# Factors Influencing PVY Development and Disease Expression in Three Potato Cultivars

Martin D. Draper[1], Julie S. Pasche[2], and Neil C. Gudmestad[2]*

[1]Present address of first author: Plant Science Department, South Dakota State University, Box 2108, PSB 113, Brookings, SD 57007-1090.
[2]Department of Plant Pathology, North Dakota State University, Walster Hall 306, Fargo, ND 58105.
*Corresponding author: Tel: 701-231-7547; Fax: 701-231-7851; E-mail: neil.gudmestad@ndsu.nodak.edu

## ABSTRACT

**Studies were performed to investigate factors affecting symptom expression of potato virus Y infection in three potato cultivars, Russet Norkotah, Shepody, and Red LaSoda. Quantitative enzyme-linked immunosorbent assay (ELISA) results revealed few differences in the relative virus titer among cultivars tested. Potato virus Y (PVY) titers developed as rapidly in Russet Norkotah as in Shepody and Red LaSoda. Additional studies were performed to determine the effect of light intensity and infections of PVY and potato virus X (PVX), alone and in combination, on the expression of mosaic symptoms in these three cultivars. Low light intensity (270-330 uE/m$^2$/sec) significantly increased plant heights and severity of mosaic disease among the cultivars compared to high light intensity (100-200 uE/m$^2$/sec). PVX and PVY, as well as the combination of PVX and PVY in the same plant, decreased plant height compared to the uninoculated (healthy) controls. Low light intensity and dual infections of PVX and PVY significantly increased mosaic disease severity in Shepody and Red LaSoda, but not in Russet Norkotah. Results of these studies refute the suggestion that Russet Norkotah is resistant to PVY infection since virus titers in this cultivar are similar to the known susceptible cultivars Shepody and Red LaSoda. These results further suggest that while Russet Norkotah is fully susceptible to infection by PVY, it resists symptom expression.**

## RESUMEN

**Este estudio se realizó con el fin de investigar los factores que afectan la expresión de los síntomas del virus Y de la papa en tres cultivares, Russet Norkotah, Shepody y Red LaSoda. Los resultados del ensayo inmunoabsorbente ligado a la enzima cuantitativa (ELISA) revelaron algunas diferencias en el título relacionado del virus entre los cultivares examinados. El título del virus Y de la papa (PVY) se desarrolló rápidamente tanto en el cv. Russet Norkotah como en los cvs. Shepody y Red LaSoda. Se realizaron estudios adicionales para determinar los efectos de la intensidad de la luz y de las infecciones de PVY y del virus X (PVX), solos y en combinación, sobre la expresión de los síntomas del mosaico en esos tres cultivares. La baja intensidad de la luz (270-330 uE/m2/sec) incrementó significativamente la altura de la planta y la severidad de la enfermedad del mosaico entre los cultivares en comparación con la alta intensidad de la luz (100-200 uE/m2/sec). La presencia de PVX y PVY así como la combinación de ambos en la misma planta, redujo la altura de la planta en comparación con los controles no inoculados (sanos). La baja intensidad de la luz y la infección dual de PVX y PVY incrementaron significativamente la severidad de la enfermedad del mosaico en los cvs. Shepody y Red LaSoda, pero no en el cv. Russet Norkotah. Los resultados del estudio refutan la sugerencia de que Russet Norkotah es resistente a la infección del PVY, ya que el título del virus de este cultivar es similar a los cultivares de Shepody y Red Lasoda de susceptibilidad conocida. Estos resultados sugieren ampliamente que mientras el cv. Russet Norkotah es altamente susceptible a la infección por PVY, es resistente a la expresión de los síntomas.**

## INTRODUCTION

Potato virus Y (PVY) infection in potatoes is typically expressed as a mosaic symptom (deBokx and Huttinga 1981). The Red LaSoda cultivar expresses severe mosaic symptoms when infected with PVY (Bagnall and Tai 1986), whereas potato

Accepted for publication November 29, 2001.
ADDITIONAL KEY WORDS: Potato virus Y, *Solanum tuberosum*, mosaic, latent carrier.

cultivars Russet Norkotah (Johansen et al. 1988) and Shepody do not typically express symptoms (Draper and Gudmestad, personal observation). Cultivars that do not express symptoms even though they are infected have been described by various authors as resistant, tolerant or symptomless carriers (Cooper and Jones 1983; Johansen et al. 1988; Whitehead 1937). Potato resistance to a plant virus is generally through inhibition of virus replication or through restriction of virus transport or movement (Maule 1991; White and Antoniw 1991), but resistance to symptom expression has not been well characterized at the genetic or physiological level. Information regarding the "resistance" responses of Shepody and Russet Norkotah to PVY is fragmented and incomplete.

The Shepody potato cultivar, released in 1983 by Ag-Canada, New Brunswick, is described as susceptible to PVY (Young et al. 1983). Apparently, Shepody develops typical symptoms from PVY infections in the Atlantic seaboard and Maritime Provinces of Canada. In the north central United States, Shepody develops typical mosaic symptoms early in the growing season, but not on later plant growth. The relationship between virus titer and the expression of symptoms has not been described in Shepody. Singh and Somerville (1987) suggested that Shepody should be classified as a group A, or very susceptible, cultivar.

The Russet Norkotah cultivar does not display severe symptoms from PVY infection, even when the virus can be readily detected by enzyme-linked immunosorbant assay (ELISA) (Johansen et al. 1988). Because the mosaic symptomatology is indistinct and may vary in intensity over the course of a growing season, visual assessments for PVY in Russet Norkotah are unreliable (Henn et al. 1995). Russet Norkotah plants with up to 28% PVY infection showed no yield loss, perhaps because the infection was from a mild strain of the virus or because Russet Norkotah was tolerant to PVY (Secor et al. 1983). When Hane and Hamm (1999) evaluated PVY-infected plants of Russet Norkotah and Shepody, they concluded that both are fully susceptible from the substantial yield losses detected in both cultivars.

Characterization of a potato virus infection by symptoms alone is very difficult. Mehdizadegan and Bourgoin (1994) found that 50% of field-grown Shepody plants with severe mosaic symptoms were infected with both PVY and PVX, 70% of plants expressing mild mosaic symptoms were infected with PVY and PVX. In this study, all surveyed plants were infected by potato virus M (PVM) and by potato virus S (PVS). In North Dakota, mosaic symptoms in potato were not associated with PVM, but PVS occurred frequently in plants with apparent mosaic symptoms (Draper 1990; Gudmestad unpublished).

Titers of some viruses in infected plants have been determined (Banik and Zitter 1990; Hewings et al. 1990). Peterschmitt et al. (1992) used quantitative ELISA to monitor the titer of maize streak virus in corn genotypes. They determined that, while the virus could be detected in the tolerant genotype, it was present at lower levels, suggesting a resistant response rather than one of true tolerance. The virus also appeared to replicate at a slower rate in the tolerant genotype. When titers of wheat streak mosaic virus (WSMV) were determined in different wheat genotypes, the Triumph 64 cultivar, described as having a low-level resistance or tolerance, also had consistently lower virus titers compared with the susceptible Centurk cultivar (Seifers and Martin 1988). The behavior of the virus in Triumph 64 suggests a host-resistant response based on reduced virus replication.

Light intensity influences symptoms of several virus diseases. Subterranean clover (*Trifolium subterraneum* L.) infected with subterranean clover red leaf virus produced more obvious red leaf symptoms under high light intensity than under low light intensity (Helms et al. 1987). Conversely, when cucumber mosaic virus was inoculated into plants of different cultivars of marrow (*Cucurbita pepo* L.) grown under different light intensities, symptoms were suppressed in plants grown at high light intensity, while virus expression in one cultivar, Goldrush, was unaffected by light intensity (Pink and Walkey 1985). Light intensity also influenced systemic movement of cauliflower mosaic virus (CaMV). Chimeric forms of CaMV were developed in the laboratory between a normal strain of the virus and a strain that lacked the ability to move systemically in any solanaceous host (Qiu and Schoelz 1992). Under low light intensity, cool temperatures and short days, systemic movement of chimeric forms of CaMV in *Nicotiana bigelovii* S. Wats. and *Datura stramonium* L. was prevented. Jensen et al. (1985) has shown that reduced light intensity did not influence titer of maize dwarf mosaic virus in sorghum, but the reduced light affected the growth of the sorghum.

The objective of this study was to categorize Shepody and Russet Norkotah as PVY-resistant or susceptible relative to Red LaSoda. Resistance was measured as the relative rate of replication of PVY, as measured by quantitative ELISA, in the cultivars over time. The impact of the virus on these cultivars was also determined by rating plants for growth after inoculation and disease development using combinations of light intensity and combinations of virus infection.

# MATERIALS AND METHODS

## *Standard Curve for PVY in ELISA*

Derivation of a standard curve from known virus concentrations is important to provide relative absorbance values that estimate virus quantity in unknown samples. Samples of 500, 100, 50, or 25 ng of purified PVY (Agdia, Inc., Elkhart, IN) were blended in a 1:20 dilution of healthy plant sap with PBST extraction buffer (Na2SO4 [1.59g/L], PVP-40 [20.0g/L] NaN3 [0.2g/L] Ovalbumin [2.0g/L] Tween 20 [2.0g/L] pH7.4), and were assessed in duplicate ELISA plates. The 500 ng sample was used to determine the development endpoint for the plate. Absorbance ($A_{405}$) was measured at 15 and 30 min after adding substrate. Mean absorbance data, as determined by simple averaging of the two plates, were plotted against known PVY concentrations. The data were analyzed using logarithmic regression to reflect the kinetics of substrate hydrolysis (Powerpoint, Microsoft Corporation, Redmond, WA).

## *Titer of PVY in Three Inoculated Potato Cultivars Over Time*

Single-eye seedpieces of Red LaSoda, Russet Norkotah, and Shepody were planted in 10-cm pots. The plants were arranged in a completely random design with replications of a single plant of each cultivar. Ten plants of each cultivar were used in each of two repetitions of the experiment. When the plants reached the two-leaf stage, half the plants were inoculated with PVY. The inoculation was performed by placing five green peach aphids (*Myzus persicae* Sulzer) on one leaf of the young plants. The aphid colony was obtained from the University of Minnesota (courtesy of D.W. Ragsdale). The colony had been established from a field collection followed by separation of individuals (Putnam 1990) and selected for resistance to the insecticide esfenvalerate (Asana®), a synthetic pyrethroid. A resistant population allowed the regular treatment of the colony with esfenvalerate to avoid contamination with parasitoids and aphids that were not resistant to this insecticide. Only apparently mature apterous aphids were used. The aphids were reared on Chinese cabbage (*Brassica pekinensis* (Lour.) Rupr.), cv. Jade Pagoda (Harris Seeds, Rochester, NY). The aphids were teased off the reservoir plants with a camel hair paintbrush and starved for 2 to 3 h. After starvation the aphids then were allowed to acquire PVY from a detached leaf of PVY-infected potato, cv. Redsen, for 30 to 120 sec. The aphids then were transferred with the paintbrush to the target plants. The inoculation process was repeated 3-5 days later with a second set of five aphids. An equal number of uninfected control plants were each exposed to five aphids, which had been starved but not allowed to acquire PVY. Aphids in all treatments were killed by spraying the plants with aerosol acephate (Orthene, Whitmire PT-1200) 12 h after being placed on the plants. The plants were grown in a controlled environment growth chamber (Conviron CMP3023, Asheville, NC) for 28 days, with sampling occurring before inoculation and every 7 days thereafter. Light conditions in the chamber were 125-200 μE/m²/sec and temperature was maintained at 21 C daylight and 18 C nighttime, ± 1-2 C.

Disks of leaf samples were collected, stored in high humidity boxes and processed according to a previously established procedure, outlined below, determined during preliminary studies. Briefly, this involved excising leaf disks weekly, from three locations within each plant using a number four cork borer (8 mm). Plant tissue was weighed immediately. As the plants grew, samples were taken from younger foliage, produced at successively higher locations on the plant, representing the bottom, middle, and top of the plant. Sampling of the middle leaf commenced 2 wk after inoculation, with the top leaf 3 wk after inoculation. A distance of approximately three nodes separated sampling sites (top, middle, and bottom). The top site on the plant was at or near the termination of growth of the plant at the end of the study period. Leaf disks were held intact in a humid box at 5 C until all tissue could be processed with sample extraction buffer 1:20 (wt:vol), ground in a microfuge tube with a pellet pestle and hand-held electric-powered motor, and loaded in duplicate ELISA wells. Samples were incubated overnight (12-16 h), and the plates were washed three times with PBST. Alkaline phosphatase conjugated anti-PVY antibody was added at 1.5 times the normal concentration and incubated for 4 h at 23 C. The plates were washed three times with PBST and loaded with PNP substrate (1 μg/ml). Plates were allowed to develop for about 30 min until the 500 ng/ml known standard reached an $A_{405}$ of about 2.0. Wells were zeroed against the average of duplicate healthy control wells of cv. Norchip sap. Data were analyzed by ANOVA (SAS Institute, Cary, NC) for each sampling date and plotted in comparison of the cultivars over time. Means were separated by LSD ($P$=0.05). The study was performed twice, and data were combined from two experiments after variances were determined to be homogeneous.

## *Effects of PVX, PVY and Light Intensity on Mosaic Symptom Expression in Three Potato Cultivars*

Ten plants each of the three cultivars in this study, Red

LaSoda, Russet Norkotah, and Shepody, were grown in a greenhouse arranged as a 4x3x2 factorial with a completely random design within each light treatment. The experiment was composed of four virus inoculation combinations, three cultivars, and two conditions of light intensity. High light intensity (270-330 μE/m²/sec) was created by supplementing natural light with 500-watt high-pressure sodium lamps. Low light conditions (100-120 μE/m²/sec) were simulated by suspending a mesh shade cloth over and around a greenhouse bench in the same cubicle in which the high light conditions were created. The same supplemental light source was used in the low light conditions as the high light conditions in order to maximize uniform light dispersion, even though the plants were shaded. Light intensity was measured with a light meter during the mid-morning hours on cloudy and clear days. Interference from external light sources in adjacent greenhouses was excluded by covering the exterior walls of the greenhouse with aluminum foil. Daytime temperatures were maintained at 23 C ± 2 C, and nighttime temperatures were maintained at 20 C ± 2 C.

Virus-inoculated treatments included PVX alone, PVY alone, dual inoculation of adjacent leaves with each virus (PVX and PVY), and a buffer control (healthy). Each treatment was replicated 10 times with a single plant per replication within each virus x cultivar x light intensity combination. Plants were mechanically inoculated with PVX and PVY (Matthews 1991). Infested plant sap used to make inoculations was extracted from reservoir potato plants (Norchip and Redsen) that were previously inoculated with purified PVX or PVY. The reservoir plants were tested by ELISA to confirm the presence of the target virus. Virus-infected sap was extracted with a ball bearing tissue macerator (Agdia, Inc., Elkhart, IN) and filtered through cheesecloth. Infected sap was diluted 1:5 (vol/vol) with 0.2 M potassium phosphate buffer supplemented with ascorbic acid and stored on ice. Plants were cut off at the second node to stimulate new leaf growth, and two basal leaves were labeled with nail polish and inoculated. PVX was inoculated by leaf rubbing on carborundum-(400 mesh) dusted plants. PVY was inoculated by high-pressure spray (413.7 kPa) delivered through a $CO_2$-driven paint sprayer. Carborundum was included in the inoculum suspension to incite wounding. Different, adjacent leaves were inoculated with each virus in the treatments that included both PVX and PVY. Inoculations were repeated 3 days later. Plants were allowed to grow for 3 wk, tested by ELISA to confirm infection, plant heights were obtained and each plant was rated for expression of visual symptoms of disease. The increase in plant height was determined by determining the growth of the plant from the inoculated leaf to the new growing point. At the time of inoculation, plants were selected based on size uniformity. The inoculated leaf was labeled with a dot of nail polish and growth was measured from that node to the growing terminal of the plant. Disease was rated on a four-point scale similar to that used by Bagnall and Tai (1986). The rating system used was as follows: 0 (zero) - no visible symptoms; 1 (one) - mild symptoms, generally mottle or mosaic, possible mild leaf crinkle; 2 (two) - moderate symptoms; and 3 (three) - severe mosaic, possible rugosity, development of necrosis. Data for plant height and disease rating were each analyzed by ANOVA (SAS Institute, Cary, NC). Means were separated by Fischer's protected LSD ($P$=0.05). The experiment was performed twice. Data from each experiment were combined after determining that variances were homogeneous.

# RESULTS

## *Standard Curve for PVY in ELISA*

Absorbance ($A_{405}$) values fit a logarithmic curve model (data not shown). The $R^2$ values for samples incubated 15 min or 30 min were 0.948 and 0.857, respectively. The data suggest that tissue samples with 500 ng/ml of PVY will reach the desired level of $A_{405}$ 2.0 in 15-30 min. They also show that ELISA absorbance values can be used to reflect relative PVY virus titer. Specifically,

TABLE 1—*Detection of PVY from inoculated potato cultivars over a 4-wk period. Absorbance values were determined from ELISA tests for PVY.*

| Cultivar | Treatment | Sampling Date (Weeks after inoculation) | | | | |
|---|---|---|---|---|---|---|
| | | 0 | 1 | 2 | 3 | 4 |
| Red LaSoda | Noninoculated | 0.010[a] | 0.019 | 0.009 | -0.005 | -0.002 |
| Red LaSoda | PVY-Inoculated | 0.010 | 0.483 | 0.667 | 2.236 | 1.996 |
| Russet Norkotah | Noninoculated | 0.012 | 0.018 | 0.014 | -0.001 | -0.005 |
| Russet Norkotah | PVY-Inoculated | 0.017 | 1.124 | 0.876 | 2.161 | 1.837 |
| Shepody | Noninoculated | 0.013 | 0.016 | 0.010 | -0.005 | -0.003 |
| Shepody | PVY-Inoculated | 0.013 | 0.683 | 0.786 | 2.120 | 2.073 |
| LSD (P=0.05) | | 0.002 | 0.419 | 0.447 | 0.260 | 0.202 |

[a]Values are mean absorbance values ($A_{405}$) from ELISA tests. Larger values reflect higher virus titer. Negative values are artifacts of zeroing absorbance against healthy plant sap.

TABLE 2—*Effect of light intensity, virus infection, and PVY infection in plants of three potato cultivars 21 days after inoculation.*

| Light Intensity | | | Virus Infection | | | Mosaic Symptoms | |
|---|---|---|---|---|---|---|---|
| Treatment | Mean Increase in Plant Height[a] (cm) | Mean Disease Rating[b] | Treatment | Mean Increase in Plant Height[a] (cm) | Mean Disease Rating[c] | Cultivar | Mean Disease Rating[b] |
| Low light | 7.60 | 0.46 | Healthy | 6.79 | 0.00 | Shepody | 0.60 |
| High light | 1.74 | 0.20 | PVX | 4.27 | 0.18 | Red LaSoda | 0.30 |
| | | | PVY | 3.85 | 0.37 | R. Norkotah | 0.09 |
| | | | PVX+PVY | 3.78 | 0.77 | | |
| LSD(P=0.05) | 0.52 | 0.22 | LSD(P=0.05) | 0.74 | 0.17 | LSD(P=0.05) | 0.15 |

[a]Means for increase in plant height are based on ten replicates.
[b]Means for disease rating are based on ten replicates.
[c]0 (zero) - no visible symptoms; 1 (one) - mild symptoms, generally mottle or mosaic, possible mild leaf crinkle; 2 (two) - moderate symptoms; and 3 (three) - severe mosaic, possible rugosity, development of necrosis.

unknown samples incubated 30 min and confirmed positive with an absorbance value of $A_{405}$ 2.0 would have a virus titer of at least 150 ng/ml.

## *Titers of PVY in Three Inoculated Potato Cultivars Over Time*

Differences in virus titer relative to leaf position were not significant for any cultivar during the sampling period (data not shown). Furthermore, few differences in virus titer were detected among the cultivars. PVY titers developed more rapidly during first week after inoculation in Russet Norkotah than in the other two cultivars, and these differences were significant (Table 1). Two weeks following inoculation, the PVY-inoculated Russet Norkotah plants had slightly lower PVY titers than they had the previous week. However, the absorbance values remained significantly higher than those of noninoculated controls. Relative virus titer increased rapidly during the third week following inoculation. PVY titer was not significantly different among the three cultivars at that date (Table 1). The PVY titer continued to increase in Red LaSoda and Shepody and there were no significant differences among the inoculated cultivars (Table 1).

During the fourth week following inoculation, the relative titer of PVY stabilized or declined slightly in all cultivars. Inoculated Shepody plants had a significantly higher PVY titer than inoculated Russet Norkotah but not higher than inoculated Red LaSoda plants. PVY titers of Red LaSoda and Russet Norkotah were not significantly different (Table 1).

TABLE 3—*Analysis of variance for plant height of Russet Norkotah, Shepody, and Red LaSoda plants, infected with PVY, PVX, or PVX+PVY under high or low light conditions.*

| Source of Variation | DF | Error | F Value | P > F |
|---|---|---|---|---|
| Rep | 9 | 17.49 | 2.14 | 0.0251 |
| Model | 33 | 193.96 | 23.74 | 0.0001 |
| Light | 1 | 4173.66 | 510.89 | 0.0001 |
| Cultivar | 2 | 5.44 | 0.67 | 0.5146 |
| Light x Cultivar | 2 | 2.64 | 0.32 | 0.7237 |
| Virus | 3 | 242.43 | 29.68 | 0.0001 |
| Light x Virus | 3 | 262.54 | 32.14 | 0.0001 |
| Cultivar x Virus | 6 | 45.42 | 5.56 | 0.0001 |
| Light x Virus x Cultivar | 6 | 44.12 | 5.4 | 0.0001 |
| Experiment | 1 | 1.41 | 0.17 | 0.6816 |
| Error | 446 | 8.17 | | |
| Corrected Total | 479 | | | |

## *Effects of PVX, PVY, and Light Intensity on Mosaic Symptom expression in Three Potato Cultivars*

Low light intensity was a critical and significant factor in plant height (Table 2). In the analysis of variance, light was a highly significant main effect ($P$=0.0001) (Table 3). Under low light intensity, plants developed elongated internodes and grew taller than plants grown under high light intensity. However, no significant interaction of light intensity with cultivar (Figure 1A, Table 3) was observed. The heights of non-inoculated control plants were significantly greater than virus-infected potato plants (Table 2, Figure 1B), with the exception of Shepody (Figure 2). Differences between non-inoculated and inoculated plants were most obvious when plants had been grown under low light (Figure 1B), and a highly significant interaction occurred between light intensity and virus infection (Table 3).

A highly significant interaction occurred between virus infection and cultivar with regard to change in plant height (Table 3). The greatest change in height was observed with virus infected plants of Russet Norkotah and Red LaSoda (Figure 2A). Differences between the various virus treatments were less evident with Shepody. In Russet Norkotah and Red LaSoda, any

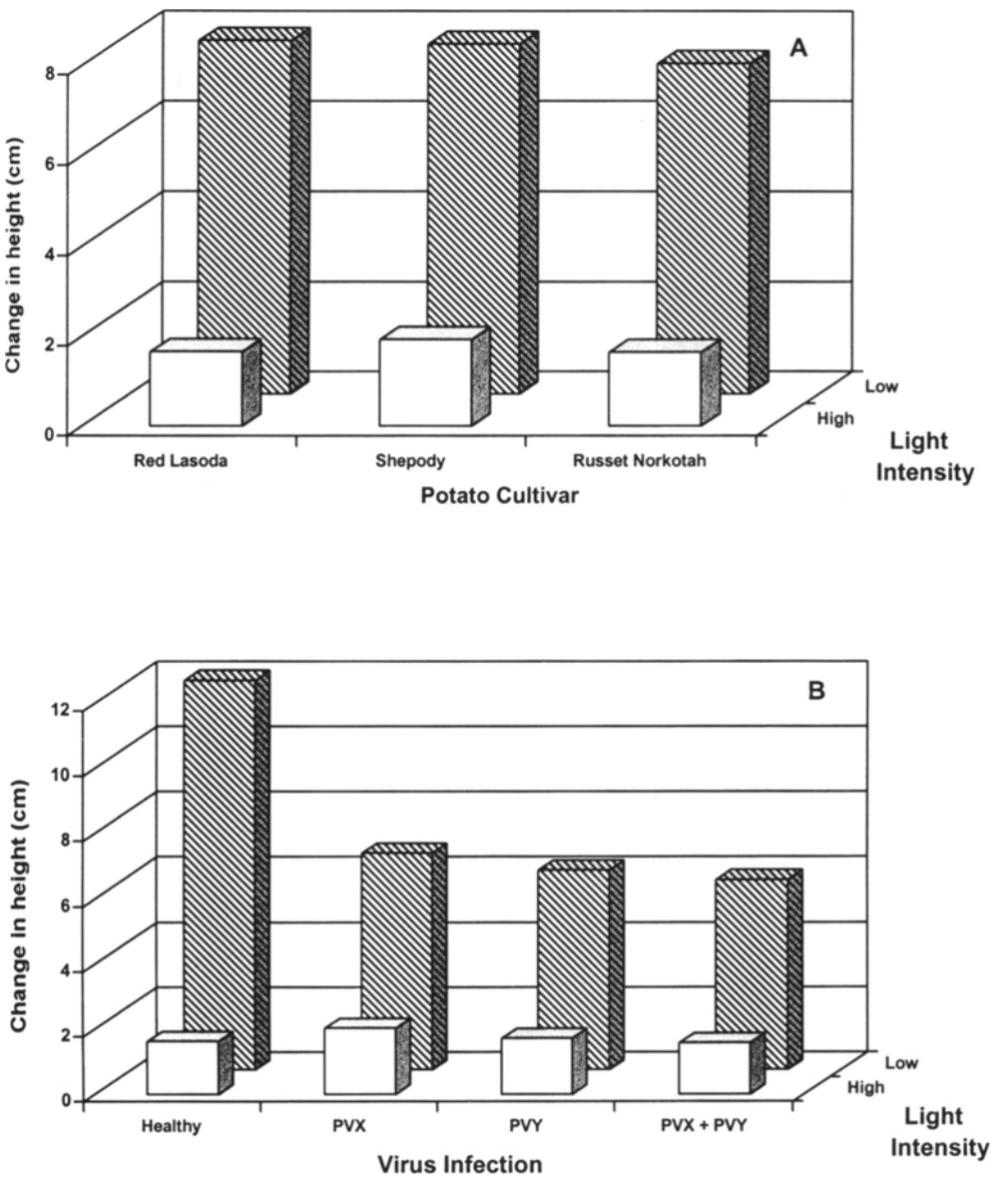


**FIGURE 1.**
**Influence of light intensity on potato cultivars and virus infection on change in plant height. (A) Effect of light on all cultivars and (B) Effect of virus infection and light intensity. Plant height measured from the inoculated leaf to the new growing point.**

virus infection resulted in reduced growth. However, this response was not observed with Shepody (Figure 2A). PVX had no effect on the growth of Shepody and the interaction of light intensity with PVX also had little effect on the growth of this cultivar (Figure 2B).

A significant three-way interaction was observed for cultivar, light, and virus infection treatments (Table 3). The data show that, at high light intensity, the effect of virus infection may be small among the cultivar-virus combinations (Figure 2B). Much greater differences in growth were observed under low light intensity. Both Red LaSoda and Russet Norkotah had much greater growth response from PVX, PVY, and PVX+PVY infection than was observed in Shepody (Figure 2B).

Differences also were detected in disease ratings between the virus infection treatments (Table 2). While all virus-infected plants among cultivars were significantly different from the non-inoculated controls, disease severity caused by PVX alone was significantly less than either treatment containing PVY (Table 2). The PVX+PVY treatment showed the greatest reduction in growth rate (Table 2, Figure 2) and highest disease rating (Table 2), regardless of light intensity (Figure 3A).

Disease development was affected significantly by cultivar, light intensity, and virus infection. Disease ratings were significantly higher on virus infected Shepody plants than on other cultivars (Figure 3B). Red LaSoda had the next highest level of disease. The disease rating of Russet Norkotah was significantly lower than the other two cultivars (Table 2, Figure 3B). Low light intensity significantly increased the expression of disease symptoms for both viruses and their combination (Figure 3). There was a significant cultivar x light intensity interaction identified for disease expression (Table 4). The interaction with light (Figure 3B) had virtually no effect on Russet Norkotah because neither PVX nor PVY was expressed in this cultivar (Figure 4). Shepody expressed symptoms of PVY infection better than either Russet Norkotah

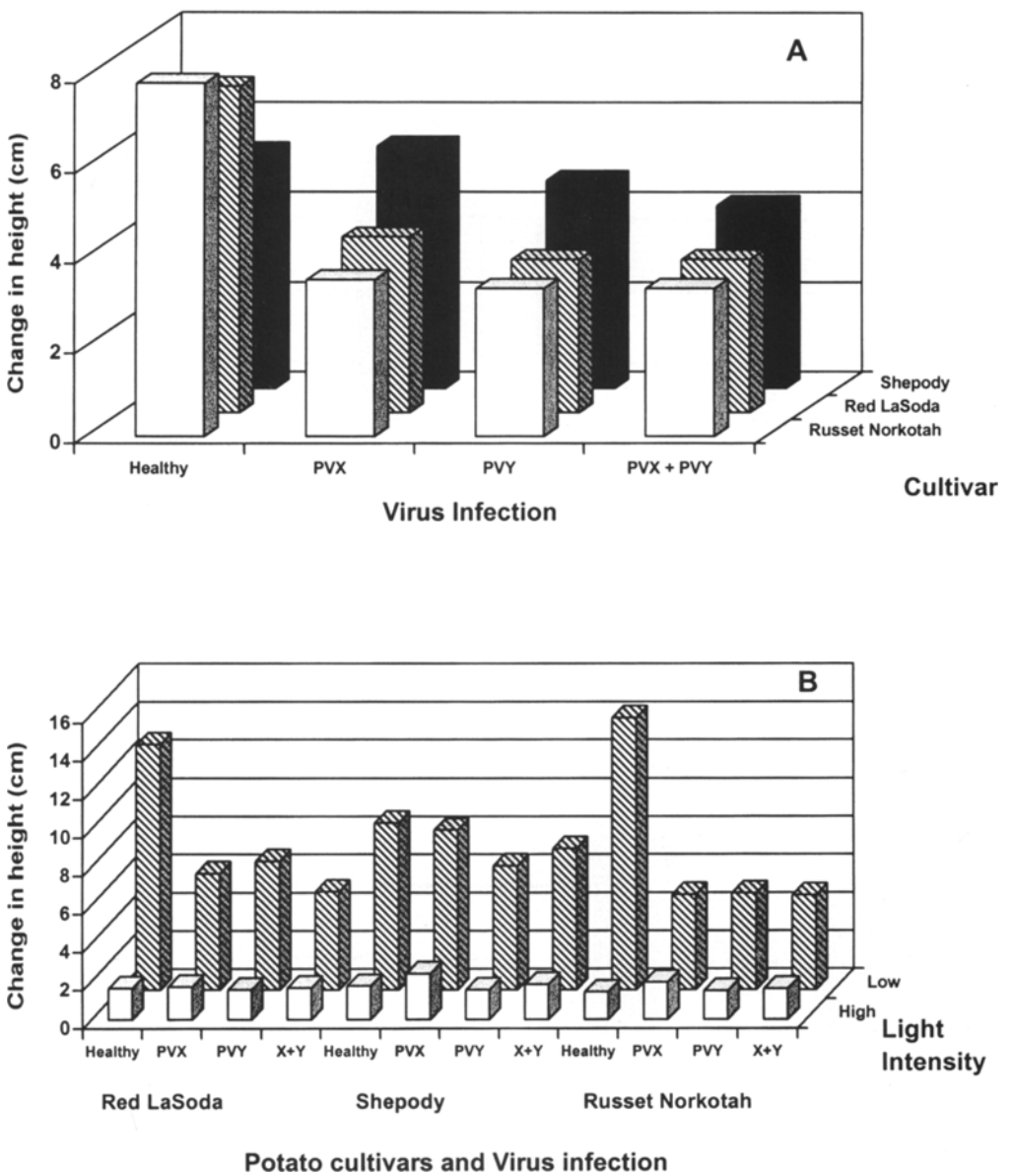


**FIGURE2.**
**Effect of combined factors on change in plant height. (A) Effect of the cultivar by virus infection interaction on plant height and (B) Effect of the three-way interaction of cultivar, virus infection, and light intensity on plant height, where H = healthy plants, X = PVX inoculated plants, Y = PVY inoculated plants, and XY = plants inoculated with both PVX and PVY. Plant height measured from the inoculated leaf to the new growing point.**

or Red LaSoda at both light intensities, whereas Red LaSoda expressed a moderate level of disease compared with the other two cultivars (Figure 3B).

Dual infection caused the most severe symptoms Shepody and Red LaSoda under each light intensity (Figure 4A). Little mosaic disease was expressed by Russet Norkotah with any treatment combination (Figure 4), although slightly more disease was observed under high light conditions (Figure 4A). The disease response of Red LaSoda was slightly less than Shepody but much greater than Russet Norkotah. The greatest disease was observed in the treatments with PVX and PVY together, followed by PVY and PVX alone, respectively (Figure 4).

## DISCUSSION

Increases in the relative titer of PVY in all three cultivars showed that all were susceptible to the virus (Table 1). Significant differences in relative PVY titer were only observed between the cultivars 1 wk and 4 wk after inoculation. Some cause for differences in the first week may be an artifact of low vector success in the transmission of the virus by green peach aphids on individual plants. Rough handling or the selection of recently molted aphids could have limited the efficiency or ability of the aphids to transmit PVY. However, such obstacles to vector efficiency would be expected to affect all three cultivars similarly. Relative virus titers of Russet Norkotah were the highest of any cultivar tested at the first sampling date.

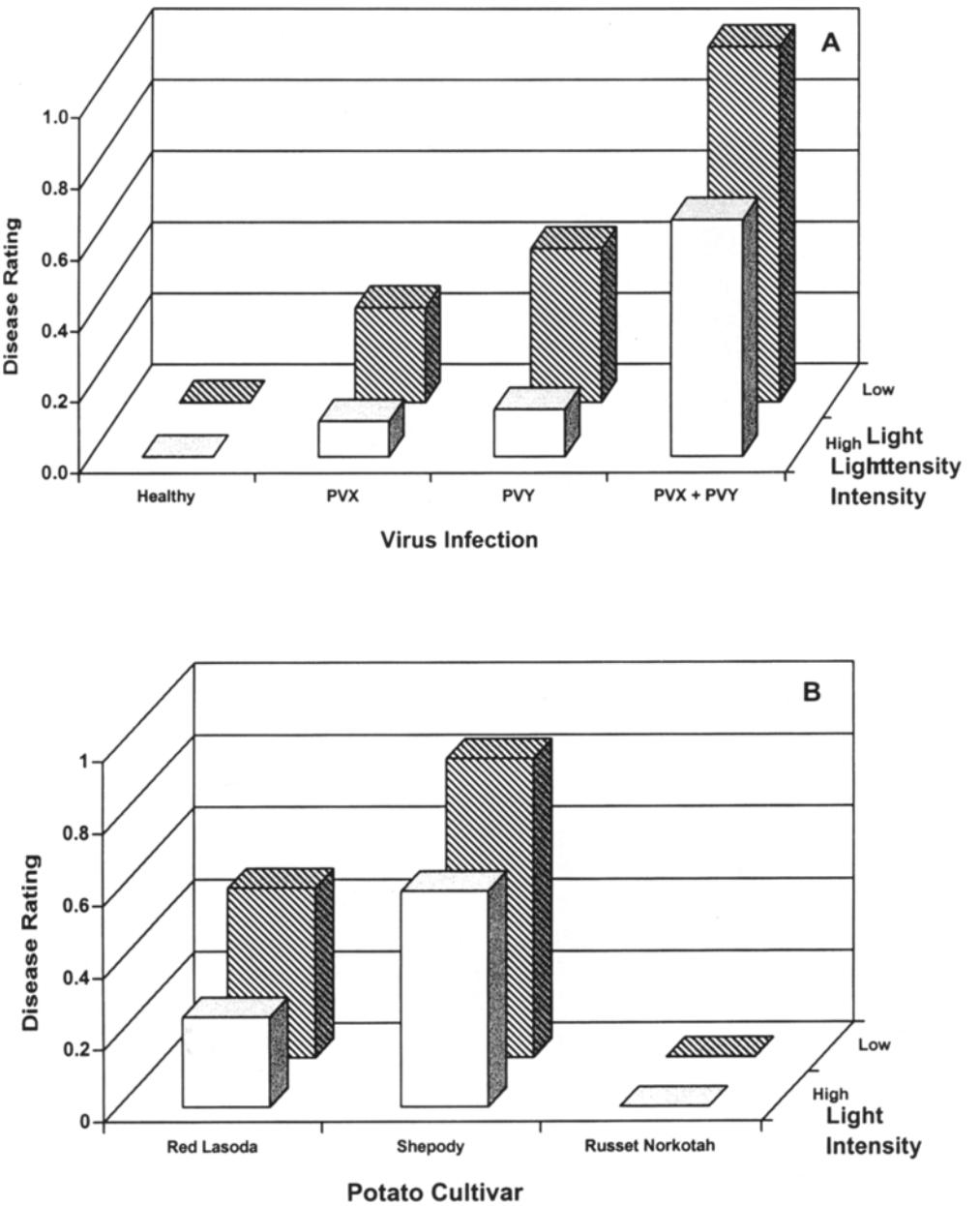


**FIGURE 3.**
**Interaction of light intensity with cultivars and virus disease rating. (A) Interaction of light intensity with cultivars and (B) Interaction of virus infection with light intensity. Ratings are as follows: 0 (zero)- no visible symptoms; 1 (one) - mild symptoms, generally mottle or mosaic, possible mild leaf crinkle; 2 (two) - moderate symptoms; and 3 (three) - severe mosaic, possible rugosity, development of necrosis. Plant height measured from the inoculated leaf to the new growing point.**

The depressed ELISA response in week two (Table 1) could have been a response to decreased virus detected in the lower leaves. By this time, many of the plants were beginning to undergo senescence in the lower canopy because of shading. Virus titer could have been lower in this senescent tissue. In the final week of the study, the PVY titer in Russet Norkotah and Red LaSoda decreased slightly (Table 1). This characteristic of the virus in the plant has been described with other potato cul-

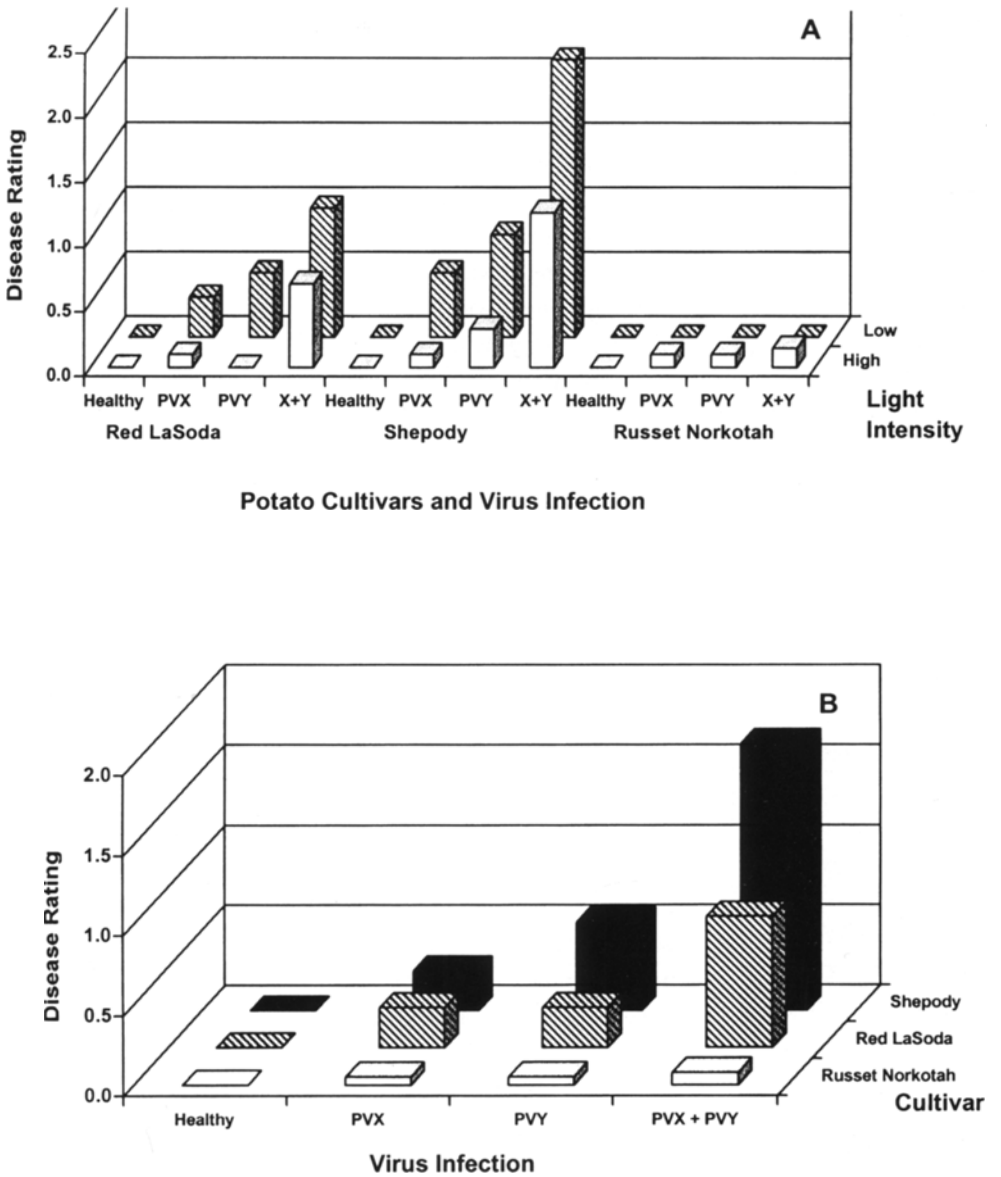


**FIGURE 4.**
**Effect of combined factors on disease rating. (A) Effect of cultivar by virus infection on disease rating and (B) Effect of three-way interaction of light intensity, cultivar, and virus infection on disease rating, where H = healthy plants, X = PVX inoculated plants, Y = PVY inoculated plants, and XY = plants inoculated with both PVX and PVY. Ratings are as follows: 0 (zero) - no visible symptoms; 1 (one) - mild symptoms, generally mottle or mosaic, possible mild leaf crinkle; 2 (two) - moderate symptoms; 3 (three) - severe mosaic, possible rugosity, development of necrosis. Plant height measured from the inoculated leaf to the new growing point.**

tivars (Singh and Somerville 1987) and with older plant tissue (Peterschmitt et al. 1992). The levels of PVY in Shepody were essentially unchanged from the measurement the previous week. These data show agreement with Singh and Somerville (1987), who identified Shepody as a potato cultivar highly susceptible to PVY.

Continued increase in relative virus titer over the five-week period indicates that there is no apparent suppression of virus replication within Russet Norkotah. Russet Norkotah did not have a relative virus titer significantly lower than the known susceptible, Red LaSoda, at any time in the 5-wk span. Further, the leaf position sampled was not a significant factor in the experiment. Restriction of virus movement is often cited as a source of host resistance (Maule 1991). Since differences were not detected between the three leaf positions sampled, it can be concluded that there is no greater inhibition of virus movement in Russet Norkotah or Shepody when compared to Red LaSoda. Shepody also appears fully susceptible to PVY$^{o}$. There was no suppression of virus titer, as would be expected in a resistant reaction, and movement of the virus did not appear to be restricted.

The light intensity studies support the premise that Shepody is highly susceptible to PVY. Shepody appears to express mosaic symptoms more readily when PVY and PVX are present in the same plant. Under low light conditions, this characteristic was exacerbated (Figure 4A). Previously, the only published study considering light effects on PVY expression showed that inoculation efficiency was not enhanced by exposing plants to a pre-inoculation dark period (Singh et al. 1988). Symptom expression can be enhanced, however, by certain environmental conditions. It is known that PVX is more

TABLE 4—*Analysis of variance for mosaic disease rating in Russet Norkotah, Shepody, and Red LaSoda, infected with PVY, PVX, or PVX+PVY under high or low light conditions.*

| Source of Variation | DF | Mean Square | F Value | P > F |
|---|---|---|---|---|
| Rep | 9 | 0.24 | 1.02 | 0.4205 |
| Model | 33 | 3.83 | 16.46 | 0.0001 |
| Light | 1 | 5.42 | 23.27 | 0.0001 |
| Cultivar | 2 | 13.23 | 56.79 | 0.0001 |
| Light x Cultivar | 2 | 2.93 | 12.56 | 0.0001 |
| Virus | 3 | 16.47 | 70.72 | 0.0001 |
| Light x Virus | 3 | 0.84 | 3.61 | 0.0134 |
| Cultivar x Virus | 6 | 5.16 | 22.15 | 0.0001 |
| Light x Virus x Cultivar | 6 | 0.61 | 2.64 | 0.0160 |
| Experiment | 1 | 0.05 | 0.22 | 0.6365 |
| Error | 446 | 0.23 | | |
| Corrected Total | 479 | | | |

likely to express a mild mosaic symptom under cooler temperatures (Beemster and deBokx 1987). PVX expression is commonly observed under cloudy conditions (low light intensity) in the field particularly in cv. Russet Burbank by seed certification officials, and by the authors (Gudmestad, personal observation).

In these studies, Shepody expressed more severe disease symptoms as a response to virus infections in the low light intensity treatments than in the high light intensity treatments. The results of this study indicate that Shepody is a susceptible cultivar that will express symptoms of disease following primary infection. Symptom expression may have a different relationship with tuber-borne PVY (secondary infection). These studies do not address the relationship of secondary PVY infection with symptom expression. The small change in plant height between the healthy and PVY-infected Shepody plants provide some evidence to suggest a tolerant relationship between PVY and Shepody (Figure 2).

Mosaic symptoms in Russet Norkotah developed very poorly when challenged with PVX, PVY, or the combination (Figure 4). However, PVY appeared to replicate and move in the plant at a rate similar to Red LaSoda, a known susceptible cultivar (Table 1). The relationship between virus titer in the two cultivars would suggest susceptibility, and, based on these characteristics, the standardized terminology suggested by Cooper and Jones (1983) would characterize Russet Norkotah as susceptible. These results also indicate that Russet Norkotah expresses characteristics of tolerance rather than sensitivity, as in Red LaSoda and Shepody. Very low disease ratings in virus-infected Russet Norkotah, regardless of light intensity, suggest few deleterious effects from any combination of virus. However, reduced plant growth under low light intensity when infected with PVX, PVY, or PVX+PVY suggests an impact of these viruses on Russet Norkotah growth (Figure 2B). It has been suggested that, if PVX had not been eliminated through latent virus testing programs throughout much of the U.S, PVY would be more readily detected through the visual inspection process. These data reject that hypothesis with regard to Russet Norkotah. Dual infections of PVX+PVY were not significantly different in disease response from plants infected with either virus alone. It is clearly evident from the high rate of apparent replication of the virus in Russet Norkotah that the cultivar is not resistant to PVY. Resistance may be imparted through a number of avenues: resistance to infection, resistance to multiplication, or resistance to movement. In each case, Russet Norkotah appears to be fully susceptible. The question of sensitivity or tolerance represents a continuum within a susceptible host. The absence of symptoms suggests that the cultivar is at least partially tolerant.

Hane and Hamm (1999) suggested that Russet Norkotah is susceptible, and presumably sensitive to PVY, based on comparisons of yield from infected plants to uninfected plants grown in commercial potato fields. However, many sources of variability are inherent with survey data from growers' fields. Studies reported here provide a better understanding of the relationship of PVY in Russet Norkotah and provides strong evidence that the cultivar is susceptible to, infection and replication of Potato Virus Y but resistant to symptom expression.

## ACKNOWLEDGMENTS

The authors wish to extend their gratitude for the financial support of this research by the Red River Valley Potato Growers Association.

## LITERATURE CITED

Bagnall, R.H., and G.C.C. Tai. 1986. Field resistance to potato virus Y in potato assessed by cluster analysis. Plant Dis 70:301-304.

Banik, M.T., and T.A. Zitter. 1990. Determination of cucumber mosaic virus titer in muskmelon by enzyme linked immunosorbent assay and correlation with aphid transmission. Plant Dis 74:857-859.

Beemster, A.B.R., and J.A. deBokx. 1987. Potato virus X (a potexvirus). *In*: Viruses of Potato and Seed Potato Production, 2nd ed. Pudoc, Wageningen, Netherlands. 259 pp.

Clarke, R.G. 1995. Director of seed potato certification. Idaho Crop Improvement Association. Personal communication.

Cooper, J.I., and A.T. Jones. 1983. Responses of plants to viruses: Proposal for the use of terms. Phytopathology 73:127-128.

deBokx, J.A., and H. Huttinga. 1981. Potato virus Y, No. 242 (No. 37 revised) In: Descriptions of Plant Viruses. CM I/AAB New Surrey, England.

Hane, D.C., and P.B. Hamm. 1999. Effects of seedborne potato virus Y infection in two potato cultivars expressing mild disease symptoms. Plant Dis 83:43-45.

Helms, K., W.J. Muller, and P.M. Waterhouse. 1987. Subterranean clover red leaf virus disease: Effects of light intensity on plant symptoms, growth and virus content. Phytopathology 77:1297-1300.

Henn, R.A., J.G. Phillips, and R.G. Brown. 1995. Russet Norkotah; A potato cultivar latently infected by PVY$^{0}$. Am Potato J 72:629-630 (Abst).

Hewings, A.D., V.D. Damsteegt, A.E. Sindermann, and S.A. Tolin. 1990. Variations in serologically detectable antigen of Soybean Dwarf Virus in soybean leaflets as a function of time after inoculation and plant age. Plant Dis 74:844-848.

Jensen, S.G., M.K. Palomar, E.M. Ball, and R. Samson. 1985. Factors influencing virus titer in maize dwarf mosaic virus infected sorghum. Phytopathology 75:1132-1136.

Johansen, R.J., B. Farnsworth, D.C. Nelson, G.A. Secor, N. Gudmestad, and P.H. Orr. 1988. Russet Norkotah: A new russet-skinned potato with wide adaptation. Am Potato J 65:597-604.

Lapidot, M., I. Paran, R. Ben-Joseph, S. Ben-Harush, M. Pilowsky, S. Cohen, and C. Shifriss. 1997. Tolerance to cucumber mosaic virus in pepper: Development of advanced breeding lines and evaluation of virus level. Plant Dis 81:185-188.

Matthews, R.E.F. 1991. Transmission, Movement, and Host Range. *In*: Plant Virology, 3rd ed. Academic Press, New York. pp. 338-378.

Maule, A.J. 1991. Virus movement in infected plants. Crit Rev Plant Sci 9:457-473.

Mehdizadegan, F., and T. Bourgoin, 1994. Relationships between mosaic symptom expression in field infection by PVM, PVS, PVX, and PVY in variety Shepody. Am Potato J 71:687-688 (Abst).

Peterschmitt, M., J.B. Quiot, B. Reynaud, and P. Baudin. 1992. Detection of maize streak virus antigens over time in different parts of maize plants of a sensitive and so-called tolerant cultivar by ELISA. Ann Appl Biol 121:642-653.

Pink, D.A., and D.G.A. Walkey. 1985. Effect of temperature and light intensity on resistance in Marrow (*Cucurbita pepo*) to cucumber mosaic virus. J Agric Sci 104:325-329.

Putnam, C. 1990. First catch your aphid then blend it. New Scientist 127:62.

Qiu, S.G., and J.E. Schoelz. 1992. Three regions of cauliflower mosaic virus strain W260 are involved in systemic infection of solanaceous hosts. Virology 190:773-782.

Ranieri, R., R.M. Lister, and P.A. Burnett. 1993. Relationships between barley yellow dwarf virus titer and symptom expression in barley. Crop Sci 33:968-973.

Secor, G.A., R. Johansen, and N.C. Gudmestad. 1983. Update on virus Y infection in ND534-4 Russ Valley Potato Grower 48:26-27.

Seifers, D.L., and T.J. Martin. 1988. Correlation of low level wheat streak mosaic virus resistance in Triumph 64 wheat with low virus titer. Phytopathology 78:703-707.

Shepard, J.F., G.A. Secor, and D.E. Purcifull. 1974. Immunochemical cross-reactivity between the dissociated capsid proteins of PVY group plant viruses. Virology 58:464-475.

Singh, R.P., S.M.P. Khurana, B.B. Nagaich, and H.O. Agrawal. 1988. Environmental factors influencing aphid transmission of potato virus Y and leafroll virus. Potato Res 31:501-509.

Singh, R.P., and T.H. Somerville. 1987. Relationship of virus concentration with the field resistance to potato virus Y in potatoes. Am Potato J 65:163-165.

White, R.F., and J.F. Antoniw. 1991. Virus-induced resistance responses in plants. Crit Rev Plant Sci 9:443-455.

Whitehead, T. 1937. Virus diseases of potato. The "carrier" problem. Its relation to symptomatology and commercial potato growing. Ann Appl Biol 24:323-341.

Young, D.A., Tarn, T.R., and Davies, H.T. 1983. Shepody: A long, smooth, white-skinned potato of medium maturity with excellent french fry quality. Am Potato J 60:109-113.