Characterization of *Solanum chomatophilum* resistance to 2 aphid potato pests, *Macrosiphum euphorbiae* (Thomas) and *Myzus persicae* (Sulzer)

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**Abstract**

The aphids *Macrosiphum euphorbiae* (Thomas) and *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) are responsible for yield reduction in potato (*Solanum tuberosum*) production by direct phloem feeding and by spreading viruses. Breeding resistant traits from *Solanum chomatophilum* into the potato germplasm provides alternative means to control aphid infestations. Integrated pest management strategy, using plant resistance, benefits from the characterization of the resistance and of its impact on aphid biology. Our objective was to characterize the resistance of *S. chomatophilum* by assessing the effects of accessions, plant parts on aphid performance, and by assessing the impact of the resistance factors on different aphid developmental stages and on alate morph production. Detailed aphid performance was obtained by measuring fecundity, survival, percentage of nymphs that reached adult moults, and population growth using whole plant and clip cage experimental designs. Accession and plant physiological age, but not aphid developmental stage, influenced all life-history parameters, except for alate morph production which was not induced on the resistant accessions. Plant part influence was independent of plant species and accession. Both experimental designs resulted in congruent resistance levels at the accession level for each of the two aphid species, supporting the use of any of them in *S. chomatophilum* resistance screening. PI243340 was resistant to both aphid species, while PI365324 and PI310990 were also resistant to *M. euphorbiae* and *M. persicae*, respectively.

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1. Introduction

*Macrosiphum euphorbiae* (Thomas) and *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) are major pests of the cultivated potato, *Solanum tuberosum* (Radcliffe, 1982; Blackman and Eastop, 1994). Both aphid species can be responsible for important yield loss by consuming phloem sap (Radcliffe, 1982) and through the spread of potato viruses (Radcliffe and Ragsdale, 2002). Aphid infestations are commonly controlled by insecticide applications but the rise of environmental concerns (Devine and Furlong, 2007) and the risk of evolution of insecticide resistance (Foster et al., 1998; Anstead et al., 2005) have led to the search for alternative strategies to control aphid populations. The breeding of resistant potato plants, which would negatively affect the performance of aphids, is one method that can achieve this goal (Smith and Quisenberry, 1994; Flanders et al., 1999). The cumulative effects of plant resistance and natural enemies can maintain aphid damages below an economic threshold (Dreyer and Campbell, 1987; Panda and Khush, 1995; Figueira and Fernando, 2004; Davis et al., 2007; Shannag and Obeidat, 2008).

Among the wide diversity of wild tuber-bearing *Solanum* species, some possess resistance to aphids and can hybridize with *S. tuberosum* (Spooner and Bamberg, 1994). *Solanum chomatophilum* has been identified as a genetic source of resistance to aphids for breeding programs (Radcliffe et al., 1981; Flanders et al., 1992; Flanders et al., 1997; Le Roux et al., 2007). *M. euphorbiae* and *M. persicae* display a lower fitness on *S. chomatophilum*, as estimated by aphid population counts and intrinsic rate of increase, compared to *S. tuberosum* (Radcliffe et al., 1981; Le Roux et al., 2007). However, variation in aphid resistance levels among different accessions of the same wild *Solanum* species has been observed (Radcliffe et al., 1981; Flanders et al., 1992), and thus resistance assessments should be conducted at the accession level. Furthermore, plant part influences aphid biological performance and thus should be considered when evaluating resistance level (Duncan and Couture, 1956; Guldemond et al., 1998; Le Roux et al., 2008). Determining the impact of plant resistance factors on aphid biology is important to predict the efficiency of the resistance factors in a pest management context. Resistance factors may have dissimilar effects on different insect

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developmental stages, as reported for Colorado potato beetle on wild *Solanum* species (Pelletier et al., 1999). Colonization of less suitable crop plants might induce the production of alate (winged) morphs in aphids (Gibson, 1971; Muller et al., 2001), which is not desirable because alate morphs can rapidly spread potato viruses (Blackman and Eastop, 1994).

Different methods have been used to assess aphid resistance. Some studies were conducted on excised leaves (Sams et al., 1975), others used clip cages to restrict aphids to certain parts of the plant in a controlled environment (Le Roux et al., 2004, 2007; Davis et al., 2007) and others were conducted in the field (Radcliffe et al., 1981; Flanders et al., 1992; Davis et al., 2007). Cutting a leaf triggers many physiological changes that can affect resistance (van Emden and Bashford, 1976). The clip cage method can impair leaf photosynthesis (Crafts-Brandner and Chu, 1999) and also results in a resistance value that is only valid for that part of the plant (Guldemond et al., 1998). However, the clip cage method has the advantage of enabling the measurement of parameters related to a single aphid, such as fecundity and survival, on a specific part of the plant, which may help to reveal the location of resistance factors. Field evaluations attempt to simulate agricultural conditions and include the effects of abiotic factors, natural enemies, and plant resistance. However, field trials are costly and time-consuming, making them unrealistic tools for high throughput screening. The resistance level may also be biased by variation of uncontrolled factors, as indicated by inconsistent results among different years (Davis et al., 2007). Timed sampling procedure, based on the number of aphids an observer counts in a given time (Radcliffe and Lauer, 1966), reduces the cost and the time associated with field studies, but neither assess the variation of resistance level within the plant nor the impacts of plant resistance on aphid biology. Finally, we favoured two methods in a controlled environment: clip cage and a protocol assessing the population growth on entire plants. This last method alleviates the drawbacks of clip cages by being less stressful to the plants and by assessing aphid preference within plants as well.

Our objective was to characterize the resistance levels of seven accessions of *S. chomatophilum* to *M. euphorbiae* and *M. persicae*. Survival and fecundity starting with 1st instar nymphs and alate adult aphids on differently aged leaves were measured with clip cages. Aphid population growth and the proportion of adult aphids that were alate were measured on entire plants while taking into account the impact of the physiological age of the plant part on which they were feeding. *S. tuberosum* (var. Shepody) served as a susceptible control in all experiments.

2. Materials and methods

2.1. Insects and plants

*S. chomatophilum* accessions (PI243340, PI243341, PI266387, PI310943, PI310990, PI365324 and PI365327), selected for their potential resistance against aphids (Radcliffe et al., 1981), were first grown from true seeds obtained from the USDA (US Potato GeneBank, Sturgeon Bay, WI, USA) and then two to three plants from each accession were propagated vegetatively by cuttings. *S. tuberosum* plants (var. Shepody, which possesses a mild resistance level to *M. euphorbiae* and *M. persicae* comparatively to other potato varieties [Davis et al., 2007]) were grown from tubers. Tuber seeds were Elite II quality (McCain Produce Inc., Florenceville, NB, Canada), meaning that less than 0.1% of tubers were infected by viruses. *M. persicae* and *M. euphorbiae* colonies were started from virginoparous aphids collected on the potato fields surrounding the Potato Research Centre (Fredericton, NB, Canada) during the summer of 2000. Aphids were subsequently reared on potted *S. tuberosum* (var. Shepody) plants placed in cages (wood frame: 1 m high, 50 cm deep and wide, all sides and ceiling screened), allowing alate aphids to engage in flight. Young alate aphids, used in the experiments, were standardized by removing all alate aphids from the ceiling and walls of the wooden cage, and collecting the alate aphids present on the ceiling of the same cage 14 h later. It was assumed that alate aphids fly from the plant less than 24 h after the final ecdysis and do not take off once settled on a suitable plant (Robert, 1988). Alate morph production in the wooden cage was induced by crowding (Muller et al., 2001). Collected alate aphids were, thus, approximately one-day old. One day-old nymphs were selected following daily observations of alate aphids individually maintained with a clip cage on *S. tuberosum* leaves. All aphid manipulations were realized with a soft-bristled paint brush. The conditions for growing plants, maintaining the aphid colonies, as well as for all the experiments were 16 h:8 h (light: dark), 24 °C: 20 °C (day: night) at 50% relative humidity.

2.2. Whole plant experiment

For each aphid species, a single large 6 to 8 week-old plant (minimum height of 45 cm, flowering with senescing leaves on the basal half of the main stem) of each *S. chomatophilum* accession or *S. tuberosum* was enclosed in a wood frame cage (as above). Ten young alate adult aphids (obtained as explained above) were released in the test cage by placing the 20 gram plastic vial (Fisher scientific, Ottawa, ON) containing them on the soil of the potted plant. Twelve days later, the plant was divided in 2 parts with respect to physiological age and each part was sampled separately. The top (i.e., young) part, which included all plant parts on the distal half of main and secondary stems (distal and basal halves were separated with respect to the length of the stems), contained part of the mature leaves and all the young leaves and reproductive buds. Secondary stems that were shorter than half the length of the main stem contained only young foliage and were assigned to the top part of the plant. The bottom (or basal) part of main and secondary stems was assigned to the bottom (i.e., old) part of the plant. The numbers of nymphs and of alate and apterous (wingless) adults were counted in each part of each plant. All accessions were studied simultaneously and the position of the different accessions was randomized within the growth chamber between trials. Four replicates of each plant accession were carried out, except for the accession PI266387 for *M. euphorbiae* and the accessions 266387 and 365327 for *M. persicae* which were replicated 3 times because the plants were not available for one replicate.

2.3. Clip cage experiment

Six large 6–8 week old plants of each *S. chomatophilum* accession (except PI365327, which was not available at the time of the experiment) and *S. tuberosum* were used. On each plant, 3 mature leaves (located on the penultimate or last level from the apex, partly senescent) and 3 young leaves (the second or third level) were studied. One young alate or one 1-day old nymph (obtained as explained above) was placed on the abaxial side of each leaf studied (18 replicates per plant accession × leaf age × aphid developmental stage combination) and covered with a clip cage. Survival and fecundity was recorded every 2 days for 14 days for alate aphids and for 20 days for nymphs. The percentage of nymphs that reached the adult moult and the average daily fecundity were calculated for the 3 aphids developing on similar-aged foliage within each plant. Daily fecundity was calculated for aphids still alive at the time of sampling. All plants of all accessions were studied at the same time and were positioned randomly within the growth chamber.
2.4. Statistical analysis

Each aphid species and insect developmental stage (i.e., nymphs versus alate adult aphids in the experiment using clip cages) was analyzed separately. Two-way ANOVAs were carried out for the whole plant experiment to determine the influence of plant accession (7 S. chomatophilum accessions and 1 S. tuberosum) and plant part within the plant (top and bottom parts) on the total number of aphids and on the proportion of alate aphids. Post-hoc Tukey’s test was applied. Missing replicates were considered as missing value in the analysis. The proportions of aphids that were winged among adult aphids, hereafter referred to as the proportions of alate aphids, were subjected to a logarithmic transformation before analysis to homogenize variances according to Cochran’s test (Underwood, 1997). Survival analysis, using the Kaplan–Meier and Cox proportional hazards algorithms, is usually applied to survival times grouped according to treatment and has become a standard data analysis method in medical research (Ma and Bechinski, 2008). Survival analysis represents the most appropriate statistical method available to handle time-to-event data, especially when the sample observation is not complete, or so-called censored (Ma and Bechinski, 2008). The event, insect death in our case, may not occur or the individual may be lost before the end of the experiment. The Cox method is a semi-parametric procedure analogous to multiple regression, does not assume any particular distribution of the data, and assume the treatment has a multiplicative effect. Plant resistance has a multiplicative effect on insect survival, as resistance effect can increase with time. The Cox proportional hazards survival

Fig. 1. Total number (±SEM) of Macrosiphum euphorbiae on Solanum tuberosum (thr) and on Solanum chomatophilum accessions (PI243340, PI243341, PI266387, PI310943, PI310990 and PI365324) 12 days after 10 young alates were placed on each plant. Bars with the same letter were not significantly different (Tukey’s test; α = 0.05).

Fig. 2. Total number (± SEM) of M. persicae on S. tuberosum (thr) and on S.chomatophilum accessions (PI243340, PI243341, PI266387, PI310943, PI310990 and PI365324) 12 days after 10 young alates were placed on each plant. Bars with the same letter were not significantly different (Tukey’s test; α = 0.05).
analysis was used to assess the effect of the categorical variables accession and leaf age on aphid survival. The significance of two-way interactions was tested using likelihood ratio tests (Lawless, 2003). The Kaplan–Meier estimator, which uses algorithms taking into account censored data, was used to produce estimates of survival. Two-way ANOVAs, followed by multiple Tukey’s tests, were used to evaluate the effects of accession and leaf age on the percentage of nymphs that reached the adult moult and on average fecundity. Statistical analyses were computed with Systat 11.0 (Systat Software Inc., California, USA), and the package “Design” in R software (http://r-project.org) was used for the survival analysis.

3. Results

3.1. Whole plant experiment

Accession explained a significant proportion of the variation in the total number of *M. euphorbiae* \( F = 4.19; \text{d.f.} = 7, 46; P < 0.001 \) and *M. persicae* \( F = 6.57; \text{d.f.} = 7, 42; P < 0.001 \) found 12 days following the placement of 10 young alates into the cages. *Macrosiphum euphorbiae* populations were significantly smaller on accessions PI243340 and PI365324 than on the control, *S. tuberosum* (Fig. 1). *M. persicae* populations were significantly smaller on accessions PI243340 and PI310990 than on *S. tuberosum* (Fig. 2). *M. euphorbiae* \( F = 150.39; \text{d.f.} = 1, 46; P < 0.001 \), but not *M. persicae* \( F = 0.02; \text{d.f.} = 1, 42; P = 0.90 \), was more abundant on the top part of the plants. The interaction between accession and plant part did not influence the abundance of *M. euphorbiae* \( F = 0.28; \text{d.f.} = 7, 46; P = 0.77 \) or *M. persicae* \( F = 0.95; \text{d.f.} = 7, 42; P = 0.47 \).

Neither accession, plant part nor their interaction influenced the proportion of alate aphids for *M. euphorbiae* \( F = 1.39; \text{d.f.} = 7, 46; P = 0.23 \), leaf part: \( F = 0.41; \text{d.f.} = 1, 46; P = 0.52 \), accession x plant part: \( F = 0.64; \text{d.f.} = 7, 46; P = 0.72 \), and for *M. persicae* (accession: \( F = 1.33; \text{d.f.} = 7, 42; P = 0.26 \), plant part: \( F = 0.008; \text{d.f.} = 1, 42; P = 0.93 \), accession x plant part: \( F = 0.60; \text{d.f.} = 7, 42; P = 0.75 \) (Fig. 3).

3.2. Clip cage experiment

Accession significantly influenced the survival of both *M. euphorbiae* nymphs and alates, but leaf age and its interaction with accession did not (Table 1). Consequently, results from old and young
leaves are pooled in Fig. 3. For both nymphs and alates, the lowest
*M. euphorbiae* survival was observed on accessions PI243340 and
PI365324 (Fig. 4). For the experiment started with 1st instar nymphs,
average daily fecundity, calculated from aphids still alive at the time
of sampling, was influenced by accession (*F* = 62.36; d.f. = 6, 238;
*P* < 0.001), but not by leaf age (*F* = 0.94; d.f. = 1, 238; *P* = 0.33) or
its interaction with accession (*F* = 0.64; d.f. = 6, 238; *P* = 0.69).
For the experiment started with young alates, average daily fecundity
was also influenced by accession (*F* = 13.39; d.f. = 6, 238; *P* < 0.001),
and not by leaf age (*F* = 2.96; d.f. = 1, 238; *P* = 0.087) or its interaction
with accession (*F* = 1.89; d.f. = 6, 238; *P* = 0.082). Average daily
fecundity of both nymphs and alates was the lowest on PI243340 and
PI365324 (Table 2). The percentage of nymphs that reached the adult
moult was significantly influenced by accession (*F* = 50.08; d.f. = 6, 70;
*P* < 0.001), but not by leaf age (*F* = 0.38; d.f. = 1, 70; *P* = 0.53) or
its interaction with accession (*F* = 0.62; d.f. = 6, 70; *P* = 0.71) and was
significantly lower on PI243340 and PI365324 than on *S. tuberosum*
(Table 2).

The survival of nymphs and alates of *M. persicae* were signifi-
cantly influenced by both accession and leaf age (Table 1). *M. per-
sicae* survival was higher on old leaves than on young ones (Fig. 5).
Regardless of leaf age, nymph and alate survivals were the lowest
on PI243340, PI266387, PI310943 and PI310990 accessions (Fig. 5).
The lowest alate survival was observed on old leaves of PI310990
and on young leaves of PI310943, and alate survival on PI243341
was low on young but not on old leaves (Fig. 5), resulting in a
significant interaction between accession and leaf age (Table 1).
For the experiment started with 1st instar nymphs, average daily
fecundity was influenced by accession (*F* = 28.88; d.f. = 6, 238;
*P* < 0.001), but not by leaf age (*F* = 2.34; d.f. = 1, 238; *P* = 0.12) or
its interaction with accession (*F* = 1.73; d.f. = 6, 238; *P* = 0.11). For
the experiment started with young alates, average daily fecundity
was influenced by accession (*F* = 10.04; d.f. = 6, 238; *P* < 0.001) and
its interaction with leaf age (*F* = 4.48; d.f. = 6, 238; *P* < 0.001), but not
by leaf age (*F* = 0.23; d.f. = 1, 238; *P* = 0.62). The interaction was
attributable to a higher fecundity for alates developing on young
versus old leaves of *S. tuberosum*, whereas fecundity was similar
for alates developing on young versus old leaves of accessions of
*S. chomatophilum*. The percentage of nymphs that reached the adult
moult was significantly influenced by accession only (accession:
*F* = 18.20; d.f. = 6, 70; *P* < 0.001; leaf age: *F* = 2.25; d.f. = 1, 70;
*P* = 0.13; accession × leaf age: *F* = 0.52; d.f. = 6, 70; *P* = 0.78).
The percentage of nymphs that reached the adult moult and the average
daily fecundity in the experiments started from nymphs and alates
were significantly lower on PI243340, PI266387, PI310943 and
PI310990 than on *S. tuberosum* (Table 2).

### 4. Discussion

In experiments using two different designs, *S. chomatophilum*
accession and plant part, but not aphid developmental stage,
influenced aphid performance as measured by daily fecundity,
survival, percentage of nymphs that reached the adult moult, and
population growth. Different insect stages may have different
physiological requirements and physical capabilities that can lead
to performance differences between stages on the same resistant
*Solanum* species, as previously reported for the holometabolous
insect, *Leptinotarsa decemlineata* (Pelletier et al., 1999). However,
our results support the hypothesis that hemimetabolous insect
stages have similar physiological and physical characteristics
(Gullan and Cranston, 1994) as the most resistant accessions were
the same for immature and mature stages of each aphid species.
Additionally, the aphid imago is able to produce either alate or
apterous morphs depending on the nutritional quality of the host
plant, natural enemy presence, and crowding (Dixon, 1998; Muller
et al., 2001). An interesting feature of *S. chomatophilum* resistance is
that it does not stimulate alate morph production and thus, does
not promote the spread of viruses through alate morphs (Blackman
and Eastop, 1994).

The effect of plant part on aphid performance was assessed by
two different methods. While the experiment with the whole plant
estimated the combined influence of preference and performance
by allowing aphids to position themselves on the preferred part of
the plant, the clip cage experiment restricted the insects on either
young or old leaves and provided information on the effect of leaf
age on performance. Overall, the intra-plant distribution was
independent from plant species and accessions for both aphid
species. This suggests that the plant characteristics involved in
the intra-plant distribution differ from the ones responsible for
*S. chomatophilum* resistance. The physiological age of different plant
parts can influence the intra-plant distribution of aphids through
the modification of preference and performance (Harrington
and Taylor, 1990; Dixon, 1998; Gould et al., 2007), which rely on many
compounds (Gibson and Plumb, 1977; Dreyer and Campbell, 1987;
Powell et al., 2006). However, sugar and amino acid composition of
the aphid diet have been reported to influence performance and

### Table 1

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Fig. 4. Survival estimated through Kaplan–Meier method of *M. euphorbiae* nymphs (A) and alates (B) placed on both young and old leaves of *S. chomatophilum* accessions (PI243340, PI243341, PI266387, PI310943, PI310990 and PI365324) and of *S. tuberosum* (tbr).
buds (Ashouri et al., 2001) may explain the higher population of young versus old leaves, and higher performance on reproductive organs. Le Roux et al. (2008) observed a high resistance of *M. euphorbiae* obtained on the top part of plants in the whole plant experiment. By contrast, *M. persicae* performed better on older leaves as previously reported (van Emden et al., 1999). Conversely, *M. euphorbiae* performance was similar on young versus old leaves, and higher performance on reproductive buds (Ashouri et al., 2001) may explain the higher population obtained on the top part of plants in the whole plant experiment. By using clip cages, Le Roux et al. (2008) observed a high resistance level to *M. euphorbiae* only on mature leaves when compared to young leaves of *S. chomatophilum* accession PI310943. This discrepancy with the present study could be explained by methodological differences. The old leaves we selected from the bottom of the plant were senescent at the end of the experiment and, thus, were physiologically different from the mature leaves of the previous study.

There was a strong variation in the level of resistance of different *S. chomatophilum* accessions to *M. euphorbiae* and *M. persicae*, as reported for other Solanum species (Flanders et al., 1992). The two aphid species behaved differently with respect to the accessions, as noticed for other Solanum species (Radcliffe et al., 1981). Consequently, the two experimental designs provided similar results at the accession level for each aphid species, respectively, providing support for using either of these methods in a screening of the *S. chomatophilum* resistance. Although fecundity measured with clip cage appears low to account for the aphid population on the whole plant, it corresponds to previous results (Le Roux et al., 2007), and may be caused by clip cage effect on plant physiology (Crafts-Brandner and Chu, 1999).

*Myzus persicae* performance was the lowest on accessions PI243340 and PI310990, but accessions PI266387, PI310943, and PI365324 could also be considered resistant. On PI266387, PI310943, and PI365324 accessions, survival and fecundity was significantly affected, and population growth tended to be reduced compared to *S. tuberosum*. PI243340, PI310990, PI266387, PI310943 and PI365324 have previously been rated as resistant to *M. persicae* (Radcliffe et al., 1981; Le Roux et al., 2007). The similar results among these studies supports the finding that wild Solanum accession resistance is stable over different *M. persicae* populations or biotypes (Radcliffe et al., 1974, 1988).

*S. chomatophilum* PI243340 and PI365324 were the most resistant accessions to *M. euphorbiae*. These results are partly in agreement with previous studies based on field resistance assessments (Radcliffe et al., 1981) and clip cage experiments (Le Roux et al., 2007). Some accessions that were found susceptible in the present study (e.g. PI310943 and PI310990) were previously rated as resistant (Radcliffe et al., 1981; Le Roux et al., 2007). Field trial resistance levels might have resulted from uncontrolled biotic or abiotic factors (Dreyer and Campbell, 1987). In addition, resistance level can vary between aphid biotypes, as different biotypes of *M. euphorbiae* perform differently on tomato plants carrying the Mi gene (Goggin et al., 2001). Variation between plant genotypes (grown from different seeds) of the same accession may also play a role. This genetic variation could explain part of the substantial variance we measured in our whole plant experiment, as well as part of the variance observed in field trials (Radcliffe et al., 1981) in which plants were grown from different seeds.

Our study indicated accessions amenable to use in a potato breeding programme. Variation in the resistance within the plant and between accessions should be taken into account when implementing resistance assessment trials. Moreover, variations in resistance level among accessions collected in different locations could be

### Table 2

<table>
<thead>
<tr>
<th>Plant accessions</th>
<th><em>M. euphorbiae</em></th>
<th><em>M. persicae</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Nymphs</td>
<td>Alate aphids</td>
</tr>
<tr>
<td></td>
<td>Average fecundity (nymphs/female)$^d$</td>
<td>Average fecundity (nymphs/female)$^d$</td>
</tr>
<tr>
<td><em>S. tuberosum</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PI243340</td>
<td>2.8 ± 2.8$^a$</td>
<td>1.0 ± 0.11$^a$</td>
</tr>
<tr>
<td>PI243341</td>
<td>94.4 ± 3.7$^b$</td>
<td>1.02 ± 0.13$^b$</td>
</tr>
<tr>
<td>PI266387</td>
<td>94.4 ± 3.7$^c$</td>
<td>1.02 ± 0.10$^c$</td>
</tr>
<tr>
<td>PI310943</td>
<td>75.2 ± 6.9$^d$</td>
<td>0.27 ± 0.05$^d$</td>
</tr>
<tr>
<td>PI310990</td>
<td>75.2 ± 6.9$^d$</td>
<td>0.27 ± 0.05$^d$</td>
</tr>
<tr>
<td>PI365324</td>
<td>4.2 ± 4.2$^d$</td>
<td>0.00 ± 0.00$^d$</td>
</tr>
</tbody>
</table>

$^a$ Means (± SEM) followed by the same letter are not significantly different from each other, analysis performed per column (Tukey's test; $a = 0.05$).
seen as a consequence of reciprocal co-evolution and serve as a model to study the geographic mosaic of co-evolution (Thompson, 2009). Future works should study the resistance mechanism by using host-plant selection assessment tools such as electric penetration graph (Tjallingii, 1995).

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Duncan, J., Couture, R., 1956. Les pucerons de la pomme de terre dans l’est du Quebec. Comité Nord des producteurs de Plant de Pomme de Terre, Cavendish Farms, and the Matching Investment Initiative program of Agriculture and Agri-Food Canada for supporting this work. Additional support was provided by a NSERC Discovery grant and the University of New Brunswick.

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