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POTATO VIRUS Y SYMPOSIUM

PVY: An Old Enemy and A Continuing Challenge

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Abstract *Potato virus Y* (PVY) is one of the most important viruses affecting potato production worldwide. The virus has been extensively studied for several decades, yet considerable economic losses continue to be suffered by the potato industry around the world. PVY is transmitted by several species of aphids in a nonpersistent manner, making control with insecticides difficult. Additionally, the virus occurs as several distinct strains, each with their own biological, serological, and molecular characteristics. This wide diversity continues to be a challenge to researchers, growers, and processors wherever the crop is grown. Here I will examine the general characteristics of PVY and touch upon some of the major facets of this important and variable virus.

Resumen El virus Y de la papa (PVY) es uno de los virus más importantes que afectan la producción de papa en el mundo. El virus ha sido estudiado extensivamente por varias décadas, pero aún continúan sufriéndose considerables pérdidas económicas por la industria de la papa alrededor del mundo. El PVY es transmitido por varias especies de áfidos de manera no persistente, dificultando el control con insecticidas. Adicionalmente, el virus se presenta como variantes diferentes, cada una con sus propias características biológicas, serológicas y moleculares. Esta amplia diversidad continúa siendo un reto para investigadores, productores, y procesadores en cualquier parte donde se siembre el cultivo. Aquí examinaré las características generales del PVY y tocaré algunas de las facetas mayores de este virus tan importante y variable.

Keywords Potato diseases · Plant viruses · PVY

Introduction

Potato virus Y (PVY) is the type member of the *Potyvirus* genus which is the largest group of plant viruses. The virus was described by Smith (1931), but probably had been known much earlier. The symptoms of infection due to this virus were almost certainly observed with the earliest cultivation of potatoes. Like other potyviruses, PVY is transmitted by aphids in a nonpersistent manner and therefore they can be acquired and transmitted in a very short period of time, perhaps less than 1 min.

In North America, the most economically important host of PVY is potato and the virus also occurs in potato crops worldwide. PVY infects a number of other important crop plants such as tobacco, tomato, and pepper, and is considered one of the most economically damaging viruses in the world (reviewed by Kerlan 2006). Approximately 400 experimental hosts of PVY have been reported (Edwardson and Christie 1997). One measure of the importance of PVY is the number of scientific journal publications on this virus. In a non-exhaustive data base search, I found 1,150 references to PVY published between 1951 and 2012. Topics included genomics, pathogenicity, epidemiology, aphid transmission, effects on yield and quality, and interactions with other viruses.

In this paper I am going to explore some of the basic concepts and characteristics associated with PVY as an introduction to the more detailed discussions to be presented by our panel of distinguished PVY researchers.

This paper is an invited presentation as part of the International Symposium on PVY sponsored by the Plant Protection Section of the Potato Association of America, August 11, 2009, in Fredericton, New Brunswick, Canada. This paper was reviewed with a view to ensure that the information was brought up-to-date beyond what was given at the time of the presentation.

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General Characteristics of PVY

The nucleoprotein particles of PVY are filamentous rods approximately 730 nm in length. The PVY genome consists of a single molecule of positive-sense single-stranded RNA of about 9,700 nucleotides, excluding the poly-A tail at the 3′ end. In infected plants, the genomic RNA is translated as a large polyprotein which is subsequently cleaved into 10 functional peptides by virus-encoded proteases (Fig. 1). One of these peptides is the capsid protein which is about 30 kDa in size (Kerlan 2006). In April of 2012, there were approximately 1,250 "hits" for PVY genomic sequence information in a computer data base search. Of these, about 100 were full-length genomic RNA sequences. Additional complete genomic sequences are being generated by active European and American research programs (Crosslin, unpublished).

PVY infections are well known to cause yield reduction in potato. De Bokx and Huttinga (1981) state PVY infections can reduce yields 10–80 %. Rykbost et al. (1999) reported reduction in yield of Number 1 tubers of Russet Norkotah by 12–40 %. Similarly, a reduction in marketable yield of 65 % in Russet Norkotah was reported by Hane and Hamm (1999). Nolte et al. (2004), studying the effect of tuber-borne PVY infections on Russet Burbank, Russet Norkotah and Shepody, reported a yield loss of 0.18 tons/ha for each 1 % increase in PVY infection. Additionally, infections with some isolates cause tuber symptoms as well, reducing quality of the crop (discussed below). Hamm et al. (2010) found that potato cultivars differed in the levels of PVY current season infections. This may relate to increased "attractiveness" of some cultivars to migrating aphids or perhaps the ease with which they become infected.

Aphid Transmission

In North America the green peach aphid, *Myzus persicae*, is considered the most efficient vector of PVY but a number of aphids are also capable of transmitting this important virus. In one study conducted at the Rothamstead Experiment Station, England, (Harrington et al. 1986), over 100 species of aphids were captured and tested for their ability to transmit PVY. Twenty of these transmitted the virus and *Myzus persicae*, *Brachycaudus helichrysi*, *Phorodon humuli* and *Aphis* spp. accounted for most of the transmissions. Other species of grain aphids such as *Sitobion avenae* and *Rhopalosiphum padi*, and the pea aphid (*Acyrthosiphon pisum*) also transmitted the virus, but at very low levels. Other researchers have reported PVY transmission by numerous species of aphids (de Bokx and Huttinga 1981; de Bokx and Piron 1990). Verbeek et al. (2010) found no difference in efficiency of transmission of N, NTN, and Wilga isolates, but other aphid species showed variability in transmission efficiencies. Other workers have reported variation in the efficiency of transmission of various isolates (Basky and Almasi 2005). The soybean aphid (*Aphis glycines*) is a relative newcomer to the United States, being first found in 2000. This aphid is also a vector of PVY and the populations of this pest can be quite high, resulting in significant transmission of the virus (Davis et al. 2005). Another recent newcomer to the United States is the Russian wheat aphid (*Diuraphis noxia*), and this aphid also has been reported as a vector of PVY (Halbert et al. 2003). Because PVY can be acquired and transmitted in so short a time, insecticides are generally considered ineffective in controlling spread of this virus within a potato crop.

"Classical" Descriptions of PVY Strains

Several biological variants, or strains, of PVY have been found infecting various crops. In potato, a number of PVY strains have been described and these were originally differentiated based on symptoms produced in tobacco and differential potato cultivars. The "ordinary" or "common" strain of PVY (PVY^O) is, as the name implies, quite common in potato crops around the world. Typically, isolates of PVY^O induce a systemic mosaic in most potato cultivars and similar symptoms in tobacco cultivars, including Burley and Samsun NN. In some cultivars, including the widely-grown Russet Norkotah and Shepody, PVY^O can be nearly symptomless (Hane and Hamm 1999). However, some other potato cultivars, such as Ranger Russet, show a systemic necrosis or hypersensitive response to PVY^O and develop severe mosaic and leaf drop. Therefore, PVY^O is generally not tuber borne in Ranger Russet. In most potato cultivars, however, PVY^O is readily perpetuated through the tubers and thus is of considerable concern to seed growers and certification agencies.

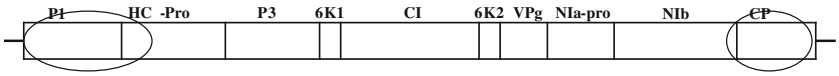

Fig. 1 Schematic of PVY genome structure. The single-stranded RNA, ~9,700 nt, is translated into a polyprotein that is subsequently cleaved into the functional peptides by virus-encoded proteases. The approximate regions coding for the 10 proteins are shown. The P1, HC-Pro, and CP (coat protein) regions, circled, are of particular importance in differentiating strains of PVY

In contrast to PVY^{O}, some isolates of PVY produce very mild mosaic in many potato cultivars and a severe systemic veinal necrosis in tobacco. These isolates are referred to as PVY^{N} and this characteristic is widely used for general biological characterization of PVY isolates (de Bokx and Huttinga 1981). PVY^{N} isolates appear to be relative newcomers to North America (MacDonald and Kristjannsen 1993) and tobacco necrosis-inducing isolates were first reported on potatoes in the western United States in 2002 (Crosslin et al. 2002). Some isolates of PVY^{N} incite potato tuber necrotic ringspot disease (PTNRD) and these have been referred to as PVY^{NTN} because of the tuber necrosis reaction. Commonly, the PVY^{NTN} isolates cause raised external rings or arcs (Fig. 2) and may cause internal tuber symptoms in some cultivars. Tubers of the cultivar Yukon Gold, for example, are very severely affected by infections with PVY^{NTN}. An additional group of PVY isolates causes tobacco veinal necrosis yet possesses the capsid protein sequence of PVY^{O} isolates. Isolates with these characteristics were first described in Europe and termed $PVY^{N\text{-}Wi}$, after being found in the cultivar Wilga. Subsequently, isolates with similar characteristics were found in North America (MacDonald and Singh 1996) where they are usually called $PVY^{N:O}$ because of the mix of properties of PVY^{O} and PVY^{N} (Singh et al. 2003; Piche et al. 2004; Crosslin et al. 2005). Some of the $PVY^{N:O}$ isolates are also known to cause internal tuber symptoms in some cultivars (Piche et al. 2004; Crosslin et al. 2005). Coupled with reductions in yield, these PVY isolates can therefore cause significant economic damage (Fig. 3).

Strain PVY^{C} causes "stipple streak" symptoms in potato cultivars possessing certain genes for resistance to PVY (Kerlan 2006). This strain is generally considered to be uncommon in North America, but its occurrence and distribution has not, to my knowledge, been studied in detail. Additional variants with a mixture of characteristics and symptomatology in tobacco and potato, such as PVY^{Z}, have been described in the literature (Kerlan 2006).

Fig. 2 Potato tuber necrotic ringspot disease (PTNRD) symptoms in Russet Burbank infected with PVY^{NTN}

Fig. 3 Internal and external symptoms in tubers of Yukon Gold infected with $PVY^{N:O}$. Photo courtesy of Phil Hamm and Jordan Eggers

Serological Reactivity and Molecular Detection

Most isolates of PVY are readily detectable by polyclonal antibodies produced by injecting animals, most commonly rabbits, with purified virus preparations. These antibodies are widely used for detection of the virus by research laboratories and seed certification agencies. The polyclonal antibodies detect all known strains of the virus, but are incapable in differentiating among the O and N groups. With the application of monoclonal antibody technology to PVY (Rose and Hubbard 1986), additional antibodies produced in mice were capable of differentiating between viruses in the "O" and "N" serotypes. The PVY^{N} and PVY^{NTN} isolates are of the N serotype whereas the O and N:O isolates are of the O serotype (Ellis et al. 1996; Crosslin et al. 2005). The fact that N:O isolates are of the O serotype possibly led to its relatively rapid spread due to misidentification as an "ordinary" isolate (Karasev et al. 2010).

Unfortunately, the serological breakdown of PVY isolates is not as simple as O and N serotypes. For example, Ellis et al. (1997) identified isolates from North America that reacted with the widely used N serotype-specific antibody 1F5 that also reacted with O serotype-specific antibodies. These isolates did not, however, react with other N-serotype specific antibodies. Ellis et al. (1997) called these "O5" isolates. These researchers went on to identify nine serotypes within the PVY^{O} group. These results indicate that the serological relationships of PVY isolates are indeed complex. Later work by Karasev et al. (2011) showed that in PVY-O5 isolates a single amino acid change was responsible for the erroneous reactivity with the 1F5 antibody.

Additional sensitivity and differentiation of PVY isolates became possible with the advent of molecular detection by reverse transcription polymerase chain reaction (RT-PCR). The technique has been widely used for detection and differentiation of PVY isolates (Weilguny and Singh 1998; Singh et al. 1998; 2003; Glais et al. 2002; Nie and Singh 2002; 2003; Boonham et al. 2002a; 2002b; Crosslin et al. 2005). An 8-primer multiplex RT-PCR was reported by Lorenzen et al. (2006b) that has been widely used due to the ability to

distinguish between O, N, NTN, and N:O strains and some strain mixtures in a single RT-PCR reaction. The RT-PCR has been especially useful for detection and identification of the $PVY^{N:O}$ isolates since this strain cannot be correctly identified as "necrotic" by serological tests (Singh et al. 2003; Crosslin et al. 2005; 2006). Coupling RT-PCR with molecular cloning and DNA sequencing has allowed comparison of whole genomes of PVY (Lorenzen et al. 2006a), and this trend is continuing to provide information on the genetic variability of this virus. Bolotova et al. (2009) conducted a statistical comparison of serological and molecular techniques for detection of PVY.

Anomalous Virus Isolates

As stated so eloquently by Smith (1931): "A serious hindrance to the study of plant—and especially of potato—viruses, is the lack of any sound system of classification". This statement certainly held true in 1931, yet the situation is only slightly better in 2012!

With an increase in the number of virus isolates that have been studied in detail has come the realization that PVY is not as simple as O, N, NTN, and N:O. For example, a PVY isolate was transmitted to tobacco from tubers of cultivar Cal White in 2000. The virus produces a systemic mosaic in tobacco and reacts with the PVY^{O}-specific monoclonal antibodies, yet it produces pronounced PTNRD symptoms in tubers of Cal White and Atlantic, but not in Russet Norkotah (Crosslin, unpublished). What do we call isolates such as this? Additional isolates are occasionally detected in virus surveys that react with PVY^{N}-specific antibodies but do not cause systemic necrosis in tobacco (Ellis et al. 1997). Ellis et al. (1997) called some of these "O5" isolates, and this designation has been used by other researchers (Karasev et al. 2010). Again, how do we refer to these isolates in a meaningful, systematic manner? Similarly, Piche et al. (2004) reported detection of the PVY^{O}, PVY^{NTN} (European), PVY^{NTN} (North American), $PVY^{N:O}$ and four groups that did not fit the current PVY pathotypes! Hu et al. (2009) described an isolate that was "NTN" based on nucleotide sequence of the whole genome, but did not induce veinal necrosis on tobacco.

Revers et al. (1996) postulated that genetic recombination among potyviruses is a relatively common phenomenon and this finding suggests that new PVY variants will continue to arise and cause problems in detection, identification, and classification. Barker et al. (2009) also stated "…clustering of isolates on the basis of genome sequence does not reflect their biological properties". The more we study this important virus the more biologically, serologically, and genetically complex it becomes.

Summary

The foci of this symposium will include attempts to describe the genomic/genetic variability between isolates, description of the research efforts on PVY in Canada, and Eastern Europe, and certification efforts aimed at controlling the incidence of PVY in seed tubers. It is hoped that this state-of-the-art information on this important potato pathogen will be of interest and use to all those involved in potato virus research, extension education, and seed certification programs around the world.

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