Effects of systemic potato response to wounding and jasmonate on the aphid *Macrosiphum euphorbiae* (Sternorryncha: Aphididae)

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Abstract

Plant induced responses are activated by multiple biotic and abiotic stresses, and may affect the interactions between a plant and phytophagous insects. The objective of this work was to evaluate the effects of different stresses inflicted to potato plants (*Solanum tuberosum*) on the potato aphid (*Macrosiphum euphorbiae*). Abiotic wounding, biotic wounding by *Leptinotarsa decemlineata* and treatment with volatile methyl jasmonate (MeJA) were evaluated with regard to the orientation behaviour, the feeding behaviour and the development of the potato aphids. Dual-choice olfactometry showed that plants treated with MeJA lost their attractiveness for the potato aphids, while both abiotic and biotic wounding did not alter the orientation of aphids. Electropenetrography revealed that the feeding behaviour of aphids was only slightly disturbed by a previous *L. decemlineata* wounding, while it was highly disturbed by mechanical wounding and MeJA treatment. Aphid nymph survival was reduced on mechanically wounded plants, the pre-reproductive period was lengthened and the fecundity reduced on plants treated with MeJA. Our results bring new information about the effects of various stresses inflicted to *S. tuberosum* on *M. euphorbiae*. We showed that wounding and MeJA treatment induced an antixenosis resistance in potato plants against *M. euphorbiae*, which may influence aphid colonization processes.

Introduction

As sessile organisms, the only way for plants to defend themselves is to develop physical and chemical barriers to counteract herbivore’s attacks. Contrary to vertebrates, and in particular mammals, the plant immune system is not based on circulative cells, but on the ability of each cell to detect an attack and spread systemic signals to non-wounded parts (Jones and Dangl 2006; Howe and Jander 2008) to set-up defence reactions. Changes arising in plants after herbivory are defined as induced responses (Karban and Baldwin 1997). They mainly rely on a shift of the phytohormone balance to redirect metabolism towards the production of defence compounds.

The phytohormone jasmonic acid (JA) is a key-player in the regulation of responses induced by wounding of both abiotic and herbivore origin. Jasmonic acid level increases in plants after herbivory within the first 2 h both locally and systemically (Maffei and Mithöfer 2007). This leads to the expression of defence proteins like proteinase inhibitors (PIs), polyphenol oxidases and lectins, which exert direct effects on phytophagous insects, mainly by reducing the digestibility of plant tissues (reviewed by Howe and Jander 2008).
Phloemophagous insects have piercing-sucking mouthparts and thus cause minimal wounding when feeding on plants (Walling 2008). Contrary to chewing herbivores, aphids (Moran and Thompson 2001; Mewis et al. 2005; de Vos et al. 2005) and whiteflies (Zarate et al. 2007) have been reported to induce the salicylate-dependant plant defence pathway rather than the JA-dependant pathway. Interestingly, aphid populations have lower population growth on plants wounded by Spodoptera exigua Hübner (Noctuidae), which induces the JA-response (Stout et al. 1998), or on mutants with constitutive expression of the JA-response (Ellis et al. 2002). The most convincing evidence of the efficiency of JA-induced response against aphids was given by field experiments conducted by Thaler et al. (2001) who reported a decrease of abundance of Macrosiphum euphorbiae Thomas (Aphididae) on tomato plants in plots treated with methyl jasmonate (MeJA).

As plant immunity rests on few different pathways, the specificity of defence mechanisms activated in response to different threats constitutes an exciting question for plant biologists. Although response to wounding is known to be JA-dependant, biotic and abiotic wounding lead to specific release of volatiles (Turlings et al. 1990), differential production of secondary compounds (McCloud and Baldwin 1997) and distinct patterns of gene expression (Reymond et al. 2000; Lawrence and Novak 2006; Sarosh and Meijer 2007). Plant response arising from an attack affects the inducer, but can also affect other species interacting with the attacked plant. For example, prior feeding on tomato plants by Helicoverpa zea Boddie (Noctuidae) increases plant resistance to S. exigua, but also to the aphid M. euphorbiae and the pathogenic bacterium Pseudomonas syringae van Hall (Pseudomonadaceae) (Stout et al. 1998). In contrast, prior herbivory by root-colonizing insects increases the density and may improve the development of aphids in field and laboratory conditions (Masters 1995).

M. euphorbiae is a highly polyphagous aphid that frequently colonizes potato plants, leading to important economic losses by transmitting phytoviruses (Boiteau et al. 1997). The effects of conspecific and heterospecific aphid pre-infections on the colonization behaviour and performances of M. euphorbiae have been researched by Brunissen et al. (2009). In contrast, we know little about the influence on this aphid species of other stresses applied to potato plants, particularly the effects of wounding and JA-activated defences. The Colorado potato beetle (CPB), Leptinotarsa decemlineata Say (Chrysomelidae), is known to induce direct responses through an increase of defence proteins expression and activity (Green and Ryan 1972; Kruzmane et al. 2002; Lawrence et al. 2008), and indirect responses through the modification of volatile blends attractive for natural enemies (Weisser et al. 1999).

Although coexistence of CPB and M. euphorbiae on a single plant may frequently occur, consequences on aphid populations are poorly documented. Short-duration mechanical and CPB wounding on potato foliage have immediate effects on the probing behaviour of aperous M. euphorbiae (Ameline et al. 2007). Our objective was to evaluate the consequences on the aphid M. euphorbiae of longer, daily-repeated mechanical and CPB wounding of potato plants (Solanum tuberosum L.), and to examine the effects of MeJA treatment on this aphid. For this purpose, the orientation behaviour, the feeding behaviour and the performances of M. euphorbiae on induced plants were studied. Besides information about the consequences of potato response induced by two types of wounding, this study brings new insight into the effects of JA-dependant defence pathway on aphids.

Materials and Methods

Plants and insects

S. tuberosum plants (cv Désirée) were grown from tubers planted in 9 cm plastic pots filled with potting compost in a growth chamber maintained at 20 ± 1°C under a photoperiod of L16:D8 (hereafter laboratory conditions) and regularly watered. Three- to four-weeks-old plants were used for experiments. The M. euphorbiae colony was established in 2004 with individuals of the clone Me LB provided by INRA-INSA Villeurbanne, France, collected in 1995 on egg-plant (Solanum melongena L.) in southern France.

The L. decemlineata colony was established in 2008 from different egg patches provided by the Max Planck Institute for Developmental Biology (Tübingen, Germany) and by the Department of Crop Protection (Ghent, Belgium). Reproduction of adults was stimulated by increasing the temperature of the growth chamber from 20 to 25 ± 1°C for 2 weeks. New egg patches were isolated and freshly hatched larvae were reared on detached potato leaves maintained on gelose medium under laboratory conditions. Aphids and CPB were reared on potato plants in distinct well-ventilated cages under laboratory conditions.
Plant treatments

Three different treatments were applied to potato plants to investigate their effects on *M. euphorbiae*. For the first treatment, three CPB larvae (L2 or L3) were allowed to feed on the third fully expanded leaf from the apex. Beetles were kept on plants for 1–2 h per day for the 4 days of treatment, so that 25–50% of the foliage was consumed. For the second treatment, abiotic lesions were performed by perforating the third leaves of potato plants with a metallic punch (three to five 0.5-cm-diameter perforations per day, for the 4 days of treatment without damaging the central vein. The plants of the third treatment were treated with MeJA by placing plants for 4 days in transparent and sealed containers (80 × 60 × 35 cm, six plants per container) in which three filters each soaked with 20 μl of MeJA (SAFC, St. Louis, MO) were suspended without any contact with plants. All plant treatments were performed under laboratory conditions. Non-damaged plants were used as control for CPB and mechanical wounding experiments. For MeJA treatment series, control plants were placed for 4 days in transparent sealed containers without MeJA.

Aphid standardization

Because of the high variability in their responsiveness, winged aphids were standardized using a setup designed to stimulate aphid flight (Brunissen et al. 2009). Briefly, winged aphids collected from the ceiling of the rearing cage were placed under a transparent ventilated box in a 2-cm-diameter receptacle surrounded by water to force aphids to leave the receptacle by flying. Two yellow paper leaves placed opposite on the outer surface of the box stimulated aphid flight. Sixty to 90 min later, only aphids present on the inner side of the box after a short flight, i.e. assumed to be searching for a host plant, were used for the experiments.

Biochemical assay

MeJA is known to induce de novo synthesis of proteinase inhibitors (Farmer and Ryan 1990). To ensure that MeJA treatment induced a response in potato plants we measured the inhibition of the degradation of azocasein (Sigma-Aldrich, St. Louis, MO) by trypsin. One gram of fresh matter was collected from the fourth leaf under the apex of treated and control plants, frozen and ground, in 0.5 M HCl buffer (pH 8.0) with 10 mg of polyvinylpolypyrrolidone. The extract was centrifugated and 0, 25, 50 and 100 μl of the supernatant were added up to a final volume of 400 μl with 0.046 M Tris–HCl (pH 8.0) containing 0.0115 M CaCl₂, and 100 μl of 1 mM HCl containing 0.1 μg/μl of trypsin. After 3 min of incubation at 30°C, 500 μl of a 0.2% azocasein solution was added and the mixture was incubated 90 min at 30°C. One millilitre of 10% trichloroacetic acid was added to the mixture, and allowed to incubate for 30 min at 4°C before centrifugation. The decrease of the absorbance of the supernatant was measured at 340 nm. For each measure point, a blank was run without plant extract, and the inhibition of the trypsin activity was calculated relative to the blank. The protein concentration of extracts was measured using the method of Bradford (1976).

Olfactometry study

To study the attractiveness of treated plants to winged *M. euphorbiae*, we used a dual-choice olfactometer described by Ameline et al. (2007). Briefly, the apparatus consisted of one cylinder (14 cm in diameter × 5 cm high) divided into two equal chambers where two non-excised fourth leaves of plants were each introduced via two opposite holes. The floor of the apparatus was made of a double polyethylene screen (holes = 0.09 mm²). For each replicate 30 standardized winged aphids were placed into a Petri dish under the double polyethylene screen. The experiments were carried out for 1 h in the dark, under laboratory conditions. Because of their negative geotaxis most aphids climbed to the screen. Aphids’ preference was measured by recording their position beneath each chamber. Aphids on the bottom of the Petri dish were considered as non-responding. An empty chamber was used as negative control. To avoid any bias the olfactometer was rotated by 180° and cleaned with the TFD4 detergent (Franklab S.A., St-Quentin-en-Yvelines, France) between each replication. Ten to 12 replications were performed for each experiment (a given pair of treatments). For each experiment, the distribution of responding aphids was analysed using a Wilcoxon test (Z) for paired samples. We used a Kruskal–Wallis test (H) to compare the percentages of non-responding aphids between experiments.

Electropenetrography study

Electropenetrography (EPG) (Tjallingii 1988) was used to study the feeding behaviour of standardized winged *M. euphorbiae*. Briefly (for details, see
Wounding MeJA treatment

<table>
<thead>
<tr>
<th>EPG classes and related parameters</th>
<th>Wounding</th>
<th>MeJA treatment</th>
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<tbody>
<tr>
<td></td>
<td>Control</td>
<td>Mechanical wounding</td>
</tr>
<tr>
<td></td>
<td>n = 31</td>
<td>n = 22</td>
</tr>
<tr>
<td>1. Pathway phase</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number</td>
<td>19.6 ± 2.3</td>
<td>20.3 ± 12.2</td>
</tr>
<tr>
<td>Total duration (min)</td>
<td>154.4 ± 13.1</td>
<td>204.6 ± 17.6*</td>
</tr>
<tr>
<td>Mean duration (min)</td>
<td>9.5 ± 0.8</td>
<td>12.3 ± 1.3</td>
</tr>
<tr>
<td>2. Salivation phase in phloem</td>
<td></td>
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<tr>
<td>Number</td>
<td>5.9 ± 0.8</td>
<td>6.2 ± 0.8</td>
</tr>
<tr>
<td>Total duration (min)</td>
<td>19.3 ± 3.5</td>
<td>23.6 ± 5.9</td>
</tr>
<tr>
<td>Mean duration (min)</td>
<td>19.3 ± 3.5</td>
<td>23.6 ± 5.9</td>
</tr>
<tr>
<td>3. Phloem ingestion phase</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number</td>
<td>2.9 ± 0.4</td>
<td>3.0 ± 0.4</td>
</tr>
<tr>
<td>Total duration (min)</td>
<td>159.5 ± 20.5</td>
<td>109.6 ± 25.0</td>
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<tr>
<td>Mean duration (min)</td>
<td>101.6 ± 21.5</td>
<td>49.8 ± 16.2*</td>
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<tr>
<td>4. Sustained phloem ingestion phase</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number</td>
<td>1.6 ± 0.2</td>
<td>1.0 ± 0.2*</td>
</tr>
<tr>
<td>Total duration (min)</td>
<td>155.8 ± 20.8</td>
<td>103.9 ± 25.2*</td>
</tr>
<tr>
<td>Mean duration (min)</td>
<td>113.0 ± 20.5</td>
<td>81.9 ± 23.1</td>
</tr>
<tr>
<td>5. Other parameters</td>
<td></td>
<td></td>
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<tr>
<td>Total duration of stylet derailment periods (min)</td>
<td>1.5 ± 1.2</td>
<td>2.6 ± 2.2</td>
</tr>
<tr>
<td>Total duration of xylem ingestion periods (min)</td>
<td>38.5 ± 5.1</td>
<td>55.3 ± 11.4</td>
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<tr>
<td>6. Indexes</td>
<td></td>
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<tr>
<td>Phloem index (%)</td>
<td>52.1 ± 6.1</td>
<td>41.2 ± 10.7</td>
</tr>
<tr>
<td>Salivation index (%)</td>
<td>10.1 ± 2.8</td>
<td>25.3 ± 5.6*</td>
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n, number of aphids per experimental situation. Means ± SE within a row followed by an asterisk are significantly different from control (Mann-Whitney U-test: P < 0.05).
clipped on the abaxial face of the fourth leaf of control or treated plants. Biological parameters were daily evaluated until 48 h after the moult into adults. Nymph survival was analysed with a Pearson’s chi-squared test. Effects on duration of the pre-reproductive period (period of time from birth to the onset of reproduction) and the fecundity of young adults for 48 h were analysed using a Student’s t-test to detect significant differences with controls. All statistical analyses were performed using STATISTICA 5.5 software (StatSoft, Tulsa, OK).

Results

Biochemical assay

The relative trypsic activity was decreased to ca. 40% after the MeJA treatment, which reflects the systemic increase of proteinase inhibitor activity after treatment (fig. 1). In contrast, mechanical and CPB wounding had no effect on systemic proteinase inhibitor activities.

Olfactometry study

The percentage of non-responding aphids was not statistically different between treatments ($H = 11.51; P = 0.0739$, data not shown). Following either mechanical or CPB wounding, $M. euphorbiae$ was significantly more attracted by the odour of the potato plant rather the empty chamber (mechanical wounding: $Z = 2.13, P = 0.033$; CPB wounding: $Z = 2.70, P = 0.007$; fig. 2). Aphids did not prefer control plants over wounded plants (abiotic wounding: $Z = 1.64, P = 0.100$; CPB wounding: $Z = 0.95, P = 0.343$). $M. euphorbiae$ preferred control plants instead of MeJA-treated plants ($Z = 2.31, P = 0.021$), but did not exhibit preference between a MeJA-treated plant and an empty chamber ($Z = 0.25, P = 0.799$).

Electropenetrography study

On plants mechanically wounded, the total duration of pathway phases was significantly increased ($U = 219, P = 0.028$; table 1). Neither time allocated to ingestion nor the number of ingestion periods was modified on those mechanically wounded plants, while the mean duration of the ingestion was significantly shorter than that of aphids feeding on control plants ($U = 224, P = 0.035$). The number and the total duration of sustained ingestion periods were both significantly reduced by mechanical wounding (respectively $U = 211.5, P = 0.019$ and $U = 232, P = 0.049$). After 8 h of monitoring, fewer aphids exhibited a sustained phloem ingestion period on wounded plants ($\chi^2 = 77.21$, d.f. = 7, $P = 0.0154$;...
fig. 3A). Although none of the parameters related to salivation phases in the phloem were modified, the salivation index on wounded plants was significantly increased ($U = 209, P = 0.018$).

On CPB-wounded plants, the mean duration of ingestion phases was significantly reduced ($U = 187, P = 0.036$) as well as the proportion of aphids exhibiting sustained phloem ingestion periods after 8 h of monitoring ($\chi^2 = 36.32, d.f. = 7, P < 0.001$; fig. 3A).

On MeJA-treated plants, the number of salivation phases significantly decreased ($P = 0.016$). The number and the total duration of ingestion phases ($U = 118.5, P = 0.004$ and $U = 149, P = 0.029$, respectively) were significantly decreased on treated plants. The number and the total duration of sustained ingestion phases were significantly shortened on those treated plants ($U = 112.5, P = 0.002$ and $U = 147, P = 0.025$, respectively). Furthermore, a lower percentage of aphids exhibited sustained ingestion during the 8 h recording time on treated plants ($\chi^2 = 68.60, d.f. = 7, P < 0.001$; fig. 3A) until the end of the experiment (8 h).

Demographic parameters study

Nymph survival of *M. euphorbiae* was significantly reduced on mechanically wounded plants ($\chi^2 = 75.5, d.f. = 13, P < 0.001$; fig. 4A). Pre-reproductive period duration and young adults fecundity were not modified (table 2). Plant infestation by CPB larvae had no consequence on nymph survival and development time, nor on fecundity (fig. 4A). On MeJA-treated plants, nymph survival was not altered (fig. 4B) while pre-reproductive period was significantly increased and fecundity reduced (respectively $t = 3.52, P < 0.001$ and $t = 3.01, P = 0.004$; table 2).

Discussion

Responses induced by MeJA in potato plants inhibited plant attractiveness for *M. euphorbiae* and strongly disturbed its feeding behaviour and performances. Both biotic and abiotic wounding had less consequence on *M. euphorbiae* than direct MeJA treatment.

Olfaction is an important process in plant colonization behaviour whereby aphids could locate their host plant (Pickett et al. 1992; Powell and Hardie 2001). Plants emit a large variety of volatile compounds with diverse functions, among which defence via the release of particular volatiles from plants after damage seems to be a general phenomenon (Dudareva et al. 2004). Herbivore-induced volatiles are known to act as indirect defence by attracting herbivore natural enemies (Turlings et al. 1990). In turn, herbivores can use these volatiles to get information about plant status and find the most suitable host to feed and reproduce. For example, we previously showed that aphids were more attracted by non-infested plants rather than plants infested by conspecifics, suggesting possible mechanisms to avoid competition (Brunissen et al. 2009).

Preference of aphids for healthy plants rather than mechanically or herbivore wounded ones is apparently a general phenomenon (Nottingham et al. 1991; Hardie et al. 1994; Bernasconi et al. 1998). In our case, we did not detect any altered attractiveness of wounded plants. Nonanal, the major green leaf
volatile released by potato following CPB wounding (Gosset et al. 2009), has been shown to attract the aphid *Rhopalosiphum padi* L. (Quiroz and Niemeyer 1998). This observation is consistent with our results, i.e. that mechanical or CPB wounding did not alter aphid performances. In contrast, we noticed a significant loss of attractiveness towards MeJA-treated plants, which is in accordance with the decreased performances and altered feeding behaviour of aphids we observed on these plants.

Numerous plant families respond to biotic and abiotic wounding by overexpressing defensive proteins, including PIs which synthesis and accumulation are directly related to the activation of the JA-dependant pathway (Ryan 1990). As expected, our MeJA treatment led to a high induction of PIs expression in potato leaves. Conversely, both mechanical and CPB wounding failed to induce a detectable systemic increase of the relative PI activity. A higher accumulation of PIs has been reported in MeJA-treated tomatoes and passion fruits than in herbivory and mechanically wounded plants, possibly because MeJA is a potent inducer of defence genes (Díez-Díaz et al. 2004; Botelho-Junior et al. 2008).

Some parameters of the behaviour and the development of *M. euphorbiae* were disturbed by wounding, either of mechanical or CPB nature. In particular, aphids had more difficulty to establish sustained ingestion phases on mechanically wounded plants, and ingestion periods were more often interrupted by salivation periods (salivation index increased). Salivation is often regarded as a mechanism that inhibits the normal reaction of sieve tube occlusion in response to wounding (Will and van Bel 2006). Several authors pointed out that longer salivation periods are hints of plant resistance (Caillaud et al. 1995; Chen et al. 1997; Klingler et al. 1998). Moreover, callose deposits occur into phloem tissues of distant potato leaves in response to mechanical wounding (Samaha, personal communication). We therefore suggest that mechanical wounding leads to an impairment to initiate long ingestion periods, explaining the reduction of nymph survival only observed on wounded plants. Different effects observed following CPB wounding can be explained by oral secretion deposits on damaged plant tissues, as compounds from these fluids can counteract plant defence (Musser et al. 2002). The weak potato response induced by CPB larvae feeding we observed is in accordance with Kruzmane et al. (2002) who showed that wounded potato plants responded far less to application of CPB oral secretions than non-host bean plants, underlying possible adaptive reaction on the host plant.

Our results showed that treatments with MeJA strongly disturbed both behaviour and performances of *M. euphorbiae*. As no direct toxic nor deterrent effects of JA have been found in aphids (Thaler et al. 2001; Zhu-Salzman et al. 2004), the resistance against *M. euphorbiae* provided by MeJA treatment suggests that JA-dependant mechanisms of resistance are effective against aphids. Laboratory studies have described JA-induced effects on development (Cooper and Goggin 2005; Gao et al. 2007), population’s growth (Ellis et al. 2002; Cooper et al. 2004) and preferences (Zhu-Salzman et al. 2004) of several aphid species, for several plant species. Moreover, in field conditions, a decrease of natural abundance of tomato colonizing insects, in particular aphids, has been reported after JA treatments on tomato plants (Thaler et al. 2001). Interestingly, there is growing evidence that phloem feeders could prevent the activation of JA-dependant defences, obviously effective against these insects, but conversely could induce less efficient salicylate-dependant defences (Walling 2008). Although exact mechanisms of MeJA-induced resistance against aphids still remain unclear, our study brings new information about the consequences of JA-induced defences on aphids. In addition to impairment of development and fecundity,

### Table 2 Effects of treatments on the pre-reproductive period duration (PRP) and the fecundity of young *Macrosiphum euphorbiae* adults reared on control plants, mechanically wounded plants, plants infested by CPB larvae and MeJA-treated plants

<table>
<thead>
<tr>
<th>Demographic parameters</th>
<th>Wounding</th>
<th>MeJA treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td>PRP duration (days)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>n = 28</td>
<td>Control</td>
</tr>
<tr>
<td>Mechanical wounding</td>
<td>n = 22</td>
<td>MeJA treatment</td>
</tr>
<tr>
<td>CPB wounding</td>
<td>n = 26</td>
<td></td>
</tr>
<tr>
<td>Young adult fecundity</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(nymphs/female/48 h)</td>
<td>10.36 (±0.18)</td>
<td>10.44 (±0.20)</td>
</tr>
<tr>
<td></td>
<td>10.45 (±0.21)</td>
<td>11.53 (±0.25)*</td>
</tr>
<tr>
<td></td>
<td>10.92 (±0.25)*</td>
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</table>

n, number of aphids per experimental situation. Means ± SE within a row followed by an asterisk are significantly different from control plants (Student’s t-test: P < 0.05).
aphids also exhibit clear alterations of their feeding behaviour, mainly detectable by a significant reduction of phloem ingestion. This reduction could be the consequence of deterrent components driven by the phloem or because of troubles to initiate long ingestion periods. For example, exposition of wheat to MeJA deters *Rhopalosiphum padi*, which has been correlated with the increase of hydroxamic acid content (Slesak et al. 2001). Though efficiency of PIs on the digestive processes of aphids is still debated because of apparent contradictory effects (Rahbé et al. 1995; Casaretto and Corcuera 1998), the systemic increase of PIs activity in MeJA-treated plants could partly explain the reduced ingestion rate of aphids and/or their lower performances. Cooper and Goggin (2005) did not observe any reduction of the honeydew excretion of *M. euphorbiae* on tomatoes treated with JA. They stated that JA did not induce deterrent effects on aphids and that observed resistance was due to antibiotic factors (antinutritive and/or toxic compounds). Our results showed that MeJA-induced resistance disturbed the feeding behaviour of aphids, resulting in an impairment of phloem sap ingestion. Such a behavioural alteration is characteristic of antixenosis resistance, likely because of repellent or deterrent compounds in the phloem sap. Though we cannot exclude that MeJA induces antibiotic resistance against aphids, our results suggest that MeJA induces an antixenosis resistance where the reduction of the phloem sap ingestion may account for the lower performances of aphids. In field conditions where potato plants are subjected to heavier stress and aphids are free to move from one plant to another to find the most suitable host plant, it could be hypothesized that this antixenosis, observed in laboratory conditions, might affect aphid colonization processes into potato fields.

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**References**


Slesak E, Slesak M, Gabrys B, 2001. Effect of methyl jasmonate on hydroxamic acid content, protease activ-