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Potato virus Y An Evolving Concern for Potato Crops in the United States and Canada

Potato virus Y (PVY) is the type member of the *Potyviridae* and a major economic disease agent in most solanaceous crops. PVY in potato has received a lot of attention in recent years, and indeed this virus is the most economically important disease problem in seed potatoes in many areas of the world. The virus is responsible for decreases in yield and quality, but the main issue in seed potato production is a requirement for strict virus tolerance limits for certified seed. High levels of PVY have been responsible for many seed lots being rejected as certified seed, resulting in a significant reduction in crop value, and at times in a shortage of certified seed, especially of certain cultivars that are highly susceptible to infection.

PVY has a wide host range, naturally infecting plants in more than nine families, including 14 genera of the Solanaceae, such as pepper, tomato, eggplant, and tobacco (43). Some of the nonpotato isolates will also infect potato, but others apparently will not (44,55,80). PVY isolates from each of these crops have become the subject of many classification schemes that will not be covered in this article. The reader is referred to several recent reviews that provide in-depth information on this topic and list numerous additional references (44,76,89). Here we concentrate on PVY as it has and continues to affect potato.

PVY is common in most potato production areas around the world, and there is increasing recognition of various strain types. The classification of the potato-infecting isolates is in a state of flux (89), but there are several recognized strains and groups. The ordinary strain of PVY, PVY^{O}, is the most prevalent in North American potato production and in general causes mosaic, leaf necrosis, and leaf drop symptoms, although the type and severity of symptoms will differ among potato cultivars (Fig. 1). PVY^{O} does not cause veinal necrosis in tobacco. Tobacco veinal necrotic strains include PVY^{N}, PVY^{NTN}, and $PVY^{N\text{-}Wi}$. The latter is not serologically distinct from PVY^{O}, and its genome likely arose via a recombination between PVY^{N} and PVY^{O} (Fig. 2). PVY^{N} and PVY^{NTN} are serologically distinct from PVY^{O}. PVY^{NTN} isolates were originally named for their ability to cause potato tuber necrosis in addition to tobacco veinal necrosis (2,6,48,65,93). They apparently arose from both recombination (32) and mutation events (45,59). Interestingly, the tobacco veinal necrotic strains tend to be less symptomatic in potato plants than PVY^{O} (12,96).

All of the PVYs are transmitted in nature by numerous species of aphids; the current total is more than 50 species that are able to transmit PVY with varying efficiency (74). Aphids transmit PVY in a nonpersistent manner which requires acquisition and inoculation times of less than one minute (7), allowing many species of aphids that are only casual visitors to potato plants ample opportunity to either acquire or transmit the virus. There are data that indicate some of the PVY strains may be more efficiently transmitted by some aphid vectors than by others (1,11,26), although transmission efficiency will differ among virus isolates within a strain and aphid populations within a species (94). Once the plant foliage is inoculated by aphids, virus is translocated to tubers; although the efficiency of this translocation can vary among cultivars. Nevertheless, given the vegetative propagation of the potato crop by tubers, infected tubers are a main source of initial inoculum in an emerging crop, and the planting of infected tubers is a major contributor to overall virus incidence. In many developed countries, the planting of seed lots with a high incidence of virus infection is minimized by growers adhering to the requirements of potato seed certification programs in which virus levels in seed production fields and harvested crops are effectively monitored and managed. Seed lots with virus incidence exceeding 1 to 3% are not usually certified and cannot be sold as seed. Seed certification programs can be extremely effective in limiting PVY incidence in seed stocks, but the program's success is dependent upon the ability of inspectors to visualize and/or detect the virus, the established threshold, and the willingness of growers to plant only certified seed. Some U.S. states and Canadian provinces have mandatory seed laws which require all commercial potato fields to be planted from certified seed. As you will see, seed certification programs and growers have faced some challenges in recent times whose underlying causes have contributed to the re-emergence of PVY as a serious disease problem in potato, especially in the seed potato crop.

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Fig. 1. A, Healthy (top left) and *Potato virus Y* (PVY)-infected leaves expressing the range of symptoms commonly observed on various potato varieties and caused by various PVY strains. Symptoms range from mild to severe mosaic, leaf crinkle, interveinal chlorosis/necrosis, vein necrosis, whole leaf chlorosis/necrosis. **B,** Symptoms on adaxial and abaxial surfaces of leaves.

Initial Reports of Necrotic Strains of PVY in the United States and Canada

PVY^O has been recognized as an issue for potato production at least since its description in the early twentieth century (79) and likely long before that. However, the necrotic strains of PVY are a relatively recent introduction to potato grown in both the United States and Canada. The first report of a tobacco veinal necrosis strain of PVY (PVY^N) (Fig. 3) in the United States was by Kahn and Monroe (41), but this was intercepted on potato introductions from South America, and the virus was not found in the field. PVY^N was identified in Ontario, Canada tobacco fields in 1969 (85) and again in 1989 (55). Using the tools available at the time, McDonald and Kristjansson (55) characterized several of these isolates and found they shared properties reported for other potato-infecting PVY^N isolates from Europe and South America. In 1990, PVY^N was reported in seed potatoes growing in Prince Edward Island (PEI) and New Brunswick. Summer sampling and subsequent winter tests identified PVY^N in several fields from both provinces, but all the seed originated from a single seed source in PEI (86). A massive survey (4.7 million leaves) in the summer of 1991 identified low levels of PVY^N in other eastern Canadian provinces (86). The extremely low incidence of the tobacco veinal necrotic strain of PVY found prompted a study to determine if eradication was possible. The conclusion was that an eradication effort carried out primarily through the potato seed certification program could prevent the multiplication of any PVY^N-infected seed potatoes and their spread to other geographic locations (86). A similar eradication effort had been successful in New Zealand during the 1980s (27) and remained effective well into the 1990s (28). The survey of 1991, in addition to the PVY^N disclosure, also identified other variant forms of PVY^N. For example, while investigating possible sources of the PVY^N introduction into Canada, three isolates collected in 1991 from table-stock potatoes imported from California, and apparently grown from Canadian seed, were identified as belonging to the PVY^{NTN} group on the basis of their induction of potato tuber necrotic ringspot disease (PTNRD) (57). Also, two isolates from Manitoba induced veinal necrosis in tobacco, but failed to react with four different PVY^N-specific monoclonal antibodies in ELISA (56). During this time, postharvest test samples representing seed lots from seven Canadian provinces and five American states were grown-out in California and Florida in the United States and in Jamaica as part of the seed certification process. Surveys of these seed lots by sampling leaves and testing with enzyme-linked immunosorbent assay (ELISA) for PVY and PVY^N were done by Peter Ellis, then of Agriculture and Agri-Food Canada. This survey was conducted from 1991 through 1994 with no

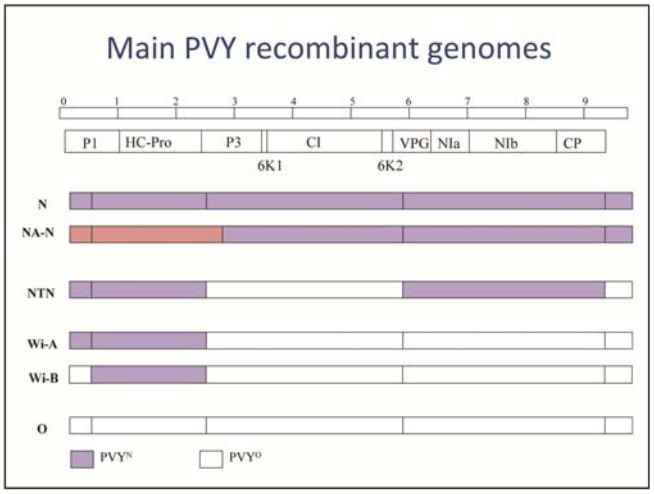

Fig. 2. *Potato virus Y* (PVY) genome organization and arrangement of the most common recombinant genomes identified during the 3-year survey of PVY isolates infecting seed potatoes in the United States. PVY^N (N) and PVY^O (O) are considered to be the parental genotypes (strains) that have recombined to form the additional strains now recognized to be present in the United States and Canada, i.e., PVY^{NTN}, both North American (NA) and European (EU) forms, and $PVY^{N\text{-}Wi}$, both A and B forms.

PVY^N found, giving additional evidence that PVY^N strains are a recent introduction into the seed potato system in North America (24).

The diagnostic tools developed from 1991 to 2002 in Canada allowed further classification of these PVY^N isolates into European and North American PVY^{NTN} (88,97) and PVY^{N-Wi} (this strain is often designated $PVY^{N:O}$ in the literature from North America and elsewhere) (61,62,69). The PVY^{N-Wi} strain was later shown to be present not only in Manitoba, but also in seed from Minnesota, Montana, and North Dakota (87). Subsequently, the determination of complete nucleotide sequences of PVY^O, PVY^{N-Wi}, PVY^N, and PVY^{NTN} (50,59,60,84) showed that some strains were molecular recombinants, while others were not.

Necrotic strains of PVY were first reported on potato growing in the United States in 2002 (15). These included isolates related to PVY^{N-Wi}, PVY^N, and both European and North American PVY^{NTN} types. Samples used to identify more than 50 isolates that induced veinal necrosis in tobacco were collected from a wide and diverse area of the Northwestern United States. These results suggested that these strains were not localized to a geographic area or to a single seed source and that introduction had likely occurred many years prior. Indeed, a PVY^N isolate was reported by McDonald and Kristjansson (55) that was obtained from tablestock potato imported into Canada from California, and data were presumably available, although not published, that additional testing of U.S. seed potatoes from several states revealed detectable levels of PVY^N (29).

How Politics Affects PVY Distribution and by Extension the Diversity of Predominant Strains

The report of PVY^N in Canada in 1990 triggered regulatory action by the United States and Canada. Canada had initiated a plan designed to test the feasibility of eradicating PVY^N by concentrating efforts on eliminating the virus from seed stocks (86). This plan advocated testing all seed lots at a recommended rate of 1,000 to 5,000 leaves per field, and in the first year of the plan there appeared to be some success in reducing the overall incidence. The annual potato trade between the United States and Canada is valued in the hundreds of millions of dollars, which facilitated a strong desire on both sides to find a solution to the quarantine measures applied following the detection of PVY^N. To facilitate continued trade of seed and commercial potatoes between the two countries, a PVY^N management plan was developed and implemented in 1994; this was amended 5 October 2001. The objective of this plan was to facilitate trade of potatoes within and between Canada and the United States, while minimizing the impact on the tobacco industry, and to protect the potato industries from widespread establishment of PVY^N in the potato crop. The plan focused on serological testing of early generation (G2) seed lots for PVY^N. Although participation was mandatory in Canada, it was voluntary in the United States, and many of the states suspected of having PVY^N opted out of participation.

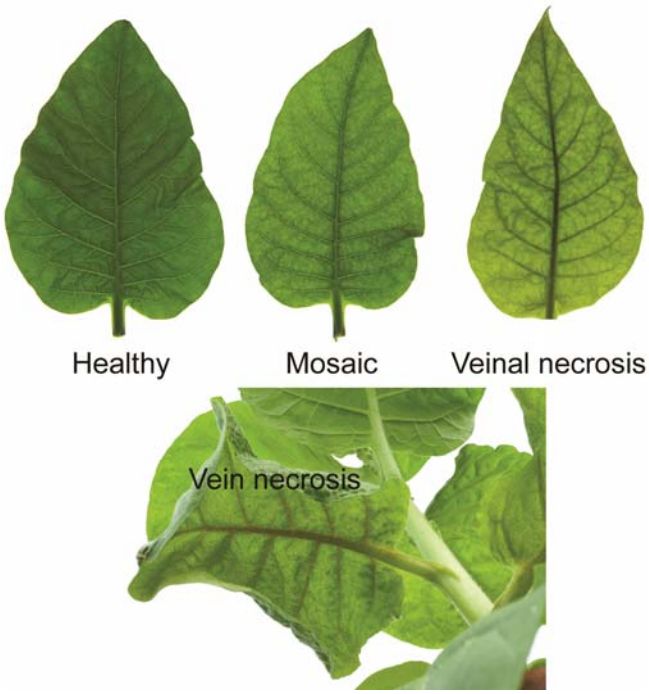

Fig. 3. Healthy and *Potato virus Y* (PVY)-infected tobacco leaves. PVY^O induces a mild mosaic or vein banding, while PVY^N, PVY^{N-Wi}, and PVY^{NTN} strains induce a characteristic veinal necrosis. The darkening and necrosis of the veins begins in the midrib of inoculated leaves and progresses to smaller veins within the inoculated leaves and then to veins in leaves above the inoculated leaves.

Hindsight is always 20:20, and we now know that even by the late 1990s, and quite possibly well before this, PVY in North America had evolved well beyond the typical PVY^O and PVY^N strains to include the recombinant PVY^{N-Wi} and PVY^{NTN} strains and likely other variants as stated earlier. Had this information been available, it would have negated any strategy to use a serological test to identify seed lots infected with a tobacco necrotic strain of PVY. Monitoring of the early generation G2 lots only detected PVY^N in a few lots over the time the management plan was in place. Testing of late generation seed lots (e.g., G4 or G5, i.e., fourth or fifth generation seed lots) may have detected an influx of PVY^N sooner. However, the plan achieved its primary goal of allowing continued trade and movement of seed potatoes.

Adoption of the 1994 PVY Management Plan did not contain the spread of PVY^N or other tobacco necrotic strains of PVY. Indeed, in the years following the adoption of the PVY management plan, many scientific publications identified a multitude of tobacco and tuber necrotic isolates of PVY from potato growing in all regions of Canada and the United States. Also during this period, *Potato mop-top virus* (PMTV) was reported for the first time in both countries (47,99), and other tuber necrotic viruses also appeared to be expanding their distribution (18,37,46,100). The PVY^N strain, now a nebulous definition for many recognized variants that could not be accurately identified by any one diagnostic assay, and other potato tuber necrotic viruses (e.g., PMTV) remained on the list of quarantined or regulated pathogens. In an effort to update the management plan and to facilitate research on appropriate disease management strategies for tuber necrotic viruses, discussions commenced in the early 2000s on the development of a revised PVY management plan that would also include other tuber necrotic viruses, specifically PMTV, *Tobacco rattle virus* (TRV), and *Alfalfa mosaic virus* (AMV).

The Canada/US-Management Plan for Potato Viruses that Cause Tuber Necrosis was finalized in October 2004 and officially adopted in February 2006 (http://www.aphis.usda.gov/plant_health/plant_pest_info/potato/downloads/pvy/NecroticVirusManagementPlan.pdf). This was the product of many bilateral discussions among scientists, seed certification officials, industry representatives, regulatory officials, and growers. The overarching goal was similar to that of the 1994 PVY management plan: to facilitate unencumbered trade of potatoes among states, provinces, and the two countries while protecting the potato industries of both countries from economically damaging levels of any of the viruses causing tuber necrosis. One immediate benefit was to exempt the finding of these viruses from any type of regulatory consequence, an action that facilitated research on the distribution, incidence, and genetic makeup of PVY affecting the U.S. and Canadian seed potato crops because growers did not fear any reprisals if necrotic strains of PVY were found on their farms. The management plan was designed to be a living document that would be continually discussed and revised as new information was acquired. The management plan was not designed to be heavy-handed, but rather to provide guidelines that would encourage additional testing and inspections to identify and facilitate the management of PVY, and more importantly for the potato industry to acknowledge the occurrence of all the tuber necrotic viruses including PVY^{NTN}, PMTV,

TRV, and AMV. Initially, testing of G2 lots for PVY^N was to continue, but within the first year a recommendation was made to discontinue the testing. This recommendation was based on results of a national survey conducted in both Canada and the United States that investigated the PVY population in all late generation (G5-G6) seed lots. The 3-year survey, discussed in detail below, was designed to identify the genetic diversity and the geographic distribution of PVY infection in U.S. and Canadian seed potato crops. The information was used to provide advice to seed certification agencies, industry representatives, and growers, and to refine the management plan so that it was based upon sound sampling, detection, and management practices.

The Re-emergence of a Genetically Diverse PVY Population and Its Effect on the Seed Potato Crop

Historically, seed certification programs have been able to keep the levels of PVY under control by using a "flush through" system in which seed potatoes are kept in the program for a limited number of generations. Each generation is assumed to accumulate virus slowly over time provided best management practices are adopted, and flushing later generations out of the certified program reduces the risk that virus will accumulate to levels that result in economic loss. Each generation of seed potatoes is carefully inspected in the field, and in many instances in postharvest tests, to determine the level of virus. If the level exceeds tolerance limits at any time, the seed lot is downgraded or removed from the certification system depending on the virus level. The success of the seed certification programs at keeping virus levels under control is dependent upon disease symptoms being expressed and observed on the crop in the field and/or on the harvested tubers, and/or being accurately identified in various postharvest testing schemes. Disease observed in the field can often be minimized by roguing virus infected plants. When virus infection cannot be observed visually, the system is less effective and seed lots that would normally be rejected may be recertified, and then the level of inoculum begins to climb. While the incidence of PVY depends to a considerable extent on whether growers utilize best management practices, three changing factors were paramount to the re-emergence of PVY: a change in the genetic composition of PVY strains, the release and widespread acceptance of cultivars that express mild or no PVY symptoms, and increased aphid pressure later in the growing season. Each of these three factors (discussed below) impedes the visual identification of infected plants, resulting in virus levels that build in each successive seed crop and consequently become more widely distributed in the commercial crop.

PVY^O induces easily recognized mosaic symptoms in most potato cultivars, but it is being displaced by tuber necrotic and/or tobacco necrotic strains (PVY^{NTN} and $PVY^{N\text{-}Wi}$) once thought to be excluded from the United States (34,51). Many of these new strains are genetic recombinants between PVY^O and the original tobacco necrotic strain, PVY^N, and the genetic diversity among these recombinants is vast (Fig. 2). In Europe, PVY^{NTN} has displaced PVY^O as the predominant strain within the past 20 years (76). Interestingly, PVY^{NTN} and $PVY^{N\text{-}Wi}$ tend to induce less severe foliar symptoms than PVY^O on most cultivars, and this has likely contributed to the rise in incidence of the necrotic and recombinant strains because they often go unnoticed during field inspections. Exacerbating the problem is that no one simple test can accurately classify the multitude of emerging necrotic PVY strains. A cocktail of biological, serological, and/or molecular diagnostic tests are required, at considerable labor and expense, to effectively classify these strains (51). Inaccurate field inspections and improper diagnosis have contributed to some unnecessary trade restrictions (42). Indeed, ELISA using antibodies specific to PVY^N and PVY^O strain types may have contributed to the spread of the recombinant isolates of $PVY^{N\text{-}Wi}$. Recall that $PVY^{N\text{-}Wi}$ is a tobacco veinal necrosis strain, but has the serological phenotype of PVY^O due to the recombinant nature of its genome. When seed lots were tested by serology for PVY^N, lots infected with $PVY^{N\text{-}Wi}$ would have tested negative and would not have been eliminated as a seed source unless the overall PVY incidence was above tolerance limits. This could have perpetuated the $PVY^{N\text{-}Wi}$ strain and increased its distribution.

The success of seed certification programs has limited the interest of potato breeding programs to include virus resistance as a trait for selection. Limited testing for virus susceptibility has resulted in the selection, release, and widespread acceptance of several potato cultivars that are tolerant to virus infection, i.e., the cultivars are symptomless carriers of the virus or symptoms are very mild and/or transient. These symptomless carriers are also good sources of virus that is spread to neighboring crops. Tolerant cultivars infected with PVY and expressing mild or transient symptoms have reduced yields, and virus is readily acquired from such plants by aphids and spread among other susceptible cultivars (39,77,78,91). Many cultivars are included in the "tolerant" category (http://oregonstate.edu/potatoes/latent to PVY list.htm), but cultivars Shepody and Russet Norkotah are two of the most problematic, and they are widely grown, accounting for over 12 and 5% of the total U.S. and Canadian seed acreage, respectively, in 2009. The demand for seed, coupled with high levels of PVY in the seed crop, has often limited the availability of certified seed for these cultivars. Resistance or susceptibility to PVY is a trait that has been included in the most recently released cultivars, but it is usually mentioned in the context of foliar symptom severity. Furthermore, the reaction to PVY is often determined from natural infections that may occur in evaluation plots. The strain of the virus is rarely considered. As early as 1978, crosses for virus resistance were begun in the USDA-ARS Aberdeen, ID breeding program. Selected clones from these crosses were evaluated in replicated plots for resistance to *Potato virus X* (PVX), PVY, and *Potato leafroll virus* (PLRV) starting in 1985 (14). These evaluations relied on natural and artificial inoculations to obtain high virus pressure. Recent releases from this program have included information regarding PVY strain reactions (90). As more breeding programs recognize the value of PVY resistance (66,98), there is a need to develop some standard materials and protocols that will allow potato genotypes to be evaluated properly against a range of PVY strains that predominate in the regions of the country that will likely produce the released cultivar. Evaluating PVY responses as part of the field testing of advanced breeding lines allows breeders, growers, and seed certification programs to identify potential problems and discover new sources of resistance.

A third factor contributing to the increase in PVY levels is the increase in aphid populations, especially in late-season flights of both colonizing and noncolonizing species. The introduction of the soybean aphid (*Aphis glycines*) to the United States in the early 2000s is a prime example. Late-season inoculation of plants by migrating aphids can result in infection, but foliar symptoms are not manifested in the mature plants while tuber infection can be significant.

Defining the PVY Problem in the United States and Canada

As mentioned above, a provision of the Canada/US-Management Plan for Potato Viruses that Cause Tuber Necrosis was to conduct a survey of all seed production areas in both countries to determine the genetic makeup and distribution of the PVY strains affecting the seed potato crop. In each of 3 years, 2004, 2005, and 2006, tuber samples were collected by growers in the United States and in Canada and submitted, in the United States to the seed certification agency in their state, and in Canada to a CFIA-approved laboratory. All U.S. seed growers were asked to collect random tubers at harvest from each field generation 5 (G5) seed lot on the farm; the sampling rate was 2 tubers per acre. If there were no G5 lots on the farm, then G4 lots or in some cases G3 lots were sampled. The certification agency submitted the tuber samples to a laboratory that they generally use for testing, which was usually associated with the state departments of agriculture. A few states

opted to send tuber samples directly to a university-based laboratory either at Idaho Falls, ID or Ithaca, NY. Each state was responsible for testing sprout or leaf tissue from sprouted tubers by ELISA using the monoclonal antibody 4C3 (Agdia), which recognizes all strains of PVY. Positive samples were retested using the PVY^N-specific monoclonal antibody 1F5. Once each of the states reported the initial findings, scientists directing the survey worked with each state's lab director or certification official to identify a subset of infected tubers that would be sent to laboratories in Idaho or New York for further strain characterization. The overall goal was to get a set of tubers that were representative of the total number of tubers collected in each state and that represented all the geographic regions and the different cultivars grown in that state. Funding allowed for ~1,000 isolates to be characterized in each of the 3 years.

In Canada, seed growers in all seed-producing provinces collected 100 tubers/seed lot of the lower classes of seed (field generation 5-6) and submitted them to one of five CFIA-approved laboratories. The approved laboratories sprouted or grew out the tubers and then tested them in composites of two by ELISA using monoclonal antibody 4C3. Both tubers of all the PVY-positive composites were sent to the CFIA reference laboratory in Charlottetown, PEI. The Charlottetown Laboratory tested individually all tubers received from the approved laboratories with monoclonal antibody 4C3 to confirm the presence of PVY. PVY-positive tubers that had adequate sprouts were inoculated directly to tobacco for further serological characterization with monoclonal antibodies Mab2 and 1F5, which are purportedly specific for PVY^O and PVY^N, respectively, and to determine the symptom type in tobacco. Inadequately sprouted tubers were grown out in the greenhouse prior to further testing. A total of ~1,700 isolates collected in Canada over the 3 years were characterized.

The original testing plan for the PVY isolates was to determine the serotype using monoclonal antibodies 4C3 and 1F5. These were previously approved by the North American Plant Protection Organization (NAPPO) for determining the presence of PVY^N. Additionally, the PVY P1 gene was to be amplified by reverse transcription–polymerase chain reaction (RT-PCR) (primers were based on Nie and Singh [61]) and sequenced. A number of diagnostic tests had previously utilized sequence diversities in the P1 gene to distinguish among several PVY strains including PVY^O, PVY^N, PVY^{NTN}, and $PVY^{N\text{-}Wi}$ (61,62).

The actual testing protocols were modified to include several other tests that allowed a more in-depth characterization of a subset of the total PVY isolates identified from the field-collected tubers. Tobacco inoculations were not originally part of the analysis for each of the PVY isolates, but many of the tubers that were eventually sent to NY or PEI were of poor quality and limited growth potential. To ensure that there was adequate material to conduct all the tests and to be able to prepare the isolates for long-term storage, the PVY-positive tubers were planted in the greenhouse and developing leaves (or sprouts) were harvested and used to mechanically inoculate tobacco plants, *Nicotiana tabacum* cv. Xanthi NN, Samsun, or Burley 21. Leaf tissue from grown-out potato or inoculated tobacco plants were subsequently lyophilized or kept frozen at –20°C for later reference. Fresh tobacco leaves from inoculated plants were observed for veinal necrosis or mosaic symptoms (Fig. 3) and tested by ELISA with monoclonal Mab2 (specific for PVY^O) and 1F5 (specific for PVY^N) to confirm presence of PVY and determine the serological type. They were also tested in ELISA with PVX antibodies to detect mixed infections. Veinal necrotic symptoms were only considered in PVX-negative tobacco plants because mixed infections of PVX and PVY can also cause veinal necrosis in tobacco (17). Leaf tissue from tobacco plants infected with the individual PVY isolates was used to amplify the P1 gene for subsequent sequencing (in 2004 and 2005), or for a RT-PCR multiplex assay (in 2005 and 2006). The multiplex assay (51) provided additional information on strain differentiation and the identification of mixed infections and was substituted for the P1 sequencing in the analysis of the 2006 samples. A subset of PVY isolates was inoculated from tobacco to potato plants (cv. Yukon Gold) to determine if the isolate would induce potato tuber necrotic ringspot disease (PTNRD) on progeny tubers (Fig. 4).

Over 214,000 tuber samples were collected from the 16 seed producing states in the United States and subsequently tested by ELISA (Table 1). Tubers from Idaho, Maine, Colorado, Montana, and North Dakota comprised nearly 75% of the samples. Accurate counts were not reported from three different states in one of the survey years. A total of 2,452 individual seed lots were tested in the United States during the 3-year survey, and PVY was detected in 836 (Table 1). Over the 3-year survey, 34.6% of the lots tested positive. The range of positive lots from any one state in any one year ranged from 0 to 100% with a median value of 30.6%. Double-antibody sandwich (DAS)-ELISA using a non-strain-specific monoclonal antibody, 4C3, detected PVY in ~4.5% of the tuber samples over the 3-year survey. The mean maximum was 11.7% in one state and ranged to a mean minimum of 0.2% with a median of 2.4%. Of the 9,093 PVY-positive tubers, 7,982 were subsequently analyzed by DAS-ELISA using the PVY^N-specific monoclonal antibody, 1F5. Many of the secondary tests were done in the Ithaca, NY lab, and by the time the tubers reached the lab they either had rotted or did not sprout. A total of 716 of the 7,982 tubers (9.0%) tested positive for PVY^N (Table 2). The percent found in the different states ranged from 20.9 to 0% with a median of 0.24%. PVY^N was not detected in seven states and was detected in less than 2% of the samples in five other states.

A total of 132,600 tubers were collected from the nine seed producing provinces in Canada (Table 1). To maintain grower anonymity, there was no attempt to maintain a collection location for the tuber samples and all data are reported as country-wide. A total of 1,326 individual lots were tested, and PVY was detected in 584. The 3-year mean of the seed lots being infested with PVY was 44.0%, with the yearly totals ranging from 39.3 to 51.8% (Table 2). PVY was detected in 2.5% of the tubers tested over the 3 years. Overall PVY detection levels were similar in 2004 and 2005 for Canada and the United States, but higher in the United States in 2006 (Table 2). Of the 3,277 PVY-positive tubers identified in Canada, 1998 were subsequently tested for PVY^N and 131 (6.6%) were positive.

The tobacco bioassay proved to be invaluable in identifying the predominant PVY strains present in the United States and in identifying the true tobacco necrotic isolates. The serological tests described above and used by all of the seed certification agencies and defined in the NAPPO standard are able to distinguish N and O serotypes, but were not able to accurately identify all isolates that cause veinal necrosis in tobacco. There was a significant discrepancy in the total number of PVY isolates that would be categorized as PVY^N depending on whether one used serology or the tobacco bioassay. In the United States, a total of 2,800 tobacco inoculations determined that 66% of the isolates induced mild mosaic and/or vein banding symptoms and 28% of the isolates induced veinal necrosis (Fig. 1). Similarly in Canada, 1,742 tobacco inoculations determined that 81 and 19% of the isolates induced mosaic/vein banding or veinal necrosis symptoms, respectively (Table 2). These totals do not include inoculations that also tested positive for PVX (i.e., mixed PVY/PVX infections). No attempt was made to separate mixed infections of PVY and PVX to determine if the PVY isolate would induce different symptoms on tobacco in the absence of PVX. The percentage of necrotic versus mosaic isolates, as determined by the tobacco bioassay, were remarkably consistent over all 3 years in each of the countries.

The real significance of both the serological and the tobacco bioassay results came when the data were combined. This allowed us to differentiate four distinct groups, PVY^O, PVY^N, $PVY^{N\text{-}Wi}$, and PVY^O-O5. The first three are recognized strains that were described above. PVY^O-O5 was initially identified by Ellis et al. (24), and recently characterized as a serological variant of PVY^O (42). PVY^O isolates do not react with the 1F5 MAb and induce mosaic symptoms in tobacco. PVY^O was the predominant strain in both Canada and the United States comprising 77 and 64%, respec-

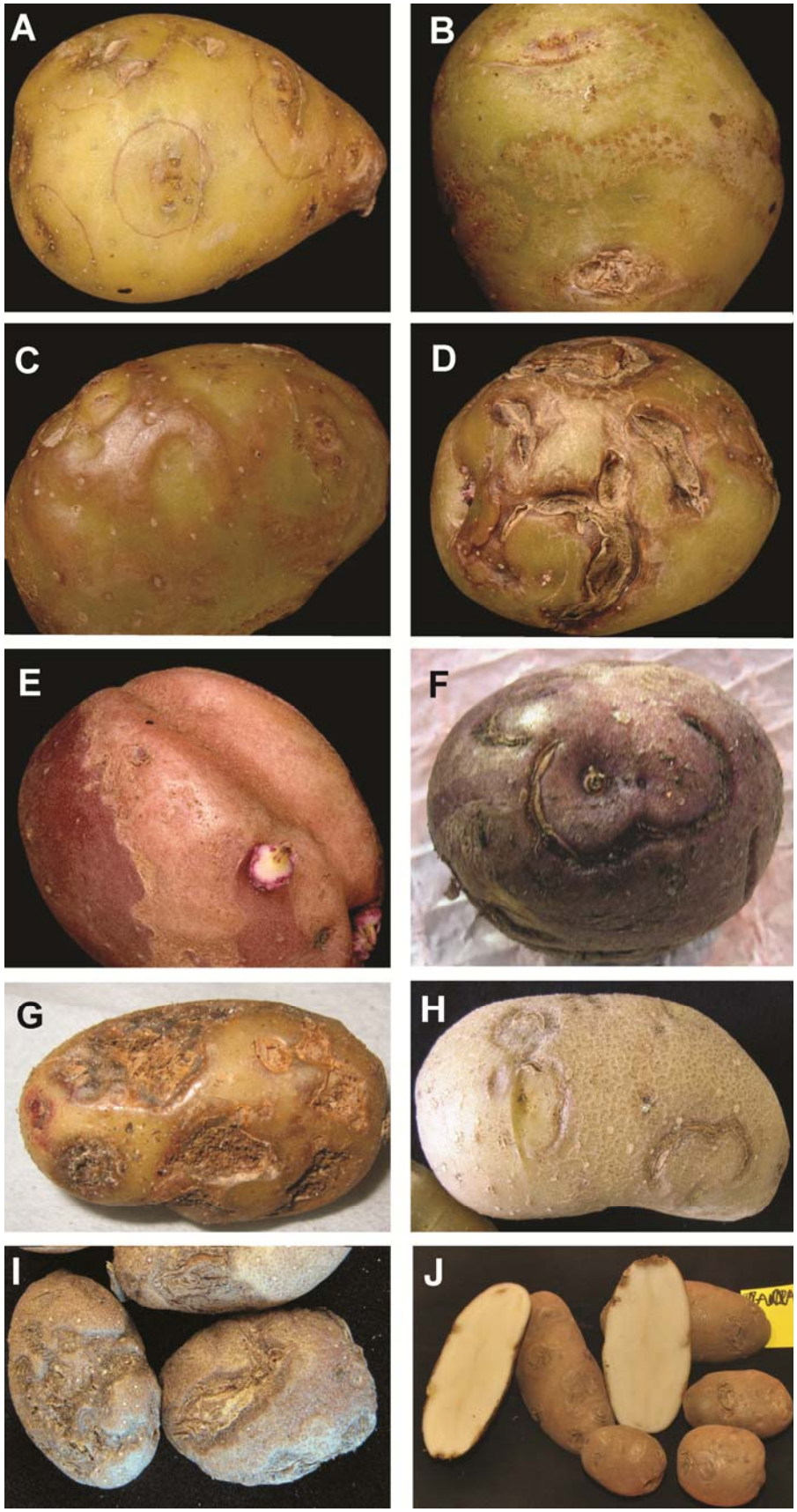

Fig. 4. Symptoms of potato tuber necrotic ringspot disease (PTNRD) on various North American potato varieties: **A–D,** varying symptoms on Yukon Gold; **E–F,** cracking and necrotic rings on Norland Red; **G,** Yukon Gem; **H,** Highland Russet; **I,** Alturas; and **J,** Ranger Russet.

tively, of the total number of isolates characterized by both serology and tobacco bioassay over the 3-year survey (Table 3). PVY^{N} isolates do react with the 1F5 MAb and induce veinal necrosis in tobacco. They accounted for 6 and 3% of the total isolates in the United States and Canada, respectively. The PVY^{N-Wi} isolates are recombinants between PVY^{O} and PVY^{N} that have PVY^{O} serological properties, i.e., they do not react with the 1F5 MAb, but they are similar to PVY^{N} in that they induce veinal necrosis in tobacco. PVY^{N-Wi} comprised 24 and 17% of the total isolates in the United States and Canada, respectively. The PVY^{N-Wi} strain has a wide distribution in both the United States and Canada (16,59,60,69, and this study) and is problematic because it is not always detected in serological tests used by certification and regulatory agencies as a tobacco necrotic strain. The PVY^{O}-O5 variant accounted for 6 and 3% of the total isolates from the United States and Canada, respectively. This variant was found in several areas of the United States, but was concentrated in one state (42). The distribution in Canada is unknown. This variant poses little disease risk to the potato or tobacco industries beyond the ordinary PVY disease, but it has caused problems for some growers in the United States since it is detected as a necrotic strain by serological tests currently sanctioned by NAPPO.

Molecular diagnostics, i.e., the P1 sequencing and the multiplex RT-PCR assay, identified additional strains and variants. The P1 sequence allowed separation of isolates into different strain classifications including PVY^{O}, PVY^{N-Wi}, and PVY^{NTN}. Only one Canadian isolate but none of the U.S. isolates were identified as PVY^{N}. The P1 sequence also distinguishes between European and North American PVY^{NTN} isolates (62,101), as does the multiplex RT-PCR method used in 2005 and 2006 (51). All of the PVY^{NTN} isolates identified in the United States from 2004 and 2005 samples using the P1 sequence were European PVY^{NTN} isolates. Another advantage of the P1 sequence was a further breakdown of the PVY^{N-Wi} isolates into two distinct groups, $PVY^{N-Wi\ a}$ and $PVY^{N-Wi\ b}$, based on the presence or absence of a recombination junction in the P1 gene (32,51). A majority of the U.S. PVY^{N-Wi} isolates were of the 'a' type. The PVY^{N-Wi} 'b' type isolates were identified from four states, but found in significant numbers in only one state (39 and 60% of the PVY^{N-Wi} isolates in 2004 and 2005, respectively) and comprised 22 of 197 and 28 of 163 samples analyzed in 2004 and 2005, respectively. The tuber-necrotic PVY^{NE} isolate (49,69) was only detected as a mixed infection with other strain variants in two samples. The presence of a unique signature sequence in all PVY^{NTN} P1 sequences and the very high homogeneity among classes of PVY^{N-Wi} isolates were more consistent with descent from single recombination events rather than multiple events recreating these strain variants.

The multiplex RT-PCR assay developed by Lorenzen et al. (51) was able to simplify the sample analysis and provide more complete data than the P1 sequencing. The assay distinguished the

Table 1. Number (and percentage) of U.S. and Canadian seed lots tested during a 3-year survey that contained detectable levels of *Potato virus Y* (PVY), and number (and percentage) of tubers that tested positive using a strain-non-specific monoclonal antibody (4C3) or a PVY^{N}-specific antibody (1F5)

	2004		2005		2006		3-year total	
United States								
Lots	266/638[a]	41.7%	219/830	26.4%	351/984	35.7%	836/2,452	34.6%[b]
4C3	2,617/79,342[c]	3.3%	1,577/57,952	2.7%	4,899/64,171	7.6%	9,093/201,465	4.6%
1F5	141/2,562	5.5%	78/1,547	5.0%	497/3,873	12.8%	716/7,982	7.8%
Canada								
Lots	250/483	51.8%	170/426	39.9%	164/417	39.3%	584/1,326	44.0%
4C3	1,422/48,300	2.9%	1,016/42,600	2.4%	839/41,700	2.0%	3,277/132,600	2.5%
1F5	44/524	8.4%	35/734	4.8%	52/740	7.0%	131/1,998	6.6%

[a] Number of seed lots with detectable levels of PVY/total number of seed lots tested.
[b] Mean percentage over the 3 years of the survey.
[c] Number of tubers testing positive for PVY or PVY^{N}/total number of tubers tested. Tubers were randomly collected (2 tubers/acre) from each late generation seed lot grown in the state. Usually fifth generation in the field seed lots were sampled, if there were no G5 lots in on the farm then G4 or G3 lots were sampled. In Canada, 100 tubers were collected from each G5 or G6 lot.

Table 2. Tobacco bioassay results and strain classification for *Potato virus Y* (PVY) isolates tested from the United States and Canada during a 3-year survey of seed potatoes

	Plants inoculated[a]	Plants with mosaic[b]	Plants with necrosis[c]	No infection[d]	Strain identification[e]			
					PVY^{O}	PVY^{N}	PVY^{N-Wi}	PVY^{O}-O5
United States								
2004	952	627	237	88	595	40	197	32
2005	903	580	272	51	550	43	229	30
2006	945	642	271	32	550	65	206	92
3 year total	2,800	1,849	780	171	1,695	148	632	154
Canada								
2004	313	272	41	0	238	12	31	12
2005	696	580	116	0	562	13	100	20
2006	733	556	177	0	482	26	145	23
3 year total	1,742	1,408	334	0	1,282	51	276	55

[a] Number of individual PVY isolates inoculated mechanically to *Nicotiana tabacum* plants.
[b] Number of tobacco plants that expressed mosaic or vein clearing symptoms following inoculation with PVY.
[c] Number of tobacco plants that expressed vein necrosis symptoms following inoculation with PVY.
[d] Number of tobacco plants that did not become infected following mechanical inoculation with sap from tuber sprouts or from leaf tissue developing from sprouted tubers.
[e] Strain identification, PVY^{O} isolates are defined as inducing mosaic symptoms on tobacco and reacting only with the 4C3 monoclonal antibody, PVY^{N} isolates are defined as inducing vein necrosis symptoms on tobacco and reacting with both the 4C3 and 1F5 monoclonal antibodies, PVY^{N-Wi} isolates are defined as inducing vein necrosis symptoms on tobacco and only reacting with the 4C3 monoclonal antibody. PVY^{O}-O5 isolates are a subgroup of PVY^{O}, they induce mosaic symptoms on tobacco and they react with both the 4C3 and 1F5 monoclonal antibodies.

major strain groups, PVY^{O}, $PVY^{N\text{-}Wi}$, and PVY^{NTN}. Additionally, it differentiates the North American and European PVY^{NTN} isolates and easily detects infections containing multiple strains of PVY. The assay does not separate the two subgroups within the $PVY^{N\text{-}Wi}$ strain, nor does it separate PVY^{O} and PVY^{O}-O5 isolates. This assay was used along with the P1 sequencing in 2005 and was the sole molecular assay used in 2006. The assay directly identified a number of mixed infections among the U.S. samples; 13 in 2005 and 66 in 2006. The 11 mixed infections defined in 2004 were done on the basis of data from all of the different assays. Fewer mixed infections were detected in Canada (Table 3). In addition, the multiplex assay defined a new group of isolates that we called $PVY^{N\text{-}Wi\ minus}$. These are isolates that have a PVY^{O} serotype and a recombinant genome organization, but do not induce vein necrosis in tobacco.

Using all of the information from all of the various assays, eight different groups of isolates can be defined (Table 4). There were 2,223 isolates from the United States that were fully characterized using serology, the tobacco bioassay, and genome data (P1 sequencing and/or multiplex RT-PCR). PVY^{O} isolates were the most common and accounted for 1,446 isolates (64%), but 131 of these isolates were the PVY^{O}-O5 variant (~6% of the 2,223 total). A total of 506 isolates (23%) belong in the $PVY^{N\text{-}Wi}$ strain, but 60 (~3% of the 2,223 total) of those were the $PVY^{N\text{-}Wi\ minus}$ variant. The $PVY^{N\text{-}Wi}$ isolates can be further divided into the 'a' and 'b' subgroups. Only two of the $PVY^{N\text{-}Wi\ minus}$ variants were from the 'b' subgroup, whereas 48 of the 353 typical $PVY^{N\text{-}Wi}$ isolates characterized from 2004 and 2005 were identified as 'b' subgroup isolates. The isolates from 2006 were only analyzed by multiplex RT-PCR, and that did not define the 'a' and 'b' subgroups. PVY^{NTN} isolates accounted for only ~5% of the total, and only three of these were identified as $PVY^{NA\text{-}NTN}$. A total of 90 samples (~4%) contained mixtures of strains or variants.

The findings were similar for the Canadian isolates. Of the 1,975 strains characterized from Canada, 67% were true PVY^{O} strains and an additional 3.6% were PVY^{O}-O5, compared to 64 and 6%, respectively, of the strains characterized in the United States. Only in 2006 were a significant number of isolates of the PVY^{NTN} type identified in Canada, perhaps because these strains are clustered in a limited geographic area or limited to a particular seed source. In any case, PVY^{NTN} strains formed only a small component (~1%) of the Canadian PVY strain mixture. As in the United States, the recombinant strain, $PVY^{N\text{-}Wi}$, comprised a sizeable percentage (~27%) of the PVY isolates in Canada. The evident displacement of PVY^{O} by the recombinant $PVY^{N\text{-}Wi}$ is perhaps a function of the greater ease with which the latter is vectored by aphids, as has been reported in European studies (12,13,33,45). A more in-depth study of the epidemiological factors determining strain incidence and distribution was beyond the scope of this study, however.

Isolates Representing all PVY Strains Can Induce PTNRD

The PVY^{NTN} strain has been historically associated with PTNRD, but it is apparent that molecular identification of PVY^{NTN} isolates does not always correlate with the isolate's ability to induce PTNRD (40,101). Similarly, isolates identified by serology or molecular analyses as belonging to strains other than PVY^{NTN} can also induce PTNRD (5). Based on these reports and a general lack of information on tuber necrosis potential in most North American cultivars, a subset of the characterized isolates described above were tested for their ability to induce PTNRD. Over 350 Canadian isolates collected during the survey were evaluated for ability to cause PTNRD by inoculation into greenhouse-grown potato plants (cv. Yukon Gold) and observation of tubers at harvest and after storage for 1 month. Of the 22 PVY^{NTN} strains tested, all caused PTNRD, but 81% of the 16 $PVY^{N\text{-}Wi}$ and an additional 11% of the 118 PVY^{O} isolates tested also caused PTNRD; none of the 50 Canadian PVY^{O}-O5 isolates caused tuber symptoms. Additionally, a total of 116 U.S. isolates representing each of the different strains and subgroups of PVY were tested for capacity to induce PTNRD on Yukon Gold (Table 4). Similar to the Canadian results, typical PTNRD symptoms were observed on tubers from plants infected with isolates of PVY^{NTN}, both North American and European subtypes; $PVY^{N\text{-}Wi}$, both the 'a' and 'b' subtypes; and PVY^{O}. In addition, plants infected with isolates representing all the strains or subgroups with the exception of $PVY^{NTN\text{-}NA}$ in general produced tubers with milder PTNRD symptoms (e.g., Fig. 4A, B, and E). Although many of the strains that induced PTNRD also caused veinal necrosis on tobacco, some exceptions were observed. A smaller subset of the U.S. isolates was also tested on Yukon Gold, Russet Burbank, and Ranger Russet in greenhouse bioassays in Idaho. These results show that Russet Burbank was resistant to PTNRD, while Yukon Gold was susceptible and Ranger Russet was moderately susceptible. PTNRD was produced on Yukon Gold from one of the PVY^{O} isolates, and this isolate also produced symptoms on Ranger Russet and Russet Burbank but at a lower incidence (Table 5).

In several studies, the North American cultivars (AC Chaleur, AC Novachip, Allegany, Atlantic, Bellisle, Century Russet, Cherokee, Conestoga, Frontier Russet, Jemseg, Kennebec, Norchip, Ranger Russet, Red Gold, Redsen, Rosegold, and Yukon Gold) have developed PTNRD when inoculated with North American or

Table 3. Identification of *Potato virus Y* (PVY) isolates from the 3-year survey that were identified to strain group based on serological reaction, molecular data, and the tobacco bioassay

	No. samples analyzed	PVY^{O}	$PVY^{N\text{-}Wi}$ [a]	$PVY^{N\text{-}Wi\ minus}$ [b]	PVY^{NTN} [c]	PVY^{O}-O5	Mix[d]	Other[e]
United States								
2004	768	483	190	20	36	28	11	
2005	696	438	163	14	39	29	13	
2006	658	364	93	26	35	74	66	
3 year total	2,122	1,285	446	60	110	131	90	
Canada								
2004	521	357	116	13	1	29	3	2
2005	729	537	148	13	1	20	0	10
2006	725	430	240	2	23	23	7	0
3 year total	1,975	1,324	504	28	25	72	10	12

[a] $PVY^{N\text{-}Wi}$ isolates can be further divided into two subgroups, 'a' and 'b'. The 'b' subgroups contain a recombination junction in the P1 gene that is not present in the 'a' subgroup.
[b] $PVY^{N\text{-}Wi\ minus}$ isolates are a variant of $PVY^{N\text{-}Wi}$ that are characterized by having a PVY^{O} serotype and a recombinant genome organization like $PVY^{N\text{-}Wi}$, but they do not induce vein necrosis in tobacco.
[c] PVY^{NTN} isolates can be further divided into two subgroups, North American ($PVY^{NTN\text{-}NA}$) and European $PVY^{NTN\text{-}Eu}$.
[d] These samples contain a mixture of PVY strains or subgroups.
[e] The combination of serological and molecular data did not clearly differentiate these strains into one of the PVY groups described in this study.

European PVY^{NTN} (57,88,97). Yukon Gold was found to be extremely susceptible and Ranger Russet moderately susceptible to PTNRD when infected with PVY^{NTN} or $PVY^{N\text{-}Wi}$ (J. L. Whitworth, *unpublished*). In a recent study, Singh et al. (2010) developed a fast-reacting, sensitive, and reliable indicator for potato tuber ringspot necrosis symptoms caused by PVY^{NTN} isolates. It was shown that AC Chaleur can develop PTNRD with both recombinant and non-recombinant PVY^{NTN} isolates within 50 to 60 days of inoculation in 50% of the tubers and up to 75 to 90% of tubers after 2 months storage at 25 to 28°C. However, it failed to develop PTNRD with PVY^{O}, PVY^{N}, and $PVY^{N\text{-}Wi}$ isolates.

Management of PVY

Results of the survey presented in this article clearly show that PVY in the Canadian/U.S. potato industry consists of a complex of strains. While the preponderance of isolates collected and characterized from the survey belonged to the ordinary PVY^{O} strain, a number of variant types that have apparently arisen at some point as a result of recombination and mutation (Fig. 2) are not uncommon and appear to be spreading within North America. It is likely that mixed infections with recombinant strains resulted in even greater strain diversity. While some of the variant strains such as those that induce PTNRD are of concern to potato producers, strains that cause veinal necrosis in tobacco would be of concern to the tobacco industry. Fortunately, the variant strains thus far form only a small percentage of the total PVY population, which is still dominated by PVY^{O}. It is also clear, however, that currently available serological and molecular tools available for PVY detection and identification are unable to efficiently and reliably differentiate the strains of concern. They can only be characterized by bioassay on tobacco and specific potato cultivars.

The inability to readily identify specific PVY strains makes any efforts to eradicate or control any specific PVY strain type difficult. The best and most practical option at this time is to control PVY as a virus complex. Given the lack of PVY symptom expression in several major cultivars and no published evidence that existing strains or variants of PVY are not detected by polyclonal antibodies or monoclonal antibodies with broad specificity, it would be advisable to use those antibodies to screen seed lots for PVY. Bringing the incidence of all PVY infections to low levels within the potato industry will concomitantly lower the incidence of variant strains to very low levels indeed. If the total PVY incidence in a seed lot is below 2 to 3%, the incidence of variant strains will be far below 0.1% and perhaps will diminish even more with diligent flushing out of seed lots with high PVY content.

Thus, PVY management on seed-producing farms needs to focus on keeping the initial inoculum in the fields at a minimum and protecting the crop from viruliferous aphids that can introduce and spread existing virus to other healthy plants. Reducing initial inoculum in seed potato fields will be accomplished by effective seed certification programs, while crop protection will result from skillful, clever, and informed management decisions on the farm.

Seed certification is the most effective means of monitoring seed grower best management practices that could reduce the overall levels of PVY and potentially eliminate the tuber necrotic strains of the virus that are not widely established nor present in significant numbers in the seed crop. However, seed certification will only be effective if PVY can be accurately identified and adequately removed from the system. Identification of the virus by inspectors will require enhanced training to recognize the wide spectrum of virus symptoms on a wide variety of cultivars (Figs. 1 and 3). Quick and accurate diagnostic assays that can be conducted in the field are useful to determine if a suspect plant is infected with PVY. Identification of infected plants to be rogued will still be an important aspect of PVY management, but postharvest testing using randomly collected samples and appropriate laboratory assays will be essential and critical to accurately determine infection levels in many cultivars and environments. As mentioned previously, several cultivars have a tolerance to PVY infection that is manifested as a lack of symptoms or their transient expression. Furthermore, some isolates of PVY may induce very mild symptoms, and late-season infections may not induce foliar symptoms, even in cultivars that normally express obvious symptoms; therefore, there is a need to incorporate a stringent virus postharvest testing component within the various seed potato certification schemes.

Planting early generation certified seed would be an ideal method to minimize PVY inoculum since these lots are less likely to be infected with PVY, but it is not currently practical due to restraints on increasing seed stocks over several years. Minitubers, the small tubers produced from tissue culture plants grown in PVY-

Table 4. Ability of *Potato virus Y* (PVY) isolates from the various strain and variant groups to induce potato tuber necrotic ringspot disease in Yukon Gold grown in the greenhouse

	United States		Canada	
	No. isolates tested	Necrotic tubers	No. isolates tested	Necrotic tubers
PVY^{O}				
2004	5	0	9	0
2005	17	2	44	0
2006	9	2	65	13
Total	31	4	118	13
PVY^{O}-O5				
2004	4	0	7	0
2005	4	0	14	0
2006	4	0	6	0
Total	12	0	27	0
$PVY^{N\text{-}Wi\text{-}a}$				
2004	10	1	45	1
2005	11	1	95	2
2006	18	1	29	0
Total	39	3	169	3
$PVY^{N\text{-}Wi\text{-}minus}$				
2004	7	0	1	1
2005	6	0	6	6
2006	5	0	1	1
Total	18	0	8	8
$PVY^{N\text{-}Wi\text{-}b}$				
2004	2	0	5	5
2005	3	0	0	0
2006	0	0	0	0
Total	5	0	5	5
$PVY^{NTN\text{-}EU}$				
2004	3	3	1	1
2005	2	1	1	1
2006	4	0	20	20
Total	9	4	22	22
$PVY^{NTN\text{-}NA}$				
2004	0	0	1	1
2005	2	1	8	1
2006	0	0	1	0
Total	2	1	10	1
Overall totals	116	12	359	52

Table 5. Bioassay results for potato tuber necrotic ringspot disease (PTNRD) and associated resistance in greenhouse trials

PVY strain	Yukon Gold	Russet Burbank	Ranger Russet
NTN	S[a] (8)[b] 86.4%[c]	R (8) 0.4%	MS (8) 11.9%
N-Wi	S (8) 15.8%	R (13) 0.6%	MS (13) 3.9%
O	S (8) 12.1%	R (5) 0.5%	MS (5) 5.5%

[a] S = susceptible (Typical PTNRD symptoms, e.g., Fig. 4C and D); MR = moderately resistant (mild surface rings, e.g., Fig. 4J); R = resistant (No PTNRD symptoms).
[b] Number of isolates for each strain used for bioassay.
[c] Percent symptomatic tubers.

free greenhouses, are the early generation seed potatoes that are subsequently grown in the field to produce conventional seed potatoes. Although the value of the minituber crop is relatively small, it is the base for the $3.2 billion U.S. potato industry. Minitubers are more expensive and more difficult to handle than field grown seed, but there is great interest in expanding minituber production among seed potato growers because they offer benefits such as disease-free planting material and a 1- or 2-year decrease in the amount of time that it takes to bring new potato cultivars to market. However, there is a potential problem, i.e., the growth of minitubers in the field differs from that of plants grown from field-grown seed (23). Plants generated from minitubers are more susceptible to aphid inoculation of PVY than plants generated from field tubers, a fact that also needs to be considered (54). More research is needed to determine if minituber production can be refined to quickly increase volume and reduce the number of field generations while avoiding increased PVY incidence. A review of existing cultural practices will be essential to maximize production of quality seed potatoes from minitubers.

Given the current situation, it is doubtful that seed certification alone will control the incidence or spread of PVY in seed and commercial crops, although some fundamental changes if adopted industry-wide would be extremely advantageous. These would include:

1. **A comprehensive seed law that dictates and enforces that only certified seed potatoes are planted.** The recent adoption of the Potato Memorandum of Understanding by all potato producing states in the United States requires that all seed exported out of state be certified to have virus levels at or below 2%. However, growers may not be required to plant only certified seed if the seed comes from their farm or another source in-state. Of the 14 states that account for 95% of the U.S. fall production (NASS 2009), only eight have a Mandatory Seed Law. This type of law requires that all potato production be planted using certified seed. In Canada, all seed potato producing farm units must plant seed potatoes of the Foundation class or better. Furthermore, all major seed potato-producing provinces have a mandatory seed planting law, some of whom do require the planting of Foundation seed class or better.
2. **Mandatory postharvest virus testing (PHVT) for the certification of all seed potatoes.** Currently, all seed that will be recertified in the United States is required to have a postharvest test, but not all seed that is sold to plant the commercial crop is required to be tested. In Canada, some provinces also require PHVT and set PVY tolerance levels for seed potatoes planted within the province. While visual inspection of plants during the growing season is helpful, these inspections (as discussed above) do not provide an accurate indication of virus infection levels in harvested tubers. To better determine virus incidence in seed lots, a sample of randomly selected tubers, collected in a manner that is representative of the entire lot, should be visually inspected for PTNRD and subsequently subjected to some type of PHVT. Lots eligible for recertification as seed or commercial planting should be free from any symptoms of PTNRD and have a low incidence of PVY.
3. **Strict adherence to reasonable virus tolerance limits allowed in certified seed.** While it is not appropriate to expect seed potatoes to be free of detectable levels of PVY or other viruses, it is prudent to move toward establishing tolerance levels that are meaningful from a virus disease management standpoint. For example, Nolte et al (63) have shown that initial levels of PVY in the seed can be expected to increase 5- to 10-fold or more during the course of a typical growing season. Furthermore, for every percent increase in PVY incidence, a 1.5 cwt/acre decrease in yield can be expected. Although more research is needed to model anticipated disease increase and yield decrease in other cultivars and environments, this research suggests that initial virus levels in the seed should be less than 5% to avoid significant yield loss in commercial plantings. Ideally, virus levels should be below 1% in seed that is planted for recertification to minimize loss and chance of rejection (63) as certified seed. Reducing initial inoculum levels in all seed will help to lower the amount of PVY overall and thereby decrease the probability of virus spread. Current tolerances are higher than these ideal levels in many seed production areas, but the industry should consider adopting stricter standards that would include refraining from relaxing these stricter standards when seed for a particular cultivar may not be widely available due to high virus levels in certain years. Relaxing tolerance standards may help maintain supply in the short term, but it will invariably lead to an increase in virus levels in the overall crop and a shortage of quality seed over the longer term.

On-Farm Management Strategies

Effective on-farm PVY control can also be realized by adopting strategies used to reduce virus availability to aphids and to reduce the potential for aphids to inoculate plants. These would include eliminating weed reservoirs of aphids and virus, the use of border crops to effectively cleanse aphids of virus before they enter the seed potato crop, and the use of chemicals that would impede aphids from feeding on potato plants (25,68,72,75,92). The success of these methods will depend somewhat on knowledge of what the major vector species are and when they are moving into or through the potato crop. The seasonal phenology of aphid flights and population dynamics of colonizing and noncolonizing aphids affecting the potato crop have been studied in various localities. Numbers are generally variable from year to year, although seasonal phenologies are relatively consistent; still it has been difficult to develop any useful predictive models for most geographic regions (22,73,75,83,102). One significant change in recent years has been the emergence of the soybean aphid in the United States and Canada. Although not an efficient vector of PVY, the sheer numbers of soybean aphids moving through the potato crop late in the season can result in significant spread of the virus within the potato crop. Soybean aphid has not been a major problem in the Western United States, but grain aphids, especially the bird-cherry oat aphid (*Rhopalosiphum padi*), are potential contributors to the spread of PVY in potato in this and other potato growing regions (22,31,38, 67,82,94). Late-season inoculation of plants by these and other migrating aphids will result in infection, and although foliar symptoms are not manifested in the mature plants, tuber infection can be significant. This will contribute to the discrepancy between field ratings of virus in the crop and results of postharvest tuber testing. Another consideration, in addition to the numbers and diversity of the aphid populations, is the efficiency with which they transmit the various strains of PVY. One hypothesis for the spread and increased incidence of the necrotic and recombinant strains of PVY is that they are spread more effectively by aphids than the ordinary strain. There are limited data on aphid transmission efficiency of various PVY strains, and results are inconsistent with some studies reporting no difference (26,58,94) and others reporting significant differences (1,11). Furthermore, differences among aphid species and clones of the same species, as well as differences among virus isolates within a strain, are likely to affect the outcome of these types of experiments.

Identification of and minimizing local sources of PVY and aphid reservoirs will also be critical to the success of on-farm management practices. In most seed production areas, there are a limited number of cultivated hosts of PVY, but volunteer potato and solanaceous weeds, especially the nightshades, can be significant sources of virus. Hairy nightshade is widespread in many of the seed production areas of the United States and has been introduced to the Maritime provinces of Canada in recent years. Hairy nightshade is a natural host of PVY and several other potato viruses including PMTV and TRV. Although the viruses are not known to be seed transmitted in hairy nightshade, the weed can overwinter in some areas and serve as a source of virus inoculum early in the

growing season. More importantly, infected hairy nightshade plants have been shown to be very attractive to aphids and therefore are a good source of viruliferous aphids especially later in the growing season. In fact, transmission of PVY from hairy nightshade to potato was more efficient than transmission between potato plants (11).

Another PVY management tool that has been successful, especially for high value crops such as early generation seed potatoes, is the use of border crops (3,9,21,25). Surrounding crops with rows of a PVY nonhost crop provides a barrier to immigrating aphids. This method is most effective for small acreages (<0.2 ha) (22,74). Aphids flying long distances tend to land at the edges of crops, especially when there is fallow land surrounding the crop. Since PVY is a stylet-borne, nonpersistently transmitted virus, aphid landing in a nonhost border will probe those plants and have a tendency to clean their stylets of virus, thus reducing the chance of transmitting virus to potato as they move further into the field. Skips in the planting of fields can mimic fallow borders in the eye of an aphid, so it is important that plantings be solid to minimize the attractiveness to immigrating aphids (19). Crop borders will not stop or reduce the spread of PVY when the inoculum source is within the seed lot, so keeping PVY levels low through effective certification programs remains a critical tool.

Insecticide applications are generally not effective in the management of PVY due to the short acquisition and inoculation times; however, they can be effective at controlling populations of colonizing aphids and reducing within-field spread of the virus by these aphids. Mineral oil sprays have generated mixed results in completely controlling PVY (3,4,8,20,30,52,53,71,81,95), and when initially registered were considered prohibitively expensive to apply at the frequencies prescribed for effective control. More promising is the recent introduction of chemicals and oils that have antifeedant properties. These compounds work by reducing the ability of the aphid to probe on epidermal tissues or by impeding the uptake or release of virus during feeding. While several studies have shown these compounds to be somewhat effective at reducing the spread of persistent and semipersistent viruses, i.e., those viruses that require relatively long transmission times such as PLRV (10,35), there are few studies on viruses like PVY that only require feeding times measured in seconds (36). Combining these compounds with other management practices such as border crops may also improve their efficacy (3).

Clearly, the success of on-farm management practices will vary across geographic ranges and will be influenced by the timing of crop cycles, the diversity of crops in the region, as well as by potato cultivar, predominant PVY strains affecting the crop, and seasonal phenology and species composition of vector populations. The ultimate goal would be to develop regional "best management practices" for PVY in seed potatoes, a portion of which would also be useful in the commercial crop. However, there is a need to develop fundamental information on the transmission efficiency of the new PVY strains, the susceptibility of various potato cultivars to different PVY strains, and the carryover of virus in seed.

Resistant Cultivars

Potato cultivars that are resistant to PVY infection would be the ideal management tool for controlling virus incidence. Unfortunately, there are few cultivars grown widely in North America that express any type of resistance that would significantly reduce virus incidence or transmission. Effective PVY resistance genes are well described and are widely used in breeding programs outside of North America, but as previously mentioned, the success, until recently, of seed certification programs at maintaining virus disease below economic thresholds has limited the enthusiasm of breeding programs to concern themselves with virus resistance. 'Eva', released by NY and PA, expresses the *Ry-adg* gene and has extreme resistance to all strains of PVY and PVX (70), but is not widely grown. Some older cultivars such as Kennebec, Sebago, and Katahdin, which have some level of field resistance conferred by unknown genes to some PVY strains, have been replaced by other cultivars that do not have PVY resistance. However, breeding programs in the Western United States have been looking more carefully at incorporating PVY resistance genes related to those in materials used to develop 'Eva' (66,98). These programs have also been testing new cultivar releases for resistance to the range of PVY strains, and some have significant levels of resistance against PVY^{O} (64,90).

Summary

North American potato production differs from other geographical regions such as Europe in that it is essentially a closed system, i.e., seed potatoes are not imported and production is dominated by only a few cultivars. The lack of significant seed imports provides a mechanism for seed certification to be extremely effective at minimizing virus levels in seed lots, especially if the changes in seed laws, postharvest testing, and tolerance limits discussed above are adopted. This is an opportunity to effectively manage PVY at levels that are at or below detection and well below economic significance. Aiding the seed certification programs in the adoption of the Canada/US-Management Plan for Potato Viruses that Cause Tuber Necrosis has and continues to build consensus and cooperation within the industry to reform and modernize seed certification practices and, as importantly, modernize best management practices that growers can implement so that their production meets or exceeds virus tolerances set within the seed certification standards. Seed inspectors could also benefit from continually updated information from the research community to help them better recognize the spectrum of symptoms caused by the various strains and variants of PVY in all the different cultivars now being grown in their states and provinces. They could also benefit from improved field diagnostics that will assist them and the growers in identifying problem plants that should be rogued. If PVY levels in seed can be minimized and on-farm management strategies can be optimized, then PVY incidence in the potato crop will be marginalized. The restricted distribution of the tuber necrotic strains also offers an opportunity to prevent these strains from becoming economically significant if appropriate testing of seed lots in those areas could prevent them from being planted. Shipping point inspections of tubers will also help in identifying and eliminating tuber necrotic viruses.

The dominance of a few cultivars has been eroding in recent years. Russet Burbank, a cultivar introduced over 100 years ago, still accounts for 40 to 50% of the U.S. acreage, but acreage in the Northwestern United States has been declining steadily as other russet cultivars come on the market and gain acceptance. Potato cultivar has had a significant impact on the PVY problem, as with the release and widespread acceptance of Shepody, Russet Norkotah, and other asymptomatic carriers of PVY (http://oregonstate.edu/potatoes/latenttoPVYlist.htm), which in 2008 comprised more than 15 and 12% of the total U.S. and Canadian seed acreage, respectively. These cultivars have certainly contributed to the overall increase in PVY in the seed potato crop and by extension the commercial potato crop. The increased diversity of potato cultivars grown in both countries has also introduced a wider spectrum of PVY symptoms, most notably the milder symptoms that are characteristic of the $PVY^{N/NTN}$ and $PVY^{N\text{-}Wi}$ strains on many cultivars. Since the success of seed certification is dependent upon visual assessment of the crop, mild or absent symptoms means that many more infected plants go unnoticed. The more symptomatic PVY^{O} strains are observed and removed, but the other strains remain in the crop and are passed along in the seed, contributing to an overall increase in PVY incidence and more importantly to a shift in PVY strain composition.

The U.S. and Canadian potato industry stakeholders are increasingly aware of the PVY-associated challenges and have been moving rapidly to work with researchers and all aspects of the industry to implement plans to suppress PVY incidence. Continued education of growers, seed certification officials, and researchers alike, coupled with the development and adoption of new or revised best management practices and diagnostic tools, and the renewed inter-

est of breeders to develop virus resistant cultivars, will be the keys to success in bringing PVY incidence under control and in minimizing tuber necrotic strains.

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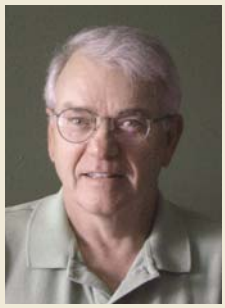
Stewart Gray

Solke De Boer

James Lorenzen

Alexander Karasev

Jonathan Whitworth



Phillip Nolte

Rudra Singh

Alain Boucher

Huimin Xu

Dr. Gray is a senior scientist with the USDA Agricultural Research Service and an adjunct professor of plant pathology at Cornell and The Pennsylvania State Universities and has conducted research on plant virus diseases in Ithaca, NY since 1987. He received his M.S. in entomology and Ph.D. in plant pathology from North Carolina State University. His main areas of research include: mechanisms of virus transmission by insects, virus epidemiology, host plant resistance to viruses, and virus disease management and control. He has responsibilities in virus disease management in small grain crops and potato. For the past 8 years, he has worked closely with the U.S. and Canadian potato industries and regulatory agencies to develop and implement the BiNational Canada – U.S. Management Plan for Potato Viruses that helped maintain trade between the countries. He serves on the National Potato Council subcommittee for Seed Certification and Plant Disease Management, and he has served as a senior editor for Plant Disease and associate editor for Virology and Journal of General Virology.

Dr. De Boer is a senior research scientist at the Canadian Food Inspection Agency's Charlottetown Laboratory. He received his B.Sc. and M.Sc. degrees in plant protection from the University of British Columbia and a Ph.D. in plant pathology from the University of Wisconsin-Madison. He researched bacterial plant diseases of potato at the AAFC Vancouver Research Station for almost 20 years before joining CFIA in 1996, where he continued work on bacterial diseases as well as initiating research on various other pathogens of potato and other crop plants. His research is directed toward increasing the understanding of the diversity of plant-pathogenic species and the development of methods for their identification and detection.

Dr. Lorenzen is a banana breeder and program leader for the Banana & Plantain Systems program of the International Institute of Tropical Agriculture. He received his B.Sc. degree from Washington State University in horticulture and M.Sc. and Ph.D. degrees from Cornell University in Vegetable Crops, working with Elmer Ewing on potato physiology. He then continued in potato research for nearly 20 years in Nepal, North Dakota, and Idaho, working on potato improvement, germplasm enhancement, molecular biology, and molecular characterization of PVY. His current research focuses on breeding for disease and pest resistance, and mapping economically useful traits in banana.

Dr. Karasev is a plant virologist in the State of Idaho. He received his Ph.D. degree in virology from Moscow State University, Russia, and did his postdoctoral research on molecular biology and genetic diversity of closteroviruses. He joined the Department of Plant, Soil, and Entomological Sciences of the University of Idaho in 2006. His main responsibilities include virus diseases of potato, legumes, and small grains. His research activities are focused on plant virus–host interactions, virus transmission, and virus evolution. He teaches a graduate course in plant virology and advises both graduate and undergraduate students.

Dr. Whitworth received his B.S. degree from Utah State University and his M.S. and Ph.D. from Oregon State University in 1993. Most of his work has involved studying potato viruses and working with seed potato growers. He has worked in seed potato certification for 10 years in Oregon, Colorado, and Idaho. He started work as a research plant pathologist for the USDA-Agricultural Research Service at Aberdeen, ID in 2003. His current work involves host resistance for PVY. His work contributes to a USDA Potato Breeding Program which involves traditional breeding to incorporate resistance genes and marker-assisted selection to identify parental material and offspring with PVY and other resistance genes.

Dr. Nolte received his B.Sc. in biology from Moorhead State University in Moorhead, MN, and his M.S. and Ph.D. in plant pathology from NDSU in Fargo, ND. Dr. Nolte has worked on potato and seed potato problems since 1979. He became the extension seed potato specialist for the University of Idaho at the District IV Extension office in Idaho Falls in June of 1991. Nolte's program focuses on seed potatoes but also includes seed-related problems in commercial production and general potato disease diagnosis and management. Recent research includes work on the potato mosaic virus complex (PVY and PVA), management of potato late blight, fungicide resistance studies in Fusarium dry rot, and the effect of chemical application on wound healing (suberization) in cut seed. He serves as the technical editor for the Potato Grower Magazine and as a contributing editor for the American Vegetable Grower Magazine. He also served as president of The Potato Association of America 2009 to 2010.

Dr. Singh earned his Ph.D. degree in plant pathology in 1966 from North Dakota State University. His thesis project was to study potato spindle tuber virus (PSTV). After completing a postdoctorate fellowship, he joined Canada Department of Agriculture (Fredericton) in 1968 as a research scientist to work on PSTV and other potato viruses. Rudra retired in 2008 after 40 years of service as a research scientist 5 from Agriculture and Agri-Food Canada. Since PSTV was a problem of seed certification, Rudra worked with Food Production and Inspection Branch personnel very closely and developed several methods for virus and viroid detections. His main contributions to potato virology were the discovery of PSTV as low-molecular-weight infectious RNA, the viroid (PSTVd); development of a modification of return polyacryamide gel electrophoresis, which was used to diagnose viroids in different countries; eradication of PSTVd from Canada in the mid-1980s; modifying testing protocol for necrotic strain of PVY; RT-PCR methods for the specific detection of four strains of PVY; and the development of multiplex RT-PCR for the simultaneous detection of six viruses or various strains of PVY by competitive RT-PCR.

Alain Boucher is the Canadian Food Inspection Agency (CFIA) National Manager of the potato section. He graduated from Université Laval, Quebec, with a degree in agronomy, concentration in plant science, in 1984. Subsequently, worked for Agriculture and Agri-Food Canada research branch, under the guidance of Dr. Rudra Singh, and contributed in the development of various virus and viroid detection and identification techniques. Alain has held various positions since 1993 to foster the design and support the delivery of various plant health and seed potato certification programs. He is presently responsible for the continuous improvement of the Canadian seed potato certification program standards.

Dr. Xu is a research scientist at the Charlottetown Laboratory of Canadian Food Inspection Agency (CFIA). He received his B.Sc. and M.Sc. degrees in plant protection from Shenyang Agricultural University. He received his second M.Sc. degree and his Ph.D. degree in virology from the University of Toronto. He studied the genome structure, gene functions, and mutation effects on virus replication and gene expression, internal initiation of translation, transgenic potato for virus resistance, and the diagnosis of Potexvirus and Potyvirus before taking a postdoctoral position at the Pacific Agri-Food Research Centre of Agriculture and Agri-Food Canada in Summerland, British Columbia. He joined CFIA in 1997, and since then he has been serving the agency at the Charlottetown Laboratory in Charlottetown, Prince Edward Island as a virologist, specializing in diagnosis and characterization of potato viruses and viroids using molecular approaches.