Classifying the Relative Host Reaction in Potato Cultivars and Breeding Lines to the US-8 Strain of *Phytophthora infestans* in Minnesota

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ABSTRACT

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A total of 32 commercial cultivars grown in the United States and 15 potato breeding lines and non-U.S. cultivars were evaluated at Rosemount, MN for their reaction to the US-8 strain of *Phytophthora infestans*. Commercial red-, russet-, and white-skinned cultivars tested in the commercial cultivar trial (COMC) in 1996 and 1997 were susceptible (S) to moderately susceptible (MS) to this organism, except for Elba, which ranked as moderately resistant (MR). Yellow-fleshed cvs. Hertha, Santé, and Agria were screened in the late blight nursery (LB1) in 1997 and 1998 and classified as S to MS while Island Sunshine, Brador, and Aziza were classified as MR. The Scottish breeding line G6582-3 and U.S. breeding lines A90586-11, AWN86514-2, AWN85624-5, B0692-4, B0718-3, and B0767-2 were classified as resistant (R). Comparison among entries was based on the area under the disease progress curve (AUDPC). Spearman rank correlation for AUDPC in the 1996 and 1997 COMC trials at 14 to 18 days after inoculation ($r = 0.65$, $P < 0.01$) was greater than any other interval tested. The Spearman rank correlation for AUDPC in the 1997 and 1998 LB1 trials at 14 to 18 days after inoculation was $r = 0.87$, $P < 0.01$ and increased only slightly in successive assessment dates, suggesting that, in Minnesota, effective evaluation of the foliar infection of late blight can occur at 18 days after inoculation or later. The average tuber blight incidence for the COMC trials at harvest was 10.0% in 1996 and 9.7% in 1997. The average tuber blight incidence for the LB1 trials at harvest was 4.3% in 1997 and 14.6% in 1998. Pearson correlations between tuber blight incidence and foliar disease for the COMC trials was very low; however, for the LB1 trials, it was significant in both 1997 ($r = 0.53$, $P < 0.01$) and 1998 ($r = 0.53$, $P < 0.01$). Asymptomatic tubers harvested from the COMC trials developed additional tuber blight when stored 28 days at ambient temperatures and still more when stored for another 5 months at 5°C. Surviving tubers of nine entries were planted in field trials during 1997 and 1998 to determine if plants that develop from tubers exposed to *P. infestans* could manifest late blight in the subsequent season. Late blight failed to develop throughout the trials in either year.

Additional keywords: disease resistance screening, late blight

In Minnesota, potato (*Solanum tuberosum* L.) is grown annually on more than 32,000 ha and the state ranks seventh nationally in plantings (3). Commercial production is diverse and includes all market classes (chips, fries, and tablestock red-, russet-, and white-skinned types). The majority of the plantings are irrigated and more than 80% of the harvested crop is stored for varying lengths of time prior to sale. Approximately 7,000 ha (all types) are raised annually for certified seed (2).

The recent migration of the US-8 strain (A_2 mating type) of *Phytophthora infestans* (Mont.) de Bary has led to the reemergence of late blight as an important disease of potato in Minnesota and throughout the United States and the world (11,17,32,33,37). Prior to the introduction of US-8, the US-1 strain (A_1 mating type) predominated in Minnesota and outbreaks of the disease in the early 1990s were effectively controlled by treatments of the systemic fungicide metalaxyl. The US-8 strain, which is insensitive to metalaxyl (17,18), was first found in Minnesota in 1994 and now requires 5- to 7-day spray schedules of protectant fungicides to maintain control. Additional measures recommended to minimize late blight include the elimination of cull piles, control of volunteer potato plants, and planting disease-free seed (40).

Currently, many breeding programs are attempting to develop resistance to the US-8 strain of *P. infestans*. In order to minimize pathogen selection pressure, it is considered desirable to breed genotypes

with general resistance that is durable (36). One criterion used to characterize general resistance is a reduced rate of disease progress as reflected by area under the disease progress curve or AUDPC (5). The difficult task facing potato breeding programs in introducing effective resistance is compounded by the diversity of market types and specific quality attributes required in cultivars accepted by industry and the public. Therefore, it has become extremely important to develop effective screening procedures to identify and quantify resistance in potato.

Resistance to the US-1 strain of *P. infestans* has been reported in the round, white-skinned cvs. Elba, Kathadin, Kennebec, and Sebago (1,7,15,35,39,43). Several yellow-skinned, yellow-fleshed cultivars have been reported as having resistance to the US-8 strain of late blight in Canada and Europe (4,42). Selected breeding lines have been identified as highly resistant to US-8 in preliminary trials (9). These cultivars and breeding lines were included in our trial to test their reaction to US-8 under Minnesota environmental conditions.

Our first objective was to evaluate commercial cultivars across all major skin types (red, russet, and white) grown in Minnesota, for their reaction to both foliar and tuber blight caused by the US-8 strain of *P. infestans*. Our second objective was to develop a classification scheme to separate cultivars and breeding lines into resistant (R), moderately resistant (MR), moderately susceptible (MS), and susceptible (S) classes based on the relative disease progress in foliage compared with defined check entries. A third objective of this study was to determine if tubers exposed to the US-8 strain of *P. infestans* in foliar inoculation trials could serve as a source of primary inoculum in initiating epidemics of late blight when planted in subsequent years.

MATERIALS AND METHODS

Plot design for foliar disease evaluation. Field experiments were established at the Rosemount Experiment Station located near Rosemount, MN in the southeast region of the state. Selection of this location was based on its remoteness from the potato-growing regions of Minnesota and the availability of suitable irrigation facilities. The soil type in the experimental areas was a Waukegan silt loam and the fields had no history of potato production.

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Thirty-two commercial potato cultivars were screened for their relative resistance in 1996 and 1997 commercial cultivar (COMC) trials (Table 1). Selection of entries was based on acreage of plantings obtained from the Minnesota Certified Seed Potato Directory (2). Cv. Elba was included for comparison due to its reported resistance to late blight (43). Plots were planted with certified seed on 6 June 1996 and 2 June 1997 in a randomized complete block design. Plots were two 3-by-1-m rows of 11 seed pieces, each on 28-cm spacings. Plots were bordered on either side by a 3-by-1-m spreader row of S cv. Norchip. Alleys 3 m long separated treatment blocks within the row, preventing disease spread along treatment rows.

In 1997 and 1998, the late blight nursery (LB1) trial was established using 15 entries which had been received from other sources (Table 2). Some of these entries had been screened in preliminary evaluations conducted in 1996 (9) and some were reported as being relatively resistant to US-8 in other studies (4,10,19,20). LB1 trials were planted 2 June 1997 and 9 June

1998. The experimental designs were as described above for the COMC trials. Cvs. Shepody, Kennebec, and Elba were included in the LB1 trials as S, MS, and MR checks, respectively, based on results from the 1996 COMC trials (27).

In all plots in all years, fertilization (200 kg of N and 90 kg of P at 365 kg/ha) was done at planting and an additional 200 kg of N/ha was broadcast and incorporated at hilling (32 days later). Colorado potato beetle (*Leptinotarsa decemlineata*) control was accomplished by an application of imidacloprid (1.2 kg a.i./ha) at planting. Chemical weed control included a pre-emergence application of penethalin (1.08 kg a.i./ha) and was supplemented with cultivation and hand weeding to maintain weed-free plots. A preventive spray of metalaxyl (Ridomil 4E at 4.5 kg a.i./ha) was applied 30 days after planting (30 days prior to inoculation) to minimize the potential for natural infection from indigenous US-1 strains of the fungus. All plots in all years were free of late blight at the time of inoculation. Stand counts were made 40 days after planting (DAP).

Foliar inoculation and disease assessment. For all plots in each year, spreader rows of Norchip were inoculated with a suspension of US-8 (isolate ND 95-2) at 1,000 sporangia/ml at 60 DAP. The suspension was prepared by inoculating tuber slices (cv. Red Norland) with an agar plug of isolate ND 95-2. Tuber slices were incubated at 18°C for 7 days. Sporangia were harvested by rinsing the tuber slices with sterilized well-water. Sporangia concentrations were determined with a hemacytometer and then diluted to 1,000 sporangia/ml using well water. The inoculum then was stored on ice and transported to the field site. Inoculum was applied with a single-nozzle, low-pressure (100 kPa) hand sprayer at a rate of 6.7 ml/row meter. Inoculum was applied at dusk in order to provide optimum conditions for spore survival. Plots were sprinkler irrigated (1.3 cm) immediately after inoculation and every other day during the morning hours for 28 days to prolong the duration of leaf wetness. Disease assessment was based on the 1-to-9 (nonlinear) Centro Internacional de la Papa (CIP) scale (21), where the

Table 1. Entry, origin, tuber characteristics, foliar area under the disease progress curve (AUDPC), foliar relative (R)AUDPC, and tuber blight incidence at harvest for commercial potato cultivars inoculated with the US-8 strain of *Phytophthora infestans* and evaluated in the field for late blight in 1996–1997 at Rosemount, MN

Cultivar or line	Released by ^b	Skin type	AUDPC		RAUDPC ^a		Tuber blight incidence (%)	
			1996	1997	1996	1997	1996	1997
Elba	New York	White	486	639	0.34	0.41	8.7	8.1
Sebago	USDA-Maine	White	591	1,161	0.41	0.71	1.6	5.2
Kennebec	USDA-Maine	White	693	1,086	0.49	0.69	7.6	9.9
Russet Burbank	California	Russet	809	1,311	0.57	0.84	12.1	8.2
Katahdin	USDA-Maine	White	892	1,256	0.63	0.80	7.6	8.5
R. B. New Leaf ^c	Monsanto	Russet	906	1,321	0.63	0.84	14.1	9.6
Red Pontiac	Michigan	Red	941	1,319	0.66	0.84	5.5	5.5
Snowden	Wisconsin	White	964	1,303	0.68	0.83	17.0	11.4
Chieftain	USDA-Iowa	Red	972	1,340	0.68	0.85	5.4	4.3
Krantz	Minnesota-Texas	Russet	992	1,311	0.70	0.84	3.5	4.3
Ranger Russet	Agriculture Canada, MB	Russet	1,073	1,340	0.75	0.85	8.9	14.8
Eide Russet	Minnesota	Russet	1,099	1,382	0.77	0.88	7.7	8.5
Nordonna	North Dakota	Red	1,110	1,305	0.78	0.83	11.7	6.6
Superior	Wisconsin	White	1,126	1,493	0.79	0.95	6.7	1.8
Itasca	Minnesota	White	1,143	1,393	0.80	0.89	7.3	5.5
La Rouge	Louisiana	Red	1,143	1,361	0.80	0.87	17.5	20.4
ND 2471-8	North Dakota	White	1,150	1,414	0.81	0.90	20.5	13.1
NorValley	North Dakota	White	1,152	1,376	0.81	0.88	8.2	5.1
Red Ruby	Minnesota	Red	1,156	1,426	0.81	0.91	9.2	10.9
FL 1533	Frito-Lay	White	1,180	1,338	0.83	0.85	10.6	16.4
Red La Soda	USDA-Louisiana	Red	1,183	1,371	0.83	0.87	21.9	18.9
Cascade	USDA-WSU	White	1,185	1,348	0.83	0.86	3.7	9.3
Yukon Gold	Agriculture Canada, University of Guelph	Yellow	1,185	1,434	0.83	0.91	13.0	11.6
Russet Norkotah	North Dakota	Russet	1,250	1,382	0.88	0.88	13.6	14.6
Goldrush	North Dakota	Russet	1,281	1,456	0.90	0.93	6.1	6.5
Norchip	North Dakota	White	1,286	1,409	0.90	0.90	11.3	5.6
Red Norland	North Dakota	Red	1,296	1,524	0.91	0.97	8.1	7.1
Shepody	Agriculture Canada, NB	White	1,300	1,404	0.91	0.89	21.3	18.4
Atlantic	USDA-ME, FL, NJ	White	1,322	1,382	0.93	0.88	4.6	5.3
Monona	Frito-Lay	White	1,340	1,433	0.94	0.91	12.5	10.7
Dark Red Norland	Nebraska	Red	1,364	1,570	0.96	1.00	7.7	9.9
Reddale	Minnesota	Red	1,428	1,465	1.00	0.93	19.1	14.1
LSD ($P = 0.05$) ^d	...	...	170	67	...	...	9.7	6.9

^a RAUDPC as a proportion of the most susceptible cultivar.

^b USDA = United States Department of Agriculture, WSU = Washington State University.

^c Russet Burbank New Leaf.

^d Fisher's protected least significant difference.

mean percent values are 1 = no late blight observable, 2 = 2.5, 3 = 10, 4 = 25, 5 = 50, 6 = 75, 7 = 90, 8 = 97.5, and 9 = 100% of stems and leaves of plants in plots were killed by the disease. Assessments were initiated 4 days after inoculation (DAI) and continued at 3- to 4-day intervals for 28 days (eight assessments).

Foliar data analysis. Statistical analysis was performed using the Student Edition of Statistix for Windows (version 1.0; Analytical Software, Tallahassee, FL). Stand counts were recorded as a percentage of emerged seed pieces from the total number of seed pieces planted in each cultivar or line. An analysis of variance (ANOVA) was computed and the comparison of means was done using Fisher's protected least significant difference (LSD). The disease index (CIP ratings) was converted to percentage data and AUDPCs were calculated according to the method described by Campbell and Madden (5). AUDPCs for each cultivar or line were subjected to ANOVA and years were analyzed separately. Comparisons of cultivar or line means were made using Fisher's protected LSD mean separation procedure with $P \leq 0.05$. AUDPC values were converted to relative area under the disease progress curve (RAUDPC) values by dividing the mean AUDPC of each cultivar or line by the mean AUDPC value of the most susceptible cultivar (16). For the COMC trials, Reddale was the most susceptible cultivar in 1996 and Dark Red Norland was the most susceptible cultivar in 1997. In the LB1 trials, RAUDPCs were derived by comparison with cv. Shepody (susceptible check). Entries were separated into R (0.0 to 0.25), MR (0.25 to 0.50), MS (0.50 to 0.75), and S (0.75 to 1.00)

classifications based on their RAUDPC. Spearman rank correlations were determined for successive measures of disease severity over six time intervals: 7 to 11, 11 to 14, 14 to 18, 18 to 21, 21 to 25, and 25 to 28 days. These were used to compare the relative rank order of entries.

Postharvest assessments. Potato vines were killed with two applications of diquat dibromide (0.43 liter a.i./ha), 5 days apart, beginning at 100 DAP. Tubers were harvested 110 DAP in both trials for each year. After harvest, tubers were washed with pressurized water and assessed visually for tuber blight. Healthy and diseased tubers were sorted, counted, and weighed. Tuber blight incidence (number of diseased tubers/total tubers harvested) and tuber blight severity (weight of diseased tubers/total weight harvested) then were determined for each cultivar. An ANOVA was performed and comparisons were made between cultivar or line means for tuber blight incidence and tuber blight severity. Pearson correlations were calculated for tuber blight incidence and severity among years and for AUDPC versus tuber blight incidence and AUDPC versus tuber blight severity for each year. A regression analysis was performed between foliar AUDPC and tuber blight incidence for the 1997 and the 1998 LB1 trials. After harvest, asymptomatic tubers (20/replicate in the COMC trials and 25/replicate in the LB1 trials) were selected and stored in paper bags at 20°C for 28 days and then rated for tuber blight incidence. Tubers without symptoms were bagged and stored an additional 5 months at 5°C. Following the storage period, tubers were sliced longitudinally and rated visually for tuber blight. Pearson correlations were used to

examine the relationship between tuber blight incidence at harvest and tuber blight incidence following storage.

Tuber transmission study. Plantings were established at a separate location at the Rosemount Experiment Station and consisted of paired plots of tubers exposed to *P. infestans* as one source and healthy tubers as the other source (certified seed). Tubers originating from plants that had been infected with the US-8 strain (ND 95-2 isolate) of *P. infestans* in the COMC field trials were used as the seed source. Tubers planted in 1997 and 1998 originated from the 1996 and 1997 COMC trials, respectively. Criteria for selection included three categories of skin color: red, russet, and white. Within skin type, cultivars were selected to represent low, medium, and high percentages of tuber blight incidence based on the percentage of tuber blight assessed at harvest of the proceeding season. Actual values are shown in Table 1. Selected cultivars for 1997 and 1998 trials were Red Pontiac (5.5 and 5.5%), Red Norland (8.7 and 7.1%), Red LaSoda (21.9 and 18.9%), Krantz (3.5 and 4.3%), Russet Burbank (12.1 and 8.2%), Russet Norkotah (13.6 and 14.6%), Sebago (1.6 and 5.2%), Kennebec (7.6 and 9.9%), and Shepody (21.3 and 18.4%). Tubers of these entries were sliced longitudinally and 10 seed pieces were planted on 15-cm spacings in 3-m rows. Each subplot consisted of one 3-m row of tubers that had been exposed to *P. infestans* and one 3-m row of healthy, certified seed of the same cultivar planted adjacent to one another. Tubers from both sources were planted on 10 April 1997 and 23 April 1998. Plots were arranged in a split plot design. Plot dimensions were 0.91 by 3 m with 3-m alleys between

Table 2. Entry, origin, tuber characteristics, foliar area under the disease progress curve (AUDPC), AUDPC rank, and tuber blight incidence for potato breeding lines and non-U.S. cultivars inoculated with the US-8 strain of *Phytophthora infestans* and evaluated in the field for late blight in 1997-1998 at Rosemount, MN

Cultivar or line	Origin or source ^a	Skin (flesh) ^b	AUDPC		AUDPC rank		Tuber blight incidence (%)	
			1997	1998	1997	1998	1997	1998
B0767-2	R. Goth, USDA	Russet (W)	45	49	1	1	0.0	0.0
AWN86514-2	J. Pavék, USDA	White (W)	63	49	2	1	1.6	11.5
B0718-3	R. Goth, USDA	White (W)	98	49	3	1	0.8	9.4
AWN85624-5	J. Pavék, USDA	White (W)	131	49	4	1	2.5	18.2
A90586-11	J. Pavék, USDA	White (W)	132	66	5	7	3.2	5.8
G6582-3	G. Mackay, Scotland	White (W)	176	49	6	1	0.6	5.8
B0692-4	R. Goth, USDA	Russet (W)	204	63	7	6	0.0	8.3
Bzura	Z. Zamarte, Poland	White (W)	395	143	8	8	4.3	8.8
Elba	New York	White (W)	639	251	9	10	8.1	27.0
Brador	Agriculture Canada, NB	Yellow (Y)	719	337	10	12	4.7	20.7
AWN85540-1	J. Pavék, USDA	White (Y)	738	238	11	9	9.9	19.1
Aziza	Netherlands, AGRICO	Yellow (Y)	768	258	12	11	2.2	6.7
Island Sunshine	G. Loo, P.E.I., AGRICO	Yellow (Y)	825	451	13	13	1.9	24.7
Agria	Germany, AGRICO	Yellow (Y)	1,015	453	14	14	1.1	2.2
Kennebec	USDA-Maine	White (W)	1,086	847	15	16	9.9	37.7
Santé	Netherlands, AGRICO	Yellow (Y)	1,143	664	16	15	5.2	11.0
Hertha	Netherlands, AGRICO	Yellow (Y)	1,207	861	17	17	3.7	21.2
Shepody	Agriculture Canada, NB	White (W)	1,404	1,276	18	18	18.4	28.4
LSD ($P = 0.05$) ^c	...	...	123	84	...	...	3.7	10.1

^a USDA = United States Department of Agriculture, AGRICO = Agrico Canada Limited.

^b W = white-fleshed and Y = yellow-fleshed cultivars.

^c Fisher's protected least significant difference.

repeated blocks with four replications for each treatment. After planting, plots were mist irrigated with 2.5 cm of water twice weekly unless natural rainfall exceeded 2.5 cm. Cultural management of insects and weeds were as described in the previous experiments. Soybean plants were planted as buffers between plots in an attempt to minimize interplot interference. Stand counts, emergence, and disease assessments were taken at 28, 35, and 42 DAP. Plots continued to be monitored for the appearance of late blight until they reached 100 DAP.

RESULTS

COMC trials. The mean stand count for entries in the COMC trials was greater than 90% in both 1996 and 1997. Symptoms of late blight were first observed in the spreader rows of cv. Norchip approximately 7 DAI. At 14 DAI, all treatment plots in both years of the trial were infected. Disease progressed rapidly between 14 and 21 DAI. Among all cultivars, the mean CIP values (and percent foliage destruction) at 14 and 21 DAI were 3.3 (18.9%) and 7.5 (86.2%) for 1996 and 5.1 (51.5%) and 7.8 (95.0%) for 1997. By 28 DAI, the foliage of most of the commercial cultivars was completely destroyed and plots were assessed as either 8 (97.5%) or 9 (100%) on the CIP scale.

The mean AUDPC value for 1996 was 1,094 (ranging from 486 for Sebago to 1,428 for Shepody) and was significantly ($P = 0.05$) less than the mean 1997 AUDPC value of 1,346 (ranging from 639 for Sebago to 1,570 for Shepody). Rainfall events were likely to have had a direct impact on the resulting scores. Seasonal rainfall accumulation for the months of July to September was 19.0 cm in 1996 and 49.9 cm in 1997. Precipitation was measurable on 8 of 28 days during the August assessment period in 1996 compared with 16 of 28 in 1997. Significant differences ($P = 0.05$) were observed among cultivars each year in disease index values at 14, 21, and 28 DAI (*data not shown*) and in AUDPC for each year (Table 1). At 18 DAI, differences in resistance levels were visible between Elba (later selected as MR check) and Kennebec (later selected as MS check) and between

Kennebec and Shepody (later selected as S check). At 25 DAI, differences in resistance levels were visible in Elba compared with Kennebec and Shepody as well as most other cultivar entries, which were completely destroyed by this time.

Cultivars that have similar genetic background showed similar reactions to the US-8 strain of *P. infestans*. Red Norland and Dark Red Norland were not significantly different from each other in their AUDPC values (Table 1). A similar result was seen when comparing AUDPC values for Russet Burbank with the transgenically derived cv. Russet Burbank-New Leaf (Table 1).

The AUDPC values for the 1996 and 1997 COMC trials, at 18 DAI, showed a relatively high coefficient of correlation (r value) using the Spearman rank test when compared with earlier dates. Spearman rank correlation for 1996 versus 1997 data sets at the 14- to 18-day interval was $r = 0.65$ ($P < 0.01$). Correlations at subsequent intervals were $r = 0.52$ (18 to 21 DAI), $r = 0.59$ (21 to 25 DAI), and $r = 0.44$ (25 to 28 DAI) (Table 3).

Tuber blight incidence at harvest averaged 10.0% in 1996 and 9.7% in 1997. Tuber blight incidence ranged from 1.6% for Sebago to 21.3% for Shepody in 1996 and 5.2% for Sebago to 18.4% for Shepody in 1997. Significant differences ($P = 0.05$) were observed among the 32 entries in each year (Table 1). Correlation for tuber blight incidence between 1996 and 1997 was low but significant (Pearson, $r = 0.32$, $P < 0.01$). Foliar disease (AUDPC) and tuber blight incidence correlations were low but significant in 1996 (Pearson, $r = 0.18$, $P < 0.05$) and were not significant in 1997 (Pearson, $r = -0.05$, $P > 0.05$). Pearson correlations between tuber blight severity and tuber blight incidence were significant in 1996 ($r = 0.80$, $P < 0.01$) and in 1997 ($r = 0.93$, $P < 0.01$). Tuber blight incidence for Red Norland and Dark Red Norland were not significantly different from each other (8.1 versus 7.7% in 1996 and 7.1 versus 9.9% in 1997). The average tuber blight incidence for Russet Burbank was 10.1 versus 11.9% for Russet Burbank-New Leaf (Table 1). Differences were not significant ($P = 0.05$) in either year.

Stored tubers developed symptoms of tuber blight following incubation at ambi-

ent temperatures for 28 days and additional tuber blight developed in asymptomatic tubers after storage for an additional 5 months at 5°C. Tuber blight incidence, after 28 days of storage, for all cultivars combined, was 3.0% in 1996 and 8.6% in 1997. Total tuber blight incidence, after 5 months, for all cultivars combined, was 5.6% in 1996 and 13.1% in 1997. Among cultivars, there was a significant positive correlation between tuber blight at harvest and tuber blight after 5 months of storage in 1996 ($r = 0.33$, $P < 0.01$) and in 1997 ($r = 0.36$, $P < 0.01$).

LB1 trials. The mean stand count for entries in the LB1 trials was greater than 95% in both 1997 and 1998. The mean AUDPC for entries in 1997 was 600 (ranging from 45 for B0767-2 to 1,404 for Shepody) and was significantly ($P < 0.01$) greater than the mean AUDPC for entries in 1998 of 341 (ranging from 49 for B0767-2 to 1,276 for Shepody). Rainfall events were likely to have had a direct impact on the resulting scores. Seasonal rainfall accumulation for the months of July to September was 49.9 cm in 1997 and 26.8 cm in 1998. Precipitation was measurable on 16 of 28 days during the August assessment period in 1997 compared with 10 of 28 in 1998. Significant differences were observed among cultivars or breeding lines each year (Table 2). Spearman rank correlations for the 1997 versus 1998 data sets was $r = 0.87$ ($P < 0.01$) at the 14- to 18-day interval. Correlations at subsequent intervals were $r = 0.90$ (18 to 21 DAI), $r = 0.93$ (21 to 25 DAI), and $r = 0.94$ (25 to 28 DAI) (Table 4). At 18 DAI, differences in resistance levels were visible between resistant entries such as Awn86514-2, B0718-3, and B0767-2 compared with the MS check Kennebec and the S check Shepody (differences were visible at 25 DAI for the MR check, Elba). These differences remained apparent through 28 days of assessment. Cultivars or lines could be separated into four classes using 25th percentiles of the RAUDPC of Shepody (Fig. 1). The relative placement of Elba, Kennebec, and Shepody served to characterize these quartiles and could be used as relative checks.

Tuber blight incidence at harvest averaged 4.3% in 1997 and 14.6% in 1998. Tuber blight incidence ranged from 0.0% for B0767-2 to 18.4% for Shepody in 1997 and 0.0% for B0767-2 to 28.4% for Shepody in 1998. Significant differences in tuber blight were observed among the 18 entries in each year (Table 2). The correlation for tuber blight incidence between years was significant (Pearson, $r = 0.47$, $P < 0.01$). Tuber blight severity averaged 5.4% in 1997 and 14.6% in 1998. The correlation for tuber blight severity between years was significant (Pearson, $r = 0.49$, $P < 0.01$). Pearson correlations between tuber blight severity and tuber blight

Table 3. Spearman rank correlation matrix for six disease progress intervals in the 1996 and 1997 commercial cultivar trials^a

1997	1996					
	7–11 DAI ^b	11–14 DAI	14–18 DAI	18–21 DAI	21–25 DAI	25–28 DAI
7–11 DAI	0.32	...	...	...	...	...
11–14 DAI	0.40	0.47	...	...	...	...
14–18 DAI	0.40	0.54	0.65	...	...	...
18–21 DAI	0.30	0.38	0.48	0.52	...	...
21–25 DAI	0.26	0.32	0.46	0.55	0.59	...
25–28 DAI	(0.21)	0.25	0.39	0.45	0.46	0.44

^a All values are significant at $P = 0.01$ except the value shown in parenthesis (not significant at $P = 0.05$).

^b DAI = days after inoculation.

incidence was very high in both 1997 ($r = 0.96$, $P < 0.01$) and in 1998 ($r = 0.95$, $P < 0.01$), suggesting that infection of tubers by *P. infestans* is independent of tuber size and that either measure is adequate to characterize the reaction of cultivars.

Correlations between foliar disease (AUDPC) and tuber blight incidence were significant at $P < 0.01$ in both years (Pearson, $r = 0.53$ in 1997 and 1998). Regression analysis of tuber blight incidence versus foliar AUDPC showed the relationship to be linear but with only a modest fit ($R^2 = 0.41$ in 1997 and 0.39 in 1998; Fig. 2). Tuber blight in resistant entries averaged only 1.2% in 1997 and 8.3% in 1998 despite experimental conditions within hills that exposed tubers to large quantities of inoculum from adjacent border rows of the S cv. Norchip.

Stored tubers developed symptoms of tuber blight following incubation at ambient temperatures for 28 days and additional rot developed in asymptomatic tubers after storage for an additional 5 months at 5°C. Tuber blight incidence, after 28 days of storage, for all entries combined, was 1.9% in 1997 and 1.2% in 1998. Total tuber blight incidence, after 5 months, for all entries combined, was 8.1% in 1997 and 2.9% in 1998. There was a significant correlation between tuber blight at harvest and tuber blight after 5 months of storage in 1997 ($r = 0.41$, $P = 0.03$) but not in 1998 ($r = 0.18$, $P = 0.12$).

The yield for the LB1 trials averaged only 22.13 metric tons (t)/ha in 1997 and 20.54 t/ha in 1998. Although significant ($P = 0.05$) differences were observed between entries (26; data not shown), it should be noted that an appreciable number of tubers developed tuber blight to such an extent that they were not capable of being harvested. Many of these could be seen after digging as tuber carcasses (portions of the periderm which remained intact while the majority of the internal tuber contents had been rotted away). These were especially evident in rows of the check cultivars (particularly Shepody but also Elba and Kennebec) in 1998. These could not be included accurately in the tuber count.

Tuber transmission trial. All treatments in both 1997 and 1998 field trials had greater than 80% emergence at 42 days (6 weeks) after planting. Stand differences were observed at 28 DAP and tubers that had been exposed to *P. infestans* were slower to emerge compared with certified seed of the same cultivar. Late blight was not observed at any of the assessment timings (28, 35, and 42 DAP). At 42 DAP, tubers that had not emerged were dug and examined for characteristic signs and symptoms (6) of tuber blight caused by the late blight fungus. None were found. All plots in both years were allowed to develop until maturity (100 DAP). Throughout the course of these studies, late blight did not develop in any planting at any time.

DISCUSSION

Results of this study indicate that there is inadequate resistance to US-8 available in potato cultivars adapted to the North Central Region. Cultivars important to Minnesota and the Upper Midwest ranged from S to MS. Reduced susceptibility was identified in the commercial round-white cvs. Elba, Kennebec, and Sebago. These same cultivars have been reported to exhibit resistance to the US-1 strain of *P. infestans* (1,15,23,35,43). Elba, an MR cultivar from New York, is a late-maturing tablestock potato, but it is not suitable for

chipping or processing purposes. Russet Burbank was characterized as MS in our trials and was identified as the least susceptible russet-skinned cultivar among those tested in both 1996 and 1997. The russet-skinned cv. Krantz is reported to have very high field resistance to US-1 (31), yet we found it to be as susceptible or more susceptible than Russet Burbank to US-8 (Table 1). There were few red-skinned cultivars with significant resistance to US-8. The red-skinned cvs. Chieftain and Red Pontiac were less susceptible to the US-8 strain than other commercially

Table 4. Spearman rank correlation matrix for six disease progress intervals in the 1997 and 1998 breeding line and non-U.S. cultivar trials^a

1998	1997					
	7–11 DAI ^b	11–14 DAI	14–18 DAI	18–21 DAI	21–25 DAI	25–28 DAI
7–11 DAI	(0.23)	...	...	...	...	...
11–14 DAI	0.41	0.48	...	...	...	...
14–18 DAI	0.77	0.84	0.87	...	...	...
18–21 DAI	0.78	0.84	0.89	0.90	...	...
21–25 DAI	0.78	0.86	0.90	0.91	0.93	...
25–28 DAI	0.78	0.86	0.89	0.91	0.93	0.94

^a All values are significant at $P = 0.01$ except the value shown in parenthesis (not significant at $P = 0.05$).

^b DAI = days after inoculation.

Fig. 1. Late blight reaction classes based on relative area under the disease progress curve (RAUDPC) for 1997–98 potato breeding line and non-U.S. cultivar (LB1) trials. Entries highlighted in black are the check entries used. Bars represent standard error of the mean.

important red-skin cultivars, such as Norland and Dark Red Norland (Table 1).

Resistance to US-8 has been reported previously in certain yellow-skinned, yellow-fleshed cultivars developed by Canadian and European breeding programs (4,20,42). We found that Aziza (4), Brador (42), and Island Sunshine exhibited some resistance to US-8 and that the Polish cv. Bzura (41) was the most resistant released cultivar tested (Fig. 1). However, not all yellow-fleshed cultivars were found to be resistant. Yukon Gold, the most popular yellow-fleshed cultivar grown in the United States, was identified as S (Table 1). Hertha also was characterized as S, whereas Agria and Santé were placed in the MS category (Fig. 1). In general, our results for the European entries agree with those given in the Netherlands Catalog of Potato Varieties (4) except that we found Hertha to be more susceptible than the Dutch rating.

An evaluation of resistant materials from breeding programs outside the region suggests that moderate to high levels of resistance are present in materials that are unadapted or unacceptable for production in Minnesota. Resistance to US-8 was identified in seven breeding lines. These included AWN86514-2 and AWN85624-5 from the United States Department of Agriculture-Agricultural Research Service (USDA-ARS) program at Aberdeen, ID and B0692-4, B0718-3, and B0767-2 from the USDA-ARS program at Beltsville, MD. Resistance to US-8 has been previously reported for the Aberdeen lines in greenhouse screening tests (14). A90586-11 (from the Tri-State Breeding program in the Pacific Northwest) and G6582-3 (from the Scottish Crop Research Institute) also were characterized as resistant to US-8. These entries were late maturing. In general, tubers from the breeding lines were equal in number but smaller in size than standard cultivars, and the yields averaged only 18.6 t/ha (26) under our conditions. At present, available resistance to US-8 will not influence the cultivar

selection process for commercial producers in Minnesota until substantial improvements are made. Thus, there is some urgency in seeking a more long-term solution to the current late blight situation through breeding for resistance.

Adult plant evaluations of field reactions to late blight, in terms of experimental design and disease assessment for late blight resistance screening, can be approached in several ways. Methods of inoculation, inoculum dose, and disease assessment techniques affect and contribute to the variability and variation of collected data. The experimental design employed in this study used two-row treatments with border rows of Norchip on both sides, allowing for uniform disease pressure on all experimental rows and furrows. This design also allowed for the recovery of an adequate number of tubers (mean = 18.1/row-meter) to statistically evaluate tuber blight.

The CIP scale was chosen for use in this study in preference to other assessment scales (20,22,25). The CIP scale scores disease as 9 different categories as opposed to 13 categories present in the Horsfall-Barratt scale (21). The CIP scale is designed to read whole plots as opposed to individual plants and provides a good description of disease symptoms for each percentage of infection. It complies most favorably with the basic rules of a good assessment key, which are efficiency and the ability to reproduce the same score between two readers. The scale's simplicity combined with its uniform distribution of disease severity categories allows for the reader to more readily distinguish and differentiate between index values. We also found the CIP scale easy to teach to individuals with limited training in plant pathology.

Evaluating RAUDPC values relative to the performance of standard check cultivars allows entries to be separated into classes that can be reproduced under environmental conditions that are variable from year to year. Haynes et al. (20) reported

that AWN86514-2, B0718-3, B0692-4, and B0767-2 ranked 1, 2, 3, or 4 out of 16 entries in their 1996 evaluation of resistance to US-8 across eight locations in the United States. The cultivar Elba exhibited great variability in these trials, ranking from 7 to 14 out of 16 entries. In their evaluation at Rosemount, MN in 1996, Elba ranked ninth (20). Providing a screening technique that delivers consistency in measuring moderate resistance is paramount. In general, this can be accomplished by inoculating adult plants at 60 DAP and assessing them twice a week within a 28-day period to minimize the variation that is normally seen when assessing AUDPCs over an entire growing season. Check cvs. Elba, Kennebec, and Shepody used in this study maintained their relative rank among the 3 years of both the COMC and the LB1 trials, which suggests the reliability of using cultivars like these as standards for comparisons of resistance in screening nurseries. The addition of a resistant entry (such as B0767-2) would further facilitate the standardization of evaluations. Using standardized check cultivars is routine in many breeding programs. Preplanning for the use of standardized check cultivars would allow breeding programs the time required to produce the modest quantities of (virus-free) seed stocks that would be necessary to use this approach in potato-breeding programs. Space needed to screen large amounts of breeding material can be a limiting factor using this type of experimental design. These evaluation methods may be most suitable for advanced selections.

The high correlation between consecutive time intervals suggests that the relative ranking of entries in these trials did not change as disease progressed and that a one-time evaluation at 18, 21, or 25 DAI would provide a good estimate of the disease reaction. The r value in the COMC trials was lower ($r = 0.65$) than the comparable r value of the LB1 trials ($r = 0.87$). This lower r value may have been due to a

Fig. 2. Regression analysis between foliar area under the disease progress curve (AUDPC) (y axis) and tuber blight incidence (x axis) for the breeding line and non-U.S. cultivar (LB1) trials in 1997 and 1998.

lack of resistant entries and the presence of relatively large numbers of susceptible cultivars in the COMC trial. Cultivars that are close in their AUDPC values could more easily fluctuate in rank from interval to interval. This should not present difficulties in trials that include a full range of disease reaction classes (from R to S). In addition, cultivar checks should be chosen to match the maturity class of materials under investigation in order to reduce error in comparison of AUDPC values. Elba, Kennebec, and Shepody are all about 110- to 120-day cultivars under Minnesota conditions.

Although significant, there was low correlation between AUDPC and tuber blight for both the COMC and the LB1 trials. Correlations for incidence or severity of tuber blight and foliar disease produced similar results. The lack of a strong relationship between foliar disease and tuber blight has been reported previously (23,44). In Europe and Canada, foliar reactions and tuber blight reactions are scored and reported as separate reactions (4,42). We feel that at-harvest measurements of tuber blight may have been the cause of the low correlations observed in this study.

Many factors can confound the outcome of both incidence and severity readings. Tuber blight is difficult to score and not all infected tubers exhibit classic symptoms (6). Variability in environmental factors and inoculum dose will affect the amount of tuber blight (13). Tuber placement (depth and orientation) within the hill also can affect the amount of symptoms that result. The accuracy of rating incipient infections can be subjective and, in other instances, tubers that are infected can be symptomless. Techniques are needed to overcome the ambiguity in rating tuber blight. Developing methods to harvest tuber carcasses from the field (which would improve incidence, not severity) and minimizing the presence of other diseases that affect tuber quality (such as soft rots) also may be beneficial and improve the uniformity of results. Tuber blight reactions also can be influenced by the genotype of the pathogen (29,34). The US-8 strain has proven to be more aggressive on tubers and results in an increased rot in fields (29) and storage (17). This increases the importance of developing some means to standardize tuber blight ratings in late blight screening programs.

Yields for the COMC and LB1 trials averaged 28.7 and 21.3 t/ha (26). This compares with statewide yield averages of 33.8 t/ha. Lower yields may have been due to indirect effects that late blight causes through foliar destruction and reduction of nutrient transfer from leaves to tubers during potato bulking. In addition, disease directly destroyed some of the tubers prior to harvest. Most of the resistant breeding lines that were included in the LB1 trials had a high percentage of immature tubers

when compared with commercial cultivars. In addition, all entries were intentionally planted 4 to 6 weeks late to minimize exposure of commercial potato planted in the region. This delayed tuber maturity and undoubtedly affected yield, but may have had a relatively greater effect on the "late-maturing" resistant entries than on mid- or early-season cultivars.

Tubers exposed to *P. infestans* failed to transmit late blight in either year of our experiments. Despite these results, field observations of transmissions of late blight from affected (or suspect) seedlots in commercial settings seem related to initial outbreaks of the disease in Minnesota (R. K. Jones, unpublished data). It is possible that the frequency of successful transmission is so low that it could not be demonstrated experimentally with the limited number ($n = 720$) of tubers tested. The combined result of increased rot on asymptomatic tubers in storage and the lack of transmission from the seed piece to the sprout suggests that specific conditions in the infection court may be necessary for infection of the sprout and its aboveground survival. At harvest and during storage, we observed both complete rot and partial infection of tubers. In storage, tubers that were completely rotted (mummified) at 28 days and at 5 months of storage were surrounded by tubers that remained apparently healthy until cut for planting. We saw no direct evidence that would indicate *P. infestans* spread from tuber to tuber during storage periods. Therefore, controlling late blight in seed production fields remains a critical recommendation for managing late blight. Lambert et al. (30) evaluated transmission and transfer of *P. infestans* from tubers artificially infected during seed cutting. Transmission occurred in 2 of 50 seed pieces inoculated, which suggests that infection during seed cutting may be an additional means by which transmission occurs. Currently registered fungicides have protective but not curative properties for seed treatment (24).

The ability to establish a protocol to effectively screen for resistance to late blight has become a high priority in potato-breeding programs (12,13,20,38). The trials that we conducted gave reproducible results in separating entries into four categories of resistance. Further exploration of this categorization might be useful in accurately defining moderate to high levels of field resistance. The characterization and deployment of MR cultivars could reduce fungicide use and help combat the escalating costs associated with chemical control programs (28). Clayton et al. (8) and Fry (16) demonstrated that cultivars with general resistance to US-1 required fewer fungicide applications for adequate disease management. Future research that matches general resistance classes with increasing interval lengths for fungicide applications may provide an integrated approach that

benefits growers and reduces the losses caused by US-8.

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