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Assessing Potato Cultivar Sensitivity to Tuber Necrosis Caused by *Tobacco rattle virus*

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Abstract

Tobacco rattle virus (TRV) causes the economically important corky ring spot disease in potato. Chemical control is difficult due to the soilborne nature of the TRV-transmitting nematode vector, and identifying natural host resistance against TRV is considered to be the optimal control measure. The present study investigated the sensitivity of 63 cultivars representing all market types (evaluated at North Dakota and Washington over 2 years) for the incidence of TRV-induced tuber necrosis and severity. This article also investigates the cultivar–location interaction (using a mixed-effects model) for TRV-induced necrosis. TRV-induced tuber necrosis ($P < 0.0001$) and severity ($P < 0.0001$) were significantly different among cultivars evaluated separately in North Dakota and Washington trials. Mixed-effects model results of pooled data (North Dakota and Washington) demonstrated that the interaction of cultivar and location had a significant effect ($P = 0.03$) on TRV-induced necrosis. Based on the virus-induced tuber necrosis data from both years and locations, cultivars were categorized into sensitive, moderately sensitive, insensitive, and moderately insensitive groups. Based on data from North Dakota, 10 cultivars, including Bintje, Centennial Russet, Ciklamen, Gala, Lelah, Oneida Gold, POR06V12-3, Rio Colorado, Russian Banana, and Superior, were rated as insensitive to TRV-induced tuber necrosis. Similar trials assessing TRV sensitivity among cultivars conducted in Washington resulted in a number of differences in sensitivity rankings compared with North Dakota trials. A substantial shift in sensitivity of some potato cultivars to TRV-induced tuber necrosis was observed between the two locations. Four cultivars (Centennial Russet, Oneida Gold, Russian Banana, and Superior) ranked as insensitive for North Dakota trials were ranked as sensitive for Washington trials. These results can assist the potato industry in making cultivar choices to reduce the economic impact of TRV-induced tuber necrosis.

Tobacco rattle virus (TRV) is an important virus pathogen of potato, with worldwide distribution capable of infecting a wide range of crops (Ghazala and Varrelmann 2007; Harrison and Robinson 1978). Primary transmission of TRV in the field occurs by soil-inhabiting nematodes of the genera *Trichodorus* and *Paratrichodorus* (Sahi et al. 2016). When transmitted, TRV incites corky ring spot disease (Crosslin et al. 1999). Tuber necrosis symptoms caused by TRV are similar to those caused by *Potato mop-top virus* (PMTV) and are characterized by rust-colored arcs, concentric rings, or extensive browning of tuber tissue that later dry into cork-like tissue (Mojtahedi et al. 2001). Relatively low levels of TRV-induced tuber defect may render entire crops unmarketable (Brown and Sykes 1973; Dale et al. 2004). If more than 6% of tubers are graded as culls due to TRV symptoms, crops are often rejected or downgraded in value (Ingham et al. 2000). Furthermore, continuous planting of TRV-susceptible cultivars will have implications on seed, ware, and processing sectors of the potato industry (Dale et al. 2004). Because the tuber necrosis symptoms caused by PMTV and TRV are very similar and indistinguishable to a layperson, the term "spraing" is frequently used to describe the disease complex in Europe (Beuch et al. 2014; Carnegie et al. 2010a, b; Mumford et al. 2000).

Prior to 1990, nematode control, including stubby-root nematodes, was managed with the use of fumigants and aldicarb (a carbamate insecticide), which was widely used in the Pacific Northwest. Aldicarb was used for Colorado potato beetle control (*Leptinotarsa decemlineata*) but also provided good control of the stubby-root nematode (Weingartner and Shumaker 1990). When aldicarb use was discontinued in 1989, there was a noticeable increase in TRV and corky ring spot disease in the Columbia Basin (Thomas et al. 1993). Natural virus resistance in potato genotypes is the only available and probably the most satisfactory means for managing TRV in the field (Ghazala and Varrelmann 2007; Solomon-Blackburn and Barker 2001b; Vaikonen 1994). However, the breeding of genetic resistance to a virus in potato cultivar can be time consuming. A major difficulty in breeding experimentation is the practical difficulty of producing a TRV infection in potato (Sahi et al.2016). Information on resistance reactions in potato against TRV infection is further complicated due to lack of correlation between resistance to spraing by natural nematode-mediated infection and resistance to mechanical leaf infection (Ghazala and Varrelmann 2007). Therefore, determining the sensitivity of potato cultivars to the expression of TRV-induced tuber necrosis may be a viable alternative.

Only a few studies in Europe have assessed cultivars for sensitivity to TRV-induced tuber necrosis (Harrison 1968; Xenophontos et al. 1998). In the United States, comprehensive evaluation of potato cultivars for sensitivity to TRV-induced tuber necrosis is limited. As per the information of The European Cultivated Potato Database, only three cultivars (Desiree, Bintje, and Kennebec) grown in the United States were previously evaluated for sensitivity to TRV-induced necrosis. One study conducted several years ago investigated the distribution of TRV in symptomatic and asymptomatic tubers of U.S. cultivars and breeding clones (Crosslin et al. 1999). However, no studies have been conducted to assess currently grown potato cultivars of each market type in the United States for sensitivity to TRV-induced tuber necrosis. Therefore, the first objective of the current study was to assess the sensitivity of the most commonly grown U.S. potato cultivars for their reaction to TRV-induced tuber necrosis. Furthermore, TRV-induced necrosis expression in potato was shown (in Europe) to be influenced by environmental conditions (Ghazala and Varrelmann 2007). Varying temperatures in greenhouse and field conditions were seen to influence TRV symptom expression in tubers (Mojtahedi et al. 2001). Therefore, studies conducted at two sites (locations) were used to test the hypothesis that TRV-induced necrosis is not affected by location. Another objective was to evaluate the

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interaction of potato cultivars and location for studying cultivar sensitivity to TRV-induced tuber necrosis.

Materials and Methods

TRV trials in North Dakota. Two field trials were conducted near Brampton, ND during summer 2015 and 2016 to screen cultivars for sensitivity to TRV-induced tuber necrosis. The experimental design was a randomized complete block design with six replications. In total, 63 and 60 cultivars were planted in 2015 and 2016, respectively (Table 1). Each row consisted of 15 tubers per cultivar planted at 12-cm soil depth and 0.3-m spacing. At the end of the growing season, potato vines were killed by flailing using a mechanical vine beater and harvested tubers were transported to a storage facility located at North Dakota State University for postharvest assessment. Harvested tubers for each cultivar were placed in two bags (approximately 50% in each). In order to determine whether tuber necrosis symptoms could develop during postharvest storage, one bag of each cultivar was stored at room temperature (23°C) and another retained under storage conditions of 10°C and 85% humidity. Tubers from bags stored at room temperature and under storage conditions were used for the first assessment and second assessment, respectively, of TRV-induced tuber necrosis symptoms.

Postharvest assessment of tubers for TRV was performed in the same manner as previous PMTV studies because the tuber necrosis symptoms caused by the viruses are similar (Domfeh et al. 2015a,b). Published protocols were used for the visual assessment of TRV-induced tuber necrosis severity in two postharvest assessments (Domfeh et al. 2015a,b; Nielsen and Molgaard 1997; Yellareddygari et al. 2017). For the 2015 and 2016 TRV trials, first tuber necrosis assessments (room temperature) were performed 20 and 27, 162 and 27, and 147 days postharvest (DPH), respectively. The second assessment of tuber necrosis (tubers in storage) for 2015 and 2016 trials was performed 162 and 147 DPH, respectively. For each evaluation, a sample consisting of 20 random tubers per cultivar from each replication was assessed for TRV-induced tuber necrosis. After tubers were rinsed with water, a mandolin slicer (Jaccard Corporation) was used to cut tubers lengthwise into 1-cm-thick slices and disease incidence and severity were evaluated. The number of tubers with necrosis symptoms from the total number of tubers assessed was used to calculate TRV incidence. Virus severity was measured in two steps. In the first step, the number of slices showing symptoms from the total number of slices was determined. In the next step, a transparent sheet consisting of 1-cm squares in a grid pattern was placed over the tuber slice showing maximum necrosis (visually identified) and the number of squares overlapping necrosis symptoms were recorded. The results from two steps were multiplied to obtain disease severity index for TRV. Severity index is expressed as values between 0 and 1, where 1 indicates that whole tuber has necrosis and 0 indicates absence of necrosis.

TRV trials in Washington. Two field trials (2015 and 2016) were established on a Washington State University research farm near Prosser, WA to screen cultivars for sensitivity to TRV-induced tuber necrosis in a randomized complete block design with six replications. This trial location has been specifically cultivated for years to be infested with TRV viruliferous *Paratrichodorus allius* (Jensen) Siddiqi and has been used to previously evaluate the sensitivity of potato cultivars and advanced potato breeding selections. In total, 59 cultivars were planted in 2015 and 2016; however, there were three substitutions in 2016 (Lelah, Rio Colorado, and Dakota Rose were substituted with Atlantic, Dakota Ruby, and Yukon Gold) (Table 1). Each replication consisted of eight tubers per cultivar planted at 13-cm soil depth and 0.23-m spacing. Potato vines were desiccated by flailing using a mechanical vine beater 10 days prior to harvest (143 and 145 days after planting in 2015 and 2016, respectively) and harvested tubers were transported to the potato storage facility located at the headquarters of the Irrigated Agriculture Research and Extension Center for postharvest assessment.

TRV-induced tuber necrosis incidence and severity evaluation methodologies were similar to North Dakota trials. A commercial-grade fruit and vegetable slicer (Nemco 56750-3) was used to provide consistent 1-cm tuber slices to evaluate for internal necrosis. Per the protocol for postharvest assessment, 50 tubers (if available) were evaluated for necrosis symptoms (approximately within 12 DPH for 2015 and 7 DPH for 2016). The remaining tubers were maintained at storage conditions of 5.6°C and 85% humidity until their evaluation for TRV-induced necrosis (second assessment). Second assessment was performed by evaluating 100 tubers (if available) for internal TRV-associated necrosis (115 and 112 DPH for 2015 and 2016, respectively).

Detection of TRV in tubers. Detection was performed only to test whether the infection was actually due to TRV. Because visual testing is not completely reliable for confirming TRV infection, diagnosis based on viral nucleic acid detection was used. For both North Dakota trials, tubers were randomly selected across all cultivars for TRV detection. TRV detection for Washington trails was not performed because the experiments were conducted in a field previously confirmed to be infested with TRV and that has been used for several years for this purpose. For the North Dakota trials, RNA was extracted from approximately 30 random symptomatic tubers from the second assessment (for both trials) and reverse-transcription polymerase chain reaction (RT-PCR) was used for detection of TRV. Infected tissue from individual potato tubers was cut using a fresh scalpel and

Table 1. Potato cultivars (sorted by market type) evaluated for tuber necrosis induced by *Tobacco rattle virus*

Russet (French fry, processing)	White (chipping)	Red	Russet tablestock	Specialty	Yellow
Alpine Russet	Atlantic	Chieftain	Goldrush	Austrian Crescent	Bintje
Alturas	Chipeta	Ciklamen	Russet Norkotah	Desiree	Gala
POR06V12-3[z]	Dakota Crisp	Colorado Rose	Russet Norkotah 278	French Fingerling	Oneida Gold
Bannock Russet	Dakota Pearl	Dakota Jewel	Russet Norkotah 296	Huckleberry Gold	Yukon Gold
Centennial Russet	Kennebec	Dakota Ruby	Russet Norkotah CO3	Russian Banana	…
Classic Russet	Lamoka	Dark Red Norland	Russet Norkotah CO8	Snowden	…
Clearwater Russet	Lelah[z]	Modoc	…	…	…
Dakota Russet	Marcy	Red Endeavor	…	…	…
Dakota Trailblazer	Mega Chip	Red Gold	…	…	…
Freedom Russet	Nicolet	Red LaSoda	…	…	…
Gemstar Russet	Pike	Red Norland	…	…	…
Premier Russet	Pinnacle	Red Thumb	…	…	…
Ranger Russet	Snowbird	Rio Colorado[z]	…	…	…
Russet Burbank	Superior	…	…	…	…
Sage Russet	Waneta	…	…	…	…
Silverton Russet	…	…	…	…	…
Teton Russet	…	…	…	…	…
Umatilla Russet	…	…	…	…	…

[z] Three cultivars (POR06V12-3, Lelah, and Rio Colorado) were not planted during the 2016 Brampton, ND trial due to lack of seed material.

stored at −80°C. The samples were then crushed in liquid nitrogen and TRIzol reagent (Life Technologies) was used to extract total RNA, as per the manufacturer's instructions. TRV was tested using RT-PCR and TRV primers complimentary to nucleotides 6,555 to 6,575 (TRV-A: CAGTCTATACACAGAACAGA) and 6,113 to 6,132 (TRV-B: GACGTGTACTCAAGGGTT), which yielded a 463-bp product (Robinson 1992). Furthermore, another 20 random asymptomatic tuber samples per trial were tested for PMTV and TRV using multiplex real-time fluorescent RT-PCR, according to a previously published protocol (Mumford et al. 2000). A multiplex assay (duplex) was used to further confirm that tuber necrosis was actually caused by TRV.

Table 2. Mean incidence and severity of *Tobacco rattle virus* induced tuber necrosis in 63 cultivars, 2015 North Dakota trial (first assessment)[y]

Cultivar	Incidence (%)	Severity index
Premier Russet	23.4 a	0.31 a
Ranger Russet	21.9 ab	0.22 ab
Sage Russet	16.4 abc	0.18 bcdef
Dakota Russet	14.5 bdc	0.18 bcde
Lamoka	14.5 bdc	0.22 abc
Russet Burbank	12.8 cde	0.16 b–h
Huckleberry Gold	10.6 cdef	0.22 abc
French Fingerling	10.5 cdef	0.15 b–j
Viking	10.2 cdefg	0.08 e–m
Russet Norkotah CO8	9.4 c–h	0.12 b–m
Silverton Russet	9.3 c–h	0.10 c–m
Alpine Russet	8.8 c–i	0.04 h–m
Snowbird	8.7 c–i	0.05 g–m
Dakota Trailblazer	8.6 c–i	0.06 f–m
Dakota Pearl	7.8 d–j	0.22 ab
Yukon Gold	7.5 d–j	0.17 b–g
Russet Norkotah CO3	6.9 d–j	0.11 b–m
Red Endeavor	6.8 d–j	0.22 abc
Bannock Russet	6.1 e–j	0.14 b–l
Colorado Rose	5.8 e–j	0.21 abcd
Rio Colorado	5.5 e–j	0.11 b–m
Chieftain	5.3 e–j	0.14 b–l
Clearwater Russet	5.3 e–j	0.10 b–m
Red Thumb	5.1 e–j	0.14 b–l
Freedom Russet	4.9 e–j	0.12 b–m
Gemstar Russet	4.8 e–j	0.07 e–m
Nicolet	4.7 e–j	0.07 e–m
Kennebec	4.5 e–j	0.04 h–m
Russet Norkotah	4.5 fghij	0.03 ijklm
Red Norland	4.4 fghij	0.09 d–m
Snowden	4.2 fghij	0.06 f–m
Dakota Jewel	4.1 fghij	0.11 b–m
Red LaSoda	3.9 fghij	0.10 b–m
Russet Norkotah 278	3.6 fghij	0.10 b–m
Russet Norkotah 296	3.6 fghij	0.08 e–m
Desiree	3.5 fghij	0.03 jklm
Dark Red Norland	3.4 fghij	0.15 b–i
Marcy	3.0 fghij	0.03 jklm
Umatilla Russet	3.0 fghij	0.10 c–m
Alturas	2.4 fghij	0.06 f–m
Waneta	2.4 fghij	0.01 m
Red Gold	2.3 fghij	0.03 h–m
Pinnocle	2.2 ghij	0.08 d–m
Modoc	1.8 hij	0.02 klm
Lelah	1.4 hij	0.03 h–m
Ciklamen	0.1 ij	0.02 klm
Teton Russet	0.9 ij	0.01 m
POR06V12-3	0.8 ij	0.06 e–m
Chipeta	0.7 ij	0.01 m
Goldrush	0.6 ij	0.02 m
Others[z]	0.0 j	0.00 m
$LSD_{0.05}$	8.2	0.12

[y] Means followed by the same letter are not significantly different according to Fisher's protected least significant difference (LSD; $\alpha < 0.05$).

[z] Others indicates cultivars (Atlantic, Austrian Crescent, Bintje, Centennial Russet, Classic Russet, Dakota Crisp, Dakota Ruby, Gala, Mega Chip, Oneida Gold, Pike, Russian Banana, and Superior) with no apparent *Tobacco rattle virus*-induced tuber necrosis symptoms and that are not listed in the table.

Statistical analysis. All statistical analyses were performed using statistical analysis software (SAS, version 9.3). Overall means of virus-induced tuber necrosis incidence and severity data were calculated (SAS PROC GLM statistical procedure) separately for North Dakota and Washington TRV trials. In both location trials, Levene's homogeneity of variance test was significant for virus-induced necrosis incidence ($P < 0.0001$) and severity ($P < 0.001$) and data from experimental runs (assessments) were analyzed separately. Because the number of cultivars varied between years, statistical analysis was performed separately for each year. TRV trials at North Dakota and Washington were analyzed separately and data were pooled to evaluate the interaction of potato cultivars and trial location. A mixed model (SAS PROC Mixed statistical procedure) was performed with cultivar and location as the fixed effect and the virus-induced necrosis variance across time (year) as the random effect. A paired t test was used to test whether the mean of the dependent variable (virus-induced tuber necrosis) is the same in two groups (two assessments and 2 years).

The relationship between virus-induced tuber necrosis versus severity index and first assessment versus second assessment was measured using Pearson's correlation coefficient (r). Furthermore, cultivar sensitivity ranking or grouping for TRV trials was performed based on the virus-induced tuber necrosis incidence rating from both assessments and years (Domfeh et al. 2015a). Potato cultivars were classified in four categories: insensitive (overall incidence <5%), moderately insensitive (overall incidence >5 to 10%), moderately sensitive (overall incidence >10 to 15%), and sensitive (overall incidence >15%).

Results

TRV field trial (North Dakota), 2015. TRV-induced tuber necrosis incidence ($P < 0.0001$) and severity ($P < 0.0001$) were significantly different among cultivars in the first disease assessment. Incidence and severity indices among potato cultivars ranged from 0 to 23.4 and 0 to 0.31%, respectively (Table 2). Potato cultivars Premier Russet, Ranger Russet, and Sage Russet had the highest incidence of TRV-induced tuber necrosis.

TRV-induced tuber necrosis incidence ($P = 0.0004$) and severity ($P < 0.0001$) were significantly higher in the second disease assessment. TRV tuber necrosis incidence and severity indices ranged from 0 to 33.3 and 0 to 0.68%, respectively (Table 3). Cultivars Classic Russet, French Fingerling, and Ranger Russet exhibited an incidence of TRV tuber necrosis greater than 30%.

TRV field trial (North Dakota), 2016. The incidence of TRV-induced tuber necrosis was higher in 2016 compared with that of 2015. There were significant differences among cultivars for incidence ($P < 0.0001$) and severity of TRV-induced tuber necrosis ($P < 0.0001$) in the first evaluation (Table 4). Potato cultivars French Fingerling, Russet Norkotah CO8, and Ranger Russet had the highest incidence (>66%) of TRV-induced tuber necrosis compared with other cultivars.

There was also a significant difference among cultivars for TRV-induced tuber necrosis incidence ($P < 0.0001$) and severity ($P < 0.0001$) in the second assessment (Table 5). The majority of the cultivars (58 in total) exhibited disease symptoms, whereas only 2 cultivars (Gala and Oneida Gold) exhibited no TRV necrosis symptoms. TRV incidence ranged from 0 to 73.2% and severity from 0 to 0.48 among the potato cultivars. Cultivar French Fingerling had the highest incidence of TRV tuber necrosis, followed by Chieftain and Clearwater Russet (Table 5).

The combined results of 2 years (including both assessments) were used to rank cultivars for sensitivity to TRV-induced tuber necrosis incidence (Table 6). Of 63 cultivars, 42 were ranked as sensitive and 10 were ranked as insensitive (Table 6). All other cultivars were ranked as either moderately sensitive or moderately insensitive to TRV-induced tuber necrosis (Table 6).

In the 2015 trial, paired *t* test results demonstrated that incidence of TRV-induced tuber necrosis was significantly higher in the second assessment (8.49%) compared with first assessment (5.06%) ($P < 0.0001$), with a mean difference of −3.42% between the two assessments. In the 2016 trial, incidence of TRV-induced tuber necrosis in the second assessment (38.19%) was significantly ($P < 0.0001$) higher than the first assessment (31.03%). Across years, *t* test results demonstrated that the incidence of TRV-induced tuber necrosis was higher in the 2016 trial (34.61%) compared with the 2015 trial (6.87%), indicating a significant ($P < 0.0001$) increase in tuber necrosis caused by this virus.

Detection of TRV in North Dakota trials. RT-PCR and multiplex assay results from randomly selected tubers confirmed TRV and detected only this virus. For 2015 and 2016 trials, 100% of the TRV-symptomatic tubers tested (RT-PCR) contained detectable TRV. However, only 20% (2016) and 15% (2015) of asymptomatic tubers tested (multiplex assay) were positive for TRV and none of the tubers tested positive for PMTV, an indication that tuber necrosis was caused only by TRV.

TRV field trial (Washington), 2015. The incidence of TRV-induced tuber necrosis was very high during the first assessment and all cultivars were affected by the virus. Significant differences were found among cultivars for TRV-induced tuber necrosis incidence ($P < 0.0001$) and severity ($P < 0.0003$). TRV tuber necrosis incidence ranged from 8 to 91% and severity ranged from 0.01 to 0.57 (Table 7).

The incidence of TRV-induced tuber necrosis increased among most cultivars during the second evaluation. Similar to the first assessment, all cultivars tested were affected by TRV tuber necrosis (Table 8). TRV-induced tuber necrosis incidence ($P < 0.0001$) and severity ($P < 0.0001$) were significantly different among cultivars. TRV-induced tuber necrosis ranged from 14 to 87%, while severity ranged from 0.01 to 0.51 (Table 8). French Fingerling, followed by Red Endeavor, Ranger Russet, and Marcy, had the highest incidence of (>75%) TRV-induced necrosis in tubers.

TRV field trial (Washington), 2016. In the first assessment of TRV-induced tuber necrosis, the number of cultivars with TRV-induced tuber necrosis was lower in 2016 compared with 2015 (56 cultivars with symptoms). TRV-induced tuber necrosis ($P < 0.0001$) and severity ($P < 0.0001$) indices were significantly different among the cultivars. Cultivars Red Norland, Dark Red Norland, and Dakota Crisp had the highest TRV-induced tuber necrosis incidence (Table 9).

Significant differences in the incidence ($P < 0.0001$) and severity ($P < 0.0001$) of TRV-induced tuber necrosis was detected among potato cultivars during the second assessment of tubers. TRV-induced necrosis incidence ranged from 0 to 51% (Table 10). TRV tuber necrosis severity ranged from 0.0 to 0.2. Similar to the first assessment, Dakota Crisp and Dark Red Norland cultivars expressed the highest incidence of TRV-induced tuber necrosis (>45%).

In the 2015 trial, paired *t* test results demonstrated that incidence of TRV-induced tuber necrosis was significantly higher in the second assessment (50.51%) compared with the first assessment (47.68%), with a mean difference of −2.23% ($P = 0.01$). Similarly, in the 2016 trial, incidence of TRV-induced tuber necrosis in the first assessment (21.48%) was significantly ($P = 0.001$) higher than the second assessment (17.78%). Across years, *t* test results demonstrated that the incidence of TRV-induced tuber necrosis was higher in the 2015 trial (49.09%) compared with the 2016 trial (19.63%), indicating a significant ($P < 0.0001$) increase in tuber necrosis caused by this virus. Furthermore, *t* test results (combined data) demonstrated that there was significant ($P < 0.0001$) difference between TRV-induced necrosis incidence between the North Dakota trial (20.57%) and the Washington trial (33.97%).

The combined results of 2 years (including both assessments) was used to rank cultivars for sensitivity to TRV-induced tuber necrosis incidence (Table 11). Of 61 cultivars, 57 were ranked as sensitive and none were ranked as insensitive (Table 11). All other cultivars were ranked as either moderately sensitive or moderately insensitive to TRV-induced tuber necrosis (Table 11).

Cultivar–environment interaction effect on TRV-induced tuber necrosis. Mixed-effects model results of pooled data demonstrated that cultivar ($P < 0.0001$) and location had a significant effect on TRV-induced necrosis ($P < 0.0001$). This could be due to the difference in magnitude of TRV-induced tuber incidence observed between the two locations. Also, a significant cultivar–location interaction effect ($P = 0.03$) on TRV-induced tuber necrosis was observed. A significant interaction suggests that TRV-induced necrosis

Table 3. Mean incidence and severity of *Tobacco rattle virus* induced tuber necrosis in 63 cultivars, 2015 North Dakota trial (second assessment)[y]

Cultivar	Incidence (%)	Severity index
Classic Russet	33.3 a	0.07 efgh
French Fingerling	31.6 ab	0.33 bc
Ranger Russet	31.0 abc	0.28 bcde
Lamoka	27.4 abcd	0.26 b–g
Alpine Russet	26.2 abcde	0.21 b–h
Huckleberry Gold	22.3 a–f	0.28 bcdef
Russet Norkotah CO8	19.4 a–g	0.19 b–h
Red Endeavor	17.6 a–h	0.68 a
Sage Russet	16.9 a–h	0.14 b–h
Premier Russet	16.1 b–i	0.14 b–h
Yukon Gold	15.4 b–i	0.30 bcd
Clearwater Russet	14.1 c–i	0.07 efgh
POR06V12-3	13.8 d–i	0.27 bcdef
Bannock Russet	13.3 d–i	0.17 b–h
Russet Burbank	13.0 d–i	0.20 b–h
Gemstar Russet	12.1 d–i	0.07 efgh
Freedom Russet	11.4 d–i	0.21 b–h
Dakota Trailblazer	11.2 d–i	0.09 efgh
Snowbird	10.8 efghi	0.10 defgh
Umatilla Russet	10.3 efghi	0.09 defgh
Desiree	10.2 efghi	0.16 b–h
Colorado Rose	10.0 efghi	0.19 b–h
Russet Norkotah 296	9.9 efghi	0.17 b–h
Russet Norkotah CO3	9.5 efghi	0.12 c–h
Dakota Ruby	9.2 fghi	0.35b
Nicolet	8.5 fghi	0.14 b–h
Alturas	8.1 fghi	0.14 b–h
Russet Norkotah 278	8.1 fghi	0.18 b–h
Viking	8.0 fghi	0.05 gh
Kennebec	7.8 fghi	0.06 fgh
Red Gold	7.1 fghi	0.14 b–h
Snowden	7.1 fghi	0.06 efgh
Silverton Russet	6.3 fghi	0.04 gh
Red Thumb	5.8 fghi	0.11 defgh
Goldrush	5.5 fghi	0.10 defgh
Dark Red Norland	5.4 fghi	0.16 b–h
Red Norland	5.1 ghi	0.16 b–h
Rio Colorado	4.4 ghi	0.20 b–h
Waneta	4.2 ghi	0.08 efgh
Chipeta	3.9 ghi	0.08 efgh
Lelah	3.8 ghi	0.03 h
Atlantic	3.5 ghi	0.15 b–h
Russet Norkotah	3.1 ghi	0.06 efgh
Pinnocle	2.8 ghi	0.05 gh
Dakota Jewel	2.3 hi	0.05 gh
Red LaSoda	2.3 hi	0.05 gh
Dakota Pearl	1.9 hi	0.05 gh
Teton Russet	1.7 hi	0.05 gh
Chieftain	1.4 hi	0.06 gh
Others[z]	0.0 i	0.00 h
$LSD_{0.05}$	16.9	0.22

[y] Means followed by the same letter are not significantly different according to Fisher's protected least significant difference (LSD; $\alpha < 0.05$).

[z] Others indicates cultivars (Austrian Crescent, Bintje, Centennial Russet, Ciklamen, Dakota Crisp, Dakota Russet, Gala, Marcy, Mega Chip, Modoc, Oneida Gold, Pike, Russian Banana, and Superior) with no apparent *Tobacco rattle virus*-induced tuber necrosis symptoms and that are not listed in the table.

Table 4. Mean incidence and severity of *Tobacco rattle virus* induced tuber necrosis in 60 cultivars, 2016 North Dakota trial (first assessment)[y]

Cultivar	Incidence (%)	Severity index
French Fingerling	73.2 a	0.56 abc
Russet Norkotah CO8	71.1 ab	0.24 e–p
Ranger Russet	66.7 abc	0.47 abcd
Yukon Gold	59.8 abcd	0.58 ab
Viking	59.2 abcde	0.21 f–km–r
Russet Norkotah	57.6 abcde	0.37 defgh
Premier Russet	57.6 abcde	0.38 defg
Lamoka	54.8 a–f	0.38 cdefg
Freedom Russet	54.6 a–f	0.24 e–p
Snowbird	52.6 a–g	0.41 bcde
Chieftain	51.7 bcdefh	0.39 cdef
Dakota Russet	51.1 b–i	0.25 e–mop
Russet Burbank	51.0 b–j	0.29 d–n
Red Endeavor	47.2 c–k	0.62 a
Marcy	45.9 c–l	0.36 defgh
Kennebec	44.1 d–l	0.33 d–k
Dark Red Norland	42.4 d–ln	0.34 d–j
Sage Russet	42.4 d–ln	0.29 d–m
Waneta	41.7 d–ln	0.29 defgijklm
Russet Norkotah 296	40.3 d–lno	0.30 d–l
Bannock Russet	39.7 d–lno	0.26 e–o
Red LaSoda	38.4 e–ln	0.39 cdefg
Snowden	38.3 e–lno	0.34 d–k
Dakota Trailblazer	34.8 f–p	0.13 l–t
Russet Norkotah 278	34.4 f–p	0.21 f–r
Umatilla Russet	32.5 g–q	0.19 h–t
Red Norland	32.3 g–q	0.35 d–i
Russet Norkotah CO3	32.0 g–q	0.36 defgh
Dakota Pearl	31.0 h–q	0.29 d–iklm
Silverton Russet	30.3 i–q	0.20 g–r
Huckleberry Gold	29.9 j–q	0.29 d–m
Dakota Jewel	29.6 k–q	0.41 bcde
Gemstar Russet	25.8 l–pr	0.16 j–t
Desiree	25.5 l–r	0.11 m–t
Atlantic	25.3 l–s	0.23 e–q
Alpine Russet	24.9 l–s	0.04 qrst
Nicolet	24.3 m–qs	0.27 e–o
Pinnocle	23.8 m–t	0.34 d–k
Modoc	23.2 m–u	0.21 f–mopqr
Red Thumb	22.5 n–u	0.17 i–t
Pike	22.2 noprstu	0.10 n–t
Teton Russet	21.8 n–v	0.09 o–t
Clearwater Russet	21.4 n–v	0.23 e–q
Chipeta	21.4 n–v	0.28 e–n
Classic Russet	19.4 opr–w	0.05 qrst
Colorado Rose	19.2 opr–w	0.19 h–s
Red Gold	13.9 p–w	0.26 e–o
Mega Chip	13.1 q–w	0.11 m–t
Dakota Ruby	12.5 q–w	0.15 k–t
Dakota Crisp	11.9 q–w	0.13 l–t
Austrian Crescent	6.7 r–w	0.03 rst
Goldrush	4.2 stuvw	0.03 rst
Centennial Russet	3.2 tuvw	0.07 pqrst
Bintje	2.8 tuvw	0.07 pqrst
Alturas	2.4 uvw	0.01 st
Oneida Gold	1.0 vw	0.05 qrst
Russian Banana	0.8 vw	0.01 st
Others[z]	0.0 w	0.00 t
$LSD_{0.05}$	21.1	0.19

[y] Means followed by the same letter are not significantly different according to Fisher's protected least significant difference (LSD; $\alpha < 0.05$).
[z] Others indicates cultivars (Ciklamen, Gala, and Superior) with no apparent *Tobacco rattle virus*-induced tuber necrosis symptoms and that are not listed in the table.

varies in cultivars grown under different field and environmental conditions.

Pearson correlation studies. The correlation between TRV-induced tuber necrosis incidence and severity was strong and significant for the North Dakota trial ($P < 0.0001$). First and second assessment (2015 trial) correlation associations between TRV-induced necrosis incidence and severity were 0.69 and 0.61, respectively. Correspondingly, first and second TRV assessments for the 2016 trial resulted in $r = 0.66$ ($P < 0.0001$) and $r = 0.63$ ($P < 0.0001$), respectively. There was a significant and strong correlation between TRV-induced tuber necrosis incidence and severity among cultivars across years ($r = 0.76$, $P < 0.0001$). There was also a significant correlation of TRV-induced tuber necrosis incidence between the first and second assessment: 0.59 ($P < 0.0001$) and 0.78 ($P < 0.0001$) for the 2015 and 2016 trials, respectively. The incidence of TRV-tuber-necrosis was significantly correlated between years for the first assessment ($r = 0.54$, $P < 0.0001$). A significant correlation between years for the second assessment of TRV-induced tuber necrosis was also observed ($r = 0.46$, $P < 0.0001$).

In the first assessment of TRV-induced necrosis in the Washington trials, the correlation between incidence and severity was strong and significant in 2015 ($r = 0.68$, $P < 0.0001$) and 2016 ($r = 0.80$, $P < 0.0001$). In the second assessment, the r between TRV-induced necrosis incidence and severity was also strong and significant for 2015 ($r = 0.73$, $P < 0.0001$) and 2016 ($r = 0.85$, $P < 0.0001$) trials. Furthermore, the correlation between TRV-induced tuber necrosis incidence and severity among cultivars across years was strong and significant ($r = 0.82$, $P < 0.0001$). The correlation of TRV-induced tuber necrosis incidence between the first and second assessment was also high: 0.84 ($P < 0.0001$) and 0.82 ($P < 0.0001$) for 2015 and 2016 trials, respectively. The correlation between years for the first assessment of TRV-tuber-necrosis incidence was weak but statistically significant ($r = 0.33$, $P = 0.013$). A significant and moderately strong correlation between years for the second assessment of TRV-induced tuber necrosis was observed ($r = 0.40$, $P = 0.002$). Furthermore, overall correlation between North Dakota and Washington trials for TRV-induced tuber necrosis was statistically significant but weak ($r = 0.26$, $P = 0.03$).

Discussion

Cultivars differed in TRV-induced tuber necrosis incidence and severity levels, an indication that TRV tuber disease development varied among potato cultivars. It appears that several factors may influence the TRV-tuber necrosis levels in cultivars after harvest. An increase in TRV-induced tuber necrosis incidence among potato cultivars was observed over the postharvest storage period. The mean percent increase in TRV-induced necrosis during storage was 23.07 and 67.79% in 2015 and 2016 North Dakota trials, respectively. This indicates that potato tubers should be evaluated over postharvest storage for accurate assessment of TRV-induced necrosis. Most commonly, tubers can be stored for 6 to 7 months at temperatures and humidity levels of 5 to 10°C and 85 to 95%, respectively. Further studies are warranted to determine whether storage conditions used by the potato industry or duration of storage influence TRV symptom development. We also know from previous studies on PMTV-induced necrosis that, when tubers are evaluated immediately after harvest, false conclusions regarding cultivar sensitivity can be reached because symptom development continues in tubers over the postharvest storage period (Yellareddygari et al. 2017). When molecular testing is not accessible, visual tuber evaluation over storage is important for growers planning to market their crop. The timing of TRV-induced necrosis assessment after harvest may affect the number of cultivars showing symptoms. A 7-day difference between assessments in the 2015 and 2016 North Dakota trials resulted in an additional seven cultivars affected by TRV-induced necrosis. Therefore, the optimal time for evaluating tubers stored at room temperature may be within 1 to 3 weeks postharvest. The difference between the 2015 and 2016 trials could also be due to varying environmental conditions because it has been demonstrated that varying temperatures in a greenhouse or in the field can influence TRV symptom expression in tubers (Mojtahedi et al. 2001).

Table 5. Mean incidence and severity of *Tobacco rattle virus* induced tuber necrosis in 60 cultivars, 2016 North Dakota trial (second assessment)[y]

Cultivar	Incidence (%)	Severity index
French Fingerling	73.2 a	0.49 abc
Chieftain	68.7 ab	0.31 d–k
Clearwater Russet	68.3 ab	0.32 d–j
Red Endeavor	66.1 abc	0.60 a
Dark Red Norland	61.8 abcd	0.59 a
Alpine Russet	61.6 abcd	0.19 i–q
Marcy	61.0 abcde	0.31 d–k
Kennebec	59.8 abcde	0.25 g–n
Red Norland	58.6 abcde	0.57 ab
Russet Burbank	58.5 abcde	0.30 e–l
Lamoka	58.1 abcde	0.32 d–j
Dakota Russet	57.4 a–f	0.32 d–j
Snowbird	52.3 a–g	0.34 c–i
Russet Norkotah	51.3 a–h	0.29 e–m
Bannock Russet	51.1 a–h	0.40 cdefg
Russet Norkotah CO3	50.9 a–h	0.31 d–k
Russet Norkotah CO8	50.8 a–h	0.25 f–n
Waneta	50.0 a–h	0.22 h–p
Ranger Russet	50.0 a–h	0.42 bcde
Freedom Russet	48.9 b–i	0.22 h–p
Russet Norkotah 278	47.6 b–j	0.27 e–n
Dakota Trailblazer	47.2 b–j	0.13 l–r
Dakota Ruby	46.8 b–j	0.29 e–m
Premier Russet	46.6 b–j	0.31 d–k
Silverton Russet	44.5 c–k	0.21 h–p
Viking	44.4 c–k	0.14 l–r
Snowden	43.8 c–k	0.28 e–n
Yukon Gold	42.8 c–l	0.47 abcd
Red LaSoda	40.9 d–m	0.31 d–k
Russet Norkotah 296	40.8 d–m	0.32 d–j
Sage Russet	38.9 d–m	0.27 e–n
Dakota Pearl	38.6 d–m	0.33 c–j
Atlantic	37.8 e–n	0.29 e–m
Teton Russet	34.4 f–o	0.15 k–r
Gemstar Russet	33.6 g–o	0.17 j–q
Dakota Jewel	32.9 g–o	0.41 bcdef
Red Thumb	32.9 g–o	0.19 h–q
Colorado Rose	32.4 g–o	0.24 g–o
Nicolet	31.5 g–o	0.21 h–p
Pinnocle	31.5 g–o	0.35 c–h
Dakota Crisp	30.0 g–o	0.19 h–q
Desiree	28.7 h–p	0.12 nopqr
Alturas	26.0 i–q	0.19 i–q
Huckleberry Gold	25.7 i–q	0.21 h–p
Austrian Crescent	25.3 j–q	0.28 e–n
Classic Russet	24.6 j–q	0.06 pqr
Modoc	22.9 k–r	0.12 nopqr
Red Gold	22.8 k–r	0.28 e–n
Chipeta	19.8 l–r	0.07 pqr
Umatilla Russet	18.8 m–r	0.15 k–r
Pike	18.3 m–r	0.08 opqr
Superior	18.2 m–r	0.04 qr
Mega Chip	14.6 nopqr	0.08 opqr
Centennial Russet	13.9 opqr	0.04 qr
Goldrush	13.3 opqr	0.04 qr
Bintje	11.1 opqr	0.07 pqr
Russian Banana	5.2 pqr	0.06 pqr
Ciklamen	3.3 qr	0.01 r
Others[z]	0.0 r	0.00 r
$LSD_{0.05}$	23.5	0.16

[y] Means followed by the same letter are not significantly different according to Fisher's protected least significant difference (LSD; $\alpha < 0.05$).

[z] Others indicates cultivars (Gala and Oneida Gold) with no apparent *Tobacco rattle virus*-induced tuber necrosis symptoms and that are not listed in the table.

Table 6. Sensitivity ranking of potato cultivars to *Tobacco rattle virus* induced tuber necrosis incidence based on 2015 and 2016 North Dakota trials

Cultivar	Incidence (%)	Sensitivity[z]
French Fingerling	46.0	S
Lamoka	37.2	S
Russet Norkotah CO8	36.4	S
Premier Russet	36.1	S
Red Endeavor	35.6	S
Dakota Russet	34.9	S
Russet Burbank	34.5	S
Chieftain	33.6	S
Freedom Russet	31.6	S
Yukon Gold	31.3	S
Ranger Russet	31.2	S
Viking	31.1	S
Snowbird	30.2	S
Sage Russet	30.2	S
Russet Norkotah	29.4	S
Kennebec	29.1	S
Dark Red Norland	28.8	S
Marcy	28.4	S
Alpine Russet	27.7	S
Clearwater Russet	27.6	S
Dakota Trailblazer	26.7	S
Bannock Russet	26.2	S
Russet Norkotah 278	25.1	S
Red Norland	24.9	S
Russet Norkotah 296	24.6	S
Russet Norkotah CO3	24.3	S
Silverton Russet	23.6	S
Snowden	23.1	S
Waneta	22.1	S
Huckleberry Gold	20.6	S
Red LaSoda	20.5	S
Dakota Pearl	19.7	S
Desiree	18.1	S
Gemstar Russet	18.1	S
Atlantic	17.4	S
Nicolet	17.2	S
Dakota Jewel	17.0	S
Umatilla Russet	16.5	S
Colorado Rose	16.1	S
Classic Russet	15.8	S
Red Thumb	15.6	S
Pinnacle	15.3	S
Teton Russet	14.0	MS
Dakota Ruby	12.8	MS
Modoc	11.9	MS
Red Gold	11.3	MS
Chipeta	11.3	MS
Dakota Crisp	10.5	MS
Pike	10.1	MS
Alturas	8.5	MI
Austrian Crescent	7.2	MI
Mega Chip	6.9	MI
Goldrush	5.0	MI
Superior	4.9	I
Centennial Russet	4.7	I
Rio Colorado	4.6	I
POR06V12-3	3.8	I
Bintje	3.5	I
Lelah	2.7	I
Russian Banana	1.3	I
Ciklamen	1.1	I
Oneida Gold	0.3	I
Gala	0.0	I

[z] Sensitivity: rankings are insensitive (I), moderately insensitive (MI), moderately sensitive (MS), and sensitive (S). Sensitivity ranking of potato cultivars was calculated by first averaging two assessments per year and then averaging data across 2 years. Sensitivity ranking of cultivars Lelah, POR06V12-3, and Rio Colorado were calculated using data from 1 year.

However, our study did not compare the temperature or other environmental conditions between the two locations used in this study. It is very likely that the soil conditions and temperatures between the locations varied substantially because they are geographically separated within United States. Furthermore, the Pacific Northwest has a much longer growing season than exists in North Dakota, which may also influence TRV infection and symptom development. Future studies should investigate the role of specific soil and environmental

Table 7. Mean incidence and severity of *Tobacco rattle virus* induced tuber necrosis in 59 cultivars, 2015 Washington trial (first assessment)[z]

Cultivar	Incidence (%)	Severity index
French Fingerling	90.7 a	0.57 a
Red LaSoda	88.2 ab	0.30 bc
Russet Burbank	72.7 abc	0.20 bcde
Gemstar Russet	71.9 abc	0.08 bcde
Pike	69.9 abc	0.13 bcde
Ranger Russet	69.9 abc	0.18 bcde
Marcy	69.7 abc	0.18 bcde
Clearwater Russet	68.5 abc	0.19 bcde
Nicolet	68.0 abc	0.12 bcde
Chieftain	67.1 abc	0.31 ab
Red Endeavor	66.9 abc	0.29 bcd
Alpine Russet	63.2 abcd	0.13 bcde
Dakota Russet	61.5 abcd	0.17 bcde
Mega Chip	60.6 abcde	0.07 bcde
Umatilla Russet	59.5 abcde	0.13 bcde
Sage Russet	59.0 abcde	0.12 bcde
Silverton Russet	56.2 abcde	0.09 bcde
Bannock Russet	56.0 abcde	0.07 bcde
Pinnacle	56.0 abcde	0.11 bcde
Premier Russet	55.6 abcde	0.10 bcde
Teton Russet	55.5 abcde	0.10 bcde
Snowden	52.8 abcde	0.10 bcde
Red Norland	52.5 abcde	0.14 bcde
Alturas	51.8 abcde	0.11 bcde
Huckleberry Gold	50.2 abcde	0.10 bcde
Dark Red Norland	48.4 abcde	0.14 bcde
Russet Norkotah CO8	47.9 abcde	0.16 bcde
Dakota Crisp	46.9 abcde	0.06 bcde
Red Thumb	46.7 abcde	0.14 bcde
Freedom Russet	46.0 abcde	0.09 bcde
Dakota Rose	44.7 abcde	0.16 bcde
Kennebec	44.2 abcde	0.14 bcde
Snowbird	44.0 abcde	0.15 bcde
Red Gold	43.7 abcde	0.06 bcde
Colorado Rose	42.1 abcde	0.11 bcde
Chipeta	41.7 abcde	0.07 bcde
Goldrush	41.4 abcde	0.04 de
Russet Norkotah 296	41.2 abcde	0.15 bcde
Rio Colorado	40.7 abcde	0.06 bcde
Oneida Gold	40.3 abcde	0.02 e
Russet Norkotah	40.0 abcde	0.07 bcde
Lamoka	38.9 abcde	0.11 bcde
Dakota Trailblazer	38.6 abcde	0.03 e
Russet Norkotah CO3	38.2 abcde	0.06 bcde
Dakota Jewel	35.6 bcde	0.05 cde
Dakota Pearl	35.4 bcde	0.08 bcde
Desiree	35.4 bcde	0.04 de
Waneta	35.2 bcde	0.06 bcde
Modoc	34.5 bcde	0.02 e
Classic Russet	34.2 bcde	0.04 de
Centennial Russet	33.3 bcde	0.05 bcde
Russian Banana	32.4 bcde	0.04 cde
Lelah	30.3 cde	0.03 e
Russet Norkotah 278	27.8 cde	0.05 cde
Gala	21.5 cde	0.01 e
Superior	19.4 cde	0.01 e
Austrian Crescent	10.0 ed	0.01 e
Ciklamen	9.7 ed	0.02 e
Bintje	7.9 e	0.01 e
$LSD_{0.05}$	25.7	0.12

[z] Means followed by the same letter are not significantly different according to Fisher's protected least significant difference (LSD; $\alpha < 0.05$).

Table 8. Mean incidence and severity of *Tobacco rattle virus* induced tuber necrosis in 59 cultivars, 2015 Washington trial (second assessment)[z]

Cultivar	Incidence (%)	Severity index
French Fingerling	87.3 a	0.51 a
Red Endeavor	81.1 ab	0.21 bcd
Ranger Russet	79.1 abc	0.21 bcd
Marcy	76.9 abcd	0.17 bcd
Red LaSoda	74.9 abcde	0.24 bc
Umatilla Russet	71.2 a–f	0.19 bcd
Pike	71.0 a–f	0.11 bcd
Dakota Russet	69.9 a–f	0.17 bcd
Clearwater Russet	68.7 a–g	0.22 bcd
Russet Burbank	68.4 a–g	0.17 bcd
Chieftain	68.2 a–g	0.26 b
Huckleberry Gold	65.2 a–g	0.11 bcd
Sage Russet	65.1 a–g	0.15 bcd
Alturas	64.8 a–h	0.15 bcd
Alpine Russet	64.1 a–h	0.17 bcd
Red Gold	62.9 a–h	0.10 bcd
Oneida Gold	59.9 a–i	0.04 cd
Snowden	59.9 a–i	0.10 bcd
Silverton Russet	59.4 a–i	0.15 bcd
Dakota Crisp	59.0 a–i	0.13 bcd
Premier Russet	58.1 a–i	0.11 bcd
Nicolet	55.7 b–j	0.15 bcd
Russian Banana	55.4 b–j	0.13 bcd
Teton Russet	55.2 b–j	0.09 bcd
Lelah	54.9 b–j	0.11 bcd
Dark Red Norland	53.2 b–j	0.21 bcd
Bannock Russet	53.0 b–j	0.09 bcd
Kennebec	52.7 b–j	0.12 bcd
Mega Chip	52.3 b–j	0.08 bcd
Red Norland	52.2 b–j	0.12 bcd
Red Thumb	51.8 b–j	0.10 bcd
Dakota Rose	50.3 b–j	0.17 bcd
Lamoka	47.8 b–j	0.13 bcd
Dakota Pearl	47.4 b–j	0.09 bcd
Chipeta	47.2 b–j	0.10 bcd
Russet Norkotah CO8	46.3 b–j	0.12 bcd
Pinnacle	45.9 b–j	0.12 bcd
Russet Norkotah CO3	44.5 b–j	0.09 bcd
Gemstar Russet	44.0 b–j	0.06 bcd
Snowbird	42.9 b–j	0.10 bcd
Waneta	40.0 c–j	0.10 bcd
Russet Norkotah	39.0 c–j	0.07 bcd
Colorado Rose	38.2 c–j	0.13 bcd
Goldrush	38.1 c–j	0.03 cd
Classic Russet	37.4 c–j	0.05 bcd
Freedom Russet	37.1 c–j	0.07 bcd
Rio Colorado	36.1 c–j	0.03 cd
Modoc	35.5 c–j	0.03 cd
Desiree	35.4 c–j	0.05 bcd
Russet Norkotah 296	34.1 d–j	0.06 bcd
Austrian Crescent	31.8 d–j	0.06 bcd
Dakota Trailblazer	30.3 e–j	0.04 cd
Centennial Russet	29.9 e–j	0.03 cd
Superior	28.9 fghij	0.01 d
Dakota Jewel	24.8 ghij	0.04 cd
Gala	24.3 hij	0.02 cd
Russet Norkotah 278	21.9 ij	0.05 bcd
Ciklamen	14.3 j	0.01 d
Bintje	14.1 j	0.01 d
$LSD_{0.05}$	21.3	0.11

[z] Means followed by the same letter are not significantly different according to Fisher's protected least significant difference (LSD; $\alpha < 0.05$).

conditions affecting TRV-induced tuber necrosis. Furthermore, additional studies should focus on postharvest survival times (percentage of tubers without symptoms) of a large set of cultivars to improve marketing decisions based on TRV-induced tuber necrosis development in storage, as has been done with PMTV necrosis (Yellareddygari et al. 2017). Varying levels of sensitivity to TRV in cultivars can influence marketing and storage timelines. For example, a cultivar sensitive to TRV-tuber-necrosis development may require less time to manifest

Table 9. Mean incidence and severity of *Tobacco rattle virus* induced tuber necrosis in 59 cultivars, 2016 Washington trial (first assessment)[z]

Cultivar	Incidence (%)	Severity index
Red Norland	61.1 a	0.15 abcd
Dark Red Norland	60.6 a	0.19 ab
Dakota Crisp	52.1 ab	0.18 abc
Atlantic	49.7 ab	0.09 cdef
Kennebec	44.2 abc	0.14 abcd
Russet Norkotah	42.5 abc	0.03 fghi
Freedom Russet	40.3 abc	0.06 cdef
Yukon Gold	40.0 abc	0.17 abcd
Red Thumb	39.8 abc	0.07 cdef
Chieftain	39.6 abc	0.13 abcd
Red Gold	38.7 abc	0.23 a
Teton Russet	38.4 abc	0.05 efgh
Red Endeavor	37.5 abc	0.11 bcde
Ranger Russet	37.3 abc	0.09 cdef
French Fingerling	36.1 abc	0.19 ab
Huckleberry Gold	34.0 abcd	0.07 cdef
Bannock Russet	30.8 bcde	0.08 cdef
Nicolet	27.8 bcde	0.05 defg
Sage Russet	27.8 bcde	0.03 fghi
Modoc	27.5 bcde	0.09 cdef
Premier Russet	26.8 bcde	0.11 bcde
Pike	24.8 bcde	0.02 fghi
Dakota Pearl	24.3 bcde	0.12 bcde
Colorado Rose	20.8 cdefg	0.03 fghi
Marcy	20.4 cdefg	0.06 defg
Russet Norkotah 296	18.7 defg	0.02 fghi
Russet Burbank	18.7 defg	0.05 efgh
Clearwater Russet	17.5 defg	0.01 ghi
Dakota Trailblazer	16.4 defg	0.04 efgh
Desiree	16.4 defg	0.03 fghi
Classic Russet	16.2 defg	0.01 ghi
Silverton Russet	15.6 defg	0.04 efgh
Dakota Russet	14.6 defg	0.03 efgh
Lamoka	14.2 defg	0.07 cdef
Dakota Jewell	13.9 defg	0.01 ghi
Alpine Russet	13.7 defg	0.01 hi
Goldrush	13.7 defg	0.02 fghi
Pinnacle	13.6 defg	0.01 ghi
Waneta	12.5 defg	0.04 efgh
Chipeta	12.0 defg	0.00 i
Gemstar Russet	11.8 defg	0.00 i
Oneida Gold	11.8 defg	0.00 i
Russet Norkotah 278	10.2 efg	0.02 fghi
Superior	9.9 efg	0.04 efgh
Umatilla Russet	9.5 efg	0.00 i
Mega Chip	8.3 efg	0.00 i
Red LaSoda 10	8.1 efg	0.02 fghi
Snowbird	7.4 efg	0.00 i
Gala	7.2 efg	0.00 i
Snowden	6.9 fg	0.02 fghi
Austrian Crescent	6.2 fg	0.01 hi
Centennial Russet	5.8 fg	0.00 i
Russet Norkotah CO3	5.0 fg	0.00 i
Dakota Ruby	4.4 fg	0.01 ghi
Russian Banana	2.2 g	0.00 i
Ciklamen	1.8 g	0.00 i
Alturas	0.0 g	0.00 i
Bintje	0.0 g	0.00 i
Russet Norkotah CO8	0.0 g	0.00 i
$LSD_{0.05}$	30.0	0.12

[z] Means followed by the same letter are not significantly different according to Fisher's protected least significant difference (LSD; $\alpha < 0.05$).

Table 10. Mean incidence and severity of *Tobacco rattle virus* induced tuber necrosis in 59 cultivars, 2016 Washington trial (second assessment)[z]

Cultivar	Incidence (%)	Severity index
Dakota Crisp	51.0 a	0.16 abcd
Dark Red Norland	49.6 ab	0.20 ab
Kennebec	45.9 abc	0.20 a
Red Gold	38.2 abcd	0.11 bcde
Chieftain	37.9 abcde	0.17 abc
Yukon Gold	37.8 abcde	0.13 abcd
Red Norland	35.5 a–f	0.12 abcd
Freedom Russet	30.8 a–g	0.12 abcd
Alpine Russet	30.6 a–g	0.04 efgh
Bannock Russet	30.6 a–g	0.05 cdef
French Fingerling	30.3 a–g	0.14 abcd
Red Endeavor	28.6 b–h	0.11 bcde
Modoc	28.5 b–h	0.10 bcde
Pike	27.3 b–i	0.03 efgh
Colorado Rose	27.0 b–i	0.07 cdef
Red Thumb	25.1 b–i	0.05 defg
Dakota Pearl	24.8 c–j	0.14 abcd
Red LaSoda	24.1 c–j	0.07 cdef
Ranger Russet	23.5 c–j	0.07 cdef
Marcy	23.3 c–j	0.07 cdef
Atlantic	22.4 c–j	0.03 efgh
Teton Russet	22.0 c–j	0.02 efgh
Huckleberry Gold	19.3 d–j	0.09 bcde
Silverton Russet	19.1 d–j	0.07 cdef
Pinnacle	18.9 d–j	0.05 cdef
Clearwater Russet	16.9 d–j	0.08 bcde
Snowbird	15.7 d–j	0.01 fgh
Waneta	15.7 d–j	0.03 efgh
Russet Norkotah	15.3 d–j	0.06 cdef
Dakota Trailblazer	14.4 d–j	0.06 cdef
Lamoka	13.1 d–j	0.08 cdef
Russet Norkotah 296	12.5 d–j	0.05 cdef
Sage Russet	12.2 d–j	0.03 efgh
Dakota Jewell	12.1 d–j	0.03 efgh
Nicolet	12.0 d–j	0.01 gh
Russet Norkotah 278	12.0 d–j	0.03 efgh
Desiree	11.7 e–j	0.01 fgh
Oneida Gold	11.7 e–j	0.00 h
Dakota Ruby	10.6 fghij	0.05 cdef
Russet Burbank	10.3 fghij	0.04 efgh
Classic Russet	10.3 fghij	0.01 fgh
Dakota Russet	10.3 fghij	0.02 efgh
Mega Chip	9.9 fghij	0.01 fgh
Premier Russet	9.4 fghij	0.03efgh
Centennial Russet	8.9 ghij	0.00 h
Umatilla Russet	8.9 ghij	0.01 gh
Gemstar Russet	8.1 ghij	0.00 h
Chipeta	6.1 ghij	0.01 gh
Snowden	5.9 ghij	0.02 efgh
Russet Norkotah CO3	4.7 ghij	0.00 h
Austrian Crescent	4.6 ghij	0.01 gh
Alturas	3.7 hij	0.01 fgh
Goldrush	2.5 hij	0.00 h
Superior	2.2 hij	0.01 gh
Ciklamen	1.9 ij	0.00 h
Russian Banana	1.2 ij	0.01 gh
Russet Norkotah CO8	1.2 ij	0.00 h
Bintje	0.0 j	0.00 h
Gala	0.0 j	0.00 h
$LSD_{0.05}$	26.3	0.12

[z] Means followed by the same letter are not significantly different according to Fisher's protected least significant difference (LSD; $\alpha < 0.05$).

Table 11. Sensitivity ranking of potato cultivars to *Tobacco rattle virus* induced tuber necrosis incidence based on 2015 and 2016 Washington trials

Cultivar	Incidence (%)	Sensitivity[z]
French Fingerling	61.1	S
Red Endeavor	53.5	S
Chieftain	53.2	S
Dark Red Norland	52.9	S
Ranger Russet	52.4	S
Dakota Crisp	52.3	S
Red Norland	50.3	S
Red LaSoda	48.8	S
Pike	48.3	S
Marcy	47.6	S
Kennebec	46.7	S
Red Gold	45.9	S
Clearwater Russet	42.9	S
Alpine Russet	42.9	S
Teton Russet	42.8	S
Lelah	42.6	S
Bannock Russet	42.6	S
Russet Burbank	42.5	S
Huckleberry Gold	42.2	S
Sage Russet	41.0	S
Nicolet	40.9	S
Red Thumb	40.9	S
Dakota Russet	39.1	S
Yukon Gold	38.9	S
Freedom Russet	38.5	S
Rio Colorado	38.4	S
Silverton Russet	37.6	S
Premier Russet	37.5	S
Umatilla Russet	37.3	S
Atlantic	36.1	S
Russet Norkotah	34.2	S
Gemstar Russet	33.9	S
Pinnacle	33.6	S
Dakota Pearl	32.9	S
Mega Chip	32.8	S
Colorado Rose	32.0	S
Modoc	31.5	S
Snowden	31.4	S
Oneida Gold	30.9	S
Alturas	30.1	S
Lamoka	28.5	S
Snowbird	27.5	S
Dakota Rose	27.5	S
Chipeta	26.8	S
Russet Norkotah 296	26.6	S
Waneta	25.8	S
Dakota Trailblazer	24.9	S
Desiree	24.7	S
Classic Russet	24.5	S
Goldrush	23.9	S
Russet Norkotah CO8	23.8	S
Russet Norkotah CO3	23.1	S
Russian Banana	22.8	S
Dakota Jewel	21.6	S
Centennial Russet	19.5	S
Russet Norkotah 278	17.9	S
Superior	15.1	S
Gala	13.3	MS
Austrian Crescent	13.2	MS
Ciklamen	6.9	MI
Bintje	5.5	MI

[z] Sensitivity: rankings are insensitive (I), moderately insensitive (MI), moderately sensitive (MS), and sensitive (S). Sensitivity ranking of potato cultivars was calculated by first averaging two assessments per year and then averaging data across 2 years. Sensitivity ranking of cultivars Atlantic, Dakota Rose, Dakota Ruby, Lelah, Rio Colorado, and Yukon Gold were calculated using data from 1 year.

symptoms in storage and require earlier and more timely marketing compared with a less sensitive cultivar.

In this study, TRV-induced tuber necrosis and severity were positively correlated, indicating that an increase in one variable increases another variable and vice versa. Moderate to strong correlations between assessments and between years were observed (based on virus-induced tuber necrosis), an indication that virus-induced tuber necrosis in potato cultivars is consistent and reproducible across years. Due to significant correlations between assessments and between years, we felt it was appropriate to combine the data for cultivar sensitivity rankings.

For TRV cultivar sensitivity ranking, russet (French fry or processing) and russet tablestock market-type cultivars were mostly sensitive. Out of 24 russet-type cultivars screened, 19 and 24 cultivars had 15% or more TRV-induced tuber necrosis incidence during the North Dakota and Washington trials, respectively. Also, it appears that most other cultivars evaluated were either sensitive or moderately sensitive to TRV-induced necrosis, regardless of tuber skin color. Of the 63 cultivars (North Dakota trial) tested, only 10 cultivars were categorized as insensitive to TRV tuber necrosis. Interestingly, seven of these cultivars (Bintje, Centennial Russet, Lelah, Oneida Gold, Rio Colorado, Russian Banana, and Superior) were also insensitive to PMTV-induced tuber necrosis (Yellareddygari et al. in press). Furthermore, three cultivars (Bintje, Desiree, and Kennebec) that were previously screened for TRV-induced necrosis in Europe produced similar results in our study. The current study categorized potato cultivars Bintje as insensitive and Desiree and Kennebec as sensitive cultivars, which were similar to European cultivar sensitivity rankings (https://www.europotato.org/)). This indicates the uniformity and reproducibility of sensitivity ranking of some potato cultivars to virus-induced necrosis across regions. However, none of the potato cultivars from Washington trials were ranked as insensitive and two cultivars (Ciklamen and Bintje) were ranked as moderately insensitive to TRV-induced tuber necrosis. It was previously reported that resistance to TRV is controlled by a single resistance gene in some potato genotypes (Barker and Dale 2006; Ghazala and Varrelmann 2007). Because only a few plants derived from necrosis-affected tubers develop systematic symptoms, TRV-induced necrosis generally represents a hypersensitive resistance reaction (Ghazala and Varrelmann 2007; Harrison 1968). However, this resistance assessment has a drawback of lacking experimental proof (Ghazala and Varrelmann 2007). Further studies for identifying resistance genes that control host reactions to TRV infection are needed.

We observed that a major shift in sensitivity ranking between two locations were observed for four potato cultivars (Russian Banana, Superior, Oneida Gold, and Centennial Russet). These cultivars were ranked as insensitive in North Dakota and sensitive to TRV-induced necrosis in Washington trials. This further illustrates the importance of the observation that the environmental conditions specific to a location may influence TRV-induced necrosis incidence in potato cultivars. Varying levels of TRV-induced tuber necrosis in cultivars by location (North Dakota and Washington) may be the consequence of the interaction of cultivars and location due to the changes in soil or other environmental properties. The vector nematode species present in the soil may also influence the transmission of the TRV strain infecting the potato (Ploeg et al. 1992; Xenophontos et al. 1998). The environmental conditions could be the reason why TRV-induced necrosis incidence in cultivars varied from location to location and year to year (Crosslin et al. 1999; Ghazala and Varrelmann 2007).

In some cases, TRV may infect the tubers and not manifest into tuber necrosis. It was demonstrated that lack of visual necrosis symptoms in tubers is no guarantee that high levels of virus are not present (Sahi et al. 2016). Resistance assessment (by scoring symptoms) of potato cultivars grown in naturally infected soils is erroneous because of uneven distribution of the vector and varying weather conditions in field trials (Ghazala and Varrelmann 2007). Additionally, in this study, we categorized asymptomatic cultivars as insensitive rather than resistant because they may have systemic TRV infections despite the lack of any symptom expression (Xenophontos et al. 1998).

Based on our results, growers can select cultivars that are less sensitive to expressing TRV-induced tuber necrosis that will help them reduce the economic consequences of the disease. These cultivars are readily available, although seed supplies of some of the less-frequently used cultivars may be regionalized. Further research on developing host resistance and identifying appropriate marketing timelines for potato in postharvest storage is warranted.

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Literature Cited

Barker, H., and Dale, M. F. B. 2006. Resistance to viruses in potato. Pages 341-366 in: Natural Resistance Mechanisms of Plants to Viruses. G. Loebenstein and J. P. Carr, eds. Springer, Dordrecht, The Netherlands.

Beuch, U., Persson, P., Edin, E., and Kvarnheden, A. 2014. Necrotic diseases caused by viruses in Swedish potato tubers. Plant Pathol. 63:667-674.

Brown, E. B., and Sykes, G. B. 1973. Control of *Tobacco rattle virus* (spraing) in potatoes. Ann. Appl. Biol. 75:462-464.

Carnegie, S. F., Cameron, A. M., and McCreath, M. 2010a. Foliar symptoms caused by *Potato mop-top virus* on potato plants during vegetative propagation in Scotland and their association with tuber yield, spraing and tuber infection. Potato Res. 53:83-93.

Carnegie, S. F., Davey, T., and Saddler, G. S. 2010b. Effect of temperature on the transmission of *Potato mop-top virus* from seed tuber and by its vector, *Spongospora subterranea*. Plant Pathol. 59:22-30.

Crosslin, J. M., Thomas, P. E., and Brown, C. R. 1999. Distribution of *Tobacco rattle virus* in tubers of resistant and susceptible potatoes and systemic movement of virus into daughter plant. Am. J. Potato Res. 76:191-197.

Dale, M. F. B., Robinson, D. J., and Todd, D. 2004. Effects of systemic infections with *Tobacco rattle virus* on agronomic and quality traits of a range of potato cultivars. Plant Pathol. 53:788-793.

Domfeh, O., Bittara, F. G., and Gudmestad, N. C. 2015a. Sensitivity of potato cultivars to *Potato mop-top virus*-induced tuber necrosis. Plant Dis. 99: 788-796.

Domfeh, O., Thompson, A. L., and Gudmestad, N. C. 2015b. Sensitivity to tuber necrosis caused by *Potato mop-top virus* in advanced potato (*Solanum tuberosum* L.) breeding selections. Am. J. Potato Res. 92:636-647.

Ghazala, W., and Varrelmann, M. 2007. *Tobacco rattle virus* 29K movement protein is the elicitor of extreme and hypersensitive-like resistance in two cultivars of *Solanum tuberosum*. Mol. Plant Pathol. 11:1396-1405.

Harrison, B. D. 1968. Reactions of some old and new British potato cultivars to *Tobacco rattle virus*. Eur. Potato J. 11:165-176.

Harrison, B. D., and Robinson, D. J. 1978. The tobraviruses. Adv. Virus Res. 23:25-77.

Ingham, R. E., Hamm, P. B., Williams, R. E., and Swanson, W. H. 2000. Control of *Paratrichodorus allius* and corky ringspot disease of potato in the Columbia Basin of Oregon. J. Nematol. Ann. Appl. Nematol. 32:566-575.

Mojtahedi, H., Crosslin, J. M., Santo, G. S., Brown, C. R., and Thomas, P. E. 2001. Pathogenicity of Washington and Oregon isolates of *Tobacco rattle virus* on potato. Am. J. Potato Res. 78:183-190.

Mumford, R. A., Walsh, K., Barker, I., and Boonham, N. 2000. Detection of *Potato mop top virus* and *Tobacco rattle virus* using a multiplex real-time fluorescent reverse-transcription polymerase chain reaction assay. Phytopathology 90:448-453.

Nielsen, S. L., and Molgaard, J. P. 1997. Incidence, appearance and development of *Potato mop-top furovirus*-induced spraing in potato cultivars and the influence on yield, distribution in Denmark and detection of the virus in tubers by ELISA. Potato Res. 40:101-110.

Ploeg, A. T., Brown, D. J. F., and Robinson, D. J. 1992. Acquisition and subsequent transmission of *Tobacco rattle virus* isolates by *Paratrichodorus* and *Trichodorus* nematode species. Neth. J. Plant Pathol. 98:291-300.

Robinson, D. J. 1992. Detection of *Tobacco rattle virus* by reverse transcription and polymerase chain reaction. J. Virol. Methods 40:57-66.

Sahi, G., Hedley, P. E., Morris, J., Loake, G. J., and MacFarlane, S. A. 2016. Molecular and biochemical examination of spraing disease in potato tuber in response to *Tobacco rattle virus* infection. Mol. Plant Pathol. 10:822-828.

Solomon-Blackburn, R. M., and Barker, H. 2001b. Breeding virus resistant potatoes (*Solanum tuberosum*): A review of traditional and molecular approaches. Heredity 86:17-35.

Thomas, P. E., Santo, G. S., and Brown, C. R. 1993. Corky Ringspot in the Columbia Basin. Spud Topics 38: No. 24. Washington Potato Commission, Moses Lake, WA.

Vaikonen, J. P. T. 1994. Natural genes and mechanisms for resistance to viruses in cultivated and wild potato species (*Solanum* spp.). Plant Breed. 112:1-16.

Weingartner, D. P., and Shumaker, J. R. 1990. Control of nematodes and soil-borne diseases in Florida potatoes with aldicarb and 1,3-D. J. Nematol. 22:775-778.

Xenophontos, S., Robinson, D. J., Dale, M. F. B., and Brown, D. J. F. 1998. Evidence for persistent, symptomless infection of some potato cultivars with tobacco rattle virus. Potato Res. 41:255-265.

Yellareddygari, S. K. R., Domfeh, O., Bittara, F. G., and Gudmestad, N. C. 2017. Analysis of *Potato mop-top virus* survival probability in post-harvest storage. Am. J. Potato Res. 94:632-637.

Yellareddygari, S. K. R., Whitworth, J. L., and Gudmestad, N. C. Assessing potato cultivar sensitivity to tuber necrosis caused by *Potato mop-top virus*. Plant Dis. In press. doi.org/10.1094/PDIS-12-17-1918-RE