



# Relationship between balsam fir sawfly density and defoliation in balsam fir

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## Abstract

Field studies were carried out to examine the relationships between balsam fir sawfly, *Neodiprion abietis* (Harris), density and resultant defoliation on young balsam fir, *Abies balsamea* (L.) Mill., in western Newfoundland. Densities of early- and late-instar larvae explained 57 and 70% of variation in defoliation in a sleeve-cage study. Densities of both early- and late-instar larvae were significantly related to defoliation on 1 to 5-year-old, but not always on 6 and 7-year-old foliage, due to the preference of larvae for young, but not current-year, foliage. Defoliation was strongly related to the densities of eggs and larvae in field surveys. Sawfly density and whether or not a population had increased or decreased in density during the previous year explained 77% (eggs), 64% (early-instar larvae) and 83% (mid-instar larvae) of the annual variation in defoliation. Our results suggest that establishment of robust density–damage relationships are possible for *N. abietis* on balsam fir, using egg densities to estimate defoliation and previously established relationships to predict both the amount of foliage remaining and growth loss. © 2004 Elsevier B.V. All rights reserved.

**Keywords:** *Abies balsamea*; Density–damage relationships; *Neodiprion abietis*; Pest management; Defoliation

## 1. Introduction

Relationships between insect density and subsequent damage to host plants are an essential component of pest management programs and have been established for many agricultural (Pedigo et al.,

1986) and forest systems (Waters and Stark, 1980; Gansner et al., 1985; Lysyk, 1990; Alfaro, 1991; Williams et al., 1991; Carroll and Quiring, 1993; Liebhold et al., 1993; Fang and Hart, 2000). Studies that attempt to relate insect density to host damage within forested systems often compare natural egg or larval densities to defoliation (e.g., Williams et al., 1991; Carroll and Quiring, 1993). The degree of relatedness between defoliation at the end of the season and egg or larval density at the beginning of the

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season is influenced by the amount of defoliation in previous years (Morris, 1955), larval survival (Lysyk, 1990), larval preferences for certain foliage age classes (Géri et al., 1993) and larval dispersal (Quiring, 1993; Carroll and Quiring, 1993).

The balsam fir sawfly, *Neodiprion abietis* (Harris) complex, (hereafter referred to as BFS), has recently become a serious pest of balsam fir, *Abies balsamea* (L.) Mill., stands in western Newfoundland, Canada. Outbreaks of the BFS have historically been short in duration (Martineau, 1984). However, the current outbreak is the longest ever recorded (Moreau, 2004) and has affected an area of approximately 50,000 ha (Anonymous, 2001). We recently showed that the amount of foliage remaining on balsam fir after defoliation by BFS was correlated to volume increment, and that feeding by sawfly larvae can reduce volume growth by approximately 40%, 2 years after the start of an outbreak (Parsons et al., 2003). These large reductions in tree growth were similar to those reported in a more extensive study of the effects of feeding by BFS on balsam fir tree growth (Piene et al., 2001). A naturally occurring nucleopolyhedrosis virus has been successfully applied to suppress sawfly populations (Lucarotti et al., 2000) and may provide an efficacious yet environmental-friendly tactic to suppress BFS populations. However, entomologists currently lack the information to predict defoliation from the densities of overwintering eggs or early-instar larvae to determine where suppression is warranted. Here, we present results of a manipulated field study and of field surveys carried out to determine the relationship between the density of eggs and larvae of BFS and defoliation in balsam fir.

## 2. Material and methods

### 2.1. Description of insect

The life history of BFS has been described by Carroll (1962) and Anstey et al. (2002). Briefly, BFS overwinter as eggs and usually hatch in late June to mid July. Newly emerged larvae feed gregariously but become more solitary in later instars. Larvae feed on all age-classes except current-year foliage, which they only consume occasionally (Moreau et al., 2003; Parsons et al., 2003). At the end of the fourth-instar

(males) or fifth-instar (females), larvae spin cocoons and pupate. Adults usually emerge in August and September, after which females use a serrated ovipositor to make slits in the edges of current-year needles in which they deposit one egg. In Newfoundland, the primary host of the BFS is balsam fir, but larvae also feed on white spruce (*Picea glauca* [Moench] Voss), black spruce (*P. mariana* [Mill.] B.S.P.), and eastern larch (*Larix laricina* [Du Roi] K. Koch).

### 2.2. Sleeve-cage study

A manipulative study with sleeve cages was carried out in a stand approximately 15 km southwest of Corner Brook, Newfoundland (48°49'N; 58°3'W). The 1 ha stand was dominated by 10 to 15-year-old, naturally regenerated, precommercially thinned ( $\geq 1.5$  m spacing, hereafter referred to as 'thinned') balsam fir 3–4 m in height, but contained small numbers of black spruce, white spruce, American mountain ash (*Sorbus americana* Marsh.), yellow birch (*Betula lutea* Michx. f.), and mountain maple (*Acer spicatum* Lam.). Ground vegetation consisted primarily of bunchberry (*Cornus canadensis* L.) and American star flower (*Trientalis borealis* Raf.). Scattered patches of squashberry (*Viburnum edule* [Michx.] Raf.) were found in the understory. Balsam fir trees in this study area contained <20 BFS eggs per branch and percentage of needle fall was <10% at the start of the study in spring 1999. The few eggs found on study branches were poked with a needle to kill them immediately prior to the experiment. The site was a typical balsam fir forest found within the Corner Brook subregion of the western Newfoundland ecoregion (Meades and Moores, 1994).

In June 2000, prior to egg hatch, 19 dominant balsam fir trees were selected. On each tree, three south-facing branches in both the sixth and seventh whorls (where the apical whorl was considered the first whorl) were selected and identified with flagging tape. Visual defoliation estimates, using defoliation classes of 0, 1–10, 11–20, 21–40, 41–60, 61–80, 81–99, and 100% were made for all shoots on each of the six selected branches per tree, as described by Parsons et al. (2003). Following initial defoliation estimates, first-instar BFS larvae were collected in a stand with a high population density approximately 15 km south-

east of this study site (48°46'N; 57°52'W). Shoots containing first-instar larvae were clipped from trees, placed in open tubs and transported to the study site. Densities of either 0, 5, 10, 25, or 50 larvae per branch (i.e., one density per branch) were randomly assigned to each branch, after which the branch was covered with a sleeve cage (i.e., 19 trees  $\times$  5 sleeve cages per tree = 95 sleeve cages). The remaining branch received neither larvae nor a sleeve cage (0 control) and was included to determine whether sleeve cages influenced branch development.

First-instar BFS larvae were placed in a group on 1-year-old foliage on the distal portion of the branch to mimic their natural feeding behaviour. To prevent larval injury during placement, needlepoint forceps were used to move needles containing larvae from shoots in tubs to the experimental branches without contacting the larvae. A fine-mesh cloth sleeve cage (1 m  $\times$  0.75 m) was placed over each branch and attached with string to prevent entry by parasitoids and predators. Cotton was placed under the string to allow branch growth and to ensure that larvae did not escape from the sleeve cage.

In early September, study branches were removed with pruning shears and transported to the laboratory where sleeve cages were removed from each branch, defoliation per shoot was visually estimated using the method described above, and the number of BFS that formed cocoons, counted. The number of cocoons per cage was used to estimate the number of late-instar larvae per cage. To express insect density in terms of branch surface area, branch length and width were recorded for all branches and surface area estimated as (length  $\times$  maximum width)/2. We used branch area instead of a branch as the sample unit because there is often a large variation in the sizes of branches (Parsons et al., 2003). The amount of defoliation caused by BFS was estimated by subtracting initial defoliation estimates (calculated using the midpoints of defoliation classes) from final defoliation estimates.

In addition, 1 terminal current-year shoot from the central axis of the branch and one 1-year-old lateral shoot were removed from the 0 control and 0 density branches of 10 trees at the end of the growing season. Shoot length and the lengths of four needles in the middle portion of these shoots were measured to determine the influence of caging on shoot and needle extension of current-year shoots.

### 2.3. Field survey of natural defoliation

Data from an independent field survey was used to determine whether results from the experimental studies were applicable in the field at a stand level. Surveys were initiated in several stands, starting in 1997, and continued until 2003. Thus, the levels of defoliation caused by natural populations of BFS were monitored in 1997 in one thinned stand, in 1998 in two thinned and one unthinned stand, in 1999 in three thinned and two unthinned stands and from 2000 to 2003 in four thinned and three unthinned stands of varying sawfly and tree densities. Stands were 22–32 years old, contained 2500–5000 (thinned stands) or 14,000–24,000 (unthinned stands) trees per ha, and were located between Stephenville (48°32'N; 58°33'W) and Corner Brook (48°57'N; 57°57'W) on the west coast of Newfoundland.

In each stand, one plot was established every 30 m on a 150 m linear transect for a total of five plots per stand. The 20 dominant and co-dominant balsam fir trees that were closest to the centre of each plot were selected. The first plot was located 30 m from the edge of the stand. In the spring of each year, five of the 20 marked trees in each plot were randomly selected without repetition, by picking numbers out of a hat. One southwest-facing mid-crown branch was sampled on each of these trees prior to egg hatch, for a total of 25 branches per site per year. The number of eggs present on each branch was recorded and branch length and width measured. Defoliation was visually estimated as described above except that defoliation was categorized in 10% classes. Natural needle fall was subtracted from defoliation estimates to obtain defoliation due to balsam fir sawfly. Estimates of natural needle fall were obtained from a sample of 120 branches collected in spring 1999 and 2000 from undefoliated sites surrounding the sawfly outbreak. Using the same sampling methods as above, sawfly densities, but not defoliation, were monitored between the first and second instar (early instars) and between the third and fourth instar (mid instars), except when densities were very low (i.e.,  $\leq 0.5$  larvae per square meter of branch surface area). Frequent monitoring of field populations enabled us to determine when populations had reached previously specified stages of development. The sample size was 30 stands for eggs, 28 stands for L<sub>1</sub>–L<sub>2</sub> and 25 stands for L<sub>3</sub>–L<sub>4</sub>.

The relationship between sawfly density and defoliation may differ for increasing versus declining populations, due to higher larval mortality in the latter. Consequently, for each stand, mean egg density in calendar year  $t-1$  was compared to the mean egg density in calendar year  $t$  to determine whether populations had increased or decreased during the previous year (i.e.,  $(\log \text{egg density in year } t-1) - (\log \text{egg density in year } t)$  is  $>0$  for decreasing and  $<0$  for increasing populations). The yearly change in defoliation in year  $t$  at a site was obtained by subtracting defoliation in spring of year  $t$  at this stand from defoliation in spring of year  $t+1$  at the same stand.

#### 2.4. Statistical analyses

Linear and multivariate regression analysis was employed to examine the relationship between BFS density (i.e., mean number of larvae per square meter of branch surface area) and percent defoliation per shoot for the sleeve-cage study. Percentages from the sleeve-cage study were subjected to the arcsine square root transformation to normalize the distribution of

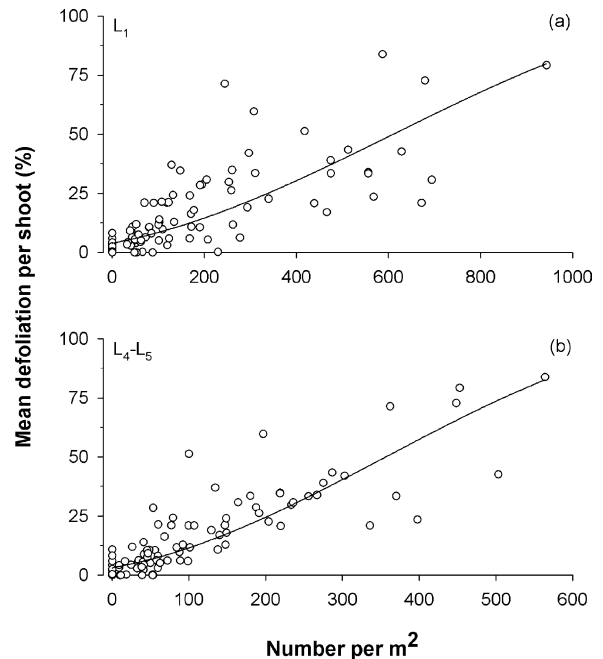


Fig. 1. Relationships between the number of (a) early- or (b) late-instar larvae of balsam fir sawfly larvae per square meter of branch surface area in sleeve cages and mean percent defoliation per shoot per branch in the sleeve-cage study.

Table 1

Summary of linear regression analyses describing relationships between densities of early- and late-instar balsam fir sawfly larvae in sleeve cages and mean percent defoliation for each shoot age in 2000

Predictor	Age of shoots	Coefficient	Intercept	d.f.	<i>F</i>	<i>P</i>	<i>r</i> <sup>2</sup>
Initial density	<i>C</i> + 1	0.05	12.03	1, 92	90.64	<0.001	0.49
	<i>C</i> + 2	0.06	12.17	1, 92	123.01	<0.001	0.57
	<i>C</i> + 3	0.05	9.87	1, 92	83.87	<0.001	0.47
	<i>C</i> + 4	0.05	9.11	1, 92	69.05	<0.001	0.42
	<i>C</i> + 5	0.05	9.05	1, 92	47.26	<0.001	0.33
	<i>C</i> + 6	0.02	18.65	1, 92	2.66	0.106	0.02
	<i>C</i> + 7	0.02	5.36	1, 42	5.35	0.026	0.03
	Overall <sup>a</sup>				7, 36	8.67	<0.001
Final density	<i>C</i> + 1	0.09	10.90	1, 92	134.38	<0.001	0.59
	<i>C</i> + 2	0.10	10.97	1, 92	195.06	<0.001	0.68
	<i>C</i> + 3	0.10	8.11	1, 92	162.31	<0.001	0.63
	<i>C</i> + 4	0.10	7.46	1, 92	123.02	<0.001	0.57
	<i>C</i> + 5	0.10	6.92	1, 92	87.80	<0.001	0.48
	<i>C</i> + 6	0.04	17.80	1, 92	4.10	0.046	0.03
	<i>C</i> + 7	0.03	6.27	1, 42	3.04	0.088	0.05
	Overall <sup>a</sup>				7, 36	24.07	<0.001

Larval densities are expressed per square meter of branch surface area. Results from a multivariate regression incorporating all age classes (i.e., overall) are also shown.

<sup>a</sup> Multivariate regression in which  $\{C + 1, C + 2, C + 3, C + 4, C + 5, C + 6, C + 7\}$  = predictor. Significance indicates that the multivariate model is significant.

residuals and/or to correct heteroscedasticity. Paired sample *t*-tests were used to compare shoot and needle lengths of current-year shoots on caged and uncaged branches at the end of the growing season.

Multiple regressions (Steel and Torrie, 1980) were carried out to determine the effects of population density, thinning and population trend (increasing or declining) on yearly changes in defoliation in the field surveys.

### 3. Results

#### 3.1. Sleeve-cage study

The density of larvae initially placed on branches explained 57% (arcsine  $\sqrt{y} = 0.06\{\text{density of early instars}\} + 11.41$ ;  $F_{1,92} = 124.42$ ,  $P < 0.001$ ) (Fig. 1a) of the variation in defoliation for all shoot ages combined. Similarly, the density of late-instar BFS, estimated by the density of cocoons, explained 70% (arcsine  $\sqrt{y} = 0.10\{\text{density of late instars}\} + 10.11$ ;  $F_{1,92} = 221.50$ ,  $P < 0.001$ ) (Fig. 1b) of the variation in defoliation. Densities of both early- and late-instar larvae of BFS were significantly related to defoliation on shoots 1–5 years old ( $r^2 \geq 0.33$ ), but not always for shoots 6 or 7 years old (Table 1). There was negligible feeding on current-year shoots.

There were no significant differences in the final mean ( $\pm$ S.E.) length of terminal current-year shoots on caged and uncaged branches, either on the central axis (caged =  $67.40 \pm 5.43$  mm, uncaged =  $61.50 \pm 7.70$  mm;  $t_9 = 0.84$ ,  $P = 0.425$ ) or on 1-year-old laterals (caged =  $44.20 \pm 3.30$  mm, uncaged =  $43.10 \pm 4.81$  mm;  $t_9 = 0.21$ ,  $P = 0.838$ ). Similarly, caging did not influence mean needle lengths on current-year shoots on the central axis of the leader (caged =  $12.80 \pm 0.66$  mm, uncaged =  $13.10 \pm 0.78$  mm;  $t_9 = 0.34$ ,  $P = 0.738$ ), or on 1-year-old laterals (caged =  $12.80 \pm 0.49$  mm; uncaged =  $13.80 \pm 0.95$  mm;  $t_9 = 1.36$ ,  $P = 0.204$ ).

#### 3.2. Field survey of natural defoliation

In both increasing and declining populations, the level of defoliation caused by natural populations of BFS increased linearly with population density. Thinning did not explain a significant portion of the

variation in defoliation ( $P \geq 0.220$  for regressions with eggs, early and mid instars) and therefore, two-way multiple regressions, incorporating only the effects of population density and trend, were used to predict defoliation. The densities of eggs ( $y = 0.10\{\text{egg density}\} + 15.23\{\text{trend}\} - 11.26$ ; trend = 1 in increasing populations and trend = 0 in declining populations;  $r^2 = 0.77$ ;  $F_{2,27} = 50.11$ ;  $P < 0.001$ ) (Fig. 2a), early

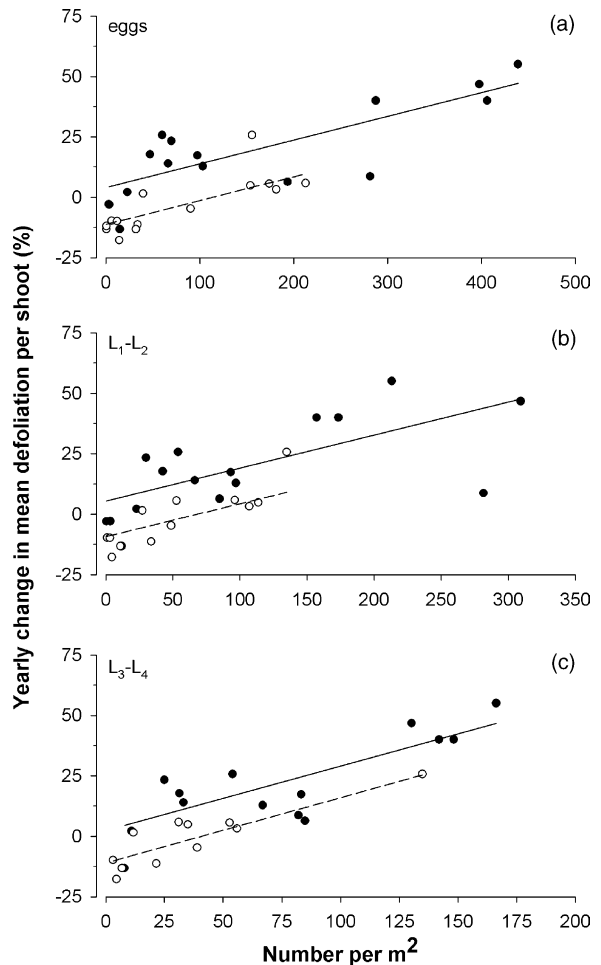


Fig. 2. Relationship between balsam fir sawfly population density per square meter of branch surface area of (a) eggs, (b) early instars or (c) mid instars, and yearly change in mean defoliation per shoot per branch in increasing (solid circles) and declining (open circles) populations. Annual variations in foliage availability can sometimes result in a negative value for annual percent change in defoliation for increasing populations and a positive value for decreasing populations. Larval densities were not determined when inferior to 0.5 larvae per square meter, resulting in different numbers of data points in figures (a–c).

instars ( $y = 0.14\{L_1-L_2 \text{ density}\} + 14.80\{\text{trend}\} - 9.31$ ;  $r^2 = 0.64$ ;  $F_{2,25} = 25.22$ ;  $P < 0.001$ ) (Fig. 2b) and mid-instar larvae ( $y = 0.27\{L_3-L_4 \text{ density}\} + 12.94\{\text{trend}\} - 11.03$ ;  $r^2 = 0.81$ ;  $F_{2,22} = 52.60$ ;  $P < 0.001$ ) (Fig. 2c) were all strongly related to defoliation. In all three relationships, increasing populations caused 13% (Fig. 2c) to 15% (Fig. 2a) more defoliation than declining populations of similar density ( $t_{22-27} > 3.18$ ;  $P \leq 0.004$ ).

#### 4. Discussion

Defoliation by the BFS was significantly related to egg and larval density in both the sleeve-cage study and in field surveys carried out over several years, suggesting that egg and larval densities are useful predictors of future defoliation.

Relationships between defoliation and larval density were weaker for young than old larvae in both studies, probably because most of the foliage consumed during larval development is eaten by third, fourth and fifth instars (Parsons et al., 2003) combined with variations in larval mortality. Other variations in defoliation not attributable to sawfly density may have resulted from differences in the actions of natural enemies (Moreau, 2004), the availability of different age-classes of foliage (Moreau et al., 2003) and foliage quality (e.g., Krause et al., 1993; Wagner and Zhang, 1993; Géri et al., 1993; McMillan and Wagner, 1997; Moreau, 2004).

Defoliation was most closely related to larval densities on young (excluding current-year) shoots in the sleeve-cage study. This is attributable to larval feeding behaviour. Early-instar larvae are gregarious and usually initiate feeding on the 1-year-old shoot on which they emerged, or on an adjacent shoot (Anstey et al., 2002). As larvae develop they slowly disperse to nearby shoots, most of which are of similar age. When a range of foliage ages is available, BFS larvae consume more 1 to 3-year-old foliage than current or older foliage (Parsons et al., 2003; Moreau et al., 2003). The low levels of defoliation recorded for sleeve cages without larvae (Fig. 1) are attributable to small errors in visual estimations of defoliation before versus after larval feeding, and perhaps due to small amounts of needle fall.

The relationship between BFS egg density and defoliation differed for increasing and decreasing

populations, probably due to differences in juvenile mortality. Survival of BFS larvae is much higher during the initial phase of an outbreak than during the period of population decline (Moreau, 2004). Consequently, larvae emerging from a given number of eggs in the early phase of an outbreak, when survival is high, cause more defoliation than larvae emerging from the same number of eggs in a declining population, when fewer individuals survive to become late instars.

Results of this study suggest that BFS egg and larval density may be used to predict defoliation on balsam fir. Larval sampling is perhaps the best method to establish density–defoliation relationships because it accounts for egg and larval mortality, as well as larval dispersal. However, larval sampling may not permit enough time to implement management tactics, such as application of a nucleopolyhedrosis virus (Lucarotti et al., 2000) that is directed against larvae. Fortunately, knowledge of whether a population is increasing or decreasing, which requires egg density estimates in consecutive years, can be used along with egg density to produce good predictions of future defoliation by *N. abietis*. Thus our results suggest that establishment of robust density–damage relationships are possible for BFS on balsam fir using egg densities to estimate future defoliation and therefore, the percentage of foliage remaining. These data can be combined with previously reported foliage weight estimates (Piene, 1983) to obtain the weight of foliage remaining and previously established relationships (Parsons et al., 2003) between foliage weight and volume growth, to estimate growth loss.

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