

Potato Plants Grown from Minitubers are Delayed in Maturity and Lower in Yield, but are not at a Higher Risk of *Potato virus Y* Infection than Plants Grown from Conventional Seed

Ana C. Fulladolsa^{1,2} · Kyle E. LaPlant^{1,3} · Russell L. Groves⁴ · Amy O. Charkowski²

Published online: 7 December 2017 © The Potato Association of America 2017

Abstract *Potato virus Y*(PVY) is the most important virus in North American seed potato (Solanum tuberosum L.) production. Planting virus-free minitubers in place of field-grown seed, which usually has a low PVY incidence, reduces initial PVY inoculum in the field. However, plants grown from minitubers are smaller and emerge later than those grown from conventional seed, which could make them more likely to become infected with PVY. We tested the effects of seed type of three potato cultivars (Dark Red Norland, Goldrush, and Red La Soda) on PVY incidence, tuber yield, and flowering time. The incidence of PVY in plants grown from minitubers did not differ from that of plants grown from conventional seed. Minituber-grown plants produced lower tuber yields than plants grown from conventional seed. Plants from minitubers also emerged and flowered later, but this did not increase their incidence of PVY. Cultivar-specific differences were observed in tuber yield and flowering times, suggesting that this variation may influence PVY incidence more than seed type.

Ana C. Fulladolsa ana.fulladolsa_palma@colostate.edu

- ¹ Department of Plant Pathology, University of Wisconsin-Madison, 1630 Linden Dr., Madison, WI 53706, USA
- ² Department of Bioagricultural Sciences and Pest Management, Colorado State University, 307 University Ave., Fort Collins, CO 80523, USA
- ³ Section of Plant Breeding and Genetics, School of Integrative Plant Sciences, Cornell University, Ithaca, NY 14853, USA
- ⁴ Department of Entomology, University of Wisconsin-Madison, 1630 Linden Dr., Madison, WI 53706, USA

Resumen El virus Y de la papa (PVY) es el más importante en la producción de semilla de papa (Solanum tuberosum L.) en Norteamérica. La siembra de minitubérculos libres de virus en lugar de la semilla obtenida del campo, que generalmente tiene una baja incidencia de PVY, reduce el inóculo inicial de PVY en el campo. No obstante, las plantas a partir de minitubérculos son más pequeñas y emergen más tarde que aquellas cultivadas de semilla convencional, que las pudiera hacer más propensas a infectarse con PVY. Nosotros probamos los efectos del tipo de semilla de tres variedades de papa (Dark Red Norland, Goldrush, y Red La Soda) sobre la incidencia de PVY, rendimiento de tubérculo y tiempo de floración. La incidencia de PVY en las plantas cultivadas a partir de minitubérculos no difirió de las cultivadas de semilla convencional. Las plantas de minitubérculos produjeron rendimientos de tubérculo más bajos que las de semilla convencional. Las plantas de minitubérculos también emergieron y florecieron más tarde, pero esto no aumentó su incidencia de PVY. Las diferencias específicas por variedad se observaron en rendimiento de tubérculo y tiempos de floración, lo que sugiere que esta variación pudiera influenciar la incidencia de PVY más que el tipo de semilla.

Keywords Potato virus $Y \cdot Solanum tuberosum \cdot Potato \cdot$ Seed potatoes \cdot Minitubers

In North America, certified seed potatoes (*Solanum tuberosum* L.) are produced under regulation by agencies that inspect seed lots in order to keep cultivar mixture and disease incidence below established thresholds known to cause significant production losses (Frost et al. 2013; Whitworth and Davidson 2008). Over 30 viruses infect potato (Stevenson et al. 2001). *Potato virus Y* (PVY) is the most economically important virus disease problem for production of seed

potatoes in many areas of the world (Gray et al. 2010). For example, Wisconsin certification records from 2002 to 2010 show that over 90% of seed lot rejections due to plant pathogens were attributed to PVY infection (Frost et al. 2013).

PVY has a wide natural host range and can infect plants in 14 genera of Solanaceae (Kerlan 2006). More than 50 species of aphids can transmit PVY in a non-persistent manner (Radcliffe and Ragsdale 2002). Infected plants show symptoms that range from mild to severe mosaic, leaf drop, leaf crinkle, leaf chlorosis, leaf necrosis, cracking and necrotic rings on tubers (Gray et al. 2010). In the past decade, seed potato certification programs have been challenged by the emergence of recombinant strains of PVY that produce mild foliar symptoms, as well as widespread adoption of cultivars that are asymptomatic when infected with the virus (Gray et al. 2010; Karasev and Gray 2013). The majority of North American certification agencies continue to rely upon visual identification of disease symptoms, and the lack of clear, visual symptoms limits PVY detection (Gray et al. 2010; Karasev et al. 2010; MacKenzie et al. 2015).

Management of PVY in seed potato production is accomplished mainly by minimizing initial inoculum through seed certification, by using resistant cultivars, and by growing the crop in northern areas where the aphid vector populations are low and migrating aphid flights typically occur late in the growing season. The use of resistant cultivars in North America is still limited and breeding for PVY resistance takes many years (Fulladolsa et al. 2015). Chemical insecticide applications to control aphid vector populations are not efficient due to the nature of non-persistent transmission of the virus (Perring et al. 1999; Radcliffe and Ragsdale 2002). Isolation of the seed crop away from other inoculum sources (e.g. commercial potato), together with early vine-killing to avoid lateseason aphid landings and virus spread, are other methods that seed farmers can employ to limit transmission of PVY (Frost et al. 2013; Love et al. 2003; Radcliffe 2006).

In North America, potato cultivars of commercial interest are maintained in tissue culture. For commercial use, potatoes are propagated first in tissue culture, and then plantlets are transplanted into pots or hydroponic systems in greenhouses or screenhouses to produce minitubers. Certification agencies require a 0 % tolerance for any virus in micropropagated plants or plants grown in greenhouses or screenhouses (Halterman et al. 2012). Greenhouse-grown minitubers are then field-planted by certified seed potato farmers to produce conventional seed, which is subsequently multiplied in the field for three to five generations, before it is sold to commercial farms to grow potatoes destined for tablestock or processing.

The yield of plants grown from microtubers and minitubers is lower than that of plants grown from conventional seed in a field environment (Allen et al. 1992; Chae et al. 2008; Lommen and Struik 1994; Lommen and Struik 1995). Microtubers are produced in vitro on tissue culture plantlets and their average weight varies from 0.13 to 4 g (Lommen and Struik 1992; Lommen and Struik 1994; Wiersema et al. 1987). Across a range of cultivars, the typical weight of a minituber produced by planting a tissue culture plantlet in a hydroponic system or in pots is 8 to 25 g (Monteiro Corrêa et al. 2008; Ritter et al. 2001). Field observations indicate that plants grown from minitubers grow differently than plants grown from conventional seed. Even when pre-sprouted, they emerge later, they produce fewer stems per plant, and canopy closure occurs later in the production season (Allen et al. 1992; Arsenault and Christie 2004; Chae et al. 2008; Lommen and Struik 1995; Wróbel 2014). In general, seed size and stem number are positively correlated with tuber yield (Barry et al. 2001; Lommen and Struik 1995).

Previous observations suggest that minituber-grown plants are more likely to become infected with PVY than those grown from conventional seed (McDonald 1987). Reduced plant size and age may delay canopy closure, increasing aphid vector attraction due to open canopies (Boiteau et al. 2000; Davis et al. 2009; Halbert and Irwin 1981; Kennedy et al. 1961). However, aphid probing behavior, residency time, and plant colonization are similar on plants grown from field tubers, minitubers, and tissue culture plantlets (Boiteau et al. 2000). The age of plants at the time of inoculation affects the incidence of PVY in progeny tubers, perhaps due to mature plant resistance (Beemster 1979). However, different cultivars show distinct responses to early- and late-season inoculations, and the rate of infection may also be influenced by environmental factors and the magnitude of insect populations (Beemster 1976; Gibson 1991; Hamm et al. 2010; Sigvald 1985).

Few studies have investigated PVY susceptibility of plants grown from minitubers, compared to those grown from conventional seed (Boiteau et al. 2000; Wróbel 2014). We designed a factorial experiment and collected data on PVY incidence, yield, emergence, and flowering times of plants grown from minitubers and conventional seed. Our main objective was to test whether plants grown from minitubers are more likely to become infected with PVY than those grown from conventional seed. We were unable to detect a difference in PVY incidence between tubers harvested from minitubergrown plants and those from conventional seed.

Materials and Methods

Plant Materials

Foundation class, field-grown seed potatoes (WI administrative code chapter ATCP 156) and minitubers were provided by the Wisconsin Seed Potato Certification Program (Antigo, WI). In both 2012 and 2013, two red potato cultivars, Dark Red Norland and Red La Soda were used. The russet cultivar Goldrush was also included in the experiments, but only in 2012.

Experimental Design and Crop Management

Treatments consisting of all combinations of seed type (minituber and conventional) and cultivar were planted in a randomized complete block design with eight replications at the Hancock Agricultural Research Station (HARS) in Hancock, WI in 2012 and 2013. Each year, the experiments were in different field locations at HARS. Experimental plots consisted of 80 plants arranged in four rows (20 plants row⁻¹) with 30 cm spacing between plants within rows and 46 cm spacing between rows. Conventional seed tubers were machine planted at a depth of 12 to 15 cm, while minitubers were hand-planted at a depth of 2.5 to 5 cm.

The soil type at the HARS is a Plainfield loamy sand (sandy, mixed, mesic, Typic Udipsamments) (Copas et al. 2009). In both years of the study, conventional horticultural crop management and plant protection practices were implemented and were aligned with the recommendations for commercial potato production developed by the University of Wisconsin-Madison (Colquhoun et al. 2016).

In-Season Data Collection

In 2012, planting was carried out on May 9. The number of plants per plot was recorded at 23, 30, and 47 days after planting (dap). Each year, emergence was determined in two ways: as the final number of plants per plot and as the time (dap) when 80% of expected plants (64/80) had emerged. Flowering data were recorded at 47, 55, 72, 84, and 96 dap. The flowering start time was determined for each plot as the number of days after planting in which at least 10% of the plants were observed to have buds or open flowers. The flowering end time was recorded as the number of days after planting in which at least 90% of the plants in the plot had abscised all flowers. In 2013, planting was carried out on May 10. The number of plants per plot was recorded at 28, 42, 60, 74, and 101 dap and flowering data were recorded at 60, 70, 74, 82, and 101 dap.

Harvest Data Collection

Potato tubers were mechanically harvested from each plot from the two innermost rows. In 2012, the tubers were harvested on September 13 (127 dap) and subsequently washed and graded as described in Copas et al. (2009). In 2013, tubers were again harvested from the two innermost rows on September 18 (131 dap), and weight, length, width, and height of all tubers in the plot were measured. In both years, B-sized tubers were classified as those with a diameter ≤ 4.45 cm.

PVY Incidence Determination

All harvested tubers were initially stored at 4 °C for a period of three months. PVY incidence was determined by testing a sample of 104 progeny tubers from each plot, or all tubers from plots where less than 104 total tubers were collected. After the initial storage period, tubers from the 2012 season were taken to the Walnut Street Greenhouses, Madison, WI, to warm and green-sprout. After approximately 14 days, tuber dormancy was broken by surface treatment with a 10 ppm gibberellic acid (GA) solution. The treatment consisted of soaking the tubers in the solution for 10 min (Bryan 1989), and then drying them overnight on the greenhouse bench before planting. Tubers from the 2013 season were not treated with GA solution because they were all adequately sprouted following the three-month storage interval. Tubers were grown in trays (one tuber per 6 cm² insert), containing Metro-Mix 300 (Sungro Horticulture, Agawam, MA).

Leaves from each plant were collected and sap was extracted using a sap extractor (Banttari 1980). Virus was detected using a chemiluminescent dot-blot immunoassay (Fulladolsa Palma et al. 2013) or enzyme-linked immunosorbent assay (PVY PathoScreen® Kit, Agdia, Inc., Elkhart, IN).

Statistical Analyses

Analysis of variance (ANOVA) and least square means comparisons were performed using PROC MIXED (SAS software, version 9.4 of the SAS System for Windows) on raw or transformed data to determine main and interaction effects of seed type and cultivar. When transformations failed to satisfy ANOVA assumptions, analogous non-parametric analyses were performed by using the ranks of the data. Emergence and flowering data were analyzed and pairwise comparisons were performed using a Friedman's test in R statistical software version 3.3.1 (R Core Team 2016). Data from 2012 and 2013 were analyzed separately due to the variation in location, weather, cultivar availability, and post-harvest grading methods.

Results

Effects of Seed Type and Potato Cultivar on Disease Incidence

We measured PVY incidence in experimental plots resulting from natural virus inoculations likely by alate aphids at the HARS in 2012 and 2013. Seed type had no effect on the incidence of PVY in progeny tubers (Table 1). In both years, virus incidence varied depending on the cultivar used (P < 0.01). Red La Soda had the highest mean number of

 Table 1
 Mean incidence (%) of *Potato virus Y* (PVY) by cultivar and seed type averaged over experimental replicates, and the effects of the factors on the progeny tubers in 2012 and 2013

Cultivar	Seed type	PVY incidence (%)		
		2012	2013	
Dark Red Norland	Conventional	2.04	13.71	
	Minitubers	2.88	13.63	
Goldrush	Conventional	2.28	nd	
	Minitubers	3.49	nd	
Red La Soda	Conventional	5.41	50.17	
	Minitubers	11.97	35.52	
Fixed effects	Cultivar	**	***	
	Seed type	NS	NS	
	Interaction	NS	NS	

**Significant at the 0.01 probability level

***Significant at the 0.001 probability level

nd, no data

NS, non-significant at the 0.05 probability level

infected plants with the greatest amount of variation compared with other cultivars (Figure 1). In comparison to 2012, average PVY incidence in 2013 was at least three times higher across all seed type and cultivar combinations.

Fig. 1 Boxplots of PVY incidence (%) averaged over seed type for each cultivar planted in 2012 and 2013. Dark gray boxes represent Dark Red Norland (DRN), light gray boxes represent Goldrush (GDR), and white boxes represent Red La Soda (RLS). Means are represented by a plus symbol (+) and the median is represented by a horizontal line within the box

Effects of Seed Type and Potato Cultivar on Yield

The total harvested tuber yield of plants grown from minitubers was significantly lower (P < 0.0001) than that of plants grown from conventional seed (Table 2). Total tuber yield represents the sum of four tuber classes: standard-sized tubers (diameter > 4.45 cm, weight ≥ 113 g), overweight tubers (weight ≥ 368 g), B-sized tubers (diameter ≤ 4.45 , weight < 113 g), and culls (Copas et al. 2009). The use of minitubers as seed significantly reduced standard-sized tuber yields across cultivars (P < 0.0001), compared to yields from conventional seed (Figure 2).

Potato cultivar significantly influenced total tuber yield of plants, as well as the yield of standard-sized and overweight tubers (Table 2). It was anticipated that yield would be influenced by cultivar, therefore we also analyzed proportion data for all tuber classes. The proportion of standard-sized tubers and culls was influenced by seed type and cultivar in both years. However, the proportion of overweight potatoes was only influenced by cultivar and there was no consistent effect of either seed type or cultivar on the yield or proportion of B-sized tubers (Table 2).

The combination of seed type and cultivar had an interactive effect on the weight of standard-sized tubers, but not on the proportion of tubers (Table 2; Figure 3). In particular, when grown from conventional seed, Red La Soda showed

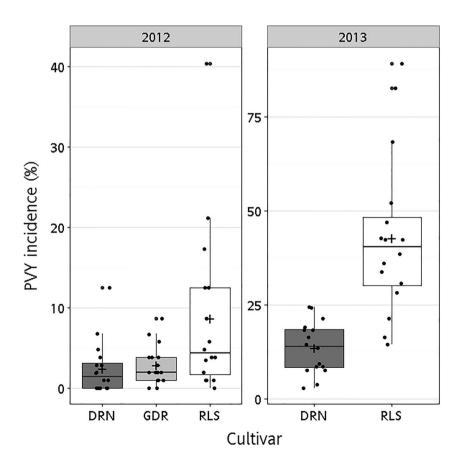


 Table 2
 Effects of cultivar and seed type on mean tuber yields (wgt) and on the proportion of total yield (pro) of four distinct tuber classes (standard-sized, overweight, B-sized, and culls), in 2012 and 2013

Year	Cultivar	Seed type	Total (kg)	Standard		Overweight		B-sized		Culls	
				wgt (kg)	pro (%)	wgt (kg)	pro (%)	wgt (kg)	pro (%)	wgt (kg)	pro (%)
2012	Dark Red Norland	Conventional	65.16	58.39	89.73	3.22	4.84	1.39	2.13	2.16	3.30
		Minitubers	46.26	37.67	81.58	1.66	3.91	2.52	5.11	4.40	9.40
	Goldrush	Conventional	65.38	57.12	87.44	4.28	6.45	2.26	3.52	1.72	2.58
		Minitubers	36.99	32.32	87.08	1.67	5.08	2.37	6.13	0.63	1.71
	Red La Soda	Conventional	78.75	65.50	83.53	5.35	6.65	1.74	2.08	6.15	7.74
		Minitubers	41.60	27.66	65.82	6.14	15.06	1.39	3.31	6.41	15.81
	Fixed effects	Cultivar	***	NS	***	***	***	NS	NS	***	***
		Seed type	***	***	***	***	NS	NS	**	NS	**
		Interaction	***	***	NS	**	**	NS	NS	**	**
2013	Dark Red Norland	Conventional	79.38	56.64	71.20	3.35	4.17	17.33	22.08	2.07	2.55
		Minitubers	53.95	31.03	57.88	7.88	14.10	8.32	15.55	6.72	12.47
	Red La Soda	Conventional	99.99	64.48	64.90	21.97	21.61	7.49	7.56	6.05	5.94
		Minitubers	58.29	30.70	52.46	9.89	17.15	6.27	10.74	11.42	19.65
	Fixed effects	Cultivar	***	*	**	***	***	***	***	***	**
		Seed type	***	***	***	NS	NS	***	NS	***	***
		Interaction	**	*	NS	***	***	***	***	NS	NS

*Significant at the 0.05 probability level

**Significant at the 0.01 probability level

***Significant at the 0.001 probability level

NS, non-significant at the 0.05 probability level

Fig. 2 Boxplots of standardsized tubers for each cultivar and seed type combination planted in 2012 and 2013. Dark gray boxes represent Dark Red Norland (DRN), light gray boxes represent Goldrush (GDR), and white boxes represent Red La Soda (RLS). Means are represented by a plus symbol (+) and the median is represented by a horizontal line within the box

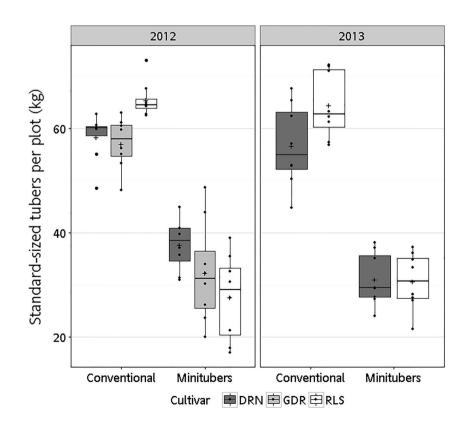
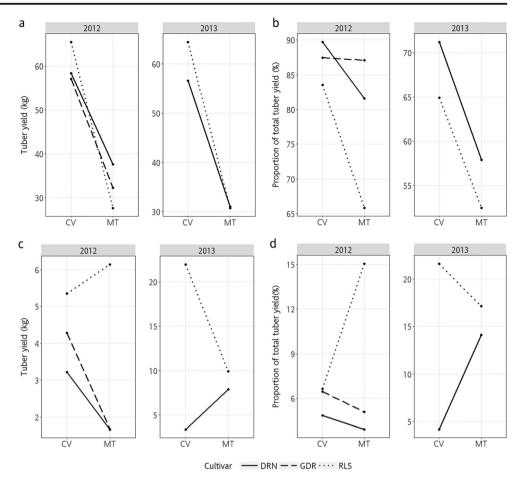


Fig. 3 Interaction plots representing mean tuber yields (kg) and proportions (%) for both standard-sized (a, b) and overweight (c, d) tuber classifications by potato cultivar and seed type in 2012 and 2013. Solid lines represent Dark Red Norland (DRN), dashed lines represent Goldrush (GDR), and dotted lines represent Red La Soda (RLS). CV, conventional seed; MT, minitubers



higher yield (weight) than the other two cultivars. However, when minitubers were used, Dark Red Norland produced higher or similar yields than the other two cultivars. The yields of overweight potatoes were also influenced by a seed typecultivar interaction. Although it was not consistent between years, the yield of Red La Soda overweight potatoes grown from conventional seed was again highly different from that of minituber-grown plants (Table 2; Figure 3).

Effects of Treatment on Plant Emergence and Flowering

Because of the discrete nature of the collected data, a nonparametric Friedman's test was used to analyze the data for emergence and flowering times, as well as for pairwise comparisons of seed type within cultivar. Emergence was measured by the final number of plants per plot (emerged over the course of the growing season) and by the time (dap) when 80% of the plants had emerged. We observed an overall effect of each combination of seed type and cultivar on the number of plants per plot, as well as on the days to 80% emergence (Table 3). In 2012, 100% emergence was achieved using conventional seed and an average of two fewer plants emerged in the minituber plots across all cultivars. In 2013, a mean of 76 plants per plot emerged and the only difference between seed type was observed for Dark Red Norland (Table 3).

In both years, the treatments strongly influenced the time to 80% emergence of plants (Table 3). In general, minitubergrown plants emerged an average of 14 days later than those grown from conventional seed. Time to 80% emergence was significantly different between seed types of Goldrush and Red La Soda, but not of Dark Red Norland.

The flowering start times significantly differed between treatments in both years (Table 3). Overall, plants grown from minitubers started and ended flowering later than those grown from conventional seed. In 2012, the red-skinned cultivars (Dark Red Norland and Red La Soda) showed similar flowering start and end times. Their flowering start times were delayed by an average of 6 days in minituber-grown plants and flowering end times were delayed by an average of 8 days. The delay in flowering was greater for minituber-grown Goldrush, starting an average of 12 days after those grown from conventional seed and ending 24 days later. In 2013, there was a significant difference in flowering start and end times between seed type treatments of Dark Red Norland. However, Red La Soda seed type treatments only influenced flowering end times. In general, minituber-grown plants

Table 3 Effects of cultivar andseed type on mean number ofplants per plot, average time to80% emergence, and averageflowering start and end times(days after planting), in 2012 and2013

Year	Cultivar	Seed type	No. plants per plot	Days to 80% emergence	Flowering start day	Flowering end day	Flowering period
2012	Dark Red	Conventional	80.00	29.13	47.00	72.00	25.00
	Norland	Minitubers	75.25	36.38	55.00	81.00	26.00
	Goldrush	Conventional	80.00	29.13	47.00	72.00	25.00
		Minitubers	78.63	47.00	59.25	96.00	36.75
	Red La Soda	Conventional	80.00	29.13	47.00	91.25	44.25
		Minitubers	79.13	47.00	54.00	99.75	45.75
Friedman's chi-square statistic			30.82***	33.54***	37.05***	33.08***	23.64***
Pairwi	se comparisons ^a						
DRN conventional vs minitubers			**	NS	**	*	NS
GDR conventional vs minitubers			*	**	**	**	NS
RLS conventional vs minitubers			*	**	**	NS	NS
2013	Dark Red Norland	Conventional	70.50	42.63	53.88	70.00	70.00
		Minitubers	78.75	42.00	62.50	96.25	96.25
	Red La Soda	Conventional	77.13	31.50	59.13	81.38	81.38
		Minitubers	77.88	42.00	60.00	101.00	101.00
Friedman's chi-square statistic			10.86^{*}	12.36**	18.40***	21.31***	20.41***
Pairwi	se comparisons ^a						
DRN conventional vs minitubers			**	NS	**	**	**
RLS conventional vs minitubers			NS	*	NS	**	**

^a DRN, Dark Red Norland; GDR, Goldrush; RLS, Red La Soda

*Significant at the 0.05 probability level

**Significant at the 0.01 probability level

***Significant at the 0.001 probability level

NS, non-significant at the 0.05 probability level

flowered for a longer period of time (37 days) than plants grown from conventional seed (26 days; Table 3).

Discussion

We performed a two-year trial to test whether plants grown from minitubers are more susceptible to PVY than those grown from conventional seed. We hypothesized that tubers harvested from minituber-grown plants would show a higher incidence of PVY than those from plants grown from conventional seed potatoes. Previous studies and observations suggest that plants grown from minitubers have a higher risk of PVY infection (Boiteau et al. 2000; Gray et al. 2010). Our results show that risk of PVY infection in plants grown from minitubers is not higher than in plants grown from conventional seed. However, there is no evidence to suggest that the risk of PVY incidence is less in minituber plants, as the differences in virus incidence in progeny tubers between plants from each seed type were not significant. This is consistent with the findings of Wróbel (2014), who did not observe differences in aphid landings or incidence of PVY, Potato virus

M (PVM), or *Potato leafroll virus* (PLRV) between minitubers and conventional seed.

The clearest effect of the use of minitubers as seed was a reduction of tuber yield as compared to that of conventional seed-grown plants. This was not unexpected, as other researchers have shown that minituber-grown plants produce lower tuber yields (Lommen and Struik 1994; Lommen and Struik 1995) and that yield is correlated with seed size (Iritani et al. 1972). We collected yield data from four tuber classes. The results showed that standard-sized tuber yields from minituber-grown plants were lower than those from conventional seed-grown plants. Nevertheless, the use of minitubers did not show a consistent effect on the yield or proportion of B-sized or overweight tubers. North American certification agencies require that tubers are highly uniform in size. For example, in Wisconsin, seed bags should contain no more than 3% of B-sized tubers and no more than 10-15% of overweight tubers. Our results were inconsistent across years and cultivars; therefore, we cannot conclude that either seed type will reliably produce a crop that meets certification standards. The proportion of culls (i.e. unmarketable tubers) was influenced by seed type and minituber-grown red cultivars tended to produce a higher proportion of culls, suggesting that using minitubers may increase the likelihood of crop loss at harvest or during grading.

We observed that plants emerged from minitubers later than from conventional seed. Others found that the emergence of plants is influenced by seed type (Ranalli et al. 1994), but also by planting depth (Pavek and Thornton 2009). Allen et al. (1992) suggested that seed size does not have a direct effect on time to emergence, but the effective planting depth of small and large tubers can result in later emergence from smaller seed. This could explain the later emergence of plants from minitubers. Although we planted minitubers at a shallower depth than conventional seed, the minitubers varied in size. Smaller tubers with smaller reserves may develop smaller root systems, which could lead to delayed emergence and varying emergence times within each plot (Barry et al. 2001). Additionally, row hilling was done approximately two weeks after most conventional seed-grown plants had emerged, but the minitubers-grown plants had yet to fully emerge, which may have resulted in a delayed emergence of minituber-grown plants.

Since the minituber-grown plants emerged later than those from conventional seed, we expected them to also flower at a later time. Some potato cultivars show mature plant resistance (Beemster 1976; Gibson 1991), therefore we investigated the relationship between maturity and PVY incidence with respect to seed type. We used flowering start and end times as indicators of maturity. Our data show that although minituber-grown plants mature later than plants grown from conventional seed, this does not result in higher PVY incidence. Interestingly, Red La Soda plants flowered for a longer period of time and ended flowering later, and they also had the highest incidence of PVY. This suggests that there are maturity-related factors that could affect the likelihood of PVY infection.

Concluding Remarks

In North America, minitubers are the starting point for field propagation of seed potatoes. The harvested tubers are usually field-multiplied for another three to four generations, before being sold to commercial potato growers, as long as certification standards for replanting are met (Frost et al. 2013; Halterman et al. 2012). If seed growers increased the proportion of minitubers planted, the time that it takes to bring the seed to commercial growers could be reduced by one or more years (Donnelly et al. 2003; Gray et al. 2010), which could reduce the accumulation of virus in the crop. The main question addressed in this study was whether planting minitubers as primary seed increases the risk of PVY incidence. Although minitubers are disease-free, there are two main concerns related to their use as primary seed: i) they produce smaller plants, which could result in the occurrence of a color contrast in the field (due to more open canopies) that is likely to influence aphid landings (Davis et al. 2009); and ii) their later emergence results in plants maturing later in the season, coinciding with late-season aphid flights of both potato-colonizing and non-colonizing species (Frost et al. 2013; Karasev and Gray 2013). In this study, we found that minituber-grown plants produce lower tuber yields than plants grown from conventional seed. This is likely due to the plants having a smaller size and later emergence (Allen et al. 1992; Arsenault and Christie 2004). However, no differences were found in PVY incidence between plants grown from the different seed types. This suggests that, despite the differences in plant growth and maturity, plants grown from minitubers do not have a higher likelihood of becoming infected with PVY than plants grown from conventional seed. This should be considered when revising PVY management and seed certification protocols. Additionally, the information generated through this study can be useful for further investigation of improved seed production from minituber-grown plants of cultivars Dark Red Norland, Goldrush, and Red La Soda. For example, we could use the data on the distribution of tuber classes of each cultivar to better estimate the amount of seed required to obtain a fixed yield of standard-sized tubers. Making such considerations can better predict the production cost of conventional seed from minitubers, as well as the cost of minituber production (Guenthner et al. 2014).

Acknowledgements This material is based upon work that is supported by the National Institute of Food and Agriculture, U.S. Department of Agriculture, under award numbers 2009-51181-05894 and 2014-51181-22373. We thank Scott Chapman for his help with the field setup, the staff at the Hancock Agricultural Research Station, and Sarah Page and Michael Drilias for their help in managing the drip irrigation plot in 2013. We also thank Nicholas Keuler and Peter Crump for their assistance with statistical analyses. All the experiments performed complied with the current regulations of the United States of America.

References

- Allen, E.J., P.J. O'Brien, and D. Firman. 1992. An evaluation of small seed for ware-potato production. *The Journal of Agricultural Science* 118: 185–193.
- Arsenault, W.J., and B.R. Christie. 2004. Effect of whole seed tuber size and pre-plant storage conditions on yield and tuber size distribution of Russet Burbank. *American Journal of Potato Research* 81: 371– 376.
- Banttari, E. 1980. Sap extraction device for sampling potato leaves and tubers. *American Journal of Potato Research* 57: 345–348.
- Barry, P., P. Clancy, and M. Molloy. 2001. The effect of seed size and planting depth on the yield of seed potatoes grown from minitubers. *Irish Journal of Agricultural and Food Research* 40: 71–81.
- Beemster, A.B.R. 1976. Translocation of the potato viruses Y^N and Y^O in some potato varieties. *Potato Research* 19: 169–172.
- Beemster, A.B.R. 1979. Acquisition of *Potato virus Y^N* by *Myzus persicae* from primarily infected 'Bintje' potato plants. *Netherlands Journal of Plant Pathology* 85: 75–81.
- Boiteau, G., L.M. Moore, and D. Wattie. 2000. Comparative analysis of aphid vector behavior in response to potato plants grown from field

tubers, minitubers or plantlets. American Journal of Potato Research 77: 71–75.

- Bryan, J.E. 1989. *Breaking dormancy of potato tubers. CIP Research Guide 16.* Lima: International Potato Center.
- Chae, W.B., H.L. Kim, H. Choi, Y.B. Kwack, and D.W. Lee. 2008. Comparison of mini-tuber and conventional tuber: the effect of the number of eyes and tuber size on the growth and yield of potato (Solanum tuberosum L.). Horticulture Environment and Biotechnology 49: 387–392.
- Colquhoun, J., A. Gevens, R. Groves, D. Heider, B. Jensen, G. Nice, et al. 2016. Commercial Vegetable Production in Wisconsin. In *Publication A3422*. Madison: University of Wisconsin-Extension.
- Copas, M.E., A.J. Bussan, M.J. Drilias, and R.P. Wolkowski. 2009. Potato yield and quality response to subsoil tillage and compaction. *Agronomy Journal* 101: 82–90.
- Core Team, R. 2016. R: A language and environment for statistical computing. In *R Foundation for Statistical Computing*. Vienna: Austria https://www.R-project.org/.
- Davis, J.A., E.B. Radcliffe, and D.W. Ragsdale. 2009. Planter skips and impaired stand favors *Potato virus Y* spread in potato. *American Journal of Potato Research* 86: 203–208.
- Donnelly, D.J., W.K. Coleman, and S.E. Coleman. 2003. Potato microtuber production and performance: a review. American Journal of Potato Research 80: 103–115.
- Frost, K.E., R.L. Groves, and A.O. Charkowski. 2013. Integrated control of potato pathogens through seed potato certification and provision of clean seed potatoes. *Plant Disease* 97: 1268–1280.
- Fulladolsa Palma, A.C., R. Kota, and A.O. Charkowski. 2013. Optimization of a chemiluminescent dot-blot immunoassay for detection of potato viruses. *American Journal of Potato Research* 90: 306–312.
- Fulladolsa, A.C., F.M. Navarro, R. Kota, K. Severson, J.P. Palta, and A.O. Charkowski. 2015. Application of marker assisted selection for *Potato virus Y* resistance in the University of Wisconsin Potato Breeding Program. *American Journal of Potato Research* 92: 444–450.
- Gibson, R.W. 1991. The development of mature plant resistance in four potato cultivars against aphid-inoculated potato virus Y^O and Y^N in four potato cultivars. *Potato Research* 34: 205–210.
- Gray, S., S. De Boer, J. Lorenzen, A. Karasev, J. Whitworth, P. Nolte, et al. 2010. *Potato virus Y*: an evolving concern for potato crops in the United States and Canada. *Plant Disease* 94: 1384–1397.
- Guenthner, J.F., A. Charkowsi, R. Genger, and G. Greenway. 2014. Varietal Differences in Minituber Production Costs. *American Journal of Potato Research* 91: 376–379.
- Halbert, S.E., and M.E. Irwin. 1981. Effect of soybean canopy closure on landing rates of aphids with implications for restricting spread of soybean mosaic virus. *Annals of Applied Biology* 98: 15–19.
- Halterman, D., A. Charkowski, and J. Verchot. 2012. Potato, viruses, and seed certification in the USA to provide healthy propagated tubers. *Pest Technology* 6: 1–14.
- Hamm, P.B., D.C. Hane, M.J. Pavek, L.D. Leroux, S.L. Gieck, and N.L. David. 2010. Potato cultivars differ in current season *Potato virus Y* (PVY) infection. *American Journal of Potato Research* 87: 19–26.
- Iritani, W.M., R. Thornton, L. Weller, and G. O'Leary. 1972. Relationships of seed size, spacing, stem numbers to yield of Russet Burbank potatoes. *American Potato Journal* 49: 463–469.
- Karasev, A.V., and S.M. Gray. 2013. Continuous and emerging challenges of *Potato virus Y* in potato. *Annual Review of Phytopathology* 51: 571–586.
- Karasev, A.V., O.V. Nikolaeva, X. Hu, Z. Sielaff, J. Whitworth, J.H. Lorenzen, et al. 2010. Serological properties of ordinary and necrotic isolates of *Potato virus Y*: a case study of PVY^N misidentification. *American Journal of Potato Research* 87: 1–9.

- Kennedy, J.S., C.O. Booth, and W.J.S. Kershaw. 1961. Host finding by aphids in the field. *Annals of Applied Biology* 49: 1–21.
- Kerlan, C. 2006. *Potato virus Y.* CMI/AAB Descriptions of plant viruses 414.
- Lommen, W.J.M., and P.C. Struik. 1992. Production of potato minitubers by repeated harvesting: Effects of crop husbandry on yield parameters. *Potato Research* 35: 419–432.
- Lommen, W.J.M., and P.C. Struik. 1994. Field performance of potato minitubers with different fresh weights and conventional seed tubers: crop establishment and yield formation. *Potato Research* 37: 301–313.
- Lommen, W.J.M., and P.C. Struik. 1995. Field performance of potato minitubers with different fresh weights and conventional seed tubers: multiplication factors and progeny yield variation. *Potato Research* 38: 159–169.
- Love, S.L., P. Nolte, D.L. Corsini, J.C. Whitmore, L.L. Ewing, and J.L. Whitworth. 2003. Seed production and certification. In *Potato Production Systems*, ed. Jeffrey C. Stark and Stephen L. Love, 49– 69. Moscow: University of Idaho Extension.
- MacKenzie, T.D., X. Nie, and M. Singh. 2015. RT-PCR and real-time RT-PCR methods for the detection of *Potato virus Y* in potato leaves and tubers. In *Plant Virology Protocols: New Approaches to Detect Viruses and Host Responses*, ed. Ichiro Uyeda and Chikara Masuta, 3rd ed., 13–26. New York: Humana Press.
- McDonald, J. 1987. Comparative levels of potato viruses S and Y infection of microplants and tuber-propagated plants in the field. *American Potato Journal* 64: 517–521.
- Monteiro Corrêa, R., J.E.B.P. Pinto, C.A.B.P. Pinto, V. Faquin, É.S. Reis, A.B. Monteiro, et al. 2008. A comparison of potato seed tuber yields in beds, pots and hydroponic systems. *Scientia Horticulturae* 116: 17–20.
- Pavek, M.J., and R.E. Thornton. 2009. Planting depth influences potato plant morphology and economic value. *American Journal of Potato Research* 86: 56–67.
- Perring, T.M., N.M. Gruenhagen, and C.A. Farrar. 1999. Management of plant viral diseases through chemical control of insect vectors. *Annual Review of Entomology* 44: 457–481.
- Radcliffe, E.B. 2006. Use of non-chemical alternatives to synthetic pesticides in maintaining plant health in a clonally propagated crop: potato. Arab Journal of Plant Protection 42: 170–173.
- Radcliffe, E.B., and D.W. Ragsdale. 2002. Aphid-transmitted potato viruses: the importance of understanding vector biology. *American Journal of Potato Research* 79: 353–386.
- Ranalli, P., F. Bassi, G. Ruaro, P. Del Re, M. Di Candilo, and G. Mandolino. 1994. Microtuber and minituber production and field performance compared with normal tubers. *Potato Research* 37: 383–391.
- Ritter, E., B. Angulo, P. Riga, C. Herrán, J. Relloso, and M. San Jose. 2001. Comparison of hydroponic and aeroponic cultivation systems for the production of potato minitubers. *Potato Research* 44: 127–135.
- Sigvald, R. 1985. Mature-plant resistance of potato plants against *Potato* virus Y^O (PVY^O). *Potato Research* 28: 135–143.
- Stevenson, W.R., R. Loria, G.D. Franc, and D.P. Weingartner. 2001. Compendium of potato diseases. St. Paul: APS Press.
- Whitworth, J., and R.D. Davidson. 2008. Quality Seed: seed improvement, cultivar and healthy seed lot selection, and the certification process. In *Potato Health Management*, ed. D.A. Johnson, 2nd ed., 31–41. St. Paul: APS Press.
- Wiersema, S., R. Cabello, P. Tovar, and J. Dodds. 1987. Rapid seed multiplication by planting into beds micro tubers and in vitro plants. *Potato Research* 30: 117–120.
- Wróbel, S. 2014. Assessment of possibilities of microtuber and in vitro plantlet seed multiplication in field conditions. Part 1: PVY, PVM and PLRV spreading. *American Journal of Potato Research* 91: 554–565.