Biology of *Caloptilia fraxinella* (Lepidoptera: Gracillariidae) on ornamental green ash, *Fraxinus pennsylvanica* (Oleaceae)

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Abstract—The ash leaf cone roller, *Caloptilia fraxinella* (Ely), is a leaf-mining moth that has recently become a significant pest of horticultural ash, *Fraxinus* L., species in communities throughout the western prairie provinces of Canada. The study examines the spatial and temporal within-host distribution of immature stages of *C. fraxinella* on green ash, *Fraxinus pennsylvanica* Marsh. Female *C. fraxinella* showed a preference for oviposition sites in the lower canopy and on the south side of the tree at the beginning and middle of the 3-week oviposition period, respectively, but no preference at the end of the period. Oviposition was constrained temporally and occurred mainly just after green ash bud flush. Immature stages were sampled throughout the growing season, and measured widths of larval head capsules showed five instars. Fourth-instar larvae disperse from the mined leaflet to a new leaflet, roll it into a cone, and pupate. Neither canopy height nor ordinal direction affected the position of larvae in the canopy, but numbers of immature stages varied by tree within a site. Female and male moths eclose from rolled leaf cones synchronously throughout the emergence period. The study provides some of the basic biological information required to design an integrated pest management program to target this emerging pest of horticultural ash trees.

Résumé—*Caloptilia fraxinella* (Ely) est un papillon de nuit à larve mineuse de feuilles qui est récemment devenu un important ravageur d'espèces du frêne horticole, *Fraxinus* L., dans les communautés de l'ensemble des provinces des prairies de l'ouest du Canada. La présente étude examine la répartition spatiale et temporelle sur l'hôte des stades immatures de *C. fraxinella* sur le frêne rouge, *Fraxinus pennsylvanica* Marsh. Les femelles de *C. fraxinella* montrent des préférences de sites de ponte sur la canopée inférieure et sur le côté sud de l'arbre, respectivement au début et au milieu de la période de ponte, qui dure 3 semaines; elles ne montrent aucune préférence à la fin de la période. La ponte est restreinte dans le temps et se fait principalement juste après le débourrement des bourgeons du frêne rouge. Les stades immatures ont été échantillonnés durant toute la saison de croissance et les largeurs des capsules céphaliques des larves indiquent l'existence de cinq stades larvaires. Les larves de quatrième stade quittent les petites feuilles qu'elles minaient, se déplacent vers une nouvelle jeune feuille qu'elles enroulent en un cône pour y faire leur nymphose. Il n'y a pas d'effet de la hauteur de la canopée, ni de l'orientation sur l'emplacement des larves dans la canopée, mais le nombre d'immatures varie d'un arbre à l'autre dans un même site. Les papillons femelles et mâles émergent de façon synchrone des cônes de feuilles durant toute la période d'émergence. Cette étude fournit les données biologiques de base nécessaires pour planifier un programme de lutte intégrée contre ce nouveau ravageur des frênes horticoles qui est en progression.

[Traduit par la Rédaction]

Introduction

Caloptilia fraxinella (Ely) (Lepidoptera: Gracillariidae) is known from eastern North America, but it was first detected in the western Canadian prairie provinces on ornamental ash, *Fraxinus* L. (Oleaceae), species in Saskatoon, Saskatchewan, in 1998 (T. Wist, personal communication) and Edmonton, Alberta, in 1999 (Pohl *et al.* 2004). Like several other invasive leaf-mining species

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Received 2 May 2008. Accepted 27 September 2008.

doi: 10.4039/n08-036

(New 1981; Potter 1992), *C. fraxinella* quickly increased in density in horticultural ash plantings following its initial introduction (Pohl *et al.* 2004). It is considered a nuisance pest when the larvae disperse in large numbers on silken threads and an aesthetic pest when the larvae roll leaflets into cones in which to pupate. Feeding by *C. fraxinella* does not seriously affect tree health, and acceding to requests from concerned citizens for its control may threaten the integrated pest management program currently in place in Edmonton (C. Saunders, personal communication). Introductions of *C. fraxinella* have recently been reported in several other western communities, and may occur in many prairie communities where ornamental ash is grown.

Caloptilia fraxinella overwinter as adults (Pohl *et al.* 2004) in reproductive diapause (Evenden *et al.* 2007) and emerge to mate and oviposit on fresh ash leaflets in early spring. Eggs (0.4 mm × 0.3 mm) are laid singly on the adaxial surface of the leaflet and neonates hatch after approximately 1 week at 20 °C (Pohl *et al.* 2004). Young larvae mine the leaflets just below the cuticle and later instar larvae create blotch mines on leaflet margins. Larvae disperse on silken threads to other leaflets that they roll into cones in which to pupate (Pohl *et al.* 2004). Before pupation, larvae feed on the underside of the leaflet to create an exit window for adult emergence (Pohl *et al.* 2004). Pupation lasts between 10 and 14 days under field conditions in Edmonton and adults eclose starting in mid-July (Pohl *et al.* 2004).

To develop an integrated pest management system to monitor and control (Evenden *et al.* 2008) this new pest of urban landscapes across the Canadian prairies, it is necessary to better understand the life history of this insect on ornamental ash plantings. In the present study, eggs, larvae, and pupae were followed during development to determine the temporal and spatial distribution of these life stages on their ash hosts. Further, adult eclosion of male and female moths was monitored.

Materials and methods

Immature stages

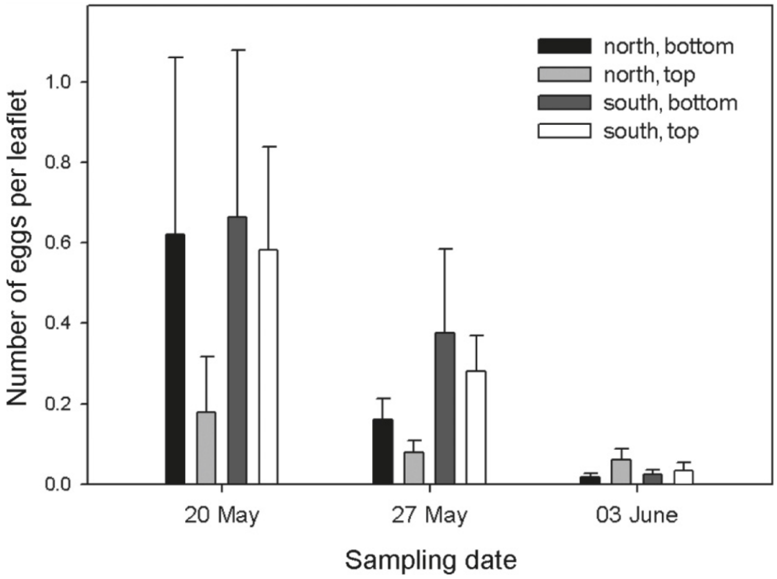
Immature stages of *C. fraxinella* were monitored on green ash, *Fraxinus pennsylvanica* Marsh., at five study sites all separated by at least 1 km in Edmonton, Alberta (53°34′N, 113°31′W), in 2005. At each site, three trees were chosen for weekly sampling throughout the development *C. fraxinella* from egg to pupa. The terminal 30 cm was removed from a branch at each of four different positions on every sampled tree: (1) the north side of the tree in the upper third of the canopy; (2) the north side of the tree in the lower third of the canopy; (3) the south side of the tree in the upper third of the canopy; and (4) the south side of the tree in the lower third of the canopy. Branches were individually bagged, transported to the laboratory, and frozen at –20 °C before enumerating immature stages. Numbers of immature stages sampled were standardized among branches by dividing the total number of individuals by the number of leaflets per sample. Numbers of eggs per leaflet sampled at each position on each tree at each site were log(x + 1)-transformed prior to analysis to improve normality and compared using one split-plot ANOVA with tree nested within site (PROC GLM; SAS Institute Inc. 1998) for each sampling date.

To determine the number of larval instars, the width of the head capsules of at least five larvae per sample was measured throughout the monitoring period using an ocular micrometer attached to a dissecting microscope. In samples with fewer than five individuals, the head capsules of all larvae were measured, for a total of 1892 head-capsule widths throughout the monitoring period. The number of larvae and (or) pupae per leaflet was log(x + 1)-transformed and their positions within the tree were compared using one split-plot ANOVA with tree nested within site (PROC GLM; SAS Institute Inc. 1998) for each sampling date.

Adult eclosion

In July 2004, six study sites were established in urban plantings of green ash all separated by at least 1 km in Edmonton. One sleeve cage constructed of white nylon organza (30 cm in diameter × 75 cm long) was positioned in each of seven selected trees at each site so that it encircled the terminal 75 cm of a branch in the midcanopy, 2–3 m off the ground. Both ends of the sleeve were sealed with flagging tape. Branches supporting sleeve cages were removed after 2–3 days in the field and a new sleeve cage was positioned on a new branch in the same tree. Branches in sleeve cages were bagged individually, transported to the laboratory, and frozen (–20 °C) prior to enumeration of adult moths and separation by sex. Moth emergence was monitored throughout the adult eclosion period from 6 July to 7 August 2004. Moth cap-

Fig. 1. Numbers (mean + SE) of *Caloptilia fraxinella* eggs per leaflet sampled at different locations in the canopy of green ash trees at five field sites in Edmonton, Alberta, throughout the oviposition period in 2005.



tures in all seven sleeve cages were pooled at each site for each collection time and log(x + 1)-transformed prior to analysis. The numbers of male and female moths that eclosed over time were compared using a repeated-measures ANOVA with time of collection specified as the repeated measure (PROC GLM; SAS Institute Inc. 1998).

Results

Immature stages

During the first sampling period (20 May 2005), there was a significant effect of canopy height on the number of eggs sampled ($F_{1,11}$ = 12.24, P = 0.0050), and female *C. fraxinella* seemed to prefer leaflets lower in the canopy (Fig. 1). However, this effect varied by site, as there was a significant site × height interaction effect ($F_{1,11}$ = 11.80, P = 0.0006). During the second sampling period (27 May 2005) there was a significant effect of ordinal direction within the canopy on the number of eggs sampled ($F_{1,26}$ = 5.95, P = 0.0218), with more eggs laid on the south side of the tree (Fig. 1). Canopy position still influenced oviposition during the second sampling period, but this effect was only seen through a significant site × height interaction effect on the number of eggs sampled ($F_{4,26}$ = 3.17, P = 0.0302). Female *C. fraxinella* showed no oviposition preference for a particular canopy position or direction during the third sampling period (6 June 2005) (Fig. 1). Female *C. fraxinella* are constrained in time to exploit fresh ash leaflets, as the oviposition period lasts only 3 weeks (Fig. 1).

Based on head-capsule widths, *C. fraxinella* larvae develop through five instars (Fig. 2). Third- and fourth-instar larvae were found in blotch mines along the margin of the leaflets. Fourth- and fifth-instar larvae were found in leaflets that had been rolled into cones, suggesting that the transition from leaflet mining to rolling occurs when larvae disperse to a new leaflet at the fourth instar. In 2005, most larval development was condensed into 4 weeks commencing at the beginning of June and continuing until the beginning of July (Fig. 3). Early in the larval activity period there was significant overlap in the instar stages sampled. Fourth-instar larvae dominated samples for 2 weeks in the middle of June, and fifth-instar larvae and pupae dominated samples toward the end of June. Pupae were found predominantly in samples retrieved during the first half of July (Fig. 3).

The particular tree sampled at each site significantly affected the number of larvae in the 10 June 2005 sample ($F_{8,21}$ = 5.82, P = 0.0006) and the 17 June 2005 sample ($F_{9,26}$ = 2.74, P = 0.0215). Similarly, the tree that was sampled at each site had a significant effect on the number of larvae and pupae in the 24 June 2005 sample ($F_{10,30}$ = 2.76, P = 0.0152), the 30 June 2005 sample ($F_{9,26}$ = 3.55, P = 0.0055), and the 11 July 2005 sample ($F_{10,30}$ = 2.13, P = 0.054). Height

Fig. 2. Larval instars (L1–L5) of *Caloptilia fraxinella* determined by measuring head-capsule widths.

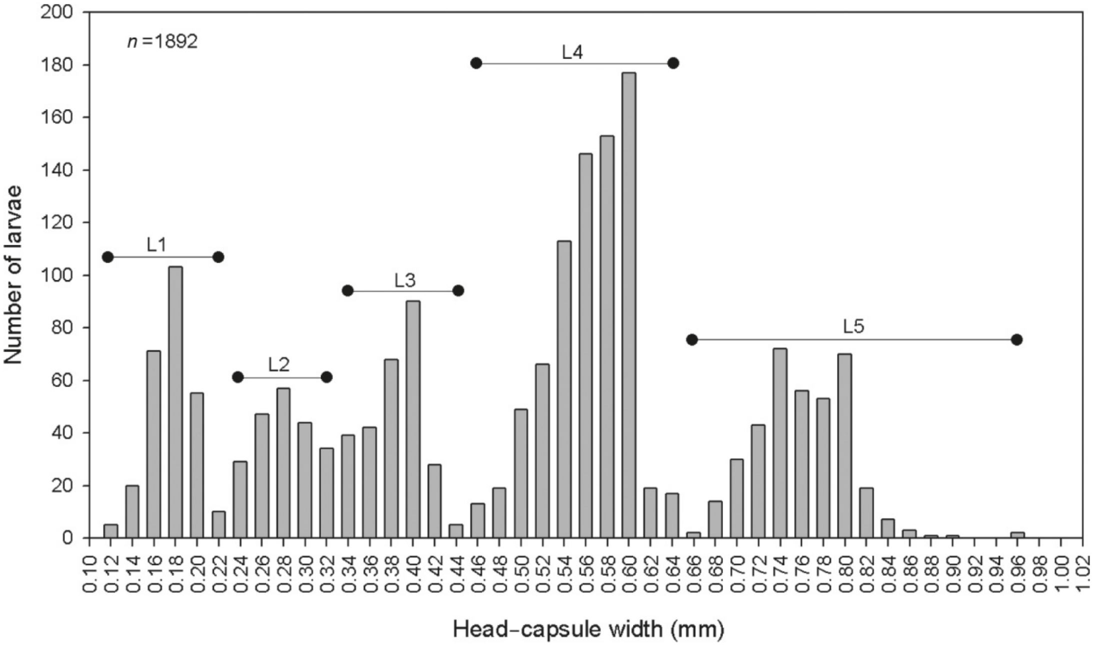
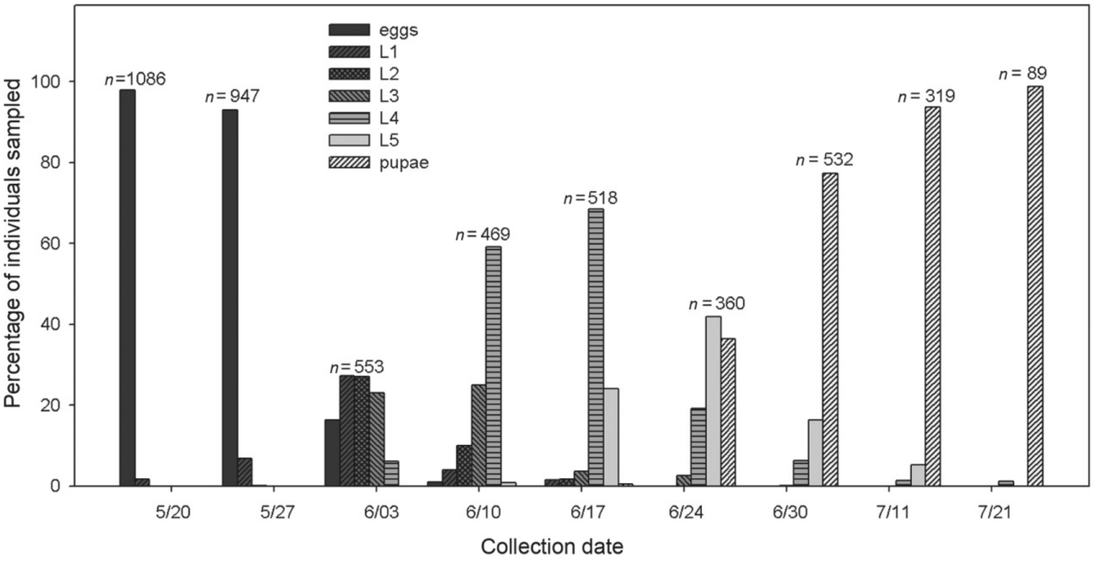
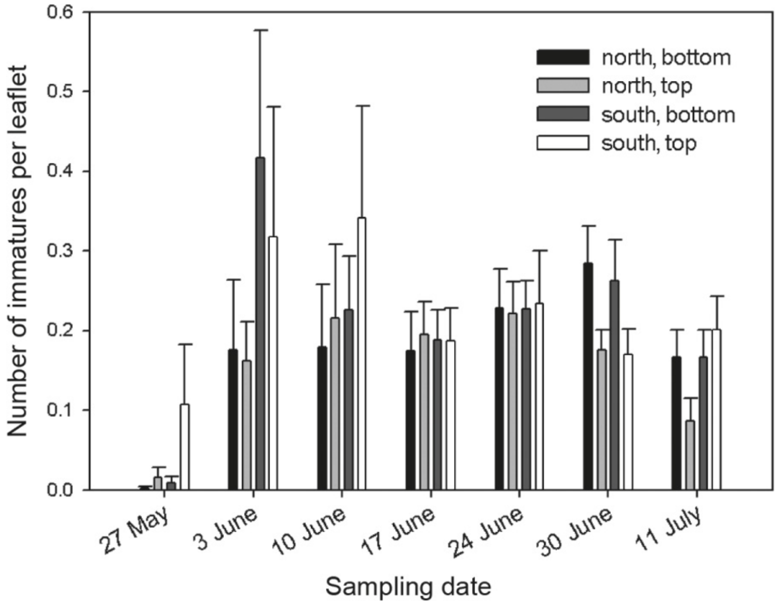


Fig. 3. Percentages of various immature life stages of *Caloptilia fraxinella* sampled on green ash trees at five field sites in Edmonton throughout the growing season in 2005.



within the canopy had a significant effect on the number of larvae and pupae only in the 30 June 2005 sample ($F_{8,21}$ = 5.82, P = 0.0006), when more immatures were found low in the canopy (Fig. 4). There was no effect of ordinal direction on the number of larvae or pupae sampled at any date, but there was a significant site × direction × height interaction ($F_{4,26}$ = 2.80, P = 0.0466) effect on the 17 June 2005 sample. Leaflet cones rolled post larval dispersal first appeared on 10 June 2005, and leaflet cones dominated samples from 17 June 2005 until the end of the study.

Fig. 4. Numbers (mean + SE) of immature *Caloptilia fraxinella* (larvae and pupae) sampled at different locations in the canopy of green ash trees at five field sites in Edmonton in 2005 (day/month).



Adult eclosion

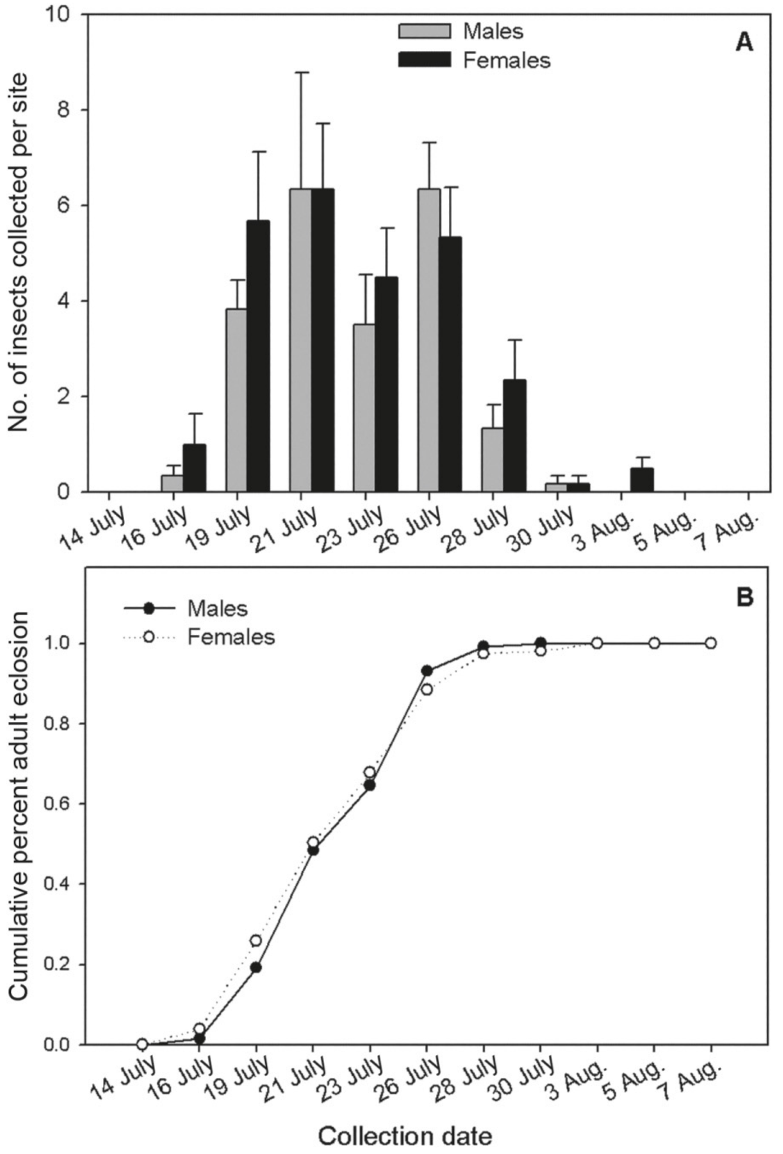
Moth eclosion from leaflet cones at field sites started in mid-July, peaked at the end of July, and ended by the beginning of August in 2004 (Fig. 5A). There was no difference between the numbers of eclosed males and females ($F_{1,5}$ = 3.31, P = 0.1287). Further, the rates of emergence of the two sexes over the eclosion period were almost identical (Fig. 5B) as indicated by the nonsignificant time × sex interaction term ($F_{7,35}$ = 0.57, P = 0.7766). Sampling time had a significant effect on the number of eclosed moths ($F_{7,35}$ = 43.82, $P < 0.0001$), but this simply reflects phenological variation in emergence time (Fig. 5A).

Discussion

Leaf-mining insects should select oviposition sites that are suitable for larval development, as larvae cannot disperse (Bultman and Faeth 1986; Reavey and Gaston 1991). This selection can vary with the host plant (Maier 1995; Furniss *et al.* 2001), the position or size of foliage within the host plant (Jones and Raske 1976; Mopper *et al.* 1984; Bultman and Faeth 1986; Basset 1991; Sato 1991; Brown *et al.* 1997; Pena and Schaffer 1997; Shibata *et al.* 2001), the position within the leaf or leaflet (Stiling *et al.* 1987; Green and Prokopy 1991, 1998; Kozlov and Koricheva 1991; Reavey and Gaston 1991), and at specific times during foliage ontogeny (Basset 1991; Kozlov and Koricheva 1991; Pena and Schaffer 1997; Shibata *et al.* 2001). Selection can depend on environmental factors such as temperature and humidity (Yarnes and Boecklen 2005) and light level (Bultman and Faeth 1988; Koricheva 1990). Further, female leaf-miners may select oviposition sites based on the nutritive value of the substrate or the level of secondary plant defense compounds in the tissue (Kitamura *et al.* 2007). Female oviposition behaviour may also be constrained by the population density of other leaf-miner species (Green and Prokopy 1991) or by natural enemies that target the female or her offspring (Brown *et al.* 1997).

In this study, *C. fraxinella* was present at high population densities, and the number of eggs per leaflet was higher in the lower canopy at the beginning of the oviposition period just after bud flush (Fig. 1). At the second sampling period, on 27 May 2005, more eggs were found on the south side of the tree (Fig. 1). Although the intensity of direct light on these leaflets was not measured, leaflets low in the canopy on the north side would be expected to experience the most shade, whereas leaflets high in the canopy on the south side would receive the most sunlight. Although some leaf-mining insects actively choose leaves in sun (Bultman and Faeth 1988) or shade (Bultman and Faeth 1988; Basset 1991; Kozlov and Koricheva 1991) for oviposition, sev-

Fig. 5. Numbers of adult male and female *Caloptilia fraxinella* (mean + SE) that emerged into sleeve cages positioned on green ash trees at six field sites in Edmonton throughout the eclosion period in 2004 (A), with cumulative percent eclosion of male and female moths (B).



eral species do not show any preference (Potter 1992; Connor 2006). Light conditions at the oviposition site would not be expected to have a major influence on female leaf-mining moths that are active in the evening (Connor 2006), such as *C. fraxinella* (Evenden *et al.* 2007). However, other leaf-mining moths are more common in the lower canopy in more shaded conditions (Kitamura *et al.* 2007). The finding that *C. fraxinella* eggs were more common in the lower canopy at the beginning of the oviposition period (Fig. 1) may indicate a true preference for a particular oviposition location. Oviposition that occurred throughout the rest of the canopy later in the oviposition period may have been due to the high population density at these sites. Although as many as 30 *C. fraxinella* eggs have been found on field-collected leaflets (Pohl *et al.* 2004), females that oviposit at the end of the egg-laying period may increase their fitness by avoiding leaflets that already contain many conspecific eggs.

Oviposition was constrained in time, and peaked immediately following bud flush (Fig. 1).

New foliage is often exploited by herbivorous insects because of its higher nutritional quality and lower levels of mechanical and chemical defense compared with older foliage. However, many leaf-mining moths occur on ontogenetically older leaves, presumably to avoid external leaf-feeders that specialize on new leaves (Shibata *et al.* 2001). Except for the newly introduced spiny ash sawfly, *Eupareophora parca* (Cresson) (Hymenoptera: Tenthredinidae) (Williams 2007), there are no major external leaf-feeders on ash in the urban forest of Edmonton where this study was done. *Caloptilia fraxinella* larvae may require soft, young leaflets in order to initiate mines; alternatively, females, because they overwinter as adults, may be constrained to oviposit on fresh leaflets (Furniss *et al.* 2001).

Head-capsule widths of larvae collected throughout the season indicate that larvae develop through five instars (Fig. 2) in a condensed 4-week period (Fig. 3). Pohl *et al.* (2004) found shed head capsules of five different sizes in dissections of mines and cones after infestation by *C. fraxinella*. In mine dissections, Pohl *et al.* (2004) found head capsules from one larval instar in the initial meandering mines, from two or three different instars in blotch mines on the margins of leaflets, and from the final two instars in leaflet cones. In the present study, third- and fourth-instar larvae were found in blotch mines and fourth- and fifth-instar larvae in leaflet cones. Both the present study and that of Pohl *et al.* (2004) indicate that dispersal of larvae to leaflets for cone-rolling occurs at the fourth instar.

Except for the 30 June 2005 sample, where more larvae and pupae were found in the lower canopy, there was no difference in the numbers of immature stages recovered from samples taken at different heights or directions within the canopy (Fig. 4). Although females preferred the lower canopy and the south side of the tree for oviposition (Fig. 1), the high population density at these sites probably resulted in an even distribution of larvae throughout the canopy (Fig. 4). Interestingly, the individual tree had an effect on the numbers of larvae and pupae sampled from 10 June to 11 July 2005. This suggests that there are tree-specific effects on survivorship, as there was no effect of the individual tree on oviposition behaviour. The number of individuals sampled per leaflet varied less later in the season; this may be associated with the position of larvae in the canopy post dispersal of fourth-instar larvae. Normally, only one pupa is recovered per leaflet cone, but Pohl *et al.* (2004) found up to three larvae successfully pupated and eclosed (T. Wist, unpublished data) within leaflet cones at high densities of infestation. Larvae of the congeneric species *Caloptilia serotinella* (Ely) use vibrational signals to defend leaf shelters under construction from intruding conspecifics (Fletcher *et al.* 2006). Such encounters may also occur in *C. fraxinella* and serve to distribute larvae in leaflet cones throughout the canopy.

Male and female moths eclosed from leaflet cones beginning in mid-July in 2004 (Fig. 5A). Eclosion continued for approximately 2 weeks, during which time maximum daily temperatures ranged between 17.55 and 33.32 °C. Unlike many other insect species, *C. fraxinella* does not exhibit protandry, as male and female moths eclosed at the same rate over the entire emergence period (Fig. 5B). It is likely that there is no selective advantage to protandry in this species because most moths eclose in a state of reproductive diapause and do not mate until they have overwintered (Evenden *et al.* 2007). Moths disperse from ash trees after eclosion and are often seen exhibiting searching behaviour in early September. Overwintering hosts are unknown (Pohl *et al.* 2004; Evenden *et al.* 2007).

Caloptilia fraxinella that have invaded the urban forests of western Canada are host-specific, and larvae only mine leaves of *Fraxinus* spp. (Pohl *et al.* 2004). It appears that some females ovipositing on green ash hosts choose the lower portion of the canopy and the south side of the tree. This preference may be more obvious at lower population densities. Oviposition is constrained temporally, occurring just after bud flush. It remains to be tested whether female *C. fraxinella* show a preference for a particular oviposition location within a leaf or leaflet. *Caloptilia fraxinella* larvae develop through five instars, but the present study did not determine whether feeding habit was associated with different instars or larval morphology as is the case for many gracillariid moths that exhibit distinct sap- and tissue-feeding stages (Kumata 1978). However, third- and fourth-instar larvae inhabit blotch mines and fourth- and fifth-instar larvae are found in rolled leaflet cones, which strongly suggests that dispersal and leaf cone rolling occur at the fourth instar. Male and female adult moths eclose simultaneously over a 2.5-week period and there is no evidence for protandry in this species. Further work on the phenology and biology of this species should include an examination of specific feeding habits of larvae within the leaflet, the effect of population density on oviposition-site preference, and the behaviour of moths in reproductive diapause that aestivate and overwinter away from their ash hosts.

Acknowledgements

I thank A. Argals, G. Armitage, W. Luth, C.M. Whitehouse, and A.M. Woytkiw for laboratory and field assistance. G.R. Pohl and C. Saunders helped to initiate this project and contributed scientific and logistical assistance throughout the study. R.-C. Yang provided statistical assistance. T. Wist and two anonymous reviewers provided helpful comments on an earlier version of the manuscript. This work was supported by grants from the Alberta Sport, Recreation, Parks and Wildlife Foundation and the Alberta Crop Industry Development Fund Ltd., and contributions from the Landscape Alberta Nursery Trades Association and the Canadian Nursery Landscape Association.

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