

The influence of understory nectar resources on parasitism of the spruce budworm *Choristoneura fumiferana* in the field

Naomi Cappuccino,^{1,2} Marie-José Houle² and Jayson Stein¹

¹Department of Zoology, University of Texas at Austin, Austin, TX 78712, U.S.A. and ²Groupe de Recherche en Écologie forestière, Université du Québec à Montréal, CP 8888, succ. Centre-ville, Montréal (Québec), H3C 3P8 Canada

- Abstract**
- 1 Nectar provided by flowering plants has been suggested as an important factor enhancing parasitism rates of herbivorous insects. Artificial nectar has been shown to increase parasitoid longevity and fecundity in laboratory studies.
 - 2 We studied the influence of understory nectar on parasitism of the spruce budworm *Choristoneura fumiferana* in a field experiment in which we either removed understory flowering herbs or sprayed a sucrose solution on the understory vegetation in 0.25 ha quadrats.
 - 3 Cohorts of laboratory-reared second instars were transferred the field to evaluate parasitism in the quadrats. The larvae were harvested as fifth instars and reared for parasitoids.
 - 4 Parasitoids of early instars caused greater mortality in the supplemental sucrose treatment than in the vegetation-removal treatment or the control. Parasitoids of older larvae did not respond to the treatments. Larger-scale treatments may be necessary to elicit a response by the larger parasitoids that attack older larvae.

Keywords Artificial nectar, boreal forest, *Choristoneura fumiferana*, *Elachertus cacoeciae*, parasitoids, spruce budworm.

Introduction

Numerous studies, mostly from agricultural systems, have established the importance of diverse vegetation in promoting greater parasitism rates of phytophagous insect pests (Sheehan, 1986; Russell, 1989; Andow, 1991). Parasitoids may be more abundant or more effective in diverse vegetation for several reasons, including the presence of favourable microhabitats, alternate hosts or more abundant nectar resources for foraging adults (Root, 1973; Russell, 1989). Leius (1967) reported higher parasitism of forest tent caterpillars *Malacosoma disstria* by the generalist ichneumonid *Itoplectis conquisitor* in orchards with a richer community of understory wildflowers. Stephen *et al.* (1997) argue that homogeneous loblolly pine plantations, with their barren understories, lack the nectar resources required by parasitoids of the southern pine beetle *Dendroctonus frontalis*. Several authors have shown that providing flowers, nectar, honey or sugar-water to parasitic wasps in laboratory cultures increases their longevity, fecundity or both (Leius, 1961; Syme, 1975; Foster & Ruesink, 1984; Dyer & Landis, 1996; Mathews

& Stephen, 1997; Fidgen & Eveleigh, 1998). Evans & Swallow (1993) demonstrated that artificial honeydew applied to alfalfa fields attracted a variety of natural enemies.

Forest diversity has been suggested to play a role in determining the severity of outbreaks of perhaps the most destructive forest pest in North America, the spruce budworm *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). The impact of the budworm on its main host plant, balsam fir *Abies balsamea*, following an outbreak is quite variable, with more diverse stands often suffering lower mortality (MacLean & Ostaff, 1989; Bergeron *et al.*, 1995). By transferring laboratory-reared larvae and pupae to field sites in both contiguous coniferous forest and fir stands surrounded by deciduous vegetation, Cappuccino *et al.* (1998) demonstrated that certain budworm parasitoids, including the ichneumonid *Itoplectis conquisitor* and the tachinid *Actia interrupta*, were more important in the more diverse landscape. The potential importance of understory flowers in promoting higher budworm parasitism rates in more diverse forests has been suggested by Simmons *et al.* (1975) and Bradette (1994).

The present experiment was designed to test the effect of understory nectar resources on parasitism of the spruce budworm, both by removing understory flowering herbs and by supplementing the available nectar resources with a sucrose

Correspondence: Naomi Cappuccino, Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada. E-mail: ncappucc@ccs.carleton.ca

solution sprayed on the understory vegetation. Although a sucrose solution together with a protein supplement better mimics natural nectar and honeydew (Hagen, 1986), Evans & Swallow (1993) found that most parasitoids and predators in alfalfa fields responded consistently to applications of sucrose only; adding protein increased enemy abundance in some cases, but this additional response was not consistent. We therefore opted for a simple sugar-water solution as a nectar supplement.

Materials and methods

The study plots were located in and adjacent to the Forêt d'enseignement et de recherche du lac Duparquet (79°12' W; 48°28' N) in the Abitibi region of Québec. On 21 and 22 May 1996, before the understory vegetation had begun to emerge, three 50 × 50 m quadrats were set up along each of seven transects in deciduous or mixed forest. At least 50 m separated the borders of adjacent quadrats; transects were at least 1 km apart. The main criterion for the placement of each quadrat was the presence of a cluster of at least eight balsam fir saplings 1–3 m in height; the quadrats were centred on these clusters. The understory vegetation had not emerged at this time, so the abundance of species that flower during the period of spruce budworm development could not be used as a criterion in choosing sites. The three quadrats along each transect were assigned one of the following treatments randomly: removal of understory herbs, addition of sucrose solution or untreated control.

A pre-treatment herbaceous biomass sample was taken in each quadrat, on 6 June, as soon as the understory herbs had emerged, but before flowering stems were apparent. All herbaceous vegetation in four 1 m² microquadrats randomly placed in each large quadrat was removed, dried and weighed.

From 7 to 14 June, herbaceous understory vegetation in the removal-treatment quadrats was cut at ground level with a swing-blade. Care was taken to remove all species that flower during the period of budworm larval and pupal development. To assess the effectiveness of the removal treatment, flowering stems were counted in four 1-m² microquadrats in each control and removal plot on 4 July.

The solution applied to the sucrose-addition treatment was prepared by mixing 100 g of granulated sugar per litre of water. The water was taken from Lake Duparquet and passed through a cotton filter before mixing. The treatment consisted of 30 l of solution sprayed on each quadrat with a 7.5-litre hand-held sprayer set to a fine mist. The first treatment was applied on 14 June, at which time the larvae had reached third instar. Heavy rains required us to repeat the treatment on 18 and 26 June.

Laboratory-reared spruce budworm larvae, obtained from the Canadian Forest Service (Sault Ste. Marie, Ont.) were introduced to the balsam fir saplings on 23 May, well in advance of budburst. The larvae had overwintered as diapausing second instars in rolls of parafilm-backed gauze. Four segments of gauze, each containing 10–25 larvae, were pinned to the branchlets of each sapling. Larvae introduced in this manner break diapause at the same time as naturally occurring larvae, move out to the tips of the branches and begin feeding.

The larvae were harvested on 1 July, when the most advanced were sixth instars. In addition to searching the saplings

thoroughly for live larvae, we also collected all foliage with larval webbing and feeding damage, since these sites often harbour cadavers, parasitoid cocoons or larvae paralysed by the eulophid *Elachertus cacoeciae* (Howard). Collected larvae and foliage were transported to the laboratory in large plastic bags kept in a cooler. All live larvae were placed on benomyl-free artificial diet (McMorran, 1965) in individual plastic cups to be reared for parasitoids. The foliage was meticulously searched for cadavers, paralysed larvae and parasitoid cocoons, which were placed in cups without diet.

The results were analysed as a series of two-way analysis of variance (ANOVA) with the main effects being transect (block) and treatment. Only the treatment effects are reported. Parasitism rates were arcsin transformed before analysis.

Results

No significant difference in the pre-treatment biomass of understory herbs was observed between the three treatments ($F = 0.981$, $P = 0.403$). By mid-June, the following species were in flower (in approximate order of abundance): *Clintonia borealis*, *Maianthemum canadense*, *Trientalis borealis*, *Rubus pubescens*, *Streptopus roseus*, *Cornus canadensis*, *Aralia nudicaulis*, *Ribes lacustre*, *Viburnum trilobum* and *Sambucus pubens*. The density of flowering stems in the control treatment was $15.29 \pm 3.12/4 \text{ m}^2$. Flowering stem density was significantly reduced in the removal treatment to a mean of 0.57 ± 0.30 stems/4 m² ($F = 22.65$, $P = 0.003$).

Careful examination of foliage bearing larval feeding damage and needles webbed together with silk revealed numerous cadavers, paralysed larvae and parasitoid cocoons, in addition to live larvae. The total number of budworms collected in each quadrat ranged from 19 to 46 (mean = 27.3). The parasitoids can be grouped into two categories: those that had already killed or paralysed the larvae at the time of harvest, and those that emerged from larvae that were collected live and reared on artificial diet. The first group includes the braconid *Apanteles morrisoni* Mason and the eulophid *Elachertus cacoeciae*. These early species attack small larvae (Dowden *et al.*, 1950) and pupated either before or shortly after the harvest. The second group includes the tachinids *Actia interrupta* (Curr.), *Lypha setifacies* (West) and *Phryxe pecosensis* (Townsend), and the ichneumonids *Tranosema rostrale* (Brischke) and *Exochus nigripalpis tectulum* (Townes). These late species attack large larvae and emerge from sixth instars and pupae (Dowden *et al.*, 1950).

A significant treatment effect was observed for the early parasitoids; the addition of sugar resulted in a parasitism rate that was significantly higher than that in the control ($F = 5.01$, $P = 0.026$). The parasitism rate in the removal treatment was not significantly lower than that of the control. The eulophid *Elachertus cacoeciae* accounted for most of the parasitism by this group; it alone showed a significant treatment effect (Fig. 1). *Apanteles morrisoni* responded in the same fashion, but it was not abundant enough to analyse separately, occurring in only four of the 27 quadrats (mean \pm SE for the three treatments: removal 0.011 ± 0.011 ; control 0.014 ± 0.014 ; addition 0.049 ± 0.026).

No single species from the group of late parasitoids was abundant enough to warrant separate analysis. The dipteran

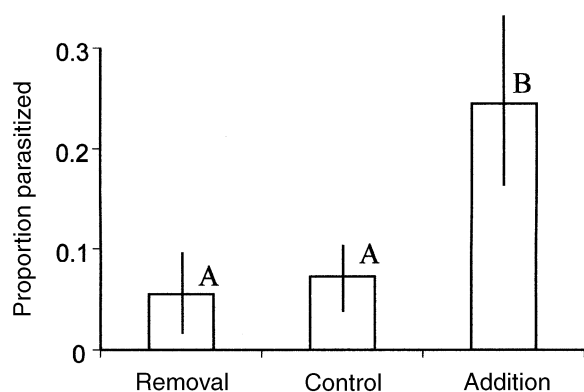


Figure 1 Parasitism of budworm larvae by *Elachertus cacoeciae* in the flower-removal treatment, control treatment and sucrose-supplement treatment. Means that are not significantly different at $\alpha=0.05$ according to Fisher's Protected LSD test are indicated by the same letter. ANOVA performed on arcsin-transformed data revealed a significant treatment effect ($F=5.87$, $P=0.017$).

parasitoids showed a non-significant tendency towards higher abundance in the control (0.190 ± 0.59) than in either the addition (0.054 ± 0.36) or the removal (0.03 ± 0.2 ; $F=3.65$, $P=0.057$) treatment. Considered as a group, late parasitoids (the dipterans plus *Tranosema* and *Exochus*) showed no significant treatment effect ($F=0.88$, $P=0.44$).

Discussion

Most species of parasitic wasps are synovigenic, that is, they emerge with a small number of eggs and must feed to produce more (Flanders, 1950). Some synovigenic parasitoids acquire nutrients for egg production by host-feeding, others rely on a source of nectar in the habitat (Mathews & Stephen, 1997). Although *Elachertus cacoeciae*, a eulophid parasitoid of the spruce budworm, benefits from both sources of nutrients, Fidgen & Eveleigh (1998) found that adult females lived just two weeks when host-feeding was supplemented with water only. However, female longevity increased nearly six-fold when a honey-water solution was provided in addition to budworm larvae (Fidgen & Eveleigh, 1998). Based on our results, it appears that the benefits of a source of carbohydrates to laboratory-reared *Elachertus* also apply to *Elachertus* foraging in the field, at least in the forest understory.

Elachertus cacoeciae, *Apanteles morrisoni* and other early parasitoids of the spruce budworm are small wasps (<2 mm). The dipteran and hymenopteran parasitoids of later instars, which did not show a significant response to supplemental sugar in the present study, are much larger (4–8 mm). These larger parasitoids may forage on a much broader spatial scale than the 0.25 ha plots used in the present study. In addition, at the time when the larger parasitoids are active, the presence of abundant natural sugar in the understory in the form of honeydew raining down from the canopy, as well as the flowering of mountain maple *Acer spicatum* in the subcanopy, may have overwhelmed the differences in sugar availability imposed by our treatments. Mountain maple flowers are visited by flies (personal observa-

tion) and may be an important resource for tachinid parasitoids of the budworm, such as *Actia interrupta*.

In the absence of rain, the effect of sucrose can last up to 7 days in agricultural fields (Evans & Swallow, 1993). Application of sugar-water solutions, or of more complex solutions that more closely meet the nutritional needs of parasitoids (e.g. Mathews & Stephen, 1997), may thus have potential as a component of integrated pest management in some systems. Large-scale application of nutrients for parasitoids would probably be difficult in most years in the boreal forest, because frequent rains would quickly wash the nutrients from the foliage. On the other hand, increasing the abundance of natural nectar sources in the boreal forest understory may be feasible. Gaps in the forest, open canopies and mixed forests all have more abundant understory flowering herbs than dense, pure stands of conifers (Simmons *et al.*, 1975; DeGrandpré *et al.*, 1993). If deciduous stands, in addition to having richer understories, also influence budworm parasitism by providing alternate hosts for parasitoids (e.g., Maltais *et al.*, 1989), managing forests to preserve a rich mosaic of stand types could prove to be an effective means of minimizing budworm impact in times of outbreak (Bergeron *et al.*, 1995; Cappuccino *et al.*, 1998). Further studies, performed at both a larger spatial scale and at different times during the budworm's cycle, will be necessary to understand how best to enhance the efficacy of its parasitoids.

Acknowledgements

We thank Robert McCron of the Canadian Forest Service (Sault Ste. Marie, Ontario) for providing the larvae as well as Jacques Régnière and Pierre Duval of the Canadian Forest Service (Ste-Foy, Québec) for sending the artificial diet. This study was funded by a Reeder Fellowship from the Zoology Department of the University of Texas at Austin.

References

- Andow, D.A. (1991) Vegetation diversity and arthropod population response. *Annual Review of Entomology*, **36**, 561–586.
- Bergeron, Y., Leduc, A., Morin, H. & Joyal, C. (1995) Balsam fir mortality following the last spruce budworm outbreak in north-western Québec. *Canadian Journal of Forest Research*, **25**, 1375–1384.
- Bradette, C. (1994) *Étude de l'influence de facteurs biotiques sur l'intensité du parasitisme chez la tordeuse des bourgeons de l'épinette*, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae). PhD Dissertation, Université de Sherbrooke, Sherbrooke, Québec, Canada.
- Cappuccino, N., Lavertu, D., Bergeron, Y. & Régnière, J. (1998) Spruce budworm impact, abundance and parasitism rate in a patchy landscape. *Oecologia*, **114**, 236–242.
- DeGrandpré, L., Gagnon, D. & Bergeron, Y. (1993) Changes in the understory vegetation of the southern boreal forest following fire. *Journal of Vegetation Science*, **4**, 803–810.
- Dowden, P.B., Carolin, V.M. & Dirks, C.O. (1950) Natural control factors affecting the spruce budworm in the Adirondacks during 1946–48. *Journal of Economic Entomology*, **43**, 774–783.
- Dyer, L.E. & Landis, D.A. (1996) Effects of habitat, temperature, and sugar availability on longevity of *Eriborus terebrans* (Hymenoptera: Ichneumonidae). *Environmental Entomology*, **25**, 1192–1201.
- Evans, E.W. & Swallow, J.G. (1993) Numerical responses of natural

- enemies to artificial honeydew in Utah alfalfa. *Environmental Entomology*, **22**, 1392–1401.
- Fidgen, J.G. & Eveleigh, E. (1998) Life history characteristics of *Elachertus cacoeciae* (Hymenoptera: Eulophidae), an ectoparasitoid of spruce budworm larvae, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Canadian Entomologist*, **130**, 215–229.
- Flanders, S.E. (1950) Regulation of ovulation and egg disposal in the parasitic Hymenoptera. *Canadian Entomologist*, **82**, 134–140.
- Foster, M.A. & Ruesink, W.G. (1984) Influence of flowering weeds associated with reduced-tillage in corn on a black cutworm (Lepidoptera: Noctuidae) parasitoid, *Meteorus rubens* (Nees von Esenbeck). *Environmental Entomologist*, **13**, 664–668.
- Hagen, K.S. (1986) Ecosystem analysis: plant cultivars (HPR), entomophagous species and food supplements. *Interactions of Plant Resistance and Parasitoids and Predators of Insects* (ed. by D. J. Boethel and R. D. Eikenbary), pp. 151–197. Wiley, New York.
- Leius, K. (1961) Influence of food on fecundity and longevity of adults of *Itopectis conquisitor* (Say) (Hymenoptera: Ichneumonidae). *Canadian Entomologist*, **93**, 771–780.
- Leius, K. (1967) Influence of wildflowers on parasitism of tent caterpillar and codling moth. *Canadian Entomologist*, **99**, 444–446.
- MacLean, D.A. & Ostaff, D.P. (1989) Patterns of balsam fir mortality caused by an uncontrolled spruce budworm outbreak. *Canadian Journal of Forest Research*, **19**, 1087–1095.
- Maltais, J., Régnière, J., Cloutier, C. & Perry, D.F. (1989) Seasonal biology of *Meteorus trachynotus* Vier. (Hymenoptera: Braconidae) and of its overwintering host *Choristoneura rosaceana* (Harr.) (Lepidoptera: Tortricidae). *Canadian Entomologist*, **121**, 745–756.
- Mathews, P.L. & Stephen, F.M. (1997) Effect of artificial diet on longevity of adult parasitoids of *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Environmental Entomology*, **26**, 961–965.
- McMorran, A. (1965) A synthetic diet for the spruce budworm *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). *Canadian Entomologist*, **97**, 58–62.
- Root, R.B. (1973) Organization of a plant–arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs*, **43**, 95–124.
- Russell, E.P. (1989) Enemies hypothesis: a review of the effect of vegetational diversity on predatory insects and parasitoids. *Environmental Entomology*, **18**, 590–599.
- Sheehan, W. (1986) Response by specialist and generalist natural enemies to agroecosystem diversification: a selective review. *Environmental Entomology*, **15**, 456–461.
- Simmons, G.A., Leonard, D.E. & Chen, C.W. (1975) Influence of tree species density and composition on parasitism of the Spruce Budworm, *Choristoneura fumiferana* (Clem.). *Environmental Entomology*, **4**, 832–836.
- Stephen, F.M., Lih, M.P. & Browne, L.E. (1997) Augmentation of *Dendroctonus frontalis* parasitoid effectiveness by artificial diet. *Proceedings: Integrating Cultural Tactics Into the Management of Bark Beetle and Reforestation Pests* (ed. by J. C. Grégoire, A. M. Liebhold, F. M. Stephen, K. R. Day and S. M. Salom), pp. 15–22. USDA Forest Service General Technical Report NE-236. Northeastern Experimental Station, Radnor, PA.
- Syme, P.D. (1975) The effects of flowers on the longevity and fecundity of two native parasites of the European pine shoot moth in Ontario. *Environmental Entomology*, **4**, 337–346.

Accepted 4 January 1999