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Impact of the arrival of *Harmonia axyridis* on adults of *Coccinella septempunctata* and *Coleomegilla maculata* (Coleoptera: Coccinellidae)

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Abstract. The impact of the arrival of the exotic coccinellid *Harmonia axyridis* on the biological control and dispersion of apple mites and aphids, and on the vertical distribution of the established coccinellids *Coccinella septempunctata* and *Coleomegilla maculata* have been studied. Assemblages of adults of the three coccinellid species were tested on apple saplings and on apple trees against *Aphis citricola* and *Tetranychus urticae*. The presence or substitution of adults of *H. axyridis* for adults of *C. maculata* or *C. septempunctata* did not reduce the predation impact on mite or aphid prey. *H. axyridis* was a more efficient predator of mites than was *C. septempunctata* and generated lower prey dispersal from host plants. Substitutions of adults of *H. axyridis* for those of *C. maculata*, and in some cases of *C. septempunctata*, resulted in greater reduction in number of aphids. On apple trees, the three coccinellid species occurred at different heights. Neither *C. maculata* nor *C. septempunctata* modified their vertical distribution on apple tree over a 24 hour period in response to the presence of *H. axyridis*.

INTRODUCTION

In 1994, an exotic coccinellid, *Harmonia axyridis* (Pallas), was recorded for the first time in Canada (Coderre et al., 1995). The east-palearctic species was introduced in 1916, 1964 and 1965 in Hawaii and California, USA and from 1978 to 1982 in the eastern United States and is now well established in the United States (Chapin & Brou, 1991; Gordon & Vandenberg, 1991; Colunga-Garcia & Gage, 1998). *Harmonia axyridis* is a polyphagous predator consuming numerous species of aphids (Lucas, 1994), coccids (McLure, 1987) and psyllids (Iablokoff-Khnzorian, 1982). Since its arrival in Canada, *H. axyridis* has became one of the dominant species in several crops (Chouinard, 2000; Coderre, in prep.; see also Colunga-Garcia & Gage, 1998).

The arrival of a new coccinellid species may have important consequences on the guild of established species. Both intruder and local coccinellids can interact directly or indirectly and may be implicated in intraguild predation (Agarwala & Dixon, 1992; Hironori & Katsuhiro, 1997; Lucas et al., 1998a; Dixon, 2000), or in exploitative competition (Evans, 1991). In alfalfa, maize and small grain crops, the establishment of *Coccinella septempunctata* L. was associated with significant changes in the local guilds of coccinellids (Elliot et al., 1996). The populations of *Coccinella transversoguttata richardsoni* Brown and *Adalia bipunctata* (L.) were drastically reduced (more than 20 times less after invasion). The establishment of *H. axyridis* in natural and agricultural ecosystems was also associated with significant population reductions of *Brachiacantha ursine* (F.), *Cycloneda munda* (Say) and *Chilocorus stigma* (Say) (Colunga-Garcia & Gage, 1998).

Such modifications in the dynamics and composition of the coccinellid guilds may also have significant impact on the biological control of prey. Previous experiments on larvae showed that interactions between *C. septempunctata* and *Coleomegilla maculata* (DeGeer) did not significantly affect the control of *Myzus persicae* (Sulzer) (Obrycki et al., 1998). However, no such studies have been conducted on adults. Adults have an important role in the outcome of competition as they are the only flying stage and will select the habitat of their offspring by oviposition. Adults are active predators and their contribution may be maximum early in the season when large larvae are absent. Moreover, no intraguild predation among adult coccinellids has been reported.

In Eastern Canada, more than 70 coccinellid species have been recorded (Bousquet, 1991), including 10 to 15 predominant aphidophagous species (LeRoux, 1960; Bouchard et al., 1982; Tourneur et al., 1992). The seven spotted ladybeetle, *C. septempunctata* is one of the commonest species in several crops (Angalet et al., 1979; Chouinard et al., 1992; Mareida et al., 1992). This palearctic species was first introduced in United States in 1956 and thereafter had an important geographical expansion (Schaefer et al., 1987; Humble, 1991). *C. septempunctata* had been recorded to attack more than 97 different prey species (Lucas, 1994). This predator prefers aphids over mites (Lucas et al., 1997b) and lepidopteran larvae (Mohan et al. 1991). The indigenous coccinellid *C. maculata* is found in North America, South America and Northern Europe. This predator is common in many herbaceous crops as well as in apple and peach orchards (Putman, 1964; Mack & Smilowitz, 1980; Coderre & Tourneur, 1986; Groden et al., 1990; Giles et al., 1994). *Coleomegilla maculata* is one of the most polyphagous coccinellid species (Hodek, 1996). The three coccinellid species, *H. axyridis*, *C. septempunctata* and *C. maculata,* share overlapping diets and have been recorded at the same time in several natural and agricultural ecosystems (Angalet et al., 1979; Coderre & Tourneur, 1986; Elliot et al., 1996; LaMana & Miller, 1996; Obrycki et al., 1998).

The aim of this study is to evaluate the potential impact of the arrival of *H. axyridis* adults on the predation efficacy by adults of two local aphidophagous coccinellids, *C. septempunctata* and *C. maculata*. Three questions were formulated: 1) According to their different voracities and to the possibility of interference between *H. axyridis* and *C. maculata* or *C. septempunctata,* may the overall impact on pest species be affected?, 2) May the arrival of *H. axyridis* modify pest dispersion generated by local coccinellid species?, 3) May *H. axyridis* displace spatially other coccinellid species by modifying their vertical distribution?

MATERIAL AND METHODS

Coccinella septempunctata adults were collected in an apple orchard near Montreal (73°36'W, 45°30'N) (Quebec, Canada). *Harmonia axyridis* adults (population of Chinese origin) and *Coleomegilla maculata* came from mass rearing on *Ephestia kuehniella* Zeller eggs (Lepidoptera: Pyralidae) and an artificial diet of pork liver and ground pollen. All coccinellids were reared on the spirea aphid, *Aphis citricola* van der Goot, at 25°C, 70% R.H. and a 16L : 8D photoperiod, one month before tests. The two-spotted spider mites, *Tetranychus urticae* Koch, were mass reared on Lima bean plants, *Phaseolus limensis*. *Aphis citricola* were collected from apple orchards near Montreal.

Prey consumption and dispersion effect on apple saplings

The first experiment was carried out on four- to six-week old apple saplings (McIntosh cultivar) grown in a greenhouse and carefully washed to clear all arthropods before the experiments. The saplings with five equal-sized and undamaged leaves were fixed with Plasticine in a hole pierced in the bottom of a plastic container (8,1 cm high with a 15,0 cm diameter). This container was placed in a second plastic container with water in which soaked the sapling roots. The adult coccinellids were fed *ad libitum* and then starved for 24 h before the experiment. Adult mites (n = 60) or 3rd instar nymphs of the aphid (n = 100) were placed on the apple sapling leaves. After 1 h, predators were added on the plant. The set up was hermetically sealed using a transparent tightened plastic film placed on the top of first container and held by the plastic cover pierced at its center. The set up was placed in an incubator (25°C, 70% RH, 16L : 8D). Two sets of treatments were carried out, one with aphids and one with spider mites. The treatments were as follows: 1) two adults of *C. septempunctata*, 2) two adults of *H. axyridis*, and 3) one adult of *C. septempunctata* and one of *H. axyridis*. All treatments were replicated 28 times. After 24 h, uneaten prey on and out of the sapling tree were counted with a binocular microscope. The number of prey eaten as well as the proportion of dispersed prey (surviving individuals that had left the plant compared to the total of the survivors) were then compared using a one-way ANOVA followed by an LSD Fisher's protected post-hoc test (Sokal & Rohlf, 1981). Controls without predators were included to evaluate natural prey mortality. Data were adjusted accordingly. All analyses were performed with SuperAnova ® (Abacus Concepts, 1989).

In order to evaluate heterospecific treatment results, an expected consumption value (E) was calculated for each replicate using the number of prey consumed in the monospecific treatments:

$E = (C + H)/2$ where:

C = number of prey consumed by 2 adults of *C. septempunctata*, H = number of prey consumed by 2 adults of *H. axyridis.*

The expected mean number of prey consumed in the heterospecific treatment was then compared to the mean of observed prey consumed in the heterospecific treatment by a Wilcoxon-Mann Whitney test. Non parametrical statistics were used because of the unequal variances in the treatments. The same formula and test were used to compare the observed and the expected proportion of prey that left the plant. Analyses was performed with JMP IN ® (Sall & Lehman, 1996).

Prey consumption and vertical distribution on apple trees

The second experiment was done on potted apple trees in controlled conditions (23°C, 70% RH, 24L : 0D). Dwarf apple trees (180 cm) were caged with a closed muslin. Nine aphid colonies were established at three heights on the tree, low (> 100 cm), medium (110–130 cm) and high (> 170 cm) height on the tree. At each height, three aphid colonies of 10 4th instar nymphs of *A. citricola* were established. In this experiment, adults of *C. maculata* were included with those of *H. axyridis* and/or *C. septempunctata* in the experiment design. After 24 h, starved coccinellids were introduced in the system, at the base of the tree. Seven treatments were considered: 1) 6 adults of *C. maculata*, 2) 6 adults of *C. septempunctata*, 3) 6 adults of *H. axyridis*, 4) 3 adults of *C. maculata* + 3 adults of *C. septempunctata*, 5) 3 adults of *C. maculata* + 3 adults of *H. axyridis*, 6) 3 adults of *C. septempunctata* + 3 adults of *H. axyridis*, and 7) 2 adults of *C. maculata* + 2 adults of *C. septempunctata* + 2 adults of *H. axyridis*. Fifteen replicates were carried out. Control trees without predators were included and data were adjusted accordingly. After 24 h, the number of living aphids at the different heights and the height position of coccinellids on the tree were recorded. The number of predated aphids was compared on the entire tree (all levels pooled), and then for each vertical level with a one-way ANOVA followed by a LSD Fisher's protected post-hoc test. The mean height position of each coccinellid species was compared among the three monospecific treatments also by using a one-way ANOVA. The height position of each species was compared also by an ANOVA in monospecific and multispecific assemblages to evaluate whether the presence of another coccinellid species may result in modification of a particular species height position.

RESULTS

Prey consumption and dispersion effect on apple saplings

Two adults of *C. septempunctata* together consumed significantly fewer mites in 24h tests than did two adults of *H. axyridis* or two adults of the heterospecific treatment ($F_{2,83}$ = 4.54, P = 0.013) (Fig. 1). Adults in the heterospecific treatment (22.8 mites) consumed significantly more mites than expected (20.9 mites) (Wilcoxon, Z = 2.19, P = 0.029). *H. axyridis* adults also consumed significantly more aphids than did *C. septempunctata* adults ($F_{2,86}$ = 5.89, P = 0.004). Adults in the heterospecific treatment (30.3 aphids) consumed similar number of aphids as expected (30.9 aphids) (Wilcoxon, Z = 0.38, P = 0.702).

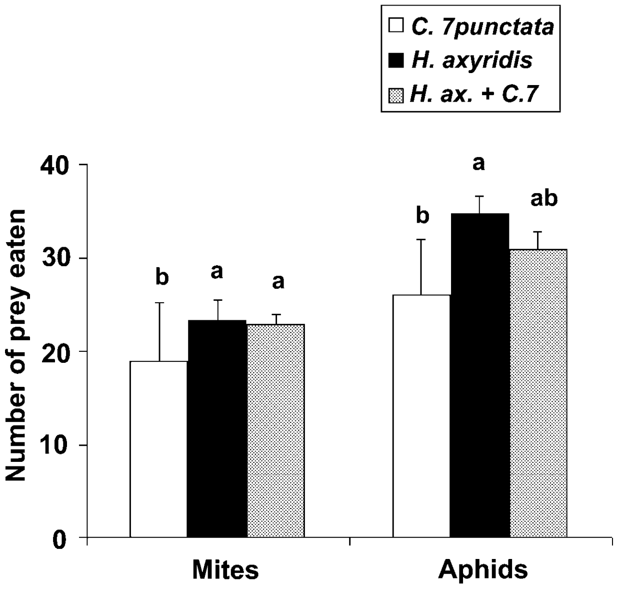

Fig. 1. Mean number of prey consumed by adult coccinellids in 24 h on apple saplings. *C. 7 = Coccinella septempunctata, H. ax. = Harmonia axyridis*. Different letters indicate a significant difference among the different combinations of coccinellids for the same prey ($P < 0.05$).

Table 1. Mean vertical position of adult coccinellids on apple trees.

Treatments*	Coccinellid vertical position (m)	
	Mean	S.E. **
	Coccinella septempunctata	
C. septempunctata	1.35	0.07 (a)***
C. 7 + C. mac.	1.18	0.09 (a)
C. 7 + H. ax.	1.37	0.09 (a)
3 species	1.36	0.14 (a)
	Coleomegilla maculata	
C. maculata	0.56	0.05 (a)
C. mac. + C. 7	0.7	0.14 (a)
C. mac. + H. ax.	0.68	0.14 (a)
3 species	0.63	0.13 (a)
	Harmonia axyridis	
H. axyridis	1.58	0.06 (a)
H. ax. + C. 7	1.37	0.09 (a)
H. ax. + C. mac.	1.6	0.08 (a)
3 species	1.51	0.09 (a)

* *C. 7 = Coccinella septempunctata, H. ax. = Harmonia axyridis, C. mac. = Coleomegilla maculata.*
** S.E. = Standard Error
*** Different letters indicate significant differences between means in the same subsection (for one coccinellid species) (ANOVA, $\alpha = 0.05$).

After 24 h, a mean of 26% of the mites had left the sapling in the control treatment without predators. A greater percentage of mites left the sapling in the presence of *C. septempunctata* adults (75.7%) than in the presence of *H. axyridis* (54.0%) ($F_{2,83} = 3.32$, $P = 0.041$) (Fig. 2). No difference was recorded between observed (66.8%) and expected (64.3%) mean proportion of mites that left the plant in the heterospecific treatment (Wilcoxon, Z = 0.38, $P = 0.702$). After 24 h, only 5.4% of the aphids had left the plant in the control treatment. In the presence of adult coccinellids, the percentage of aphids that left the apple sapling was similar among the different treatments ($F_{2,74} = 0.01$, $P = 0.993$). As with mites, expected (15.4%) and observed (18.2%) percentages of aphids leaving the plant for the heterospecific treatment were similar (Wilcoxon, Z = 0.33, $P = 0.735$).

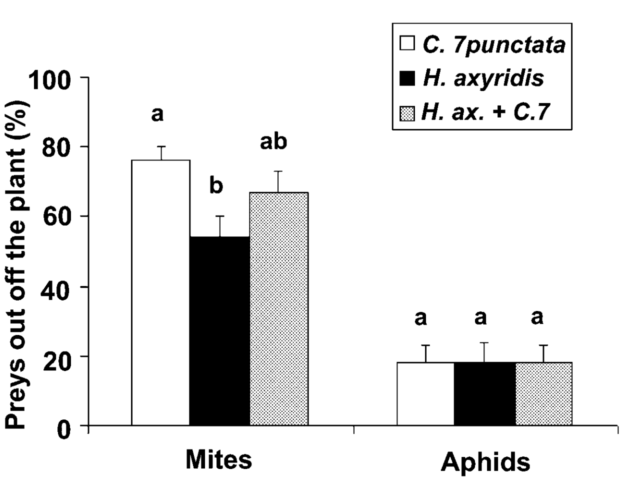

Fig. 2. Mean percentage of prey that had left the apple sapling after 24 h. *C. 7 = Coccinella septempunctata, H. ax. = Harmonia axyridis*. Different letters indicate a significant difference among the different combinations of coccinellids for the same prey ($P < 0.05$).

Prey consumption and vertical distribution on apple trees

In monospecific treatments, *C. maculata* was recorded at a mean height of 0.562 m ± 0.055 (X ± SE), *C. septempunctata* at 1.347 m ± 0.069 and finally *H. axyridis* at 1.578 m ± 0.069. All heights were significantly different ($F_{2,43} = 68.81$, $P < 0.001$). The height position of the coccinellids were not affected by the presence of the others species; *C. septempunctata* ($F_{3,58} = 0.82$, $P = 0.491$), *C. maculata* ($F_{3,60} = 0.23$, $P = 0.892$) and *H. axyridis* ($F_{3,59} = 1.64$, $P = 0.191$) (Table 1).

Considering the entire apple tree, in monospecific treatments, *C. septempunctata* and *H. axyridis* consumed more aphids than *C. maculata* ($F_{6,103} = 22.68$, $P < 0.001$) (Fig. 3). The presence of *H. axyridis* or *C. septempunctata* in the same tree as *C. maculata* significantly increased the number of aphids consumed by the guild compared to the trees where *C. maculata* occurred alone. Considering each vertical level, this pattern was observed in high ($F_{6,103} = 13.21$, $P < 0.001$) and medium height ($F_{6,103} = 7.85$, $P < 0.001$) in the tree (Fig. 4). No difference was observed at the lower height ($F_{6,103} = 7.38$, $P < 0.001$; LSD $P > 0.05$) (Fig. 4). At all levels, the presence of both *C. septempunctata* and *H. axyridis* in the tree did not significantly affect the number of aphids consumed, compared to trees where only *C. septempunctata* or only *H. axyridis* occurred. Finally the trispecific combination

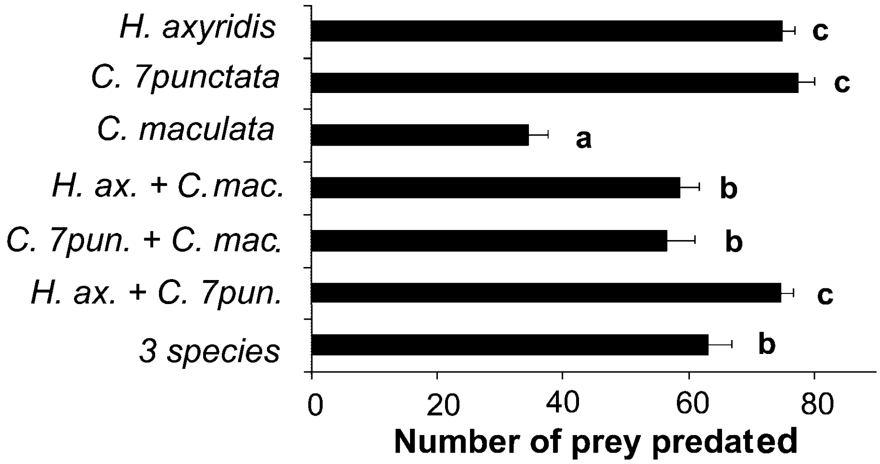

Fig. 3. Mean number of prey consumed by adult coccinellids in 24 h on the entire apple tree, (all vertical levels pooled). *C. 7* = *Coccinella septempunctata, H. ax.* = *Harmonia axyridis, C. mac.* = *Coleomegilla maculata.* For details about the treatments, see Material and Methods section. Different letters indicate a significant difference among the different combinations of coccinellids ($P < 0.05$).

generated a stronger impact on aphid populations than the *C. maculata* treatment at each height.

DISCUSSION

We draw three primary conclusions from our experiments. First, the replacement of *C. maculata* adults or *C. septempunctata* adults by *H. axyridis* adults did not reduce the impact of the coccinellids on spider mites or on aphids. Second, mite dispersal from plants was lower in the presence of *H. axyridis* than in the presence of *C. septempunctata.* Third, in our short-term experiment, neither *C. maculata* nor *C. septempunctata* modified their vertical distribution on apple trees in response to the presence of *H. axyridis*.

In our study, adults of *H. axyridis* or adults of heterospecific combinations consumed more mites than did *C. septempunctata* adults. Furthermore, more mites were consumed by adults in heterospecific combination than expected, suggesting that some kind of facilitation or stimulation may have occurred. In apple orchards, several mite species including the two spotted spider mites, *T. urticae,* and the European red mites, *Panonychus ulmi* (Koch), can become important pests (Van de Vrie, 1985). Among large coccinellids, several species attack these mites but, except for *C. maculata,* mites appear to constitute a low-quality prey (Putman, 1957; Lucas et al., 1997b, 1998b). Previous studies on *C. septempunctata* and *H. axyridis* have shown that both species can consume mites but have a significant preference for aphids (Lucas et al., 1997b). Furthermore, despite its large size, *C. septempunctata* had a very low voracity confirming its inefficiency as a biological control agent against *T. urticae* (Lucas et al., 1997b) and *P. ulmi* (Lucas et al., 1998b). Thus, the arrival of *H. axyridis* may possibly improve the control of mites but only during periods of aphid scarcity.

Our results also revealed that replacing *C. maculata* adults with *H. axyridis* adults improved the impact of coccinellids on aphid populations in apple trees, and that replacing *C. septempunctata* by *H. axyridis* improved or maintained their impact. These results were consistent among the different heights in the tree. The overall voracity of the coccinellid assemblage was probably enhanced when *H. axyridis* was included because of the greater voracity of this species. Moreover, the number of aphids consumed by adults in heterospecific combination was as expected, suggesting that no unusually strong exploitative interspecific competition (i.e., superior to intraspecific competition between two individuals) occurred between *C. septempunctata* and *H. axyridis*. The three coccinellid species are primarily aphidophagous and prey on numerous aphid species in natural and agricultural systems (Blackman, 1965 ; Hodek, 1973; Angalet et al., 1979 ; Lucas, 1994). Thus, because of their preference for aphids which constitute their essential food source (allowing egg maturation and complete development), the arrival of *H. axyridis* may have a greater impact on aphid than on mite control.

Adults of *C. septempunctata* caused greater mite dispersal from the plants than did *H. axyridis* adults. Aphids responded similarly to both predators. Prey dispersal as a defensive response to predation has been poorly studied but may be important from a biological control perspective (Roitberg & Myers, 1978, 1979; Roitberg et al., 1979; Evans, 1991). One should believe that a predator with a low capture success and a high disturbing effect may generate a strong dispersal response effect of the prey without significantly reducing prey number. Since *C. septempunctata* has a low efficacy on mites, its overall effect may be to propagate the infestation in other parts of the plant or of the crop. Furthermore, by dispersing prey, the predator may reduce the local densities of mites such that the consequent numerical and functional response of other predators could be delayed or weaken. In our situation, *H. axyridis* consumed more mites than did *C. septempunctata* and generated less dispersal by the mites, indicating greater potential of this beetle against this prey.

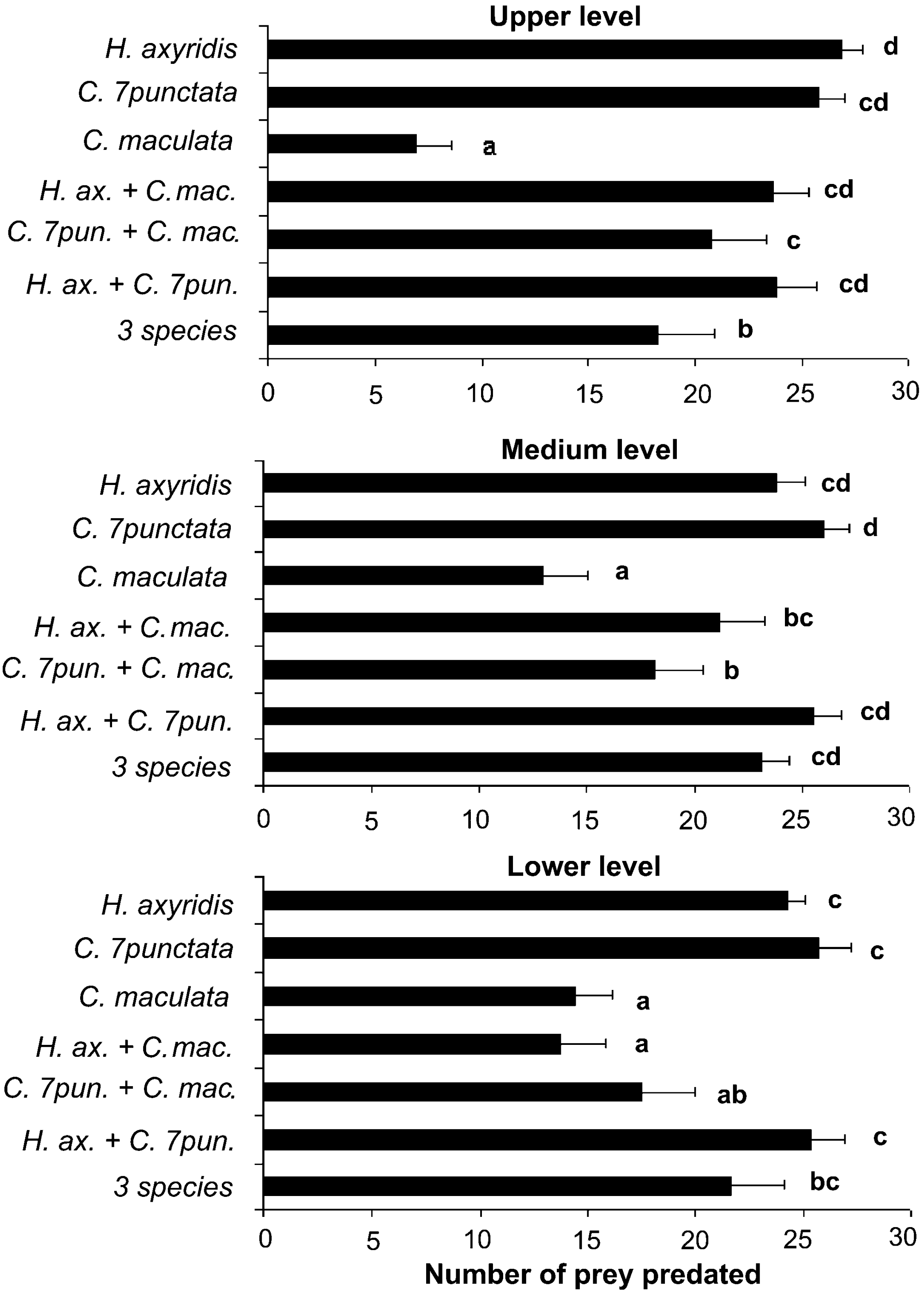

Fig. 4. Mean number of prey consumed by adult coccinellids in 24 h on apple tree, at upper, medium and lower level. *C. 7 = Coccinella septempunctata, H. ax. = Harmonia axyridis, C. mac. = Coleomegilla maculata.* For details about the treatments, see Material and Methods section. Different letters indicate a significant difference among the different combinations of coccinellids ($P < 0.05$).

These results should be confirmed in field or semi-field experiments.

In our short-term study, the mean vertical position of *H. axyridis* in the tree was different from those of the other species. Such different vertical positions may reduce potential interaction; in addition, in the fields the three species exploit a considerable array of different habitats (Angalet et al., 1979; Mareida et al., 1992; LaMana & Miller, 1996; Colunga-Garcia & Gage, 1998; Obrycki et al., 1998). According to our results and also to the fact that *C. maculata* is mainly encountered in the herbaceous stratum (Coderre & Tourneur, 1986), competition between *H. axyridis* and *C. maculata* should be less important than between *H. axyridis* and *C. septempunctata.* In maize, while some other indigenous species such as *Hippodamia tredecimpunctata tibialis* (Say) were severely affected, *C. maculata* has remained a predominant species despite the arrival of other coccinellids such as, *Propylea quatuordecimpunctata* (L.) and *C. septempunctata* (Coderre unpubl.). In our study, neither *C. septempunctata,* nor *C. maculata* modified their vertical position in the presence of *H. axyridis*; however a long-term study in the field may generate a different response. For example, according to Iablokoff-Khnzorian (1982), *Adalia bipunctata* (L.) in Siberia avoid plants where *H. axyridis* is present, mainly *Salix* sp.

This study is an initial evaluation of the impact of *H. axyridis* on the aphidophagous and acarophagous guilds and on biological control of aphids and mites in apple orchards. It would be risky to speculate on the potential long-term impact of *H. axyridis* in the field. However, *H. axyridis* is eurytopic and polyphagous and may be implicated in exploitative or interference competition as well as in intraguild predation with local predatory species (Evans, 1991; Agarwala & Dixon, 1992; Hironori & Katsuhiro, 1997; Lucas et al., 1997a, 1998a; Dixon, 2000). In the field, its arrival in natural and agricultural ecosystems is associated with significant reductions of several coccinellid species populations (Colunga-Garcia & Gage, 1998). To obtain an overall pattern of the effect of the arrival of *H. axyridis* on the local guild of coccinellids and consequently on their prey, the next step would be to evaluate the impact on immature stages of local ladybeetles (selection of oviposition sites, selection of pupating and molting sites, interactions among larvae, etc.) and to carry out *in situ* studies in different agricultural and natural systems.

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