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See table of contents

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Article abstract

The hemlock looper, *Lambdina fiscellaria*, pupal distribution was studied through a 3-year outbreak cycle near Lac Princeton on Anticosti Island in Quebec. Over the 3 years, 10 balsam fir trees were cut and all pupae were counted on the stem and branches (non-foliated vs foliated parts) of the lower, middle and upper crowns and on the stem below crown. In pre-outbreak conditions, pupae were mostly found on branches of the middle and upper crowns. During the outbreak, pupal density did not increase on these parts of the trees, since pupae were mostly found on the stem, from the ground to the middle crown, and on branches of the lower crown. Few pupae were found on the foliated portion of branches in post-outbreak conditions but most were found on the basal non-foliated part of branches, which appears to be a preferred location for hemlock looper pupation. In order to optimize detection of population increases in monitoring networks, we suggest using pupal traps at breast height on balsam fir trees.

Changes in hemlock looper [Lepidoptera: Geometridae] pupal distribution through a 3-year outbreak cycle

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[Changements dans la distribution des chrysalides de l'arpenteuse de la pruche [Lepidoptera : Geometridae] au cours d'un cycle épidémique de trois ans]

La distribution des chrysalides de l'arpenteuse de la pruche, *Lambdina fiscellaria,* a été étudiée au cours d'un cycle épidémique d'une durée de trois ans près du Lac Princeton sur l'île d'Anticosti au Québec. Au total, 10 sapins ont été coupés et toutes les chrysalides ont été comptées sur le tronc et les branches (partie non-foliée vs foliée) de la cime inférieure, médiane et supérieure, ainsi que sur le tronc sous la cime. En condition pré-épidémique, les chrysalides ont principalement été trouvées sur les branches des cimes médianes et supérieures. Durant l'épidémie, la densité des chrysalides n'a pas augmenté dans ces sites de pupaison et les larves se sont surtout transformées en chrysalides sur le tronc, à partir du sol jusque dans la cime médiane, ainsi que sur les branches de la cime inférieure. Peu de chrysalides ont été trouvées sur la partie foliée des branches en période post-épidémique, la plupart étant trouvées sur la partie basale non-foliée

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qui apparaît comme un endroit préférentiel pour la pupaison de l'arpenteuse de la pruche. De façon à optimiser la détection des augmentations de populations dans les réseaux de surveillance, des pièges à chrysalides devraient être placés à hauteur de poitrine sur le tronc de sapins baumiers.

INTRODUCTION

The hemlock looper, *Lambdina fiscellaria* (Guenée) [Lepidoptera: Geometridae], is one of the most important defoliators of coniferous forests in eastern Canada (Jobin and Desaulniers 1981; Otvos *et al.* 1979). Populations of this species are known for their rapid increase and sudden disappearance (Watson 1934), with outbreaks rarely lasting more than 2 or 3 yr at a specific location (Otvos *et al.* 1979). Larvae feed on both current- and previous-year needles without eating them completely (Carroll 1956; Watson 1934). This results in the drying out of damaged needles that eventually fall during autumn (Watson 1934). This may rapidly result in tree death, even in the first yr in which damage is observed (Hudak *et al.* 1978; Jobin and Desaulniers 1981). Widespread areas of tree mortality have resulted from hemlock looper outbreaks in the past in Newfoundland (Otvos *et al.* 1979) and on Anticosti Island in Quebec (Jobin and Desaulniers 1981). More recently on the North Shore in Quebec, the looper defoliated 472 000 ha (of which 95% were severely defoliated; Bordeleau 1999) and 925 000 ha (Bordeleau 2000) of forest in 1999 and 2000 respectively.

The hemlock looper has only one generation per yr and overwinters in the egg stage. At the end of their development, looper larvae show a negative photo-taxis (Carroll 1956) and begin seeking dark pupation sites. Pupae are often found on trees, in bark crevices, lichens or under strips of bark (Watson 1934). Large numbers of pupae have also been observed in old stumps (Carroll 1956; Jobin and Desaulniers 1981; Tessier 1930) and on the ground, in the angles formed by roots (De Gryse and Schedl 1934). It is important to know the spatial distribution of insect life stages for developing efficient sampling techniques (Batzer *et al.* 1995; Dajoz 1998). Carroll (1956) and Otvos (1974) reported that most looper pupae were found on the stem and below the crown level of trees in Newfoundland. However, these studies were done in outbreak conditions, when defoliation is severe, which increases late-instar larval wandering in search of food to complete development (Carroll 1956). Pupal distribution in pre- and post-outbreak conditions, when larval wandering should be reduced because of greater food availability (particularly in pre-outbreak conditions), has never been studied.

In 1993, on Anticosti Island in Quebec, we found an incipient outbreak (no observable defoliation) of the hemlock looper and took the opportunity to study pupal distribution through a 3-yr outbreak cycle in a single site. The objective of this study was to test the hypothesis that hemlock looper pupal distribution is different during an outbreak, compared with pre- and post-outbreak conditions.

MATERIALS AND METHODS

Distribution of hemlock looper pupae was studied during 3 consecutive yr, from 1993 to 1995, in a 75-yr-old balsam fir (*Abies balsamea* (L.) Mill.) forest located near Lac Princeton (49°52' N, 64°11' W) on Anticosti Island, in Quebec. In 1993, the looper population was increasing but did not cause any observable damage on trees cut to study pupal distribution. In 1994, the population was high and caused light (6–25%) to moderate (26-75%) defoliation. In 1995, the population crashed suddenly and dropped below the 1993 population level. Annual defoliation was very low in 1995 (trace level: 1-5%), but total defoliation remained at a light to moderate level due to 1994 defoliation. Almost no tree mortality resulted from this outbreak.

Three codominant balsam fir trees were cut in 1993 and 1995, and four in 1994 to study the spatial distribution of hemlock looper pupae. Diameter at breast height (DBH) was measured before tree cutting and tree height, crown length and length of stem below the crown were measured after cutting. Then, trees were divided into several parts. First, the stem below the crown was isolated from the rest of the tree. The tree crown was divided into three equal sections: the upper, middle and lower crown levels. In each level, the stem was isolated from branches and each branch was divided into two parts: the first 30 cm from the stem (the basal non-foliated part which is usually covered by lichens) and the remaining foliated part (> 30 cm). All pupae were counted on each part of the trees.

Tree characteristics were compared between yr of study using the GLM procedure from SAS (SAS Institute 1989). Chi-square tests were used to compare the spatial distribution of pupae as a function of vertical stratification (below crown, lower, middle and upper crown) and location (stem below crown, stem within crown, branches < 30 cm and branches > 30 cm) between yr of study.

RESULTS

The characteristics of the balsam fir trees sampled were not significantly different between yr, with averages ranging from 17 to 21 cm DBH and from 11.4 to 12.9 m in height (Table 1). Crowns were well developed, covering 59 to 68% of tree height. Therefore, differences in the distribution of hemlock looper pupae were considered to result mostly from changes in population density, defoliation, and climatic conditions through the 3-yr outbreak cycle.

Significant differences were observed between yr in pupal distribution as a function of vertical stratification (below crown, lower, mid and upper crown; $\chi^2 = 140.2$, df = 6, $P < 0.001$) and location (stem below crown, stem within crown, branches < 30 cm and branches > 30 cm; $\chi^2 = 152.4$, df = 6, $P < 0.001$).

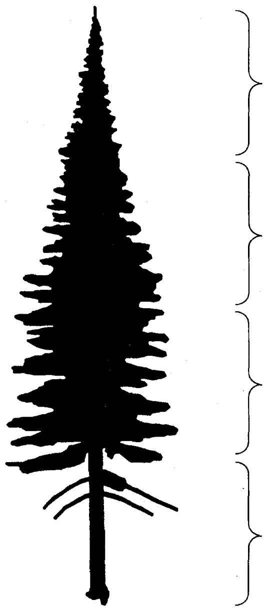
In 1993, 50% of pupae were found in the middle crown (Fig. 1), and on the whole, 83% of pupae were found on branches, with only 17% being found on tree stems (Fig. 2). In 1994, the average number of pupae on branches of the middle and upper crowns remained similar to 1993 (Table 2). However, abundance of pupae increased on branches of the lower crown and on tree stems, where more than 50% of pupae were found, particularly below the crown. It resulted in a more uniform distribution of pupae on trees, except for the upper crown which obviously offers a lower number of pupation sites due to smaller stems and branches (Table 2). On tree stems, a general trend of increasing number of pupae toward ground level was observed each yr, and this trend was particularly noticeable in 1994, when defoliation was light to moderate (Table 2).

In 1995, pupal abundance decreased below the level observed in 1993 (pre-outbreak conditions) and only one pupa was found in the upper crown, with most individuals (64%) being found on branches of the middle and lower crowns (Table 2; Fig. 1). Three times

Table 1. Outbreak status and characteristics (mean ± SE) of balsam fir trees cut at Lac Princeton on Anticosti Island, Quebec, to study hemlock looper pupal distribution

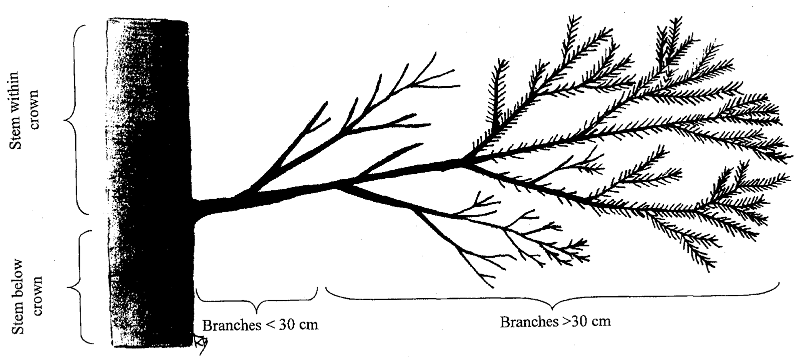
Year	Outbreak status	Annual defoliation	Trees sampled	DBH[a] (cm)	Height[a] (m)	Crown length[a] (m)	Stem below crown[a] (m)
1993	Pre	None	3	20.0 ± 0.3	11.4 ± 0.3	7.2 ± 0.3	4.2 ± 0.3
1994	Peak	Light–mod.	4	17.0 ± 1.4	11.4 ± 0.9	6.7 ± 0.9	4.6 ± 0.9
1995	Post	Trace	3	21.1 ± 1.8	12.9 ± 0.5	8.8 ± 0.4	4.1 ± 0.1

[a] No significant difference (ANOVA; $P > 0.05$) between years.



	1993	1994	1995
Upper crown	22 ± 6 (18)	16 ± 13 (6)	1 ± 1 (1)
Middle crown	65 ± 17 (50)	81 ± 37 (31)	15 ± 4 (37)
Lower crown	26 ± 8 (20)	88 ± 21 (34)	16 ± 5 (41)
Stem below crown	16 ± 5 (12)	78 ± 22 (29)	9 ± 6 (21)

Figure 1. Mean numbers (± SE) and percentage (in parentheses, under mean ± SE) of hemlock looper pupae found at different heights in balsam fir trees in 1993 (pre-outbreak), 1994 (outbreak) and 1995 (post-outbreak) at Lac Princeton on Anticosti Island, Quebec.



	Stem		Branches	
Year	Below crown	Within crown	< 30 cm	>30 cm
1993	16 ± 5 (12)	6 ± 1 (5)	55 ± 14 (43)	52 ± 14 (40)
1994	78 ± 22 (30)	55 ± 24 (21)	71 ± 16 (27)	60 ± 27 (23)
1995	9 ± 6 (21)	6 ± 6 (15)	20 ± 4 (49)	6 ± 5 (15)

Figure 2. Mean numbers (± SE) and percentage (in parentheses, under mean ± SE) of hemlock looper pupae found at different locations on balsam fir stems (below vs within crown) and branches (basal non-foliated part, < 30 cm vs foliated part, > 30 cm) in 1993 (pre-outbreak), 1994 (outbreak) and 1995 (post-outbreak) at Lac Princeton on Anticosti Island, Quebec.

Table 2. Average number (± SE) of hemlock looper pupae on different parts of balsam fir trees sampled in 1993 (pre-outbreak), 1994 (peak of the outbreak) and 1995 (post-outbreak) at Lac Princeton on Anticosti Island, Quebec

Crown level	Location	1993	1994	1995
Upper crown	Stem	1 ± 1	1 ± 1	0 ± 0
	Branches < 30 cm	18 ± 6	12 ± 8	1 ± 1
	Branches > 30 cm	3 ± 1	3 ± 3	0 ± 0
Middle crown	Stem	2 ± 1	22 ± 12	1 ± 1
	Branches < 30 cm	27 ± 7	33 ± 13	9 ± 7
	Branches > 30 cm	36 ± 11	26 ± 15	5 ± 5
Lower crown	Stem	3 ± 2	31 ± 11	5 ± 5
	Branches < 30 cm	11 ± 5	26 ± 6	10 ± 6
	Branches > 30 cm	12 ± 7	31 ± 12	1 ± 1
Below crown	Stem	16 ± 5	78 ± 22	9 ± 6
Total		**129 ± 31**	**263 ± 57**	**41 ± 5**

more individuals were found on the basal non-foliated part (< 30 cm) compared with the foliated part of the branches (Table 2; Fig. 2).

DISCUSSION

Changes in pupal distribution observed through a 3-yr outbreak cycle of the hemlock looper in this study suggest that looper density and severity of defoliation, combined with differences in climatic conditions and natural enemy activity, may influence the selection of pupation sites by larvae. High larval density increases contact frequency between individuals on branch tips, forcing larvae to drop (Carroll 1956). In 1994 (light to moderate defoliation), abundance of pupae on branches of the middle and upper crowns was similar to 1993 (no visible defoliation), but abundance on branches of the lower crown increased to a level similar to that observed in the middle crown. Moreover, abundance on the stem, from the ground to the middle crown, also increased significantly, indicating that more larvae dropped to the lower crown and to the ground in 1994.

High density also causes larvae to increase their movement when searching for food (Carroll 1956; Watson 1934). In outbreak conditions, larvae use silk threads to descend to lower levels of the canopy and even to the undergrowth to find food (Hébert and Jobin 2001). This behaviour increases the number of larvae crawling on the forest floor and may explain that in outbreak conditions, many authors have also observed pupae from almost everywhere in the forest, even in old stumps (Carroll 1956; Jobin and Desaulniers 1981; Otvos 1974; Tessier 1930). This may also explain the results that Carroll (1956) and Otvos (1974) obtained in outbreak conditions. They reported respectively that 90% and 80% of pupae occurred on the stem and 62% and 60% of pupae occurred below the crown, which is much higher than in our study where a maximum of 50% of pupae were observed on the stem and 30% below the crown in 1994 (low to moderate defoliation; highest population in our study). This indicates that the low to moderate defoliation observed in 1994 in our study was an intermediate state between the pre-outbreak (1993 in our study) and severe outbreak conditions observed in the studies by Carroll (1956) and Otvos (1974). Changes in pupal distribution as a function of population density and defoliation have also been reported for the forest tent caterpillar, *Malacosoma disstria* Hübner, where cocooning shifted from trees to shrub strata as density and defoliation increased (Batzer *et al.* 1995).

In post-outbreak conditions, food shortage or lower food quality may also increase larval searching activities compared to pre-outbreak conditions. This may result in higher proportions of larvae falling from trees. This might explain that few pupae were found on the foliated part of branches and that more pupae were found on the stem in 1995 (post-outbreak) than in 1993 (pre-outbreak).

Hemlock looper population was near outbreak level in 1993 and most pupae (83%) were observed on branches within the crown, which is different from results reported by Carroll (1956) and Otvos (1974) in outbreak conditions who reported respectively 10% and 20% of pupae on branches. Thus, larvae of low-density populations may pupate mostly on branches where they feed. In situations of abundant food supply, there is no reason for the looper to spend energy in unnecessary movements, except for escaping natural enemies. Thus, the earliest possible detection of population increase might be obtained by sampling in the canopy, on the basal non-foliated part of branches (< 30 cm) which appears as a preferred location for pupation of the hemlock looper, considering the surface area available for pupation. This is probably linked to the abundance of lichens (in which the looper often pupates) found on this part of branches. However, these pupation sites would be difficult to sample in monitoring networks and, as density does not change on this part of the tree during the outbreak, sampling pupae within the canopy would no longer be useful to determine population levels. Furthermore, as population density increases, more pupae are found on tree stems at breast height. Therefore, monitoring pupae on this part of the tree with artificial shelters like burlap traps described by Otvos (1974) would provide useful estimates to detect increases of looper population near outbreak level. Moreover, using artificial shelters at DBH (Liang *et al.* 1998; Otvos 1974; Shore 1989) is much easier on an operational basis than sampling in the canopy.

A good knowledge of the spatial distribution of insect life stages is important for developing reliable monitoring systems (Dajoz 1998). Our study demonstrates that the distribution of insect life stages can change from yr to yr and that it should be taken into account when developing sampling techniques and monitoring systems. These changes in pupal distribution were associated with differences in population density, but further work is needed to determine if population density is the driving force for these changes or other factors such as weather or natural enemy activity are responsible for yr to yr changes in pupal distribution.

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