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Local and systemic responses induced by aphids in *Solanum tuberosum* plants

Sébastien Dugravot[1]†, Laurence Brunissen[1], Emilie Létocart[1], W. Freddy Tjallingii[2], Charles Vincent[3], Philippe Giordanengo[1] & Anas Cherqui[1]*

[1]*Biologie des Plantes et Contrôle des Insectes Ravageurs, UPRES EA 3900, Université de Picardie Jules Verne, 33 rue Saint Leu, 80039 Amiens cedex, France,* [2]*Laboratory of Entomology, Wageningen University, PO Box 8031, 6700EH Wageningen, The Netherlands, and* [3]*Horticultural Research and Development Centre, Agriculture and Agri-Food Canada, 430 Gouin Blvd., Saint-Jean-sur-Richelieu, QC, Canada J3B 3E6*

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Abstract

The aphids *Macrosiphum euphorbiae* (Thomas) and *Myzus persicae* (Sulzer) (Homoptera: Aphididae) are serious pests of potato (*Solanum tuberosum* L.) (Solanaceae), notably in transmitting several plant viruses. Heterospecific interactions may occur between these two species as they are often seen at the same time on the same potato plant in the field. As aphid infestation is known to induce both local and systemic changes, we conducted experiments to determine the effect of previous infestation on probing behaviour and feeding-related parameters. We used the DC electrical penetration graph technique to characterize the influence of previous infestation by conspecific *M. persicae* or by heterospecific *Ma. euphorbiae* on *M. persicae* feeding behaviour at both local and systemic levels, i.e., on previously infested leaves and on non-previously infested leaves of infested plants, respectively. Conspecific and heterospecific infestation led to similar modification of *M. persicae* feeding activities. However, the effects of previous infestation occurring at the local level were opposite to those observed at the systemic level. *Myzus persicae* food acceptance was slightly enhanced on previously infested leaves, whereas it was inhibited on non-infested leaves of infested plants, which indicated an induced resistance mechanism. Our results advance the understanding of the mechanisms involved in aphid–host plant acceptance and colonization processes on potato plants in conspecific and heterospecific situations.

Introduction

More than 100 plant species belonging to different genera and families have been shown to exhibit responses to herbivory (Karban & Baldwin, 1997). Induced plant responses may be involved in defence processes, affecting herbivore settling, feeding, oviposition, growth and development, fecundity, and fertility (Walling, 2000). Most studies on plant responses to herbivores have focused on chewing insects that extensively damage leaves (Stotz et al., 1999). However, owing to a recent increase of published information, physiological plant responses and resistance mechanisms against phloem-feeding insects are starting to be disentangled.

Aphids, the largest group of phloem feeders, can inflict considerable damage and fitness cost to several crops (Dixon, 1998). Plants have developed defence strategies to limit aphid damage. It is known that both local and systemic changes in gene expression can occur in plant response to phloem-feeding insects (van de Ven et al., 2000). For example, pathogenesis-related (PR) proteins such as β-1,3-glucanase (BGL2) are expressed by genes associated with salicylic acid-dependent responses to pathogens; they are induced during aphid infestation on *Arabidopsis* rosette leaves (Moran & Thompson, 2001). Systemic plant resistance factors against aphids can also be induced by jasmonic acid pathway activation, as application of synthetic jasmonic

*Correspondence: Anas Cherqui, Laboratoire de Biologie des Entomophages, Université de Picardie Jules Verne, 33 rue Saint Leu, 80039 Amiens cedex, France. E-mail: anas.cherqui@u-picardie.fr
†Present address: Equipe d'Ecobiologie des Insectes Parasitoïdes (UPRES EA 3193), Université de Rennes 1, Campus Beaulieu, 263 Av du Général Leclerc, 35042 Rennes, France.

acid to tomato plants triggers a decrease of *Macrosiphum euphorbiae* (Thomas) (Homoptera: Aphididae) performance (Cooper & Goggin, 2005). Both jasmonic acid and salicylic acid pathways may be involved in rapid local defence response in infested leaves. Moreover, in tomato plants, the *Mi* gene confers an induced resistance to *Ma. euphorbiae* (Kaloshian et al., 2000; Martinez de Ilarduya et al., 2003; Goggin et al., 2004). Recently, Thompson & Goggin (2006) reviewed several studies using transcription analysis of gene expression and showed that plant phloem feeders are able to considerably change the physiology of their host plants, including secondary metabolism.

Some studies have shown that previous infestation could affect subsequent insect performances. Wool & Hales (1996) reported that a previous infestation of cotton plants by *Aphis gossypii* decreased subsequent colonization by conspecific aphids. Another phloem-feeding insect, the silverleaf whitefly, *Bemisia argentifolii*, induced PR protein accumulation in collard and tomato plants, which negatively affected the colonization process of conspecific and heterospecific competitors (Mayer et al., 2002). Conversely, previous infestation by *Myzus persicae* (Sulzer) (Homoptera: Aphididae) carried out on three different peach cultivars led to an improvement of conspecific performance (Sauge et al., 2002, 2006).

Macrosiphum euphorbiae and *M. persicae* are sympatric aphid species, which are serious pests of potato crops. Direct phloem-sap feeding may cause yield losses (Radcliffe, 1982), but the most important damage consists of transmitting several plant viruses (Blackman & Eastop, 1984). As these two aphid species are often present simultaneously on the same potato plant, and even on leaves previously colonized by both species (S Dugravot, pers. obs.), heterospecific interactions may occur. Interspecific interactions often occur among sap-feeding insects and may be intense between related taxa (Miller, 1967; Moran & Whitham, 1990). Plant phloem alterations can positively or negatively affect the performance of other phloem feeders (Way & Banks, 1967; Dorschner & Baird, 1989; Bumroongsook & Harris, 1992). Understanding interactions between phytophagous insects that share a common host plant is of ecological interest when studying host-plant acceptance and colonization processes.

In the context of early colonization of potato plants by two aphid species, we addressed the following question: Do previous infestations influence plant acceptance by aphids? Consequences of both conspecific *M. persicae* and heterospecific *Ma. euphorbiae* infestations were investigated locally and systemically. For this purpose, we used the electrical penetration graph (EPG) technique (McLean & Kinsey, 1967; Tjallingii, 1988) to analyse aphid feeding activities that occur before and during sap ingestion from phloem sieve elements. EPG is also suitable to characterize a phloem-based plant resistance to sap-feeding insects, as it allows to explain interactions between aphid stylets and plant tissues (Tjallingii, 2006). Using the DC-EPG technique, we demonstrated various changes in the feeding behaviour of *M. persicae* occurring after previous infestation carried out on potato plants.

Materials and methods

Plants and insects

Potato plants [*Solanum tuberosum* L. cv. Désirée (Solanaceae)] susceptible to aphids were grown from tubers in plastic pots in an environmental chamber maintained at 20 ± 1 °C under a photoperiod of L16:D8. Four-week-old plants were used for the experiments. *Myzus persicae* and *Ma. euphorbiae* were mass reared on potato plants in environmental chambers under the same conditions. The rearing of *M. persicae* was initiated from a single virgino-apterous female collected in early summer 1999 from a potato field near Loos-en-Gohelle, France. The clone of *Ma. euphorbiae*, Me LB, was provided by Institut National de Recherches Agronomiques (INRA)-Institut National de Science appliquées (INSA), Villeurbanne, France.

Previous infestation treatments

Previous infestations were performed by placing on a single leaf of each plant either 50 *M. persicae* or 50 *Ma. euphorbiae* with a random mixture of adults and fourth-instar nymphs. The aphids were isolated on the third leaf from the apex in a ventilated plastic box during 96 h and removed carefully with a paintbrush just before the experiments. Non-infested potato plants were used as a control and treated in the same way.

EPG experiments

The probing behaviour of 2- to 3-day-old apterous adult *M. persicae* was monitored using the DC-EPG technique (Tjallingii, 1978, 1988). An aphid and a plant were connected through a thin gold wire (20 µm diameter and 2 cm length) stuck on the insect's dorsum by conductive silver glue (water based), and another electrode (copper wire) inserted in the soil of the potted plant. When the aphid started probing, the electrical circuit was completed, and EPG waveforms were produced. All plants and insects were held inside a Faraday cage during recording at 20 ± 1 °C. Recordings were performed on one aphid per plant during daytime for 8 h continuously. Acquisition and analyses of the EPG signals were done with the PROBE 3.0 software (F Tjallingii, Laboratory of Entomology, Wageningen University, The Netherlands).

Myzus persicae feeding behaviour was investigated on leaves of non-infested and previously infested plants: (i) third or

fourth leaf level from the apex of non-infested plants (hereafter 'control'); (ii) third leaf level from the apex of plants previously infested by *M. persicae* (hereafter 'conspecific local', CL); (iii) fourth leaf level from the apex, just below the leaf previously infested by *M. persicae* (hereafter 'conspecific systemic', CS); (iv) third leaf level from the apex of plants previously infested by *Ma. euphorbiae* (hereafter 'heterospecific local', HL); (v) fourth leaf level from apex, just below the leaf previously infested by *Ma. euphorbiae* (hereafter 'heterospecific systemic', HS). Preliminary experiments showed no difference between EPG parameters of aphids monitored on either third or fourth leaves of non-infested potato plants.

Seventeen EPG parameters (Table 1) were analysed using the following five EPG waveforms (Tjallingii, 1978, 1988): pathway phase waveforms (lumped waveforms A, B, C, and pd) reflecting activities during stylet pathway; E1 waveforms indicating salivation in phloem sieve elements; E2 waveforms indicating passive sieve element sap ingestion and concurrent salivation; G waveforms indicating active xylem sap ingestion; and F waveforms indicating derailed stylet mechanics (or penetration difficulties; Tjallingii, 1988). The 17 EPG parameters, calculated using the 'EPG-Calc' Visual Basic macro (P Giordanengo, unpubl.), were assigned to five categories (Table 1), namely (i) general probing behaviour class: this included the mean number of probes and the total duration of probing; (ii) pathway phase, corresponding to probing activities excluding phloem and xylem activities: this class included total duration of the pathway and the time spent by aphids before initiating the first probe; (iii) phloem salivation, with a distinction between single phloem salivation periods, phloem salivation periods followed by sap ingestion, time from the first probe to first salivation, and duration of the probe before the first salivation; (iv) phloem phase, including all parameters concerning phloem sap ingestion and the time spent by aphids before performing a first-sustained ingestion longer than 10 min. For aphids that did not exhibit E1 and sustained E2 (sE2), the complete 8-h recording time (= 480 – time to first probe in min) was used as the value for the time to first E1 and first sE2, respectively. The phloem acceptance index corresponded to the time (%) dedicated to phloem sap ingestion from first sustained phloem ingestion period (100 = maximal phloem acceptance). It was calculated only using aphids that reached sE2. The percentage of aphids showing sE2 was also calculated at every hour of probing; and (v) other EPG parameters included xylem ingestion and derailed stylet mechanics.

Statistical analysis

Because data were not normally distributed, the EPG parameters of aphids monitored on treated plants were compared pairwise with aphids monitored on control plants by non-parametric Mann–Whitney U-tests at $P = 0.05$ (Table 1). Nineteen to 45 replicates were done per treatment. The percentage of aphids with sE2 phloem phase on treatment and control plants was analysed with the Pearson χ^2-test.

Results

Myzus persicae feeding behaviour on previously infested leaves (at the local level)

Under CL conditions, none of the EPG parameters related to general probing behaviour and pathway phases was statistically different from the control (Table 1; parameters 1–4). However, aphids on CL leaves exhibited significant lower total duration of single phloem salivation bouts than aphids on control plants (parameter 6: $P = 0.033$). While parameters related to phloem phase were similar on CL and control plants (parameters 10–13), the percentage of aphids performing a sustained phloem ingestion (sE2 > 10 min) was higher on CL than on control leaves after the second hour of probing ($\chi^2 = 17.63$, $P<0.001$; Figure 1).

Under HL conditions, the number of probes was significantly lower than under control conditions (parameter 1: $P = 0.027$). Nevertheless, total duration of probing and pathway phase parameters were not significantly modified (parameters 2–5). Previous infestation by *Ma. euphorbiae* induced a significant decrease in total single phloem salivation bouts relative to that observed on CL leaves (parameter 6: $P = 0.002$). Moreover, aphids on HL leaves exhibited sustained phloem ingestion significantly earlier than on control plants (parameter 13: $P = 0.016$). Furthermore, after the first 2 h, a higher percentage of aphids showed sustained phloem ingestion on HL than on control plants ($\chi^2 = 53.16$, $P<0.001$: Figure 1).

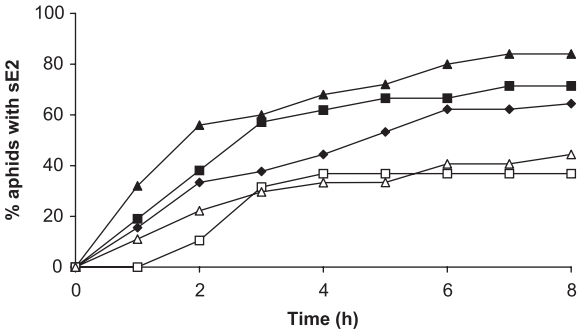

Figure 1 Cumulative percentage of aphids that initiated a sustained phloem ingestion (sE2 > 10 min): aphids tested on control potato plants ◆; aphids tested on previously infested leaves by conspecific (CL) ■ or by heterospecific aphids (HL) ▲; aphids tested on systemic leaves from previously infested plants by conspecific (CS) □ or by heterospecific aphids (HS) △.

Table 1 Probing behaviour (mean ± SEM) of *Myzus persicae* during an 8-h access to leaves from non-infested tomato plants (control); leaves previously infested by *M. persicae* (CL); leaves previously infested by *Macrosiphum euphorbiae* (HL); non-infested leaves from previously infested plants by *M. persicae* (CS); and non-infested leaves from previously infested plants by *Ma. euphorbiae* (HS).

		Non-infested plants (control)	Infested leaves		Non-infested leaves	
			From pre-infested plants (local level)		From pre-infested plants (systemic level)	
EPG parameters	Unit	n = 45	*M. persicae* (CL) n = 24	*Ma. euphorbiae* (HL) n = 25	*M. persicae* (CS) n = 19	*Ma. euphorbiae* (HS) n = 27
General probing behaviour						
1. Number of probes	number	15.2 ± 1.6	13.5 ± 1.8	10.2 ± 1.9*	15.5 ± 2.8	18.7 ± 2.2*
2. Total duration of probing	min	331.2 ± 13.7	300.8 ± 17.6	339.2 ± 12.2	260.9 ± 24.9*	281.1± 14.6*
Pathway phase						
3. Total duration of pathway	min	111.6 ± 10.4	107.5 ± 9.6	98.4 ± 16.7	114.7 ± 12.7	154.4 ± 13.5*
4. Time from start of recording to first probe	min	26.2 ± 5.6	39.2 ± 11.4	39.1 ± 13.0	44.0 ± 12.5	38.8 ± 7.9
Phloem salivation (E1 only)						
5. Number of all E1 periods	number	5.2 ± 0.6	5.7 ± 0.8	5.4 ± 1.0	3.8 ± 0.5	6.4 ± 0.8
6. Total duration of single E1 periods	min	27.5 ± 5.0	13.8 ± 4.0*	9.3 ± 3.6*	27.9 ± 7.4	23.3 ± 6.4
7. Total E1 duration followed by phloem ingestion	min	26.7 ± 8.0	15.8 ± 3.9	18.9 ± 4.2	5.0 ± 2.7*	17.7 ± 5.1
8. Time from first probe to first E1	min	91.1 ± 15.0	68.9 ± 9.1	65.8 ± 27.6	125.4 ± 31.9	129.6 ± 25.6
9. Duration of probe before first E1	min	25.6 ± 10.2	17.3 ± 2.0	52.5 ± 25.5	76.1 ± 34.7	18.3 ± 1.7
Phloem phase						
10. Number of phloem ingestion periods	number	2.1 ± 0.3	2.5 ± 0.5	3.4 ± 0.8	0.9 ± 0.4**	2.5 ± 0.6
11. Total duration of phloem ingestion	min	154.6 ± 24.8	148.7 ± 26.1	199.6 ± 28.8	80.3 ± 31.0*	59.1 ± 16.7*
12. Phloem acceptance index	%	48.6 ± 6.8	51.5 ± 8.7	66.2 ± 7.5	14.9 ± 7.1**	24.0 ± 6.6*
13. Time from first probe to first sustained E2	min	271.5 ± 26.2 (29)	224.4 ± 36.7 (15)	173.4 ± 32.7* (21)	344.5 ± 39.3 (7)	319.1 ± 35.5 (12)
Other parameters						
14. Number of stylet derailment periods	number	0.5 ± 0.2	0.3 ± 0.2	0.3 ± 0.2	0.7 ± 0.2	0.8 ± 0.3
15. Total duration of stylet derailment periods	min	11.2 ± 4.2	5.2 ± 3.5	3.3 ± 2.0	21.1 ± 7.7	20.6 ± 7.7
16. Number of xylem ingestion periods	number	0.3 ± 0.1	0.1 ± 0.1	0.4 ± 0.2	0.6 ± 0.3	0.4 ± 0.2
17. Total duration of xylem-ingestion periods	min	10.4 ± 3.7	10.7 ± 7.1	8.9 ± 4.1	13.4 ± 6.6	7.4 ± 3.0

Means followed by * or ** indicate a significant difference with control plants at $P<0.05$ and $P<0.01$, respectively.
For parameter 13, the numbers of aphids used in each treatment are given under the parameter between brackets.

Myzus persicae feeding behaviour on non-infested leaves from previously infested plants (at the systemic level)

Total duration of probing was significantly lower on CS than on control plants (parameter 2: P = 0.016), whereas the number of probes was not significantly different between these two treatments (parameter 1). Time to initiate the first probe (parameter 4) and total duration of this probe (parameter 3) were not significantly different between CS and control plants. However, total duration of phloem salivation followed by phloem ingestion, the number of phloem ingestion periods, and their total duration were significantly reduced for aphids recorded on CS leaves (parameters 7, 10, and 11: P = 0.021, P = 0.008, and P = 0.021, respectively). Consequently, the phloem acceptance index was decreased for aphids monitored on CS leaves when compared to control plants (parameter 12: P = 0.004). Furthermore, during the 8-h recording time, the percentage of aphids showing sustained phloem ingestion on CS was lower than on control plants ($\chi^2 = 53.16$, P<0.001; Figure 1).

Under HS conditions, total duration of probing was lower than under control conditions (parameter 2: P = 0.012) and the number of probes higher (parameter 1: P = 0.018). Among pathway phase parameters, only total pathway duration was increased on HS leaves (parameter 3: P = 0.019). Time until the first phloem salivation (parameters 8 and 9) was not modified. Although number of phloem ingestion periods was not affected for aphids on HS leaves, total time of phloem ingestion (parameter 11: P = 0.049) and phloem acceptance index were both significantly lower under HS than under control conditions (parameter 12: P = 0.044). Moreover, after the second hour, the percentage of aphids exhibiting sustained phloem ingestion was lower for aphids tested on HS than on control leaves ($\chi^2 = 56.84$, P<0.001; Figure 1).

Discussion

Monitoring of *M. persicae* feeding behaviour at local or systemic level of previously infested plants showed different effects for both conspecific and heterospecific pre-infestations. The plant response induced by a previous infestation seems to be slightly beneficial at the local level but somewhat detrimental at the systemic level. Generally, the effects induced by previous infestation by either *M. persicae* or *Ma. euphorbiae* were very similar.

During probing, aphids release two different types of saliva, a sheath material, and watery saliva. Whereas solid saliva is reported to protect the stylets during intercellular probing phases, the function of the watery saliva released during the phloem phase remains only partially understood (Miles, 1999; Cherqui & Tjallingii, 2000). It has been suggested that it may prevent the activation of the sieve plate sealing system in response to phloem wounding (Tjallingii & Hogen-Esch, 1993). Consequently, the decreased phloem salivation period we observed in *M. persicae* on previously infested leaves could be the consequence of a beneficial earlier salivation by conspecifics into the same or into connected sieve tubes (Sauge et al., 2002).

Previous infestation by *Ma. euphorbiae* reduced the number of probes while total probing duration remained the same, leading to longer probes. On resistant host plants, phloem feeders tended to probe more frequently and for shorter periods (McLean & Kinsey, 1967; Mesfin et al., 1995). The reduced number and extended duration of probes suggest that leaves previously infested by *Ma. euphorbiae* became more suitable than non-infested leaves of control plants. Accordingly, the prompt first sustained phloem ingestion observed on HL leaves also indicates an enhanced leaf acceptance. Although beneficial effects of previous infestation by aphids on local sites have already been reported (Way & Banks, 1967; Way & Cammell, 1970; Prado & Tjallingii, 1997; Sandström et al., 2000; Gonzáles et al., 2002; Sauge et al., 2002), we report for the first time beneficial effects of a heterospecific previous infestation. It is noteworthy that aphids are able to increase local concentrations of carbohydrates (Girousse et al., 2003) and amino acids (Sandström et al., 2000) in the sieve tubes. Such improvements in sap quality could explain the beneficial effects observed at the site of the previous infestation.

Conversely to what was observed at the local level, monitoring of *M. persicae* at the systemic level showed detrimental effects. In either conspecific or heterospecific interactions, the duration of probing and phloem ingestion and the phloem acceptance index were decreased. Moreover, on leaves previously infested by heterospecific aphids, the number of probes and total duration of the pathway increased significantly. These are typical features of the behaviour of aphids feeding on resistant plants, as reported in EPG studies on aphid/plant systems (Campbell et al., 1982; van Helden & Tjallingii, 1993; Cole, 1994; Caillaud et al., 1995; Klingler et al., 1998; Ramirez & Niemeyer, 1999; Sauge et al., 2002).

The modifications observed in the feeding behaviour of *M. persicae* tested on healthy leaves of previously infested potato plants led us to hypothesize that a mechanism of systemic resistance is induced by *M. persicae* and *Ma. euphorbiae*. Parameters pertaining to phloem element accessibility were not modified, while altered phloem activities indicated a resistance mechanism located in the phloem. The reduced acceptance could be due to induced allelochemicals in the phloem sap as it is often observed in plants after damage by chewing insects (Karban & Baldwin, 1997). Analysis of gene expression established that phloem-feeding insects induce specific plant responses (Thompson & Goggin, 2006).

Several genes involved in cell wall modification, water transport, vitamin biosynthesis, photosynthesis, carbon assimilation, and nitrogen and carbon mobilization were up-regulated in the phloem of *Apium graveolens* infested by *M. persicae* (Divol et al., 2005). This gene induction was accompanied by a systemic response of the plant to the aphid infestation. A gene-for-gene resistance is triggered when a plant resistance gene (*Mi*) recognizes the intrusion of phloem-feeding insects in tomato (Kaloshian et al., 2000; Martinez de Ilarduya et al., 2003). In *Arabidopsis*, Moran & Thompson (2001) demonstrated that infestations by *M. persicae* induced the transcription of PR and β-1,3-glucanase (BGL2) genes, both associated with salicylic acid-dependent responses to pathogens. Such induced resistance to aphids has already been shown by EPG data in the peach cultivar 'Rubira' infested by *M. persicae* (Sauge et al., 2002) and in one genotype of *Medicago truncatula* infested by *Acyrthosiphon kondoi* (Klingler et al., 2005).

Previous infestations by conspecific and heterospecific aphids induced modifications of *M. persicae* feeding activities at the local and systemic level. Therefore, it can be assumed that both conspecific and heterospecific interactions can act systemically. On the other hand, one could explain the local beneficial effects as a local suppression of the systemically spread induced resistance (E Prado and WF Tjallingii, unpubl.). The salivary sheath, a major salivary secretion, is not secreted into the sieve elements and may have mainly a local effect. Aphids might thus protect themselves against their own-induced resistance. A previous infestation of potato plants by aphids, either conspecific or heterospecific, leads to altered plant acceptance by aphids colonizing the plant afterwards.

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