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Predation on *Mindarus abietinus* infesting balsam fir grown as Christmas trees: the impact of coccinellid larval predation with emphasis on *Anatis mali*

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Abstract. The impact of natural coccinellid larval predation on the balsam twig aphid was evaluated by systematically removing coccinellid egg masses in a 6–8 year-old balsam fir (*Abies balsamea*) Christmas tree plantation in southwestern Quebec. Among coccinellid species hunting on fir foliage during development of *Mindarus abietinus* fundatrices in May, the indigenous *Anatis mali* was by far the most abundant and the main one to oviposit on trees. Comparison of trees on which coccinellid larval predation was excluded with control trees showed that *A. mali* had a marked impact both during and after the phase of rapid *M. abietinus* population growth that followed fundatrix maturation. On trees where coccinellid larvae were allowed, aphid colonies became inactive (i.e. no live aphids in the colony) about two weeks earlier than on controls. A strong dampening effect on aphid density was also observed in those colonies that remained active until the end of the aphid life cycle. Predation on aphid colonies reduced sexuals production, as the density of *M. abietinus* overwintering eggs per shoot subsequently was reduced by 32%. Predation by coccinellid larvae occurred too late to prevent needle damage to current year shoots, which affects the aesthetic value of Christmas trees. However, current year shoots measured in the mid-crown of trees late in the season were 19% longer on trees where aphid predation by coccinellid larvae was allowed, compared with trees where they were excluded. Rearing all larval stages of *A. mali* on 4th instar and adult sexuparae of *M. abietinus* indicated an average consumption of 269 aphids to complete larval development and pupate, which was equivalent to at least seven colonies of *M. abietinus* at maximum aphid density at the experimental site. *Anatis mali* is an important natural control factor of balsam twig aphid in Christmas tree plantations, hence its activity should be protected and possibly stimulated by favourable pest management practices.

Key words: natural predation, plantations, predator voracity, shoot damage, tree growth, Aphididae, Coccinellidae, *Abies balsamea*

Introduction

Coccinellids (Coleoptera: Coccinellidae) can play an important role in regulating aphid populations in various agroecosystems, their impact often being the highest of all aphidophagous insects (Hodek, 1967, 1970; Kring et al., 1985; Frazer, 1988; Elliot and Kieckhefer, 1990; Hodek and Honek, 1996). In the strongly seasonal climates of temperate regions, coccinellid larvae and adults overlap in time only partly, and thus may have very different impacts on early-season aphid population dynamics. It has been suggested that coccinellid impact on aphid density largely results from predation by the larval stages (Wright and Laing, 1980; Mills, 1982), however in most studies the impact of adults versus larvae has not been discriminated.

It should be possible to estimate the impact of either adult or larval predation by directly comparing aphid density reduction after excluding specific stages of particular interest (Hodek, 1970; Luck et al., 1988). From a practical viewpoint, measuring the impact of coccinellid predation and distinguishing larval from adult impact could be important to develop more effective Integrated Pest Management programs based on maximising alternatives to chemical insecticides (Rice and Wilde, 1988).

The balsam twig aphid, *Mindarus abietinus* Koch (Homoptera: Aphididae), is an important pest of balsam fir (*Abies balsamea* (L.) Mill.) and other fir species grown as Christmas trees in North America (Nettleton and Hain, 1982; Bradbury and Osgood, 1986; Kleintjes, 1997). As observed elsewhere in eastern Canada (Varty, 1966, 1968), *M. abietinus* has a monoecious life cycle in Quebec requiring three or four generations extending from late April – early May to mid-late July, with overwintering as diapausing eggs laid on tree foliage (Deland et al., 1998).

Feeding on fir needles from previous year shoots by immature fundatrices before bud break causes no apparent damage to fir. However, feeding by mature fundatrices and their progeny as colonies start to grow on newly opened buds and current year shoots results in needle distortion and shoot stunting (Varty, 1966; Nettleton and Hain, 1982; Bradbury and Osgood, 1986). Such damage is of little concern in natural forests, but in Christmas tree plantations, it reduces the aesthetic value of trees and can have substantial economic impact (Bradbury and Osgood, 1986). In a recent field study conducted in southwestern Quebec, we estimated that $\geqslant$5% of balsam fir shoots with *M. abietinus* damage resulted in tree rejection or downgrading at harvest, a threshold that corresponded to $\geqslant$9% of shoots being infested by aphid fundatrices in the preceding spring (Deland et al., 1998). The spraying of chemical insecticides can effectively control *M. abietinus* fundatrices and prevent damage to current year shoots in early spring (Nettleton and Hain, 1982; Bradbury and Osgood, 1986). However, insecticide spraying is costly and interferes with natural predators of the aphid as well as with other non-target organisms inhabiting Christmas tree plantations, including nesting migratory birds (Rondeau and Desgranges, 1991; Kleintjes, 1997; Deland et al., 1998).

Little is known about the diversity, abundance, and biology of natural enemies of the balsam twig aphid in North America (reviewed by Rather and Mills, 1989). Coccinellid and syrphid (Diptera: Syrphidae) larvae have frequently been observed directly preying on *M. abietinus* on fir grown as Christmas trees in plantations (Amman, 1963; Nettleton and Hain, 1982; Kleintjes, 1997), as well as in natural forests (Varty, 1969). Therefore, in a preliminary inventory of predators in several balsam fir plantations in southwestern Quebec in 1995, we concentrated on predominant species of coccinellid and syrphid predators of the aphid. Among the indigenous coccinellids, *Anatis mali* Say (Coleoptera: Coccinellidae), was the most abundant on trees both as adults and larvae, suggesting that its potential to regulate the balsam twig aphid should be investigated.

Of nearctic distribution, *A. mali* is the largest coccinellid in Canada, being widely distributed in coniferous forests (Smith, 1965; Watson, 1976; Larochelle, 1979; Gordon, 1985). Its biology is poorly known and its potential as a predator to reduce balsam twig aphid density is unknown. Kleintjes (1997) also observed *A. mali* larvae feeding on *M. abietinus* on balsam fir in Christmas tree plantations in Wisconsin. Other known prey for *A. mali* larvae are *Cinara* sp. aphids (Varty, 1969) and small larvae of the spruce budworm (*Choristoneura fumiferana*) (Clemens) (Lepidoptera: Tortricidae) (Smith, 1966). Other coccinellids that we observed foraging as adults and breeding on Christmas trees in southwestern Quebec are, in order of relative abundance: *Harmonia axyridis* Pallas which was recorded for the first time in Quebec in 1994 (Coderre et al., 1995), *Mulsantina hudsonica* Casey and *Coccinella septempunctata* L. (Berthiaume, 1998).

The objective of this study was to estimate the impact of coccinellid larval predation, mainly by *A. mali*, on balsam twig aphid density and damage to young balsam firs grown as Christmas trees.

Material and methods

We carried out field work in 1996 in a commercial Christmas tree plantation of balsam fir located near Sawyerville (45°20′ N, 71°34′ W), east of Sherbrooke, QC. Trees were 6–8 years old, about 1.5 m high, and had never previously been treated with insecticides. We selected a uniform experimental plot of 40 trees (4 rows of 10 trees) in a section where tree branches were not overlapping, so as to limit possible inter-tree dispersal of coccinellid larvae. Ground vegetation was low as a result of weed control, which may also have contributed to limit dispersal of coccinellid larvae among trees. At least 4 buffer rows of trees were kept around the plot to avoid any edge effect.

We measured the impact of coccinellid larval predation on aphid density by directly excluding all eggs (and therefore larvae), during the period of intense population growth resulting from reproduction of fundatrices and their apterous viviparous progeny. We randomly selected 20 trees in the experimental plot, each tree being randomly allocated to one of two treatments: (i) exclusion of coccinellid larvae, or (ii) unmanipulated control trees on which coccinellid larvae were allowed. For the first group of trees, we removed by hand all coccinellid egg masses at 4 day intervals (shorter than embryonic development) during the entire period of coccinellid oviposition (28 May to 13 June 1996). We estimated coccinellid egg density per tree on the first date by counting all coccinellid eggs on trees of both experimental groups. Because the trees were small, it was possible to localise visually and destroy all coccinellid egg masses found by systematic searching of the foliage. In addition, because of the large size-differential between *A. mali* and other coccinellids laying eggs on the trees, we were able to confirm that 90% of the removed egg masses belonged to *A. mali*. Exclusion was largely successful because no coccinellid larvae were observed on experimental trees during the experiment.

We determined the impact of coccinellid larval predation on aphid density by randomly sampling 4 current year (actively growing) shoots showing signs of actual or recent aphid activity (needles distortion, live or dead aphids and/or cast skins, and honeydew droplets) per tree, at 4 day intervals. The total number of shoots removed per tree was small relative to the total available (which was hundreds per tree). We collected shoot samples from 13 June (coccinellid egg hatching recently started) to 17 July (no live aphids remaining in colonies, end of the aphid cycle). Shoots collected were kept individually in 100 dram plastic bottles inside a cooler to stop development, reproduction and predation on aphids, until they could be examined under a stereomicroscope to count and sort aphids in the laboratory. The data were used to establish trends in aphid density per shoot, and proportion of aphid colonies that were ‘active’ (colonies with at least 1 live aphid).

Predation by coccinellid larvae on *M. abietinus* sexuparae in aphid colonies has the potential to limit aphid egg density. However, this needs to be verified because adult sexuparae are alate, and so both their emigration and immigration could affect any density relationship between aphid egg density and previous predation in aphid colonies. To evaluate treatment effects, we collected 10 current year shoots (1996 shoots approaching maturity) on each tree on 28 July, when egg laying had ceased. We estimated aphid egg density on current year shoots because balsam twig aphid oviparae mainly use these shoots for oviposition (Varty, 1966; Nettleton and Hain, 1982; Deland et al., 1998). *Mindarus abietinus* eggs were identified by their characteristic waxy fibre covering, and counted using a stereomicroscope in the laboratory.

To evaluate the impact of coccinellid larval predation on aphid damage, we counted all current year shoots on 1/8 of the tree periphery and classified them as with or without aphid damage at the end of the aphid's cycle on 28 July. A damaged shoot was defined as a shoot having one or more sharply distorted needles, which typically result from *M. abietinus* feeding. We also evaluated the potential impact of treatments on primary growth of the trees by measuring the length of the tree leader shoot and 20 current year shoots randomly selected at mid height of each tree on 22 August (1996 shoot elongation completed).

To estimate the maximum predation potential of *A. mali* larvae on the balsam twig aphid under controlled conditions, we randomly selected 25 newly hatched larvae from 30 egg masses collected in the plantation. They were then reared individually at 21 ± 2 °C in 10 cm diameter petri dishes in our field site laboratory, which allowed easy access to the supply of balsam twig aphids. Larvae were fed *ad libitum* with 4th instar and adult sexuparae, which is the largest morph of this aphid (Varty, 1968). Daily observations allowed monitoring of the number of aphid prey eaten and *A. mali*'s development by determining the larval instar reached. We reduced the number of coccinellid larvae under observation to fifteen at the beginning of their 4th instar, because their voracity was such that providing aphids for *ad libitum* feeding became limiting.

Statistical analysis

We calculated average values of aphid number per shoot (n = 4), aphid eggs per shoot (n = 10), and shoot length (n = 20) for each tree and each sampling date. The overall means in each experimental group (n = 10) were compared using the Student's t-test. We similarly compared tree leader length, coccinellid egg density per tree, and percentage of damage (transformed to arcsine $\sqrt{x}$) between treatments. We compared proportions of shoots containing live aphids for each date using Pearson's χ^2 tests. Statistical analyses were performed using Systat$^{\mathrm{TM}}$ (Kirby, 1993). For interpretation purposes, we refer to the 5% error rate as the threshold for significance.

Results

On first day of the experiment (28 May), coccinellid egg density was uniform, i.e. 63.8 ± 13.2 versus 70.4 ± 9.7 (mean ± SE) for trees assigned to the with and without coccinellid larvae treatments, respectively (t = 0.404; df = 18; $p = 0.691$).

After the beginning of coccinellid egg hatching, the percentage of active colonies declined steadily for trees with coccinellid larvae, while this percentage remained at 100% until 29 June for trees without coccinellid larvae (Figure 1). On 3 July and 7 July, only about 50% of previously infested shoots still contained live aphids for trees with coccinellid larvae, compared to 97.5 and 77.5% for trees without coccinellid larvae (3 July, $\chi^2 = 21.6$, df = 1, $p < 0.001$; 7 July, $\chi^2 = 6.54$, df = 1, $p = 0.011$).

On 13 June, near the start of predation by coccinellid larvae, aphid density in active colonies was similar for the two groups of trees (t = –0.57; df = 18; $p = 0.575$) (Figure 2). On 17 June, aphid density had increased twofold on trees without coccinellid larvae, but had decreased on trees with coccinellid larvae. For each sampling date from 17 June to 3 July, aphid density was at least twice higher on trees without coccinellid larvae than on trees with coccinellid larvae, these differences being significant (Figure 2). On 7 July and 11 July near the end of the aphid cycle, aphid density had already reached very low levels, and differences were no longer significant between treatments.

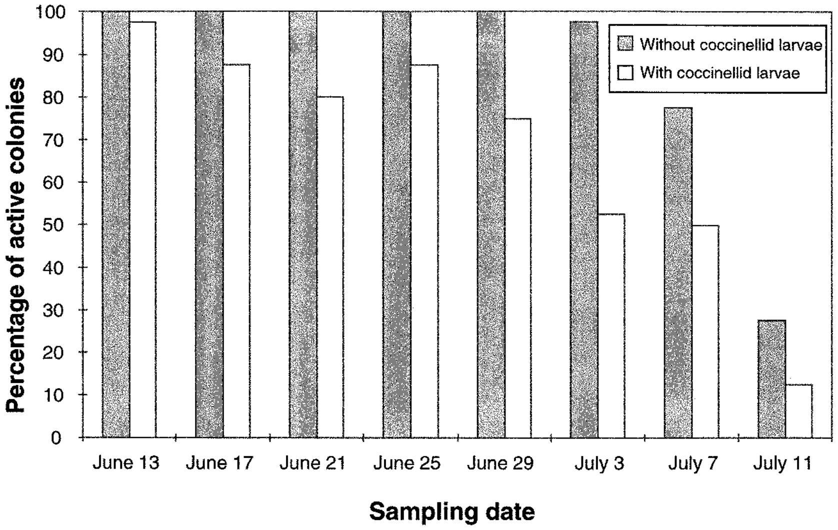

Figure 1. Trends in the percentage of active colonies (at least one live aphid per shoot) of the balsam twig aphid, *Mindarus abietinus*, on balsam fir trees with and without coccinellid larvae.

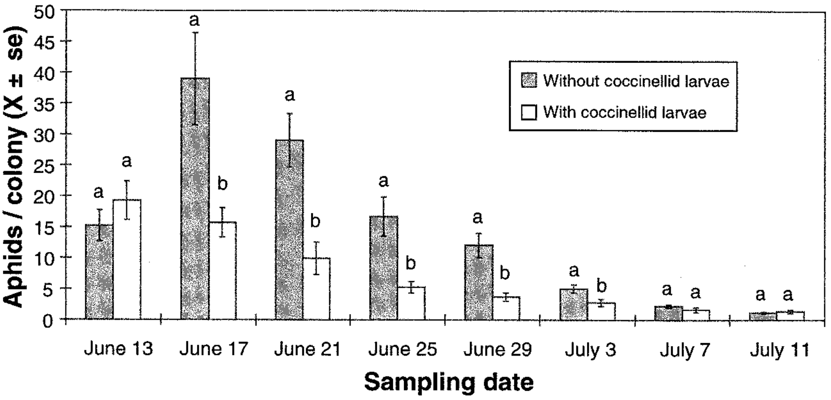

Figure 2. Trends in density of the balsam twig aphid within active colonies on balsam fir trees with and without coccinellid larvae. For each date, different letters indicate significant differences (t test, df = 18, $p < 0.05$).

At the end of the aphid cycle, trees on which coccinellid larvae were allowed had a mean aphid egg density about 32% lower than trees without coccinellid larvae (5.0 ± 0.3 versus 7.3 ± 0.4 for trees with and without coccinellid larvae respectively; t = 4.564, df = 18, $p < 0.001$). The percentage of shoots with typical needle distortion (51–54%), and the length of the tree leader (47–51 cm) were not significantly different (Table 1) among treatments. However, the current year mid-crown shoots on trees with coccinellid larvae were on average 19% longer than on trees without them (Table 1).

Table 1. Impact of excluding coccinellid larval predation during balsam twig aphid population growth, on the aphid egg density, percentage needle damage to fir shoots, mid-crown shoot length, and tree leader length, on 6–8 year-old balsam fir grown as Christmas trees, Sawyerville, QC

Variable	Coccinellid larvae		p value*
	Present	Excluded	
M. abietinus eggs (*N*/shoot)	5.0 ± 0.3	7.3 ± 0.4	< 0.001
Shoot damage (%)	53.5 ± 9.4	50.8 ± 8.0	0.770
Shoot length (cm)	15.3 ± 0.2	12.9 ± 0.3	< 0.001
Tree leader length (cm)	50.6 ± 2.7	47.4 ± 3.2	0.451

Values given are mean ± SE, with n = 10 replicate trees per treatment.
*Student's t-test, df = 18.

As expected, the number of 4th instar or adult sexuparae of balsam twig aphid eaten by *A. mali* in the laboratory increased markedly with larval instar. Maximum consumption by 4th instar larvae of *A. mali* averaged 190.1 ± 3.8 (mean ± SE), representing 71% of the average total of 269 aphids consumed during the whole larval life of *A. mali*. Consumption of first, second and third instars averaged 14.0 ± 0.7, 23.4 ± 1.0 and 39.8 ± 2.0.

Discussion

Impact assessment of entomophagous insects on pest populations is a key step, but also a major difficulty, in the evaluation of biological control programs (Lapchin et al., 1987; Luck et al., 1988). The direct hand removal of predators allows for unambiguous evaluation of their impacts but the method is rarely used because it is tedious (Luck et al., 1988; Hodek and Honek, 1996; Jervis and Kidd, 1996). However, contrary to the use of exclusion with cages, hand removal avoids microclimatic effects, which are the greatest limitation of predator exclusion with cages. Our results are mostly relevant for the specific contribution of larval stages of *A. mali* which was by far the predominant species in our study, representing 90.1% of all coccinellid larvae observed on control trees. These data are also consistent with those of a general survey of the plantation conducted in parallel with this study (Berthiaume, 1998). The systematic removal of coccinellid egg masses for the entire period of egg laying permanently excluded subsequent presence of coccinellid larvae. Complete searching of the foliage of experimental trees allowed us to verify that coccinellid larvae were absent on trees of the exclusion treatment, especially 3rd and 4th instars, which have by far the greatest predatory potential.

Coccinellid females tend to lay their eggs in a prey density-dependent manner (Hagen, 1962; Ives, 1981; Iablokoff-Khnzorian, 1982; Hodek, 1993; Hemptinne and Dixon, 1997; Dixon, 1998). The fact that coccinellid egg density between the two groups of trees was similar when the experiment began suggests equal balsam twig aphid density on the two groups of trees. This was supported by similar numbers of aphids counted per infested shoot between the two groups of trees at the beginning of coccinellid egg hatching. Thus, we attributed any differences between the two groups of trees from mid to late June to the direct or indirect consequences of excluding *A. mali* larvae.

The faster reduction in the percentage of active colonies on unmanipulated trees suggests that coccinellid larvae were able to completely destroy growing balsam twig aphid colonies once discovered. Starting on 13 June, previously active aphid colonies that were empty increased in numbers on trees that were not manipulated, while colony extinction on the coccinellid-suppressed trees did not start before the end of June (Figure 1).

The efficacy of specialised aphid predators like coccinellid larvae is largely determined by their voracity (Gurney and Hussey, 1970; Mills, 1982). In experimental conditions, larvae of *A. mali* ate an average of 269 fourth instar or adult sexuparae of balsam twig aphid before pupating, which represents approximately seven aphid colonies at the 1996 average density in the plantation. This estimate is probably conservative because aphid colonies also contained younger aphid stages. Moreover, total food consumption by coccinellid larvae usually increases under fluctuating temperatures (Gawande, 1966; Obrycki and Tauber, 1981; Hodek and Honek, 1996), suggesting that *A. mali*'s predatory potential is probably higher in field conditions than estimated here. By comparison with Varty's (1969) partial data on consumption of *M. abietinus* alates by larvae of *M. hudsonica* (also well adapted to predation on the aphid), *A. mali*'s voracity seems to be at least 10 times higher, which might be expected given the much larger size of *A. mali*.

Coccinellids are thought to be capable of preventing aphid population outbreaks in several systems (Hodek, 1967, 1970; Frazer and Gill, 1981; Frazer, 1988). Balsam twig aphid population growth in southwestern Quebec is limited to a few weeks in late spring-early summer, during parthenogenetic reproduction of fundatrices and their apterous viviparous progeny on current year shoots (Deland et al., 1998). Regulation of *M. abietinus* population by coccinellid predation would more likely depend on predation by the overwintered adults on immature aphid fundatrices, than on subsequent larval predation. Obviously, this cannot occur before first instar larvae have started to hunt for prey, which implies that overwintered female beetles have fed sufficiently to regenerate their ovaries and lay eggs on trees.

Nevertheless, our results reveal that coccinellid larval predation had an impact upon early stages of aphid population growth. The fir trees from which coccinellid larvae were excluded had a sharp increase in aphid density in mid June, which was mostly prevented on the control trees. Data on percentage of active colonies (Figure 1) and aphid density (Figure 2) over the period of 3–4 weeks starting 13 June revealed a prolonged dampening effect of coccinellid larval predation on aphid dynamics.

In aphid population dynamics, the impact of natural enemies during the regressive phase that follows population build-up is also critical, but for the next rather than the current season (Hodek, 1973). Predation then has the potential to reduce the density of aphid overwintering eggs and thus the number of fundatrices for the next growing season (Hodek, 1973). Our results show that, despite intense dispersal of sexuparae in the plantation (Deland et al., 1998), predation by coccinellid larvae on control trees reduced the density of aphid overwintering eggs by 32%. There is no evidence that coccinellid larvae eat balsam twig aphid eggs. The observed reduction can be attributed to predation on the preceding stages of the aphid, mainly on progenies of fundatrices and their apterous daughters. Coccinellid larvae may also have fed on the sexuales. However, because of their small size and spatial dispersion, *M. abietinus* sexuales probably represent unprofitable prey for coccinellid larvae, especially for older stages of *A. mali*.

Substantial mortality of balsam twig aphid fundatrices in the spring does not protect plantations from high densities of overwintering eggs later in the summer, because massive immigration of sexuparae by flight is possible (Deland et al., 1998). Predation on adult sexuparae (and its resulting impact on aphid egg density) could be expected only from highly mobile predators capable of strong numerical response through immigration. In this system, such predators include adults of some coccinellids, and especially those of the cantharid *Podabrus rugosulus* Leconte (Coleoptera: Cantharidae) which was an active predator of sexuparae in the plantation (Berthiaume 1998).

Balsam twig aphid damage through reduced tree and shoot growth is rarely considered, by contrast with aesthetic damage to shoots which generally is of greatest concern to Christmas tree growers (Smith et al., 1981; Martineau, 1985; Rose and Lindquist, 1994). Allowing coccinellid larval predation on control trees resulted in increased shoot growth at the mid-crown level, but not of the tree leader. In a study conducted simultaneously in the same plantation, Desrosiers (1998) found that on similarly infested trees, aphid control with the systemic insecticide acetylphosphoramidothioate (Acecap97^{TM}, Creative Sales, Fremont, NE) increased growth of the tree leader and apical-crown shoots, but not growth of lateral (sub-dominant) mid-crown shoots. Thus although balsam twig aphid damage is usually limited to shoots of the mid-to-low crown of balsam fir (Varty, 1966; Nettleton and Hain, 1982; Bradbury and Osgood, 1986), aphids have a general impact on tree growth, affecting even the most vigorous shoots at the tree top. In our experiment, control trees were only partly protected by coccinellid larval predation, which may explain that beneficial effects were not as complete as with insecticide treatment. Further demonstration that coccinellid larval predation on aphids could enhance growth in other conifer species is needed, as it could have practical implications for tree plantation management.

Coccinellid larvae did not reduce the incidence of shoot damage because their impact occurred too late in the phenology of the aphid. Shoot damage results from feeding by mature fundatrices and their progeny on newly opened buds and shoots at early stages of shoot elongation and needle differentiation (Varty, 1966). These events occurred in early June, when coccinellid eggs had not yet hatched. When larvae started to impact aphid colonies in mid June, it was too late to completely prevent needle damage on shoots. However, coccinellid predation may have reduced the severity of damage. The early destruction of numerous aphid colonies and the reduction of aphid density in surviving colonies may have slowed or stopped the progress of damage on aphid infested shoots. Depending on remaining growth potential (length, needle differentiation), final shoot maturation could override or reduce the visibility of aesthetic damage.

Several approaches might be tried to increase coccinellid predation and prevent balsam twig aphid damage in fir plantations. Artificial food has been used to attract many coccinellid species for pest control purposes (Ewert and Chiang, 1966; Schiefelbein and Chiang, 1966; Ben Saad and Bishop, 1976; Mensah and Madden, 1994). This approach might result in faster ovarian maturation and earlier oviposition, thus improving synchrony of larval predation with balsam twig aphid colonies, hence probably reducing the risk of shoot damage.

The impact of larval predation by *A. mali* and other coccinellids breeding on fir grown as Christmas trees cannot be generalised from our results. The abundance of *A. mali* in 1996 in the plantation may have been exceptional due to high balsam twig aphid density, the historical absence of insecticide use, and other unknown favourable conditions. Nevertheless, our data confirm that *A. mali* is an important specialist aphid predator in the balsam fir plantation system. Referring to coccinellids, Frazer (1988, p. 235) stated that effectiveness is revealed when ‘the density of an aphid population would be different if the coccinellids were not present’. According to this criterion for effectiveness, *A. mali* larvae were effective in the balsam fir system studied. Their exclusion not only provided a direct measure of their dampening effect on aphid population growth in early summer, but also of their favourable effect on tree growth and potential inter-season impact on aphid dynamics. Given a rotation cycle of nearly 10 years for balsam fir grown as Christmas trees under local climatic conditions, there is considerable opportunity for using *A. mali* in biological control on pre-harvest trees on which aesthetic damage control is not critical. More research is needed to improve our knowledge on the biology and ecology of *A. mali* and other aphid predators in this system, in order to define specific management procedures to protect and increase their effectiveness against the balsam twig aphid.

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