Field Resistance to Potato Virus Y in Potato Assessed by Cluster Analysis

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ABSTRACT

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Forty potato cultivars tested for their responses to potato virus Y (PVY) at Fredericton, NB (1972–1983), were separated into five resistance groups by the Scott-Knott cluster analysis procedure. Susceptible groups A (52.1–60.4% infection) and B (35.4–47.5%) differed significantly from the moderately to highly resistant groups C (12.9–14.6%), D (4.6–9.6%), and E (0.0–2.5%) in a supplementary Duncan's multiple range test, which otherwise gave much overlapping. Mean disease readings for the different categories of cultivars retained the same relative order (A, B, C, D, E) during each year of the trial. By comparison with these five groups, 42 additional commercial cultivars and many seedlings present in the trials for 4–8 of the 12 yr could be classified. The "old" strain of PVY was used in these trials, whereas the official Dutch variety ratings are based on the "new" strain of this virus. Nevertheless, 11 cultivars common to the two lists are rated quite similarly. In the New Brunswick seed potato crop, incidence of mosaic (caused largely by PVY) increased as cultivars progressed during 5 yr from "Elite" status through Foundation seed to Certified seed. This increase was most pronounced in groups A and B, moderate in groups C and D, and virtually absent in the most resistant group, E. To reduce the reservoir of PVY in potato crops, susceptible cultivars, now widely grown, need to be replaced with PVY-resistant cultivars.

Resistance to the potato mosaic viruses, potato virus Y (PVY) and the related potato virus A (PVA), has been available for many years (2,5,14–16,19,20,24). Cultivars such as Katahdin and Kennebec carry resistance to both of these viruses and represent a significant portion of the crops grown in the northeastern seed-producing areas, Maine and Atlantic Canada. Nevertheless, large plantings of Russet Burbank and other susceptible cultivars continue to be grown to meet particular demands, and mosaic remains a problem.

Seed inspection services use meristem-tip culture and ELISA programs to provide a continuous supply of "virus-free" seed to state and provincial seed farms and thence to the growers. Stocks of susceptible cultivars already held by growers, however, are reservoirs for virus, which is transmitted by aphids to the new potato lines. The remedy is not seen as a simple substitution of resistant for susceptible cultivars but as one of the objectives in a major breeding program.

This report describes the assessment of resistance to PVY in different potato cultivars in trials where disease incidence was analyzed by the Scott-Knott cluster analysis (SKCA) procedure (21). This was done in association with the National Potato Breeding Program of Agriculture Canada to advise on parent selection and evaluate seedlings. Some comparisons were made with official Dutch variety lists and with performance in the New Brunswick seed potato crop. The nature of resistance and the consequences of replacing susceptible with resistant cultivars in the northeastern seed-growing areas are considered. A brief report has appeared previously (4).

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MATERIALS AND METHODS

Field trials. Seed tubers of the cultivars tested were obtained from the isolated New Brunswick substations at Alma (1968–1975) and Benton (1976–1983). This seed has consistently proven to be free of PVY. The cultivars were planted at Fredericton, NB, in 3-m-long single-row plots, 10 plants per plot, with each third row planted with PVY-infected tubers of the cultivar Red LaSoda. Two replicated but independently randomized blocks were used each year. Two border rows of the cultivar Russet Burbank were planted on each side of the field, and similarly, a 3-m buffer plot at each headland. Sufficient insecticide (carbofuran) was used to combat flea beetles and Colorado beetles, and fungicide (mancozeb) was used to control the late blight fungus. Spread of PVY by aphids was allowed to proceed naturally. In other trials, these pesticides had little effect on the spread of PVY. Plots were harvested by machine, using a distinctly colored cultivar (red or blue as required) as a marker in a 1-m space between plots. Ten tubers were taken at random from each plot and eye-indexed (a plant grown from one eye of each tuber for visual diagnosis) in the greenhouse during the winter months. Representative plants were tested with a differential host (*Nicotiana tabacum* 'Samsun') simultaneously inoculated with potato virus X (PVX) (3).

Analysis. Typically for the years 1972–1983, 60–100 commercial cultivars and 200–400 Fredericton seedlings (F seedlings, the first two digits denoting year of selection) were included in the trial. During this 12-yr period, a group of 40 cultivars was tested each year. For analysis, the results from eye-indexing the two 10-tuber samples of each cultivar were treated as a single 20-unit replicate. The original data were recorded as percentages of PVY-diseased plants in each 20-unit replicate and subjected to arc sine $\sqrt{x/100}$ transformation expressed in degrees (23) before analysis of variance (ANOVA). The SKCA procedure (21) was used to separate the cultivars into discrete groups. The cultivars were also compared by Duncan's multiple range test (DMRT). The possibility of using both SKCA and one of the traditional multiple-comparison procedures such as DMRT to compare and group means has been suggested by Madden et al (17).

RESULTS AND DISCUSSION

The 40 standards. With the SKCA ($P = 0.01$), the 40 cultivars were separated into five groups, A–E (Table 1). Despite the fact that the overall disease incidence varied from year to year, the mean for each group (transformed data) for any given year retained its relative position (A, B, C, D, E) without exception (Table 2). Groups A and B (highly susceptible and susceptible, respectively) were shown to be significantly more susceptible to PVY than groups C, D, and E (moderately resistant, resistant, and highly resistant, respectively) with DMRT ($P = 0.01$). Otherwise, DMRT splits our cultivars into three susceptible and five resistant groups with much overlapping.

Pedigrees of all 40 cultivars have been checked (25). Most of the American and Canadian cultivars in groups C, D, and E can be traced to Katahdin or one of its parents, USDA seedling 24642. Because of limited access to complex European breeding programs, we can only note that Surprise and Dorita are seedlings of Libertas (group D), and Parnassia, of Richter's Jubel (Table 3). The pedigrees of susceptible Canadian and American cultivars generally lack known resistant cultivars and often contain known susceptibles such as Bliss Triumph, Green

Mountain, or Early Rose.

Other cultivars. It has been possible to classify other cultivars that have been in the trials from 4 to 8 of the 12 yr, 1972–1983, though not necessarily in successive years. This could usually be done by empirical comparisons of the performance of the individual cultivar with means and limits of groups A–E for the specific years that the particular cultivar had been in the trial. Where the classification was not obvious from empirical comparisons, a separate SKCA was done of the five means plus any cultivars (other than those in Table 1) that appeared in a particular combination of years. Thus, 42 additional commercial cultivars were classified (Table 3). A large number of F seedlings has been similarly rated.

Dutch ratings. A number of cultivars grown in Europe were included in the trials for comparison with ratings such as those given in Dutch variety lists (22,27). Although we have used what would be described as PVY^{o} (old strain) and Dutch workers have used PVY^{n} (new strain), there is good correspondence. Our group A includes Eersteling (Dutch 4, very susceptible); group B, Bintje and Homeguard (Dutch 5, fairly susceptible) and Furore (Dutch 6, moderately susceptible); groups C and D, Dorita, Aquila, Libertas, and Richter's Jubel (Dutch 7, fairly resistant); and group E, Kennebec and Surprise (Dutch 8, highly resistant). In addition, the cultivar Dore (Dutch 2, extremely susceptible) was tested for 4 yr, during which time 45 of 80 plants became infected versus 42 of 80 for Eeersteling, the most susceptible cultivar among the 40 standards. This agreement with Dutch ratings does not necessarily mean that the different cultivars are equally susceptible to the two virus strains but that each would be expected to occupy relatively the same position when listed in order of resistance to either PVY^{o} or PVY^{n}.

Cultivar groups in New Brunswick seed crop. A further assessment was made of the five groupings based on performance of the cultivars in the New Brunswick commercial seed crop. Data from the New Brunswick Florida Tests of 1981, 1982, and 1983 was used, combining the 3 yr to obtain sufficient samples from each class of seed (Elite-1 (E-1), E-2, E-3, foundation, and certified). Within each seed class, the incidence of mosaic was calculated for each of the groups, A–E. We used "mosaic" plants in the Florida readings as a percentage of the total plants in samples of all cultivars within each group. Supplementary tests at Fredericton on samples from selected growers have demonstrated that this is a reasonably accurate estimate for PVY. Only a minor

Table 1. Forty potato cultivars, tested at Fredericton, NB (1972–1983), listed in order of susceptibility to potato virus Y and grouped by Scott-Knott cluster analysis and Duncan's multiple range test

Cultivar	Origin[w]	Percent infection[x]	Mean arc sine $\sqrt{x/100}$ [y]	Cluster analysis group[z]	Duncan's multiple range[z]
Eersteling	Br	60.4	51.22	A	a
Green Mountain	OAm	56.3	49.06	A	ab
Cariboo	Can	52.9	46.41	A	abc
Shepody	Can	52.1	46.26	A	abc
Russet Burbank	OAm	47.5	42.76	B	abc
Keswick	Can	40.4	39.28	B	bc
Irish Cobbler	OAm	42.1	38.69	B	bc
Acadia Russet	Can	39.2	38.03	B	bc
Bintje	Dut	38.8	37.40	B	bc
Red Pontiac	US	35.4	36.73	B	c
Dorita	Mex	14.6	21.22	C	d
Avon	Can	18.3	21.10	C	d
Saco	US	13.3	18.09	C	d
Raritan	Can	15.8	17.77	C	d
Belleisle	Can	11.7	16.63	C	de
F52047	Can	12.9	16.63	C	de
F63050	Can	12.9	15.27	C	def
Chinook	Can	9.6	13.43	D	defg
Penobscot	US	8.3	13.28	D	defg
F67128	Can	8.8	12.87	D	defg
Aquila	Ger	8.3	11.47	D	defgh
Tobique	Can	6.7	11.06	D	defgh
Libertas	Dut	8.3	10.66	D	defgh
F59045	Can	6.3	9.84	D	defgh
Huron	Can	5.8	9.34	D	defgh
Warba	US	5.4	9.26	D	defgh
Norland	US	4.2	8.82	D	defgh
F65089	Can	4.6	8.66	D	defgh
Parnassia	Dut	2.5	4.37	E	efgh
Abnaki	US	2.1	3.07	E	fgh
Sebago	US	1.7	2.98	E	fgh
F64041	Can	0.8	2.15	E	gh
Jemseg	Can	0.8	2.15	E	gh
Golden Chipper	US	0.8	1.54	E	gh
Kennebec	US	0.4	1.08	E	gh
Surprise	Dut	0.4	1.08	E	gh
Nipigon	Can	0.0	0.00	E	h
Katahdin	US	0.0	0.00	E	h
Chippewa	US	0.0	0.00	E	h
Canus	US	0.0	0.00	E	h

[w] Br = British, Can = Canadian, Dut = Dutch, Ger = German, Mex = Mexican, OAm = older American, and US = USDA or state breeding programs.
[x] Based on greenhouse eye-index test results of 240 sample tubers harvested from field exposure trials (12 yr × 20).
[y] Where x is the percentage of PVY-infected plants grown from each of twelve 20-tuber replicates.
[z] Significance level: $P = 0.01$.

Table 2. Annual mean (arc sine $\sqrt{x/100}$)[a] infection with potato virus Y (PVY) for cultivars of different resistance groups in field exposure trials at Fredericton, NB, 1972–1983

Resistance group[b]	Number of cultivars	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983
A	4	59.97	56.03	65.32	48.68	55.24	36.78	64.75	36.49	42.77	13.53	67.49	40.73
B	6	39.17	49.66	53.36	43.15	48.17	27.68	51.41	20.51	32.37	12.99	54.28	32.96
C	7	12.38	18.28	35.64	27.85	35.76	12.75	30.98	12.65	9.22	0.00	17.95	3.69
D	11	7.77	12.69	24.02	18.90	22.85	5.19	22.54	2.34	4.69	0.00	6.37	2.07
E	12	0.00	1.07	4.36	4.76	4.51	0.00	2.61	0.00	1.07	0.00	0.00	0.00

[a] Where x is the percentage of PVY-infected plants grown from one 20-tuber sample of each cultivar per year. Summation and averaging for the groups was done with transformed data.
[b] Group A cultivars = highly susceptible to PVY, B = susceptible, C = moderately resistant, D = resistant, and E = highly resistant. Separations based on Scott-Knott cluster analysis of the data for 12 yr.

fraction of this mosaic is due to PVA or PVX. The figures given in Table 4 are ratios, where the cultivar group and seed class with the highest percentage of infection (group A cultivars, certified seed) = 1.0. Although only group means are given, there were virtually no significant discrepancies in the performance of individual cultivars.

Virus-tested seed potatoes grown on the New Brunswick provincial seed farm are classed "Pre-elite." They become E-1 class seed after the initial commercial crop and move in successive years to the E-2, E-3, Foundation, and Certified classes provided they meet standards for the particular class. The Certified seed may be used only for table or processing crops, which are not represented in the Florida test and are not used further as seed. A steady increase in mosaic is observed each year in cultivars in susceptible groups A and B. This increase is not a simple accumulation of PVY infection but occurs despite rejections and roguing. The increase is less pronounced in cultivars in groups C and D but is virtually absent from those in group E. There are no known overwintering hosts for PVY in the northeastern seed-growing areas, so it is in commercial potato stocks that the reservoir of this virus exists. If the figures for groups A and B are projected another year into the table or processing crops, it is obvious that this is where the major reservoir of PVY lies.

Significance of resistance. In our trials, for every 100 PVY-infected plants among cultivars in group A, there were, by ratio, 73.3 in an equal number of plants representative of group B, 25.6 in group C, 12.5 in group D, and 1.4 in group E. Thus if cultivars from groups A and B were eliminated from a relatively large area and this reservoir of infection were removed, the virus would probably spread sufficiently to maintain itself in group C and D cultivars only in years of relatively intense spread, and in group E cultivars, probably not at all.

Plants of group E cultivars do occasionally become infected with PVY in commercial crops. We have seen eight PVY-diseased plants in a half hectare of Kennebec. Infections such as this, those that have occurred in our trials, and some that have been obtained by aphid transmission in the greenhouse were all under circumstances of heavy infection pressure. In commercial crops, this would amount to a heavy aphid movement from infected plants in a nearby crop of a susceptible cultivar. Such heavy aphid flights are probably a regular occurrence in some areas, as suggested by the field experiments of Jones and Vincent (14) and Corbett (10)—trials in which substantial percentages of Katahdin plants became infected. In the northeastern areas, infection pressures rarely approach this intensity, and the statement (1) that "one can traverse acre upon acre of fields of Katahdin or Kennebec in northern Maine and New Brunswick without finding a trace of PVY" is true in all but exceptional years. Even then, only an occasional infected plant will be found.

Nature of resistance. It has been suggested that the Katahdin-type resistance to PVY is due in part to a necrotic response (2,10,13). The virus with accompanying necrotic lesions may become systemic in younger plants, but localization occurs in older leaves (2,10). However, plants or leaves of susceptible cultivars also become more resistant to PVY as they mature (2,6,7), and localized necrotic lesions will result from inoculation of older leaves. There appears to be a differential response, but no comprehensive explanation of the resistance has been developed.

Young plants from infected tubers of Katahdin and other highly resistant cultivars develop weakly with necrotic lesions. Tubers from these plants are often so small that the infections are virtually self-eliminating. Thus, in addition to the resistance, we have an example of Vanderplank's "population immunity" (26). By contrast, plants of susceptible cultivars with secondary infections, though somewhat stunted, show largely mosaic symptoms and only moderately reduced tuber yield.

Effect of isolation. There was an influx of the vector-persistent potato leafroll virus (PLRV) into these PVY trial plots in the early 1970s. By contrast, during the entire 12 yr of this work, no more than an occasional infection with PVY (none in group E cultivars) has occurred in a separate PLRV trial plot protected only by about 600-m isolation. Whether it is due to brief retention by the aphid vector

Table 3. Potato cultivars tested at Fredericton, NB, for four to eight of the years 1972–1983 listed in order of susceptibility to potato virus Y, classified in five resistance groups in comparison with standards

Cultivar	Origin[a]	Years[b] (no.)
	Group A[c]	
Doré	Dut	4
Kerr's Pink	Br	4
Grand Falls	Can	6
Epicure	Br	4
	Group B	
Caribe	Can	8
La Rouge	US	4
Homeguard	Br	4
Furore	Dut	4
Red La Soda	US	5
La Chipper	US	4
Batoche	Can	8
	Group C	
Pungo	US	5
Chieftain	US	6
Russet Rural	OAm	5
Viking	US	5
Fundy	Can	7
Canso	Can	6
Earlaine	US	4
Profijt	Dut	7
York	Can	8
Cascade	US	7
	Group D	
Peconic	US	6
Teton	US	5
Pentland Ace	Br	7
Norchip	US	6
Belrus	US	4
Ontario	US	4
Onaway	US	4
Hunter	Can	8
Monona	US	5
Richter's Jubel	Ger	7
	Group E	
Reliance	US	7
Pennchip	US	6
Sequoia	US	8
Norchief	US	6
Wauseon	US	4
Cherokee	US	4
Tawa	US	5
Menominee	US	6
Norgleam	US	6
Sable	Can	7
Snowflake	US	8

[a] Br = British, Can = Canadian, Dut = Dutch, and US = USDA or state breeding programs.
[b] Number of years cultivar was on trial, not necessarily consecutive.
[c] Resistance groups: A = high susceptible, B = susceptible, C = moderately resistant, D = resistant, and E = highly resistant, based on comparisons with means for standard groups for specific years the cultivar was on trial.

Table 4. Relative incidence of mosaic disease (largely potato virus Y [PVY]) in potatoes of five seed certification classes, which are further separated into five groups of cultivars on the basis of resistance to PVY in the New Brunswick Florida seed potato test (1981–1983)

Cultivar resistance group[a]	Seed class[b]				
	E-1	E-2	E-3	Foundation	Certified
A	0.05[c] (18)[d]	0.10 (23)	0.20 (28)	0.30 (27)	1.00 (36)
B	0.05 (66)	0.08 (119)	0.21 (448)	0.25 (507)	0.46 (115)
C	0.03 (10)	0.02 (11)	0.06 (33)	0.10 (27)	···
D	0.00 (3)	0.00 (3)	0.02 (4)	0.01 (4)	···
E	0.00 (37)	0.00 (63)	0.00 (479)	0.01 (387)	0.00 (46)

[a] Group A = cultivars highly susceptible to PVY, B = susceptible, C = moderately resistant, D = resistant, E = highly resistant, as determined from field exposure trials at Fredericton, NB.
[b] Pre-elite seed from the provincial seed farm becomes elite-1 (E-1) when grown commercially for 1 yr, then drops one class each succeeding year, provided it continues to meet the class inspeciton standards.
[c] Mosaic incidence as a ratio, where group A cultivars, certified seed = 1.0.
[d] Number of fields sampled, 3 yr combined.

(8,9,12), a dispersal effect, or both, spread of PVY from field to field over any distance is limited. Nevertheless, what little does occur could account for initial infections in E-1 seed crops of susceptible cultivars, setting the stage for the annual increases we have observed (Table 4).

Relative resistance and immunity. In our trials, we wished to determine relative resistance to PVY under natural conditions and not simply screen out cultivars with some degree of susceptibility. Thus, we did not introduce infective aphids to increase infection pressure as some workers have done (16,20). We have not overlooked cultivars immune to PVY (and PVA) (11,18). Some of these are included in our trial (though not listed in Tables 1 and 3) and, as parents, in the breeding program. Artificially heavy infection pressure in confined cages, and grafting with infected scions will be used to confirm that certain of the seedling selections are immune.

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