Transmission Efficiency of *Potato virus Y* strains PVY^O and PVY^{N-Wi} by Five Aphid Species

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Abstract

Mello, A. F. S., Olarte, R. A., Gray, S. M., and Perry, K. L. 2011. Transmission efficiency of *Potato virus Y* strains PVY^O and PVY^{N-Wi} by five aphid species. *Plant Dis.* 95:1279–1283.

Potato virus Y (PVY) is a reemerging problem in potato production in North America. Although the “ordinary” strain, PVY^O, is still the dominant isolate in U.S. seed potatoes, the recombinant strain of the virus PVY^{N-Wi} (= PVY^{N:O}) has become widespread. An increase in the prevalence of a PVY strain could be due to differences in the efficiency of transmission by aphid vectors. The transmission efficiency by a clone of *Myzus persicae* was determined for five isolates each of PVY^O and PVY^{N-Wi}. An aphid transmission assay was developed based on the use of potato seedlings from true potato seed, allowing for greater control of plant age and growth stage. No apparent differences in trans-

mission by *M. persicae* were observed. Single isolates of PVY^O and PVY^{N-Wi} were tested for their ability to be transmitted from potato to potato by five aphid species: *Aphis glycines*, *A. gossypii*, *A. nasturtii*, *M. persicae*, and *Rhopalosiphum padi*. Both PVY isolates showed a similar transmission phenotype in being transmitted efficiently by *M. persicae* but very poorly or not at all by *A. glycines*, *A. gossypii*, and *R. padi*. The aphid *A. nasturtii* transmitted both isolates with an intermediate level of efficiency. The data do not support a model for a differential aphid transmissibility being responsible for the increase in the prevalence of PVY^{N-Wi}.

Potato virus Y (PVY) has a worldwide distribution and is arguably the most important viral pathogen of cultivated solanaceous crops species. It is one of the most intensively studied of plant viruses, and a diversity of strains has been characterized biologically and by genomic sequencing (20). Strains of PVY are differentiated based on host responses (including an ability to overcome resistance genes), serological properties, and genomic sequencing. Isolates from potato can be classified into seven strain groups, with many synonyms and subgroupings (37). The strain historically regarded as the most common or “ordinary” has been designated PVY^O. In North American potato-production areas, new strains of the virus are emerging; in particular, recombinant isolates designated PVY^{N-Wi} (= PVY^{N:O}) and tuber necrotic strains designated PVY^{NTN} (6,22,30,36). The PVY^{N-Wi} isolates in the United States and Canada were originally designated PVY^{N:O} because they were serologically similar to PVY^O but phenotypically similar to PVY^N in giving rise to veinal necrosis symptoms on tobacco (37). Although PVY^O isolates remain those most commonly observed in North America, over the past decade there has been an increase in the detection of PVY^{N-Wi} in seed-producing states and provinces (13,27). The basis for this shift in strain prevalence is not fully understood. Infected tubers as planting stock (seed) are the primary reservoir for the spread of PVY in potato production areas. PVY can also persist in weeds, current season crops, and overwintered

volunteer potato plants. One possibility to explain the increase in prevalence of PVY^{N-Wi} isolates is that they may have gone undetected due to mild symptoms in some of the more widely grown cultivars, resulting in their becoming established in potato seed-producing areas. A second possibility is that vector relationships may have played a role in the shift in strain types.

The spread of PVY is mediated by aphid vectors and it is non-persistently transmitted by a number of aphid species (20). *Myzus persicae* is the most important aphid vector for PVY in potato (32). Other vectors, including noncolonizing aphids, can be of epidemiological significance, and the complement of aphids present will depend on the region and the production system (7,15,31,39). One explanation for the increasing incidence and spread of necrotic and recombinant strains in the United States would be a more effective transmission of these strains compared with that of PVY^O. In this study, the aphid transmission efficiencies of five isolates each of PVY^{N-Wi} and PVY^O were compared using the vector *M. persicae*. Additionally, five aphid species were compared in their ability to transmit a single isolate each of PVY^{N-Wi} and PVY^O.

Materials and Methods

PVY isolates and the differentiation of PVY strains by enzyme-linked immunosorbent assay and tobacco host responses. Virus isolates were obtained during the course of a North American survey of PVY in potato in 2004 (13). PVY confirmation was performed by double- or triple-antibody sandwich enzyme-linked immunosorbent assay (DAS-ELISA or TAS-ELISA, respectively) using three commercially available monoclonal antibodies (MAbs 4C3, 15F, and 2) (9) and one polyclonal antiserum; methods followed the manufacturer’s instructions (Agdia Inc., Elkhart, IN) for DAS-ELISA (5) and those of Ellis et al. (9) for TAS-ELISA. Samples that produced absorbance values at 405 nm greater than 0.1 and three times greater than the average of uninfected greenhouse-grown potato or tobacco controls were considered positive. To propagate the virus and for bioassays, ELISA-positive potato samples were ground in phosphate-buffered saline (PBS; 5) and rubbed onto Carborundum-dusted (325 mesh) tobacco leaves (*Nicotiana tabacum* ‘Samsum NN’) at the three- to five-leaf stage. Plants were maintained in a greenhouse and observed weekly for 28 days, and

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Accepted for publication 1 June 2011.

symptoms were recorded as veinal necrosis, mosaic, or none. Plants were tested by DAS-ELISA and positive isolates were preserved as lyophilized leaf tissue. Lateral-flow PVY immunostrips (Agdia Inc.) were also used to confirm the presence of virus.

Differentiation of PVY strains based on polymerase chain reaction. Total RNA was isolated by freezing 0.06 g of infected leaf tissue in liquid nitrogen and grinding the tissue to a fine powder using a minipestle (Argos Technologies, Elgin, IL) in a microfuge tube. After addition of 400 µl of extraction buffer (100 mM Tris [pH 8.0], 50 mM EDTA, 500 mM NaCl, and 10 mM mercapto-ethanol) and 52.8 µl of 10% sodium dodecyl sulfate, the tubes were vortexed and incubated at 65°C for 10 min; 128 µl of 5 M sodium acetate was added to each tube, followed by vortexing and centrifugation at 10,000 × g for 10 min. The RNA-containing supernatant was removed and RNA precipitated with the addition of an equal volume of isopropanol. Following centrifugation at 10,000 × g for 10 min, the pellet was washed twice with 70% ethanol and resuspended in 80 µl of sterile water.

Reverse transcription (RT) was performed using 0.6 µl of RNA extract in a 15-µl reaction volume with 3 µl of 5× buffer (Invitrogen, Carlsbad, CA), 25 mM MgCl₂, 2.5 mM dNTP, 3 µM random hexamer + oligo-dT primer mix, 6 units of RNase Out Ribonuclease Inhibitor (Invitrogen), and 60 units of SSII reverse transcriptase (Invitrogen). First-strand cDNA synthesis was performed in a thermocycler with the following regime: 25°C for 2 min, ramped to 42°C at 1°C/min, held at 42°C for 45 min, ramped to 60°C at 1°C/min, and the reaction terminated. Multiplex polymerase chain reaction (PCR) was performed in a 20-µl reaction containing 0.8 µl of cDNA, 2 µl of 10× PCR buffer, 25 mM MgCl₂, 2.5 mM dNTP, 1.0 unit of Taq DNA polymerase (New England Biolabs, Ipswich, MA), and 0.2 µM each of the primers o2172, n2258, o2439c, n2650c, n5707, o6266c, S5585m, and A6032m (23). The PCR program consisted of: 94°C for 2 min; 12 cycles of 94°C for 10 s, 66°C for 30 s (minus 0.5°C per cycle), and 72°C for 60 s; then, 20 cycles of 92°C for 10 s, 60°C for 30 s, and 72°C for 60 s; and ending with a final extension for 7 min at 72°C (23). PCR products were separated in a 2.0% agarose gel, stained with ethidium bromide (33), and visualized with a fluorescent imager Kodak Gel Logic 200 Imaging System (Kodak Scientific Imaging Systems, Rochester, NY).

Aphids, plants, and the transmission assay system. The aphid species and hosts for rearing were as follows: the green peach aphid, *M. persicae*, on turnip (*Brassica rapa* L. 'Rapa'); the cotton aphid, *Aphis gossypii*, on cucumber (*Cucumis sativus* L.); the bird cherry-oat aphid, *Rhopalosiphum padi*, on barley (*Hordeum vulgare* L.); the soybean aphid, *A. glycines*, on soybean (*Glycine max*

(L.) Merr.); and the buckthorn aphid, *A. nasturtii*, on potato (*Solanum tuberosum* 'Yukon Gold'). All aphids were collected in the northeastern United States, with the exception of *M. persicae* clone 3 (= G006). Aphids were maintained in growth chambers at 19 to 22°C with a photoperiod of 14 and 10 h (light and darkness, respectively). All of these stock colonies have been maintained for at least 3 years. The aphid transmission assay system made use of seedlings of true potato seed collected from selfed plants of advanced clone 'NY129' from the Cornell potato breeding program. This clone and selfed progeny are susceptible to systemic infection by the PVY isolates employed in this study. TPS was sown in vermiculite and incubated in a growth chamber at 27 ± 2°C with a photoperiod of 14 and 10 h (light and darkness, respectively) for approximately 1 month. Seedlings were transplanted individually into 18-cm-diameter pots and grown in a greenhouse at 21°C. The soil was a Cornell peat-lite mix (4), as prepared and sold by the College of Agriculture and Life Sciences (Ithaca, NY). Plants were fertilized twice a week with a 21-5-20 formulation (J. R. Peters, Inc., Allentown, PA). Source plants for virus acquisition were prepared by inoculating Carborundum-dusted leaves of plants grown to the first true compound leaf stage at 45 to 55 days postseeding. At 2 to 3 weeks postinoculation, leaves showing symptoms and testing positive for PVY with immunostrips were used as source leaves for virus acquisition.

Aphids used for transmission experiments were dislodged from leaves, starved for 2 h, and transferred onto source leaves infected with PVY. Aphids were observed under a dissecting microscope for feeding behavior and allowed to feed for 2 to 10 min prior to transfer onto the leaves of uninfected target plants. The target plants were seedlings from TPS, 30 to 40 days postemergence from seed, prior to the emergence of the first true compound leaf. The experimental unit consisted of a single source leaf and 10 target plants, each with five aphids per plant. Experiments were repeated at least three times, with each replicate employing a different virus source plant. As a negative control for each experiment, five starved aphids that had not fed on a source leaf were also transferred onto each of 10 target plants. Following an overnight inoculation access period in a growth chamber maintained at 22 to 25°C with constant lighting, feeding was terminated by fumigation with Dibrom (Valent USA Corp., Walnut Creek, CA) for 2 h. Plants were then placed in a greenhouse and observed for symptom development for 21 to 28 days after inoculation and infection was confirmed by DAS-ELISA. Transmission frequencies between experiments were compared using group testing methods (11,38). The estimated likelihood of virus transmission by a single aphid was represented by the maximum-likelihood estimator P*, as described in previous studies (26,29). In order to avoid underestimating transmission efficiency of species for which no transmission was observed (e.g., 0/30), the P* value was calculated assuming a single transmission event (e.g., 1/30) (12,38). Similarly, in order to avoid the bias in overestimating transmission efficiency in replicates for which 100% transmission was observed (e.g., 10/10), the P* value was calculated assuming one less transmission event (e.g., 9/10). The mean maximum-likelihood estimator P* for each combination of aphid species and virus isolate was determined; mean comparisons and analyses of variance were performed using Proc Mixed and with the use of Tukey's procedure, SAS software 9.1 (SAS Institute, Inc., Cary, NC). A 0.05 level of significance was used for all tests.

Results

Characterization of PVY strains by ELISA, tobacco host response, and multiplex PCR. The initial identification of field isolates as PVY was based on a DAS-ELISA with polyclonal antibodies or the TAS-ELISA with MAb 4C3. The MAb 4C3 reacts with all tested isolates of PVY (9). Additional serotyping was performed with MAb2, an antibody recognizing an antigen common to most PVY^O and PVY^C isolates (but not PVY^N) (23,25). A third antibody, MAb 1F5, was originally thought to specifically recognize necrotic strains of PVY (PVY^N) (9) but was subsequently

Table 1. Serological characterization and tobacco host response of *Potato virus Y* (PVY) isolates used in aphid transmission experiments^x

PVY, strain	Origin ^y	Tobacco reaction ^z	MAb 4C3	MAb 1F5	MAb 2
PVY ^O					
Oz	New York	MM	+	—	+
CO35	Colorado	MM	+	—	+
ME324-33	Maine	MM	+	—	+
ID1-7-12b	Idaho	MM	+	—	+
ME236-120	Maine	MM	+	—	+
PVY ^{N-Wi}					
ME151-25	Maine	MM/VN	+	—	+
ID1-2-9b	Idaho	MM/VN	+	—	+
MN15b-28	Minnesota	MM/VN	+	—	+
ME193-25	Maine	MM/VN	+	—	+
ID14-2-14a	Idaho	MM/VN	+	—	+

^x Monoclonal antibody (MAb) 4C3 recognizes all isolates of PVY. MAb 2 detects an antigen common to most PVY^O and PVY^C isolates. MAb 1F5 recognizes an antigen common to some but not all necrotic isolates of PVY (e.g., PVY^N).

^y State of origin for the tubers from which the isolates were obtained.

^z Symptoms on *Nicotiana tabacum* were recorded 21 to 28 days post-inoculation. MM = systemic mottle/mosaic, VN = systemic veinal necrosis.

observed not to detect some necrotic isolates (i.e., those classified as PVY^{N-Wi} or PVY^{N-O}; 27). Consistent with these specificities, all PVY isolates in this study were recognized by MAb 4C3 and MAb 2 but not MAb 1F5 (Table 1). All of the isolates gave rise to a systemic mottle-mosaic in tobacco, while half of them (those designated PVY^{N-Wi}) also induced a systemic veinal necrosis (Table 1). To further characterize the virus isolates and to confirm that each isolate consisted of a single strain type, a multiplex RT-PCR was employed using procedures previously established (23). Agarose gel electrophoresis of the PCR products from isolates PVY-Oz, CO35, ME324-22, ID1-7-12b, and ME256-120 yielded two amplicons of 689 and 267 bp each. Isolates ME151-25, ID1-2-9b, MN15b, ME193-25, and ID14-2-14a yielded amplicons of 689 and 181 bp (Fig. 1). In this multiplex PCR assay developed by Lorenzen et al. (23), the 689-bp band is common to both strains PVY^O and PVY^{N-Wi}, while the 267- and 181-bp bands are characteristic of PVY^O and PVY^{N-Wi}, respectively.

Transmission of PVY isolates by *M. persicae*. In order to test for differences in aphid transmissibility among strains of PVY^O and PVY^{N-Wi}, *M. persicae* was selected, because this PVY vector is a common colonizing aphid in potato (20,31). A transmission assay system using potato plantlets from true potato seed was set up to allow for the control of plant age and to minimize variability among source and target plants. The transmission of all isolates was evaluated with 50 aphids in each of three experiments (150 total) except for the reference isolates PVY^O-Oz and PVY^{N-Wi}-ME151-25 that were tested in six experiments. Using a single clone of *M. persicae*, there were no apparent differences in the aphid transmissibilities of PVY^O and PVY^{N-Wi} strains as groups; using five aphids per plant, the rates ranged from 53% (16/30) to 90% (27/30) and 83% (25/30) to 93% (28/30), respectively (Table 2). All isolates were transmitted to 8 of 10 plants in at least one experimental replicate and, on the whole, all isolates were relatively efficiently transmitted by *M. persicae*. For the statistical

Fig. 1. Reverse-transcription multiplex polymerase chain reaction of RNA extracted from tobacco leaf tissue infected by *Potato virus Y* (PVY) strains and isolates. Lanes 1–5, PVY^{N-Wi} isolates ME151-25, ID1-2-9b, MN15b-28, ME193-25, and ID14-2-14a, respectively. Lanes 6–10, PVY^O isolates PVY-Oz, CO35, ME324-33, ID1-7-12b, and ME236-120, respectively. Sizes of the complementary DNA amplicons are indicated to the right of the figure. An amplicon of 689 bp was present for both strains, the 181-bp amplicon was present only for PVY^{N-Wi} isolates, and the 267-bp amplicon present only for PVY^O isolates.

analysis, the data for the 10 virus isolates was bulked and the transmission frequencies considered as a single data set. In replicates where 10/10 plants were infected, the P* value of 0.369 (corresponding to 9/10 plants infected) was assumed in order to avoid the biased overestimate of 1.0 (38). Only one isolate differed from the others in transmission frequency; the estimated likelihood of transmission by a single aphid for the PVY^O isolate ID1-7-12b was 0.156, whereas that for the other nine isolates ranged from 0.27 to 0.369 (Table 2). The mean of the PVY^O isolates was also compared with the mean of the PVY^{N-Wi} isolates with a planned contrast and no significant difference was observed.

Transmission of PVY^O and PVY^{N-Wi} by five aphid species. Although *M. persicae* is considered the most important vector of viruses in potato (31), other aphids infest potato or play a role in PVY transmission. To test the transmission of PVY^O and PVY^{N-Wi} by other aphid species, four additional aphid species were selected. *A. nasturtii* and *A. gossypii* are both potato-infesting aphids of worldwide importance, while *A. glycines* and *R. padi* are PVY vectors with the potential to migrate through potato in large numbers in North America (7,15,32). PVY transmission by two additional clones of *M. persicae* was also evaluated. The PVY^O isolate Oz and the PVY^{N-Wi} isolate ME151-25 were employed in this set of transmission assays.

Using five aphids per plant, the PVY transmission efficiency by the five aphids species ranged from 0 to 90%. *M. persicae* was the most efficient (Table 3). The three clones of *M. persicae* had similar transmission efficiencies, except for clone 3 that transmitted the PVY^{N-Wi} isolate more frequently. *A. nasturtii* was able to transmit both PVY isolates, though with an intermediate level of efficiency. *A. gossypii*, *R. padi*, and *A. glycines* were relatively poor vectors, transmitting less efficiently than all three clones of *M. persicae*. Among the different aphid species, the estimated mean likelihood of transmission by a single aphid ranged from 0.003 to 0.338. Although no transmission of the PVY^O isolate Oz by *A. glycines* was observed, estimating the transmission frequency as zero would likely be an underestimate (38). A more conservative estimate was made assuming a single transmission event among all replicates (e.g., 1/30). Whereas the estimated likelihood of transmission by a single aphid would more accurately be described as <0.007, for statistical comparisons and in Table 3, the value is assumed to be 0.007. In summary, with the exception of *M. persicae* clone 3 noted above, whereas there are observed differences in transmission efficiencies between aphid species and clones to transmit a given PVY isolate, there are no differences in the ability of a given aphid clone to transmit the PVY^O versus the PVY^{N-Wi} isolate.

Discussion

To facilitate testing the efficiency of aphid transmission that more accurately reflects PVY spread into and within potato and to reduce the experimental variability inherent in transmission work, we developed a system using true potato seed to generate test plants. This allowed for greater consistency in the preparation of PVY-infected source plants from which aphids fed and acquired virus, and the size and age of uninfected target plants onto which

Table 2. Aphid transmission of isolates of *Potato virus Y* (PVY)^O and PVY^{N-Wi} by *Myzus persicae* clone 1 from and into NY 129 potato plants^z

	PVY ^O isolates					PVY ^{N-Wi} isolates				
	Oz	CO-35	ME324-33	ID1-7-12b	ME236-120	ME151-25	ID1-29b	MN15b-28	ME193-25	ID14-2-14a
	10/10	10/10	9/10	8/10	10/10	9/10	9/10	9/10	10/10	10/10
	9/10	8/10	9/10	4/10	8/10	9/10	9/10	9/10	9/10	10/10
	8/10	6/10	9/10	4/10	6/10	8/10	7/10	8/10	7/10	8/10
	7/10	—	—	—	—	8/10	—	—	—	—
	5/10	—	—	—	—	8/10	—	—	—	—
Total	39/50	24/30	27/30	16/30	24/30	42/50	25/30	26/30	26/30	28/30
P*	0.271 ab	0.270 ab	0.369 a	0.156 b	0.270 ab	0.313 a	0.317 a	0.338 a	0.317 a	0.338 a

^z Transmission expressed as the number of plants infected/number of plants exposed to aphids. The experimental unit was a single source plant and 10 target plants with five aphids per plant. P* is the mean estimated likelihood of transmission by a single aphid; different letters within the table indicate a statistical difference between means at ($P < 0.05$).

viruliferous aphids were transferred. Several of the previous studies to determine transmission efficiency of various potato-infecting PVY strains by various colonizing and noncolonizing aphid species have employed source or recipient plants other than potato (10,17–19,39). The probing behavior of PVY vectors differs significantly depending on the host and can affect the estimation of transmission efficiency (3,28). Therefore, it is important to use potato as both the source and recipient plants in determining the efficiency of PVY transmission in the potato cropping system. Potato plants are not generally grown from seed but, rather, are propagated in tissue culture or sprouted from tubers. It is difficult to obtain large numbers of plants at the same growth stage by either of these methods but both of these sources of plants have been used to determine PVY transmission efficiency by different aphid species (7,15,21,28,34). The source and age of potato plants can influence transmission efficiency (2) and, therefore, having a reliable method to generate large numbers of potato plants of the same age and morphology can minimize one potentially major source of variation in transmission efficiency. The use of true potato seed has been reported previously for PVY transmission studies but with less emphasis on plant age and methodology (7).

Although a single clone of *M. persicae* (clone 1) was used for a majority of this work, it did transmit virus at frequencies comparable with those from potato to potato reported elsewhere (28,32,39). This clone proved to be a relatively efficient vector for all tested isolates of PVY^O and PVY^{N-Wi}. Although one isolate, PVY^O ID1-7-12b, was transmitted less efficiently than a majority of the other isolates, overall there were no striking differences observed when the means of the two groups of isolates were compared by planned contrast, and it cannot be concluded that the isolates of PVY^{N-Wi} are more efficiently transmitted than those of PVY^O. To our knowledge, there have been no other direct comparisons of transmission efficiency of the PVY^O and PVY^{N-Wi} strains. Fereres et al. (10) reported similar transmission efficiencies for PVY^O and PVY^N. Interestingly, Harrington and Gibson (16) reported a greater number of field-collected aphids transmitting PVY^O than PVY^N but this was not a direct comparison of transmission efficiency and may have reflected a difference in amounts of natural inoculum in the study area. Basky et al. (1) compared the transmission of PVY^O and PVY^N and reported that PVY^N was transmitted more efficiently than PVY^O, although the differential transmission efficiency was likely due to differences in the amounts of virus available in the source tissues. More recently, Verbeek et al. (39) compared aphid transmission efficiencies for PVY^N, PVY^{NTN}, and PVY^{N-Wi}

strains and found no significant differences when source tissues containing comparable levels of virus were used. In summary, there is a lack of evidence that there are significant differences in transmission efficiency by aphids among the various PVY strains.

Aphid species and aphid populations within a species can differ markedly in transmission efficiency of the same virus (12,14,24,39). We tested two additional clones of *M. persicae* and found similar transmission efficiencies for all virus isolates, with the exception of PVY^{N-Wi} ME151-25, which was transmitted more efficiently by clone 3 than by clone 1 or 2. Although there can be considerable variability in transmission work and the experimental design included a limited number of replicates, it would not be surprising to see differences among clones in this and other aphid species with regard to their efficiency in transmitting viruses. Verbeek et al. (39) also found slight differences in transmission efficiency of various PVY isolates among *M. persicae* clones but, in general, all *M. persicae* populations are reported to be efficient vectors of PVY (32,39).

Although *M. persicae* is considered to be the most efficient and important vector of PVY in potato in many production areas, there are numerous other aphids, both potato-colonizing and migrant species, that have been identified as vectors in field and laboratory studies (32). In the northeastern United States, the foxglove aphid, *A. nasturtii*, is a common potato-colonizing aphid and it has been identified as a relatively efficient vector of PVY in potato in other geographic areas (34,39). We also found *A. nasturtii* to be a vector with intermediate efficiency, suggesting that populations of this aphid may all be similar in their ability to transmit PVY, similar to the consistency found among *M. persicae* populations. The three additional aphids tested in this study (*A. gossypii*, *R. padi*, and *A. glycines*) represent common aphids in northeastern U.S. agriculture and potential migrant aphids in potato. All have been reported to be vectors of PVY but at relatively low efficiencies. However, these species can occur in very large numbers; therefore, their vector propensity rating could be quite high. *R. padi* is abundant in many potato production areas (15,32,34) and is considered to be a principal vector of PVY, because it can emigrate from cereals in large numbers and impact overall PVY incidence (8,19,28,34,35). Our clone of *R. padi* transmitted PVY inefficiently, similar to other studies, but there does appear to be a good deal of variability in transmission efficiency among *R. padi* clones (19,28,35). Variability in transmission efficiency among *R. padi* clones extends to other viruses such as the yellow dwarf viruses (14,24). Similarly, *A. glycines* has become an abundant aphid migrating through po-

Table 3. Transmission of *Potato virus Y* (PVY) isolates PVY^O Oz and PVY^{N-Wi} ME151-25 by five aphid species from and into NY 129 potato plants

	<i>Myzus persicae</i>			<i>Aphis gossypii</i>	<i>A. nasturtii</i>	<i>Rhopalosiphum padi</i>	<i>A. glycines</i>
	Clone 1	Clone 2	Clone 3				
PVY^O isolate Oz							
	7/10 ^z	10/10	9/10	1/10	6/10	3/10	0/10
	7/10	5/10	6/10	0/10	1/10	3/10	0/10
	6/10	2/10	3/10	0/10	1/10	3/10	0/10
	6/10	—	—	0/10	—	0/10	—
	6/10	—	—	0/10	—	0/10	—
	2/10	—	—	0/10	—	0/10	—
Total	34/60	17/30	18/30	1/60	8/30	9/60	0/30
P*	0.162 bc	0.181 b	0.202 b	0.003 e	0.070 de	0.034 e	0.007 e
PVY^{N-Wi} isolate ME151-25							
	10/10	8/10	10/10	1/10	6/10	1/10	3/10
	8/10	6/10	9/10	0/10	3/10	0/10	0/10
	7/10	1/10	8/10	0/10	1/10	0/10	0/10
	7/10	—	—	0/10	—	0/10	—
	5/10	—	—	0/10	—	0/10	—
	2/10	—	—	0/10	—	0/10	—
Total	39/60	15/30	27/30	1/60	10/30	1/60	3/30
P*	0.208 b	0.154 bcd	0.338 a	0.003 e	0.086 cde	0.003 e	0.023 e

^z Transmission expressed as the number of plants infected/number of plants exposed to aphids. The experimental unit was a single source plant and 10 target plants with five aphids per plant. P* is the mean estimated likelihood of transmission by a single aphid; different letters within the table indicate a statistical difference between means at ($P < 0.05$).

tato in much of the Midwestern and northeastern United States (7). Our clone transmitted PVY inefficiently but Davis et al. (7) reported transmission efficiencies ranging from 14 to 75%. Interestingly, they found that *A. glycines* preferentially transmitted PVY^O from plants infected with mixtures of PVY strains. Although we found differences among the five aphid species in their ability to transmit PVY, there were no obvious differences in the transmission of the two virus strains. Other factors such as feeding preferences on PVY^O versus PVY^{N:O}-infected hosts and mixed infections could also influence the epidemiology.

PVY has shown itself to be remarkably complex, as illustrated by the conspicuous emergence of new genotypes and pathotypes. The determining forces of selection giving rise to emerging virus variants are not apparent but, given the “flush-through” or limited generation nature of potato seed production, the aphid vectors will remain a critical link. Ultimately, potato clean-seed production and the management of virus-tested seed crops will be the key to limiting the spread of PVY and the emergence of new pathotypes.

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