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Host preference of the major strains of *Plum pox virus* — Opinions based on regional and world-wide sequence data

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Abstract

Plum pox virus (PPV) causes sharka — the most serious viral disease of stone fruit trees. PPV is wide spread in Europe and Mediterranean Basin, its incidence has been further approved in Asia and both Americas. Nine PPV strains have been recognized until now (PPV-D, PPV-M, PPV-Rec, PPV-EA, PPV-C, PPV-T, PPV-W, PPV-CR, and PPV-An), forming molecularly distinct entities, however, only partially differentiable by their biological or epidemiological properties. The most strict virus-host linkages under natural conditions have been detected for strains naturally infecting cherries (PPV-C and PPV-CR). However, although less stringent but still clear host preference is observed also for three epidemiologically most important strains (PPV-D/plum/apricot, PPV-M/peach, and PPV-Rec/plum). So far no genetic marker has been mapped in the PPV genome, which responsibility for the host specificity/preference could be explicitly demonstrated. In this review, we focus on the host preference of three major PPV strains as evidenced by analysis of an extensive dataset of PPV isolates of Slovak and world-wide origin. Together, we discuss several performed relevant experiments and further possible research procedures aimed to better understand the genetic determinants and mechanisms of the host preference of this potyvirus.

Keywords: sharka, Prunus, virus-host interactions

1. Incidence of major strains of PPV indicates a host species preference under natural conditions

Plum pox virus (PPV) is the only potyvirus affecting woody hosts, namely the stone fruit trees of the genus *Prunus*. Its (+)ssRNA genome is translated into a polyprotein from which particular viral polypeptides are derived (P1, HC- pro, P3, 6K1, CI, 6K2, VPg, NIa-pro, NIb and CP). The frameshift in the P3 region results in an additional product P3N-PIPO. The virus is naturally spread by aphids. However, its long-distance distribution by infectious biological material in the frame of human horticulture practices is more important (Šubr and Glasa 2013). PPV currently occurs in temperate regions of all continents except Australia. Its economic impact is the highest in Europe, however, particular countries differ by the contamination level and by incidence of various virus strains. In Slovakia, PPV occurs endemically in all the Prunus-cultivation areas. Three of nine known strains have been found here: PPV-D, PPV-M and PPV-Rec, which are also the major PPV strains from the global point of view (Šubr and Glasa 2013). Because of several recombinant events in their evolutionary history, these strains are very closely related each to other and form a subclaster in the phylogenetic tree based on the

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complete PPV genomes (García et al. 2014). Recently, in frame of an international project (Sharka Containment, acronym SharCo), a systematic collection of sequence data from world-wide originating PPV isolates was generated (http://www.sharco.eu/). Isolates of the three major PPV strains share complete genome identity above 95% (ca. 96% between PPV-M and PPV-D and above 97% between PPV-D and PPV-Rec or between PPV-M and PPV-Rec). Despite of such high similarities, these strains are clearly distinguishable, mainly when comparing their most variable genome part (NIb-CP region) (Šubr and Glasa 2008). In addition to their sequence variability, the strains differ, e.g., by posttranslational modifications of the capsid protein and their biological properties, in particular their prevalent, although not clear-cut, incidence in different host species (García et al. 2014).

In the last two decades we partially sequenced and characterized more than 200 PPV isolates from various parts of Slovakia. Over 80% of them originated from plum trees (P. domestica) or myrobalans (P. cerasifera) because of traditional plum growing in our country. 60% of Slovak PPV-M isolates were found in peach trees (P. persica), supporting the preferential occurrence of PPV-M in this host (Dallot et al. 2003). Markedly stronger host preference was, however, observed for the other two strains which have been isolated mainly from plums (88% PPV-D and 94% PPV-Rec). This result might be biased by the low number of analysed Slovak samples from peach and apricot (P. armeniaca), but the results were similar when taking into account over 1 300 SharCo database isolates (with higher ratio of peach and apricot ones) originating from various countries (http:// w3.pierroton.inra.fr:8060/homes/index) (Table 1). In this case, the plum specificity is 88% for PPV-Rec and 49% for PPV-D. Indeed the last value is lower than that observed for Slovak isolates, but it is still comparable to the peach preference of PPV-M (52%).

2. Bioinformatic analyses of sequence data from natural PPV isolates

Such non-uniform incidence of PPV in *Prunus* species enables to presume some genetic predispositions of PPV

strains to infect preferentially particular hosts. Therefore we inspected the complete PPV sequences for polymorphisms correlating with the host species they were isolated from (plum for PPV-D or PPV-Rec and peach for PPV-M were considered as "typical" hosts). Analysed sequences included four "host-atypical" Slovak isolates: BOR-3, SK-514ap (PPV-Rec from apricot), SK-23pe and SK-272pe (PPV-D from peach) (acc. nos. AY028309, LN614587, LT158756 and HF585098, respectively). Only one single amino acid polymorphism correlating with the host species of PPV-D could be found along the polyprotein, T/A¹¹⁶⁴, close to the C terminus of the polypeptide 6K1. This applied, however, only for old-world PPV-D isolates. Another single relevant polymorphism Y/H⁸⁸² in the P3 protein was found in North American PPV-D. Such ambiguous results showed the weak point of strictly bioinformatic approach which should be problematic from several points of view.

Quantity and quality of relevant data remain the first limitation and bias for sequence analyses. The SharCo database contained 118 autonomous complete (or nearly complete) sequences of isolates from major PPV strains (accessed on March, 2015). After elimination of Japanese PPV isolates originating from other *Prunus* hosts and few isolates with unknown origin, 79 sequences remain: 43 PPV-D, 11 PPV-Rec and 18 PPV-M. Twenty-one PPV-D isolates (49%) originated from USA and Canada, where PPV after recent introduction is controlled and strongly geographically restricted (Gottwald 2006). These isolates show high sequence identity and distort the global picture of PPV-D diversity.

A cardinal problem of bioinformatic analysis of natural isolates remains in the fact that this approach might represent some weakness to discover genetic determinants of the host preference. There is namely no detailed information available about infection development in particular trees (including infection time, source, way of transmission, etc.) which may be important for evaluation of relevance of possible sequence changes. Fixation of genetic markers may be expected only after some virus coexistence with a new ("atypical") host.

Another problem constitutes the analysis of PPV populations in frame of each single tree, because of the uneven

Table 1 Strain affiliation of *Plum pox virus* (PPV) isolates from different *Prunus* host species¹⁾

Original host	PPV-M	PPV-D	PPV-Rec
Plum/Myrobalan	75 (5/0)	369 (36/5)	233 (29/0)
Apricot	65 (1/0)	172 (8/0)	13 (3/0)
Peach	172 (23/0)	80 (3/28)	8 (0/0)
Other/Unknown	16 (1/0)	128 (2/2)	12 (1/2)
All	328 (30/0)	749 (49/35)	266 (33/2)

¹⁾ All independent isolates from the SharCo database (March, 2016) are indicated. In the parentheses, numbers of Slovak/North American isolates are specified.

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