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Screening of Wild Potatoes Identifies New Sources of Late Blight Resistance

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Abstract

Late blight (LB) of potato is considered one of the most devastating plant diseases in the world. Most cultivated potatoes are susceptible to this disease. However, wild relatives of potatoes are an excellent source of LB resistance. We screened 384 accessions of 72 different wild potato species available from the U.S. Potato GeneBank against the LB pathogen *Phytophthora infestans* in a detached leaf assay (DLA). *P. infestans* isolates US-23 and NL13316 were used in the DLA to screen the accessions. Although all plants in 273 accessions were susceptible, all screened plants in 39 accessions were resistant. Resistant and susceptible plants were found in 33 accessions. All tested plants showed a partial resistance phenotype in two accessions, segregation of resistant and partial resistant plants in nine accessions, segregation of partially resistant and susceptible plants in four accessions, and segregation of resistant, partially resistant, and susceptible individuals in 24 accessions. We found several species that were never before reported to be resistant to LB: *Solanum albornozii*, *S. agrimoniifolium*, *S. chomatophilum*, *S. ehrenbergii*, *S. hypacrarthrum*, *S. iopetalum*, *S. palustre*, *S. piurae*, *S. morelliforme*, *S. neocardenasii*, *S. trifidum*, and *S. stipuloideum*. These new species could provide novel sources of LB resistance. *P. infestans* clonal lineage-specific screening of selected species was conducted to identify the presence of *RB* resistance. We found LB resistant accessions in *Solanum verrucosum*, *Solanum stoloniferum*, and *S. morelliforme* that were susceptible to the *RB* overcoming isolate NL13316, indicating the presence of *RB*-like resistance in these species.

Keywords: cultivar/resistance, disease management, late blight, Oomycetes, *Phytophthora infestans*, potato wild species, *RB* gene, vegetables, wild potatoes

Pests and pathogens contribute to a 17.2% yield loss in potato at a global level (Savary et al. 2019). Late blight (LB), brown rot, early blight, and cyst nematode are the most serious diseases, with LB, caused by oomycete pathogen *Phytophthora infestans*, considered to be the most devastating potato disease in the world. *P. infestans* infection of potato contributed to the Irish Famine in 1845, which resulted in an estimated 1 million hunger-associated deaths and an equal number of immigrants to North America. Even today, LB remains a major constraint for potato production and is considered a constant threat to food security (Fisher et al. 2012; Haverkort et al. 2008). After the Irish Famine, cultural management practices included the Bordeaux mixture toward the end of the 19th century and chemical products based on manganese and tin around the mid-20th century (Haverkort et al. 2008). Today, LB management strategies depend largely on the routine application of fungicides. However, the evolution of fungicide-resistant genotypes and favorable weather conditions can lead to epidemics and crop losses (Fry and Goodwin 1997; Cooke et al. 2012). Selective sweeps have been documented in the potato–*P. infestans* pathosystem (Cooke et al. 2012; Zhan and McDonald 2013). These sweeps occur when a new pathogen genotype emerges and rapidly displaces existing strains. These newly established genotypes of *P. infestans* are called clonal lineages.

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The highly destructive nature of *P. infestans* and past social and economic impacts associated with LB have led to efforts to breed LB-resistant potatoes. Initial breeding efforts were based on quantitative or field resistance, which is typically controlled by multiple genes. Because of complications that arise from breeding heterozygous tetraploids for a quantitative trait and undesirable associations between resistance and late maturity, breeding for field resistance has been only partially successful (Wastie 1991). The discovery of major LB resistance (R) genes in *Solanum demissum*, a Mexican wild relative of potato, showed some promise in the early 20th century. This discovery led to the extensive use of *S. demissum* in potato breeding programs in Europe and North America. In total, 11 R genes (R1 to R11) from *S. demissum* were transferred into cultivated potatoes. These introgressed R genes provide race-specific resistance to different strains of *P. infestans.* However, these resistance genes have systematically been overcome by new genotypes (Fry and Goodwin 1997). *P. infestans* is a highly adaptable pathogen that may undergo sexual reproduction. Frequent shifts in the existing population because of migration can also lead to the emergence of new clonal lineages (Fry 2008). Consequently, breeding efforts that incorporate single R genes will not provide durable resistance. Thus, current breeding for LB resistance must incorporate multiple R genes with different specificities. Evaluation of potato germplasm for novel sources of resistance is critical for the development of LB-resistant cultivars. The potato germplasm resource consists of wild relatives, landraces, cultivated species, and modern cultivars, which have a tremendous range of genetic and phenotypic variation (Bethke et al. 2017). Novel sources of resistance would benefit breeding efforts toward LB resistance in potato because most of the identified *R* genes are short-lived and have already been overcome by rapidly evolving *P. infestans* isolates.

Several methods have been developed to screen for foliar LB resistance, including field tests and whole plant assays (Stewart et al. 1983), laboratory tests on detached leaves (Lapwood 1961), in vitro assays (Huang et al. 2005), and detached leaf assays (DLAs) (Vleeshouwers et al. 1999). Field tests that measure the area under the disease progress curve provide the best estimate of disease resistance (Fry 1978). DLAs can be used as an alternative method, providing results similar to field tests (Vleeshouwers et al. 1999).

The potato germplasm resource includes 107 wild potato species, including diploids, triploids, tetraploids, and hexaploids from 16 countries, ranging from the southwestern United States to central Argentina and Chile (Spooner et al. 2019). The largest collections of potato germplasm are held by the International Potato Center in Peru, the U.S. Department of Agriculture Potato Genebank in Wisconsin, and the Institut für Pflanzengenetik und Kulturpflanzenforschung Gatersleben Genebank in Germany. In the past, 270 accessions of potatoes were screened for LB resistance under field conditions, and 10 highly resistant accessions were identified (Gopal and Singh 2003). Similarly, screening of up to three accessions each of 34 wild species for tuber and foliar blight resistance identified significant variation in the resistance phenotype within and between species (Khiutti et al. 2015). Recent screenings of 1,055 accessions for tuber resistance against LB identified 68 very resistant and 311 partially resistant accessions (Bachmann-Pfabe et al. 2019). In most cases, tuber and foliar blight resistance are considered different traits, and genes that confer foliar blight resistance do not provide tuber blight resistance (Stewart 1992). Unlike foliar blight, the genetics of tuber blight resistance to *P. infestans* is poorly understood, and few sources of resistance have been identified (Collins et al. 1999; Oberhagemann et al. 1999; Park et al. 2005c; Simko et al. 2006).

RB, also called *Rpi-blb1*, is a broad-spectrum LB resistance gene from *Solanum bulbocastanum* (Song et al. 2003; van der Vossen et al. 2003). *RB* and its homologs were found in tuber-bearing and non-tuber bearing *Solanum* species, suggesting its presence before the divergence of the two groups (Wang et al. 2008). Based on transgenic, resistance, and genetic assays, *RB* genes that are functionally equivalent to those in *S. bulbocastanum* have been identified in *Solanum stoloniferum* and *Solanum verrucosum* (Liu and Halterman 2006; Wang et al. 2008).

In this study, we report the screening of 384 accessions of 72 *Solanum* species against *P. infestans* using a DLA. These include a broad array of wild potato relatives available through the U.S. Potato Genebank, with three or more accessions per species when available. We focused on identifying accessions with strong foliar resistance, indicating the presence of R genes. We have also identified the presence of an *RB*-like gene in some of the selected accessions from different species.

Materials and Methods

Plant materials. True potato seeds from 384 accessions were obtained from the U.S. Potato Genebank (Sturgeon Bay, WI). At least three accessions from diploid (286 accessions), tetraploid (77

Table 1. Late blight rating scale, description of the symptoms, and disease reaction

Disease rating	Severity of symptoms	Disease reaction
1	>90% of the mean leaf area covered with blackish-brown lesions, sporulation, and water soaking	Highly susceptible
2	81–90% of the mean leaf area covered with blackish-brown lesions, sporulation, and water soaking	Highly susceptible
3	71–80% of the mean leaf area covered with blackish-brown lesions, sporulation, and water soaking	Susceptible
4	61–70% of the mean leaf area covered with blackish-brown lesions, sporulation, and water soaking	Susceptible
5	41–60% of the mean leaf area covered with blackish-brown lesions, sporulation, and water soaking,	Partially resistant
6	21–40% of the mean leaf area covered with blackish-brown lesions, sporulation, and water soaking	Partially resistant
7	Cell death at the point of inoculation accompanied by 10–20% of the mean leaf area exhibiting blackish-brown lesions, sporulation, and water soaking	Resistant
8	Cell death at the point of inoculation accompanied by <10% of the mean leaf area exhibiting blackish-brown lesions, sporulation, and water soaking	Highly resistant
9	0% infection, no visible symptoms, clean leaves	Immune

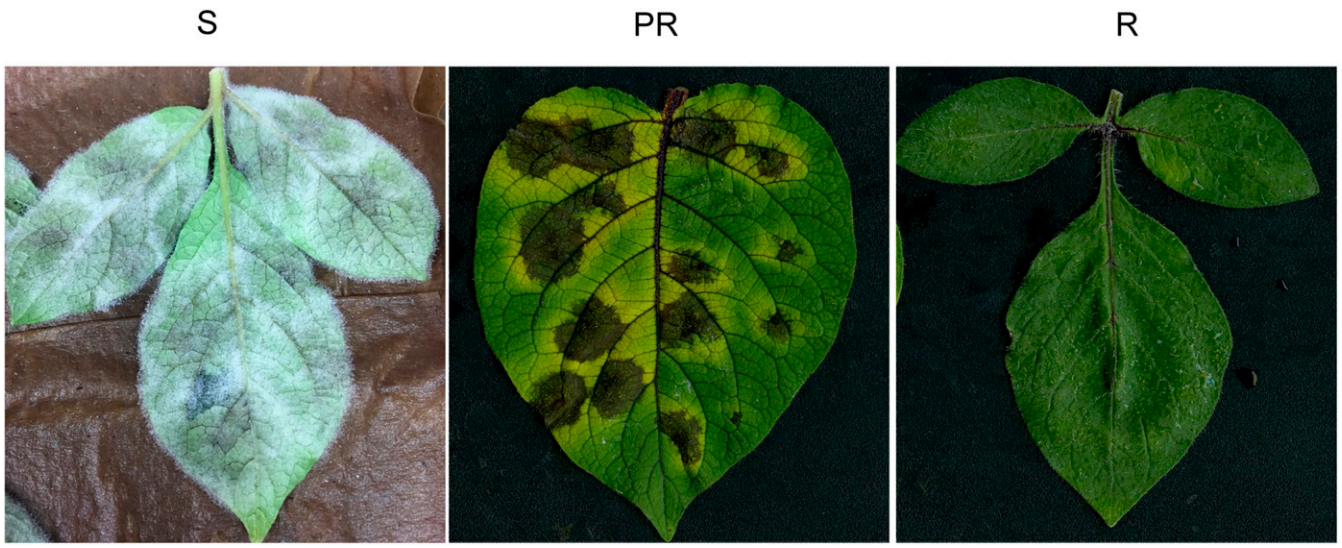

Fig. 1. Infection of *Solanum* spp. by *Phytophthora infestans* isolate US-23. Susceptible (S), partially resistant (PR), and resistant (R) phenotypes were identified after a detached leaf assay. Phenotypes were determined by the percentage of the mean leaf area covered with sporulating hyphae and water soaking: >61% indicated susceptible, 21 to 60% indicated partial resistance, and a resistant phenotype was indicated by no sign of sporulation, cell death at the point inoculation, and in some cases visible cell death at the point of inoculation accompanied by ≤20% of the mean leaf area exhibiting sporulation and water soaking. Photographs were taken 5 days after inoculation.

Table 2. Late blight-resistant *Solanum* species and accessions tested, number of plants per accession evaluated, and resistance counts[a]

				Phenotype		
Species number	**Accession number**	**Species**	**Tested plants**	**Susceptible (rating: 1–4)**	**Partial resistant (rating: 5–6)**	**Resistant (rating: 7–9)**
1	561636	*S. albornozii*	5	4	–	1
2	545748	*S. agrimoniifolium*	5	–	2	3
3	310927	*S. berthaultii*	25	6	6	13
4	498141	*S. berthaultii*	5	4	–	1
5	595507	*S. berthaultii*	17	12	1	4
6	498104	*S. berthaultii*	20	9	5	6
7	473331	*S. berthaultii*	22	10	1	11
8	310981	*S. berthaultii*	9	7	1	1
9	310925	*S. berthaultii*	23	2	7	14
10	275188	*S. bulbocastanum*	5	–	–	5
11	545751	*S. bulbocastanum*	5	–	–	5
12	275139	*S. chacoense*	25	17	3	5
13	568972	*S. chacoense*	22	13	2	7
14	458313	*S. chacoense*	27	14	3	10
15	414143	*S. chacoense*	19	2	8	9
16	275202	*S. chomatophilum*	5	–	–	5
17	283062	*S. cardiophyllum*	14	1	2	11
18	283063	*S. cardiophyllum*	5	1	2	2
19	347759	*S. cardiophyllum*	19	7	4	8
20	558041	*S. cardiophyllum*	7	2	–	5
21	595468	*S. cardiophyllum*	10	6	–	4
22	341232	*S. cardiophyllum*	15	–	–	15
23	341235	*S. cardiophyllum*	16	–	–	16
24	160208	*S. demissum*	5	4	–	1
25	230589	*S. demissum*	5	–	–	5
26	498232	*S. demissum*	5	–	–	5
27	184762	*S. ehrenbergii*	5	5	–	1
28	255519	*S. ehrenbergii*	5	1	2	2
29	473477	*S. hypacrarthrum*	5	–	–	5
30	545768	*S. hjertingii*	5	3	–	2
31	498021	*S. iopetalum*	5	3	1	1
32	558410	*S. iopetalum*	5	–	5	–
33	310979	*S. microdontum*	5	–	2	3
34	458355	*S. microdontum*	5	2	–	3
35	498123	*S. microdontum*	5	–	2	3
36	365334	*S. microdontum*	5	–	–	5
37	218225	*S. microdontum*	14	3	2	9
38	265881	*S. microdontum*	15	3	–	12
39	473170	*S. microdontum*	16	7	–	9
40	473312	*S. microdontum*	16	13	–	3
41	498124	*S. microdontum*	16	12	–	4
42	545901	*S. microdontum*	10	9	–	1
43	595511	*S. microdontum*	13	9	–	4
44	275222	*S. morelliforme*	5	2	–	3
45	545774	*S. morelliforme*	5	3	–	2
46	498129	*S. neocardenasii*	5	–	3	2
47	458367	*S. okadae*	5	–	–	5
48	498065	*S. okadae*	2	1	–	1
49	230561	*S. polyadenium*	5	–	–	5
50	320342	*S. polyadenium*	2	–	–	2
51	347770	*S. polyadenium*	5	–	–	5
52	473401	*S. palustre*	5	2	2	1
53	558169	*S. palustre*	5	–	–	5
54	184764	*S. pinnatisectum*	5	–	–	5
55	230489	*S. pinnatisectum*	5	1	3	1
56	275236	*S. pinnatisectum*	5	1	3	1
57	347766	*S. pinnatisectum*	21	9	4	8
58	653808	*S. pinnatisectum*	16	14	–	2
59	653790	*S. pinnatisectum*	16	1	5	10
60	275234	*S. pinnatisectum*	15	–	4	11
61	310997	*S. piurae*	5	2	–	3
62	365365	*S. piurae*	5	3	1	1
63	473501	*S. piurae*	5	4	–	1
64	275261	*S. schenckii*	5	–	–	5

(*Continued on next page*)

[a] Dashes indicate not found.

accessions), hexaploid (18 accessions), and unknown ploidy (3 accessions) tuber-bearing species were selected (Supplementary Table S1). Seeds of each accession were germinated in a greenhouse in soilless potting mix in a 10- × 10-cm pot and after 2 weeks, five or more seedlings per accession were transplanted into individual 15- × 15-cm pots. The greenhouse was maintained at the temperature of 22°C during the day (12 h) and 20°C at night (12 h), with a 17.5-h photoperiod. The plants were routinely irrigated and fertilized.

Pathogen propagation and inoculation. *P. infestans* isolates US-23 and NL13316 were used to screen plants for LB resistance. Periodically, a fresh culture of each isolate was grown on rye A medium at 18°C (Caten 1970). The virulence activity of the pathogen was routinely confirmed on leaflets of known LB-susceptible potatoes. For the infection assay, fresh sporangia were harvested from a 10- to 14-day-old rye A cultured plate by flooding the plate with 5 ml of ice-cold sterilized water and mixing with a spreader. The plate was kept at 4°C for about 2 to 4 h to release zoospores. The zoospores were harvested and diluted in 40 ml of ice-cold sterilized water. Motile zoospores were counted under a microscope, and the concentration was adjusted to 50,000 per ml of water. A DLA was performed as reported previously (Vleeshouwers et al. 1999) with some modifications. Briefly, compound leaves having at least three leaflets were collected from 5- to 8-week-old plants. The assay was carried out on square standard height bioassay dishes lined with wet heavy-duty paper towels. The abaxial side of each leaflet was inoculated (4 to 6 droplets per leaflet) with 10-µl droplets of inoculum (50,000 zoospores per ml). The bioassay plates were kept in a room with natural light at a temperature of 21°C. We routinely used susceptible checks such as W4 and Ranger Russet depending on the availability of fully grown young leaves during each experiment.

Disease rating. Disease ratings were made 5 days after inoculation on a 1 to 9 rating scale, with 1 being the most susceptible and 9 being the most resistant, as described previously, with some modifications (Brylińska and Śliwka 2017; Cruickshank et al. 1982; Malcolmson 1976). Detailed descriptions of the disease rating scale, the severity of symptoms, and disease reactions are presented in Table 1. The resistant and partially resistant plants were evaluated for LB resistance at least two additional times.

Table 2. (*Continued from previous page*)

				Phenotype		
Species number	**Accession number**	**Species**	**Tested plants**	**Susceptible (rating: 1–4)**	**Partial resistant (rating: 5–6)**	**Resistant (rating: 7–9)**
65	498250	*S. schenckii*	5	–	–	5
66	558456	*S. schenckii*	5	–	–	5
67	251741	*S. stoloniferum*	5	–	1	4
68	255545	*S. stoloniferum*	5	–	2	3
69	498032	*S. stoloniferum*	5	3	–	2
70	498037	*S. stoloniferum*	5	1	–	4
71	498039	*S. stoloniferum*	5	2	–	3
72	498240	*S. stoloniferum*	5	–	–	5
73	498241	*S. stoloniferum*	5	–	–	5
74	498276	*S. stoloniferum*	5	–	–	5
75	498287	*S. stoloniferum*	5	–	–	5
76	545784	*S. stoloniferum*	5	–	–	5
77	545785	*S. stoloniferum*	5	–	–	5
78	545786	*S. stoloniferum*	5	–	–	5
79	545787	*S. stoloniferum*	5	–	–	5
80	545789	*S. stoloniferum*	5	–	–	5
81	545795	*S. stoloniferum*	5	–	–	5
82	545796	*S. stoloniferum*	5	–	–	5
83	545803	*S. stoloniferum*	5	2	–	3
84	545805	*S. stoloniferum*	5	–	–	5
85	558450	*S. stoloniferum*	5	–	–	5
86	558451	*S. stoloniferum*	5	–	2	3
87	558467	*S. stoloniferum*	5	2	–	3
88	558475	*S. stoloniferum*	5	–	–	5
89	558476	*S. stoloniferum*	5	–	–	5
90	564042	*S. stoloniferum*	5	–	–	5
91	564043	*S. stoloniferum*	5	–	–	5
92	498116	*S. stipuloideum*	5	–	3	2
93	498117	*S. stipuloideum*	5	–	–	5
94	498118	*S. stipuloideum*	5	2	–	3
95	498119	*S. stipuloideum*	5	–	–	5
96	255541	*S. trifidum*	5	1	2	2
97	558478	*S. trifidum*	5	1	–	4
98	498043	*S. trifidum*	5	3	–	2
99	570642	*S. trifidum*	5	–	–	5
100	498062	*S. verrucosum*	5	4	–	1
101	365404	*S. verrucosum*	12	–	–	12
102	275260	*S. verrucosum*	15	5	–	10
103	275258	*S. verrucosum*	16	9	–	7
104	558146	*S. venturii*	5	4	–	1
105	558224	*S. venturii*	5	4	–	1
106	473310	*S. vernei*	5	3	1	1

Results

The 384 accessions of wild relatives of potato comprising 72 different *Solanum* species were screened against *P. infestans* clonal lineage US-23, the most prevalent in the United States. We broadly grouped the resistance response rating (Table 1) into three major categories: susceptible (disease rating 1 to 4), partially resistant (disease rating 5 and 6), and resistant (disease rating 7 to 9). The majority of infected leaves showed phenotypes ranging from completely susceptible to highly resistant, but some leaves showed a partial resistance phenotype (Fig. 1). Although all plants in 273 accessions (71%) were susceptible, in 39 accessions (10%) all screened plants were resistant (Table 2 and Supplementary Table S2). Both resistant and susceptible plants were found in 33 accessions (9%) and in two accessions (0.5%) all tested plants showed a partially resistant phenotype (Table 2 and Supplementary Table S2). Similarly, nine accessions (2%) showed segregation of partially resistant and resistant phenotypes, and four accessions (1%) showed segregation of partially resistant and susceptible individuals within an accession (Table 2 and Supplementary Table S2). We also found 24 accessions (6.5%) that showed segregation of resistant, partially resistant, and susceptible individuals (Table 2 and Supplementary Table S2). In summary, we found at least one LB-resistant plant in 106 (28%) accessions (Table 2); these accessions belong to 27 *Solanum* species (Table 3). Detailed descriptions of these species are listed in Table 3. Despite screening an extensive number of accessions, we could not find any resistant individuals in the remaining 45 species.

To delineate the source of LB resistance, we selected some species that are predicted to have the broad-spectrum LB resistance gene *RB*. Initially, these species were screened against the *RB* avirulent *P. infestans* isolate US-23 and subsequently the *RB* virulent *P. infestans* isolate NL13316. NL13316 was reported to overcome LB resistance provided by the *RB* gene (C. Richael, Simplot Plant Sciences, *unpublished*). We confirmed the virulence activity of NL13316 against the *RB*-expressing potato clones K41 and SP951. K41 is a tetraploid, BC3 clone which was developed from a somatic hybrid (J101) between *S. tuberosum* ('Superior') and *S. bulbocastanum* (clone PT29), which confers a high level of foliar resistance to *P. infestans* (Halterman et al. 2008; Helgeson et al. 1998). SP951 is a transgenic version of 'Katahdin' harboring a single-copy *RB* gene that confers partial resistance to *P. infestans* (Bradeen et al. 2009; Halterman and Middleton 2012). Potato 'Katahdin' was used as a susceptible check. We found that K41 and SP951 both provide resistance or partial resistance against US-23 but are highly susceptible to NL13316 (Fig. 2). We also found that isolate NL13316 is more virulent than US-23 (Fig. 2). These two *P. infestans* isolates helped to determine whether these accessions have *RB* or other sources of LB resistance. We selected accessions from *S. bulbocastanum*, *S. chacoense*, *S. cardiophyllum*, *S. ehrenbergii*, *S. microdontum*, *S. morelliforme*, *S. neocardenasii*, *S. okadae*, *S. polyadenium*, *S. pinnatisectum*, *S. piurae*, *S. stoloniferum*, *S. trifidum*, and *S. verrucosum* that showed resistance against US-23. The selected accessions were tested against isolate NL13316, and we found that accessions of *S. morelliforme* (275222, 545774, and 545775), *S. verrucosum* (141173, 275260, and 275258) and *S. stoloniferum* (498287, 545785, 545795, 545796, 558450, and 558451) are resistant or immune to isolate US-23 but susceptible to NL13316 (Table 4). These accessions probably carry the functional *RB/Rpi-blb1* gene for LB resistance.

Discussion

Primarily, LB is managed by spraying fungicides and planting resistant cultivars. Clonal lineages of *P. infestans* can change frequently, leading to the emergence of fungicide-insensitive isolates (Saville et al. 2015) and a breakdown in the resistance available in current potato cultivars. Thus, despite intensive breeding efforts to

Table 3. Late blight-resistant *Solanum* species and source of resistance[a]

Species number	Species	Ploidy	EBN	TA	RA	R gene/locus[b]	Reference
1	*S. agrimoniifolium*	4×	2	3	2	–	This study
2	*S. albornozii*	2×	2	4	1	–	This study
3	*S. berthaultii*	2×	2	11	7	*Rpi-ber1*	Rauscher et al. 2006; Vossen and Nijenhuis 2009
4	*S. bulbocastanum*	2×	1	3	2	*Rpi-blb1/RB*, *Rpi-blb2* and *Rpi-blb3*	Park et al. 2005a; Naess et al. 2000; Song et al. 2003; van der Vossen et al. 2003; van der Vossen et al. 2005
5	*S. cardiophyllum*	2×	1	8	7	*Rpi-blb3*	Lokossou et al. 2010
6	*S. chacoense*	2×	2	12	4	*Rpi-chc1*	Chakrabarti et al. 2014; Vossen and Nijenhuis 2009
7	*S. chomatophilum*	2×	2	4	1	–	This study
8	*S. demissum*	6×	4	3	3	*R1* to R*11*	Malcolmson and Black 1966; Black et al. 1953; Vossen et al. 2016
9	*S. ehrenbergii*	2×	1	3	2	–	This study
10	*S. hjertingii*	4×	2	13	1	*Rpi-blb3*/*R2*	Lokossou et al. 2010
11	*S. hypacrarthrum*	2×	1	1	1	–	This study
12	*S. iopetalum*	6×	4	3	1	–	This study
13	*S. microdontum*	2×	2	15	11	–	Sandbrink et al. 2000; Colon and Budding 1988
14	*S. morelliforme*	2×	–	3	2	–	This study
15	*S. neocardenasii*	2×	–	1	1	–	This study
16	*S. okadae*	2×	–	3	2	*Rpi-oka1*	Jones et al. 2013
17	*S. palustre*	2×	1	3	2	–	This study
18	*S. pinnatisectum*	2×	1	10	7	*Rpi1*, *Rpi2* and *Rpi-blb3*	Kuhl et al. 2001; Nachtigall et al. 2018; Lokossou et al. 2010
19	*S. piurae*	2×	2	3	3	–	This study
20	*S. polyadenium*	2×	1	3	3	–	Toxopeus 1964
21	*S. schenckii*	6×	4	3	3	*R2*	Champouret 2010
22	*S. stipuloideum*	2×	1	7	4	–	This study
23	*S. stoloniferum*	4×	2	41	25	*Rpi-sto1/Rpi-pta1*	Wang et al. 2008; Vleeshouwers et al. 2008
24	*S. trifidum*	2×	1	6	4	–	This study
25	*S. venturii*	2×	2	3	2	*Rpi-vnt1*	Colon and Budding 1988; Foster et al. 2009
26	*S. verrucosum*	2×	2	9	4	*RB* like	Liu and Halterman 2006
27	*S. vernei*	2×	2	3	1	–	Colon and Budding 1988

[a] EBN, endosperm balance number; RA, resistant accessions; TA, tested accessions. Dashes indicate not known.
[b] R gene/locus previously shown to be present in this species.

incorporate resistance over the past century, LB remains a major constraint for potato production around the world. Therefore, it is important to develop LB-resistant potato cultivars in pace with changing *P. infestans* populations. Because most cultivated potato is susceptible to LB, we rely on screening of wild relatives for LB resistance to identify germplasm needed in the development of resistant cultivars. Our study included accessions collected from Argentina, Bolivia, Brazil, Chile, Colombia, Costa Rica, Ecuador, Guatemala, Mexico, Paraguay, Peru, and the United States and represents all wild species available for distribution by the U.S. Potato Genebank. Although most accessions were susceptible, 28% contained at least one resistant plant. The high percentage (71%) of the susceptible accessions found in this study might be due in part to the use of the DLA. DLAs provide very conducive conditions for LB development, which may not accurately identify weak *R* gene-mediated resistance or quantitative resistance. In these cases, DLAs might not be suitable for screening, and a field assay would better (Jo et al. 2011). We believe that complete resistance found by DLA in this study is probably governed by single or multiple R genes. These types of *R* genes are generally race specific, exhibit Mendelian inheritance, and are easy to use in breeding. Partial resistance observed in some accessions of *S. iopetalum*, *S. pinnatisectum*, and *S. verrucosum* may be governed by weak R genes or other types of general resistance. These types of resistance are polygenic, non-race specific, and difficult to use in breeding but are still preferred over R gene-mediated resistance by many breeders because of their potential durability.

Many LB resistance genes have been mapped, cloned, and reported from wild relatives of potato. Detailed descriptions of the cloned *Rpi* genes or mapped loci for LB resistance have been outlined in Table 3. Although numerous sources of LB resistance have been found in different wild *Solanum* species, limited progress has been made in the use of these resistances in cultivated potatoes. However, current advances in marker technologies and novel approaches in mapping and cloning genes have provided momentum in deploying genes from wild *Solanum* species for LB resistance. In the past, *S. demissum* has been used extensively to transfer dominant LB resistance genes (*R1* to *R11*) into *S. tuberosum* via conventional breeding. Now, molecular markers have been developed for most of these genes to assist in marker-assisted selection (Gebhardt et al. 2004; Kim et al. 2012; Sokolova et al. 2011; Vossen et al. 2016). Similarly, LB resistance genes from *S. bulbocastanum* (*Rpi-blb1*/*RB*, *Rpi-blb2* and *Rbi-blb3*), with the assistance of molecular markers, have been widely used in potato breeding programs around the world (Lokossou et al. 2009; Park et al. 2005a; van der Vossen et al. 2003). Most LB resistance screening in previous studies was conducted with field or whole-plant assays. In harmony with previous studies, we also found LB resistance in *S. berthaultii* (2×), *S. bulbocastanum* (2×), *S. cardiophyllum* (2×), *S. chacoense* (2×), *S. demissum* (6x), *S. hjertingii* (4×), *S. microdontum* (2×), *S. okadae* (2×), *S. pinnatisectum* (2×), *S. polyadenium* (2×), *S. schenckii* (6×), *S. stoloniferum* (2×), *S. venturii* (2×), *S. verrucosum* (2×), and *S. vernei* (2×) which indicates the presence of single or multiple strong R genes (Table 3). However, we

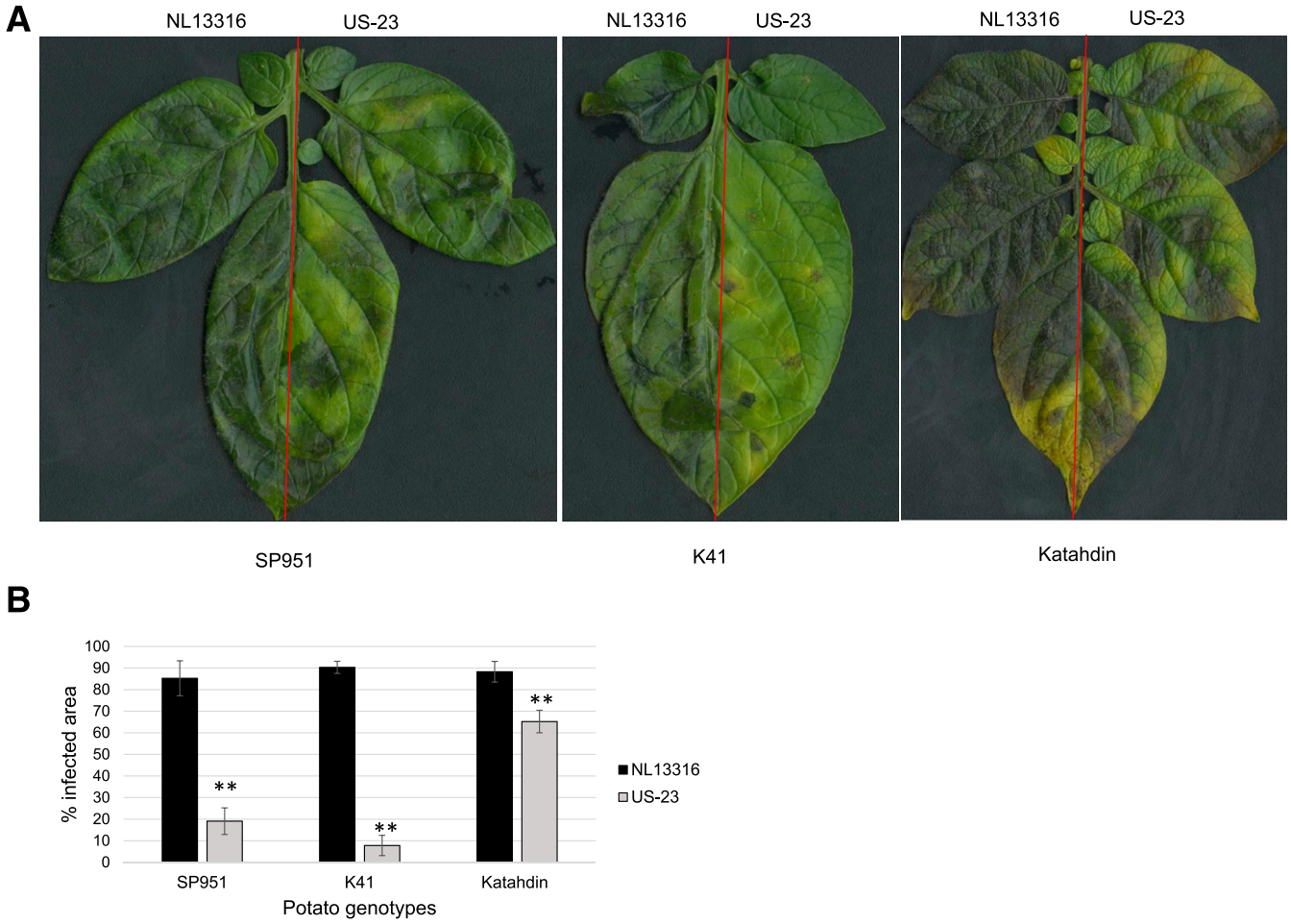

Fig. 2. *Phytophthora infestans* isolate-specific (NL13316 and US-23) disease assay. K41, SP951, and 'Katahdin' leaves were inoculated with isolates NL13316 (RB virulent) and US-23 (RB avirulent) in a detached leaf assay. **A,** The left-hand side of the leaf was inoculated with NL13316, and the right-hand side of the leaf was inoculated with US-23. A typical disease resistance response with the restricted growth of the pathogen was observed with US-23, whereas increased growth and sporulation were observed for the isolate NL13316. Potato cultivar 'Katahdin' was used as a susceptible control. The photographs were taken 5 days after pathogen inoculation. **B,** Bar diagrams represent the percentage of infected leaf area. Error bars represent standard deviations, and ** indicate the values that are statistically different ($P < 0.001$, Tukey test). Experiments were repeated at least twice with similar results.

also identified several species that have no previous documentation of LB resistance, including *S. albornozii* (2×), *S. agrimoniifolium* (4×), *S. chomatophilum* (2×), *S. ehrenbergii* (2×), *S. hypacrarthrum* (2×), *S. iopetalum* (6×), *S. palustre* (2×), *S. piurae* (2×), *S. morelliforme* (2×), *S. neocardenasii* (2×), *S. trifidum* (2×), and *S. stipuloideum* (2×) (Table 3). Our results are based on a DLA to determine resistance phenotypes. The extremely favorable conditions of DLAs, such as temperature and humidity, provide a rigorous screen to identify genotypes with resistance. However, because environmental conditions and genetic backgrounds can affect the effectiveness of R genes, whole plant assays might be warranted in germplasm developed by using these species as sources of resistance. Among novel LB resistance species found in this study, *S. agrimoniifolium* (4×, 2EBN) can be readily used in tetraploid potato breeding programs. Similarly, *S. albornozii*, *S. chomatophilum*, *S. hypacrarthrum*, and *S. piurae* are diploid, and because they are 2 EBN, they could readily be used in diploid potato breeding programs. However, other species such as *S. ehrenbergii*, *S. iopetalum*, *S. morelliforme*, *S. neocardenasii*, *S. palustre*, *S. stipuloideum*, and *S. trifidum* may need bridge crossing, embryo rescue, protoplast fusion, or chromosome-doubling techniques and additional years to be useful in breeding programs, because of differences in ploidy level barriers and endosperm balance number (EBN) incompatibility with cultivated potato. Here, we documented LB resistance only in the foliar tissue. *R* gene-derived resistance to foliar and tuber blight is not always positively correlated, and their effects vary between genetic backgrounds (Dorrance and Inglis 1998; Halterman et al. 2008; Kirk et al. 2001; Stewart et al. 1992); we expect different results if these species were screened for potato tuber resistance against *P. infestans*. The presence of strong LB resistance in the aforementioned species further verifies that wild potato germplasm is a very good source of LB resistance that should be exploited in modern potato breeding programs around the world. Introgression of R genes from wild potatoes to cultivated germplasm may take several decades because of the crossing barriers, self-incompatibility, difference in EBN number, and ploidy level (Haverkort et al. 2016). The use of genetic modification techniques to rapidly transfer single or multiple R genes from wild potatoes to elite cultivars may prove a valid tool in modern potato breeding programs. Several *Rpi* genes have been cloned from different *Solanum* species (Table 3). These *Rpi* genes can be introduced

Table 4. *Phytophthora infestans* isolate NL13316-specific screening of US-23-resistant accessions from selected *Solanum* species

			***P. infestans* isolate**[a]		
Species number	**Accession number**	**Species**	**US-23**	**NL13316**	**Source of resistance**
1	275188	*S. bulbocastanum*	R	R	Unknown
2	545751	*S. bulbocastanum*	R	R	Unknown
3	275139	*S. chacoense*	R	R	Unknown
4	283062	*S. cardiophyllum*	R	R	Unknown
5	283063	*S. cardiophyllum*	R	R	Unknown
7	255519	*S. ehrenbergii*	R	R	Unknown
9	458355	*S. microdontum*	R	R	Unknown
10	498123	*S. microdontum*	R	R	Unknown
11	275222	*S. morelliforme*	R	S	RB
12	545774	*S. morelliforme*	R	S	RB
13	545775	*S. morelliforme*	R	S	RB
14	498129	*S. neocardenasii*	R	R	Unknown
15	458367	*S. okadae*	R	R	Unknown
16	230561	*S. polyadenium*	R	R	Unknown
17	320342	*S. polyadenium*	R	R	Unknown
18	184764	*S. pinnatisectum*	R	R	Unknown
19	230489	*S. pinnatisectum*	R	R	Unknown
21	310997	*S. piurae*	R	R	Unknown
22	365365	*S. piurae*	R	R	Unknown
24	251741	*S. stoloniferum*	R	R	Unknown
25	255545	*S. stoloniferum*	R	R	Unknown
26	498032	*S. stoloniferum*	R	R	Unknown
27	498037	*S. stoloniferum*	R	R	Unknown
28	498039	*S. stoloniferum*	R	R	Unknown
29	498276	*S. stoloniferum*	R	R	Unknown
30	498287	*S. stoloniferum*	S	S	RB
31	545784	*S. stoloniferum*	R	R	Unknown
32	545785	*S. stoloniferum*	R	S	RB
33	545786	*S. stoloniferum*	R	R	Unknown
34	545787	*S. stoloniferum*	R	R	Unknown
35	545789	*S. stoloniferum*	R	R	Unknown
36	545795	*S. stoloniferum*	R	S	RB
37	545796	*S. stoloniferum*	R	S	RB
38	545803	*S. stoloniferum*	R	R	Unknown
39	545805	*S. stoloniferum*	R	R	Unknown
40	558450	*S. stoloniferum*	R	S	RB
41	558451	*S. stoloniferum*	R	S	RB
42	558467	*S. stoloniferum*	R	R	Unknown
43	255541	*S. trifidum*	R	R	Unknown
44	558478	*S. trifidum*	R	R	Unknown
45	141173	*S. verrucosum*	R	S	RB
46	275260	*S. verrucosum*	R	S	RB
47	275258	*S. verrucosum*	R	S	RB

[a] R, resistant; S, susceptible.

individually or stacked via genetic modification techniques into elite cultivars to provide resistance against LB (Ghislain et al. 2019; Haesaert et al. 2015; Zhu et al. 2012). A recent study shows that stacking three *Rpi* genes, namely *RB/Rpi-blb1*, *Rpi-blb2*, and *Rpi-vnt1*, into potato cultivars 'Desiree' and 'Victoria' completely abolished LB infection without fungicide spray (Ghislain et al. 2019).

An allele mining study in *Solanum* germplasm identified 17 *RB*-like homologs in 11 different wild species of potato (Tiwari et al. 2015). Similarly, *RB*-related marker analysis was conducted on 21 *Solanum* species of tuber-bearing species, and the *RB*-related marker was present in ≥15 different species (Pankin et al. 2011). However, both of these studies lacked a functional study of *RB*-like genes from different species. To identify functional orthologs of the *RB* gene, we screened several US-23 resistant genotypes against the *P. infestans* isolate NL13316. We confirmed that *P. infestans* isolate NL13316 is virulent to *RB*-mediated resistance. We found no significant differences in the degree of susceptibility between K41, SP951, and susceptible control 'Katahdin' against NL13316 (Fig. 2). Because a single copy of the *RB* gene is inserted in SP951, it provides partial resistance to the *RB* avirulent *P. infestans* isolate US-23. In harmony with previous findings, there were significant differences in the *RB*-mediated resistance between K41 and SP951 against *P. infestans* isolate US-23. Even with the susceptible control 'Katahdin,' isolate NL13316 showed a significantly more virulent phenotype than US-23. It would be interesting to conduct a follow-up study on the virulence activity of isolate NL13316 to other cloned *R* genes in order to determine whether its ability to overcome resistance is specific to the *RB* gene. We found that US-23-resistant genotypes from *S. morelliforme*, *S. verrucosum*, and *S. stoloniferum* are susceptible to the *RB* breaking isolate NL13316, which suggests that genotypes from these species may contain an *RB*-like gene. The source of LB resistance found in *S. bulbocastanum*, *S. chacoense*, *S. cardiophyllum*, *S. ehrenbergii*, *S. microdontum*, *S. neocardenasii*, *S. okadae*, *S. polyadenium*, *S. pinnatisectum*, *S. piurae*, *S. trifidum*, and accessions of *S. stoloniferum* against *RB*-breaking isolate NL13316 could be a novel source of resistance. However, we did not eliminate the possibility of having *Rpi-blb2* and *Rpi-blb3* in *S. bulbocastanum* (Park et al. 2005a; van der Vossen et al. 2005), *Rpi-chc1* in *S. chacoense* (Vossen and Nijenhuis 2009), *R2* in *S. microdontum* (Lokossou 2010), or *Rpi-vnt1*-like genes in *S. okadae* (Van Weymers et al. 2016). The novel sources of resistance identified in these species could be valuable in the future for LB resistance breeding in potato.

In summary, we screened a broad array of wild potato relatives available in the U.S. Potato Genebank against LB pathogen *P. infestans* and identified 106 accessions from 27 species with a high degree of resistance. Additionally, by using strain-specific screening, we determined that the *RB*-like gene is probably present in some of the selected accessions. Some of these accessions could be an important new source of LB resistance genes in potato breeding programs.

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Literature Cited

Bachmann-Pfabe, S., Hammann, T., Kruse, J., and Dehmer, K. J. 2019. Screening of wild potato genetic resources for combined resistance to late blight on tubers and pale potato cyst nematodes. Euphytica 215:48.

Bethke, P. C., Halterman, D. A., and Jansky, S. 2017. Are we getting better at using wild potato species in light of new tools? Crop Sci. 57:1241-1258.

Black, W., Mastenbroek, C., Mills, W. R., and Peterson, L. C. 1953. A proposal for an international nomenclature of races of *Phytophthora infestans* and of genes controlling immunity in *Solanum demissum* derivatives. Euphytica 2: 173-179.

Bradeen, J. M., Iorizzo, M., Mollov, D. S., Raasch, J., Kramer, L. C., Millett, B. P., Austin-Phillips, S., Jiang, J., and Carputo, D. 2009. Higher copy numbers of the potato *RB* transgene correspond to enhanced transcript and late blight resistance levels. Mol. Plant-Microbe Interact. 22:437-446.

Brylińska, M., and Śliwka, J. 2017. Laboratory assessment of potato resistance to *Phytophthora infestans*. Plant Breed. Seed Sci. 76:17-23.

Caten, C. E. 1970. Spontaneous variability of single isolates of *Phytophthora infestans*. II. Pathogenic variation. Can. J. Bot. 48:897-905.

Chakrabarti, S. K., Singh, B. P., Thakur, G., Tiwari, J. K., Kaushik, S. K., Sharma, S., and Bhardwaj, V. 2014. QTL Analysis of late blight resistance in a diploid potato family of *Solanum spegazzinii* × *S. chacoense*. Potato Res. 57:1-11.

Champouret, N. 2010. Functional genomics of *Phytophthora infestans* effectors and Solanum resistance genes. PhD dissertation. Experimental Plant Sciences, Wageningen University, Wageningen, The Netherlands.

Collins, A., Milbourne, D., Ramsay, L., Meyer, R., Chatot-Balandras, C., Oberhagemann, P., De Jong, W., Gebhardt, C., Bonnel, E., and Waugh, R. 1999. QTL for field resistance to late blight in potato are strongly correlated with maturity and vigour. Mol. Breed. 5:387-398.

Colon, L. T., and Budding, D. J. 1988. Resistance to late blight (*Phytophthora infestans*) in ten wild *Solanum* species. Euphytica 39 (S3):77-86.

Cooke, D. E. L., Cano, L. M., Raffaele, S., Bain, R. A., Cooke, L. R., Etherington, G. J., Deahl, K. L., Farrer, R. A., Gilroy, E. M., Goss, E. M., Grünwald, N. J., Hein, I., MacLean, D., McNicol, J. W., Randall, E., Oliva, R. F., Pel, M. A., Shaw, D. S., Squires, J. N., Taylor, M. C., Vleeshouwers, V. G. A. A., Birch, P. R. J., Lees, A. K., and Kamoun, S. 2012. Genome Analyses of an aggressive and invasive lineage of the Irish potato famine pathogen. PLoS Pathog 8:e1002940.

Cruickshank, G., Stewart, H. E., and Wastie, R. L. 1982. An illustrated assessment key for foliage blight of potatoes. Potato Res. 25:213-214.

Dorrance, A. E., and Inglis, D. A. 1998. Assessment of laboratory methods for evaluating potato tubers for resistance to late blight. Plant Dis. 82:442-446.

Fisher, M. C., Henk, D. A., Briggs, C. J., Brownstein, J. S., Madoff, L. C., McCraw, S. L., and Gurr, S. J. 2012. Emerging fungal threats to animal, plant and ecosystem health. Nature 484:186-194.

Foster, S. J., Park, T.-H., Pel, M., Brigneti, G., Śliwka, J., Jagger, L., van der Vossen, E., and Jones, J. D. G. 2009. *Rpi-vnt1.1*, a *Tm-2(2)* homolog from *Solanum venturii* confers resistance to potato late blight. Mol. Plant-Microbe Interact. 22:589-600.

Fry, W. 2008. *Phytophthora infestans*: the plant (and *R* gene) destroyer. Mol. Plant Pathol. 9:385-402.

Fry, W. E. 1978. Quantification of general resistance of potato cultivars and fungicide effects for integrated control of potato late blight. Phytopathology 68:1650-1655.

Fry, W. E., and Goodwin, S. B. 1997. Resurgence of the Irish potato famine fungus: after 150 years, the late blight fungus is again menacing farmers. Bioscience 47:363-371.

Gebhardt, C., Ballvora, A., Walkemeier, B., Oberhagemann, P., and Schuler, K. 2004. Assessing genetic potential in germplasm collections of crop plants by marker–trait association: a case study for potatoes with quantitative variation of resistance to late blight and maturity type. Mol. Breed. 13:93-102.

Ghislain, M., Byarugaba, A. A., Magembe, E., Njoroge, A., Rivera, C., Román, M. L., Tovar, J. C., Gamboa, S., Forbes, G. A., Kreuze, J. F., Barekye, A. and Kiggundu, A. 2019. Stacking three late blight resistance genes from wild species directly into African highland potato varieties confers complete field resistance to local blight races. Plant Biotechnol. J. 17:1119-1129.

Gopal, J., and Singh, B. P. 2003. Screening potatoes for resistance to late blight (*Phytophthora infestans*) under field conditions. Potato Res. 46:47-56.

Haesaert, G., Vossen, J. H., Custers, R., De Loose, M., Haverkort, A., Heremans, B., Hutten, R., Kessel, G., Landschoot, S., Van Droogenbroeck, B., Visser, R. G. F., and Gheysenf, G. 2015. Transformation of the potato variety Desiree with single or multiple resistance genes increases resistance to late blight under field conditions. Crop Prot. 77:163-175.

Halterman, D. A., and Middleton, G. 2012. Presence of the potato late blight resistance gene *RB* does not promote adaptive parasitism of *Phytophthora infestans*. Am. J. Plant Sci. 3:360-367.

Halterman, D. A., Kramer, L. C., Wielgus, S., and Jiang, J. 2008. Performance of transgenic potato containing the late blight resistance gene *RB*. Plant Dis. 92: 339-343.

Haverkort, A. J., Boonekamp, P. M., Hutten, R., Jacobsen, E., Lotz, L. A. P., Kessel, G. J. T., Visser, R. G. F., and van der Vossen, E. A. G. 2008. Societal costs of late blight in potato and prospects of durable resistance through cisgenic modification. Potato Res. 51:47-57.

Haverkort, A. J., Boonekamp, P. M., Hutten, R., Jacobsen, E., Lotz, L. A. P., Kessel, G. J. T., Vossen, J. H., and Visser, R. G. F. 2016. Durable late blight resistance in potato through dynamic varieties obtained by cisgenesis: scientific and societal advances in the DuRPh Project. Potato Res. 59:35-66.

Helgeson, J. P., Pohlman, J. D., Austin, S., Haberlach, G. T., Wielgus, S. M., Ronis, D., Zambolim, L., Tooley, P., McGrath, J. M., James, R. V., and Stevenson, W. R. 1998. Somatic hybrids between *Solanum bulbocastanum* and potato: a new source of resistance to late blight. Theor. Appl. Genet. 96:738-742.

Huang, S., Vleeshouwers, V. G. A. A., Visser, R. G. F., and Jacobsen, E. 2005. An accurate in vitro assay for high-throughput disease testing of *Phytophthora infestans* in potato. Plant Dis. 89:1263-1267.

Jo, K.-R., Arens, M., Kim, T.-Y., Jongsma, M. A., Visser, R. G. F., Jacobsen, E., and Vossen, J. H. 2011. Mapping of the *S. demissum* late blight resistance gene *R8* to a new locus on chromosome IX. Theor. Appl. Genet. 123:1331-1340.

Jones, J., Foster, J. S., Chu, Z., Park, T., Gerard, E. A., Pel, A. M., and Visser, G. F. 2013. Late blight resistance genes and methods. US Patent W0 2009013468 A2. World Intellectual Property Organization 20 July 2007. https://patents.google.com/patent/WO2009013468A2/en

Khiutti, A., Spooner, D. M., Jansky, S. H., and Halterman, D. A. 2015. Testing taxonomic predictivity of foliar and tuber resistance to *Phytophthora infestans* in wild relatives of potato. Phytopathology 105:1198-1205.

Kim, H.-J., Lee, H.-R., Jo, K.-R., Mortazavian, S. M. M., Huigen, D. J., Evenhuis, B., Kessel, G., Visser, R. G. F., Jacobsen, E., and Vossen, J. H. 2012. Broad spectrum late blight resistance in potato differential set plants *MaR8* and *MaR9* is conferred by multiple stacked *R* genes. Theor. Appl. Genet. 124:923-935.

Kirk, W. W., Felcher, K. J., Douches, D. S., Niemira, B. A., and Hammerschmidt, R. 2001. Susceptibility of potato (*Solanum tuberosum* L.) foliage and tubers to the US-8 genotype of *Phytophthora infestans*. Am. J. Potato Res. 78:319-322.

Kuhl, J., Hanneman, R., and Havey, M. 2001. Characterization and mapping of *Rpi1*, a late-blight resistance locus from diploid (1EBN) Mexican *Solanum pinnatisectum*. Mol. Genet. Genomics 265:977-985.

Lapwood, D. H. 1961. Laboratory assessments of the susceptibility of potato haulm to blight (*Phytophthora infestans*). Eur. Potato J. 4:117-128.

Liu, Z., and Halterman, D. 2006. Identification and characterization of *RB*-orthologous genes from the late blight resistant wild potato species *Solanum verrucosum*. Physiol. Mol. Plant Pathol. 69:230-239.

Lokossou, A. A., Park, T. H., van Arkel, G., Arens, M., Ruyter-Spira, C., Morales, J., Whisson, S. C., Birch, P. R. J., Visser, R. G. F., and Jacobsen, E. 2009. Exploiting knowledge of *R/Avr* genes to rapidly clone a new LZ-NBS-LRR family of late blight resistance genes from potato linkage group IV. Mol. Plant-Microbe Interact. 22:630-641.

Lokossou, A. A. 2010. Dissection of the Major Late Blight Resistance Cluster on Potato Linkage Group IV. PhD dissertation. Experimental Plant Sciences. Wageningen University, Wageningen, The Netherlands. https://edepot.wur.nl/138871

Lokossou, A. A., Rietman, H., Wang, M., Krenek, P., van der Schoot, H., Henken, B., Vosman, B., et al. 2010. Diversity, distribution, and evolution of *Solanum bulbocastanum* late blight resistance genes. Mol. Plant Microbe Interact. 23: 1206-1216.

Malcolmson, J. F. 1976. Assessment of field resistance to blight (*Phytophthora infestans*) in potatoes. Trans. Br. Mycol. Soc. 67:321-325

Malcolmson, J. F., and Black, W. 1966. New *R* genes in *Solanum demissum* lindl. and their complementary races of *Phytophthora infestans* (Mont.) de bary. Euphytica 15:199-203.

Nachtigall, M., König, J., and Thieme, R. 2018. Mapping of a novel, major late blight resistance locus in the diploid (1EBN) Mexican *Solanum pinnatisectum* Dunal on chromosome VII. Plant Breed. 137:433-442.

Naess, S. K., Bradeen, J. M., Wielgus, S. M., Haberlach, G. T., McGrath, J. M., and Helgeson, J. P. 2000. Resistance to late blight in *Solanum bulbocastanum* is mapped to chromosome 8. Theor. Appl. Genet. 101:697-704.

Oberhagemann, P., Chatot-Balandras, C., Schäfer-Pregl, R., Wegener, D., Palomino, C., Salamini, F., Bonnel, E., and Gebhardt, C. 1999. A genetic analysis of quantitative resistance to late blight in potato: towards marker-assisted selection. Mol. Breed. 5:399-415.

Pankin, A., Sokolova, E., Rogozina, E., Kuznetsova, M., Deahl, K., Jones, R., and Khavkin, E. 2011. Allele mining in the gene pool of wild *Solanum* species for homologues of late blight resistance gene *RB/Rpi-blb1*. Plant Genet. Resour.9: 305-308.

Park, T. H., Gros, J., Sikkema, A., Vleeshouwers, V. G. A. A., Muskens, M., Allefs, S., Jacobsen, E., Visser, R. G. F., and van der Vossen, E. A. G. 2005a. The late blight resistance locus *Rpi-blb3* from *Solanum bulbocastanum* belongs to a major late blight *R* gene cluster on chromosome 4 of potato. Mol. Plant-Microbe Interact. 18:722-729.

Park, T.-H., Vleeshouwers, V. G. A. A., Kim, J.-B., Hutten, R. C. B., and Visser, R. G. F. 2005c. Dissection of foliage and tuber late blight resistance in mapping populations of potato. Euphytica 143:75-83.

Rauscher, G. M., Smart, C. D., Simko, I., Bonierbale, M., Mayton, H., Greenland, A., and Fry, W. E. 2006. Characterization and mapping of *Rpi-ber*, a novel potato late blight resistance gene from *Solanum berthaultii*. Theor. Appl. Genet. 112:674-687.

Sandbrink, J. M., Colon, L. T., Wolters, P. J. C. C., and Stiekema, W. J. 2000. Two related genotypes of *Solanum microdontum* carry different segregating alleles for field resistance to *Phytophthora infestans*. Mol. Breed. 6:215-225.

Savary, S., Willocquet, L., Pethybridge, S. J., Esker, P., McRoberts, N., and Nelson, A. 2019. The global burden of pathogens and pests on major food crops. Nat. Ecol. Evol. 3:430-439.

Saville, A., Graham, K., Grünwald, N. J., Myers, K., Fry, W. E., and Ristaino, J. B. 2015. Fungicide sensitivity of U.S. genotypes of *Phytophthora infestans* to six oomycete-targeted compounds. Plant Dis. 99:659-666.

Simko, I., Costanzo, S., Ramanjulu, V., Christ, B. J., and Haynes, K. G. 2006. Mapping polygenes for tuber resistance to late blight in a diploid *Solanum phureja* x *S. stenotomum* hybrid population. Plant Breed. 125:385-389.

Sokolova, E., Pankin, A., Beketova, M., Kuznetsova, M., Spiglazova, S., Rogozina, E., Yashina, I., and Khavkin, E. 2011. SCAR markers of the R-genes and germplasm of wild *Solanum* species for breeding late blight-resistant potato cultivars. Plant Genet. Resour. 9:309-312.

Song, J., Bradeen, J. M., Naess, S. K., Raasch, J. A., Wielgus, S. M., Haberlach, G. T., Liu, J., Kuang, H., Austin-Phillips, S., Buell, C. R., Helgeson, J. P., and Jiang, J. 2003. Gene RB cloned from *Solanum bulbocastanum* confers broad spectrum resistance to potato late blight. Proc. Natl. Acad. Sci. USA. 100:9128-9133.

Spooner, D. M., Jansky, S., Rodriguez, F., Simon, R., Ames, M., Fajardo, D., and Castillo, R. 2019. Taxonomy of wild potatoes in northern South America (Solanum section Petota). Volume 108 of Systematic Botany Monographs. American Society of Plant Taxonomists, Ann Arbor, MI.

Stewart, H. E., Wastie, R. L., Bradshaw, J. E., and Brown, J. 1992. Inheritance of resistance to late blight in foliage and tubers of progenies from parents differing in resistance. Potato Res. 35:313-319.

Stewart, H. E., Flavelle, P. H., McCalmont, D. C., and Wastie, R. L. 1983. Correlation between glasshouse and field tests for resistance to foliage blight caused by *Phytophthora infestans*. Potato Res. 26:41-48.

Tiwari, J. K., Devi, S., Sharma, S., Chandel, P., Rawat, S., and Singh, B. P. 2015. Allele mining in *solanum* germplasm: cloning and characterization of *RB*-homologous gene fragments from late blight resistant wild potato species. Plant Mol. Biol. Report. 33:1584-1598.

Toxopeus, H. J. 1964. Treasure-digging for blight resistance in potatoes. Euphytica 13:206-222.

van der Vossen, E., Sikkema, A., Te Lintel Hekkert, B., Gros, J., Stevens, P., Muskens, M., Wouters, D., Pereira, A., Stiekema, W., and Allefs, S. 2003. An ancient *R* gene from the wild potato species *Solanum bulbocastanum* confers broad-spectrum resistance to *Phytophthora infestans* in cultivated potato and tomato. Plant J. 36:867-882.

van der Vossen, E. A. G., Gros, J., Sikkema, A., Muskens, M., Wouters, D., Wolters, P., Pereira, A., and Allefs, S. 2005. The *Rpi-blb2* gene from *Solanum bulbocastanum* is an *Mi-1* gene homolog conferring broad-spectrum late blight resistance in potato. Plant J. 44:208-222.

Van Weymers, P. S. M., Baker, K., Chen, X., Harrower, B., Lees, A. K., Lynott, J. S., Armstrong, M. R., McKenzie, G., Bryan, G. J., and Hein, I. 2016. Utilizing " omic " technologies to identify and prioritize novel sources of resistance to the oomycete pathogen *Phytophthora infestans* in potato germplasm collections. Front. Plant Sci. 7:672.

Vleeshouwers, V. G. A. A., Rietman, H., Krenek, P., Champouret, N., Young, C., Oh, S.-K., Wang, M., Bouwmeester, K., Vosman, B., Visser, R. G. F., Jacobsen, E., Govers, F., Kamoun, S., and Van der Vossen, E. A. G. 2008. Effector genomics accelerates discovery and functional profiling of potato disease resistance and *Phytophthora infestans* avirulence genes. PLoS One 3: e2875.

Vleeshouwers, V. G. A. A., Van Dooijeweert, W., Keizer, L. C. P., Sijpkes, L., Govers, F., and Colon, L. T. 1999. A laboratory assay for *Phytophthora infestans* resistance in various *Solanum* species reflects the field situation. Eur. J. Plant Pathol. 105:241-250.

Vossen, J. H., and Nijenhuis, M. A. R. M. J. 2009. Cloning and exploitation of a functional R-gene from *Solanum chacoense*. US Patent: WO 2011034433 A1. https://data.epo.org/gpi/EP2478006A1

Vossen, J. H., van Arkel, G., Bergervoet, M., Jo, K. R., Jacobsen, E., and Visser, R. G. F. 2016. The *Solanum demissum R8* late blight resistance gene is an *Sw-5* homologue that has been deployed worldwide in late blight resistant varieties. Theor. Appl. Genet. 129:1785-1796.

Wang, M., Allefs, S., Van Den Berg, R. G., Vleeshouwers, V. G. A. A., Van Der Vossen, E. A. G., and Vosman, B. 2008. Allele mining in *Solanum*: conserved homologues of *Rpi-blb1* are identified in *Solanum stoloniferum*. Theor. Appl. Genet. 116:933-943.

Wastie, R. L. 1991. Breeding for resistance. Pages 193-223 in: Advances in Plant Pathology 7: *Phytophthora infestans*, the Cause of Late Blight of Potato. D. S. Ingram and P. H. Williams, eds. Academic Press, New York, NY.

Zhan, J., and McDonald, B. A. 2013. Experimental measures of pathogen competition and relative fitness. Annu. Rev. Phytopathol. 51:131-153.

Zhu, S., Li, Y., Vossen, J. H., Visser, R. G. F., and Jacobsen, E. 2012. Functional stacking of three resistance genes against *Phytophthora infestans* in potato. Transgenic Res. 21:89-99.