Assessment of Resistance of Tubers of Potato Cultivars to *Phytophthora erythroseptica* and *Pythium ultimum*

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ABSTRACT

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Tubers of 34 potato cultivars were examined for their susceptibility to infection by zoospores of *Phytophthora erythroseptica* and mycelia of *Pythium ultimum*. Incidence of infected tubers (%) and penetration of rot (mm) were the parameters used to determine the susceptibility of each cultivar. Tubers of cv. Atlantic appeared to have some resistance to infection and colonization by *Phytophthora erythroseptica*. Cvs. Russet Norkotah and Snowden were the most susceptible to infection by *P. erythroseptica*. Snowden was found to be highly susceptible to *P. erythroseptica*, but it was the most resistant to *Pythium ultimum*. Cvs. FL-1625 and FL-1867 also were less susceptible to *P. ultimum* than the other cultivars. Cvs. Superior, Itasca, and Dark Red Norland were the most susceptible to *P. ultimum*. Cultivar susceptibility should be considered when making disease management decisions, particularly in fields where these soilborne diseases are a recurring problem.

Additional keywords: control, epidemiology, leak, pink rot, *Solanum tuberosum*

Pink rot of potato (*Solanum tuberosum* L.) caused by *Phytophthora erythroseptica* Pethybr. and leak caused by *Pythium ultimum* Trow are two important soilborne diseases of potato in the United States (32). The name pink rot describes the diagnostic pink color that appears in infected tuber tissue when cut and exposed to air for 20 to 30 min (12,24). The common disease name of leak is descriptive of the exudation of water droplets from the blackish, soft watery breakdown of tissue of infected tubers (2,16). These diseases can cause severe yield losses in fields and in storage facilities (1,16,32). In the United States, levels of pink rot infection in fields ranged from 10 to 75% (1,4,8), and often tubers in infected areas or the entire field may not be harvested. Tubers infected with *Phytophthora erythroseptica* usually are found in wet, low-lying areas during harvest, and symptom development occurs soon after tubers are placed in storage facilities (1,3,32). The leak pathogen also can cause seed-piece decay after planting (16) and kill seedlings from true potato seed (24).

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Infection of tubers by *P. erythroseptica* generally occurs via stolons (10,21,27); however, tubers also can be infected by zoospores of *P. erythroseptica* through tuber eyes (29) and wounded tubers (31). *Pythium ultimum* is incapable of penetrating the undamaged skin of the tuber (14). Thus, infections by the leak pathogen always start at cuts and wounds, and only occasionally through the stem end (1).

Studies on cultivar susceptibility to *Phytophthora erythroseptica* and *Pythium ultimum* are scarce and most are outdated, involving potato cultivars no longer in production. Most studies on cultivar susceptibility to pink rot and leak involve one pathogen or the other and do not evaluate susceptibility to both diseases. In studies involving pink rot, Cairns and Musket (6) evaluated 51 cultivars and found that all were susceptible. Similarly, Jones (17) found that none of the eight cultivars he tested were resistant. Other studies have identified that cultivars exhibited various levels of susceptibility. Goss (12), reported that cvs. Irish Cobbler (6%) and Kasota (10%) had a lower incidence of infection than cvs. Warba (46%) and Pawne (42%). Fernandez-Northcote et al. (10) reported that tubers of only four clones were found to be resistant to pink rot after screening 13 cultivars and 242 native clones from Peru. Lennard (20) found that some cultivars were more susceptible than others. More recently, Stack et al. (33) noted that differences in cultivar susceptibility may not be significant enough to affect pink rot management. Peters and Sturz (25) reported that plantlets of cvs. Butte and Russet Burbank were the least susceptible, and those of Goldrush and Yukon Gold were the most susceptible. Regarding the susceptibility of potato tubers to the leak pathogen, Jones (16) reported that none of the 15 potato cultivars grown in British Columbia, Canada was resistant to leak. Hawkins (13) found that incidence of leak in cultivars can range from 0 to 91%. Priou et al. (28) concluded that some cultivars were more susceptible than others to infection by *Pythium aphanidermatum*, the leak pathogen in tropical areas.

There is little information on the levels of resistance to the pink rot and leak pathogens of the potato cultivars currently grown in the United States; therefore, the main objective of this study was to assess the reaction of tubers of 35 cultivars to infection by zoospores of *Phytophthora erythroseptica* and mycelia of *Pythium ultimum*. Preliminary reports of this research have been published (29,30).

MATERIALS AND METHODS

Potato cultivars, cultivation, harvest, and pre-inoculation handling. A total of 34 commercial potato cultivars (Table 1) were obtained from seed potato producers in North Dakota (ND), Minnesota (MN), or private companies. Whole or cut seed tubers were used for planting. All cultivars were produced in single rows (30 m) in field plots with center pivot irrigation in McLeod (ND) in 1998, in Glyndon (MN) in 1999, and in Dawson (ND) in 2000. Cultural practices during the growing season were those recommended for the production of potato in the Red River Valley. Tubers were harvested at maturity, visually inspected for pink rot and leak symptoms, and placed in a room at 15°C and 90% relative humidity for 2 weeks to promote wound healing. Thereafter, tubers of all cultivars were stored at 10°C for 2 to 3 months before inoculations. Disease-free tubers (140 to 190 g) were acclimated to room temperature (20 to 24°C) 2 to 3 days prior to inoculations. No natural infections of pink rot or leak were observed in any year of the study. Preliminary studies showed that the frequency of infection by *Phytophthora erythroseptica* in surface sterilized tubers with 0.5% NaOCl and non-surface-sterilized tubers were similar (P = 0.05). Therefore, tubers used for inoculations were not surface sterilized or washed prior to inoculation. Tubers used for inoculation with *P. erythroseptica* had the apical and at least one lateral eye free of soil, and those used for inoculation with *Pythium ultimum* had an intact periderm.

Pathogen isolates. *Phytophthora erythroseptica* isolates PR-347 (31) from Minnesota and PE-02 obtained in 1997 from an infected tuber from Carrington, ND were used to evaluate levels of resistance to pink rot. Isolates 153-7 and Py-HS of *Pythium ultimum* obtained in 1997 from infected tubers from Idaho and North Dakota, respectively, were used to evaluate resistance to leak. All isolates were identified based on described morphological characteristics (34,35). Inoculations were made on freshly wounded Russet Burbank tubers with colonized agar plugs of the isolates. These preliminary studies showed that all isolates were highly pathogenic. Pathogenicity of all isolates was maintained every year through inoculation to Russet Burbank tubers and re-isolation on water agar culture plates.

Inoculations with *Phytophthora erythroseptica*. A method similar to that reported by Vujicic and Colhoun (36) was followed to obtain zoospores of *P. erythroseptica*. However, clarified V8 juice agar and clarified V8 juice broth were used instead of pea extract. Clarified V8 juice agar contained 100 ml of clarified V8 juice, 15 g of agar, and 900 ml of deionized distilled water. A stock of clarified V8 juice broth contained: 100 ml of V8 juice filtered through four layers of cheesecloth, and 900 ml of deionized distilled water. To obtain mycelial mats of *P. erythroseptica*, three mycelial disks (5 mm in diameter) of the pathogen grown on clarified V8 juice agar for 3 days were placed on each glass petri dish (9 cm) or plastic petri dish (8.5 cm), flooded with 10 ml of autoclaved clarified V8 broth, and incubated in darkness at room temperature (20 to 24°C) for 3 days. To induce sporangia formation, the clarified V8 juice broth was discarded, and replaced with a filtered and autoclaved soil extract (100 g of soil from potato field in 900 ml of deionized water) at 10 ml/petri plate, after rinsing the mycelial mats two to three times with sterile deionized water. These cultures were further incubated for 36 to 48 h under continuous light in an incubator (20 ± 1°C) with eight lamps (Sylvania F20T12/CW). Finally, to induce the release of zoospores, cultures were chilled at 10 ± 1°C for 1 h and rewarmed at room temperature (20 to 24°C). Abundant zoospore release occurred within 15 to 25 min. A hemacytometer was used to obtain an inoculum concentration of 2×10^4 zoospores ml^{-1}. Zoospore suspension was chilled (8 to 10°C) until inoculations were made within 10 to 60 min. Before inoculations, tubers were placed in plastic moist chambers (33 cm long by 24 cm wide by 12 cm high) lined at the bottom with plastic canvas mesh 3. Each tuber was inoculated by placing a single drop of inoculum (10 µl; approximately 200 zoospores) on each of the three apical eyes of tubers (one apical plus two next laterals). Control tubers were inoculated only with sterile distilled water. After inoculations, tubers were covered with two layers of wet paper towels before closing the moist chambers to maintain high humidity, thereby promoting infection. All inoculated tubers in moist chambers were incubated in darkness at room temperature (20 to 22°C) for 10 to 12 days.

Table 1. Potato cultivars tested for their reaction to *Phytophthora erythroseptica* and *Pythium ultimum*[a]

Cultivars	Parentage	Release	Maturity group
Red cultivars			
Dark Red Norland	Clone from Red Norland	?	Early
La Rouge	LA02-5 (LaSoda × Progress) self	1962	Medium
NorDonna	ND206-1R × ND821-6R	1995	Medium
Red LaSoda	Triumph × Katahdin	1953	Main season
Norland	Redkote × ND626	1957	Early
Red Pontiac	Triumph × Katahdin	1945	Late
Viking	Nordak × Redskin	1963	Main season
Russet cultivars			
Goldrush	ND450-3Russ × Lemhi Russet	1992	Medium
Liberty Russet	Somaclone of Lemhi Russet	2000	Medium late
Russet Burbank	Early Rose × ?	1914	Late
Russet Burbank-NL	Russet Burbank-GMO	1995	Late
Russet Burbank-NLLR	Russet Burbank-GMO	?	Late
Russet Norkotah	ND9526-4Russ × ND9687-5Russ	1987	Medium-early
Ranger Russet	Butte × A6595-3	1991	Full season
White cultivars			
Atlantic	Waseon × B5141-6 (Lenape)	1976	Medium
FL-1207	…[b]	…	…
FL-1533	…	…	…
FL-1625	…	…	…
FL-1831	…	…	…
FL-1833	…	…	…
FL-1867	…	…	…
FL-1879	…	…	…
FL-1900	…	…	…
Itasca	MN304.72-10 × ND58-3	1994	Medium
Kennebec	B127 × USDA X96-56	1948	Medium
LaChipper	Cayuga × Green Mountain	1962	Medium
Norchip	ND4731-1 × M5009-2	1968	Medium early
NorValley	Norchip × ND860-2	1996	Medium
Pike	Allegany × Atlantic	1995	Medium
Shepody	Bake-King × F58050	1980	Medium late
Shepody-NL	Shepody – GMO	?	Medium late
Snowden	B5141-6 (Lenape) × Wischip	1990	Full season
Superior	USDA X96-56 × MN59.44	1961	Early
Yukon Gold	W5279-4 × Norgleam	1980	Medium

[a] Information obtained from Love (22) and University of Maine.
[b] Information for Frito-Lay (FL) cultivars not available for public disclosure.

Inoculations with *Pythium ultimum*. All tubers were wounded on one side before inoculations. The wounding procedure involved the removal of a disc of periderm tissue (5 mm in diameter by 1 mm deep) cut with a No. 2 cork borer from an area near the middle of one side of each tuber. Inoculum of *P. ultimum* was prepared by growing the isolates on modified V8 juice agar (100 ml of V8 juice, 1.25 g of $CaCO_3$, and 900 ml of water) for 48 h. One *P. ultimum*-colonized agar plug (5 by 3 mm) cut from the colony margin was placed on the freshly wounded tuber tissue. Control tubers were inoculated with modified V8 juice agar plugs. The inoculated tubers were placed in plastic moist chambers as described above and were incubated in darkness at room temperature (20 to 22°C) for 6 days.

Disease assessment. Development of pink rot symptoms in tubers was examined 10 to 12 days after inoculations with *Phytophthora erythroseptica*, whereas development of leak symptoms was examined 6 days after inoculation with *Pythium ultimum*. Inoculated tubers were removed from moist chambers, sliced in half lengthwise through the inoculation point or points, and covered with moist paper towels to enhance the development of the pink discoloration diagnostic for pink rot and the watery blackish discoloration characteristic of leak. The number of tubers showing symptoms of pink rot or leak was recorded 30 min after cutting. Incidence of pink rot or leak rot was calculated as (number diseased tubers/number of inoculated tubers) × 100. To determine pink rot and leak severity, the maximum width (W) and depth (D) of rot from the inoculation point were measured, then penetration of rot was calculated using the formula reported by Lapwood et al. (19): Penetration = $(W/2 + [D - 5])/2$.

Experimental design and data analysis. A factorial of cultivar by isolate (35 by 2) experiment was arranged in a completely randomized design with four replicates per cultivar. A replicate consisted of a set of 10 tubers per cultivar. Ten noninoculated tubers per cultivar served as controls. Two experiments for each isolate were conducted in the first year (1998), but only one experiment per isolate was conducted in 1999 and 2000. All 35 cultivars were not included in each year of the study. Cultivars were grouped based on the appearance of the skin as russets, reds, or whites for data analysis. All data were subjected to analysis of variance (PROC GLM, SAS). Pink rot or leak did not develop in tubers used as the control; therefore, these data were not included in the statistical analysis. Data from 3 years were pooled after testing the homogeneity of error mean squares (11) and analyzed as combined experiments as outlined by Carmer et al. (7). The relationship between pink rot incidence and severity and between leak incidence and severity were analyzed with Pearson's correlation test to determine the strength of the correlation between these variables. For this, only data for cultivars that were tested for a minimum of 2 years were included.

RESULTS

Assessment of incidence and severity of pink rot. Differences on incidence of infection among the potato cultivars to *Phytophthora erythroseptica* were highly significant (reds, $P < 0.001$; russets, $P = 0.029$; and whites, $P < 0.001$). The effect of isolate and the interaction of isolate–cultivar was not significant (Table 2). Among the red cultivars, Viking (78%) and Red LaSoda (73.6%) had the highest incidence of pink rot-infected tubers, whereas Norland (52.2%) and NorDonna (51.6%) had the fewest pink rot-infected tubers (Table 3; Fig. 1). Among the russet cultivars, Russet Norkotah (88.1%) and Liberty Russet (82.5%) had the highest incidence of pink rot and, in contrast, Russet Burbank (50.1%) and Ranger Russet (43.3%) had the lowest incidence of pink rot-infected tubers (Table 3; Fig. 1). Among the white cultivars, Snowden (85.3%), FL-1207 (76.9%), Kennebec (76.3%), FL-1867 (74.8%), and Shepody-NL (74.7%) had the highest incidence of pink rot-infected tubers, whereas cultivars Atlantic (31.6%) and FL-1900 (23.4%) had the lowest (Table 3). Pink rot severity values in red, russet, and white cultivars were not significantly different (Table 3).

Assessment of the association incidence and severity of pink rot. The relationship between incidence and severity of pink rot in red cultivars was highly significant ($r = 0.8$, $P = 0.002$). Plotting of paired values of incidence and severity of pink rot in red cultivars showed that cultivars such as Viking and Red LaSoda had a high incidence of pink rot and rotted more extensively, whereas cultivars such as Nordonna and Norland had low incidence of pink rot and rotted less extensively (Fig. 1). Incidence and severity values of pink rot in white and russet cultivars were not correlated significantly; however, there were cultivars with high incidence of infected tubers and extensive rotting of tuber tissue (Russet Norkotah), and cultivars with a low incidence of pink rot and low tuber rot severity (Atlantic) (Fig. 1).

Assessment of incidence of leak. The combined analysis of data of leak incidence showed that differences in the incidence of infection by the leak pathogen among the red and russet cultivars were not significant (Table 4). In contrast, differences in the incidence of leak infection among white cultivars were highly significant ($P = 0.001$; Table 4). Cvs. Superior (97.3%), LaChipper (96.9%), FL-

Table 2. Combined analysis of variance of severity and incidence of pink rot caused by *Phytophthora erythroseptica* in 34 potato cultivars[a]

		Severity				Incidence			
Sources of variation	DF[b]	SS	MS	*F* value	*PR > F*	SS	MS	*F* value	*PR > F*
Red cultivars									
Year	1 (2)	1,161.05	1,161.05	…	…	6,716.23	3,358.12	…	…
Rep (year)	6 (9)	91.73	15.29	…	…	1,574.55	174.95	…	…
Cultivar[c]	6 (6)	126.13	21.02	0.60 NS	0.726	14,728.25	2,454.71	9.52 **	0.001
Isolate[d]	1 (1)	634.02	634.02	15.77 NS	0.157	14,307.90	14,307.90	3.96 NS	0.185
Cultivar × isolate[e]	6 (6)	367.75	61.29	1.31 NS	0.377	732.44	122.07	0.43 NS	0.847
Year × cultivar	6 (11)	210.81	35.14	0.75 NS	0.633	2,837.38	257.94	0.90 NS	0.569
Year × isolate	1 (2)	40.20	40.20	…	…	7,225.23	3,612.62	…	…
Year × cultivar × isolate	6 (11)	281.36	46.89	…	…	3,156.83	286.99	…	…
Error	78 (111)	1,131.28	14.50	…	…	29,398.37	264.85	…	…
Total	111 (159)	4,044.31	…	…	…	79,368.74	…	…	…
Russet cultivars									
Year	1 (2)	2,495.56	2,495.56	…	…	6,978.76	3,489.38	…	…
Rep (year)	6 (9)	104.43	17.41	…	…	2,111.89	234.66	…	…
Cultivar[c]	6 (6)	576.29	96.05	2.82 NS	0.137	31,683.68	5,280.61	4.10*	0.029
Isolate[d]	1 (1)	451.70	451.70	36.14 NS	0.105	2,942.24	2,942.24	8.50 NS	0.100
Cultivar × isolate[e]	6 (6)	408.40	68.07	2.16 NS	0.208	2,237.84	372.97	1.12 NS	0.423
Year × cultivar	5 (9)	170.12	34.03	1.08 NS	0.467	11,577.72	1,286.41	3.85*	0.029
Year × isolate	1 (2)	12.50	12.50	…	…	692.21	346.10	…	…
Year × cultivar × isolate	5 (9)	157.45	31.49	…	…	3,004.37	333.82	…	…
Error	69 (98)	2,654.77	38.48	…	…	…	…	…	…
Total	100 (142)	7,770.45	…	…	…	…	…	…	…
White cultivars									
Year	1 (2)	5,724.73	5,724.73	…	…	40,659.76	20,329.88	…	…
Rep (year)	6 (9)	37.82	6.30	…	…	6,449.48	716.61	…	…
Cultivar[c]	18 (19)	1,875.00	104.17	2.22 NS	0.060	67,409.20	3,547.85	4.62 **	0.001
Isolate[d]	1 (1)	399.66	399.66	1.50 NS	0.436	17,084.33	17,084.33	2.57 NS	0.250
Cultivar × isolate[e]	18 (19)	740.61	41.15	1.52 NS	0.214	7,153.81	376.52	0.81 NS	0.684
Year × cultivar[e]	16 (30)	751.92	47.00	1.74 NS	0.152	23,031.73	767.73	1.64 NS	0.090
Year × isolate	1 (2)	266.95	266.95	…	…	13,309.68	6,654.84	…	…
Year × cultivar × isolate	14(30)	377.80	26.99	…	…	14,012.53	467.08	…	…
Error	200 (300)	3,018.96	15.10	…	…	71,210.34	237.37	…	…
Total	275 (412)	13,728.98	…	…	…	268,598.51	…	…	…

[a] Values followed by NS = nonsignificant at $P = 0.05$, * = significant at $P \leq 0.05$, ** = significant at $P \leq 0.01$.
[b] Values in parenthesis are degrees of freedom for incidence of pink rot.
[c] Significance tested using year × cultivar as an error term.
[d] Significance tested using year × isolate as an error term.
[e] Significance tested using year × cultivar × isolate as an error term.

1207 (96.3%), Itasca (96.3%), Pike (95.6%), Yukon Gold (93.5%), Shepody-NL (93.1%), and Shepody (92.3%) had the highest incidence of infected tubers, whereas cv. Snowden (33.5%) had the lowest incidence of infection by *Pythium ultimum* (Table 3), followed by cultivars FL-1867 (47.5%) and FL-1625 (44.1%).

Assessment of severity of leak. Differences of severity values (rot penetration) caused by the colonization of tuber tissue by the leak pathogen were similar in all the red cultivars; however, significant differences in rot penetration were found among russet and white cultivars (Table 3). Tuber tissue of russet cultivars such as Liberty Russet, Goldrush, and Ranger Russet were more extensively rotted than tuber tissue of Russet Burbank and Russet Norkotah. Among the white cultivars, tubers of FL-1207 followed by Itasca and Superior rotted more extensively than tubers of FL-1900, FL-1867, NorValley, Yukon Gold, or Snowden (Table 3).

Assessment of the association incidence and severity of leak. Incidence and severity of leak in russet and white cultivars were highly correlated (russets: r = 0.8, P = 0.02; whites: r = 0.6, P = 0.004). However, this relationship was not evident with some cultivars. Plotting of paired values of incidence and severity divided cultivars into several groups (Fig. 2). One group included resistant cultivars showing low incidence of infection and also less extensive rotting of tuber tissue: Snowden, FL-1625, and 1867. Another group contained susceptible cultivars with a high incidence of infection accompanied with extensive rotting: Superior, Itasca, and Dark Red Norland. A third group comprised cultivars such as: Yukon Gold and LaChipper with high incidence of leak but with low tuber rot severity (Fig. 2).

Table 3. Incidence and severity of pink rot and leak caused by *Phytophthora erythroseptica* and *Pythium ultimum,* respectively, in tubers of 34 potato cultivars[a]

Cultivars[b]	Yr tested (no.)	Pink rot		Leak	
		Incidence	Severity	Incidence	Severity
Red cultivars					
Viking	3	78.0	38.6	92.6	23.8
Red LaSoda	3	73.6	38.2	88.5	23.2
La Rouge	3	66.4	37.6	89.0	22.8
Red Pontiac	3	62.3	37.9	90.6	24.0
Dark Red Norland	2	61.9	38.6	95.6	29.8
Norland	3	52.2	36.2	94.8	27.1
NorDonna	3	51.6	35.7	77.3	23.6
LSD	…	9.6	NS	NS	NS
Russet cultivars					
Russet Norkotah	3	88.1	37.6	76.7	20.3
Liberty Russet	1	82.5	45.3	97.5	30.2
Goldrush	3	64.5	34.4	85.0	26.2
Russet Burbank-NLLR	2	55.9	32.3	88.1	20.7
Russet Burbank-NL	3	54.5	32.7	77.5	21.2
Russet Burbank	3	50.1	36.0	73.0	20.4
Ranger Russet	3	43.3	37.0	88.1	25.1
LSD	…	9.2	NS	NS	1.6
White cultivars					
Snowden	3	85.3	34.7	33.5	18.9
FL-1207	1	76.9	36.3	96.3	32.3
Kennebec	3	76.6	41.3	67.4	23.0
Shepody-NL	2	74.7	35.1	93.1	26.1
Itasca	3	66.2	36.6	96.3	29.9
FL-1625	3	65.1	39.9	44.1	19.7
FL-1867	2	64.3	35.3	47.5	17.7
FL-1879	3	63.3	37.9	76.6	20.8
Shepody	3	63.1	38.1	92.3	26.0
Yukon Gold	3	62.5	36.8	93.5	18.0
FL-1831	3	59.5	39.5	70.8	24.8
FL-1533	3	59.3	35.6	70.8	21.0
Superior	3	58.5	38.9	97.3	29.4
NorValley	3	51.3	41.0	74.7	18.0
LaChipper	2	50.0	34.1	96.9	20.2
Pike	2	47.8	33.4	95.6	25.5
Norchip	3	47.0	41.2	82.9	24.0
FL-1833	2	45.9	33.7	79.7	25.2
Atlantic	3	31.6	33.2	77.3	23.1
FL-1900	1	23.4	….	77.3	15.7
LSD	…	10.0	2.9	7.3	1.8

[a] Mean incidence (%) of infection from two experiments per isolate in 1998 and one experiment in 1999 and 2000 with four replications of 10 tubers of each cultivar per replication; mean severity (mm) of penetration of rot solely based in infected tubers; NS = not significant; … = missing value.

[b] LSD = least significant difference, P = 0.05.

DISCUSSION

Results from inoculation of tubers produced in three different locations in three consecutive years revealed that the potato cultivars evaluated in this study differed in their reaction to *Phytophthora erythroseptica* and *Pythium ultimum*. Our data indicate that most of the potato cultivars currently grown in the United States are mostly susceptible to both the pink rot and leak pathogens; however, there were cultivars that have higher levels of resistance as measured by reduced incidence and colonization of tubers. Our data, therefore, agree with previous reports on these diseases (12,13,16,17,20). This high susceptibility of the current cultivars may reflect the fact that potato breeding programs have not focused on breeding for resistance to these diseases. Thus, it might be desirable for breeding purposes to survey collections of potato cultivars and lines including wild species to identify the best source of resistance. Interestingly, cv. Snowden was highly susceptible to *Phytophthora erythroseptica* while being the least susceptible to *Pythium ultimum*. Cv. Pike followed almost the same pattern. These results may indicate that a different gene or genes is involved in resistance to these two pathogens.

The susceptibility of tuber eyes to infection by *Phytophthora infestans*, a relative of *P. erythroseptica*, remains the same over an extended period after harvest (18). Thus, the use of zoospores of *P. erythroseptica* to infect eyes of whole and undamaged tubers should closely simulate how infection naturally occurs in the field. Moreover, symptoms of pink rot starting at tuber eyes in moist areas have been reported (5,6). We also have observed this type of infections in our pink rot surveys in North America, particularly under heavy disease pressure (i.e., favorable temperature, 20 to 25°C) and high inoculum density (31). Therefore, under these circumstances, less incidence of infection and less severe rotting of tuber tissue caused by the pink rot pathogen indicate that cultivar Atlantic has some resistance to *P. erythroseptica*; which is consistent with what was reported previously in that this cultivar has some resistance to "wet rot" (37). Cvs. LaChipper, Pike, and FL-1833 also may have some resistance to *P. erythroseptica*. Likewise, Nordonna and Norland among the red-skinned cultivars and Ranger Russet and Russet Burbank among the russet-skinned cultivars appear to have less susceptibility to *P. erythroseptica* relative

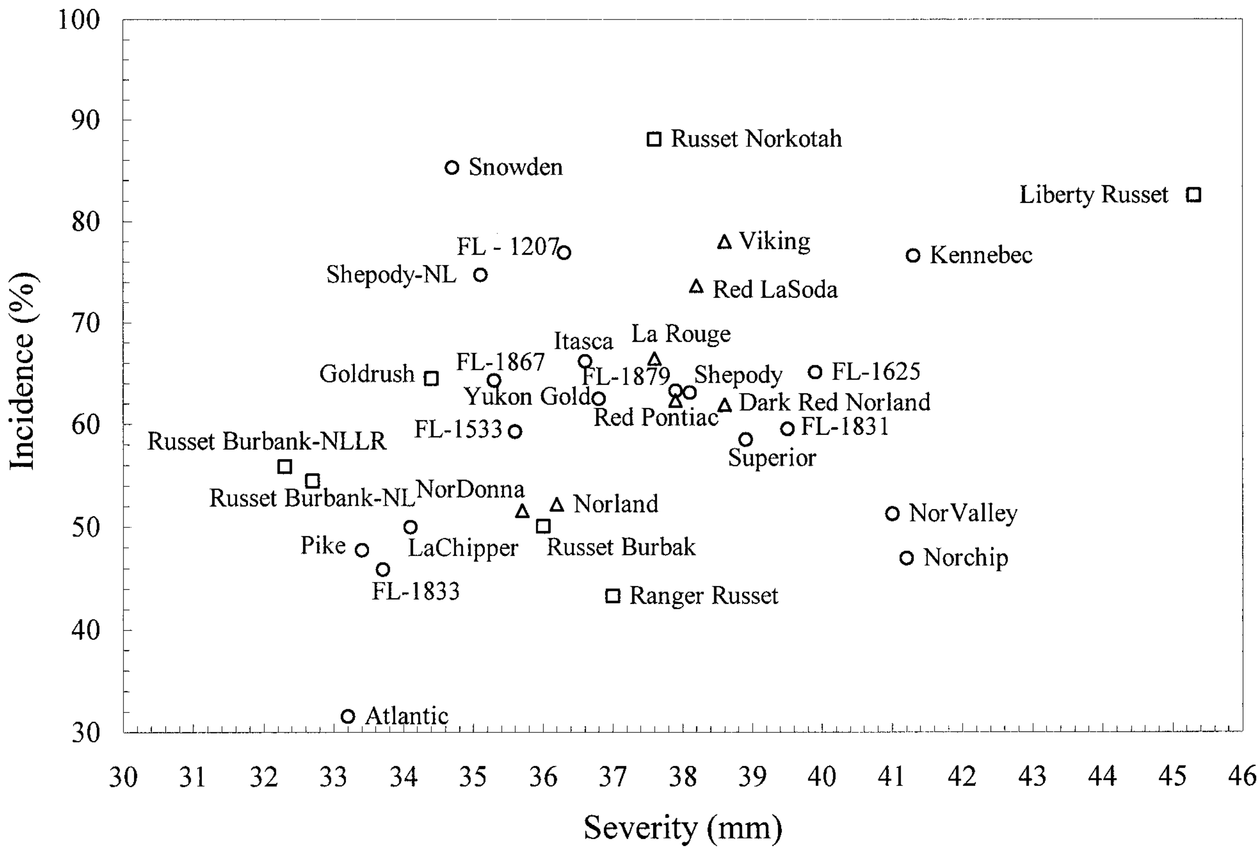

Fig. 1. Comparison of potato cultivars (red cultivars = △, russet cultivars = □, and white cultivars = ○) for resistance to *Phytophthora erythroseptica* based on paired values of incidence of infection (resistance to infection) and severity of rot penetration (resistance to colonization).

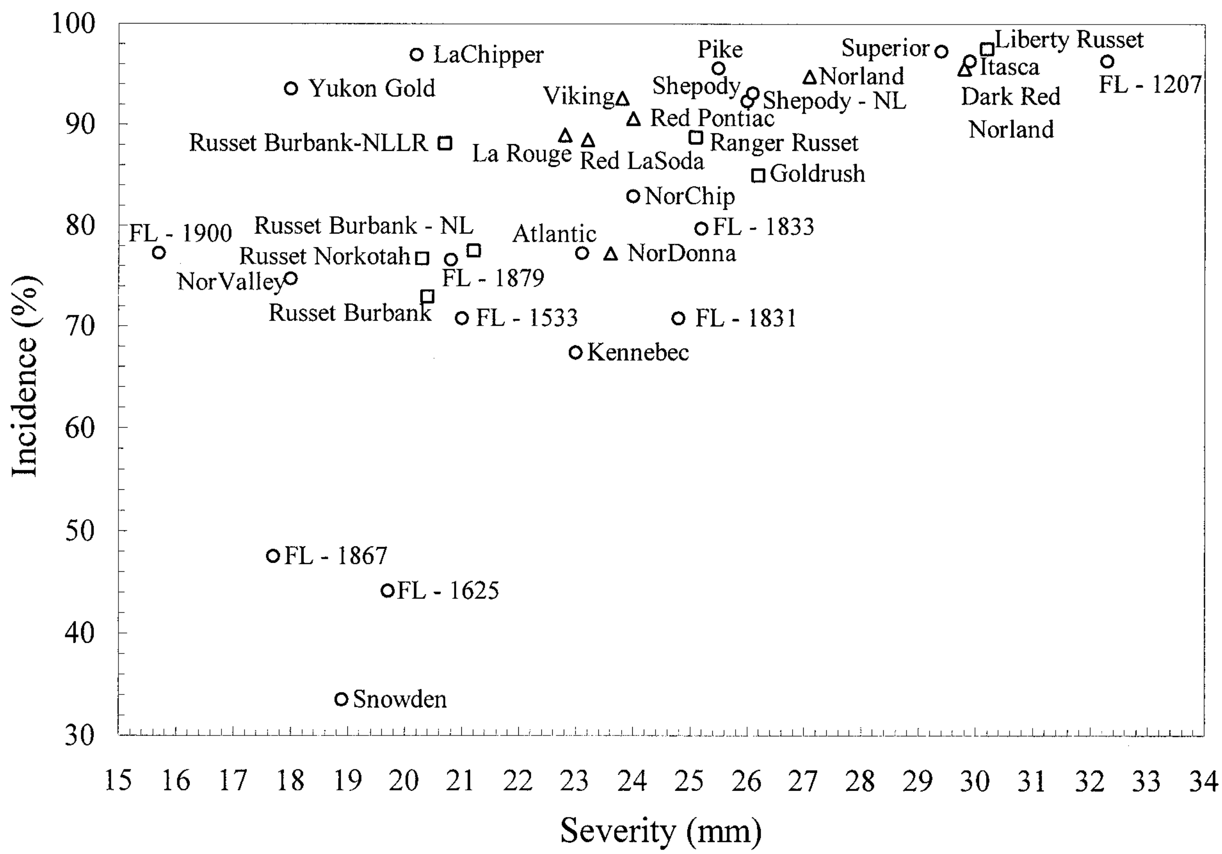

Fig. 2. Comparison of potato cultivars (red cultivars = △, russet cultivars = □, and white cultivars = ○) for resistance to *Pythium ultimum* based on paired values of incidence of infection (resistance to infection) and severity of rot penetration (resistance to colonization).

to other cultivars. Our data also agree with the finding by Peters and Sturz (25) that cv. Russet Burbank is less susceptible than cvs. Goldrush and Yukon Gold to infection by *P. erythroseptica*. These three cultivars do not differ in the severity of tuber rotting, however (Table 3; Fig. 1). Cvs. Pike and Russet Burbank had been reported to be less susceptible to *P. infestans* US-8 (9,26). That resistance to *P. infestans* also confers resistance to *P. erythroseptica* has not been demonstrated in potato cultivars and should be investigated further.

Pythium ultimum is incapable for penetrating the undamaged skin of the tuber (14); therefore, tuber infection by this pathogen occurs mainly through wounds and injuries caused during the harvest operations, and is compounded by temperatures above 20°C (32). Wounds, from minute to severe cuts, occur routinely during harvest and bin-filling operations (15). The inoculation method used here, including severe wounding and holding inoculated tubers at temperatures above 20°C, closely approximates the natural infection conditions that exist when high levels of disease occur. Thus, it is noteworthy that cvs. Snowden, FL-1625, and FL-1867 appeared to have resistance to *P. ultimum*. These cultivars all had less incidence of leak infection, and there was limited tuber rot. Snowden has been reported to have some resistance to *Phytophthora infestans* (9,14). Hawkins and Harvey (14) found that cultivars in which cell walls are resistant to mechanical puncture also are resistant to leak; this characteristic should be explored in future studies involving resistance.

The relationship of incidence and severity in these two diseases, and the high correlation between incidence of infection and severity of leak (rot) with exceptions, may indicate that these traits are adequate for screening tuber resistance, with incidence being the easier and most rapid to assess. The nonsignificant correlation between incidence and severity of pink rot in russet and white cultivars should be interpreted with caution because our severity data may be due to one, two, or three infections per tuber, which can greatly affect disease severity but leave no effect on disease incidence. Future studies should address the effect of number of infection points on pink rot severity.

Our data also demonstrate that attention to cultural management practices used for leak and pink rot control is more important with some cultivars than it is with others. For example, based on our results of disease incidence, it is obvious that it is more difficult to manage pink rot in Russet Norkotah than it is in Russet Burbank. Potato growers have experienced the same trend and the use of mefenoxam-based fungicides tends to be higher on Russet Norkotah than for Russet Burbank for this reason (*unpublished data*). A central component of any disease management program typically involves the use of resistant cultivars. Cultivars that are less susceptible to tuber infection by *P. erythroseptica* and *Pythium ultimum* could play an important role in the integrated management of pink rot and leak in potato production fields until new resistant cultivars are developed. Highly susceptible cultivars should not be planted in fields with a history of occurrence of pink rot or leak. This would be a particularly important concern in fields with wet areas or fields that are irrigated frequently. Cultivars with some resistance might be planted, but complemented with other control measures such as the use of mefenoxam-based fungicides (23,38).

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Table 4. Combined analysis of variance of severity and incidence of leak caused by *Pythium ultimum* in 34 potato cultivars[a]

		Severity				Incidence			
Sources of variation	**DF**	**SS**	**MS**	***F* value**	***PR > F***	**SS**	**MS**	***F* value**	***PR > F***
Red cultivars									
Year (location)	2	1,328.53	664.26	…	…	4,440.32	2,220.16	…	…
Rep (year)	9	17.66	1.96			652.94	72.55	…	…
Cultivar[b]	6	592.68	98.78	2.85 NS	0.063	4,605.58	767.60	2.02 NS	0.148
Isolates[c]	1	293.72	293.72	5.39 NS	0.146	347.24	347.24	0.87 NS	0.450
Cultivar × isolate[d]	6	182.76	30.46	1.12 NS	0.413	1,082.69	180.45	0.70 NS	0.655
Year × cultivar	11	381.51	34.68	1.27 NS	0.349	4,174.26	379.48	1.47 NS	0.265
Year × isolate	2	108.96	54.48	…	…	801.12	400.56	…	…
Year × cultivar × isolate	11	300.22	27.93	…	…	2,831.80	257.44	…	…
Error	111	521.93	4.70	…	…	5,569.56	50.18	…	…
Total	159	3,899.44	…	…	…	25,125.90	…	…	…
Russet cultivars						…	…	…	…
Year (location)	2	1,915.71	957.85	…	…	26,527.51	13,263.76	…	…
Rep (year)	9	93.51	10.39	…	…	727.68	80.85	…	…
Cultivar[b]	6	898.67	149.78	5.32 **	0.013	4,089.04	681.51	1.74 NS	0.219
Isolates[c]	1	261.41	261.41	3.54 NS	0.201	4,629.55	4,629.55	3.61 NS	0.198
Cultivar × isolate[d]	6	567.60	94.60	6.40 **	0.007	2,844.59	474.10	2.36 NS	0.119
Year × cultivar	9	253.61	28.18	1.91 NS	0.175	3,529.29	392.14	1.96 NS	0.166
Year × isolate	2	147.72	73.86	…	…	2,567.71	1,283.86	…	…
Year × cultivar × isolate	9	133.02	14.78	…	…	1,804.42	200.49	…	…
Error	99	578.37	5.84	…	…	…	…	…	…
Total	143	5,397.97	…	…	…	…	…	…	…
White cultivars									
Year	2	3,702.22	1,851.11	…	…	36,007.65	18,003.82	…	…
Rep (year)	9	47.77	5.31	…	…	788.33	87.59	…	…
Cultivar[b]	19	6,357.77	334.62	4.99 **	0.001	121,984.14	6,420.22	6.51**	0.001
Isolates[c]	1	1,195.35	1,195.35	4.49 NS	0.168	2,121.85	2,121.85	3.47 NS	0.204
Cultivar × isolate[d]	18	466.08	25.89	0.81 NS	0.678	6,974.27	387.46	1.70 NS	0.102
Year × cultivar[d]	28	1,879.42	67.12	2.09 *	0.028	27,618.41	986.37	4.32 **	0.001
Year × isolate	2	532.57	266.29	…	…	1,223.89	611.95	…	…
Year × cultivar × isolate	28	898.44	32.09	…	…	6,393.54	228.34	…	…
Error	276	1,821.05	6.62	…	…	29,385.78	106.47	…	…
Total	383	18,230.09	…	…	…	246,998.27	…	…	…

[a] Values followed by: NS = nonsignificant at P = 0.05, * = significant at P =≤ 0.05, ** = significant and P =≤0.01.
[b] Significance tested using year × cultivar as an error term.
[c] Significance tested using year × isolate as an error term.
[d] Significance tested using year × cultivar*isolate as an error term.

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