Do resistant plants provide an enemy-free space to aphids?

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Abstract. An experiment was conducted to compare the predation efficiency of the coccinellids *Harmonia axyridis* and *Coleomegilla maculata* on potato plants, *Solanum tuberosum*, and on a wild aphid-resistant species, *Solanum tarijense. Harmonia axyridis* females reduced aphid populations more than *C. maculata* females. Aphid predation by the predators was reduced on *S. tarijense* compared to *S. tuberosum. Coleomegilla maculata* spent less time on *S. tarijense* than on *S. tuberosum. Harmonia axyridis* spent the same amount of time on both plant species. The plant species did not affect IGP between larvae. Compared to *S. tuberosum*, the resistant plant offers *M. persicae* an enemy-free space against both coccinellid predators.

INTRODUCTION

The development of resistant plants is a management strategy that has received much attention in recent years (Le Roux et al., 2008a). Plant resistance may be based on chemical or physical characteristics that alter host-plant colonization behavior of the pest (antixenosis) or its demographic parameters (antibiosis) (Le Roux et al., 2007, 2008b). Many wild *Solanum* species are considered for hybridization with the commercial potato *Solanum tuberosum* L., based on their resistance to pests (Flanders et al., 1992; Bamberg et al., 1996) and diseases (Douches et al., 2001; Chen et al., 2003). However, plant resistance may also have an impact on the third trophic level, i.e., the predators and the parasitoids of the pest (Orr & Boethel, 1986; Obrycki, 1986). For example, the foraging abilities of many insect predators are hindered by glandular trichomes (Obrycki & Tauber, 1984; Lucas et al., 2004).

Many species contribute to aphid biocontrol (Obrycki et al., 1983; Karley et al., 2003; Koss & Snyder, 2005), and their exclusion from resistant plants could provide an enemy-free space to aphids adapted to resistant plants. The aim of this study was to evaluate the impact of an aphid-resistant plant on the behavior of two aphid predators. We studied the predation and oviposition behavior of adults of two common coccinellids of potato fields, i.e. the multi-spotted Asian ladybeetle Harmonia axyridis Pallas and the twelve-spotted ladybeetle Coleomegilla maculata lengi Timberlake (Coleoptera: Coccinellidae), on a susceptible commercial potato plant and on an aphid-resistant wild species, Solanum tarijense Hawkes (Alvarez et al., 2006). Solanum tarijense plants have type A glandular trichomes that secrete sticky exudates. In a field study S. tarijense PI 414150 has been shown to be more resistant to M. persicae than other wild Solanum and S. tuberosum (Fréchette et al., 2010). We also compared the residence time of H. axyridis and C. maculata

larvae on *S. tuberosum* and *S. tarijense* plants, as well as the occurrence of intraguild predation (IGP) between larvae as a response to host-plant species. IGP can have an impact on predators dynamics and thus possibly on herbivores populations dynamics.

MATERIAL AND METHODS

Biological material

Harmonia axyridis and C. maculata stock cultures were established from individuals collected in fields of Southwestern Quebec, Canada. Adults and larvae were reared in plastic boxes and fed with an excess of laboratory-reared green peach aphids, Myzus persicae (Sulzer). Plants were grown in a glasshouse from S. tuberosum cv. Désirée tubers and S. tarijense PI 414150 seeds. Insects were reared at 19°C, 16L: 8D.

Predation and oviposition

Plants (\approx 14 cm height) were standardized to have 5–7 fully expanded leaves and were isolated in Plexiglas® cages ($30 \times 30 \times 30$ cm). Twenty aphids (immatures and apterous adults mixed) were gently transferred with a fine hair brush to each plant. Either two *C. maculata* or two *H. axyridis* adult females older than one week were placed in each cage. Coccinellid females were removed from the plants 22 h later, and both cages and plants were thoroughly examined to count coccinellid eggs and the number of aphids remaining on each plant. Each plant was used twice (one time with *C. maculata* and one time with *H. axyridis*), and each coccinellid female was tested twice (one time with *S. tuberosum* and one time with *S. tarijense*). Half of the plants of a given species were randomly assigned to receive *C. maculata* females first, while the other half received *H. axyridis* first. Each combination was replicated 12 times.

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Intraguild predation and residence time

One 4th instar *H. axyridis* larva and one 3rd instar *C. maculata* larva were placed on a different leaf of the same plant. *Harmonia axyridis* larvae older (and thus larger) than *C. maculata* larvae were used in order to maximize IGP probability. Plants (≈ 18 cm height) were standardized to six fully expanded leaves. Five apterous aphids were gently transferred with a fine hair brush onto each plant. Larvae were then observed for 90 min: IGP occurrence, the residence time of larvae on plants, and the way in which the larvae left (falling down or walking away from the plant) were noted. Twelve replications were made on *S. tarijense*, while 11 replications were made on *S. tuberosum*.

Statistical analysis

The numbers of aphids remaining on plants were first compared with an ANOVA with plant sequence as an independent variable. As there was no significant difference (F = 0.00035; d.f. = 1,46; P = 0.985) between plant sequences, the data was further analyzed with a 2-way ANOVA (plant species and coccinellid species). The proportion of cages where coccinellid eggs were found, the proportion of replicates where IGP occurred and the proportion of coccinellid larvae residence times of less than 30 min were compared between *S. tuberosum* and *S. tarijense* with a Likelihood ratio test.

RESULTS

Predation and oviposition

The number of aphids remaining on plants differed significantly between plant species (F = 5.92; d.f. = 1,44; P = 0.019) and between coccinellid species (F = 19.58; d.f. = 1,44; P < 0.0001), with no interaction between factors (F = 0.45; d.f. = 1; P = 0.51). There were significantly more aphids remaining on S. tarijense than on S. tuberosum, and more aphids remaining in the presence of C. maculata adults than in the presence of C. axyridis adults (Fig. 1).

Coleomegilla maculata eggs were observed only in 2 of 24 experimental cages. Harmonia axyridis eggs were found in 16 of 24 experimental cages with statistically similar distributions between S. tuberosum and S. tarijense (Likelihood Ratio; $\chi^2 = 0.76$; d.f. = 1; P = 0.38). All eggs were laid on the walls of the cages.

Intraguild predation and residence time

Coleomegilla maculata larvae remained significantly longer on *S. tuberosum* than on *S. tarijense* (Likelihood ratio; $\chi^2 = 4.02$; d.f. = 1; P = 0.045). All *C. maculata* larvae left *S. tuberosum* plants by crawling, while 66.7% left *S. tarijense* plants by falling down. *Harmonia axyridis* larvae residence time was not affected by plant species (Likelihood ratio; $\chi^2 = 0.38$; d.f. = 1; P = 0.54). All *H. axyridis* larvae that left the plants did so by crawling. IGP occurred only in one replicate of each plant species and, in both cases, *H. axyridis* larvae preyed upon *C. maculata* larvae.

DISCUSSION

The behavior of the two aphid predators was altered on the aphid-resistant *S. tarijense. Coleomegilla maculata* larvae left *S. tarijense* earlier than *S. tuberosum*. Moreover, *C. maculata* and *H. axyridis* adults ate fewer aphids on the aphid-resistant *S. tarijense* than on the susceptible *S. tuberosum*. The possibility that the difference observed could be attributed to a difference in aphid reproduction rate was not evaluated. However, *M. persicae* population growth rate would be expected to be lower on *S. tarijense* (Pelletier et al., 2010).

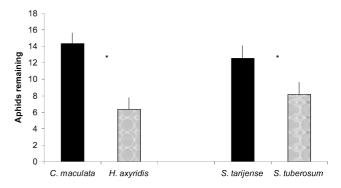


Fig. 1. Mean (\pm S.E.) number of aphids remaining on *Solanum tarijense* and *Solanum tuberosum* plants 22 h following the introduction of either two *Coleomegilla maculata* or two *Harmonia axyridis* adult females. The initial number of aphids on each plant was 20. An asterisk indicates a significant difference (ANOVA, P < 0.05).

Solanum tarijense plants have glandular trichomes (Gibson, 1971) known to hinder the normal behavior of aphids (Alvarez et al., 2006). The adult Colorado potato beetle, Leptinotarsa decemlineata L., also demonstrated an important thanatosis behavior to S. tarijense trichomes (Pelletier & Dutheil, 2006). The fact that a large proportion of C. maculata fell also might be a similar reaction to the chemicals contained in the trichomes. The present study reports for the first time altered behaviour of aphid natural enemies on S. tarijense. Such an effect was previously reported for the glandular-trichome bearing Solanum berthaultii (Hawkes) (Obrycki & Tauber, 1984), now considered as the same species as S. tarijense (Spooner et al., 2007). However, S. berthaultii has both A and B types of glandular trichomes that act together by increasing the amount of exudates sticking to the insects, whereas S. tarijense has only type A glandular trichomes (Horgan et al., 2007). The impact of type A glandular trichomes on H. axyridis and C. maculata behaviour should be further studied.

Assessing the impact of plant resistance on natural enemies is important within the context of integrated pest management. The possibility that aphids or their natural enemies may become adapted to *Solanum* spp. glandular trichomes is unknown, but previous studies have demonstrated that the Colorado potato beetle may adapt to trichome-bearing plant species (Pelletier & Smilowitz, 1991). Should aphid-resistant plants bearing trichomes be used in the field, an enemy-free space would be provided for trichome-adapted aphids until their natural enemies become likewise adapted.

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