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Soybean aphid predators in Québec and the suitability of *Aphis glycines* as prey for three Coccinellidae

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Abstract. Since its invasion of North America in 2000, the soybean aphid, *Aphis glycines* Matsumura (Homoptera: Aphididae) has notably changed the arthropod community of the soybean agroecosystem. The objectives of this study were to characterize the foliar predatory fauna associated with *A. glycines* in commercial soybean fields in Québec, Canada, and to evaluate the suitability of *A. glycines* as prey for three coccinellid species: *Harmonia axyridis* Pallas, *Propylea quatuordecimpunctata* L. and *Coleomegilla maculata lengi* Timberlake (Coleoptera: Coccinellidae). Field surveys showed that several predators responded rapidly to expanding and increasing populations of the soybean aphid. Coccinellidae were the most important aphidophagous predators observed in 2002 (58.6%) and 2003 (44.8%), with mainly four native and naturalized species co-occurring with the soybean aphid throughout the growing season. Measurement of fitness parameters under laboratory conditions (survival, development time, longevity, fecundity) indicated that *A. glycines* is an excellent prey for the development and reproduction of all three of the coccinellid species studied. The intrinsic rate of natural increase (r_m) was highest for *H. axyridis* (0.238 d^{-1}), intermediate for *P. quatuordecimpunctata* (0.215 d^{-1}) and lowest for *C. maculata* (0.134 d^{-1}).

Key words: *Aphis glycines*, biological control, *Coleomegilla maculata*, *Harmonia axyridis*, *Propylea quatuordecimpunctata*, prey suitability

Introduction

Native natural enemies may play a major role in reducing populations of invasive pest species (DeBach and Rosen, 1991). As exotic pest populations increase in abundance and disperse, they can trigger important functional and numerical responses by the native enemy fauna. The observation of such a phenomenon in the 1950's led to the development of the integrated pest control concept (Stern et al., 1959) when native coccinellids responded to the invasion of the spotted alfalfa aphid in California. This concept recognizes the beneficial role native predators and parasitoids may play in biological control of invasive organisms and promotes measures to preserve or enhance their populations.

Surveys of beneficial organisms are needed to document their identity, abundance and potential biological control contributions following the introduction of an exotic pest (Whitcomb, 1981, Van Driesche and Bellows, 1996). Identification of key natural enemies stimulates research on their ecology, management and value as biological control agents (Paine, 1969; Whitcomb, 1981). Studies on the suitability of an exotic species as prey for the native enemy fauna further provide a basis for predicting and interpreting predator-prey interactions in the field.

The soybean aphid, *Aphis glycines* Matsumura (Homoptera: Aphididae), is a multivoltine species native to Asia (Wu et al., 2004). In North America, it was first detected in Michigan in 2000 (DiFonzo and Hines, 2001) and rapidly spread through other parts of the continent (Venette and Ragsdale, 2004). Surveys in Québec, Canada, showed an immediate invasion of all soybean growing areas by the aphid following its first report in 2002 (Mignault et al., unpublished data). How the soybean aphid will ultimately affect the production of soybean in North America remains unknown, but the patterns observed since the invasion suggest that the presence of *A. glycines* is causing profound ecological changes in the agroecosystem (Heimpel et al., 2004).

The first objective of the present study was to characterize the species composition of the foliar predatory fauna associated with *A. glycines* in commercial soybean fields in Québec. Interest in aphidophagous natural enemies in soybean was low prior to the arrival of *A. glycines* because none of the three reported aphid species (*Acyrthosiphon pisum* Harris, *Aphis craccivora* Koch, *Aphis gossypii* Glover) were common or had an economic impact (Blackman and Eastop, 1984). As a consequence, there is a paucity of ecological information available on aphidophagous predators in soybean in Québec. Most were likely transient visitors to this crop as aphid populations were too low to sustain predator development and reproduction (O'Neil and Wiedenmann, 1987).

The second objective was to evaluate the suitability of *A. glycines* as prey for three coccinellid species (Coleoptera: Coccinellidae): the fourteen spotted ladybeetle, *Propylea quatuordecimpunctata* L., the Asian multicolored ladybeetle, *Harmonia axyridis* Pallas, and the pink spotted ladybeetle, *Coleomegilla maculata lengi* Timberlake. These species were selected as they were the most abundant aphid predators observed in soybean fields in Québec in 2002 (this study). Prey suitability was determined by measuring several parameters of predator fitness (survivorship, preimaginal development time, longevity, and fecundity) and by calculating their intrinsic rate of natural increase (r_m). The r_m is a useful demographic parameter to estimate the population growth potential of an organism under given ecological conditions (e.g. temperature or food resource) (Birch, 1948). It influences the outcome of predator–prey interactions (Janssen and Sabelis, 1992) and may be useful in selecting promising biological control agents (Jervis and Copland, 1996; Roy et al., 2003).

Materials and methods

Sampling of foliar predators

An intensive survey was conducted in 2002 and 2003 to determine the distribution and abundance of the soybean aphid in Québec (Mignault et al., unpublished data). A parallel study was undertaken to document the diversity of foliar aphidophagous predators in nine major soybean producing regions: Montérégie-Ouest, Montérégie-Est, Laurentides, Lanaudière, Mauricie, Estrie, Centre-du-Québec, Capitale-Nationale and Chaudière-Appalaches. In this instance, one commercial field per area (N = 9) was sampled every 2 weeks from the beginning of July, when the first soybean aphids were observed in Québec to the end of August (4 sampling dates per year). Foliar predators were sampled by sweep net. In each field, 100 sweeping movements, following a figure of eight, were performed in the upper-canopy level while walking rapidly through the vegetation; the sweeping movements were executed in 10 areas of the field (10 sweeps × 10 zones) along a zigzag transect, with each area separated by 100 paces. Samples were transferred to plastic bags, put in a cooler, and brought back to the laboratory. Aphidophagous predators were then sorted and adults were preserved in 90% ethanol. Subsequently, all specimens were examined under a microscope for identification to species level. Although the efficiency of sweep net sampling may vary considerably for different arthropod groups and is affected by several abiotic factors, this method is adequate to generate a global portrait of the predatory fauna on herbaceous vegetation (Zeiss and Klubertanz, 1994).

Suitability of the soybean aphid as prey for coccinellids

Study organisms

Coccinellid cultures were established from individuals (ca. 50 from each species) collected in St-Stanislas-de-Kostka, (45° 11′00″ N, 74° 07′00″ W) in August 2002. The three coccinellid species were reared in growth chambers at 24 ± 1°C, 50–70% relative humidity, and under a photoperiod 16L:8D. Larvae and adults were fed with a mixed diet of soybean aphids and potato aphids, *Macrosiphum euphorbiae* (Thomas) maintained on seedlings of soybean, *Glycine max* (L.) Merrill, and potato, *Solanum tuberosum* L., respectively. Predators had been in culture for 2–3 generations prior to use in the experiment. All experiments were carried out under the same climatic conditions as described above.

Development

Survivorship and developmental time (egg-to-adult) were determined for each coccinellid species using *A. glycines* as prey. Synchronous cohorts of eggs laid between 10:00 and 12:00 were obtained and incubated at 24°C in Petri dishes. Eggs were examined at 10:00 daily for eclosion, and each newly emerged larva was transferred to a soybean seedling infested with *A. glycines* of various stages. The seedlings were kept in small plastic cages (20 cm × 10 cm × 10 cm) with aeration holes covered with fine mesh. Temperature in cages was monitored at frequent intervals using thermocouples (Omega HN23). Plants were changed every 4 days or earlier to provide prey *ad libitum* to the coccinellids. All predators were examined daily at 10:00 for survival, pupation, and adult emergence. On the day of emergence, adults were collected in Petri dishes and their sex determined by observing the shape of the last abdominal segment: the hind margin of the last segment is straight or slightly convex in females whereas it is clearly or moderately concave in males (Randall et al., 1992). Coccinellid larvae that escaped from the rearing arena, mainly *P. quatuordecimpunctata*, were excluded from the analysis. Fifty larvae of each species were tested. Pearson's χ^2 test was used to determine whether percentage mortality differed among coccinellid species. For developmental period, a factorial analysis was performed with sex and species as independent variables, followed by the Student–Neuman–Keuls multirange test (SNK), when a significant difference was observed. For all experiments, statistical tests were done using SAS version 8.0 with the significance level set at $p = 0.05$ (SAS Institute, 1989–2002).

Reproduction

We measured longevity, oviposition period, and total and age-specific fecundity of coccinellid females when fed on a monotypic diet of *A. glycines*. Following emergence, all females reared from the previous experiment were isolated, returned to rearing cages, and provided with a male from the same treatment for 15 days. Female coccinellids can store sperm in their spermatheca for a long period and one or few matings are generally sufficient to ensure lifetime fertility (Hodek, 1973; Majerus, 1994). Each female was provided with soybean aphids *ad libitum* from day of emergence to death. Eggs were collected daily to determine daily and lifetime fecundity. Differences in longevity, oviposition periods, and lifetime fecundity between species were tested using one-way ANOVA. Following a significant difference, means were compared by the Student-Neuman-Keuls multirange test (SNK).

The secondary sex ratio of the progeny, measured as the proportion of males at emergence, and egg fertility, measured as the proportion of eggs hatching, were determined using sub-samples of eggs from 10 females of each species. For the sex ratio, egg masses of more than 10 eggs were collected at five-day intervals, from the fifth day after the first oviposition to the end of the oviposition period. Each egg mass was placed in a small plastic cup (26.9 ml) with a source of humidity consisting of a 1 cm piece of wet dental cotton. Following hatching, larvae were provided with aphids (*M. euphorbiae* and *A. glycines*), organic pollen grains, and a pea size bit of artificial diet (Natural Insect Control, Stevensville, ON, Canada). Individuals were checked every second day for death, pupation or emergence. Following emergence, adults were sexed. Egg fertility was measured using the remaining egg masses from the same 10 females. Egg masses were kept in plastic cups (26.9 ml) with a source of humidity until eclosion. Sibling cannibalism, a common phenomenon in Coccinellidae (Agarwala and Dixon, 1992), was avoided by removing or killing hatching larvae. As melanization is an indication of the imminent eclosion of coccinellid eggs (Rogers et al., 1972, Michaud and Grant, 2004), eggs were checked regularly when turning to a greenish-grey color. Considering that eggs belonging to the same cluster show a certain synchrony of eclosion (Michaud and Grant, 2004), eggs that did not hatch within the day after the first eclosion were considered sterile. Sex ratio and fertility data were too few to be meaningfully compared statistically among species. However, mean values of the 10 females over their reproductive period were used to calculate the intrinsic rate of population increase (r_m).

Intrinsic rate of population increase (r_m)

The r_m factor was calculated for each coccinellid species by repeated iteration of the simplified Birch formula (Birch, 1948):

$$\sum e^{-r_m x} l_x m_x = 1$$

In the equation, x is female age, l_x is the fraction of females surviving to age x, and m_x is the age-specific fertility that records the number of living females born per female of age x, calculated from the sex ratio and fertility data measured in our experiments.

Results

Predator diversity and abundance

In 2002 and 2003, foliar aphidophagous predators belonging to five main insect families were collected in soybean fields infested with *A. glycines*: Coccinellidae, Anthocoridae, Chrysopidae, Syrphidae and Nabidae. Coccinellidae were the most abundant predators observed in both years (58.6% in 2002, N = 179; 44.8% in 2003, N = 154). A total of seven coccinellid species were identified and the four most common were *Propylea quatuordecimpunctata* (67.6 and 53.6%), *Harmonia axyridis* (13.3 and 20.3%), *Coleomegilla maculata lengi* (14.3% and 7.2%) and *Coccinella septempunctata* L. (3.8 and 13.0%). Numbers in parenthesis represent the relative abundance of each coccinellid species as a percentage of the total number collected in 2002 and 2003, respectively. Few individuals of *Hippodamia variegata* (Goeze), *H. parenthesis* (Say) and *Brachiacanta ursina* (Fabricius) were also collected in soybean fields.

During both years, coccinellids were present in low numbers in early July (Figure 1). From then on population densities did not fluctuate to a great extent across the next two sampling dates. The highest densities were recorded late in the season, with *P. quatuordecimpunctata*, the

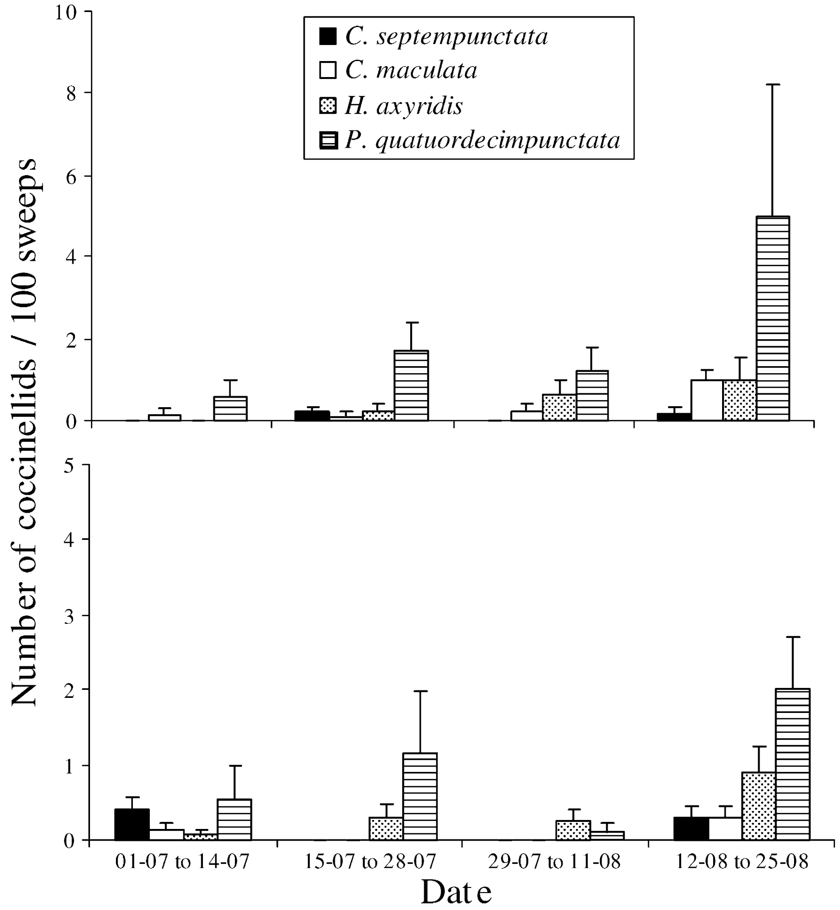

Figure 1. Seasonal fluctuation in the densities (X + SE) of adult *Coccinella septempunctata*, *Coleomegilla maculata*, *Harmonia axyridis* and *Propylea quatuordecimpunctata* in commercial soybean fields of Québec in 2002 and 2003.

dominant species throughout the season, and *H. axyridis* being responsible for this increase. Populations of *C. maculata* and *C. septempunctata* remained low throughout the season.

Coccinellid performance

All three coccinellid species had the capacity to develop and reproduce successfully when fed on *A. glycines*. Survivorship from hatching to adult emergence was high (*P. quatuordecimpunctata*, 92.9%, N = 42; *H. axyridis*, 97.9%, N = 49; *C. maculata*, 97.8%, N = 46) and similar for the three species ($\chi^2 = 2.103$, df = 2, $p = 0.349$). Preimaginal development times for females and males of each species are compared in Table 1. The development time (from oviposition to adult emergence) differed among species ($F = 20.32$; df = 2,106; $p < 0.0001$), but there was no difference between males and females within species ($F = 0.05$; df = 1,106; $p = 0.819$), and the interaction between species and sex was not significant ($F = 0.81$; df = 2,106; $p = 0.446$). Development was shorter for *P. quatuordecimpunctata*, intermediate for *H. axyridis* and longer for *C. maculata* ($F = 21.77$; df = 2,109; $p < 0.0001$).

Longevity of female coccinellids was similar among the three species ($F = 0.89$; df = 2,46; $p = 0.4186$), with a life span of about 4 months at 24°C (Table 2). None of the females died before the age of 60 days (Figure 2). No differences were observed among species in the pre-oviposition ($F = 0.12$; df = 2,46; $p = 0.8552$), oviposition ($F = 1.19$; df = 2,46; $p = 0.3125$) or post-oviposition periods ($F = 1.38$; df = 2,46; $p = 0.2623$). Oviposition began 9 days following emergence and lasted 12–15 weeks. For each species, oviposition usually ceased 5–10 days before female death.

Harmonia axyridis females produced three and five times as many eggs, on average, as did *P. quatuordecimpunctata* and *C. maculata* females, respectively (Table 2; $F = 40.47$; df = 2,46; $p < 0.0001$). As seen from the age-specific fecundity curves (Figure 2), this difference resulted from a constant higher daily production throughout the oviposition period of *H. axyridis*. Lifetime sex ratio appeared to be balanced for *H. axyridis* and *P. quatuordecimpunctata*, but male-biased to some extent for *C. maculata* (Table 2). Lifetime egg fertility values were 55.2, 53.1, and 26.6% for *H. axyridis*, *P. quatuordecimpunctata* and *C. maculata*, respectively. The production of fertile eggs ceased

Table 1. Preimaginal development time (days) of *Harmonia axyridis*, *Propylea quatuordecimpunctata* and *Coleomegilla maculata*, when reared on the soybean aphid, *Aphis glycines*, at 24 °C

Coccinellid species	Preimaginal developmental time			
	Female		Male	
	N	Days ± SE	N	Days ± SE
Harmonia axyridis	21	19.9 ± 0.2^{b}	24	19.6 ± 0.3^{b}
Propylea quatuordecimpunctata	11	18.7 ± 0.5^{a}	16	18.8 ± 0.4^{a}
Coleomegilla maculata	17	20.7 ± 0.2^{c}	23	21.1 ± 0.3^{c}

Within column values followed by the same letter are not significantly different (SNK; $\alpha = 0.05$).

Table 2. Life table parameters of female cocinellids of *Harmonica axyridis*, *Propylea quatuordecimpunctata* and *Coleomegilla maculata*, when reared on the soybean aphid, *Aphis glycines*, at 24 °C

Coccinellid species	N	Preoviposition period d ± SE	Oviposition period d ± SE	Postoviposition period d ± SE	Fecundity x ± SE	Longevity d ± SE	Sex-ratio of progeny (% of male♂)	r_m d^{-1}
Harmonia axyridis	21	9.6 ± 0.6^a	103.2 ± 7.4^a	5.7 ± 1.2^a	2008.4 ± 181.4^a	136.4 ± 7.5^a	51.4	0.238
Propylea quatuordecimpunctata	11	9.2 ± 1.2^a	97.2 ± 10.5^a	10.6 ± 3.8^a	592.8 ± 131.7^b	132.6 ± 8.9^a	42.4	0.215
Coleomegilla maculata	17	9.9 ± 1.1^a	86.8 ± 7.9^a	6.1 ± 1.8^a	390.5 ± 46.1^b	122.8 ± 7.2^a	64.9	0.134

Within column values followed by the same letter are not significvantly different (SNK; $\propto = 0.05$).

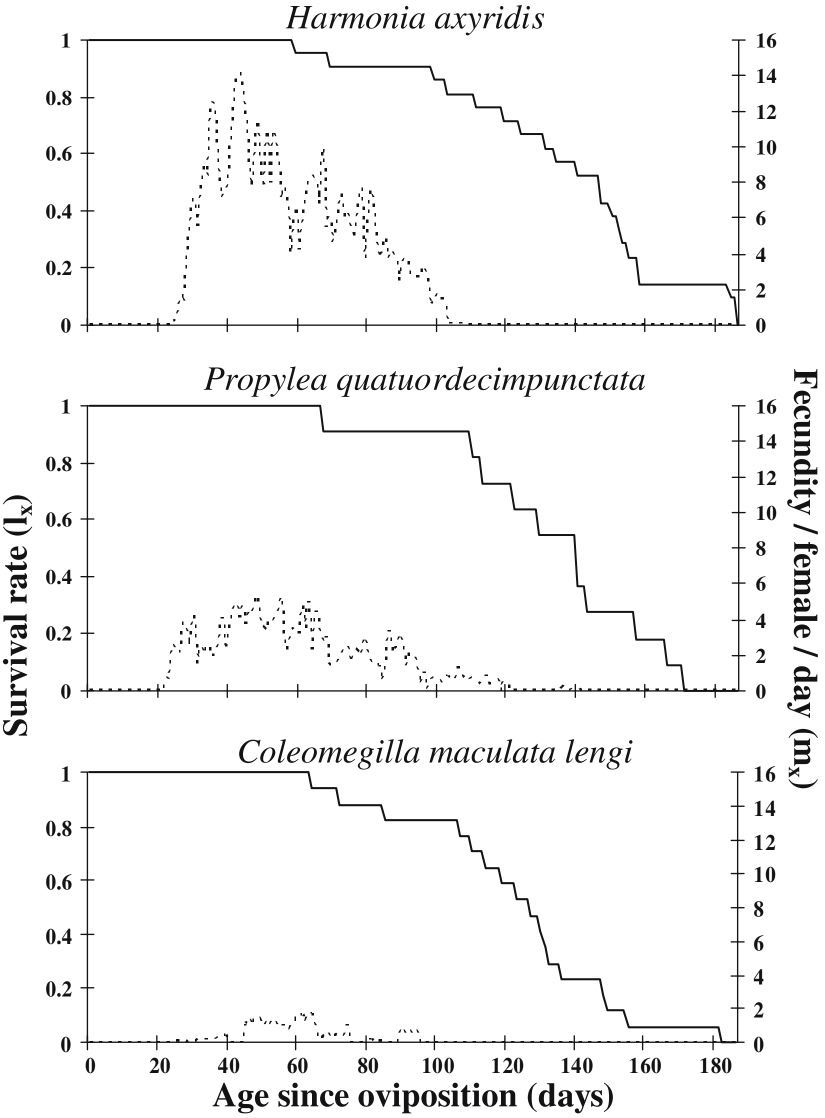

Figure 2. Age-specific survival rate (l_x) (solid line, y-axis on left) and age-specific fecundity per female (m_x) (dotted line, y-axis on right), of *Harmonia axyridis*, *Propylea quatuordecimpunctata* and *Coleomegilla maculata*, when reared at 24 °C on the soybean aphid, *Aphis glycines*.

during the 10th, 11th, and 14th week for *C. maculata*, *H. axyridis*, and *P. quatuordecimpunctata*, respectively. Either the amount or viability of sperm transferred in the 15 days following emergence were insufficient to fertilize the female's entire egg complement.

The estimate of r_m at 24 °C was highest for *H. axyridis* (0.238 d^{-1}), intermediate for *P. quatuordecimpunctata* (0.215 d^{-1}) and lowest for *C. maculata* (0.134 d^{-1}).

Discussion

Our study indicates that several aphidophagous predators have responded to the recent and massive invasion of soybean fields by *A. glycines*. Coccinellids were the most abundant natural enemies in sweep samples collected from the upper soybean canopy and four species in particular co-occurred with the soybean aphid throughout the growing season in Québec. Based on laboratory assessments of prey quality, we conclude that soybean aphids are suitable prey for the development and reproduction of *P. quatuordecimpunctata*, *C. maculata* and *H. axyridis*.

Coccinellid diversity and abundance

In Asia, *A. glycines* is attacked by the typical guild of aphid natural enemies, i.e. a diversity of aphidophagous predators, parasitoids and entomopathogenic fungi (Wang et al., 1962; Han, 1997). Recent studies in the United States indicated that several indigenous and naturalized species of predators responded to the invasion of soybean fields by *A. glycines*. In Indiana, Michigan and Kentucky, the main predators of the soybean aphid are coccinellids and predatory bugs, the dominant species being *H, axyridis* and *Orius insidiosus*(Say) (Hemiptera: Anthocoridae) [>85% of all foliar predators in Indiana in 2001 and 2002 (Rutledge et al., 2004)], and to a lesser extent *C. septempunctata*, *Hippodamia convergens* Guérin-Méneville (Coccinellidae), *C. maculata*, *Leucopis* spp. (Diptera: Chamaemyiidae) and *Scymnus louisianae* (Coccinellidae) (Fox, 2002; Brown et al., 2003; Fox et al., 2004; Rutledge et al., 2004).

In many respects, the suites of foliar-foraging predators associated with *A. glycines* in the Midwestern U.S. and Québec are similar, yet there are two important distinctions. First, the minute pirate bug *O. insidiosus* was rarely collected in soybean fields in Québec during our survey, although it was common and abundant in Michigan and Indiana, with densities as high as 1.3 individuals per soybean terminal (Fox, 2002). *Orius insidiosus* is present throughout the season in U.S.soybean fields where it feeds on arthropod prey including thrips, mites, leafhoppers and whiteflies (Isenhour and Yeargan, 1981;

Rutledge et al., 2004). These prey items are not common in soybean fields in Québec, except for leafhoppers that can be locally abundant in mid-season (M. Roy, unpublished data). Our results suggest that *O. insidiosus* populations did not move into the soybean agroecosystem until late in the season when soybean aphid densities peaked. Second, the fourteen spotted ladybeetle, *P. quatuordecimpunctata*, the dominant species in 2002 and 2003, has not been reported in the Midwestern U.S. This Palaearctic species was first collected in Québec in 1968 (Chantal, 1972) and has slowly dispersed southward (Day et al., 1994) where it can be observed on a wide range of crops (Obrycki et al. 1993). Whether the differences in abundance of *P. quatuordecimpunctata* between Québec and Midwestern U.S. result from spatial variables, intraguild interactions or other ecological factors remains to be examined.

Propylea quatuordecimpunctata was observed throughout the season, while *H. axyridis*, the second most abundant species, arrived later in the season, but reached relatively high numbers in August. In 2002 and 2003, coccinellid populations mostly peaked shortly after populations of *A. glycines* (Mignault et al., unpublished data). Coccinellid abundance in agroecosystems is often highly correlated with aphid population densities (Ives et al., 1993; Dixon, 2000).

Several studies have outlined the importance of refuge habitats for generalist predators, particularly those that play a role in reducing pest populations in annual crops (reviewed by Wissinger, 1997; Landis et al., 2000). Corn fields are probably important sources of coccinellids and other aphidophagous predators for soybean fields (Wang and Ba, 1998). Corn is typically grown in rotation with soybean in Québec and mostly shares the same guild of aphidophagous predators (Coderre, 1983). These predators colonize corn fields before and during the period that *A. glycines* starts to invade soybeans. Spatio-temporal movements from corn into soybean, and vice versa, could be a determinant of predatory guilds and understanding them necessitates a metapopulation approach between the soybean agroecosystem and other crop or natural systems.

Suitability of Aphis glycines *for coccinellids*

Under laboratory conditions *P. quatuordecimpunctata*, *H. axyridis* and *C. maculata* developed and reproduced successfully on a diet of *A. glycines*. These conclusions are consistent with results from surveys showing that these coccinellids invade soybean fields colonized by the soybean aphid.

Coleomegilla maculata is native to North America while *H. axyridis* and *P. quatuordecimpunctata* are Palaearctic species coming from the Far East and Europe, respectively (Hagen et al., 1999). They are all established east of the Rocky Mountains and more or less common in a variety of habitats (forests, orchards, row crops) and are considered to be efficient predators of several arthropod pest species. The three species are somewhat indiscriminate, opportunistic feeders, and show great nutritional plasticity (Hodek and Honek, 1996; Hagen et al., 1999). They are all primarily aphidophagous but their dietary range may include other arthropods (e.g. scales, psyllids, eggs of Lepidoptera, mites) and plant materials (e.g. pollen, fruits).

The three coccinellid species yielded similar results with respect to most fitness parameters tested (survival, development time, longevity, reproduction). The main difference observed was in fecundity as *H. axyridis* laid on average three and five times as many eggs as *P. quatuordecimpunctata* and *C. maculata*, respectively. To some extent this may be a consequence of body size as large species of coccinellids are more fecund than smaller species (see Dixon, 2000). These differences in fecundity are most likely responsible for the higher r_m value obtained for *H. axyridis* (0.238 d^{-1}) compared to *P. quatuordecimpunctata* (0.215 d^{-1}) and *C. maculata* (0.134 d^{-1}).

All aphid species are not equally suitable as food for coccinellids and we can compare the intrinsic rates of population increase obtained here with the soybean aphid to published information for each species when fed on other aphids. For each coccinellid species, r_m values are highest for larvae and adults reared on the soybean aphid compared to other aphid species (Table 3). However, these contrasts should be interpreted with caution because rearing conditions and strain differences can affect demographic parameters of an organism, thereby the maximum population growth rate (Roy et al., 2003), and because rearing temperatures do not perfectly match among the studies listed in Table 3. Nevertheless, high r_m values clearly indicate that *A. glycines* is an excellent prey to sustain larval development and oviposition of *H. axyridis*, *P. quatuordecimpunctata* and *C. maculata*. One might argue that the capacity of *H. axyridis* to exploit the soybean aphid was predictable since they have a long history of co-evolution in Asia (Rongcai et al., 1994; Han, 1997; Sun et al., 2000). Such is not the case for *P. quatuordecimpunctata* and *C. maculata* as their populations had never co-occurred with the soybean aphid prior to its arrival in North America in 2000. This attests to the nutritional plasticity of these coccinellid species as they rapidly modified their feeding habits to include a

Table 3. Daily intrinsic rate of natural increase (r_m d^{-1}) of *Harmonia axyridis*, *Propylea quatuordecimpunctata* and *Coleomegilla maculata* on different prey

Coccinellid	Prey	Temp (°C)	r_m d^{-1}	Reference
H. axyridis	*Aphis glycines*	24	0.238	Present study
	Sitotroga cerealella	27	0.153	Abdel-Salam and Abdel-Baky (2001)
	Myzus persicae	25	0.089	Lanzoni et al. (2004)
	Ephestia kuehniella	24	0.113	Michaud and Grant (2003)
P. quatuordecimpunctata	*Aphis glycines*	24	0.215	Present study
	Acyrthosiphon pisum	26	0.140	Obrycki et al. (1993)
C. maculata	*Aphis glycines*	24	0.134	Present study
	Ephestia kuehniella + artificial diet	24	0.087	Gagné et al. (1996)
	Acyrtosiphon pisum	26	0.1	Phoofolo and Obrycki (1997)
	Ostrinia nubilalis	26	0.1	Phoofolo and Obrycki (1997)
	Myzus persicae	25	0.11	Wright and Laing (1978)

suitable resource that suddenly increases in local abundance (Mooney and Cleland, 2001).

Potential role of coccinellid predators

Coccinellids are important natural enemies of aphids and contribute to their population reduction in different agricultural systems (see Obrycki and Kring, 1998). Suppression of a prey population by a predator is mainly determined by the attack rate of the predator (the functional response) and the relative population growth rates of the predator and its prey (the numerical response). In theory, following the arguments developed by Janssen and Sabelis (1992), a natural enemy that has a r_m value equal to or greater than its host/prey should have the capacity to regulate the population of its prey. The rate of increase of *A. glycines* populations is higher on young soybean plants than on mature plants, with r_m values of 0.31 d^{-1}, 0.23 d^{-1} and 0.15 d^{-1} on plants of 3, 5 and 7 weeks, respectively (Van den Berg et al., 1997). These values are much higher than those we measured for coccinellids, and may therefore limit the potential of the coccinellids as biological control agents of the soybean aphid. However, other biological traits and ecological factors such as the voracity of the predators, and their seasonal synchrony with the prey must be considered to predict the outcome of population interactions between *A. glycines* and coccinellids.

Recent empirical results in Asia (Han, 1997; Van den Berg et al., 1997; Wu et al., 2004) and North America (Fox et al., 2004, Rutledge et al., 2004) suggest that coccinellids together with other natural enemies may suppress *A. glycines* populations and mitigate their impact on soybean plants. In agreement with predator-prey models and empirical evidence (Zhang and Chen, 1991; Chang and Kareiva, 1999; Takagi, 1999; Elliott et al., 2000), some of these studies underline the determinant role Coccinellidae may play at low soybean aphid densities, when more effective specialized aphidophagous natural enemies are scarce (Van den Berg et al., 1997; Fox et al., 2004; Rutledge et al., 2004). Because of their early arrival in soybean fields and their presence throughout the growing season, the guild of indigenous and naturalized coccinellids (mostly *P. quatuordecimpunctata* and *H. axyridis*) is likely to play a significant role in biological control of the soybean aphid in Québec. These ecological circumstances suggest a cautious approach toward the introduction of exotic biological control agents (Fox et al., 2004) and the precocious use of pesticides that could be detrimental to beneficial natural enemies in soybeans.

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