Foliar Resistance to *Phytophthora infestans* (Mont.) de Bary (US-8) in 13 Mexican and South American *Solanum* Species Having EBNs of 1, 2, and 4 and Implications for Breeding

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ABSTRACT

The recent US-8 clonal lineage of *Phytophthora infestans*, the pathogen causing late blight (LB) disease, is one of the most widespread and difficult to control. Sources of foliar resistance to US-8 were evaluated in 1927 seedling genotypes by sampling 49 plant introductions (PIs) representing 13 Mexican and South American *Solanum* species having an Endosperm Balance Number (EBN) of 1, 2, or 4, and one species with an unknown EBN. Species evaluated were 2*x*(1EBN) *S. bulbocastanum, S. cardiophyllum, S. commersonii, S. pinnatisectum*, and *S. trifidum*; 2*x*(2EBN) *S. berthaultii, S. megistacrolobum, S. microdontum*, and *S. verrucosum*; 4*x*(2EBN) *S. fendleri* and *S. stoloniferum*; 6*x*(4EBN) *S. guerreroense*; 2*x* unknown EBN *S. polyadenium*; as well as 4*x* *S. tuberosum* families as controls. Foliar resistance in the field was monitored in 1998 and 1999. Resistance differed relative to species geographic origin, EBN, species themselves, PIs within a species, and genotypes within a PI. In 1998 Mexican germplasm had a lower area under the disease progress curve (AUDPC, 1140) and greater resistance than South American germplasm (1601), while the 1EBN (1119) and unknown EBN (1075) species had greater resistance than 2EBN (1470) and 4EBN (1888) species. AUDPC ranged among species from 555 (*S. cardiophyllum*) to 1932 (*S. megistacrolobum*) and among PIs within a species most widely for *S. bulbocastanum* (267-1007) and least widely for *S. polyadenium* (1019-1179). In 1999 LB symptoms were not observed on the species before an early freeze; however, all 1999 *S. tuberosum* families showed LB symptoms and segregated for resistance, pointing to greater resistance in the species than in cultivated germplasm. Resistance found in diploid 2EBN germplasm is more accessible due to greater crossability with cultivated germplasm; however, though more difficult to introgress, resistance found in some of the more reproductively isolated 1EBN germplasm is worth pursuing.

RESUMEN

El nuevo linaje clonal US-8 de *Phytophthora infestans* causante de la enfermedad conocida como tizón tardío (LB) es uno de los más difundidos y difícil de controlar. Se evaluaron las fuentes de resistencia foliar en 1927 genotipos de plántulas, muestreando 49 introducciones de plantas (PIs) que representan 13 especies de *Solanum* mexicanas y sudamericanas, con un número de balance del endospermo (EBN) de 1, 2, o 4 y una especie de EBN desconocido. Las especies evaluadas fueron 2*x*(1EBN) *S. bulbocastanum, S. cardiophyllun, S. commersonii S. pinnatisectum* y *S. trifidum*; 2*x*(2EBN) *S. bertaulthii, S. megistacrolobum, S. microdontum* y *S. verrucosum*; 4*x*(2EBN) *S. fendleri* y *S. stoloniferum*; 6*x*(4EBN) *S. guerreroense*; *S. polyadenium* 2*x* de EBN desconocido y familias de *S. tuberosum* 4*x*, fueron también incluidas como testigo. La resistencia foliar en el campo fue monitoreada en 1998 y 1999. La resistencia

Accepted for publication 10 August 2004.
ADDITIONAL KEY WORDS: Endosperm Balance Number, EBN, late blight, *Phytophthora infestans*, potato breeding, *Solanum* species

ABBREVIATIONS: AUDPC, area under the disease progress curve; EBN, Endosperm Balance Number; LB, late blight; NRSP-6, USDA/ARS Potato Introduction Station; PIs, plant introductions; UMORE, University of Minnesota, Outreach, Research and Extension Park

fue relativamente diferente en especies de origen geográfico distinto, EBN, especie, PIs dentro de la especie y genotipos dentro de un mismo PI. En 1998, el germoplasma mexicano presentó menor área bajo la curva de progreso de la enfermedad (AUDPC, 1140) y mayor resistencia que el germoplasma sudamericano (1601), mientras que el 1EBN (1119) y la especie de EBN desconocido (1075) tuvieron mayor resistencia que las especies 2EBN (1470) y 4EBN (1888). El AUDPC varió entre especies de 555 (*S. cardiophyllum*) a 1932 (*S. megistacrolobum*) y entre PIs dentro de una especie, más amplio para *S. bulbocastanum* (267-1007) y más restringido para *S. polyadenium* (1019-1179). En 1999, no se observaron síntomas de LB en esta especie antes de la primera helada, sin embargo, todas las familias de *S. tuberosum* mostraron síntomas de LB y segregaron para resistencia, indicando mayor resistencia en la especie que en el germoplasma cultivado. La resistencia encontrada en el germoplasma diploide 2EBN es más accesible debido a una mayor posibilidad de cruzamiento con el germoplasma cultivado, sin embargo, aunque es más difícil la incorporación de genes por hibridación, vale la pena hacer un seguimiento de la resistencia hallada en el germoplasma 1EBN aislado de los cruzamientos más reproductivos.

INTRODUCTION

The potato disease late blight (LB), caused by the pathogen *Phytophthora infestans*, is one of the most important diseases that affects the potato industry worldwide. The disease reduces yield through rapid foliar destruction in the field as well as tuber decay during growth and development and during storage (Hooker 1981). Today both A1 and A2 mating types of *P. infestans* exist worldwide. Since the first A2 collection in Europe (1981) (Hohl and Iselin 1984) and in the United States (1987) (Deahl et al. 1991), reports abound that the clonal lineages of A2 are displacing A1 lineages in many areas (Goodwin et al. 1995, 1996; Koh et al. 1994; Marshall-Farrar et al. 1998; Platt 1994; Sujkowski et al. 1994). The US-8 (A2) clonal lineage is more virulent than the once predominant US-1 (A1) lineage and has displaced it in many growing regions within the United States and Canada (Fry and Goodwin 1997; Goodwin et al. 1995, 1996; Marshall-Farrar et al. 1998; Miller et al. 1998; Platt 1994). Compared to US-1, the US-8 has greater lesion-area expansion capacity (Kato et al. 1997; Miller et al. 1998) and greater tuber infection potential (Lambert and Currier 1997; Marshall and Stevenson 1996). In addition, US-8 and other recent clonal lineages are insensitive to metalaxyl, a once commonly used systemic fungicide that was effective in late blight control (Goodwin et al. 1996; Kato et al. 1997).

The potential for sexual recombination and the emergence of more aggressive races of *P. infestans* has resulted in renewed interests to identify new sources of resistance among the wild *Solanum* species for introgression into cultivars. Genetic variability for traits having economic importance is well documented among the 228 recognized wild potato species; including resistance to *P. infestans* (Bamberg et al. 1994; Colon and Budding 1988; Hanneman and Bamberg 1986; Hawkes 1994; Toxopeus 1964). Race-specific resistance to *P. infestans* derived from *S. demissum* has been extensively used (Toxopeus 1964). Unfortunately, all 11 race-specific resistance alleles identified in this species have been overcome by virulence alleles in the pathogen (Turkensteen 1993). Non-race-specific resistance to *P. infestans* is also found among the wild potato species and promises the most potential for durable protection of cultivated potatoes (Black 1970). The center of origin for *P. infestans* is most likely the Toluca Valley in central Mexico, where the pathogen's greatest genetic variability can be found (Niederhauser 1991). Douches et al. (2001) found greater resistance to *P. infestans* (US-8) among Mexican PIs than South American PIs evaluated.

Late blight is becoming an increasingly difficult disease to control and there is a growing need to explore and to integrate diverse strategies for successful management. One strategy is to introgress and pyramid diverse genetic resistance found in wild *Solanum* species into adapted breeding lines and cultivars. The objective of this research was to determine sources of foliar resistance to *P. infestans* (US-8) among *Solanum* germplasm previously reported as having resistance to *P. infestans* clonal lineages other than US-8 (Bamberg et al. 1994, Hanneman and Bamberg 1986). Germplasm was chosen to represent Mexican and South American origin and various breeding systems, ploidy, and Endosperm Balance Number (EBN) values to explore their implications towards breeding progress.

MATERIALS AND METHODS

1998 Field Season

Botanical seed of 49 PIs representing 13 Mexican and South American *Solanum* species was obtained from the Inter-Regional Potato Introduction Project (NRSP-6) in Sturgeon Bay, WI (Table 1). All PIs selected had resistance to *P. infestans* using clonal lineages other than US-8 from earlier work reported to NRSP-6 and documented by Bamberg et al. (1994) and Hanneman and Bamberg (1986), with the exception of *S. commersonii*. One-hundred seeds of each PI were sown in a commercial peat-based germination mix and up to 48 seedlings per PI were transplanted to 7.7-cm square pots. To facilitate testing over years, one herbaceous stem cutting was

TABLE 1—*Area under the disease progress curve (AUDPC) and % defoliation at final reading caused by* Phytophthora infestans *in 1998 field evaluations for 49* Solanum *plant introductions from 13* Solanum *species.*

Origin Species (ploidy)[a]	EBN[a]	Plant Introductions[b]	N	AUDPC Mean[c]	AUDPC +/- SD	% Defoliation at final reading Mean[c]	% Defoliation at final reading +/- SD	% Defoliation at final reading Range
MEXICO								
S. bulbocastanum (2*x*)	1	7 PIs[d]	297	649 A	344	55 B	24	0–100
		243345	37	840 de	232	61 cd	14	25–75
		243504	44	746 cd	233	61 cd	18	10–90
		243505	47	548 b	257	44 b	22	1–75
		243506	48	574 bc	299	47 b	21	0–75
		243509	38	727 cd	384	51 bc	24	1–100
		243512	48	267 a	198	26 a	18	2.5–75
		275192	35	1007 d	237	73 d	15	25–98
S. cardiophyllum (2*x*)	1	2 PIs	55	555 A	306	39 A	21	10–90
		283062	47	460 a	210	34 a	16	1–75
		283063	8	1113 b	129	74 b	11	50–90
S. fendleri (4*x*)	2	1 PI	31	1265 CD	269	76 CD	11	50–100
		225661	31	1265	269	76	11	50–100
S. guerreroense (6*x*)	4	1 PI	39	1888 FG	177	95 GH	8	90–100
		161727	39	1888	177	95	8	90–100
S. pinnatisectum (2*x*)	1	11 PIs	492	1178 BC	146	75 CD	4	50–100
		184764	47	1268 de	102	76 ab	4	75–90
		184774	46	1184 cd	100	75 ab	0	75–75
		190115	46	1225 cd	125	74 ab	4	50–75
		230489	45	1196 cd	133	75 ab	0	75–75
		253214	48	1207 cd	128	75 ab	2	75–90
		275231	48	1146 bc	107	75 ab	0	75–75
		275232	48	1172 c	157	77 bc	5	75–907
		275233	39	1074 ab	172	75 ab	6	50–100
		275234	30	1325 e	101	80 c	7	75–90
		275236	47	1020 a	145	74 a	6	50–90
		347766	48	1183 cd	98	74 ab	4	50–75
S. polyadenium (2*x*)	Unknown	5 PIs	178	1075 B	250	73 C	13	25–100
		230480	47	1019 a	202	70 a	13	50–98
		275237	35	1049 a	240	71 ab	14	25–100
		275238	44	1035 a	126	68 a	11	50–75
		310963	33	1175 a	352	80 c	9	75–100
		320342	19	1179 a	319	79 bc	9	75–90
S. stoloniferum (4*x*)	2	6 PIs	274	1435 E	260	76 CDE	10	50–100
		161158	48	1332 b	184	76 b	3	75–90
		161178	48	1458 c	95	75 b	0	75–75
		195166	48	1711 d	139	85 c	7	75–100
		205510	34	1748 d	116	76 b	5	75–100
		230490	48	1296 b	106	82 c	8	75–90
		239410	48	1157 a	228	65 a	12	50–75
S. trifidum (2*x*)	1	3 PIs	127	1542 E	390	87 FG	13	50–100
		283064	36	1272 a	354	79 a	14	50–100
		283065	44	1418 a	301	87 b	12	75–100
		283104	47	1866 b	238	95 c	8	75–100

TABLE 1—*Continued.*

Origin Species (ploidy)[a]	EBN[a]	Plant Introductions[b]	N	AUDPC Mean[c]	AUDPC +/- SD	% Defoliation at final reading Mean[c]	% Defoliation at final reading +/- SD	% Defoliation at final reading Range
S. verrucosum (2*x*)	2	1 PI	21	1404 DE	464	82 DEF	17	50–100
		161173	21	1404	464	82	17	50–100
SOUTH AMERICA								
S. berthaultii (2*x*)	2	3 PIs	124	1458 E	243	83 DEF	10	75–100
		265857	48	1571 b	207	87 b	10	75–100
		265858	30	1538 b	164	84 b	10	75–100
		473331	46	1287 a	227	78 a	7	75–100
S. commersonii (2*x*)	1	4 PIs	144	1726 F	289	85 EF	11	50–100
		320267	43	1534 a	225	77 a	8	50–90
		320269	47	1764 b	310	85 b	11	75–100
		473408	28	1732 b	223	87 b	11	75–100
		476412	26	1970 c	182	93 c	11	75–100
S. megistacrolobum (2*x*)	2	1 PI	23	1932 G	191	100 H	1	98–100
		195210	23	1932	191	100	1	98–100
S. microdontum (2*x*)	2	4 PIs	122	1536 E	370	81 DEF	14	50–100
		195185	21	1543 b	481	81 ab	19	50–100
		218224	48	1313 a	228	75 a	9	75–90
		473166	15	1701 bc	241	87 b	12	75–100
		473171	38	1748 c	337	87 b	14	50–100

[a]*Solanum* species origin, ploidy, and Endosperm Balance Number (EBN) from Hanneman and Bamberg (1986).
[b]Plant introductions obtained from NRSP-6, USDA/ARS Potato Introduction Station, Sturgeon Bay, WI 54235.
[c]AUDPC and % defoliation followed by the same letter do not differ significantly between species (upper case letters) or within a species (lower case letters) using Hochberg's GT2 with $P \leq 0.05$ (Sokal and Rohlf 1995).
[d]The first row within each species summarizes all genotypes for that species.

taken from each genotype and rooted under intermittent mist. Having two genetically identical groups allowed the original seedlings to be used the first field-season for disease assessments, while the rooted cuttings were reserved for tuber increase under natural, shortening day length from August to December 1998 at the University of Minnesota, St. Paul, MN.

On 23 August 1998 seedlings were transported to the University of Minnesota LB disease screening nursery at the University of Minnesota, Outreach, Research, and Extension (UMORE) Park, Rosemount, MN. The number of genotypes within each PI was equally divided for replication of PIs in the field and placed in plastic trays and arranged in the field in two randomized complete blocks. Thus, each PI was represented twice in the field. The median number of genotypes evaluated for each PI was 44. To ensure uniform exposure to *P. infestans* inoculum, genotypes were positioned between adjacent border rows (0.9 m apart) of the susceptible cultivar Norchip, which had been previously inoculated (10 August 1998) with a suspension of 6,000-8,000 sporangia mL^{-1} of *P. infestans* (US-8, strain ND 95-2) (Jenkins 2000). Twelve days after field placement, genotypes were directly inoculated with US-8, ND 95-2 (6,000-8,000 sporangia mL^{-1}), to guard against escapes. Throughout the epidemic the field was sprinkler irrigated (1.3 cm) every other day during the morning hours to prolong leaf wetness and to facilitate disease development.

Foliar LB disease assessments were taken on each seedling genotype twice a week for a total of seven readings. The rating scale of 1 to 9 was used, where 1 = no visible lesions to 9 = 100% necrotic tissue (Henfling 1987). The scores were converted to mean percent defoliation for the corresponding range (i.e., 1 = 0%, 5 = 50%, and 9 = 100%) and used to calculate the area under the disease progress curve (AUDPC) for each genotype (Shaner and Finney 1977).

1999 Field Season

Despite efforts to optimize 1998 greenhouse environmental conditions, not all genotypes set tubers from rooted cuttings. Tubers were harvested December 1998 and stored at 4 C for two months and were then planted in the greenhouse. Every genotype that emerged was clonally replicated by rooting two herbaceous stem cuttings. On 29 June 1999, following sufficient growth, rooted cuttings were field-transplanted at the UMORE

Park using a randomized complete block design with two blocks. Each PI was represented once per block and genotypes were nested within respective PI. Plants were spaced 30 cm within rows and 91 cm between rows. Additionally, between 8 and 26 seedling tuber genotypes from each of 18 *S. tuberosum* 4*x* families were randomized as family plots and planted among the *Solanum* species plots. The 4*x* families were comprised of crosses involving S (US-8 susceptible) x R (US-8 resistant) and S x S 4*x* breeding lines and cultivars. Each seedling tuber genotype was represented once in the field.

As in 1998, experimental plots were planted adjacent to border rows of a susceptible cultivar; Russet Burbank was used in 1999. Border plants were inoculated with *P. infestans* (6,000-8,000 sporangia mL^{-1}, US-8, ND 95-2) on 16 August 1999. Sprinkler irrigation was used to prolong leaf wetness and to facilitate disease development. Foliar LB disease assessments were made twice a week totaling five readings before a freeze killed all plants on 2 October 1999.

Analysis of variance was used to test for significant differences in resistance between various germplasm groups and Hochberg's GT2 (Sokal and Rohlf 1995) was used for mean separation to account for unequal sample sizes using $P \leq 0.05$.

RESULTS

1998 Field Season

Variability for resistance to *P. infestans* (US-8, ND 95-2) was found between germplasm grouped by origin and EBN (Tables 1 and 2). Mexican germplasm was significantly more resistant (AUDPC 1140; final defoliation 71%) than germplasm of South American origin (AUDPC 1601; final defoliation 84%). The mean AUDPC and percent defoliation at the final reading for the 1EBN species (1119; 70%) and *S. polyadenium* (unknown EBN, 1075; 73%) were not significantly different, but were significantly lower than the 2EBN (1470; 80%) and the 4EBN (1888; 95%) species (Table 2). In addition, AUDPC and percent defoliation between the 2EBN species and 4EBN *S. guerreroense* were significantly different.

Variability for resistance to *P. infestans* was observed between *Solanum* species; both between and within EBN groups (Table 1). *Solanum cardiophyllum* had an AUDPC (555) significantly lower than any other species followed by *S. bulbocastanum* (649), *S. polyadenium* (1075), and *S. pinnatisectum* (1178). These four species are diploid and of Mexican origin. The 1EBN species, *S. bulbocastanum* and *S. cardiophyllum*, had AUDPC scores nearly two times lower than any other species evaluated. Species within the 2EBN group, regardless of origin, had >75% defoliation or greater at the final reading, whereas three 1EBN species and *S. polyadenium* had defoliation ≤75% at the final reading (Table 1). *Solanum commersonii* was included in this research even though it was not previously characterized as a resistant species; it had one of the highest AUDPC values. When *S. commersonii* is removed from analysis, the significant differences observed between origin and EBN groups did not change. Resistance in the 1EBN species *S. commersonii* and *S. trifidum* were more similar to 2EBN species, while *S. polyadenium* was more similar to the 1EBN Mexican species.

TABLE 2—*Area under the disease progress curve (AUDPC) and % defoliation at final reading to* Phytophthora infestans *in 1998 field evaluations of* Solanum *germplasm grouped by origin and Endosperm Balance Number (EBN).*

Origin and EBN	No. of plant introductions	No. of plants	AUDPC Mean[a]	AUDPC +/- SD	% Defoliation at final reading Mean[a]	% Defoliation at final reading +/- SD
MEXICO (M)[b]	37	1514	1140A	420	71A	19
1 EBN	23	971	1029a	418	67a	21
2 EBN	8	178	1417b	282	77c	10
4 EBN	1	326	1888c	177	95d	8
Unknown EBN	5	39	1075a	250	73ab	13
SOUTH AMERICA (SA)[b]	12	413	1601B	328	84B	12
1 EBN	4	144	1726a	289	85a	11
2 EBN	8	269	1534b	329	84a	13
M and SA[b]	49	1927	1239	444	74	19
1 EBN	27	1115	1119a	466	70a	21
2 EBN	16	595	1470b	309	80b	12
4 EBN	1	39	1888c	177	95c	8
Unknown EBN	5	178	1075a	250	73a	13

[a]AUDPC and % defoliation followed by the same letter between origin (upper case letters) or EBN (lower case letters) do not differ significantly using a t-test for origin ($P < 0.001$) and Hochberg's GT2 at $P \leq 0.05$ for EBN (Sokal and Rohlf 1995).

[b]The first row of each location of origin summarizes the *Solanum* species within that location.

Variability for resistance to *P. infestans* was found between PIs within a species and between genotypes within a PI (Table 1). For example, within *S. bulbocastanum* the most susceptible PI (275192, AUDPC 1007) had an AUDPC nearly four times that of the most resistant PI (243512, AUDPC 267). Likewise, from the 2EBN group, *S. berthaultii* PI 473331 (AUDPC 1287) had significantly more resistance than *S. berthaultii* PIs 265857 (1571) and 265858 (1538). This trend of observing PI within species differences occurred across all species tested, even when sampling only two PIs as with *S. cardiophyllum*. Variability between genotypes was observed with respect to segregation of resistance within a PI as shown by wide standard deviation ranges for both AUDPC and percent plant defoliation (Table 1). *Solanum pinnatisectum* had the lowest standard deviations for AUDPC and percent defoliation (146 and 4, respectively), while *S. verrucosum* had the highest AUDPC standard deviation (464) and *S. bulbocastanum* the highest percent defoliation standard deviation (24).

1999 Field Season

Disease progression on inoculated border rows of Russet Burbank occurred very slowly due to generally warm and dry weather conditions. Late blight symptoms did not progress rapidly enough to be observed on species germplasm prior to an early, killing freeze. However, the epidemic progressed sufficiently to observe late blight symptoms on all *S. tuberosum* families and to observe significant differences between them for resistance. *Solanum tuberosum* families having one resistant parent (AUDPC 140) had significantly greater resistance ($P < 0.001$) than families arising from crosses between two susceptible parents (AUDPC 210) (Table 3). The species exhibited greater resistance than the *S. tuberosum* families.

DISCUSSION

Genetic variability for resistance to *P. infestans* (US-8, strain ND 95-2) was found between *Solanum* species and PIs

TABLE 3—*Area under the disease progress curve (AUDPC) and % defoliation at final reading caused by* Phytophthora infestans *for 18* Solanum tuberosum *families in 1999 field evaluations.*

Cross no.	No. of plants	Parentage female	Parentage male	AUDPC Mean[a]	AUDPC +/- SD	AUDPC 95% Confidence interval	% Defoliation at final reading Mean[a]	% Defoliation at final reading +/- SD	% Defoliation at final reading Range
				S x R[b]					
52	11	MaineChip	BO718-3	59a	84	2–116	11a	16	0–50
56	11	Pike	Jacqueline Lee	89ab	40	62–116	36abc	13	25–50
51	12	Chipeta	Zarewo	90ab	49	59–121	35abc	20	10–75
54	16	ND2470-27	Jacqueline Lee	121abc	79	79–164	43bcd	24	10–75
55	12	NY103	Jacqueline Lee	133abc	97	71–195	40bcd	20	25–75
53	19	MN86118	Penta	156abcd	74	121–192	48bcd	21	10–75
50	17	Atlantic	Jacqueline Lee	264de	126	199–328	61cde	30	10–100
Total	98			140	105		41	25	0–100
				S x S					
63	18	MN86119	Chipeta	87ab	51	62–112	32ab	18	2.5–75
67	12	NY103	Yukon Gold	114abc	45	85–142	43bcd	18	10–75
66	11	MSA091-1	ND2676-10	154abcd	72	105–202	41bcd	20	25–75
61	17	MN16478	Agassiz	165abcd	68	130–200	46bcd	23	10–75
58	13	MaineChip	Chipeta	167abcd	64	128–205	52bcd	25	10–90
57	10	Chipeta	Chipeta	186bcd	76	132–240	48bcd	14	25–75
59	22	MaineChip	Yukon Gold	192bcd	100	148–236	58bcde	18	25–97.5
64	26	MN86129	ND2676-10	212cd	85	177–246	66def	19	25–90
65	8	MN86131	Yukon Gold	219cd	105	131–307	59bcde	19	25–75
62	19	MN85439	ND2676-10	362ef	119	304–419	80ef	15	50–97.5
60	15	Mainestay	MN86125	404f	92	353–455	91f	10	75–100
Total	171			210	124		57	25	2.5–100

[a]AUDPC and % defoliation at final reading followed by the same letter do not differ significantly using Hochberg's GT2 at $P < 0.05$ (Sokal and Rohlf 1995).

[b]S x R = Susceptible x Resistant cross; S x S = Susceptible x Susceptible cross.

previously identified as having resistance to clonal lineages other than US-8. Caution should be taken from making broad categorical judgments about a species resistance to *P. infestans*, since this research did not randomly sample species acquisitions at NRSP-6 or other international genebanks. Nevertheless, this research points to multiple wild *Solanum* sources possessing high levels of resistance to the tested US-8 isolate that breeders can access for introgression into cultivated potatoes. Moreover, the potential exists to identify in this germplasm greater durability to *P. infestans* since resistance was found to both US-8 in this research as well as other clonal lineages in previous research (Bamberg et al. 1994; Hanneman and Bamberg 1986).

Individuals with relatively high late blight resistance were observed in both Mexican and South American germplasm; despite finding a significant overall difference between the groups. Mexico is suspected to be the center of origin of *P. infestans* (Niederhauser 1991). Geographical separation between Mexico and South America and the hypothesized center of origin of *P. infestans* being proximal to the Toluca Valley of Mexico (Niederhauser 1991) may account for greater resistance being found among Mexican germplasm due to longer co-evolution between host and pathogen compared to South American species. Finding greater resistance (US-8) among *Solanum* species originating in Mexico relative to species originating in South America (Table 2) is in agreement with Douches et al. (2001) also evaluating Mexican and South American PIs for resistance to US-8. Species PIs used in this research do not overlap with those of Douches et al. (2001) and thus this research expands the knowledge and characterization of NRSP-6 inventories. Mexican PIs tested herein having collection locality data reported by Bamberg et al. (1996b) and by the USDA in the Germplasm Resources Information Network database, http://www.ars-grin.gov, were located relatively close (~300 kilometers) to the Toluca Valley.

The Mexican 1EBN germplasm seems in particular to be a valuable source of resistance to *P. infestans* (Tables 1 and 2). Perhaps not only evolving in a region with high selection pressure for *P. infestans* resistance led to generally high resistance among the Mexican 1EBN germplasm, but also sharing a common EBN would not by itself exclude gene exchange between the 1EBN germplasm. Researchers have pursued accessing resistance to biotic and abiotic stress within the Mexican 1EBN germplasm for introgression into cultivated potato. Sexual crosses between cultivated potato and Mexican and/or South American 1EBN species has been difficult, but successful by ploidy and EBN manipulation (Carputo et al. 1997; Ehlenfeldt and Hanneman 1988; Louwes et al. 1992; Novy and Hanneman 1991; Zlesak and Thill 2001); by utilizing bridging species between *S. tuberosum* and *S. bulbocastanum* (2*x*, 1EBN) such as *S. acaule* (4*x*, 2EBN), *S. phureja* (2*x*, 2EBN), and *S. verrucosum* (2*x*, 2EBN) (Hermsen and Ramanna 1973, 1976); and by embryo rescue in crosses of *S. tuberosum* haploids (2*x*, 2EBN) and *S. pinnatisectum* (2*x*, 1EBN) (Hanneman et al. 1999). In addition, successful cultivated potato + 1EBN species somatic fusion hybrids and backcross progenies possessing heritable resistance to *P. infestans* (Dorrance et al. 2001) have been produced by (Helgeson et al. 1998) and (Thieme et al. 1997). Given the level of variability found in this research combined with the presence of 2*n* pollen (Zlesak and Thill 2002) in this same population, adds yet another approach to introgress *P. infestans* resistance into cultivated potatoes (Hanneman 1999).

Genetic variability was observed among genotypes within PIs for LB resistance (Table 1). Depending on the genetic variation within a species or PI for any trait, a breeder may choose to employ fine-screening techniques to identify superior genotypes for use as parents in breeding (Bamberg et al. 1996a; Douches et al. 2001). If there is relatively little genetic variability in a species or PI for a particular trait of interest, resources deployed to fine-screen and select superior genotypes may be better allocated on those having greater genetic variance. For example, *S. bulbocastanum* PIs 243504 (AUDPC 746 +/- 233) and 243509 (AUDPC 727 +/- 384) had similar mean AUDPC values; however, PI 243509 had a broader distribution for resistance. Theoretically, it would be of greater benefit to fine-screen PI 243509 to identify parental genotypes segregating for superior resistance than PI 243504. In addition, multi-trait introgression can increase efficiency in developing breeding lines and cultivars. PIs and individual genotypes selected for introgression of resistance to *P. infestans* can be screened for other desirable traits that are limited in current cultivars or are useful for introgression. Hayes and Thill (2002) screened tubers of genotypes from this study for the ability to produce chips with acceptable color after six months storage at 4 C, and *S. pinnatisectum* and *S. verrucosum* were identified as sources of superior chip color. Although the PI of *S. verrucosum* screened had a relatively high AUDPC compared to all other species PIs examined, fine-screening this PI for genotypes possessing both resistance to *P. infestans* and good chip color after cold storage should identify superior parental

genotypes from which desirable levels of both traits may be introgressed simultaneously. Similarly, Zlesak and Thill (2002) screened genotypes from this population for the presence of $2n$ pollen to identify genotypes having both $2n$ pollen and resistance for more efficient introgression efforts.

Although in 1999 the LB epidemic did not progress enough on the species germplasm to detect disease symptoms, it did progress enough to observe symptoms and find significant differences in resistance between the *S. tuberosum* families used as controls (Table 3). The difference in LB symptoms between species and *S. tuberosum* families illustrates three points: (1) the high level of resistance in some wild germplasm, (2) the continued potential to improve the resistance in cultivated potatoes, and (3) the diversity of species from which to draw upon. This is not to say that LB resistance is not currently available in the cultivated gene pool. Within the *S. tuberosum* families evaluated, those with one parent possessing some degree of resistance (S x R) as a group had greater resistance than those with two susceptible parents (S x S). However, among families there were some S x S crosses that had greater resistance than some S x R families. Cultivated potato has complex tetrasomic inheritance and finding differences in combining ability among *S. tuberosum* parents for LB resistance, even when parents themselves show similar resistance levels, was found by Colon et al. (1995) and highlights the benefit of using progeny tests to identify superior *S. tuberosum* parents for imparting resistance.

Our results point to a wide array of wild *Solanum* germplasm with various ploidy levels and EBN from which *P. infestans* resistance can be introgressed into cultivated potato. The decision of which species, PIs within a species, and genotypes within a PI to use as a source of resistance to *P. infestans* can be made clearer for breeders by taking into account traits important to the overall breeding objectives, germplasm and laboratory resources, and breeding system. Diploid 2EBN germplasm generally crosses more readily with cultivated germplasm than diploid 1EBN germplasm (Hanneman 1999) and may be most suitable for developing resistant cultivars in the short term. In the long term using germplasm that is more reproductively isolated, i.e., Mexican 1EBN, is justifiable since exceptionally high levels of resistance can be found.

ACKNOWLEDGMENTS

This manuscript is Scientific Journal Series No. 011210092 of the Department of Horticultural Science, University of Minnesota. This research has been supported in part by the University of Minnesota, College of Agriculture, Food, and Environmental Sciences (COAFES), Minnesota Rapid Agricultural Response Fund (RARF), United States Department of Agriculture USDA/ARS grant 59-1920-8-028 and grant 59-0500-0-046, Northern Plains Potato Growers Association (NPPGA), and the Minnesota Area II Potato Research and Promotion Council.

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