

Potato Virus Y

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1. Introduction

Potato virus Y (PVY) is the type species of the genus *Potyvirus*, one of the largest groups of plant viruses, containing c. 160 species ^{[1][2]}. Potyviruses are transmitted by aphids and cause economically damaging diseases in crop plants. PVY exists as several strains and has become one of the most economically important pathogens of potato and the most important virus ^[3], and it occurs commonly wherever potatoes are grown. The Andean region of South America is the centre of origin of potato and many wild and domesticated species grow there (Figure 1a). After the discovery and colonization of the Americas by Europeans in the 16th century, tubers of one species of domesticated potato, *Solanum tuberosum*, were taken to Europe, and from there, over time, to the rest of the world ^{[4][5]}. Potato consumption grew in popularity in the 19th century, and it became an established staple food in many countries. Potatoes are vegetatively propagated, with progeny “seed” tubers being used to establish the next crop, and, unknown at the time, potato viruses were also transported with tubers. Potato viruses were first identified in the 1930s ^{[6][7]}, and now more than 50 viruses affecting potato are known, although only a few, including PVY, cause economically important diseases ^[3]. Potato is the world's third most important staple food crop and an important crop supporting food security in developing countries, where potato production now exceeds that in the developed world, and viruses are major constraints on potato production systems ^{[3][8]}.



Figure 1 (a) Potato cultivation in the high Andes of Bolivia; (b) symptoms of O (ordinary) strain Potato virus Y (PVY^O) on leaves of *Solanum tuberosum* Group Phureja (c) necrotic local lesions (indicated by white arrow heads) elicited by PVY^O in the inoculated leaves of potato cv Atlantic; (d) necrotic symptoms induced by N (necrotic) strain Potato virus Y (PVY^N) in tobacco leaves.

Human activity has played a major part in the spread of PVY from the South American Andes to the rest of the world, particularly through trade in plant material of unknown disease status. Since emerging from the Andean region, PVY has also become a major pathogen of tobacco and solanaceous vegetable crops [9][10][11][12][13]. This review highlights current knowledge of PVY population structure, epidemiology and economic impacts, mostly drawn from research on virus infections in potato. We believe that to effectively control the virus and prevent the emergence of new strains in key crops, future research should be strongly focused on host resistance and factors driving virus evolution and spread. Therefore, we also describe natural resistance mechanisms to PVY and how they can be modulated by rising temperatures under global warming. Modern biotechnology can play a role by developing genetically edited PVY-resistant crops as well as producing “vaccinated” plants by priming their antiviral defences through RNA silencing.

2. PVY Population Structure

PVY was first identified by Smith [6], and several strains infecting potato were subsequently described in the early 20th century. Five major strain groups have now been recognised [14][15][16]. The first strains to be recognised were the O (ordinary) (Figure 1b), N (necrotic) and C (common) strains. These strains were characterised by biological properties and symptoms in potato hosts carrying strain-specific resistance genes (hypersensitive (HR) or *N* genes) [16][17][18]. The O, N and C strains were distinguished using potato cultivars carrying the genes *Ny* or *Nc*, which displayed necrotic spots on leaves when inoculated with O or C, respectively (Figure 1d) [17]. The N strain induces a systemic veinal necrosis in tobacco (Figure 1c) but generally no HR and only mild or no symptoms in potato leaves, and the C strain (PVY^C) causes economically important diseases in other solanaceous crops including tobacco, tomato and pepper. In the 1980s, additional strains were reported where although mild or no symptoms were observed in leaves, some induced severe symptoms in potato tubers, such as potato tuber necrotic ringspot disease (PTNRD) [19][20]. Genome sequencing has revealed that the virus genomes of these isolates comprise sequences derived from O and N strains, these recombinant isolates included PVY^{NTN} and PVY^{N-Wi} [19][21][22][23]. The resistance gene *Nz* is effective against PVY^Z (shown to be the recombinant NTN). However, other recombinant strains such as PVY^{N-Wi} were not controlled by *Nz*, and they induce mild foliar symptoms with no PTNRD [18].

Phylogenetic analysis of 460 whole-genome sequences of PVY, collected from infected plants worldwide, showed that PVY originated in the Andes of South America, the centre of origin of the potato and where potatoes were first domesticated [14][15]. The date of origin (time to most recent common potyvirus ancestor) of the PVY population was estimated to be 1860 YBP. The maximum likelihood tree analysis largely supported the previous classification of strains based on host reactions, and five phylogroups were identified. Analysis of the nonrecombinant sequences produced three main lineages: the N phylogroup, which is widespread in South America and may only have spread to the rest of the world recently; the O phylogroup, isolates of which were found mostly from plants outside South America, and a branch of O, the C phylogroup, with no isolates found among South American samples. Moreover, the C isolates were often found in non-potato hosts, suggesting they may have diverged outside the Andes, possibly in Europe [15]. The analysis suggests that diversification and emergence of some of the current strains of PVY may have occurred outside South America, possibly in Europe. The first potato breeding programmes were based on a narrow genetic foundation of only a few introductions of potato, developing varieties through in-breeding and selection [4][14]. The introduction of new germplasm to combat susceptibility to late blight into potato breeding programmes in the mid-19th century probably led to PVY strain diversification, as this material also contained PVY resistance genes. Approximately half of the sequences analysed in the study by Fuentes et al. [15] comprised recombinants from N and O sequences and formed two further lineages, the R1 and R2 phylogroups. Recombinant isolates came to prominence in the 1980s and quickly spread, displacing other PVY strains in potato production systems, probably because they were uncontrolled by *N* genes and the mild foliar symptoms in many modern varieties enabled them to proliferate in seed crops because they escaped visual inspections [18]. Thus, since PVY was distributed from the Andes in potato tubers, the PVY population has evolved, with new strains emerging to infect non-potato hosts as well as overcome resistance of potato hosts, and human activity has been an important driver of this process [18].

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