

Sensitivity of Potato Cultivars to *Potato mop-top virus*-Induced Tuber Necrosis

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Abstract

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Potato (*Solanum tuberosum*) cultivars representing four market classes were assessed for sensitivity to *Potato mop-top virus* (PMTV)-induced tuber necrosis in three separate trials in a field in North Dakota known to be infested with PMTV. Reverse-transcription polymerase chain reaction confirmed the presence of PMTV in randomly selected samples. Results of tuber necrosis assessments conducted during storage demonstrated that sensitivity to PMTV-induced tuber necrosis among cultivars follows a continuum of tolerant to sensitive. As a group, the russet-skinned cultivars had a lower incidence of tuber necrosis than red-, yellow-, and white-skinned cultivars. The incidence and severity of PMTV-induced tuber necrosis in trial 1 were significantly correlated with those parameters in

trial 2 across years. Significant correlations also existed between the incidence of powdery scab on tubers and the incidence of PMTV-induced tuber necrosis in trial 1 across years. A significant correlation was also found between root gall numbers and powdery scab incidence and severity on tubers as well as PMTV-induced tuber necrosis incidence in trial 2. The results of this study provide growers with disease management options by avoiding cultivars highly sensitive to PMTV-induced tuber necrosis development and potentially replacing them with tolerant cultivars in the same market class. It is apparent from these studies that field assessments can be used for the development of PMTV-resistant germplasm for use in future breeding strategies.

The *Potato mop-top virus* (PMTV) causes serious economic losses in potato (*Solanum tuberosum* L.) production in affected countries (33,40,47,49). PMTV, the type member of the genus *Pomovirus* (29,57), is a rod-shaped, tripartite, single-stranded RNA virus (33,50–52,56). PMTV has been reported in northern and central Europe, Asia, and North and South America (2,7,23,24,26,27,31,32,38–40,45,62). In the United States, PMTV was first reported in Maine in 2003 (32), North Dakota in 2010 (16), Washington State in 2011 (14), Idaho in 2013 (61), and Colorado in 2014 (N. C. Gudmestad, unpublished).

PMTV is both seed- and soilborne. PMTV is vectored by *Spongospora subterranea* f. sp. *subterranea* (4,7), the causal agent of powdery scab in potato. PMTV has been reported to remain infective in a field after 18 years without potato (6), surviving in the resting spores of *S. subterranea* f. sp. *subterranea*, which themselves are also long lived. This clearly indicates that, when PMTV is present in a field, it cannot be eliminated through normal or even prolonged periods of crop rotation. PMTV infection is partially systemic and only a proportion of the progeny tubers from an infected plant carry the infection (8,15,30). This can lead to the elimination of the virus from potato crops after a few generations when the tubers are planted in soil free of PMTV and *S. subterranea* f. sp. *subterranea* (6,15,30,56). Unlike its vector, PMTV has a narrow host range, infecting members of only three families: namely, Solanaceae, Tetragoniaceae, and Chenopodiaceae (1,5,25). Humid soil and cool weather are conducive to PMTV because these conditions favor its vector (12,21,58,60). The success of PMTV transmission by *S. subterranea* f. sp. *subterranea* has been reported to be greatest at 12 to 20°C, while little or no infection occurs above 24°C (9).

Cultivar and environmental conditions greatly influence symptoms induced by PMTV (12,20). Symptoms of primary infection include brown-colored lines, arcs, and rings on the surface of the tubers or internal rusted arcs and flecks in the tuber flesh of sensitive cultivars (7,21,31). In secondary infections, tubers may show reticulate or deep cracks, blotchy surface markings, or distortions (7,21). The symptoms described above are similar to those induced by *Tobacco rattle virus* (TRV), both of which render affected tubers unmarketable.

The leaves of plants grown from infected tubers may show different shades of yellow markings which can easily be confused with leaf symptoms induced by *Alfalfa mosaic virus* and *Potato aucuba mosaic virus* (7). PMTV may cause shortening of internodes, which results in a dwarfed appearance (mop-top) (6). Virus-specific methods such as reverse-transcription polymerase chain reaction (RT-PCR), real-time RT-PCR, immunocapture RT-PCR, qualitative amplification based specific hybridization, RT-PCR-microplate hybridization, and enzyme-linked immunosorbent assay (ELISA) have been used for the detection of PMTV in potato (3,19,33,38,44,48,53,55). In the absence of suitable chemical treatments or other methods for effective control of *S. subterranea* f. sp. *subterranea* or PMTV, the most efficient measure for the prevention of this disease is avoidance; that is, to plant non-infected seed and avoid soils infested with virus-carrying *S. subterranea* f. sp. *subterranea* (35). However, ensuring that only disease-free potato seed are planted is difficult to achieve because PMTV is currently not tested or evaluated under seed certification regulations in the United States (17). Thus, genetic resistance remains the best option for the management of this disease once it has been introduced into a field or onto a farm. Field trials have been conducted to assess the sensitivity of potato cultivars to PMTV-induced tuber necrosis in Europe (6,11,31,39,40,46,47). Despite PMTV becoming more important in the United States, there has not been a detailed evaluation of potato cultivars for sensitivity to PMTV-induced tuber necrosis. The primary objective of this study was to screen some commonly grown U.S. potato cultivars for their reaction to tuber necrosis caused by PMTV to determine whether variability in symptom expression in tubers exists. To accomplish this, three cultivar trials were conducted in 2011, 2012, and 2013 in a potato field in North Dakota known to be infested with PMTV-carrying *S. subterranea* f. sp. *subterranea*.

Materials and Methods

Cultivar trial 1. Fourteen potato cultivars, consisting of seven russet-, three white-, three red-, and one yellow-skinned market types (Table 1), were evaluated for sensitivity to PMTV-induced tuber necrosis in a randomized complete block design with four replications in 2011 and 2012. Each replication consisted of 15 seed tubers per cultivar planted 0.3 m apart with potato spacers ('Russet Burbank') planted between cultivars. The potato spacers between replications were used to provide continuous ground cover to decrease variability in soil moisture and soil temperature which can affect *S. subterranea* f. sp. *subterranea* infection (58,60).

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Cultivar trial 2. Twenty-four cultivars of russet-, white-, red-, and yellow-skinned market types were planted in 2011 (Table 1). In 2012, due to unavailability of seed, ‘Puren’ and ‘Patagonia’ were not evaluated but five additional cultivars—‘Dakota Crisp’, ‘Dakota Pearl’, ‘Colorado Rose’, ‘Alturas’, and ‘Atlantic’—were included. In both years, a randomized complete block design with three replications was used. Each replication consisted of 5 and 10 seed tubers per cultivar in 2011 and 2012, respectively, planted in rows 0.3 m apart. To ensure ground cover, seed tuber spacers (Russet Burbank) were planted between cultivars.

Cultivar trial 3. Five white-skinned potato cultivars in addition to a tolerant internal control (‘Ivory Crisp’), previously included in trial 1 and trial 2 (Table 1), were evaluated for sensitivity to PMTV-induced tuber necrosis in a randomized complete block design with three replications in 2013. Each replication consisted of 10 seed tubers per cultivar planted 0.3 m apart. Seed tuber spacers (Russet Burbank) were planted between cultivars to ensure ground cover.

Seed tubers used in all trials were obtained from seed potato farms which were free of PMTV, as revealed by recent surveys. Each tuber was carefully examined during hand cutting to prepare seed for planting and none of them had *S. subterranea* f. sp. *subterranea* lesions or internal symptoms of tuber necrosis. All trials were conducted on a sandy loam soil. In 2011, the average air and soil temperatures of the experimental site during the growing season, as recorded by the North Dakota Agricultural Weather Network, were 18 and 19°C, respectively. The amount of rainfall during the growing season totaled 355.6 mm while sprinkler irrigation amounted to 95.3 mm. In 2012, the average air and soil temperatures were 15.6 and 17°C, respectively. A total of 518.2 mm of sprinkler irrigation was applied while rainfall amounted to 262.4 mm. In 2013, the average air and soil temperatures were 18.9 and 19°C, respectively. The amount of sprinkler irrigation applied was 355.6 mm while rainfall amounted to 176 mm. The amount of nitrogen applied was 110 kg/ha in

2011, 319 kg/ha in 2012, and 333 kg/ha in 2013. Each year, the herbicides pendimethalin and rimsulfuron were applied at the rates of 2.8 liters/ha and 105 g/ha, respectively. To control leafhoppers, green peach aphid, and Colorado potato beetles, insecticides such as thiamethoxam, imidachloprid, abamectin, and esfenvalerate were applied at rates recommended by manufacturers. Fungicides, including chlorothalonil, fluopyram/pyrimethanil, boscalid, and azoxystrobin, were applied to control early and late blight as appropriate for an irrigated commercial potato crop in the Upper Great Plains of the United States.

Root gall evaluation. Five plants were carefully removed 90 days after planting. Roots were gently shaken to release attached soil and galls were evaluated under a magnifying glass. Galls on roots were counted and expressed as number of galls per plant in accordance with the method used by Hernandez Maldonado (22). Data on root galls were collected for trials 1 and 2 in 2012 only.

Postharvest tuber sampling. After harvest, tubers were cured at a temperature of 10°C for 3 weeks and stored at 8 to 10°C thereafter. The tubers were evaluated three times for trial 1 and two times for trial 2 during storage for powdery scab infection on tubers and PMTV-induced tuber necrosis. For trial 1, evaluations were conducted 37, 117, and 204 days postharvest (DPH) in 2011 and 56, 167, and 214 DPH in 2012. For trial 2, evaluations were done 70 and 136 DPH and 126 and 190 DPH in 2011 and 2012, respectively. Tubers were evaluated twice in trial 3 for PMTV-induced tuber necrosis at 63 and 133 DPH. For each trial, a sample consisting of 100 tubers per cultivar and replication was taken at random and one-third (trial 1) or half (trials 2 and 3) of the tubers were graded at each evaluation. All harvested tubers were used when less than 100 tubers were available. In trial 1, 15,636 and 26,181 tubers were examined in 2011 and 2012, respectively. The total number of tubers examined in trial 2 was 1,975 and 3,834 in 2011 and 2012, respectively, while 1,254 tubers were examined in trial 3. This brings the total number of tubers evaluated for PMTV-induced tuber necrosis

Table 1. Potato cultivars evaluated in this study^z

Trial 1			Trial 2				Trial 3 2013		
Cultivar	Skin	Year	2011 Cultivars	2012 Cultivars	Skin	Year	Cultivar	Skin	Year
Russet Burbank	Russet	1914	Nicolet	Nicolet	White	2012	Nicolet	White	2012
Russet Norkotah	Russet	1987	Alpine Russet	Alpine Russet	Russet	2008	Snowden	White	1990
Ranger Russet	Russet	1991	Dakota Jewel	Dakota Jewel	Red	2004	Dakota Crisp	White	2005
Umatilla Russet	Russet	1998	Yagana	Yagana	Yellow	1983	Atlantic	White	1976
Alpine Russet	Russet	2008	Kennebec	Kennebec	White	1948	Ivory Crisp	White	2002
Bannock Russet	Russet	1999	Dark Red Norland	Dark Red Norland	Red	1957	Lamoka	White	2011
Dakota Trailblazer	Russet	2009	Puren	...	Yellow	1993
Ivory Crisp	White	2002	Snowden	Snowden	White	1990
Shepody	White	1980	Viking	Viking	Red	1963
Kennebec	White	1948	Red Pontiac	Red Pontiac	Red	1945
Yukon Gold	Yellow	1980	Yukon Gold	Yukon Gold	Yellow	1980
Red LaSoda	Red	1953	Red Norland	Red Norland	Red	1964
Red Pontiac	Red	1945	Lamoka	Lamoka	White	2011
Red Norland	Red	1964	Red LaSoda	Red LaSoda	Red	1953
...	Patagonia	...	Red	2009
...	Ivory Crisp	Ivory Crisp	White	2002
...	Ranger Russet	Ranger Russet	Russet	1991
...	Bannock Russet	Bannock Russet	Russet	1999
...	Russet Burbank	Russet Burbank	Russet	1914
...	Karu	Karu	Red	2002
...	Umatilla Russet	Umatilla Russet	Russet	1998
...	Russet Norkotah	Russet Norkotah	Russet	1987
...	Shepody	Shepody	White	1980
...	Dakota Trailblazer	Dakota Trailblazer	Russet	2009
...	Dakota Crisp	White	2005
...	Dakota Pearl	White	1999
...	Colorado Rose	Red	2000
...	Alturas	Russet	2002
...	Atlantic	White	1976

^z The same 14 potato cultivars were planted in 2011 and 2012 for trial 1. Skin = skin color and Year = year of release.

in this study to 48,880. PMTV incidence and severity index were determined using previously published protocols (40). Washed tubers were cut lengthwise into 1-cm-thick slices with a SafeHands Professional Mandolin slicer (Jaccard Corporation, NY). PMTV incidence was calculated as the number of tubers showing symptoms of PMTV-induced necrosis per the total number of tubers examined for each sample. The number of slices per tuber with internal necrosis was determined (a). The slice with the most severe necrosis was then covered with a mask of 1-cm-broad strips and the number of strips with necrosis was recorded (b). An index of PMTV severity was calculated by multiplying the two measurements (a × b) and expressing the values between 0 and 1, where 0 indicates no necrosis and 1 indicates the presence of necrosis throughout the tuber. Cultivars were ranked based on the overall incidence means of tuber necrosis according to the following categorization: tolerant = <5%, moderately tolerant = >5 to 10%, moderately sensitive = >10 to 15%, and sensitive = >15%. The overall incidence was calculated by adding the incidence of each cultivar for 2011 to that of 2012. Only cultivars planted in 2011 and 2012 were included in the classification.

Powdery scab on tubers was visually assessed and severity scored by comparing the area of tuber covered by disease with a modified graphic scale (18). An average percentage of the sample disease severity was calculated. Symptoms were confirmed by observation of cystosori under the microscope (×400) when required. Incidence was obtained by calculating the percentage of symptomatic tubers from the total number of tubers in the sample.

Detection of PMTV and TRV. Necrotic tissues were taken from slices of potato tubers with a sharp scalpel sterilized in 75% ethanol and flamed until red-hot between samples. The tissues were crushed in liquid nitrogen and stored at -80°C until used for RNA extraction. Total RNA was extracted using TRIzol reagent (Life Technologies,

Grand Island, NY) according to the manufacturer's instructions, with the exception that 0.8 ml was added to each tube for tissue homogenization instead of 1 ml. The RNA pellets were air dried for 5 to 10 min and, thereafter, the pellets were dissolved in 100 µl of RNase-free water. Detection of PMTV in tubers was done by RT-PCR according to a previously published protocol (38), with the only modification being the use of 0.2 µl of random primers (500 µg/ml) and 3.3 µl of RNase-free water instead of 1 and 2.5 µl, respectively. To further demonstrate that tuber necrosis was caused by PMTV, RNA from tuber extractions were also tested for TRV using RT-PCR according to Robinson (43). For trials 1 and 2, 150 and 200 randomly selected symptomatic tubers were tested for PMTV and TRV in 2011 and 2012, respectively, while 50 tubers were tested for trial 3.

Statistical analysis. Statistical analyses of the experimental data were carried out using the Statistical Analysis Software, version 9.3. Separate analyses of variance (ANOVA) were conducted on the percentage of data for incidence and severity of powdery scab and PMTV-induced tuber necrosis for each year due to nonhomogeneity of variance between years (Levene's test: $P < 0.000$) (36). In each trial, combined ANOVA analyses were carried out for data evaluated two or three times during storage because variances across evaluation periods were homogeneous (36). Residual plots of the percentage data sets (PMTV-induced tuber necrosis and powdery scab on tubers) as well as root gall data for trial 2 revealed that ANOVA could be performed without prior transformation because major assumptions were satisfied. Root gall number for trial 1 was square root transformed prior to ANOVA. Treatments were compared using the Fisher's protected least significant difference test at $P \leq 0.05$. The Pearson's correlation coefficient was calculated to demonstrate the degree of association between parameters. The calculation of correlations between trials involved the 14 cultivars common to trials 1 and 2 over a 2-year period.

Results

Susceptibility of potato cultivars to powdery scab infection. In trials 1 and 2, cultivars differed significantly ($P < 0.0001$) in susceptibility to root gall formation caused by *S. subterranea* f. sp. *subterranea*. In trial 1, the mean number of galls per plant ranged from 0.8 in 'Russet Norkotah' to 110.3 in 'Kennebec' (Table 2). 'Kennebec', 'Red Pontiac', 'Umatilla Russet', 'Red Norland', Ivory Crisp, and 'Shepody' were among the most susceptible cultivars while Russet Norkotah, 'Bannock Russet', and 'Yukon Gold' were among the least affected. In trial 2, the mean number of galls per plant ranged from 3.2 in 'Dakota Jewel' to 149.6 in 'Lamoka' (Table 2). Root gall formation was most severe in Lamoka, Kennebec, Red Pontiac, 'Snowden', and Shepody while Dakota Jewel, Russet Norkotah, 'Karu', 'Dakota Trailblazer', and Dakota Crisp were among the least affected.

In trials 1 and 2, powdery scab lesion incidence and severity on tubers differed significantly ($P < 0.0001$) in 2011 and 2012. In trial 1, the incidence of powdery scab lesions on tubers across cultivars was 0 to 47.5% while severity was 0 to 2.9% in 2011 (Table 3). In 2012, powdery scab lesion incidence on tubers was 0 to 57% while severity was 0 to 2.7% (Table 3). Powdery scab incidence and severity were highest in Shepody, 'Red LaSoda', Kennebec, and Ivory Crisp across years. As expected, powdery scab incidence and severity were lowest in the russet-skinned cultivars across years. Russet Norkotah and Bannock Russet did not have powdery scab lesions on tubers in 2011, as was observed in 'Alpine Russet' and Umatilla Russet in 2012. In trial 2, the incidence of powdery scab lesions on tubers ranged from 0% in several russet-skinned cultivars to 50.8% in Kennebec while severity was 0 to 0.7% in 2011 (Table 4). Kennebec, Shepody, Red LaSoda, and 'Viking' were among the cultivars with the highest incidence while Alpine Russet, 'Ranger Russet', Bannock Russet, Russet Burbank, Russet Norkotah, Umatilla Russet, and Dakota Trailblazer had no powdery scab lesions on tubers. In 2012, the incidence of powdery scab on tubers was 0 to 52.8% while severity was 0 to 3.5% (Table 4). Kennebec, Red LaSoda, Dakota Pearl, Shepody, and Red Pontiac were among the cultivars most susceptible to powdery scab lesion on tubers while Bannock

Table 2. Mean number of *Spongospora* galls per plant on potato roots 90 days after planting in trials 1 and 2 (2012 only)^z

Trial 1		Trial 2	
Cultivar	Galls	Cultivar	Galls
Kennebec	110.3 a	Lamoka	149.6 a
Red Pontiac	65.0 b	Kennebec	115.3 ab
Umatilla Russet	46.3 bc	Red Pontiac	77.8 bc
Red Norland	38.0 bcd	Snowden	76.0 bc
Ivory Crisp	36.6 cde	Shepody	64.2 bcd
Shepody	26.1 def	Nicolet	43.7 cd
Russet Burbank	14.8 efg	Red LaSoda	32.6 cd
Red LaSoda	12.5 fgh	Umatilla Russet	26.3 cd
Alpine Russet	10.0 fghi	Yagana	25.1 cd
Ranger Russet	3.4 ghij	Alpine Russet	22.4 cd
Dakota Trailblazer	2.5 ghij	Dakota Pearl	16.2 cd
Yukon Gold	2.3 hij	Russet Burbank	12.9 cd
Bannock Russet	1.7 ij	Colorado Rose	12.2 cd
Russet Norkotah	0.8 j	Ivory Crisp	12.1 cd
...	...	Viking	11.9 cd
...	...	Dark Red Norland	10.0 d
...	...	Alturas	9.5 d
...	...	Atlantic	9.1 d
...	...	Yukon Gold	8.5 d
...	...	Bannock Russet	8.1 d
...	...	Red Norland	6.3 d
...	...	Ranger Russet	5.8 d
...	...	Dakota Crisp	5.6 d
...	...	Dakota Trailblazer	4.1 d
...	...	Karu	3.5 d
...	...	Russet Norkotah	3.4 d
...	...	Dakota Jewel	3.2 d
LSD ($P = 0.05$)	25.8	...	66.0

^z Galls = mean number of root galls. Means with the same letter are not significantly different based on Fisher's protected least significant difference (LSD) ($P = 0.05$). Root gall numbers were square root transformed prior to analysis. Reported means are based on the untransformed data.

Russet, Russet Burbank, Umatilla Russet, and Dakota Trailblazer did not have lesions.

Sensitivity of potato cultivars to PMTV-induced tuber necrosis. Cultivar trial 1. PMTV-induced tuber necrosis incidence and severity differed significantly among cultivars ($P < 0.0001$) in both years. In

2011, incidence ranged from 0% in Bannock Russet to 5.2% in Red Norland, while severity indices ranged from 0 in Bannock Russet to over 0.1 in Red Norland (Table 5). In 2012, the incidence of PMTV-induced tuber necrosis ranged from over 0.3% in Bannock Russet to 17% in Red LaSoda while severity indices ranged from

Table 3. Mean incidence and severity of powdery scab caused by *Spongospora subterranea* f. sp. *subterranea* in 14 potato cultivars planted in 2011 and 2012 and evaluated three times during a 7-month storage period (trial 1)^z

Cultivar	Powdery scab on tubers			
	2011		2012	
	Incidence (%)	Severity (%)	Incidence (%)	Severity (%)
Shepody	47.5 a	2.9 a	50.6 a	1.3 bc
Red LaSoda	43.1 ab	1.4 b	57.0 a	2.7 a
Kennebec	37.7 bc	1.5 b	55.7 a	1.5 b
Ivory Crisp	32.4 cd	0.7 c	27.8 b	0.4 bcd
Red Pontiac	29.1 d	0.8 c	17.1 bcd	0.2 cd
Red Norland	16.3 e	0.2 cd	21.9 bc	0.2 cd
Yukon Gold	14.4 e	0.1 d	8.6 cde	0.1 d
Ranger Russet	1.3 f	>0.0* d	1.3 de	>0.0* d
Russet Burbank	0.6 f	>0.0* d	0.3 e	>0.0* d
Alpine Russet	0.2 f	>0.0* d	0.0 e	0.0 d
Umatilla Russet	0.2 f	>0.0* d	0.0 e	0.0 d
Dakota Trailblazer	0.2 f	>0.0* d	2.8 de	>0.0* d
Russet Norkotah	0.0 f	0.0 d	0.9 e	>0.0* d
Bannock Russet	0.0 f	0.0 d	0.9 e	>0.0* d
LSD($P = 0.05$)	7.8	0.6	15.9	1.1

^z Means with the same letter are not significantly different based on Fisher's protected least significant difference (LSD) ($P = 0.05$). An asterisk (*) indicates that severity of powdery scab is not a true zero because there were a few tubers with powdery scab lesions.

Table 4. Mean incidence and severity of powdery scab caused by *Spongospora subterranea* f. sp. *subterranea* in potato cultivars planted in 2011 and 2012 and evaluated twice during storage (trial 2)^z

Cultivar	Powdery scab on tubers			
	2011		2012	
	Incidence (%)	Severity (%)	Incidence (%)	Severity (%)
Kennebec	50.8 a	0.7 a	52.8 a	3.5 a
Shepody	24.1 b	0.2 bcd	35.1 b	1.5 c
Red LaSoda	21.8 bc	0.2 bc	51.4 a	2.6 b
Viking	20.4 bcd	0.3 b	21.5 cd	0.3 ef
Lamoka	14.1 bcde	0.1 bcd	16.5 cdef	0.2 ef
Yukon Gold	13.0 bcdef	0.2 bcd	7.1 fgh	0.1 f
Ivory Crisp	13.0 bcdef	0.1 cd	27.3 bc	0.8 cde
Puren	9.4 cdefg	>0.0* cd
Dakota Jewel	9.0 defg	0.1 bcd	6.2 fgh	0.1 f
Red Pontiac	7.4 efg	0.1 cd	37.0 b	1.1 cd
Yagana	6.4 efg	>0.0* cd	6.4 fgh	>0.0* f
Dark Red Norland	4.3 efg	0.1 bcd	9.4 efg	0.0 f
Nicolet	3.1 efg	>0.0* d	16.7 cdef	0.2 ef
Red Norland	3.0 efg	>0.0* d	20.7 cde	0.5 def
Karu	1.3 gf	>0.0* d	3.6 gh	>0.0* f
Patagonia	1.0 gf	>0.0* d
Snowden	0.6 gf	>0.0* d	4.1 gh	>0.0* f
Alpine Russet	0.0 g	0.0 d	0.7 h	>0.0* f
Ranger Russet	0.0 g	0.0 d	0.6 h	>0.0* f
Bannock Russet	0.0 g	0.0 d	0.0 h	0.0 f
Russet Burbank	0.0 g	0.0 d	0.0 h	0.0 f
Russet Norkotah	0.0 g	0.0 d	1.1 h	>0.0* f
Umatilla Russet	0.0 g	0.0 d	0.0 h	0.0 f
Dakota Trailblazer	0.0 g	0.0 d	0.0 h	0.0 f
Dakota Pearl	50.7 a	1.4 c
Dakota Crisp	20.4 cde	0.4 def
Colorado Rose	13.9 defg	0.3 ef
Atlantic	5.6 fgh	>0.0* f
Alturas	1.0 h	>0.0* f
LSD($P = 0.05$)	12.5	0.2	12.1	0.7

^z Means with the same letter are not significantly different based on Fisher's protected least significant difference (LSD) ($P = 0.05$). An asterisk (*) indicates that severity of powdery scab is not a true zero because there were a few tubers with powdery scab lesions.

0.002 in Bannock Russet to 0.14 in Red Pontiac (Table 5). There was a highly significant correlation between PMTV-induced tuber necrosis incidence and severity among cultivars in 2011 ($r = 0.97$, $P = 0.001$) and 2012 ($r = 0.66$, $P = 0.01$). The overall correlation between incidence and severity among cultivars across years was also significant ($r = 0.79$, $P = 0.001$). This means that cultivars with the highest incidence of PMTV-induced tuber necrosis also had the highest severity of the disease. Based on the 2-year results of PMTV-induced tuber necrosis incidence, the cultivars can be ranked as follows: tolerant = Bannock Russet, Dakota Trailblazer, Yukon Gold, Ivory Crisp, and Umatilla Russet (overall incidence of <5%); moderately tolerant = Ranger Russet, Alpine Russet, Russet Burbank, Red Pontiac, Russet Norkotah, and Shepody (overall incidence of >5 to 10%); moderately sensitive = Kennebec (13.8% overall incidence); and sensitive = Red Norland and Red LaSoda (overall incidence of 17.6 and 18.6%, respectively) (Table 6).

In 2011 and 2012, PMTV-induced tuber necrosis incidence increased significantly during storage ($P < 0.0001$). A significant interaction ($P < 0.0001$) was found between period of evaluation and cultivar in PMTV-induced tuber necrosis incidence. Generally, more PMTV-induced tuber necrosis symptoms were found in the second and third evaluations than the first. The highest increase in incidence occurred in Kennebec, Red Norland, Red LaSoda, Red Pontiac, and Shepody but remained unchanged in several cultivars. However, the severity of PMTV-induced tuber necrosis did not change during storage in 2011 ($P > 0.47$) but increased significantly ($P < 0.0001$) in 2012, with the highest increase occurring in Kennebec, Ranger Russet, Red LaSoda, Russet Norkotah, Red Norland, and Russet Burbank. The presence of PMTV was readily confirmed in randomly

selected symptomatic tubers by RT-PCR. TRV was not detected in any of tubers tested.

Cultivar trial 2. As with trial 1, the incidence of PMTV-induced tuber necrosis was low among cultivars in 2011; therefore, differences in incidence and severity were not statistically significant among cultivars (Table 7). However, in 2012, differences among cultivars in PMTV-induced tuber incidence and severity were highly significant ($P < 0.0001$). PMTV-induced tuber necrosis incidence ranged from 0% in Bannock Russet to 29.9% in Dakota Crisp while severity indices ranged from 0 in Bannock Russet to 0.49 in Lamoka (Table 7). Cultivars such as Dakota Jewel, Dakota Crisp, and 'Dark Red Norland' had significantly higher PMTV-induced necrosis incidence than both Red Norland and Red LaSoda while Bannock Russet, Umatilla Russet, Ivory Crisp, Russet Norkotah, Yukon Gold, and 'Nicolet' were among those least sensitive. There was no correlation between PMTV-induced tuber necrosis incidence and severity among cultivars in 2011 ($r = 0.24$, $P = 0.20$) and 2012 ($r = 0.49$, $P = 0.10$). However, the incidence of PMTV-induced tuber necrosis was significantly correlated with severity among cultivars across years ($r = 0.53$, $P = 0.05$). Based on the 2-year results of PMTV tuber necrosis incidence, the cultivars can be ranked as follows: tolerant = Bannock Russet, Dakota Trailblazer, Russet Norkotah, Umatilla Russet, Yukon Gold, Ivory Crisp, Russet Burbank, Karu, and Shepody (overall incidence of <5%); moderately tolerant = Viking, Red Pontiac, Red Norland, and Ranger Russet (overall incidence of >5 to 10%); moderately sensitive = Nicolet, Kennebec, and Red LaSoda (overall incidence of >10 to 15%); and sensitive = Alpine Russet, Snowden, Lamoka, Dakota Jewel, Dark Red Norland, and 'Yagana' (overall incidence of >15%) (Table 6).

Table 5. Mean incidence and severity index of *Potato mop-top virus* (PMTV)-induced tuber necrosis in 14 potato cultivars planted in 2011 and 2012 and evaluated three times during a 7-month storage period (trial 1)^z

Cultivar	PMTV tuber necrosis			
	2011		2012	
	Incidence (%)	Severity index	Incidence (%)	Severity index
Red Norland	5.2 a	0.10 a	12.4 b	0.10 bd
Red LaSoda	1.7 b	0.03 b	17.0 a	0.11 abc
Ranger Russet	0.9 bc	>0.0* bc	6.4 d	0.11 ab
Alpine Russet	0.5 bc	0.01 bc	5.5 de	0.11 abc
Kennebec	0.7 bc	>0.0* c	13.2 b	0.05 de
Yukon Gold	0.7 bc	>0.0* c	4.0 df	0.03 eg
Russet Burbank	0.4 bc	>0.0* bc	4.7 df	0.05 def
Ivory Crisp	0.4 bc	0.01 bc	2.9 efg	0.05 def
Red Pontiac	0.4 bc	0.02 bc	9.4 c	0.14 a
Russet Norkotah	0.4 bc	>0.00* c	5.7 d	0.06 cde
Dakota Trailblazer	0.2 c	>0.00* bc	0.5 g	>0.00* fg
Umatilla Russet	0.1 c	>0.00* c	2.3 fg	0.02 eg
Shepody	0.1 c	>0.00* bc	6.3 d	0.04 eg
Bannock Russet	0.0 c	0.00 c	0.3 g	>0.00* g
LSD($P = 0.05$)	1.41	0.03	2.68	0.05

^z Means with the same letter are not significantly different based on Fisher's protected least significant difference (LSD) ($P = 0.05$). Index is given as a value between 0 and 1, where 0 indicates no tuber necrosis and 1 presence of necrosis through the tuber. An asterisk (*) indicates that severity of PMTV-induced tuber necrosis is not a true zero because there were a few tubers with internal necrosis.

Table 6. Summary of sensitivity rankings of potato cultivars based on *Potato mop-top virus* (PMTV)-induced tuber necrosis incidence values summed for 2011 and 2012

Trial	Tolerant cultivars (overall incidence <5%)	Moderately tolerant cultivars (overall incidence >5 to 10%)	Moderately sensitive cultivars (overall incidence >10 to 15%)	Sensitive cultivars (Overall incidence >15%)
Trial 1	Bannock Russet, Dakota Trailblazer, Yukon Gold, Ivory Crisp and Umatilla Russet	Ranger Russet, Alpine Russet, Russet Burbank, Red Pontiac, Russet Norkotah and Shepody	Kennebec	Red Norland and Red LaSoda
Trial 2	Bannock Russet, Dakota Trailblazer, Russet Norkotah, Umatilla Russet, Yukon Gold, Ivory Crisp, Russet Burbank, Karu and Shepody	Viking, Red Pontiac, Red Norland and Ranger Russet	Nicolet, Kennebec and Red LaSoda	Alpine Russet, Snowden, Lamoka, Dakota Jewel, Dark Red Norland and Yagana

In 2011, PMTV-induced tuber necrosis incidence increased significantly ($P < 0.0001$) during storage. As noted in cultivar trial 1, a significant interaction ($P < 0.0002$) was found between time of evaluation and cultivar in PMTV tuber necrosis incidence. Generally, incidence was higher in the second evaluation than the first and cultivars such as Alpine Russet, Dakota Jewel, Kennebec, Nicolet, Puren, and Yagana had the highest increase. The severity of PMTV tuber necrosis did not change during storage ($P > 0.17$). In 2012, changes in PMTV tuber necrosis incidence ($P > 0.28$) and severity ($P > 0.67$) during storage were not significant. However, a significant interaction was found between the time of evaluation and cultivar ($P = 0.02$) in PMTV tuber necrosis incidence. A large decrease in incidence (25.8%) was observed in Dakota Jewel between the first and second evaluations but incidence increased in a number of cultivars such as Snowden, Red LaSoda, Alpine Russet, Red Norland, and Dark Red Norland during the same period. Presence of PMTV was confirmed in randomly selected symptomatic tubers by RT-PCR, and TRV was not detected in any of the tubers tested.

Cultivar trial 3. Significant differences ($P < 0.0001$) in PMTV-induced tuber necrosis incidence and severity were found among cultivars. PMTV tuber necrosis incidence ranged from 1.6% in Lamoka to 47% in Nicolet (Table 8). Dakota Crisp and Snowden had incidences of PMTV-induced tuber necrosis not significantly different

Table 7. Mean incidence and severity of *Potato mop-top virus* (PMTV)-induced tuber necrosis in potato cultivars planted in 2011 and 2012 and evaluated twice during storage (trial 2)^z

Cultivar	PMTV tuber necrosis			
	2011		2012	
	Incidence (%)	Severity index	Incidence (%)	Severity index
Nicolet	9.0	0.16	1.6 hi	>0.00* g
Alpine Russet	8.9	0.02	8.6 defgh	0.10 defg
Dakota Jewel	8.3	0.16	24.3 ab	0.27 c
Yagana	5.1	0.11	15.7 cd	0.30 bc
Kennebec	3.3	>0.00*	10.8 cdefg	0.03 g
Dark Red Norland	3.1	0.04	25.0 ab	0.18 cde
Puren	3.0	0.07
Snowden	2.2	0.06	13.9 cde	0.42 ab
Viking	2.1	0.18	6.3 efghi	0.08 efg
Red Pontiac	2.0	0.08	7.5 efghi	0.17 cdef
Yukon Gold	1.5	>0.00*	2.1 hi	>0.00* g
Red Norland	1.4	0.06	7.0 efghi	0.03 g
Lamoka	1.0	0.05	18.8 bc	0.49 a
Red LaSoda	0.1	0.02	12.4 cdef	0.05 efg
Patagonia	0.1	0.12
Ivory Crisp	>0.0*	>0.00*	1.5 hi	0.06 efg
Ranger Russet	0.0	0.00	5.8 efghi	0.05 efg
Bannock Russet	0.0	0.00	0.0 i	0.00 g
Russet Burbank	0.0	0.00	4.7 fghi	0.04 fg
Karu	0.0	0.00	3.6 ghi	0.04 efg
Umatilla Russet	0.0	0.00	0.5 hi	0.02 g
Russet Norkotah	0.0	0.00	0.9 hi	0.00* g
Shepody	0.0	0.00	3.6 ghi	0.06 efg
Dakota Trailblazer	0.0	0.00	0.8 hi	0.00* g
Dakota Crisp	29.9 a	0.23 cd
Dakota Pearl	11.5 cdefg	0.11 defg
Colorado Rose	7.0 efghi	0.01 g
Alturas	4.9 fghi	0.06 efg
Atlantic	4.4 fghi	0.02 g
LSD($P = 0.05$)	NS	NS	8.4	0.14

^z Means with the same letter are not significantly different based on Fisher's protected least significant difference (LSD) ($P = 0.05$). Index is given as a value between 0 and 1, where 0 indicates no tuber necrosis and 1 presence of necrosis through the tuber. An asterisk (*) indicates that incidence or severity of PMTV-induced tuber necrosis is not a true zero because there were a few tubers with internal necrosis. NS = no significance.

from that of Nicolet. The severity of PMTV-induced necrosis ranged from 0.007 in Lamoka to 0.66 in Nicolet. A very strong positive correlation ($r = 0.98$, $P = 0.001$) was found between PMTV-induced tuber necrosis incidence and severity. Changes in PMTV-induced tuber necrosis incidence ($P > 0.98$) and severity ($P > 0.99$) during storage were not statistically significant. PMTV was confirmed in randomly selected symptomatic tubers by RT-PCR but none tested positive for TRV.

Comparison between PMTV-induced tuber necrosis sensitivity trials. A significant correlation was found between trials 1 and 2 in 2011 for PMTV-induced tuber necrosis severity ($r = 0.60$, $P = 0.02$) but not incidence ($r = 0.09$, $P = 0.20$) using the data from the 14 potato cultivars common between the two trials. However, highly significant and strong correlations were observed in incidence ($r = 0.89$, $P = 0.001$) and severity ($r = 0.76$, $P = 0.001$) between trials 1 and 2 in 2012. Overall, PMTV-induced tuber necrosis incidence and severity in trial 1 were significantly correlated with those parameters in trial 2 across years ($r = 0.69$ and $P = 0.01$, respectively).

Relationship between powdery scab infection and PMTV-induced tuber necrosis. In trial 1, root gall number was significantly correlated with powdery scab incidence ($r = 0.51$, $P = 0.05$) but not severity ($r = 0.41$, $P = 0.20$) on tubers. There was no correlation between root gall number and PMTV-induced tuber necrosis incidence ($r = 0.45$, $P = 0.20$) or severity ($r = 0.16$, $P = 0.20$). A significant correlation ($r = 0.62$, $P = 0.02$) was found between powdery scab incidence on tubers and PMTV-induced tuber necrosis incidence across years. However, there was no correlation ($r = 0.14$, $P = 0.20$) between powdery scab severity on tubers and PMTV-induced tuber necrosis severity across years.

In trial 2, root gall number was significantly correlated with incidence ($r = 0.76$, $P = 0.01$) and severity ($r = 0.81$, $P = 0.001$) of powdery scab on tubers. Root gall number was also significantly correlated with PMTV-induced tuber necrosis incidence ($r = 0.54$, $P = 0.05$) but not severity ($r = 0.45$, $P = 0.20$). There was no correlation between powdery scab incidence and PMTV-induced tuber necrosis incidence ($r = 0.48$, $P = 0.10$) or severity ($r = 0.17$, $P = 0.20$) across years.

Discussion

This is the first study evaluating potato cultivars for sensitivity to PMTV-induced tuber necrosis conducted in the United States or North America, although some North American cultivars were evaluated previously under South American conditions (54). This study was prompted by the increasing importance of PMTV in North America, which poses a serious economic threat to growers. The results obtained in this study demonstrate the existence of a continuum of sensitivity to PMTV-induced tuber necrosis among commonly grown North American potato cultivars from tolerant to sensitive. Therefore, potato growers have the option of replacing cultivars highly sensitive to the development of PMTV-induced tuber

Table 8. Mean incidence and severity of *Potato mop-top virus* (PMTV)-induced tuber necrosis in six white-skinned potato cultivars planted in 2013 and evaluated two times during storage (trial 3)^z

Cultivar	PMTV tuber necrosis	
	Incidence (%)	Severity index
Nicolet	47.0 a	0.66 a
Snowden	42.0 a	0.41 a
Dakota Crisp	36.4 a	0.41 a
Atlantic	10.0 b	0.03 b
Ivory Crisp	9.4 b	0.13 b
Lamoka	1.6 b	>0.00* b
LSD(0.05)	10.9	0.18

^z Means with the same letter are not significantly different based on Fisher's protected least significant difference (LSD) ($P = 0.05$). Index is given as a value between 0 and 1, where 0 indicates no tuber necrosis and 1 presence of necrosis through the tuber. An asterisk (*) indicates that incidence or severity of PMTV-induced tuber necrosis is not a true zero because there were a few tubers with internal necrosis.

necrosis with tolerant ones in the same market class in production areas where PMTV exists. The identification of cultivars tolerant to PMTV-induced tuber necrosis also provides breeders with useful information for future breeding strategies.

In our study, we made no attempt to ascertain whether the absence of tuber necrosis was due to resistance to PMTV infection or resistance to the expression of tuber necrosis. The results were based on disease response of plants. The occurrence of asymptomatic PMTV infections in tubers has been reported by many researchers (11,33,49,53). The possibility of latent infections occurring means that incidence of PMTV infection among the cultivars could be higher than what has been reported based on tuber necrosis expression. Investigations to reveal the extent of symptomless infection were beyond the scope of this study and are the focus of future research.

The overall significant correlations ($r = 0.69$, $P = 0.01$) in both incidence and severity of PMTV-induced tuber necrosis between trial 1 and trial 2 demonstrate that levels of sensitivity among cultivars in 2011 and 2012 were consistent, an indication of the reliability and reproducibility of the results reported in this study. This evidence demonstrates that field trials can be used to effectively evaluate potato cultivars for sensitivity to PMTV tuber necrosis under North American conditions. The results also show some level of seasonal variation in PMTV tuber necrosis incidence across cultivars even though the ranking of cultivars within a particular season changed very little. Generally, the incidence of PMTV tuber necrosis increased from 2011 through 2013. Due to the low levels of PMTV tuber necrosis incidence observed in 2011, more water was applied via irrigation in 2012 and 2013 than 2011 in order to increase *S. subterranea* f. sp. *subterranea* infection. Therefore, the low incidence in 2011 could be due to the low frequency of irrigation applied in late summer, which is the practice among some growers in an attempt to reduce pink rot (caused by *Phytophthora erythroseptica* Pethybr.) disease pressure. Seasonal variability in PMTV infection among cultivars has also been observed in previous studies (11,53). The occurrence of seasonal variation in PMTV tuber necrosis emphasizes the importance of multiyear assessments for cultivar classification (40,49). Even though the cultivar classification reported in this article is based on the results of trials conducted over two growing seasons, the data offer valuable information upon which future work in this area could be built.

Despite the fact that trial 3 of this study was conducted in only one year (2013), all the cultivars evaluated in this trial were evaluated at least once in trial 2, and the high PMTV tuber necrosis incidence observed in three of the six cultivars tested in trial 3 made its inclusion in this report appropriate. Furthermore, the inclusion of trial 3 offered the opportunity to confirm the high incidence of tuber necrosis observed in Dakota Crisp in 2012 because this cultivar was not evaluated in 2011.

PMTV tuber necrosis incidence (and severity, to some extent) increased more in sensitive cultivars during storage. The most notable exception of a sensitive cultivar which had a large decrease in incidence between the first and second evaluations is Dakota Jewel in trial 2 (2012). A large decrease in PMTV tuber necrosis during storage was recorded in 'Saturna' (39,40), widely regarded to be one of the cultivars most sensitive to tuber necrosis in the Nordic countries (31,46,49). The reasons for the disappearance of tuber necrosis remain unknown but reabsorption of the brown color by the tuber has been implicated (40).

Because PMTV is vectored by *S. subterranea* f. sp. *subterranea*, susceptibility of cultivars to powdery scab at root and tuber phases was also evaluated. The results demonstrated significant variability in susceptibility to root gall formation (34) and powdery scab on tubers among cultivars. Generally, the russet-skinned cultivars were less susceptible than the red-, white-, and yellow-skinned cultivars to powdery scab infection on tubers (42) but susceptibility to root gall formation did not appear to be associated with skin color. The absence of overall correlation ($r = 0.48$, $P = 0.2$) between incidence of powdery scab on tubers and incidence of PMTV-induced tuber necrosis in trial 2 is consistent with previously published results (13,30,37,41,47,54). However, in trial 1, the strong overall correlation

($r = 0.62$, $P = 0.02$) found between incidence of powdery scab on tubers and PMTV tuber necrosis incidence contradict the reports cited above. A study conducted in Scotland to investigate the transmission of PMTV from infected seed tubers to daughter plants found statistically significant correlations ($r = 0.48$ and 0.61 in 2004 and 2005, respectively) between the incidence of PMTV and powdery scab for those crops in which both PMTV and powdery scab were present (15). The low or complete absence of correlation between powdery scab on tubers and PMTV infection has been attributed to differences in the optimal environmental conditions required by *S. subterranea* f. sp. *subterranea* and PMTV (9,10) and the fact that *S. subterranea* f. sp. *subterranea* infection of other parts of the potato plant such as roots and stolons also causes PMTV transmission (10,15,28,49). However, in the present study, it is likely that the strong correlation between powdery scab on tubers and PMTV-induced tuber necrosis is due to the fact that 50% of the cultivars evaluated were russet-skinned and not very sensitive to either disease.

The results reported in the present study indicate statistically significant correlations between root gall formation and powdery scab on tubers in trials 1 and 2 as well as PMTV tuber necrosis in trial 2. The strongest correlation occurred between root gall formation and powdery scab incidence and severity ($r = 0.76$, $P = 0.01$ and $r = 0.81$, $P = 0.001$, respectively) in trial 2. While the low correlation found between root gall formation and powdery scab as well as PMTV tuber necrosis supports the findings of other workers (9,59), the very strong association between powdery scab and root gall numbers in trial 2 contradicts the report of Van de Graaf et al. (59), who noted that the optimum temperature range required for *S. subterranea* f. sp. *subterranea* infection of roots is higher than the 12 to 15°C required for tuber phase infection. The work of Van de Graaf et al. (59) and Carnegie et al. (9) was carried out under constant (controlled) conditions whereas our work was done in the field, where temperature fluctuates day and night during the growing season, and this could explain differences in results.

It is evident from the results that russet-skinned cultivars were the least susceptible to powdery scab lesions on tubers, and this appeared to be associated with low sensitivity to PMTV-induced tuber necrosis. In contrast, many russet-skinned cultivars were susceptible to root gall formation. It is interesting to note that cultivars such as Dakota Crisp, Dakota Jewel, Dark Red Norland, and Red Norland, which were sensitive to both PMTV-induced tuber necrosis and powdery scab infection on tubers, had low levels of *S. subterranea* f. sp. *subterranea* root infection. These data, therefore, suggest that powdery scab infection on tubers is better linked with and may be more important in leading to PMTV-induced necrosis expression in tubers than the presence of root galls. Here again, we did not investigate symptomless infection by *S. subterranea* f. sp. *subterranea* on roots or on tubers but this will be the focus of future studies.

In this study, we found that, among the commonly grown potato cultivars in the United States, the russet-skinned cultivars, in comparison with red-, yellow-, and white-skinned cultivars, are not only less susceptible to powdery scab infection on tubers but also are less sensitive to PMTV-induced tuber necrosis. Differences in sensitivity to PMTV-induced tuber necrosis found among cultivars confirms the idea that natural variability exists in North American potato cultivars, which could provide economic relief to potato producers affected by this disease. Potato growers now have the option to plant less-sensitive cultivars in the same market class, especially in areas with a history of *S. subterranea* f. sp. *subterranea* and PMTV. Cultivars found to be tolerant to the tuber necrosis phase of PMTV can also be utilized in future breeding programs. The results of this and other studies indicate that soils in parts of the United States are already infested with powdery scab and PMTV in some cases. It is important that a comprehensive survey be conducted to assess the extent of infestation of these two pathogens in the United States. By using harmonized sampling and virus detection procedures, joint PMTV surveys involving 10 countries in Northern Europe were carried out from 2005 to 2008 (49). The experience gained through this project will be useful for planning the surveys in North America. Strict seed surveillance measures need to be put in place to help prevent

infestation of disease-free soils. In addition, the evaluation of cultivars for sensitivity should be expanded to cover more cultivars and other germplasm, including advanced breeding materials. Furthermore, the extent of latent infections in cultivars should be investigated through techniques such as RT-PCR or ELISA.

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