Relative Resistances of Potato Clones in Response to New and Old Populations of *Phytophthora infestans*

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ABSTRACT

Inglis, D. A., Johnson, D. A., Legard, D. E., Fry, W. E., and Hamm, P. B. 1996. Relative resistances of potato clones in response to new and old populations of *Phytophthora infestans*. Plant Dis. 80:575-578.

Potato cultivars and clones were evaluated in Washington and New York in 1993 and 1994 for field reaction to recent immigrant genotypes of *Phytophthora infestans*. Plants were visually evaluated at regular intervals for percent blighted foliage. Relative cultivar susceptibilities were compared by ranking the values obtained for areas under disease progress curves (AUDPC) of each line tested. Cultivar rankings in response to infection by new, immigrant isolates of *P. infestans* were nearly identical to rankings obtained previously with isolates prevalent prior to 1990. The cultivars Norchip, Hilite, Russet Norkotah, Goldrush, Superior, and Shepody were more susceptible than Russet Burbank. White Rose and Ranger Russet were similar in susceptibility to Russet Burbank. CO08-3008-1, ND-2438-7R, Kennebec, and Elba were less susceptible than Russet Burbank. Comparisons of the number of blighted tubers at harvest showed that foliage and tuber susceptibilities differed among cultivars. Shepody and Russet Norkotah tubers were most susceptible to tuber blight of those tested.

Additional keywords: fungicide resistance, host resistance, late blight

Recently, many potato (*Solanum tuberosum* L.) production regions in the United States and Canada have sustained significant losses from late blight, caused by *Phytophthora infestans* (Mont.) de Bary. Coastal areas of the Pacific Northwest in 1990, 1991, and 1993; sprinkler-irrigated areas in the arid Columbia basin of Washington and Oregon in 1993 (11) and 1995; and production areas in New York in 1992 and 1993 have been among those seriously affected.

Coincident with these disease outbreaks has been the detection of new genotypes of *P. infestans* (9) and an increase in genetic variation in *P. infestans* populations throughout the United States and Canada; this is apparently the result of migration of *P. infestans* genotypes from northern Mexico (7,10). Prior to 1990, the US-1 *P. infestans* genotype (all references herein to *P. infestans* genotypes designated "US" are sensu Goodwin et al., 1994 [7]) is believed to have been predominant throughout North America (6,10). The US-1 genotype is sensitive to the fungicide metalaxyl and is of the A-1 mating type. Many of the new immigrant genotypes are insensitive to metalaxyl and of the A-2 mating type. Other distinctions among newly identified genotypes exist and are being elucidated using various genetic and phenotypic markers (6).

In western Washington, the US-6 genotype of *P. infestans* was isolated from 1990 to 1993. This strain is of the A-1 mating type and insensitive to metalaxyl (2). US-11, a variant of US-6 that was possibly generated by mitotic recombination, also is of the A-1 mating type and is insensitive to metalaxyl; US-11 was isolated from western Washington in 1994 (S. B. Goodwin and W. E. Fry, *unpublished*). Throughout most of the United States and in New York, the US-8 genotype was the cause of late blight epidemics in 1994. US-8 is characterized by metalaxyl-insensitivity and the A-2 mating type (7,11).

In 1994, more than 60% of the acreage planted to potatoes in the United States was devoted to three cultivars, Russet Burbank, Russet Norkotah, and Shepody (14). For Washington, these cultivars constituted over 80% of the potato acreage in 1994, but their reaction to late blight has not been considered until now. The reactions of other potato cultivars such as Elba, Kennebec, Superior, and Norchip to late blight have already been published (3–5,15).

Information about the late blight susceptibility of commercially important cultivars is needed by those making decisions regarding late blight management and could help to optimize the success of integrated control strategies, especially in areas like eastern Washington where late blight previously has been of only limited concern. Incorporation of host resistance into a strategy of reduced fungicide applications (19) could enable a reduction in the amount of fungicide required for acceptable disease suppression. The same information used in concert with disease forecasting models could be used to identify fields where disease is most likely to develop so that monitoring programs could be initiated early in the growing season.

In this study during the 1993 and 1994 growing seasons, we evaluated the field reactions of some of the most important potato cultivars grown commercially in the United States to US-6, US-8, and US-11 clonal populations of *P. infestans* in Washington and New York.

MATERIALS AND METHODS

Washington. Field evaluations were done in Puget Silt Loam soil not previously cropped to potato at the Washington State University-Mount Vernon Research and Extension Unit near Mount Vernon. This location was chosen because of proximity to neighboring commercial potato fields and the known presence of an aggressive, metalaxyl-insensitive *P. infestans* population of the US-6 genotype throughout the area (2,7). Certified seed of potato cultivars and clones selected for evaluation were cut to approximately 70 g and immediately hand-planted in single rows arranged in four replicated randomized complete blocks. White Rose (of intermediate susceptibility) was planted as border and/or spreader rows every fourth treatment row. Blocks were 6 m long and had a 1-m row spacing and 23-cm seed spacing. Blocks also were separated by 3-m alleys on all sides to reduce interblock interference and to provide adequate access for irrigation and pesticide applications with a tractor-mounted sprayer. All blocks received fertilizer as preplant broadcast applications of potassium at 39 kg/ha. At the time of planting, nitrogen at 94 kg/ha and phosphorus at 69 kg/ha also

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Accepted for publication 5 February 1996.

Publication no. D-1996-0305-04R

Table 1. Rankings[y] (least to most susceptible) of the area under the disease progress curve (AUDPC) of potato cultivars evaluated in New York between 1979 and 1983 against *Phytophthora infestans*[z]

Year tested cultivar	AUDPC	Rank
1979		
NY59 = Elba	1,133	a
Kennebec	1,542	ab
Sebago	1,719	abc
NY 61	2,011	bcd
Katahdin	2,238	cde
FL-657	2,432	def
Bake King	2,461	efg
Hudson	2,534	fgh
Atlantic	2,662	gh
Monona	2,749	h
1980		
Sebago	848	a
Kennebec	993	b
Katahdin	1,374	c
Monona	1,694	d
1981		
Elba	1,921	a
Rosa	2,511	b
Kennebec	2,682	bc
Katahdin	2,791	c
Hudson	3,002	d
Belchip	3,134	e
Belrus	3,186	e
1983		
Rosa	396	a
Chipbelle	863	b
Hudson	1,222	c
Chieftain	1,286	c

[y] Ranks determined according to Proc Rank procedure in SAS (SAS Institute, Cary, NC). Common letters within years do not differ significantly according to analysis of variance of ranked AUDPCs and least significant difference analysis ($P = 0.05$).
[z] The genotype was probably US-1 because it existed in the United States prior to 1990 (7,8).

were liquid-injected 5 cm below and 10 cm to the side of each seedpiece. Weed control was obtained by spraying metribuzin at 0.34 kg a.i./ha plus paraquat dichloride at 1.05 kg a.i./ha prior to plant emergence. Emergence was recorded 30 DAP (days after planting) and ranged between 90 and 100% for all plots except ND02438-7R, which in 1994 had 50% emergence. No fungicides were applied to test plots, and late blight developed naturally in both years.

In 1993, plots were planted 25 May. Permethrin at 0.09 kg a.i./ha was applied for insect control, 21 DAP. Total monthly rainfalls May through August were 8.0, 4.3, 6.5, and 0.9 cm, respectively (total = 19.7 cm). The 30-year average at Mount Vernon for these months is 17 cm. An additional 2.5 cm of water (1.25 cm/month) was applied during the last 2 months of the growing season with an irrigation gun. Beginning 60 DAP and continuing weekly until 100 DAP, plants in each plot were visually evaluated for percent foliage affected by late blight. Late blight was assessed as percent infected leaf area following James (13). Because of high late blight pressure on the last three dates, each row was divided into five equal parts so that five ratings could be made and then averaged. No other foliar diseases were evident. The presence of US-6 in infected potato tissues was verified (S. B. Goodwin and W. E. Fry, *unpublished*). Vines were chopped and sprayed with Diquat dibromide at 0.52 kg a.i. (salt)/ha 101 DAP, and sprayed again 107 DAP prior to harvest 115 DAP. The total number of tubers and the percent blighted tubers per plot were assessed visually at harvest.

In 1994, plots were planted 24 May. Total monthly rainfalls May through August were 1.2, 5.4, 1.6, and 1.2 cm, respectively (total = 9.4 cm). Due to the relatively dry growing season, supplemental irrigation began 48 DAP with sprinklers that delivered 0.36 cm of water, in a morning plus evening irrigation, three times a week for 4 weeks. Beginning 57 DAP and continuing until 90 DAP, plots were rated visually every week. Each row was divided into three equal parts so three ratings could be made and then averaged. Vines were chopped 92 DAP, but desiccation sprays were deliberately omitted to maximize the development of tuber blight infections. Plots were harvested and tubers were rated for blight 94 DAP, sooner than in 1993, to maximize detection of tuber infections. The presence of US-11 in infected potato tissues was verified (S. B. Goodwin and W. E. Fry, *unpublished*).

New York. Experiments consisted of three replicated complete blocks in both 1993 and 1994. Plot size was four rows, each 4 m long with 0.9 m between rows and a 0.23-m spacing between potatoes within rows. Each plot was surrounded by at least 4 m of fallow soil on all sides. A pre-emergence herbicide (linuron 50W, 1.7 kg a.i./ha) was used. Fertilizer was 168 kg each of nitrogen, phosphorus, and potassium per hectare applied at planting. Certified seed tubers (ca. 50 g) were planted during 2 to 6 June each year. For disease assessments, a modification of the Commonwealth Mycological Institute key (3) was used. Sprinkler-irrigation was applied approximately three evenings a week.

Plots were inoculated in late July in both years. Inoculations in 1993 were with *P. infestans* US-6. The inoculum was prepared from plates of Rye A agar medium (1) approximately 14 days old and adjusted to a concentration of approximately 1,500 sporangia per ml. Approximately 50 ml of inoculum were delivered to a single plant in the center of each plot. Inoculation

Table 2. Area under the disease progress curve (AUDPC) and rankings[y] (least to most susceptible) of potato cultivars evaluated in Washington and/or New York in 1993 and/or 1994 against genotypes of *Phytophthora infestans* identified after 1990[z]

		Washington				New York			
		AUDPC		Rank		AUDPC		Rank	
Cultivar/clone	Maturity class	1993	1994	1993	1994	1993	1994	1993	1994
Elba	Late	527	135	a	a	...	397	...	a
Kennebec	Medium-late	748	247	b	ab	...	407	...	a
ND24387R	Medium-late	...	407	...	c	...	242	...	a
C00830081	Medium-late	...	362	...	bc	120	500	a	ab
Ranger Russet	Medium-late	1,101	389	bc	bc	361	731	bc	bc
Russet Burbank	Late	1,035	650	b	d	521	744	b	bcd
White Rose	Medium	1,060	834	bc	de	...	...	...	...
Shepody	Medium-late	1,169	807	cd	cd	608	824	b	f
Superior	Early	1,516	1,079	f	ef	...	742	...	cd
Goldrush	Medium	...	1,194	...	fg	...	793	...	de
Russet Norkotah	Medium-early	1,214	1,424	de	g	833	800	c	ef
Hilite	Medium-early	1,388	1,456	ef	g	1,017	793	c	de
Norchip	Medium-early	...	...	...	...	925	834	c	f

[y] Ranks determined according to Proc Rank procedure in SAS (SAS Institute, Cary, NC). Common letters within years do not differ significantly according to analysis of variance of ranked AUDPCs and least significant difference analysis ($P = 0.05$).
[z] Genotypes of *Phytophthora infestans* in plots in Washington and New York in 1993, in Washington in 1994, and in New York in 1994 were US-6, US-11, and US-8, respectively, sensu Goodwin.

in 1994 was done with *P. infestans* US-8, using approximately 1,000 sporangia per ml (50 ml per plant).

Potato cultivars tested in New York between 1979 and 1983 (Table 1) were also screened against *P. infestans* following the same general procedures. The isolates used in these studies were probably all US-1 (7,8).

Data analysis. Relative potato cultivar susceptibilities in Washington and New York were compared in each year by ranking area under the disease progress curve values (AUDPC) using the Proc Rank procedure in SAS (SAS Institute, Cary, NC) and then applying a one-way analysis of variance to the ranks. Results were statistically analyzed, and if F values were significant, Fisher's protected LSD test was used at $P = 0.05$. According to Quade (17), a one-way analysis of variance applied to ranks is equivalent to the Kruskal-Wallis k-sample test, and the F test generated by the parametric procedure applied to the ranks is often better than the X^2 approximation used by Kruskal-Wallis.

RESULTS

Thirteen potato cultivars and clones were evaluated two or more years in Washington and/or New York for field reaction to recently identified genotypes of *P. infestans*. Rankings of mean AUDPC values of the lines tested indicated that Norchip, Hilite, Russet Norkotah, and Goldrush were the most susceptible to the new *P. infestans* genotypes. Superior, White Rose, and Ranger Russet were similar to Russet Burbank; and CO08-3008-1, ND-2438-7R, Kennebec, and Elba were the least susceptible (Table 2). Moreover, Shepody in four of four tests had higher, and in two of four tests significantly higher, AUDPC values than Russet Burbank.

Several cultivars showed the same relative susceptibility to late blight whether tested before 1990 or after 1990. Late blight evaluations prior to 1990 (Table 1 and 3–5,15) and New York and Washington evaluations in 1993 and 1994 (Table 2) ranked Elba and Kennebec consistently lower in susceptibility than most other tested potato cultivars. Superior ranked among the highest in susceptibility in separate tests in New York in 1974, 1976, and 1984 (3–5), and in Washington and New York tests in 1993 and 1994 (Table 2). Norchip ranked among the highest in susceptibility in New York in 1977 (4,5) and in 1993 and 1994 (Table 2). Russet Burbank ranked intermediate in susceptibility in New York in 1976 and 1977 (4) and in Washington and New York in 1993 and 1994 (Table 2).

Foliage and tuber susceptibilities to late blight differed for each cultivar tested. Russet Norkotah and Shepody had the highest incidence of tuber infection at harvest in Washington in both 1993 and 1994 (Table 3).

DISCUSSION

In this field study, several potato cultivars ranked nearly the same for resistance to new, immigrant isolates of *P. infestans* as they ranked to US-1 isolates prior to the 1990s. Evaluations in New York in the 1970s and 1980s consistently ranked Kennebec lower in susceptibility than other cultivars, Superior and Norchip among the highest in susceptibility, and Russet Burbank intermediate. Furthermore, Norchip and Superior generally are regarded as susceptible, Russet Burbank as moderately susceptible, and Kennebec as moderately resistant to late blight (18). The ranking of these cultivars as a result of a different population of *P. infestans* remains unchanged. However, we do not have data on the relative aggressiveness of previous and immigrant strains.

Recent epidemics in the United States caused by the new, immigrant genotypes have been dominated by one or only a few clones, and usually no genetic variation has existed among the isolates collected from a specific site at different sampling times throughout an epidemic (7,8,10). New genotypes of *P. infestans* in this study included US-6 in Washington and New York in 1993, US-8 in New York in 1994, and US-11 in Washington in 1994. These genotypes are insensitive to metalaxyl. US-6 and US-11 are of the A-1 mating type, whereas US-8 is A-2. Cultivar evaluations done prior to 1990 probably involved populations of the US-1 genotype, which is sensitive to metalaxyl and of the A-1 mating type (7,8).

The increased aggressiveness ascribed anecdotally to the new genotypes of *P. infestans* cannot be explained by R-gene selection because cultivars have not varied in R-gene composition. Instead, the severity of disease noted in recent epidemics may, in part, be a reflection of metalaxyl-insensitivity and the absence of the suppressive effects of a once successful disease control technology. Increased aggressiveness may also be the result of an increase in parasitic fitness of immigrant strains.

New potato selections such as ND2438-7R and C008-3008-1 were more resistant to late blight than Russet Burbank, while cultivars such as Russet Norkotah, Goldrush, Hilite, and Shepody, which have been widely grown in recent years, were more susceptible than Russet Burbank. Of the cultivars evaluated, the foliar response of Shepody at the two locations during the 2 years (Table 2) was somewhat variable considering field observations that consistently confirm that Shepody is more susceptible than Russet Burbank. Cultivars with variable responses to late blight from year to year would be more difficult to manage in integrated pest management programs than cultivars with stable responses (16).

In this study, cultivar susceptibilities as a function of maturity class resembled those reported previously (5). Earlier maturing cultivars generally are more susceptible than late maturing cultivars. By example, late blight developed earlier and more quickly on Superior, Hilite, Russet Norkotah, and possibly Shepody than on Russet Burbank. These results also are in agreement with field observations made by the first and second authors in the Columbia Basin and western Washington during epidemics of the past few years. Very susceptible, early-maturing cultivars are probable sources of early season inoculum buildup, and their advanced development of a mature crop canopy would create a microenvironment earlier in the season that could promote disease development. Fields of early-season cultivars are conceivable targets for intense fungicide spray programs and should be monitored and managed accordingly for early development of late blight.

The rankings of foliage disease severity sometimes differed from the rankings of tuber disease severity. Differences in foliage and tuber reactions to late blight also have been reported previously (20). Russet Norkotah and Shepody had relatively high incidence of tuber infection at harvest in Washington in both 1993 and 1994, whereas Shepody and Ranger Russet had relatively high incidence of tuber infection 3 months poststorage (12). Many areas have recently described serious tuber blight in Ranger Russet (W. Stevenson, *personal communication*).

Table 3. Percentage of tubers with visible late blight symptoms at harvest in selected potato cultivars and clones infected with new clonal populations of *Phytophthora infestans*[x] at Mount Vernon, WA, in 1993 and 1994

	% Tuber rot at harvest[y]	
Cultivar/clone	**1994**	**1993**
ND02438-7R	0 a	...
C008-3000-1	0.5 a	...
Rosa	...	2.2 a
Red LaSoda	1.1 a	...
Superior	1.1 a	2.0 a
Elba	2.1 a	1.5 a
Ranger Russet	2.8 a	2.3 a
Russet Burbank	2.7 a	3.7 ab
Allegany	4.2 a	...
Kennebec	4.7 a	2.3 a
Goldrush	4.7 a	...
Hilite	2.9 a	1.6 a
White Rose	6.2 a	3.1 a
Norkotah	15.0 b	5.9 bc
Shepody	18.7 b	7.1 bc
LSD (P = 0.05)[z]	0.0662	0.0259

[x] Clonal populations of *Phytophthora infestans* identified as US-6 and US-11, sensu Goodwin, existed in plots in Washington in 1993 and 1994, respectively.

[y] Percent data transformed before analysis using square root of $x + 0.5$.

[z] Common letters in the same column do not differ significantly according to analysis of variance and least significant difference analysis.

ACKNOWLEDGMENTS

We thank L. Johnson and B. Gundersen for technical assistance. Support was provided in part by the Washington State Potato Commission, the Oregon Potato Commission, and Cornell University Hatch Projects 153430 and 153447. Plant Pathology New Series 0215, project 5112, College of Agriculture and Home Economics Research Center, Washington State University, Pullman, WA.

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