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Divergent effects of PVY-infected potato plant on aphids

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Abstract Host plant selection by aphids can be positively or negatively affected when plants are infected by phytoviruses. Potato plants infected by *Potato virus Y* (PVY), a non-persistent virus, are reported to affect settling behaviour and growth parameters of *Myzus persicae* Sulzer and *Macrosiphum euphorbiae* Thomas. Using the Electrical penetration graph system (EPG), we demonstrated that PVY-infection of potato plants influences the feeding behaviour of these two aphid species. *Myzus persicae* exhibited increased phloem sap ingestion and reduced non-probing duration. *Macrosiphum euphorbiae* showed delayed stylet insertion, reduced activity in the phloem vessels and an enhanced non-probing duration. In addition, we showed that these two species exhibited different transmission rates. The opposite effects of PVY-infected potato plant on these two aphids are discussed in terms of PVY spreading in the field.

Keywords Virus infection · *Potato virus Y* · Feeding behaviour · *Macrosiphum euphorbiae* · *Myzus persicae*

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Plant infection by phytoviruses has been reported to affect behaviour and physiology of vectoring aphids. A myriad of effects have been observed on aphids, from positive through neutral to negative (Fereres and Moreno 2009) modifying the different steps of host plant colonization. Eigenbrode et al. (2002) showed that volatiles from potato plants infected by the *Potato leaf roll virus* (PLRV), a persistently transmitted circulative virus that depends on aphids for dispersal, are attractive for vector aphids. After landing, aphid feeding behaviour (particularly superficial tissue probing and sustained phloem sap ingestion) can be enhanced on plants infected by PLRV (Alvarez et al. 2007). Finally, PLRV infection was also reported to enhance host plant preference and acceptance, thus improving aphid fitness (Castle and Berger 1993; Srinivasan and Alvarez 2007). In contrast to the effect of persistent viruses, mechanically transmitted infection of potato plants by the vector-independent virus *Potato virus X*, induced no effect on aphids (Alvarez et al. 2007; Castle et al. 1998; Eigenbrode et al. 2002; Srinivasan and Alvarez 2007). *Potato virus Y* (PVY), a less vector-dependent virus, transmitted in a non-persistent manner by a broad range of aphid species, induces various modifications of aphid behaviour and physiology depending on the species (Srinivasan and Alvarez 2007). PVY infection enhanced settling behaviour and growth parameters of *Myzus persicae* whereas it had no effect on *Macrosiphum euphorbiae*.

It appears that, according on their dependency to a vector, viruses could induce different degrees of modification in the colonization of infected plants by the vector aphids. Our objective was to study the effect of PVY infection of potato plants on its two main aphids *M. persicae* and *M. euphorbiae*. Electrical penetration graph system (EPG) was used to compare feeding behaviour of aphids on PVY-infected potato plants (*Solanum tuberosum* L.) and healthy ones. In accordance with previous work reporting differential effects on these two-aphid species' fitness (Castle and Berger 1993; Srinivasan and Alvarez 2007), we hypothesized that PVY-infection would enhance the feeding activity of *M. persicae* whereas it would have no effect on *M. euphorbiae* feeding behaviour.

Potato plants (*Solanum tuberosum* L. cv. Bintje) were grown from healthy or infected (PVY^{NTN}) tubers in 9-cm plastic pots under controlled greenhouse conditions (20±1°C, 60±5% relative humidity, under 16 L:8D photoperiod) before experiments. Five week-old plants were used for both feeding behaviour experiments and virus acquisition process in transmission efficiency experiments. Two week-old in vitro plants were used for the inoculation process in transmission efficiency experiments. NTN isolate of PVY was obtained from potato tubers collected in potato fields (Cambrai, France) and was maintained in laboratory through aphid transmission on potato cv. Bintje plants. Plant infection status was determined by RT-PCR (Glais et al. 2005). The *M. euphorbiae* and the *M. persicae* colonies were initiated from a single apterous parthenogenetic female originating respectively from the clone Me LB05 (INRA-INSA, Villeurbanne, France) and from a potato field in northern France (1999). Aphids were reared on potato plants raised under the same conditions as above in a separated growth room. Experiments were conducted with alate aphids synchronized according to Brunissen et al. (2009). The DC Electrical Penetration Graph system (Tjallingii 1978) was used to investigate aphid probing behaviour on the abaxial face of the third fully developed leaf of an infected or healthy plant. To insert one aphid and one plant in an electrical circuit, a thin gold wire (20 μm diameter and 2 cm long) was stuck on the insect's dorsum by conductive silver glue and the other electrode was inserted in the soil of the potted plant. For each PVY-infected or healthy plant, 19 to 22 replicates were done and recordings were performed continuously for 8 h during daytime. Acquisition of the EPG waveforms (C, E1, E2) (Tjallingii 1988) was carried out with PROBE 3.5 software (EPG-Systems, Wageningen, The Netherlands). Analysis of EPG parameters was calculated using the EPG-Calc 4.9 software (Giordanengo 2009). C waveforms corresponded to stylet pathways in plant tissues except phloem and xylem, E1 waveforms to salivation in phloem elements and E2 waveforms to passive phloem sap ingestion. Statistical analyses were performed using STATISTICA 6.0 software (StatSoft, Tulsa, Oklahoma, USA). Within each species, for each EPG parameter, a pairwise comparison between healthy and PVY-infected plant was performed using a Mann & Whitney *U*-test. Transmission bioassays were performed with PVY^{NTN} infected leaflets, detached from infected potato plants and placed in a Petri dish (diameter: 9 cm) for a 30 min acquisition access period (AAP). Then, aphids were individually deposited on healthy in vitro plants for a 24-h inoculation access period (IAP). At the end of the IAP, aphids and possible progeny produced were removed from the in vitro plants, which were then placed in a growth chamber for 2 weeks before determining their infection status. Transmission efficiency analysis revealed that *M. persicae* exhibited the best rate with 80% (24 infected plants out of 30 inoculated ones) compared to the 20% obtained in *M. euphorbiae* (6 infected plants out of 30 inoculated ones).

In *M. euphorbiae*, all the selected parameters related to probing behaviour were significantly modified on PVY-infected plants compared to healthy ones (Fig. 1a): first stylet insertion was delayed (142.8±32.8 vs 26.1±7.7, U=109, $p<0.01$), number of probes was reduced (4.4±0.7 vs 13.2±1.9, U=82, $p<0.01$) and a longer non-probing period was observed (379.1±23.9 vs 158.5±27.6 min, U=42, $p<0.01$). Total duration of pathway phase, salivation in phloem elements and phloem sap ingestion were significantly shortened on PVY-infected plants (respectively 49.2±10.7 vs 140.0±17.4 min, U=74, $p<0.01$; 4.7±2.6 vs 43.4±12.2 min, U=65, $p<0.01$; 29±13.6 vs 98.5±24.7 min, U=105.5, $p<0.01$). Analysis of feeding behaviour of *M. euphorbiae* revealed that PVY-infection reduced the suitability of potato plants compared to healthy ones whereas we hypothesized no effect. The delayed first puncture, and decreased pathway and phloem sap ingestion phases observed on infected plants could result from the modification of chemical (e.g. deterrent com-

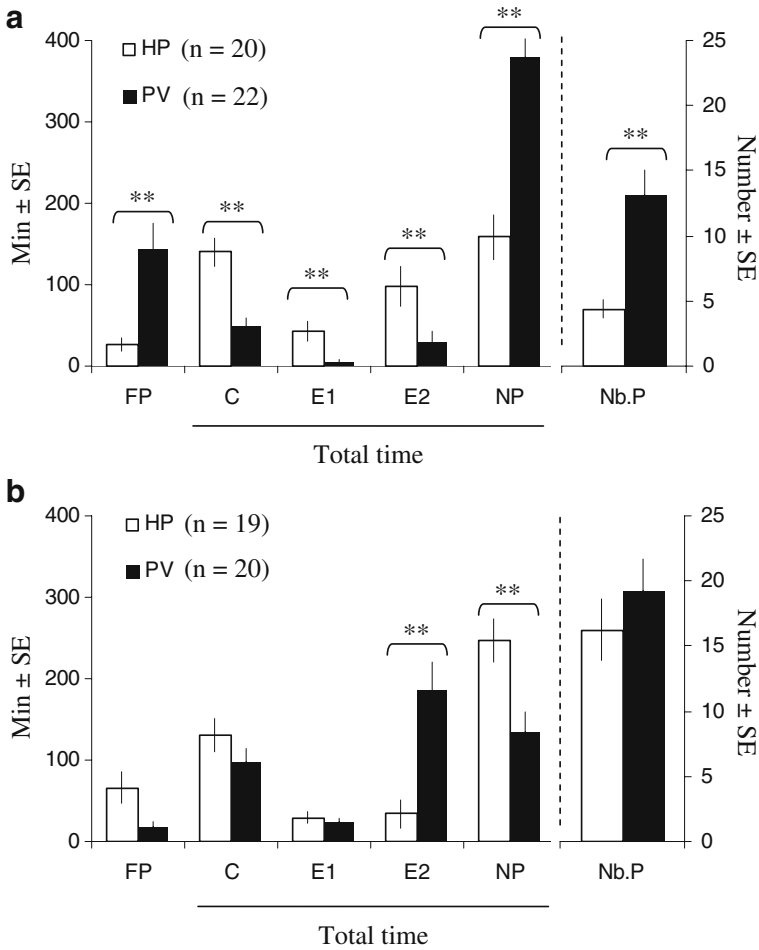

Fig. 1 Electronically monitored probing characteristics (mean ± SE) of *Macrosiphum euphorbiae* (**a**) and *Myzus persicae* (**b**) on healthy (HP) or PVY-infected (PVY) plants during the 8 h access experiment. FP: Time from start to the first probe, C: Searching phase in epidermic and mesophyll tissues, E1: Salivation phase in phloem vessels, E2: Phloem sap ingestion phase in phloem vessels, NP: Non-probing phase, Nb.P: Number of probing phase. Significant differences were determined at $P<0,01$ (**) according to Mann & Whitney *U*-test

pounds) and physical properties of the plant tissues. Indeed, pathogen infection can modify plant chemistry inducing defence reactions, which can in turn influence host plant acceptance (Felton et al. 1999; Hatcher et al. 2004). However, decreased pathway, salivation and ingestion phase durations observed on infected plants may be considered as a result of both increased non-probing activity and delayed first probe. Srinivasan and Alvarez (2007) showed that PVY-infected plants did not affect either the fecundity or the settling behaviour of *M. euphorbiae*. PVY-infection of potato plants seems to only affect events linked to *M. euphorbiae* probing activity. Furthermore, as reported by Pescod et al. (2007), *M. euphorbiae* and *M. persicae* do not respond in the same way to nutrients from phloem sap.

In *M. persicae*, duration of non-probing was reduced (135.2±24,7 vs 247.4±26.2 min, U=88, $p<0.01$, Fig. 1b) and duration of phloem sap ingestion was extended on plants infected by PVY (186.6±34.0 vs 33.7±18.2 min, U=64, $p<0.01$). Enhancement of phloem sap ingestion and probing duration induced by PVY-infection of potato plants could result from either a difficulty to obtain the required nutrients or an easier host acceptance. Regarding the literature, the second hypothesis seems to be the most suitable. Indeed, infection by phytoviruses has been reported to increase the amount of carbohydrates and amino acids in leaves (Castle and Berger 1993; Markkula and Laurema 1964) and the greater nutritional quality of virus-infected plants is believed to be partly responsible for enhanced vector life history on such plants (Fereres et al. 1989). Together with our results, such variations in their diet may explain the enhanced growth rate of *M. persicae* populations on PVY-infected plants observed by Castle and Berger (1993) and the preference exhibited by alates of this species to settle on infected plants reported by Srinivasan and Alvarez (2007).

Former work, in addition to the putative virus-induced biochemical or physical changes in the host plant, could explain the divergent effects of PVY-infected plant on feeding activity between these two species. Depending on the insect species, our study highlights, for the first time, positive or negative effects on the aphid feeding behaviour induced by a non-persistent virus infection of their host plant. PVY-infection positively affects all the stages of host plant colonization and population growth of *M. persicae*. For *M. euphorbiae,* only plant acceptance is reduced on PVY-infected plants, without effect on aphid fitness. As reported for plants infected by persistent viruses (Alvarez et al. 2007; Eigenbrode et al. 2002), non-persistent viruses could be responsible for variations in plant colonization and aphid performance. Thus, in *M. persicae,* the increase of feeding activity observed on infected plants could reinforce its sedentary status and consequently decrease its interplant movement ability. By contrast, colonizing *M. euphorbiae,* less accepting of infected plants, are more likely to perform interplant movements. Thus, PVY seems to exhibit different spreading strategies depending on its vector. *M. persicae* is a sedentary species but with a high virus transmission rate whereas *M. euphorbiae* is potentially a very mobile species but with a very low virus transmission rate. Moreover, on infected plants, *M. persicae* produce more numerous progeny which will in turn spread the virus, contributing to the very high transmission efficiency of the species.

Deciphering the ecology of such a pathosystem thus appears as a prerequisite to understanding how plant, insect and pathogen communities are structured. Future studies will be required to evaluate the significance of our findings on the propagation strategies of non-persistently transmitted viruses.

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