Comparative Use of *Mindarus abietinus* (Homoptera: Aphididae) by Two Coccinellids (Coleoptera: Coccinellidae), the Native *Anatis mali* and the Exotic *Harmonia axyridis*, in a Christmas Tree Plantation

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ABSTRACT The exotic coccinellid *Harmonia axyridis* (Pallas) recently expanded its range into eastern Canada and elsewhere in North America. We hypothesized that this coccinellid should be less well adapted to the prey *Mindarus abietinus* Koch. on balsam fir trees than the native coccinellid *Anatis mali* (Say), which evolved in close association with aphids on conifers in North America. We compared, under field conditions, prey use by both species by collecting data on their synchrony with *M. abietinus*, their prey searching and predation behaviors, life stage distribution in fir canopy, and their overall reproductive success in this system. The seasonal life cycle of *A. mali* was better synchronized with that of *M. abietinus* compared with that of *H. axyridis*. In spring, *A. mali* adults appeared nearly 2 wk earlier on trees than *H. axyridis* and were active predators of the aphid fundatrices. *A. mali* oviposition thus began before the aphid population started to grow, and its larvae were most active during peak aphid colonies. Behavioral observations showed that both adults and larvae of the native *A. mali* searched for prey more actively than those of *H. axyridis*. Distribution of life stages also showed that eggs and pupae had different distributions on trees and that the adult-to-adult net reproductive rate of *A. mali* was three times higher than that of *H. axyridis*. Thus, the native *A. mali* was better adapted than *H. axyridis* to prey on *M. abietinus*, possibly because it evolved for a much longer period of time with this prey in conifer habitats.

KEY WORDS Coccinellidae, *Anatis mali*, *Harmonia axyridis*, behavior, predator–prey synchrony, specialist versus generalist species, exotic species, *Abies balsamea*

Species coevolution occurs in most ecosystems and is a major driving force of specialization for numerous species (Abrams 1986, Berlocher and Feder 2002). The level of specialization differs among species and follows a continuum; some use numerous hosts or prey, whereas others use only one or a limited number of hosts or prey or even only a part of this host (Futuyma and Wasserman 1981, Albuquerque et al. 1997). One of the major costs of specialization is the reduction of host or prey range, which makes the specialist species dependent on only one or a few resource species. However, this has some advantages because specialist species are more efficient exploiters of their specific resources (Thompson et al. 1990). For herbivorous insects, numerous studies (Hsiao 1978, Scriber and Slansky 1981, Berlocher and Feder 2002) showed that exploitation strategies, including host plant synchrony and behavior, vary between a generalist and a specialist species that feed on the same host plant. However, few studies have considered the impact of specialization for predators, as they are often considered to be mostly generalists. Nevertheless, some level of specialization has been shown for predators of aphids (Albuquerque et al. 1997). Long-term coevolution between predators and prey can result in strong associations in natural ecosystems and can lead to the development of better-adapted predator strategies for optimal use of a specific prey. Coccinellidae are important aphidophagous predators that often play a determinant role in limiting aphid populations, and multispecific coccinellid associations on particular host plants are very common at local aphid outbreaks (Hagen 1962, Iperti 1966, Hodek 1967, 1970, Dean 1982, Kring et al. 1985, Elliott and Kieckhefer 1990, Evans 1991, Agarwala and Dixon 1992). Different levels of specialization have been shown in aphidophagous coccinellids, mainly based on prey range and habitat specificity (Hodek and Honek 1996, Dixon 2000, Symondson et al. 2002), and thus, multispecific associations observed under field conditions provide interesting opportunities to compare use strategies between coccinellid species using the same prey that feed on the same host plant in a specific ecosystem.

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The balsam twig aphid, *Mindarus abietinus* Koch., is an important pest of balsam fir (*Abies balsamea* L. Mill.) grown as Christmas trees in North America (Varty 1968, Renault 1983, Bradbury and Osgood 1986, Rather and Mills 1989, Kleintjes 1997, Fondren and McCullough 2003). This aphid has a complex life cycle involving different morphs over three or four generations from May to July before it overwinters as eggs on the foliage of its conifer host (Amman 1963, Varty 1966, Bradbury and Osgood 1986, Berthiaume et al. 2001b). *M. abietinus* colonies develop rapidly on growing shoots shortly after bud break, causing needle distortion and shoot stunting, thus reducing the esthetic value of Christmas trees (Amman 1963, Varty 1966, Nettleton and Hain 1982, Bradbury and Osgood 1986, Rather and Mills 1989, Kleintjes 1997, Fondren and McCullough 2003). Many coccinellid species have been observed during *M. abietinus* outbreaks either in Christmas tree plantations (Amman 1963, Kleintjes 1997, Berthiaume 1998, Berthiaume et al. 2001b, Cloutier and Jean 2002, Fondren et al. 2004) or in natural forests (Varty 1966, 1969, Rather and Mills 1989). However, the biology and ecology of most species involved in these systems are poorly known. A preliminary inventory (Berthiaume 1998), carried out in Christmas tree plantations in Quebec in 1995, showed that several species of coccinellidae attacked the balsam twig aphid: *Anatis mali* (Say) was the most abundant but *Harmonia axyridis* (Pallas) was also encountered.

Although both *A. mali* and *H. axyridis* attack all morphs and instars of the balsam twig aphid (Berthiaume 1998), their relationship to this aphid strongly differs. *A. mali* is a nearctic univoltine species, known to be closely associated with conifers, and with a limited range of prey and habitats (Smith 1965a, Gagné and Martin 1968, Watson 1976). Thus, it may be considered as a relatively specialized conifer–aphid predator. However, *H. axyridis* is a recently introduced multivoltine species (Coderre et al. 1995, Lamana and Miller 1996, Nalepa et al. 1996), originating from south Asia (Chapin and Brou 1991, Koch 2003), with a wide range of aphid prey and various host plants in a range of habitats (Iablokoff-Khnzorian 1982, Chapin and Brou 1991, Tedders and Schaefer 1994, Dreistadt et al. 1995, Lamana and Miller 1996). Thus, it can be considered to be a clearly more generalist aphid predator than *A. mali.*

The relatively high abundance of the recently introduced *H. axyridis* in the balsam fir plantation system provided an interesting opportunity to compare their use strategies on *M. abietinus* with those of the native *A. mali.* We hypothesized that *A. mali* would be more efficient at exploiting the balsam twig aphid than *H. axyridis*, assuming that it coevolved more closely with this aphid on conifers and for a longer period of time. More specifically, we collected field data and directly observed predator–prey interactions on balsam fir to compare predator synchrony with the *M. abietinus* cycle; adult and larval behavior of both species while searching for prey on balsam fir and their life stage distributions on balsam fir trees. A first list of predacious coccinellids of the balsam twig aphid in balsam fir plantations is also provided for eastern Canada.

Materials and Methods

Field work was carried out from May to August 1996 in a commercial balsam fir plantation located near Sawyerville, Québec, Canada (45°20′ N, 71°34′ W). Trees were 6–8 yr old and had never been treated with insecticides. Twice weekly from 9 May to 26 July 1996, the foliage of 30–50 randomly selected trees (≈2 m in height) was examined between 0900 and 1900 hours to identify and record the presence and activity of coccinellid predators. Coccinellids were identified at species level and developmental stage (eggs, larvae, pupae, and adults) and their location within the tree crown (upper, middle, or lower third) and on shoots (current year, 1 yr old, 2 yr old, etc.) were recorded. The behavior of each coccinellid was observed for 15 s and recorded as (1) local searching and predation (i.e., systematic walking along needles on fir shoots, with antennation of the substrate, or attacking or consuming aphids), (2) mating, (3) moving (i.e., rapid walking along the shoot axis), and (4) resting (i.e., immobile for >10 s) (Berthiaume et al. 2001a). Because they are usually observed in the same sequence, local searching and predation were grouped into a single category. When predation was observed, the morph (fundatrix, fundatrigenea, sexupara, or sexual) of the aphid prey was determined whenever possible. Coccinellid species were considered to have completed one generation of their summer cycle on the balsam twig aphid in this plantation when adults were observed on balsam fir trees in spring (May and June), followed by the larvae and/or pupae in early summer (June and early July), and finally by adults later in the summer (mid-late July).

To evaluate coccinellid synchrony with prey abundance, balsam twig aphid density was estimated twice weekly from 29 April to 15 July by collecting four fir branch apices (i.e., the tip comprising the 1-yr-old shoot plus its current year buds and/or newly developing shoots) from each of 10 randomly selected trees. Apices were randomly selected within the midcrown, where most colonies of *M. abietinus* are usually found (Nettleton and Hain 1982). Each apex was kept in a 100-dram plastic bottle inside a cooler to stop development, reproduction, and predation on aphids, until it could be examined under a stereomicroscope in the laboratory. All aphids were counted, and the average density per apex was determined for each sampling date over the 10 replicate trees.

To compare *A. mali* and *H. axyridis* oviposition and pupation sites on balsam fir and to estimate pupal mortality, direct observations were made on 25 randomly selected trees from 22 May (before coccinellid oviposition started) to 20 July. More than 99% of coccinellid egg masses observed on balsam fir trees were those of *A. mali* and *H. axyridis.* At 4-d intervals, *A. mali* and *H. axyridis* egg masses and pupae were sought over the whole tree, identified (*A. mali* eggs are
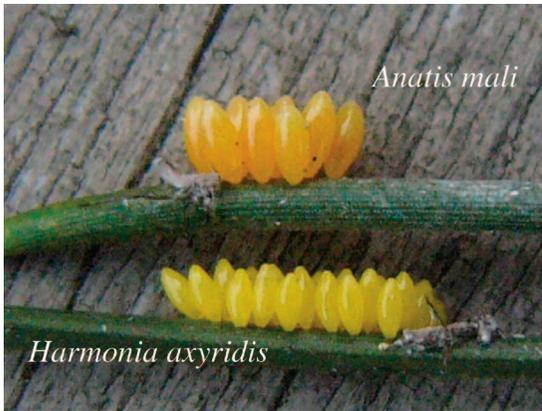
Fig. 1. Egg masses of *A. mali* and *H. axyridis.*

substantially larger than those of *H. axyridis*; Fig. 1), located with respect to the upper, middle, or lower crown and shoot age (current year, 1 yr old, 2 yr old, etc.), and marked using colored forest flags. Eggs were counted in each mass, and their position (upper or underside of needles or twigs) was also recorded. Previously marked egg masses and pupae were reobserved at 4-d intervals to record egg hatching or adult emergence and thus estimate stage-specific mortality. Furthermore, to determine if coccinellid eggs and pupae of both species were randomly distributed within the crown of balsam fir trees, we compared their vertical distributions with a theoretical one, based on the volume of each third of the crown and calculated using the cone formula: volume of each third = (radius^2 × π)(1/3 × height). Radius was measured at the base of each third of the crown, in each cardinal direction, and averaged to have more precise estimates. Tree height and radius were measured at the end of the growing season.

We compared adult and larval coccinellid distributions (versus crown height and shoot age) between species on balsam fir trees using χ^2 tests. The number of shoot ages used varied for different life stages and was adjusted to respect distribution on trees. For example, larvae are exclusively found on current year shoots, 1-yr shoots, and 2-yr shoots, and thus, the number of classes used for the χ^2 test was three (df = 2). We also compared spring (9 May to 18 June) and summer (5–26 July) adult and larval coccinellid behavior and distribution on fir trees between species using χ^2 tests (pooled data for all sampling dates). Furthermore, we also compared the egg and pupal distributions between species and with a theoretical distribution based on the volume of foliage in each part of the trees using χ^2 tests. The number of eggs per mass was compared between species using Student's *t*-test. Statistical analyses were performed using SAS programs (SAS Institute 1999). For interpretation purposes, we refer to the 5% error rate as the threshold for significance.

Results

Coccinellid Diversity. Adults of eight coccinellid species were observed attacking the balsam twig aphid in the balsam fir plantation (Table 1); five of these species completed one generation on this aphid. During field observations for monitoring activity of coccinellid predators on trees, we observed 1,651 adults, 3,150 larvae, and 3,090 pupae. In terms of abundance, *A. mali* was by far the dominant species followed by *H. axyridis*, with these two species accounting for nearly 97% of all observed adult coccinellids on balsam fir trees (Table 1). The two dominant species and *Mulsantina hudsonica* Casey preyed on fundatrices, colonies (including fundatrices, fundatrigenea, and sexuparae), and sexuals of the balsam twig aphid. For the two other species that completed one generation on this aphid (*Coccinella trifasciata* L. and *Coccinella septempuntata* L.), no predation on sexuals was observed, but they preyed on fundatrices and colonies.

Predator–Prey Seasonal Synchrony. Fundatrices of the balsam twig aphid emerged in early May, and their density remained relatively constant until the end of May (Fig. 2A), when most of them became adults. Then, fundatrices moved toward the bursting buds and began reproduction. Aphid density increased rapidly to a maximum of 50.0 ± 12.9 aphids per apex on 6 June. From 6 to 24 June, alate sexuparae matured and dispersed by flight to colonize other balsam fir trees. This resulted in a gradual decrease in aphid density within colonies on current year shoots. The alate sexuparae produced a generation of apterous sexuals that lay eggs on balsam fir trees. The first sexuals of the balsam twig aphid were observed on 10 June. Density

Table 1. Coccinellid beetles observed preying on different morphs and stages of the balsam twig aphid, *M. abietinus*, on balsam fir grown as Christmas trees in Sawyerville, Québec, Canada

Species	Number observed	Relative abundance	Complete generation	Prey
Anatis mali Say	1,422	86.13	Yes	F, C, S
Harmonia axyridis Pallas.	176	10.66	Yes	F, C, S
Coccinella trifasciata L.	16	0.97	Yes	F, C
Coccinella septempuntata L.	16	0.97	Yes	F, C
Mulsantina hudsonica Casey	10	0.60	Yes	F, C, S
Chilocorus stigma Say	6	0.36	No	F
Adalia bipunctata L.	3	0.18	No	C
Propylea quatuordecimpunctata L.	2	0.12	No	C

F, fondatrix; C, colony; S, sexuals.
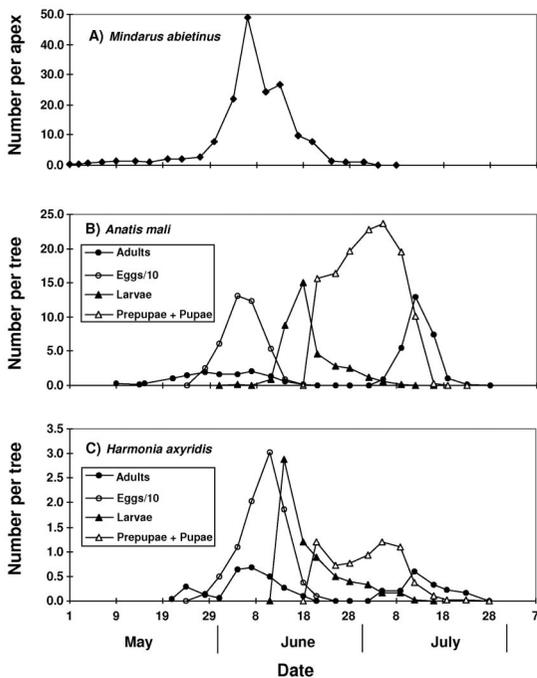
Fig. 2. Phenology and seasonal abundance of *M. abietinus* (A), *A. mali* (B), and *H. axyridis* (C) in a balsam fir Christmas tree plantation. Note that coccinellid egg density was divided by 10.

remained low from 24 June to 8 July, near the end of the aphid annual cycle.

The first spring *A. mali* adults were observed in an adjacent red pine plantation (*Pinus resinosa* Ait.) on 2 May, and in the balsam fir plantation 1 wk later (9 May), whereas adults of *H. axyridis* were first observed on 21 May (Fig. 2). Density of *A. mali* adults increased slowly to a maximum of 1.9 ± 0.3 (SE) adults per tree on 28 May, whereas *H. axyridis* reached a maximum of 0.6 ± 0.2 adult per tree on 4 June. Oviposition by both *A. mali* and *H. axyridis* began between 22 and 26 May and was completed by 16 June for *A. mali*, but continued until 24 June for *H. axyridis* (Fig. 2). An average density of 224.9 ± 22.0 eggs per tree was observed for *A. mali* compared with 59.9 ± 8.0 eggs per tree for *H. axyridis*. The maximum egg density was observed on 3 June for *A. mali* and on 12 June for *H. axyridis* (Fig. 2). For both species, no adult was

observed on trees between 21 June and 2 July, suggesting that overwintered adults had mostly died out by the third week of June (Fig. 2). The first *A. mali* larvae appeared on 4 June, whereas those of *H. axyridis* were first observed on 14 June. Thus, the first larvae of *A. mali* appeared ≈10 d before those of *H. axyridis*. Combined larval and prepupal mortality was estimated at 90% for *A. mali* and 93.6% for *H. axyridis* (number of pupae per tree/initial egg density on the same trees). The first pupae of both species appeared on 21 June, and the summer adults began to emerge by 5 July (Fig. 2). Pupal mortality was estimated at 11.0 and 32.2% for *A. mali* and *H. axyridis*, respectively. An average of 23.7 ± 3.1 summer adults of *A. mali* and 2.5 ± 0.5 summer adults of *H. axyridis* emerged per tree, representing a factor of population increase over a single generation (emerged adults/maximum density per tree in spring) of 12 and 4, respectively. Peaks of the different life stages of *H. axyridis* were seasonally more compressed than those of *A. mali* (Fig. 2).

Coccinellid Behavior. Mating of *A. mali* was observed on fir trees from 9 May until the first week of June (data not shown) compared with the end of May to the middle of June for *H. axyridis*. For both species, no mating of summer adults was observed in the balsam fir plantation (Table 2). Adults of *A. mali* fed on *M. abietinus* fundatrices that were the only aphid prey available on trees until the end of May, and began to feed within colonies (fundatrices and their viviparous progeny) when they became available. We observed that adult *A. mali* used its head to create openings between compact needles and penetrate bursting buds, whereas adult *H. axyridis* remained on the buds and were unable to feed on colonies until the shoot elongation stage. Spring adults of *H. axyridis* were significantly less active in food searching and predation than adults of *A. mali* (30.9% versus 65.1%; $\chi^2 = 48.89$; df = 1; $P < 0.0001$; Table 2). Summer adults of both species were mainly observed resting or walking toward the top of trees (especially *A. mali*), and were less active predators than spring adults (*A. mali* $\chi^2 = 78.91$; df = 1; $P < 0.0001$; *H. axyridis* $\chi^2 = 15.93$; df = 1; $P < 0.0001$; Table 2). Furthermore, summer adults of *A. mali* searched more and attacked aphids more frequently than those of *H. axyridis* (41.4% versus 5.7%; $\chi^2 = 33.95$; df = 1; $P < 0.0001$; Table 2). *A. mali* larvae were significantly more active in searching and attacking aphids (87.9%) than those of *H. axyridis* (72.5%; $\chi^2 = 30.78$; df = 1; $P < 0.0001$). Overall, 24.3%

Table 2. Behavioral activities on balsam fir trees of spring and summer adults and larvae of the coccinellids A. mali and H. axyridis in a Christmas tree plantation

Developmental stage	Species	N	Mating	Local searching and predation	Resting	Moving
Spring adults	*Anatis mali*	588	9.2	65.1	19.0	6.6
	Harmonia axyridis	123	9.8	30.9	41.5	17.9
Summer adults	*Anatis mali*	834	0.0	41.4	50.9	7.7
	Harmonia axyridis	53	0.0	5.7	73.6	20.7
Larvae	*Anatis mali*	1,205		87.9	8.9	3.2
	Harmonia axyridis	222		72.5	24.3	3.2

Behavioral data are expressed as relative abundance (%) for each species and stage. *N* is the total no. individuals observed.

Table 3.　Vertical distribution within balsam fir trees of spring and summer adults and larvae of the coccinellids *A. mali* and *H. axyridis* in a Christmas tree plantation

Developmental stage	Species	N	Lower crown	Middle crown	Upper crown
Spring adults	*Anatis mali*	588	22.4	44.4	33.2
	Harmonia axyridis	123	10.6	39.8	49.6
Summer adults	*Anatis mali*	834	12.8	21.3	65.8
	Harmonia axyridis	53	32.1	54.7	13.2
Larvae	*Anatis mali*	1,205	39.7	43.9	16.4
	Harmonia axyridis	222	38.7	45.9	15.3

Distribution data are expressed as relative abundance (%) for each species and stage. *N* is the no. individuals observed.

of *H. axyridis* larvae were observed resting on trees compared with only 8.9% for *A. mali* ($\chi^2 = 36.98$; df = 1; $P < 0.0001$; Table 2).

Within-Tree Distribution of Coccinellids. The vertical distributions of both spring and summer adults of *A. mali* on balsam fir trees were significantly different from those of *H. axyridis* (spring adults: $\chi^2 = 15.74$; df = 2; $P = 0.0004$; summer adults: $\chi^2 = 59.43$; df = 2; $P < 0.0001$; Table 3). Nearly 50% of all spring adults of *A. mali* were observed in the middle crown of trees, whereas most *H. axyridis* were observed in the upper crown (Table 3). However, the reverse was true for summer adults. Furthermore, for each species, the vertical distribution of spring versus summer adults was significantly different (*A. mali:* $\chi^2 = 151.08$; df = 2; $P < 0.0001$; *H. axyridis:* $\chi^2 = 26.28$; df = 2; $P < 0.0001$). For spring adults, the horizontal distribution on branches as a function of shoot age (year of shoot growth) was not significantly different between species ($\chi^2 = 4.42$; df = 2; $P = 0.1097$). Both species were observed predominantly on current year shoots (48.2 and 36.8%, respectively, for *A. mali* and *H. axyridis*) and on 1-yr-old shoots (45.1 and 53.7%, respectively, for *A. mali* and *H. axyridis*). In contrast, a significant difference was observed for summer adults ($\chi^2 = 10.37$; df = 2; $P = 0.0056$), with more *A. mali* being observed on current year shoots compared with *H. axyridis* (75.8% versus 66.7%). With respect to larvae, the vertical and horizontal distributions within trees were not significantly different between species (vertical: $\chi^2 = 0.36$; df = 2; $P = 0.8341$; horizontal: $\chi^2 = 0.79$; df = 2; $P = 0.6738$). Most larvae of both species were found on current year shoots (80.2 and 91.5%, respectively, for *A. mali* and *H. axyridis*) in the lower and middle crowns, locations where balsam twig aphid colonies developed (Table 3).

About five times more egg masses per tree were observed for *A. mali* (16.4 ± 1.5) than for *H. axyridis* (3.0 ± 0.4; $t = 8.72$; df = 48; $P < 0.0001$), but egg masses of *H. axyridis* had ≈30% more eggs per mass (20.5 ± 1.2 versus 13.7 ± 0.3 eggs; $t = -8.114$; df = 482; $P < 0.0001$). With respect to location, egg masses of *A. mali* were more often in the lower crown (77.1%) than those of *H. axyridis* (56.8%; Fig. 3), with their vertical distributions being significantly different ($\chi^2 = 38.69$; df = 2; $P < 0.0001$). No egg masses of *A. mali* were found on current year shoots (Fig. 3), and they were always laid on the under side of needles or twigs of balsam fir. In contrast, few egg masses of *H. axyridis*

were found on current year shoots, and nearly 20% were laid on the upper side of fir needles or twigs. Egg mass distribution was significantly different from a theoretical distribution based on the estimated volume of each third of the fir tree crown for *A. mali* ($\chi^2 = 64.63$; df = 2; $P < 0.0001$) but not for *H. axyridis* ($\chi^2 = 3.55$; df = 2; $P = 0.1700$), indicating that, for the latter species, egg masses were randomly distributed in balsam fir trees.

Most pupae of both species were found in the middle and lower crowns (Fig. 4), and their vertical distribution differed from the theoretical distribution of foliage for *A. mali* ($\chi^2 = 9.66$; df = 2; $P = 0.008$), but not for *H. axyridis* ($\chi^2 = 5.85$; df = 2; $P = 0.0544$). Thus, the two species had different vertical pupal distribution in balsam fir trees ($\chi^2 = 8.02$; df = 2; $P = 0.0183$). With respect to horizontal distribution, nearly 50% of *A. mali* pupae were found on 1-yr-old shoots, with only 16.9% being found on current year shoots, whereas most pupae of *H. axyridis* (73.3%) were found on the
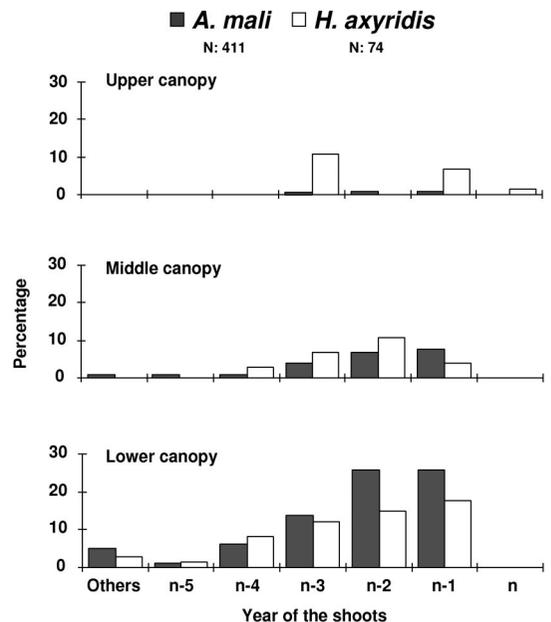
Fig. 3.　Egg mass distribution as a function of crown level and year of shoot development on balsam fir for two coccinellids, *A. mali* and *H. axyridis*, attacking the balsam twig aphid on balsam fir in a Christmas tree plantation.
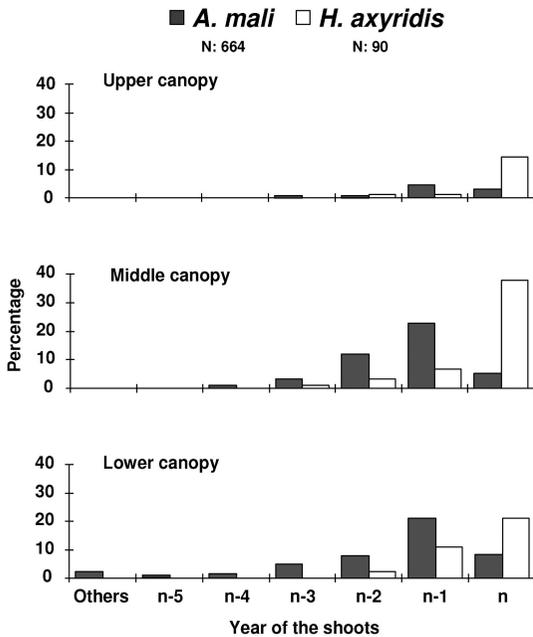
Fig. 4. Pupal distribution as a function of crown level and year of shoot development on balsam fir for two coccinellids, *A. mali* and *H. axyridis*, attacking the balsam twig aphid on balsam fir in a Christmas tree plantation.

current year shoots, the difference being highly significant ($\chi^2 = 112.41$; df = 4; $P < 0.0001$; Fig. 4). Furthermore, *A. mali* pupae were mostly found on the underside of needles and twigs of fir trees (nearly 80%), whereas those of *H. axyridis* were mainly found on the upper side.

Direct observations in the field indicated that *A. mali* pupae were attacked by conspecific adults and larvae, by larvae of *H. axyridis*, and by adults and nymphs of *Podisus serieventris* Uhl. (Heteroptera: Pentatomidae). *H. axyridis* pupae were also attacked by adults and larvae of *A. mali*, but no events of cannibalism or predation by *P. serieventris* were observed on this species. *A. mali* pupae were attacked more frequently on current year shoots than on older shoots ($\chi^2 = 10.095$; df = 3; $P = 0.0178$; Table 4). Such difference was not observed for *H. axyridis* ($\chi^2 = 0.801$; df = 3; $P = 0.8492$). For both species, pupal mortality was not linked with vertical distribution in balsam fir tree crowns (Table 4).

Discussion

Coccinellid communities associated with aphid outbreaks are generally dominated by two to four species accounting for >90% of overall abundance (Kring et al. 1985, Agarwala and Dixon 1992, Hodek and Honek 1996, Fondren et al. 2004). This was also the case in our study because the coccinellid community was clearly dominated by *A. mali* and, to a lesser extent, by *H. axyridis*, which, despite its very recent introduction into this region, was relatively abundant. If we assume that both species overwintered outside the study plantation (Gagné and Martin 1968, Obata 1986, Sakurai et al. 1993), the native *A. mali* colonized more rapidly the balsam fir plantation in spring than the exotic *H. axyridis*.

Synchrony with prey in space and time is an important characteristic of specialized predators, because they should evolve to optimize use of their specific prey in this as in other respects. The two dominant species of coccinellidae in our study appeared in May, but at different times. Spring adults of the native *A. mali* appeared in the first days of May when balsam twig aphid eggs were hatching, whereas those of the exotic *H. axyridis* appeared only a few weeks later when fundatrices were maturing. In Ontario, Gagné and Martin (1968) also reported *A. mali* in early May in red pine (*Pinus resinosa* Ait.) plantations, the same habitat where we first observed this coccinellid species in early May. Moreover, our direct observations of behavior showed that adults of *A. mali* were consistently more active searchers and predators of balsam twig aphid than those of *H. axyridis*. The high searching capacity and mobility of *A. mali* adults is adaptive because it feeds on aphid fundatrices whose density is always low and also because the density of the balsam twig aphid, and other aphids, is usually low in natural coniferous forests (Smith 1965b, Gagné and Martin 1968, Varty 1969). Coccinellidae that attack the fundatrix stage, such as *A. mali*, can have a significant impact on aphid populations because it precludes the formation of colonies (Kieckhefer and Kantack 1980, Frazer and Gill 1981, Elliott and Kieckhefer 1990).

Seasonal synchrony between coccinellid oviposition and peaks in aphid density on particular host plants has been often observed; it would allow optimal growth and development of larvae on ephemeral food resources (Dixon 1970, Honek 1980, Wright and Laing 1980, Evans and Dixon 1986, Hemptinne and Dixon 1997). Although oviposition began simultaneously for

Table 4. Pupal mortality (%) for the coccinellids *A. mali* and *H. axyridis* as a function of their location on balsam fir trees (shoot age and crown height) in a Christmas tree plantation

Species	Shoot growth unit relative to current year				Location in tree crown		
	n	$n-1$	$n-2$	$n-3$	Upper	Middle	Lower
A. mali	20.5 (112)	10.6 (321)	7.2 (138)	6.9 (58)	13.8 (58)	10.1 (297)	11.0 (309)
H. axyridis	31.8 (66)	29.4 (17)	50.0 (4)	—	40.0 (15)	20.5 (44)	45.2 (31)

Numbers in parentheses represent the no. pupae observed.

both species, *A. mali* maximum egg density and oviposition period were better synchronized with the peak of the aphid population. In comparison, oviposition by *H. axyridis* peaked slightly out of phase with it, when aphid density actually was decreasing during alate dispersal. This indicates that the native *A. mali* was better synchronized with the balsam twig aphid than the exotic *H. axyridis*, probably because it has evolved over a much longer period of time with this prey in North American coniferous forests. Adults of *A. mali* also began to feed earlier on young aphid colonies because they were able to penetrate the bursting buds of balsam fir and prey on developing aphid colonies before the shoot elongation stage, whereas *H. axyridis* was not observed doing so. This inability of *H. axyridis* adults to feed early within colonies (the most abundant resource) might also explain why its oviposition period was prolonged compared with that of *A. mali*, which closely matched the availability of large aphid colonies.

Niche partitioning is an important mechanism that permits coexistence of species (Rosenzweig 1981), including coccinellids (Honek 1985, Coderre and Tourneur 1986, Coderre et al. 1987). Partitioning of oviposition sites can be achieved temporally or spatially (Blackman 1965, Coderre et al. 1987). Because *H. axyridis* is a new exotic species in this ecosystem, our data may provide a reference for future studies on niche partitioning between these two species. For aphidophagous predators, oviposition site selection is critical for the survival of young larvae (Hodek 1973, Iperti and Quilici 1986, Coderre et al. 1987, Kairo and Murphy 1995, Lucas and Brodeur 1999). In addition to the differences in oviposition period observed in our study, a difference in preferred oviposition sites was also observed. Although Watson (1976) reported the inverse (on unidentified coniferous trees), we observed that *A. mali* females always laid their eggs on the underside of needles and twigs of the balsam fir. Other species such as *Anatis ocellata* L. also lay their eggs on the underside of leaves (Kesten 1969). *H. axyridis* also laid most of its eggs on the underside of needles and twigs of balsam fir, but nearly 20% were found on the upper side. This may accelerates hatching of these eggs because they are exposed to higher temperatures on the upper side. The egg distribution of both species varied also as a function of height within trees, with *A. mali* selecting the middle and lower crowns and *H. axyridis* showing no height preference. Nettleton and Hain (1982) reported that balsam twig aphid colonies develop mostly in the middle and lower crowns of trees, suggesting that adult *A. mali* may have evolved some host location strategies to deposit their eggs in close association with the natural distribution of this aphid. Egg laying at lower levels in the canopy by *A. mali* may reflect a good capacity of movement of larvae; these are known to disperse in all parts of trees after hatching (Smith 1965b, Gagné and Martin 1968). Preferential oviposition of *A. mali* in the lower parts of trees might also be linked to some microclimatic preferences of this species that evolved in natural coniferous forests. On the contrary, no oviposition height preference was observed for *H. axyridis* in balsam fir trees, indicating no microclimatic preference or a higher heat tolerance of this exotic species. Egg distribution of both species might be also influenced by predation and intraguild predation.

Searching activity and attack frequency are key determinants of predators efficacy, especially for coccinellid larvae, and this influences their potential to reduce aphid populations (Hodek 1967, Gurney and Hussey 1970, Murdoch 1973, Ehler and Miller 1978, Jervis and Kidd 1996, Elliott et al. 1996). Our direct observations over several weeks show that larvae of *A. mali* were searching for prey more actively than those of *H. axyridis* and that larvae of both species were more actively searching balsam fir foliage than the adults. Considering that larvae consume food to grow and adults mainly to reproduce and also because adults can disperse more efficiently than larvae, foraging success on a particular tree is crucial for larvae. Coccinellid mortality during larval development is usually high (Banks 1957, Frazer et al. 1981) and was estimated to exceed 90% for both species in this study. Cannibalism and intraguild predation have been reported elsewhere as major sources of larval mortality and appeared to be the primary factors responsible for high larval mortality in the balsam fir plantation. Cannibalism was observed with *A. mali* in this study and has also been observed in natural populations of most coccinellids (Hodek 1967, 1970, Fox 1975, Polis 1981, Mills 1982, Polis et al. 1989, Evans 1991, Agarwala and Dixon 1992). *A. mali* larvae attacked individuals of the same or smaller size. Although several studies reported cannibalism in *H. axyridis* (McClure 1987, Osawa 1989), including in balsam fir plantations (Cloutier and Jean 2002), this behavior was not observed in our study, probably because of the low density of this recent exotic species. Considering that *A. mali* larvae appeared earlier and are larger than those of *H. axyridis* (for same larval instars), intraguild predation was unidirectional in favor of *A. mali* during larval development. However, the last larval instar of both species are reciprocal intraguild predators of prepupae and pupae. This is the only stage in which *H. axyridis* has a direct impact on the native species *A. mali*.

Coccinellid last-instar larvae typically search for a protected site to pupate some distance away from their feeding site (Ng 1986, Hoelmer et al. 1993, Hodek and Honek 1996). In our study, pupal distribution on trees was significantly divergent between the two coccinellid species, *A. mali* pupae being most frequently localized on previous year shoots, whereas *H. axyridis* was mostly found on current year shoots where balsam twig aphid colonies developed (Nettleton and Hain 1982, Kleintjes 1997). Thus, larvae of *H. axyridis* do not follow the usual pattern found for coccinellid species in selecting a pupation site, at least on balsam fir (Osawa 1992). Our data suggest that the pupation site selection behavior of *A. mali* is more adaptive in reducing cannibalism and intraguild predation as such mortality decreased for pupae located away from

aphid colonies (current year shoots). Furthermore, vertical distribution of *A. mali* pupae on balsam fir was in agreement with its reported distribution in young red pine plantations (Gagné and Martin 1968). This species seems to prefer pupating in the lower crown of coniferous trees.

In this study, the native *A. mali* was much better synchronized with the early spring activity of its holocyclic prey, as its spring adults appeared in the habitat at the time of fundatrix emergence, about 2 wk earlier than *H. axyridis.* Direct observations of large numbers of individuals over several weeks also indicated that adults and larvae of *A. mali* were more active than those of *H. axyridis* in searching and predation on balsam fir foliage. Our observations also suggest that *A. mali*, because of its relatively large size, has a significant potential as intraguild predator of other coccinellids. Stage-specific density data showed that this *A. mali* population had a substantially higher net rate of increase on the aphid than that of *H. axyridis*, the adult-to-adult net reproductive rate of *A. mali* being three times higher than that of *H. axyridis.* The fact that *H. axyridis* was the second most abundant species in this plantation, only 2 yr after its first report in Quebec (Coderre et al. 1995), indicates that this species has a high potential of establishment in this region. In many cases, such as in balsam fir plantations, community structure before the introduction of invasive species such as *H. axyridis* is mostly unknown, and thus their real impact will be difficult to determine. However, this study evaluated the situation relatively early after *H. axyridis* arrival and further research should be carried out to observe the evolution of this new association.

Acknowledgments

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