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Sensitivity to Tuber Necrosis Caused by *Potato Mop-Top Virus* in Advanced Potato (*Solanum tuberosum* L.) Breeding Selections

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Abstract *Potato mop-top virus* (PMTV) is transmitted by the powdery scab pathogen (*Spongospora subterranea* f.sp. *subterranea* (Sss)) and no effective disease control methods are currently available for either pathogen. Eighty-one advanced breeding selections of potato (*Solanum tuberosum* L.) from different market classes and a broad genetic base were evaluated for sensitivity to PMTV-induced tuber necrosis in a field in North Dakota known to be infested with PMTV. Commercial cultivars, ranging from sensitive to tolerant in their reaction to PMTV-induced tuber necrosis incidence were included in each market class as internal controls. Results of tuber assessments revealed high variability in PMTV-induced tuber necrosis incidence and severity among selections. Based on PMTV-induced tuber necrosis incidence results over a two-year period, a total of 17 advanced selections were found to be tolerant, nine - moderately tolerant, eight - moderately sensitive, and six were found to be sensitive. The russet-skinned types had lower tuber necrosis incidence than the red-, white- and yellow-skinned types. Increases in the incidence of PMTV tuber necrosis during the storage period was influenced significantly by selection type and skin-color. Further studies are needed to investigate if tolerant selections are resistant to the virus to determine their suitability as parents in breeding programs to introduce PMTV resistance into commercial potato cultivars. In the short term, tolerant selections with other desirable agronomic characteristics could be released as commercial cultivars for growers to utilize as a means to limit the economic impact of PMTV-induced tuber necrosis.

Resumen El virus de trapeador de la papa (potato mop top virus, PMTV) se transmite por el patógeno de la roña polvorienta (*Spongospora subterránea* f. sp. *subterránea* (Sss)) y no hay métodos efectivos disponibles actualmente de control de las enfermedades para cualquiera de estos patógenos. Se evaluaron 81 selecciones avanzadas de papa (*Solanum tuberosum* L.) de diferentes tipos de mercado y de una amplia base genética, para la sensibilidad de la necrosis de tubérculo inducida por PMTV, en un campo en Dakota del Norte que se sabe que esta infestado con PMTV. Las variedades comerciales, comprendidas desde sensibles a tolerantes en su reacción a la incidencia de la necrosis del tubérculo inducida por el PMTV, se incluyeron en cada clase de mercado como testigos internos. Los resultados en las evaluaciones de tubérculo revelaron alta variabilidad en la incidencia de la necrosis del tubérculo inducida por el PMTV y en la severidad entre selecciones. Con base a los resultados de la incidencia de la necrosis del tubérculo en un período de dos años, se encontraron un total de 17 selecciones avanzadas que fueron tolerantes, nueve moderadamente tolerantes, ocho moderadamente sensibles y seis susceptibles. Las de piel tipo russet tuvieron incidencia más baja de necrosis de tubérculo que las de tipo de piel roja, blanca y amarilla. El incremento en la incidencia de la necrosis de tubérculo por PMTV durante el período de almacenamiento fue influenciado significativamente por el tipo de selección y por el color de la piel. Se necesitan más estudios para determinar si las selecciones tolerantes son resistentes al virus, para decidir si pueden utilizarse como progenitores en programas de mejoramiento para introducir la resistencia a PMTV a variedades comerciales de papa. En el corto plazo, las

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selecciones tolerantes con otras características agronómicas deseables pudieran liberarse como variedades comerciales, para que las usen los productores como un medio para limitar el impacto económico de la necrosis del tubérculo inducida por PMTV.

Keywords Potato mop top virus · Powdery scab · Tuber necrosis · Cultivar sensitivity

Introduction

Potato mop-top virus (PMTV), the type member of the genus *Pomovirus*, is seed- and soil-borne, and has straight tubular, rod-shaped particles (Torrance and Mayo 1997; Sokmen et al. 1998). PMTV has a tripartite genome consisting of three single-stranded, positive sense RNA molecules (Scott et al. 1994; Torrance et al. 1999). PMTV is a serious pathogen of potato and can cause significant economic losses in sensitive potato cultivars (Harrison and Jones 1970; Sandgren et al. 2002) and is believed to have originated from the Andean region of South America (Hinostroza and French 1972; Salazar and Jones 1975; Tenorio et al. 2006). PMTV has been recognized as a threat to potato production in Northern Europe, Asia, South and North America (Calvert and Harrison 1966; Crosslin 2011; David et al. 2010; Harrison et al. 1997; Lambert et al. 2003; Latvala-Kilby et al. 2009; Mallik and Gudmestad 2015; Wale 2000; Whitworth and Crosslin 2013; Xu et al. 2004). PMTV is vectored by *Spongospora subterranea* f.sp. *subterranea* (Sss) (Arif et al. 1995; Calvert and Harrison 1966; Harrison and Jones 1970; Jones and Harrison 1969), a fungal-like organism that causes powdery scab on potato. Cool temperature and high soil moisture enhance infection with Sss by favoring germination and movement of zoospores (Merz 2008; Sandgren et al. 2002). PMTV survives in the resting cystosori of Sss which can persist in the soil for many years (Jones and Harrison 1972), making eradication of PMTV from an infested field difficult, if not impossible. Field to field spread of PMTV occurs through infected seed and movement of virus-carrying cystosori of Sss attached to seed tubers or in adhering soil (Sandgren et al. 2002). Typical primary symptoms of PMTV infection include brown arcs and rings in the flesh of tubers (Calvert and Harrison 1966; Harrison and Jones 1971) and are sometimes visible on the tuber surface (Jeffries 1998). Symptoms induced when PMTV-infected tubers are planted include misshapen or deep cracks on tubers (Calvert 1968; Tenorio et al. 2006) and foliar symptoms such as mottling, shortening of internodes and yellow blotches or rings (Xu et al. 2004). Foliar symptoms are strongly affected by prevailing environmental conditions (Calvert 1968; Carnegie et al. 2010). Tuber symptoms render affected tubers unsuitable for processing or consumption (Carnegie et al. 2012).

Genetic resistance remains the best option for the management of PMTV once it has been introduced into a field or onto a farm. Field trials have been conducted to assess the susceptibility/sensitivity of potato cultivars to PMTV-induced tuber necrosis in Europe (Calvert 1968; Carnegie et al. 2009; Kurppa 1989; Nielsen and Molgaard 1997; Sandgren et al. 2002), North America (Domfeh et al. 2015) and in the Andean Region of South America (Tenorio et al. 2006). Results of these trials suggest that natural variability exists in potato germplasm in susceptibility/sensitivity to PMTV infection. With recent reports of PMTV occurring in many parts of USA (Crosslin 2011; David et al. 2010; Lambert et al. 2003; Mallik and Gudmestad 2015; Whitworth and Crosslin 2013; Xu et al. 2004), it has become important to screen a wide range of potato germplasm for their reaction to PMTV infection. The primary objective of this study was to screen some North and South American advanced potato breeding selections for their reaction to tuber necrosis caused by PMTV. To accomplish this, a trial was conducted in 2011 and 2012 in a potato field in North Dakota known to be infested with PMTV-carrying Sss.

Materials and Methods

Sixty-four advanced breeding selections made up of 14 russet-, 19 white-, 21 red- and 10 yellow-skinned market types were planted in 2011 (Table 1). In 2012, 23 russet-, 12 white-, 17 red- and 5 yellow-skinned genotypes were planted (Table 1). Due to unavailability of seed of some breeding selections that were dropped from further evaluation, a number of clones across all skin-types planted in 2011 were not planted in 2012 but additional clones were included in 2012 (Table 1). A total of 91 potato genotypes were evaluated and of these, 10 were commercial cultivars included as internal controls. Fifty genotypes were tested in both years. The majority of the genotypes evaluated for PMTV tuber necrosis sensitivity were obtained from the North Dakota State University (NDSU) potato breeding program from genetic material that the program evaluates on an annual basis. Clones beginning with ND, CO, W, NY, A, and O belong to the potato breeding programs of North Dakota, Colorado, Wisconsin, New York (Cornell), Idaho (USDA-ARS, Aberdeen) and Oregon, respectively. "AOND", "AND", and "ATND" clones were bred and selected through collaborations among the potato breeding programs of Idaho, Oregon, North Dakota and Texas. Clones that start with RC, RG, RA, R, RK, SPA and T (T10-12) originated from the INIA-Remehue National Potato Breeding Program of Chile. Internal controls, consisting of commercial cultivars with known reactions to PMTV induced tuber necrosis ranging from sensitive to tolerant (Domfeh et al. 2015) were used in all field trials. For the russet-skinned genotypes, cvs. Alpine Russet (sensitive), Ranger

Table 1 Advanced breeding selections planted in 2011 and 2012

Red-skinned selections[a]	Russet-skinned selections[a]	White-skinned selections[a]	Yellow-skinned selections[a]
AND00272-1R	AND00618-1RussY[d]	ND060835C-4	R87009-28
ATND98459-1RY	AND01804-3Russ	ND6956b-13	R91007-5
ND060728-5R	AND97279-5Russ[d]	ND7519-1	RA517-123
ND4659-5R	AND99362B-1Russ[d]	ND7550C-1	RC06-109
ND8314-1R	AOND95292-3Russ[d]	ND8229-3[d]	RK24-48[d]
ND8555-8R[b]	ND039194AB-1Russ[d]	ND8304-2	RA82-4[c]
R90070-8	ND049289-1Russ	ND8305-1[d]	RA362-54[c]
R90096-5[d]	ND049381C-2Russ[d]	ND8307C-3	RA519-50[c]
R91129-11	ND049423b-1Russ	ND8331Cb-2	R89045-35[c]
RA20-6	ND049517B-1Russ[d]	ND8331Cb-3	RA148-48[c]
RA89044-45	ND049546b-10Russ	ND8559-20	RA16-5[c]
RA90213-60	ND050082Cb-2Russ	RA151-24	Yukon Gold
RC72-35	ND050105C-1Russ	ND060601CAB-2[c]	Yagana
RC89-25[d]	ND060735-3Russ[d]	ND060715B-15 i	
RG47-3[d]	ND060742C-1Russ	ND060847CB-1[c]	
SPA161	ND060761B-3Russ[d]	MLS-292A[c]	
T10-12	ND060766b-4Russ	CO95051-7 W[c]	
R90134-6[c]	ND060770B-5Russ[d]	R65A-70[c]	
ND050167C-3R[c]	ND060796AB-1Russ	W2717-5[c]	
R90213-60[c]	ND070927-2Russ[d]	NY-138[c]	
ND8058-11[c]	ND6400C-1Russ	NY-139[c]	
ND028842b-1RY[c]	ND8068-5Russ	Ivory Crisp	
ND060733b-4RY[c]	ND8413-7Russ	Kennebec	
R90160-5[c]	ND8229-3[b,c]	Lamoka	
Dakota Jewel	ND060796AB-1Russ[c]		
Red Pontiac	Bannock Russet		
	Alpine Russet		
	Ranger Russet		

[a] Commercial cultivars Dakota Jewel, Red Pontiac, Bannock Russet, Alpine Russet, Ranger Russet, Ivory Crisp, Kennebec, Lamoka, Yukon Gold and Yagana were included as internal controls. These cultivars range from tolerant to sensitive in their reaction to PMTV-induced tuber necrosis incidence (Domfeh et al. 2015)

[b] ND8229-3 was released in 2012 as Dakota Russet; ND8555-8R was released in 2014 as Dakota Ruby

[c] Selections were planted in 2011 only

[d] Selections were planted in 2012 only

Russet (moderately tolerant) and Bannock Russet (tolerant) were included. Among the white-skinned genotypes, cvs. Lamoka (sensitive), Kennebec (moderately sensitive) and Ivory Crisp (tolerant) were used. With the red-skinned clones, cvs. Dakota Jewel (sensitive) and Red Pontiac (moderately tolerant) were included. Cultivars Yagana (sensitive) and Yukon Gold (tolerant) served as internal controls for the yellow-skinned genotypes. In both years, a randomized complete block design with three replications was used. Each replication consisted of 5 seed pieces per selection planted in 2011 and 10 seed pieces in 2012 in rows 0.3 m apart. To ensure ground cover, seed tuber spacers (cv. Russet Burbank) were planted between cultivars. The trial was conducted on a sandy loam soil with approximately 3.0 % organic matter.

Seed tubers used in this trial were obtained from seed potato farms which were free of PMTV as revealed by recent surveys (Gudmestad, unpublished). During the survey, soil was collected from seed farms and assayed using *Nicotiana debneyi* as bait plants which were subsequently tested by reverse transcription polymerase chain reaction (RT-PCR). Each seed tuber was also carefully examined during hand-cutting to prepare seed for planting and none of them had Sss lesions or internal symptoms of tuber necrosis. 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 (NDAWN) were 18 °C 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 °C and 17 °C, respectively. A total of 518.2 mm of sprinkler irrigation was applied, while rainfall amounted to 262.4 mm. Each year, the herbicides pendimethalin and rimsulfuron were applied at the rate of 2.8 l/ha and 105 g/ha respectively. To control leafhoppers, green peach aphid and Colorado potato beetles, insecticides such as thiamethoxam, imidacloprid, 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 USA. The 2011 and 2012 field trials were planted on 24-25th May and 30th April; and harvested on 5th October and 5th September, respectively.

Post-Harvest Tuber Sampling After harvest, tubers were cured at a temperature of 10 °C for three weeks and stored at 8 - 10 °C thereafter. The tubers were evaluated twice during storage for PMTV-induced tuber necrosis. Evaluations were performed at 70 and 136; 126 and 190 days post-harvest in 2011 and 2012, respectively. Samples consisting of 100 tubers per clone and replicates were taken at random and half of the tubers were graded at each evaluation date. All harvested tubers were used when less than 100 tubers were available. A total of 6078 and 8042 tubers were examined in 2011 and 2012 respectively, bringing the total number of tubers evaluated in this study to 14,120.

PMTV incidence and severity index were determined using previously published protocols (Nielsen and Molgaard 1997). 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 tuber necrosis per the total number of tubers examined for each sample. The number of slices per tuber with internal necrosis was determined (a). The tuber slice with the most severe internal necrosis was covered with a clear transparency with 1 cm wide vertical and horizontal strips. The number of squares 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 and advanced selections were ranked based on the overall incidence means of tuber necrosis according the following categorization: tolerant -<5 %; moderately tolerant - >5 % to 10 %; moderately sensitive - >10 % to 15 %; sensitive - >15 %.

Detection of PMTV and TRV Necrotic tissues were taken from slices of potato tubers with a sterilized scalpel. 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 5–10 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 (Nakayama et al. 2010) 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 μl and 2.5 μl, respectively. To further demonstrate that tuber necrosis was caused by PMTV, RNA from tuber extractions were also tested for *Tobacco rattle virus* (TRV) using RT-PCR (Robinson 1992). A total of 150 randomly selected symptomatic tubers were tested for the presence of PMTV and TRV in 2011 and 2012. For each year, 60 red-, 50 white-, 20 yellow and 20 russet-skinned tubers were tested.

Statistical Analysis Statistical analyses of the experimental data were carried out using the Statistical Analysis Software (SAS) version 9.3. Separate analyses of variance (ANOVA) were conducted on PMTV tuber necrosis incidence and severity data for each year due to non-homogeneity of variance between years (Levene's test: $P<0.000$) (Millikin and Johnson 1992). Preliminary analysis of the data revealed significant differences among skin-types in PMTV tuber necrosis incidence (2011) and severity. The data were subsequently partitioned into skin-types using the Proc Sort function in SAS prior to analysis. Combined ANOVA analyses were carried out on the data obtained after two evaluations, as variances across evaluation periods were homogeneous (Millikin and Johnson 1992). Residual plots of the data sets revealed that ANOVA could be performed without prior transformation as major assumptions were satisfied. Treatments were compared using the Fisher's Protected Least Significance Difference (LSD) test at $P\leq0.05$. The Pearson's Correlation Coefficient was calculated to demonstrate the degree of association between parameters. The calculation of correlations between years involved those selections planted in 2011 and 2012 (red-skinned - 16; russet-skinned - 15; white-skinned - 13, yellow-skinned - 6 and overall - 50).

Results

Tuber necrosis evaluated was determined to be caused by PMTV and not TRV based on RT-PCR results. In 2011, RT-PCR results revealed that 54/60 red- (90 %), 47/50 white- (94 %), 18/20 yellow- (90 %) and 19/20 russet-skinned (95 %) randomly selected symptomatic tubers were positive for PMTV but TRV was not detected in any of them. Similar results were obtained in 2012 with 58/60 (97 %), 47/50 (94 %), 17/20 (85 %) and 18/20 (90 %) red-, white- yellow

and russet-skinned symptomatic tubers, respectively, testing positive for PMTV, while none was positive for TRV. Due to non-homogeneity of variance between years, separate analyses were done for each year and the results are presented accordingly. Data on PMTV-induced tuber necrosis incidence ($P<0.003$) and severity ($P<0.0001$) differed significantly across skin-types in 2011. Mean tuber necrosis incidence ranged from 2.3 % in yellow-skinned selections to 7.5 % in red-skinned selections (Table 2). The mean tuber necrosis incidence among white-skinned selections was not significantly different from those of red- and russet-skinned selections. Russet- and yellow-skinned selections had statistically similar mean tuber necrosis incidence (Table 2). PMTV tuber necrosis severity was significantly higher in the red-skinned selections than the other selections, all of which had similar severity indexes. In 2012, differences in tuber necrosis incidence were not statistically significant ($P<0.06$) but severity differed significantly ($P<0.0004$) across skin-type (Table 2). PMTV tuber necrosis incidence ranged from 4.7 % in russet-skinned selections to 7.6 % in yellow-skinned selections. PMTV tuber necrosis severity ranged from 0.04 in russet-skinned selections to 0.13 in white- skinned selections (Table 2). White- and yellow-skinned selections had significantly higher tuber necrosis severity than russet-skinned selections.

PMTV-induced tuber necrosis incidence and severity differed significantly among red-skinned advanced breeding selections in 2011 ($P<0.0039$ – incidence; $P<0.0001$ - severity) and 2012 ($P<0.0001$). In 2011, the incidence of PMTV tuber necrosis ranged from zero in two selections (RA20-6 and RA89044-45) to 29.9 % in selection SPA161, while severity ranged from zero in selection RA20-6 and RA89044-45 to 1.0 in selection ND8314-1R (Table 3). None of the selections had significantly lower PMTV tuber incidence than the moderately tolerant cv. Red Pontiac internal control. Two selections, SPA161 and ND8314-1R had significantly higher tuber incidence and severity than the sensitive standard, Dakota Jewel (Table 3). In 2012, incidence ranged from zero in two selections, R90096-5 and T10-12, to 30.4 % in selection ND060728-5R, while severity ranged from zero in selections R90096-5 and T10-12 to 0.36 in selection SPA161 (Table 3). None of the selections had significantly lower tuber necrosis incidence than the moderately tolerant cv. Red Pontiac and none proved significantly more sensitive than the sensitive cv. Dakota Jewel (Table 3). PMTV tuber necrosis incidence ($r=0.57$, $P<0.02$) and severity ($r=0.48$, $P<0.05$) data in 2011 were significantly correlated with those parameters in 2012. Highly significant correlations were found between incidence and severity among red-skinned selections in 2011 ($r=0.96$, $P>0.001$) and in 2012 ($r=0.94$, $P<0.001$).

Differences in PMTV-induced tuber necrosis incidence among the russet-skinned selections were not statistically significant but severity differed significantly among the genotypes ($P<0.0006$) in 2011. Tuber necrosis incidence ranged from zero in cv. Bannock Russet and five selections to 9.6 % in ND060742C-1Russ, while severity ranged from zero in cv. Bannock Russet and five other genotypes to 0.39 in ND060742C-1Russ (Table 4). PMTV-induced tuber necrosis incidence ($P<0.0001$) and severity ($P=0.0005$) differed significantly in 2012. Tuber necrosis incidence ranged from zero in five selections and cv. Bannock Russet to 19 % in AND97279-5Russ, while severity ranged from zero in five selections and cv. Bannock Russet to 0.25 in ND060742C-1Russ (Table 4). A total of 19 selections had tuber necrosis incidence statistically similar to that of the tolerant cv. Bannock Russet, while AND97279-5Russ had significantly higher incidence than the sensitive cv. Alpine Russet (Table 4). Significant correlations were found in tuber necrosis incidence ($r=0.53$, $P<0.05$) and severity ($r=0.91$, $P<0.001$) between the 2011 and 2012 data. Significant correlations were also found between incidence and severity in 2011 ($r=0.70$, $P<0.01$) and in 2012 ($r=0.74$, $P<0.01$).

Differences in PMTV-induced tuber necrosis incidence among white-skinned selections were not statistically significant but severity differed significantly ($P<0.0001$) in 2011. Tuber necrosis incidence ranged from zero in selection ND8331Cb-3 to 23.2 % in ND060601CAB-2, while severity ranged from zero in ND8331Cb-3 to 0.64 in ND060601CAB-2 (Table 5). In 2012, both incidence and severity differed significantly ($P<0.0001$) among the potato genotypes. Tuber necrosis incidence ranged from 0.5 % in selection RA 151–24 to 18.8 % in cv. Lamoka, while severity ranged from 0.01 in

Table 2 Summary of *Potato mop-top virus* (PMTV)-induced tuber necrosis incidence (%) and severity index of several advanced breeding selections across skin-types in 2011 and 2012

Skin color[d]	PMTV tuber necrosis incidence (%)[e]		PMTV tuber necrosis severity index[e,f]		Skin color[d]	PMTV tuber necrosis incidence (%)		PMTV tuber necrosis severity index[e,f]	
	2011					2012			
Red	7.5	a	0.22	a	Yellow	7.6		0.12	a
White	5.6	ab	0.11	b	Red	7.5		0.09	ab
Russet	2.5	bc	0.05	b	White	6.4		0.13	a
Yellow	2.3	c	0.06	b	Russet	4.7		0.04	b
$LSD_{0.05}$	3.2		0.07			NS		0.05	

[d] Tuber necrosis assessments were conducted twice during storage and analyses were performed on the combined data. Evaluations were performed at 70 and 136; 126 and 190 days post-harvest in 2011 and 2012, respectively

[e] Means with the same letter are not significantly different based on Fisher's protected LSD ($P=0{\cdot}05$)

[f] Index is given as a value between 0 and 1, where 0 indicates no tuber necrosis and 1 presence of necrosis through the tuber (Nielsen and Molgaard 1997)

Table 3 *Potato mop-top virus* (PMTV)-induced tuber necrosis incidence (%) and severity index of several advanced breeding selections with red skin-type planted in 2011 and 2012

Advanced breeding selection[i,j]	PMTV tuber necrosis incidence (%)[k]		PMTV tuber necrosis severity index[k,l]		Advanced breeding selection[i,j]	PMTV tuber necrosis incidence (%)[k]		PMTV tuber necrosis severity index[k,l]	
2011					2012				
SPA161	29.9	a	0.80	ab	ND060728-5R	30.4	a	0.32	a
ND8314-1R	26.0	ab	1.00	a	SPA161	24.4	ab	0.36	a
ND060728-5R	23.5	abc	0.61	bc	Dakota Jewel	24.3	ab	0.27	ab
R90134-6	14.4	abcd	0.30	def	RC89-25	19.0	bc	0.15	bcd
ND050167C-3R	12.5	abcd	0.36	de	ATND98459-1RY	10.1	cde	0.14	bcde
AND00272-1R	9.7	bcd	0.23	defg	Red Pontiac	7.5	def	0.17	bc
R90213-6	8.3	cd	0.32	def	ND8555-8R	4.8	def	0.08	cdef
Dakota Jewel	8.3	cd	0.16	efgh	RC72-35	4.2	def	0.01	def
ND8058-11R	8.3	cd	0.41	cd	RA90213-60	3.8	def	0.06	cdef
RA90213-60	7.5	cd	0.31	def	ND8314-1R	3.7	def	0.03	def
T10-12	4.6	d	0.02	h	R91129-11	3.4	def	0.06	cdef
ND028842b-1RY	4.3	d	0.21	defgh	ND4659-5R	2.2	ef	0.03	def
ND060733b-4RY	4.3	d	0.14	efgh	RA89044-45	1.7	ef	0.02	def
ND8555-8R	2.5	d	0.05	gh	RA20-6	1.5	ef	0.01	ef
R91129-11	2.1	d	0.02	h	RG47-3	0.9	ef	>0.00[m]	ef
Red Pontiac	2.0	d	0.08	fgh	AND00272-1R	0.8	f	0.01	ef
R90160-5	1.4	d	0.01	h	R90070-8	0.5	f	>0.00[m]	f
R90070-8	1.1	d	0.02	h	R90096-5	0.0	f	0.0	f
ND4659-5R	0.9	d	0.01	h	T10-12	0.0	f	0.0	f
ATND98459-1RY	>0.0[m]	d	0.02	h					
RC72-35	>0.0[m]	d	0.01	h					
RA20-6	0.0	d	0.00	h					
RA89044-45	0.0	d	0.00	h					
$LSD_{0.05}$	16.3		0.24			9.3		0.14	

[i] Commercial cultivars Dakota Jewel and Red Pontiac were included as internal controls

[j] Tuber necrosis assessments were conducted twice during storage and analyses were performed on the combined data. Evaluations were performed at 70 and 136; 126 and 190 days post-harvest in 2011 and 2012, respectively

[k] Means with the same letter are not significantly different based on Fisher's protected LSD (P=0·05)

[l] Index is given as a value between 0 and 1, where 0 indicates no tuber necrosis and 1 presence of necrosis through the tuber (Nielsen and Molgaard 1997)

[m] Incidence or severity of PMTV-induced tuber necrosis is not a true zero as there were a few tubers with internal necrosis

selection ND8307C-3 to 0.5 in selection ND7550C-1 (Table 5). None of the selections had significantly lower tuber necrosis incidence or severity than the tolerant cv. Ivory Crisp. There was no correlation in PMTV tuber necrosis incidence data between 2011 and 2012 (r=0.55, P<0.10). However, the tuber necrosis severity data in 2011 were significantly (r=0.62, P<0.05) correlated with those of 2012. A significant correlation was also found between incidence and severity in 2011 (r=0.85, P>0.01) and in 2012 (r=0.66, P<0.02).

Differences in PMTV-induced tuber necrosis incidence among yellow-skinned selections were not statistically significant but severity differed significantly (P<0.0088) in 2011. Tuber necrosis incidence ranged from zero in three selections to 9.7 % in selection RA82-4, while severity ranged from zero to 0.32 in RA82-4 (Table 6). In 2012, incidence (P<0.0002) and severity (P<0.0389) differed significantly among yellow-skinned selections. Tuber necrosis incidence ranged from 1.7 % in RK24-48 to 15.7 % in cv. Yagana (Table 6). None of the selections had significantly lower tuber necrosis incidence or severity than the tolerant cv. Yukon Gold or higher incidence/severity than the sensitive cv. Yagana. There was no correlation in the tuber necrosis incidence or severity data between 2011 and 2012. Significant correlation was found between tuber necrosis incidence and severity in 2011 (r=0.87, P<0.05).

Based on the two-year PMTV tuber necrosis incidence data, selections and internal controls were classified as tolerant, moderately tolerant, moderately sensitive or sensitive.

Table 4 *Potato mop-top virus* (PMTV)-induced tuber necrosis incidence (%) and severity index of several advanced breeding selections with russet skin-type planted in 2011 and 2012

Advanced breeding selection[d,e]	PMTV tuber necrosis incidence (%)	PMTV tuber necrosis severity index[f,g]		Advanced breeding selection[d,e]	PMTV tuber necrosis incidence (%)[f]		PMTV tuber necrosis severity index[f,g]	
2011				2012				
ND060742C-1Russ	9.6	0.39	a	AND97279-5Russ	19.0	a	0.20	ab
Alpine Russet	8.9	0.02	b	ND060735-3Russ	13.7	ab	0.08	c
ND6400C-1Russ	7.5	0.10	b	ND060742C-1Russ	12.9	abc	0.25	a
ND049289-1Russ	4.2	0.03	b	ND070927-2Russ	9.0	bcd	0.02	c
ND8229-3	3.4	0.09	b	Alpine Russet	8.6	bcde	0.10	bc
ND050082Cb-2Russ	3.0	0.03	b	ND050105C-1Russ	8.6	bcde	0.02	c
ND050105C-1Russ	2.8	0.06	b	ND8413-7Russ	6.6	bcdef	0.03	c
ND059769Ab-1Russ	2.4	0.09	b	AND99362B-1Russ	6.5	bcdef	0.11	bc
ND049423b-1Russ	1.1	0.01	b	ND049381C-2Russ	6.4	bcdef	0.10	bc
ND8068-5Russ	0.0	0.00	b	Ranger Russet	5.8	cdef	0.05	c
Ranger Russet	0.0	0.00	b	ND060796AB-1Russ	5.8	cdef	0.05	c
ND060796AB-1Russ	0.0	0.00	b	ND039194AB-1Russ	5.1	def	0.02	c
AND01804-3Russ	0.0	0.00	b	ND049517B-1Russ	4.3	def	0.03	c
ND049546b-10Russ	0.0	0.00	b	ND049289-1Russ	3.0	def	0.00	c
ND060766b-4Russ	0.0	0.00	b	ND050082Cb-2Russ	2.8	def	0.00	c
ND8413-7Russ	0.0	0.00	b	ND049423b-1Russ	1.5	ef	0.00	c
Bannock Russet	0.0	0.00	b	ND8068-5Russ	1.5	ef	0.01	c
				AOND95292-3Russ	0.6	f	>0.00[h]	c
				ND060761B-3Russ	0.6	f	>0.00[h]	c
				AND01804-3Russ	0.5	f	>0.00[h]	c
				Bannock Russet	0.0	f	0.00	c
				AND00618-1RussY	0.0	f	0.00	c
				ND060766b-4Russ	0.0	f	0.00	c
				ND6400C-1Russ	0.0	f	0.00	c
				ND060770B-5Russ	0.0	f	0.00	c
				ND049546B-10Russ	0.0	f	0.00	c
$LSD_{0.05}$	NS	0.15			7.3		0.11	

[d] Commercial cultivars Alpine Russet, Bannock Russet and Ranger Russet were included as internal controls

[e] Tuber necrosis assessments were conducted twice during storage and analyses were performed on the combined data. Evaluations were performed at 70 and 136; 126 and 190 days post-harvest in 2011 and 2012, respectively

[f] Means with the same letter are not significantly different based on Fisher's protected LSD (P=0·05)

[g] Index is given as a value between 0 and 1, where 0 indicates no tuber necrosis and 1 presence of necrosis through the tuber (Nielsen and Molgaard 1997)

[h] Incidence or severity of PMTV-induced tuber necrosis is not a true zero as there were a few tubers with internal necrosis

The red-skinned selections and internal control cultivars were classified as follows – tolerant: RC72-35, RA20-6, RA89044-45, ND4659-5R, R90070-8 and T10-12 (overall incidence <5 %); moderately tolerant: R91129-11, ND8555-8R and Red Pontiac (overall incidence >5 % to 10 %); moderately sensitive: ATND98459-1RY, RA90213-60 and AND00272-1R (overall incidence >10 % to 15 %) and sensitive: SPA161, ND8314-1R, ND060728-5R and Dakota Jewel (overall incidence >15 %) (Table 7). The russet-skinned selections and internal control cultivars were classified as follows – tolerant: ND060766b-4Russ, ND049546b-10Russ, AND01804-3Russ, ND8068-5Russ, ND049423b-1Russ and Bannock Russet (overall incidence <5 %); moderately tolerant: ND050082Cb-2Russ, ND060796AB-1Russ, ND8413-7Russ, ND049289-1Russ, ND6400C-1Russ and Ranger Russet (overall incidence >5 % to 10 %); moderately sensitive: ND050105C-1Russ (overall incidence >10 % to 15 %) and sensitive: ND060742C-1Russ and Alpine Russet (overall incidence >15 %) (Table 7). The white-skinned selections and internal control cultivars were ranked as follows – tolerant: ND8331Cb-3, ND8331Cb-2, ND7519-1, ND8559-20, ND8307C-3 and Ivory Crisp (overall incidence <5 %);

Table 5 *Potato mop-top virus* (PMTV)-induced tuber necrosis incidence (%) and severity index of several advanced breeding selections with white skin-type planted in 2011 and 2012

Advanced[g,h] breeding selection	PMTV tuber necrosis incidence (%)	PMTV tuber[i,j] necrosis severity index		Advanced[g,h] breeding selection	PMTV tuber[i] necrosis incidence (%)		PMTV tuber[i,j] necrosis severity index	
2011				2012				
ND060601CAB-2	23.2	0.64	a	Lamoka	18.8	a	0.49	a
ND060715B-15	14.7	0.19	bcd	ND8304-2	17.7	ab	0.13	b
ND8304-2	14.1	0.20	bcd	ND7550C-1	11.7	ab	0.50	a
ND7550C-1	11.9	0.28	b	Kennebec	10.8	bc	0.03	b
ND060847CB-1	11.8	0.12	bcd	ND8229-3	10.0	cd	0.16	b
MSL-292A	8.4	0.16	bcd	ND6956b-13	8.2	cde	0.05	b
RA151-24	5.4	0.05	cd	ND060835C-4	5.3	cdef	0.17	b
ND060835C-4	5.4	0.19	bcd	ND8305-1	3.2	def	0.03	b
ND6956b-13	5.2	0.02	d	ND8307C-3	2.5	ef	0.01	b
CO95051-7 W	4.2	0.05	cd	ND8331Cb-2	1.9	ef	0.02	b
Kennebec	3.3	0.01	d	ND8559-20	1.8	ef	0.02	b
R65A-70	2.9	0.26	bc	Ivory Crisp	1.4	ef	0.05	b
W2717-5	2.7	0.03	cd	ND8331Cb-3	1.0	ef	0.08	b
ND7519-1	2.4	0.04	cd	ND7519-1	1.0	ef	0.09	b
ND8307C-3	2.2	0.03	cd	RA151-24	0.5	f	0.02	b
ND8559-20	2.2	0.01	d					
NY-138	1.7	>0.00[k]	d					
Lamoka	1.0	0.05	bcd					
NY-139	>0.0[k]	0.01	d					
Ivory Crisp	>0.0[k]	>0.00[k]	d					
ND8331Cb-2	>0.0[k]	0.00[k]	d					
ND8331Cb-3	0.0	>0.00	d					
$LSD_{0.05}$	NS	0.23			7.5		0.17	

[g] Commercial cultivars Ivory Crisp, Lamoka and Kennebec were included as internal controls

[h] Tuber necrosis assessments were conducted twice during storage and analyses were performed on the combined data. Evaluations were performed at 70 and 136; 126 and 190 days post-harvest in 2011 and 2012, respectively

[i] Means with the same letter are not significantly different based on Fisher's protected LSD (P=0·05)

[j] Index is given as a value between 0 and 1, where 0 indicates no tuber necrosis and 1 presence of necrosis through the tuber (Nielsen and Molgaard 1997)

[k] Severity of PMTV-induced tuber necrosis is not a true zero as there were a few tubers with internal necrosis

moderately tolerant: RA151-24 (overall incidence >5 % to 10 %); moderately sensitive: ND060835C-4, ND6956b-13 and Kennebec (overall incidence >10 % to 15 %) and sensitive: ND7550C-1, ND8304-2 and Lamoka (overall incidence >15 %) (Table 7). The yellow-skinned selections and internal controls were classified as follows – tolerant: R91007-5 and Yukon Gold (overall incidence <5 %); moderately tolerant: RC06-109 (overall incidence >5 % to 10 %); moderately sensitive: R87009-28 and RA517-123 (overall incidence >10 % to 15 %) and sensitive: Yagana (overall incidence >15 %) (Table 7).

The overall correlations in tuber necrosis incidence (r= 0.55, P<0.001) and severity (r=0.41, P<0.01) data across skin-types between 2011 and 2012 were statistically significant. Significant interactions were found in PMTV-induced tuber necrosis incidence between selection and period of evaluation (P<0.0001) as well as between skin-color and evaluation period (P<0.0001) in 2011. Across skin-type, the increase in incidence during storage was higher in red- and white-skinned selections than in yellow- and russet-skinned types. Generally, incidence was higher in the second evaluation than the first and selections such as SPA161, ND8314-1, ND060728-5R (all red-skinned) and ND060601CAB-2 (white-skinned) had the highest increase. The severity of PMTV tuber necrosis did not change during storage. In 2012, changes in PMTV tuber necrosis incidence and severity during storage were not significant.

Table 6 *Potato mop-top virus* (PMTV)-induced tuber necrosis incidence (%) and severity index of several advanced breeding selections with yellow skin-type planted in 2011 and 2012

Advanced[d,e] breeding selection	PMTV tuber necrosis incidence (%)	PMTV tuber[f,g] necrosis severity index		Advanced[d,e] breeding selection	PMTV tuber[f] necrosis incidence (%)		PMTV tuber[f,g] necrosis severity index	
2011				2012				
RA82-4	9.7	0.32	a	Yagana	15.7	a	0.30	a
RA362-54	5.4	0.07	b	RA517-123	12.4	ab	0.04	bc
Yagana	5.1	0.11	b	R87009-28	11.9	ab	0.23	abc
R87009-28	3.0	0.11	b	RC06-109	7.2	bc	0.24	abc
RA519-50	1.3	0.02	b	Yukon Gold	2.1	c	>0.00[h]	c
Yukon Gold	1.5	0.01	b	R91007-5	2.0	c	0.01	c
RA517-123	1.0	0.05	b	RK24-48	1.7	c	0.03	bc
R91007-5	0.9	0.03	b					
R89045-35	>0.0[h]	0.02	b					
RA148-48	0.0	0.00	b					
RA16-5	0.0	0.00	b					
RC06-109	0.0	0.00	b					
$LSD_{0.05}$	NS	0.18			6.8		0.23	

[d] Commercial cultivars Yagana and Yukon Gold were included as internal controls

[e] Tuber necrosis assessments were conducted twice during storage and analyses were performed on the combined data. Evaluations were performed at 70 and 136; 126 and 190 days post-harvest in 2011 and 2012, respectively

[f] Means with the same letter are not significantly different based on Fisher's protected LSD (P=0·05)

[g] Index is given as a value between 0 and 1, where 0 indicates no tuber necrosis and 1 presence of necrosis through the tuber (Nielsen and Molgaard 1997)

[h] Severity of PMTV-induced tuber necrosis is not a true zero as there were a few tubers with internal necrosis

Discussion

This is the first study conducted in the Americas on the reaction of advanced potato selections to PMTV-induced tuber necrosis. This study demonstrated the existence of natural variability among advanced potato breeding selections in their reaction to PMTV-induced tuber necrosis. The advanced breeding materials were selected from a broad genetic base across North and South America, representing different market classes. This information may offer assistance to potato growers who encounter PMTV by identifying genetic material within a particular market type that is tolerant to the virus. The use of potato genotypes tolerant to PMTV that do not express the tuber necrosis phase of the virus can reduce the economic impact of the disease if and when the selections are released as commercial cultivars.

Russet-skinned selections had lower PMTV tuber necrosis incidence compared to the white-, red- and yellow-skinned types, which is in agreement with a previous study (Domfeh et al. 2015). It is worth noting that none of the tubers of two russet-skinned selections, ND060766b-4Russ and ND049546b-10Russ had tuber necrosis over two seasons. High levels of tolerance to PMTV tuber necrosis in russet-skinned cultivars has been reported (Domfeh et al. 2015). Russet-skinned potato selections have been found to be resistant to the tuber phase of powdery scab (Miller 2001; Nitzan et al. 2008; Perla et al. 2014). This could, in part, explain the tolerance to PMTV tuber necrosis, assuming some degree of correlation between powdery scab incidence on tubers and PMTV-induced tuber necrosis incidence existed in this study and as reported elsewhere (Davey et al. 2014; Domfeh et al. 2015). High physiological levels of the storage protein lipoxygenase (LOX; EC 1.13.11.12) found in russet-skinned tubers has been linked with resistance to powdery scab (Perla et al. 2014). Mechanisms such as accumulation of phytoalexins, hypersensitive response-mediated cell death and accumulation of suberin in the periderm of the tubers are believed to be activated at higher physiological levels of LOX protein (Perla et al. 2014). In contrast, tubers of two red-skinned selections, SPA 161 and ND060728-5R were the most sensitive to tuber necrosis in both years of the study. The high level of sensitivity to tuber necrosis among some red-skinned cultivars is also supported by results of a previous study (Domfeh et al. 2015).

Incorporation of host plant resistance to Sss and PMTV may be effective management tools for both pathogens. The nature and control of resistance to Sss has not been determined, but it is likely multigenic and root gall and tuber scab symptoms are most likely under separate genetic control (Wastie 1994). Resistance to Sss tuber scab has been found to be highly heritable based on assessment of progeny families, and that the resistance could be predicted based on the phenotype of the parents (Wastie 1991). Similarly, the nature of resistance to PMTV has also not been determined. However, based upon previous work and the results presented here, it appears highly heritable. Tolerant russet-skinned selections reported in this study include ND049546b-10Russ and ND049423b-1Russ, both of which have Dakota Trailblazer as the male parent. Dakota Trailblazer was found to be tolerant to Sss-induced root galling and tuber scab incidence and tolerant to PMTV-induced tuber necrosis (Domfeh et al. 2015). Incidentally, the female parent of ND049546b-10Russ is Dakota Russet (evaluated as ND8229-3) which in 2011 exhibited tolerance to PMTV induced tuber-necrosis (incidence of 3.4 %). Russet Norkotah also showed tolerance to Sss-induced root galling and tuber scab incidence, and was moderately tolerant to PMTV-induced tuber necrosis (Domfeh et al. 2015). ND8413-7Russ has Russet Norkotah as

Table 7 Summary of sensitivity rankings of advanced breeding selections based on *Potato mop-top virus* (PMTV)-induced tuber necrosis incidence values summed for 2011 and 2012

Skin color[a,b]	Tolerant selections (Overall incidence <5 %)	Moderately tolerant selections (Overall incidence >5 % to 10 %)	Moderately sensitive selections (Overall incidence >10 % to 15 %)	Sensitive selections (Overall incidence >15 %)
Red	RC72-35	R91129-11	ATND98459-1RY	SPA161
	RA20-6	ND8555-8R	RA90213-60	ND8314-1R
	RA89044-45	Red Pontiac	AND00272-1R	ND060728-5R
	ND4659-5R			Dakota Jewel
	R90070-8			
	T10-12			
Russet	ND060766b-4Russ	ND050082Cb-2Russ	ND050105C-1Russ	ND060742C-1Russ
	ND049546b-10Russ	ND060796AB-1Russ		Alpine Russet
	AND01804-3Russ	ND8413-7Russ		
	ND8068-5Russ	ND049289-1Russ		
	ND049423b-1Russ	ND6400C-1Russ		
	Bannock Russet	Ranger Russet		
White	ND8331Cb-3	RA151-24	ND060835C-4	ND7550C-1
	ND8331Cb-2		ND6956b-13	ND8304-2
	ND7519-1		Kennebec	Lamoka
	ND8559-20			
	ND8307C-3			
	Ivory Crisp			
Yellow	R91007-5	RC06-109	R87009-28	Yagana
	Yukon Gold		RA517-123	

[a] Commercial cultivars Dakota Jewel, Red Pontiac, Kennebec, Ivory Crisp, Lamoka, Bannock Russet, Ranger Russet, Alpine Russet, Yagana and Yukon Gold are internal controls

[b] Evaluations were performed at 70 and 136; 126 and 190 days post-harvest in 2011 and 2012, respectively

the male parent and was rated as moderately tolerant in the current study.

Wild relatives have been used as reliable sources of resistance traits in potato genetic improvement (Rudorf 1958). An assessment of the russet-skinned advanced selections evaluated here found that *Solanum chacoense*, *S. berthaultii*, *S. tuberosum*, *S. kurtzianum*, *S. phureja*, and *S. raphanifolium* were represented within the four-generation pedigrees, in addition to *Solanum tuberosum*. Advanced russet selections evaluated represent a range of tolerance and sensitivity to PMTV tuber necrosis. For example, ND049546b-10Russ, rated as tolerant has *S. raphanifolium* in its pedigree on the side of the female parent. Moderately tolerant clones ND060796AB-1Russ and ND6400C-1Russ have *S. tuberosum* and *S. berthaultii* and *S. chacoense* and *S. phureja* in their pedigrees, respectively. Given the natural variation present in the cultivars (Domfeh et al. 2015) and in advanced selections studied here, assessment of wild *Solanum* spp. relatives is warranted.

In the study reported here, tubers were evaluated for symptom expression (disease response of plants), with those which reacted severely described as "sensitive" while those with little or no apparent effect are considered "tolerant" (Cooper and Jones 1983). PMTV was readily confirmed by RT-PCR in randomly selected tubers but none were positive for TRV. The tuber necrosis symptoms observed (conspicuous brown-colored arcs, rings and lines) were, thus, likely caused by PMTV. In some cultivars (e.g., Cara and Saturna), a good correlation has been found between PMTV infection and the occurrence of tuber necrosis (Davey 2009), indicating that tuber necrosis may be a good indicator of PMTV infection (Cooper and Harrison 1973; Jones and Harrison 1972; Kurppa 1989). In future studies, it would be advantageous to determine if some of the selections tested here that did not show tuber necrosis are resistant to the virus or only tolerant to necrosis expression.

Transmission of PMTV to potato plants is dependent on the successful infection of the Sss vector, which is heavily influenced by environmental conditions (Cooper and Harrison 1973; Harrison 1974; Sandgren et al. 2002; Sokmen et al. 1998). Relatively cool soil temperatures (12–15 °C) and high soil moisture enhance infection with Sss by favoring germination and movement of zoospores (Merz 2008; Sandgren et al. 2002). The differences in environmental conditions between the two study years may have influenced the results of these trials. Significant differences in PMTV tuber necrosis

incidence were detected only among the red-skinned selections in 2011, yet in 2012, significant differences were found among selections of all skin-types. In 2011, the average air and soil temperatures of the experimental site during the growing season were 18 °C and 19 °C, respectively. The total amount of moisture applied to the crop via rainfall and irrigation during the growing season totaled 450.9 mm. In 2012, the average air and soil temperatures were 15.6 °C and 17 °C, respectively and a total of 780.6 mm of sprinkler irrigation and rainfall was applied to the crop. The lower moisture level and higher average temperatures in 2011 may have contributed to the overall lower tuber necrosis incidence observed. The lower overall incidence in 2011 made it difficult to detect statistically significant differences, except in the more sensitive red-skinned selections. The lower temperatures and higher moisture levels in 2012 resulted in higher tuber necrosis incidence levels, enabling the detection of significant differences among all skin-types. The inability to detect statistical differences in tuber necrosis incidence data among the white-skinned selections in 2011 could partly be attributed to higher variability among replications. While it would be virtually impossible to control air and soil temperatures in field trials such as those conducted here, it is feasible to ensure that soil moisture levels are high, as they were in 2012 compared to 2011, to provide a favorable environment for zoospore development and movement in the soil which will favor virus infection (Carnegie et al. 2012; Cooper and Harrison 1973; Davey et al. 2008; Jones 1988).

The overall significant correlation observed between the 2011 and 2012 PMTV tuber necrosis incidence and severity across skin-types indicate the reliability and reproducibility of the results and further demonstrate that field trials can be used to screen potato germplasm for their reaction to PMTV infection under North American conditions. Increase in PMTV tuber necrosis incidence during storage has been reported (Harrison and Jones 1971; Kurppa 1989; Molgaard and Nielsen 1996; Nielsen and Engsbro 1992; Ryden et al. 1989; Sandgren 1995; Sandgren et al. 2002). Our results show that PMTV tuber necrosis incidence was significantly higher in the second evaluation than the first in 2011 and this occurred mainly in the tubers of sensitive red- and white-skinned selections. This evidence suggests that PMTV tuber necrosis incidence increased more in sensitive selections during storage, consistent with previously published reports (Domfeh et al. 2015; Harrison and Jones 1971). The results also imply that conducting tuber necrosis assessment at harvest may underestimate the incidence of the disease.

In the study reported here we have demonstrated the existence of natural variability among advanced potato breeding selections in their reaction to PMTV-induced tuber necrosis. A total of 17 advanced breeding selections made up of six red-, five russet-, five white and one yellow-skinned types have been found to be tolerant to PMTV tuber necrosis. This information provides potential assistance to potato growers in areas where PMTV causes significant economic losses. In the short term, tolerant selections which have other desirable agronomic characteristics could be released as commercial cultivars for growers to plant. In the long term, tolerant selections which combine absence of tuber necrosis with little or no accumulation of PMTV can be utilized in breeding programs to introduce resistance into commercial cultivars. The screening of potato germplasm for reaction to PMTV infection should be widened to include more genetically diverse material such as wild *Solanum* species.

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