Testing Taxonomic Predictivity of Foliar and Tuber Resistance to *Phytophthora infestans* in Wild Relatives of Potato

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ABSTRACT

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Potato late blight, caused by the oomycete phytopathogen *Phytophthora infestans*, is a devastating disease found in potato-growing regions worldwide. Long-term management strategies to control late blight include the incorporation of host resistance to predominant strains. However, due to rapid genetic changes within pathogen populations, rapid and recurring identification and integration of novel host resistance traits is necessary. Wild relatives of potato offer a rich source of desirable traits, including late blight resistance, but screening methods can be time

intensive. We tested the ability of taxonomy, ploidy, crossing group, breeding system, and geography to predict the presence of foliar and tuber late blight resistance in wild *Solanum* spp. Significant variation for resistance to both tuber and foliar late blight was found within and among species but there was no discernable predictive power based on taxonomic series, clade, ploidy, breeding system, elevation, or geographic location. We observed a moderate but significant correlation between tuber and foliar resistance within species. Although previously uncharacterized sources of both foliar and tuber resistance were identified, our study does not support an assumption that taxonomic or geographic data can be used to predict sources of late blight resistance in wild *Solanum* spp.

Microorganisms that cause plant diseases present a substantial burden to agriculture through yield losses due to plant stress, costs associated with disease control, and efforts to detect infections and limit disease epidemics. In particular, species of the phytopathogenic genus *Phytophthora* are well known for their ability to cause disease of economically important crops, with almost 100 recognized species targeting close to 300 different hosts. *Phytophthora infestans*, the causal agent of late blight on potato and tomato, is a problem everywhere these crops are grown. The cost associated with late blight control is significant and is estimated at more than \$3 billion/year worldwide (Fry 2008).

Plant breeders are interested in the identification and incorporation of simply inherited genes that confer robust resistance to diseases. These resistance (*R*) genes typically encode proteins that recognize the presence of very specific pathogen molecules, termed effectors, resulting in the activation of defense responses. However, deletion or mutation of effectors can allow individuals in pathogen populations to elude recognition, cause disease, and pass this advantage on to subsequent generations. This breakdown in resistance has been observed many times in potato varieties containing major late blight resistance genes. In fact, *P. infestans* has been termed an “*R*-gene destroyer” (Fry 2008).

Race-specific recognition of late blight effectors in potato results in a predictable series of responses, including activation of hypersensitive cell death surrounding the site of ingress, induction of pathogenesis-related gene transcription, and initiation of a systemic resistance response (systemic acquired resistance). Eleven *R* genes with this resistance phenotype have been identified in the Mexican hexaploid potato species *Solanum demissum* and

were introduced into cultivated potato varieties grown worldwide (Malcolmson and Black 1966; Umaerus and Umaerus 1994; Wastie 1991). However, all of these genes have been overcome by specific *P. infestans* strains due to mutation or deletion of corresponding effectors, although some still provide moderate resistance in certain geographic regions.

A second type of resistance has been identified that is capable of defending against a broader spectrum of *P. infestans* strains (Simmonds and Wastie 1987; Umaerus and Umaerus 1994). This type of resistance has been reported in several different species of *Solanum*, including the diploid potato species *S. bulbocastanum* and *S. verrucosum*. The host genes involved in this resistance still conform to the gene-for-gene interaction with *P. infestans* but they likely target effector molecules that are widespread among different pathogen clonal lineages.

Another type of plant resistance response to pathogens is partial (quantitative or rate-reducing) resistance (Agrios 1997). This partial resistance is assumed to be polygenic, nonrace specific, and potentially more durable than *R*-gene-mediated race-specific resistance. Some *S. tuberosum* cultivars such as ‘Surprise’, ‘Pimpernel’, and ‘Robijn’ and some wild tuber-bearing *Solanum* spp. (section *Petota* Dumort.) display partial resistance to late blight (Colon et al. 1995). Different levels of partial resistance, from immunity to susceptibility, can also be found in several wild *Solanum* spp. (Vleeshouwers et al. 2000). In most cases, the hypersensitive response (HR) or a late or trailing HR (hyphae can escape from HR-responding cells) has been observed in the interaction between *P. infestans* and hosts with partial resistance (Vleeshouwers et al. 2000). This suggests that the “weak” *R* gene and effector interactions cause an ineffective HR in blocking the pathogen, resulting in partial resistance phenotypes. The molecular mechanism of partial resistance is still unknown. Partial resistance is day-length dependent; therefore, breeding for partial resistance to late blight usually results in late maturity cultivars under long-day conditions (Umaerus et al. 1983). Finally, nonhost resistance—resistance of all members of a plant species to all isolates of a given

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pathogen species—is present in some nontuber-bearing solanaceous species, such as *S. nigrum* and *S. villosum* (Colon et al. 1993). To date, no sexually compatible relatives of cultivated potato have been found to contain nonhost resistance to *P. infestans*.

The genetics of tuber resistance to *P. infestans* is less understood, and relatively few sources of tuber resistance have been identified (Collins et al. 1999; Oberhagemann et al. 1999; Park et al. 2005b; Simko et al. 2006). Although some genes that confer foliar late blight resistance also provide protection in the tubers (Park et al. 2005b; Platt and Tai 1998; Stewart et al. 1994), correlation between foliar and tuber resistance is not consistent and is likely gene dependent (Kirk et al. 2001; Simko et al. 2006; Stewart et al. 1992). In the case of the *RB* resistance gene from *S. bulbocastanum*, the level of gene transcription in tubers correlates with the resistance phenotype, suggesting that expression of resistance genes, as opposed to their presence or absence, could be responsible for tuber resistance (Bradeen et al. 2009; Kramer et al. 2009).

Recently, the relationship between the presence of foliar resistance to *P. infestans* in many potato accessions and their position within a phylogenetic tree of some wild relatives of potato has been evaluated (Vleeshouwers et al. 2011). These data have facilitated the identification of *P. infestans* resistance gene homologs in closely related germplasm.

As outlined by Jansky et al. (2006) and Spooner et al. (2009), a widely held assumption is that taxonomically related organisms, or those found in geographic proximity, are likely to share traits (Chapman 1989; Daly et al. 2001; Marshall and Brown 1975; Spooner et al. 2002; Warburton 1967). This concept arises from knowledge that plant populations are not randomly arranged assemblages of genotypes but are structured in space, time, and history, resulting from the combined effects of mutation, migration, selection, and drift (Loveless and Hamrick 1984). Species-specific statements of disease and pest resistances are made in wild potato (Hawkes 1990; Ross 1986; Ruiz de Galarreta et al. 1998) as well as other crops, such as species of *Allium* (Kik 2002), *Brassica* (Ellis et al. 2000), Cucurbitaceae (Robinson and Decker-Walters 1997), *Daucus* (Simon 2000), or *Phaseolus* (Freytag and Debouck 2002).

These assumptions have rarely been subjected to empirical tests, however. We have carried out a series of studies, using a common set of accessions, including various taxonomic and biogeographic accessions, to determine whether there is a relationship between taxonomic or biogeographic variables and resistance to insect and nematode pests and bacterial, fungal, and viral pathogens of potato (Cai et al. 2011; Chung et al. 2011; Jansky et al. 2006, 2008, 2009). The present study is an extension of such tests with the most serious disease of potato worldwide, late blight of potato.

MATERIALS AND METHODS

Plant material and preparation. Up to three accessions of each of 34 wild species were evaluated for foliar and tuber late blight resistance. These wild potato species were chosen to represent the taxonomic and geographic diversity of wild potato (Fig. 1). They were used in previous studies of taxonomic predictivity of resistance to Colorado potato beetle, soft rot, early blight, *Potato virus Y*, and white mold (Cai et al. 2011; Chung et al. 2011; Jansky et al. 2006, 2008, 2009). Botanical seed was obtained from United States Potato Gene Bank (NRSP-6) in Sturgeon Bay, WI.

This study was designed to test associations of foliar and tuber late blight resistance to species, series (groups of putatively interrelated species), plastid-based molecular clade, ploidy, crossability groups, and elevation. Many wild species cross with each other and with cultivated potato. Ploidy does not always predict crossing success in potato, and species are grouped according to endosperm balance numbers (EBN) based on their ability to hybridize with each other (Hanneman 1994). Barring other crossing barriers, successful hybridization is expected when male and female gametes have matching EBN values.

For tuber resistance assays, in October 2012, seed were soaked in gibberellic acid at 1,500 ppm for 24 h to promote uniform germination. Then, they were sown in soilless potting mix and grown under an 18-h photoperiod. Seedlings were transplanted to 50-well flats 3 weeks after sowing and, 3 weeks later, 18 plants per accession were planted into 10-cm pots. In January, the photoperiod was reduced to 12 h to induce tuber production. Tubers were harvested in February 2013 and were inoculated in March 2013. Four species did not produce enough tubers for the tuber resistance assay. Family bags (one tuber from each plant of an accession per bag) were collected and served as replications for the tuber inoculation trials. Tubers were inoculated in March 2013, as described below.

For foliar resistance evaluations, another set of seed was planted as described above, in December 2012. Seedlings (18 to 24 per accession) were transplanted to individual 10-cm pots in January 2013. Seedlings were inoculated (described below) in March 2013. An 18-h photoperiod was provided throughout this experiment.

Source of late blight inoculum. One late blight isolate was used in both the foliar and tuber resistance tests. Isolate US-23 of *P. infestans* (mating type A1) was provided by Dr. Amanda Gevens, Department of Plant Pathology, University of Wisconsin-Madison.

Foliar inoculation. A whole-plant inoculation method was used to determine levels of foliar late blight resistance. Late blight inoculum was prepared as follows. *P. infestans* isolate US-23 was grown on rye A agar medium in the dark at 15°C. Cultures from petri dishes were washed with sterile distilled water and combined to obtain a suspension with a concentration of approximately 50,000 to 70,000 sporangia/ml. A hemacytometer was used to quantify the inoculum. Before inoculation, the suspension was incubated at 12°C for 2.5 to 3 h to release zoospores and plants were placed in a controlled environment chamber with a misting system (>95% relative humidity). Chamber temperatures were set at 23°C during the day and 15°C at night with a 14-h photoperiod. Plants were inoculated on both the underside and topside of the leaves using a hand sprayer. Two plants per accession were sprayed with water, serving as negative controls.

Fig. 1. Geographic localities of accessions evaluated in this study. The location of accessions with an average foliar resistance score at 8.0 or above (highly resistant) are shown with filled circles.

At 7, 10, and 13 days after inoculation (dai), each plant was scored using Malcolmsen's 9-score scale, where 9 is resistant (Cruickshank et al. 1982). The score was determined based on the percentage of infected leaf tissue, as follows: 1 = >90%, 2 = 81 to 90%, 3 = 71 to 80%, 4 = 61 to 70%, 5 = 41 to 60%, 6 = 26 to 40%, 7 = 11 to 25%, 8 = 1 to 10%, and 9 = 0%.

Tuber inoculation. Tubers were inoculated using a puncture inoculation method. Inoculum of *P. infestans* was prepared as described above but adjusted to a concentration of 20,000 sporangia/ml. Freshly harvested tubers were washed and allowed to air dry before inoculation. Each tuber was punctured with a sterile pipette tip to a depth of 5 to 6 mm. Then, 20 µl of the sporangia suspension was injected into the tuber at each of the puncture sites. Following inoculation, tubers were placed in heavy-duty plastic bags lined with wet paper towels to maintain high humidity. The bags containing the tubers were then moved to incubation chambers at 15°C for 14 days. After the incubation period, each tuber was cut with a knife blade at each inoculation site. Each tuber was scanned and the image was used to measure the necrotic area of the cut surface of the tuber (transverse plane) using ImageJ (Schneider et al. 2012). The necrotic area was divided by the surface area of the tuber and then multiplied by 100 to obtain a disease score (percent of area affected).

Foliar and tuber resistance data were analyzed using the General Linear Model in SAS (v9.3; SAS Institute Inc., Cary, NC). Residuals were normally distributed; therefore, no transformation was necessary.

All effects were considered fixed. The average score of each accession within a species was used to calculate the mean and standard deviation for that species. Means comparisons were based on a protected Fisher's least significant difference test in SAS. Correlations were calculated using Spearman's Rank Correlation procedure in SAS.

RESULTS

Comparison of foliar resistance among species. Foliar resistance scores were taken at 7, 10, and 13 dai in two separate trials. Significant differences were found among means for each trial. Therefore, each trial was treated separately. The average mean resistance score in trial 1 was 8.2, with a range of 4.5. Trial 2 had an average mean resistance score of 6.8, with a range of 7.9. There was a moderate and significant correlation between species ranks between the two trials ($r = 0.49$, $P = 0.003$). Significant differences were found among species at each time point in each trial. However, very few disease symptoms were observed at 7 dai, with a lowest average resistance score of 6.8 for *S. colombianum* (data not shown). A rank correlation analysis of the 10- and 13-dai scores resulted in a correlation of 0.95 ($P < 0.000001$). Therefore, we focused on the 10-dai time point for our analyses, because data were collected in the middle of the rating period (Fig. 2). Using means from both trials at 10 dai, the most resistant species was *S. bulbocastanum*, represented by four different accessions, with

Fig. 2. Mean foliar *Phytophthora infestans* resistance scores (9 = resistant and 0 = susceptible) for 34 wild *Solanum* spp. at 10 days after inoculation. Species were ordered based on the average means of two trials, with the most resistant at the top of the graph. Black bars represent means from trial 1 and gray bars represent means from trial 2. Error bars denote standard deviations. Data in parentheses include series, clade, ploidy, and endosperm balance numbers (EBN).

an average score of 8.9. *S. bulbocastanum* ranked 11/34 in trial 1 and 1/34 in trial 2. Other species with high average resistance scores were *S. schenckii* (six accessions; tie1/34 and 4/34), *S. albicans* (four accessions; 16/34 and 2/34), *S. brevicaulis* (eight accessions; 14/34 and 3/34), *S. polyadenium* (four accessions; tie1/34 and 9/34), and *S. lesteri* (four accessions; tie1/34 and 5/34), each with average scores of 8.6. The most susceptible species was *S. colombianum* (13 accessions), with an average score of 3.6. *S. colombianum* ranked 34/34 in trial 1 and 33/34 in trial 2.

Comparisons of foliar resistance among plastid DNA-based clade, series, ploidy, and EBN. Species in clade 1 exhibited the most foliar resistance to late blight, with an average resistance score of 8.2 (Table 1). This was followed by clades 2, 4, and 3, with foliar resistance scores of 7.5, 7.3, and 7.1, respectively. However, average resistance score differences among clades were not found to be significant ($P = 0.115$). Similarly, no significant differences were found among ploidy levels using average means from both trials.

The species represented in this screen were divided into 13 series following Hawkes (Hawkes 1990); species determinations follow Spooner et al. (2014). Significant differences were observed among series within each trial. However, a rank correlation between trials was not significant. The most resistant species, ranked by most to least resistant, belong to the series *Bulbocastana*, *Polyadenia*, *Demissa*, and *Acaulia* (Table 1).

No significant differences among species with different EBN were observed using average means from both trials. However, significant within-trial differences were observed. In each trial, 1 EBN species had the highest level of resistance, followed by the 4 EBN and 2 EBN species.

Correlation between foliar resistance and elevation. A test for correlation between foliar resistance score and the distance above sea level where the accession was collected resulted in a weak but significant correlation ($r = 0.20$, $P = 0.03$) with accessions collected from higher elevations exhibiting higher resistance. No discernable pattern of accessions containing foliar resistance scores above 8.0 was observed because these accessions were found throughout all regions where the wild potato in this study were collected (Fig. 1).

Comparison of tuber resistance among species. Significant differences were found among tubers of 30 wild potato species after inoculation with *P. infestans* (Fig. 3). No species was found to be completely resistant after wounding and inoculation. Tubers of the species *S. andreaeanum* had the lowest percent infection, with an average of only 10.9% of the tuber surface area damaged by *P. infestans* (Fig. 4). Tubers of *S. bulbocastanum*, the species with the best average foliar resistance score, had the second lowest percent tuber diameter infection (14.2%). *S. colombianum* and *S. commersonii*, two of the most foliar susceptible species, also had the highest level of tuber susceptibility with 44.4 and 62.6% of the tuber surface area, respectively, showing necrosis.

Comparisons of percent tuber resistance among plastid DNA-based clade, series, ploidy, and EBN Significant differences were found among species belonging to the four potato clades (Table 2). Clade 3 contained species with the lowest percentage of tuber tissue infected, with an average of 14.0%. This was marginally different ($P = 0.08$) from clades 1 and 4, with average tuber infections of 27.0 and 25.7%, respectively. In contrast to foliar resistance scores, there were no significantly different tuber resistance scores among ploidy levels of potato species.

Significant differences were found among series ($P < 0.0001$), with species in series *Bulbocastana* and *Piurana* having the lowest tuber disease scores. However, each of these series was represented by only one species. Tubers of the series *Commersoniana*, represented solely by *S. commersonii*, had significantly more susceptibility to tuber infection than the other series.

Differences among tubers from species with different EBN values were also significant ($P = 0.04$). Species with EBN 4 were

the most resistant, with an average tuber resistance score of 19.3%. Tubers of species with EBN 1 were the most susceptible to infection, with an average score of 29.3%.

Correlation between tuber resistance and elevation. No significant correlation was found between the level of tuber resistance and the distance above sea level (elevation) where the accession was collected.

Correlation between foliar and tuber results. A moderate and significant correlation ($r = 0.47$, $P = 0.009$) was found between tuber and foliar resistance scores among species. The correlation was reduced to 0.11 and was no longer significant ($P = 0.28$) when accessions were compared individually. The correlation between tuber and foliar resistance based on series means was moderate and significant ($r = 0.58$, $P = 0.04$). No significant correlation between tuber and foliar resistance was found for ploidy, EBN, or clade.

DISCUSSION

Germplasm screening and the identification of novel disease resistance traits is a time-consuming process. Most plant breeders rely on primary germplasm pools (cultivated relatives) to move resistance between existing and new varieties. However, due to the maintenance of monocultures in most agricultural productive practices, pathogen strains that overcome resistance can quickly become established and problematic. In these cases, it becomes necessary to identify new resistance traits in secondary or tertiary germplasm pools. In potato, this includes wild *Solanum* relatives that may or may not be sexually compatible with cultivars.

It can be assumed that major *R* genes segregate among individuals in wild populations of potato due to the selective pressure of pathogens and the effectors they harbor, similar to other plant systems (Jones and Dangl 2006). The presence of a functional *R* gene allows individuals to survive infection, whereas defeated *R* genes may only provide limited value to the population and can be lost. Likewise, the presence or absence of specific effectors

TABLE 1. Comparison of foliar resistance scores among taxonomic, ploidy, and endosperm balance number (EBN) classes

Class ^a	Score ^b	SD ^c
Clade		
1 (6)	8.2	±0.9
2 (2)	8.1	±2.4
3 (3)	7.0	±7.1
4 (23)	7.4	±2.2
Series		
<i>Bulbocastana</i> (1)	8.7	±0.3
<i>Polyadenia</i> (2)	8.6	±0.5
<i>Demissa</i> (4)	8.4	±1.1
<i>Acaulia</i> (2)	8.3	±0.7
<i>Tuberosa</i> (7)	7.9	±1.6
<i>Pinnatisecta</i> (5)	7.9	±1.6
<i>Longipedicellata</i> (2)	7.9	±1.6
<i>Megistacroloba</i> (2)	7.7	±2.0
<i>Yungasensa</i> (2)	7.6	±2.1
<i>Piurana</i> (1)	6.8	±1.7
<i>Commersoniana</i> (1)	6.6	±2.8
<i>Cuneoalata</i> (1)	6.1	±2.3
<i>Conicibacata</i> (5)	5.9	±3.0
Ploidy		
6x (5)	8.4	±2.4
4x (5)	6.8	±2.2
2x (24)	7.6	±1.9
EBN		
1 (9)	8.0	±1.6
2 (20)	7.2	±2.1
4 (5)	8.4	±2.4

^a Number of species in each category is indicated in parentheses.

^b Mean *Phytophthora infestans* resistance score (9 = resistant and 0 = susceptible) at 10 days after inoculation.

^c Standard deviation of each mean is shown.

segregates within pathogen populations, with their value to the population based primarily on their contribution to virulence. A combination of balancing selection between *R* genes and their corresponding effectors, along with the rare creation of new *R* genes with novel specificities, results in the maintenance of multiple *R* genes within host populations, each with its own specificity and stability (Van der Hoorn et al. 2002). Therefore, when screening populations for disease resistance, it is necessary to include multiple individuals from each population (accession) of each species. Ideally, one would also include multiple pathogen strains to encompass a larger suite of effector molecules. In the case of potato, where thousands of accessions are available within over 100 species, screening for new resistance traits for a pathogen such as *P. infestans*, which is estimated to contain hundreds of potential effectors (Haas et al. 2009), can be cost and time prohibitive. A predictive component to germplasm screening would be extremely helpful. Several studies have investigated the potential relationship between disease and pest resistance phenotypes and geographic origin, taxonomy, ploidy, and breeding system of the species being studied (Cai et al. 2011; Chung et al. 2011; Jansky et al. 2006, 2008, 2009; Khiutti et al. 2012; Limantseva et al. 2014; Pérez et al. 2014; Spooner et al. 2009; Uribe et al. 2014). All of these studies found high intraaccession and intraspecific variation for disease and pest resistance but none of them found a conclusive association with geography alone. Hence, the current way to find genetic variation for such traits continues to be broad screening studies of large populations until a more efficient strategy using taxonomic,

molecular, or biogeographic parameters can predict discovery of such useful traits. The results of our late blight resistance screen provided no exception to this premise, because we found no strong correlation of any taxonomic component with either foliar or tuber resistance.

Our results verified the presence of well-documented foliar resistance in several wild potato species for which *R* genes have been identified, such as *S. bulbocastanum* (Park et al. 2005a; Song et al. 2003; Van Der Vossen et al. 2003; van der Vossen et al. 2005), *S. schenckii* (Jacobs et al. 2010), *S. microdontum* (Tan et al. 2008), *S. polyadenium* (Toxopeus 1964), *S. pinnatisectum* (Kuhl et al. 2001), and *S. demissum* (Black and Gallegly 1957). However, we also identified several species that have little or no previous documentation of late blight resistance, such as *S. albicans*, *S. brevicaulis*, *S. lesteri*, *S. jamesii*, and *S. immite*. All five of these species with previously uncharacterized resistance were ranked within the top 10 most foliar-resistant species. Although documentation of resistance in these species is limited, our results correlate with results of previous resistance screens. Accessions from each of these species were determined to contain resistance as documented in the SolRgene database (Vleeshouwers et al. 2011), which includes results of *P. infestans* resistance screening using two different pathogen strains. Additionally, a few individual accessions of *S. albicans*, *S. brevicaulis*, *S. immite*, and *S. jamesii* also have documented resistance or medial resistance in the Germplasm Resource Information Network (USDA-ARS National Genetic Resources Program 2014). The presence of resistant and susceptible individuals

Fig. 3. Percentage of the tuber transverse plane (generated after slicing through the infection point) damaged by *Phytophthora infestans* for 34 wild *Solanum* spp. after puncture inoculation. Species were ordered with the most resistant at the top of the graph. Error bars denote standard deviations. Data in parentheses include series, clade, ploidy, and endosperm balance numbers (EBN).

within accessions of these species provides the opportunity for crossing and generation of segregating populations for the purpose of map-based identification or cloning of novel *R* genes, when crosses to cultivated potato is not possible due to EBN barriers.

In contrast to the well-documented foliar resistance present in potato and its wild relatives, genes controlling tuber late blight resistance are less characterized, despite its importance in controlling postharvest losses and seed tuber transmission of *P. infestans*. Difficulties in obtaining tubers from many species due to specific day-length requirements, and documentation of resistance phenotypes, impede large-scale screening. Our evaluation of tubers from 97 accessions of 30 species is one of the largest published to date. Similar to our foliar results, we found little predictive power in the association between tuber resistance and taxonomic components. Additionally, we found only a modest correlation between tuber and foliar resistance within species, and this correlation was eliminated when accessions were analyzed individually. A lack of correlation between tuber and foliar resistance was not surprising. It has been suggested that any correlation between foliar and tuber resistance is dependent on the genes involved (Park et al. 2005b). Some genetic evidence indicates that there may be little or no correlation between foliar and tuber resistance (Kirk et al. 2001; Liu and Halterman 2009; Simko et al. 2006; Stewart et al. 1992), while other results indicate that some resistance genes have the ability to confer both foliar and tuber resistance (Park et al. 2005b; Platt and Tai 1998; Stewart et al. 1994).

P. infestans is found in most regions where wild potato species are located (CABI 2013). However, in our screen, resistance was also found in species accessions collected in regions where pathogen pressure is presumably intermittent or nonexistent, such as accessions of *S. jamesii* collected from the southwestern United States, where dry weather conditions are not ideal for late blight disease. The maintenance of resistance in *S. jamesii* accessions is a potentially interesting topic for future research. It is possible that *P. infestans* resistance in this species is not associated with a strong fitness penalty, resulting in very little selection against presence of resistance in the absence of the pathogen. *P. infestans* resistance in *S. jamesii* could also be closely linked to resistance to another pathogen that is more prevalent in the region, and susceptibility in

some accessions is the result of the linkage being broken. It is also possible that reporting of *P. infestans* incidence in the southwestern United States is inadequate due to the scarcity of agricultural hosts, and that pathogen populations are actually more common than we realize. Regardless, this presents a potentially interesting

TABLE 2. Comparison of tuber infection among taxonomic, ploidy, and endosperm balance numbers (EBN) classes

Class ^a	Area (%) ^b	SD ^c
Clade		
3 (3)	14.0	±10.1
2 (2)	17.6	±6.9
4 (20)	25.7	±13.0
1 (5)	27.0	±7.8
Series		
<i>Bulbocastana</i> (1)	14.2	±2.5
<i>Piurana</i> (1)	15.6	±18.5
<i>Acaulia</i> (2)	17.0	±7.0
<i>Demissa</i> (2)	17.4	±4.1
<i>Polyadenia</i> (1)	19.4	±5.7
<i>Longipedicellata</i> (2)	20.3	±6.3
<i>Tuberosa</i> (6)	21.5	±10.3
<i>Yungasense</i> (2)	23.7	±8.8
<i>Pinnatisecta</i> (5)	26.7	±8.1
<i>Megistacroloba</i> (2)	29.4	±14.5
<i>Conicibacata</i> (5)	30.7	±10.3
<i>Cuneoalata</i> (1)	32.4	±12.1
<i>Commersoniana</i> (1)	62.6	±2.0
Ploidy		
6x (3)	17.3	±4.9
4x (5)	22.1	±9.4
2x (22)	25.9	±12.7
EBN		
4 (3)	17.3	±4.9
2 (19)	23.8	±11.0
1 (8)	29.3	±14.6

^a Number of species in each category is indicated in parentheses.

^b Percent transverse surface of the tuber damaged by *Phytophthora infestans* after wound inoculation.

^c Standard deviation of each mean is shown.

Fig. 4. Tubers showing different levels of resistance to *Phytophthora infestans* 14 days after wound inoculation. A, Resistant tuber from accession 561645, species *Solanum andreaeanum*; B, moderately susceptible tuber from accession 275173, species *S. jamesii*; and C, completely susceptible tuber from accession 472846, species *S. commersonii*.

phytopathological phenomenon that warrants further study in addition to the genetic characterization of *P. infestans* resistance in *S. jamesii*.

The lack of a strong correlation between foliar or tuber resistance to *P. infestans*, as in all of our similar studies to date, and any taxonomic characteristic of the host species suggests that high-throughput screening is still a necessary process in identifying novel resistance traits. We also observed only a moderate correlation between tuber and foliar resistance within species, supporting previous data suggesting that genetic mechanisms involved in each phenotype are host specific. The methodology used in our screen for tuber resistance included evaluation of tuber infection with a rapid and unbiased quantification of diseased tissue using digital scans. Although the production of tuber tissue for some species was problematic, once suitable growth conditions were established, the inoculation and evaluation process was relatively straightforward and now serves as a practical tool for future screening studies. Many of the species with tuber and foliar resistance identified in our screen can be crossed easily with cultivars, allowing for rapid introduction of late blight resistance. Others may serve as useful sources of *R* genes though map-based cloning once segregating populations are developed.

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