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Relationships between yellowheaded spruce sawfly, *Pikonema alaskensis*, density and defoliation on juvenile black spruce

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Abstract

Manipulative field experiments and field surveys were carried out to evaluate the relationship between the density of yellowheaded spruce sawfly, *Pikonema alaskensis* (Roh.), and resultant defoliation on young open-grown black spruce, *Picea mariana* ([Mill.] B.S.P.), in central Newfoundland. In sleeve-cage experiments, the number of early and late-instar larvae per current-year shoot explained greater than 73 and 69%, respectively, of variation in mid-crown branch defoliation and 34–75% of variation in leader defoliation. In field surveys, densities of eggs, mid-, and late-instar larvae in whorls 2 and 4 explained greater than 34, 46, and 75% of variation, respectively, of defoliation in leaders and in whorls 1 and 2 of black spruce. Estimates of adult female and male abundance obtained from sticky traps explained 66 and 40% of variations, respectively, in defoliation among trees within stands and almost 90% of variations in defoliation among stands. Relationships were slightly improved by incorporating previous defoliation into analyses as a covariate. Our results indicate that density–defoliation relationships for all stages of *P. alaskensis* on black spruce are robust and suitable for incorporation into a management program for this pest.

Keywords: *Pikonema alaskensis*; *Picea mariana*; Integrated pest management; Intra-crown dispersal

1. Introduction

Efficiently implementing suppression tactics in integrated pest management requires a basic understanding of the herbivore density–plant damage relationship. These relationships can be used to establish an economic injury level (Pedigo et al., 1986), and thereby facilitate decision-making regarding the application of suppression tactics (Binns and Nyrop, 1992). In response to increasing pressure to fulfill the conflicting economic and ecological demands of effective suppression with minimal environmental effects, the establishment of density–defoliation relationships has become increasingly prevalent in forest pest management (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; Nealis and Turnquist, 2003; Parsons et al., 2005).

Heterogeneity in the temporal and spatial distribution of insects, and in the response of host-plants to associated injury, may complicate the establishment of relationships between herbivore density and defoliation. For example, the spatial distribution of insect herbivores is determined by their foraging behavior, which is often influenced by variations in food quality (Hassell and Southwood, 1978; Stamp and Bowers, 1990; Carroll and Quiring, 1993; Williams et al., 2001), foraging patterns of natural enemies (Quiring and Butterworth, 1994; McMillan and Wagner, 1998; Williams et al., 2001), and climatic or microclimatic conditions (Knapp and Casey, 1986; Stamp and Bowers, 1990; Alonso, 1997; Bryant et al., 2002). Similarly, responses of host-plants to herbivory can be highly variable due to variations in site quality (Morse and Kulman, 1986), defoliation intensity (Kulman, 1971; Piene and Little, 1990) or history (Vanderklein and Reich, 1999), and/or the location of plant tissue consumed (Honkanen and Haukioja, 1994). A basic understanding of an insect's foraging behavior (Carroll and Quiring, 1993; Parsons et al., 2005) and/or the capacity of its host to compensate for the injury inflicted (Trumble et al., 1993) are needed to establish robust relationships relating current pest density to future host-plant damage.

Severe outbreaks of yellowheaded spruce sawfly, *Pikonema alaskensis* (Roh.) (Hymenoptera: Tenthredinidae) in intensively managed black spruce (*Picea mariana* [Mills.] B.S.P.)

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stands throughout central Newfoundland (Hall et al., 1998) and in isolated regions of New Brunswick (Lavigne, 1996) have slowed tree growth and caused widespread top-kill (upper crown branch mortality). Top-kill halts the apical growth of trees resulting in squat bushes with little commercial value. Reports of extensive top-kill, as high as 88% of the trees in some stands (unpubl. data), and associated losses in height and volume growth have generated concern for the future wood supply in the region. This pattern of injury is related to the propensity of late-instar larvae, which consume the most foliage, to disperse acropetally (sensu Quiring, 1993) from lower to upper apical crown positions to complete development (unpubl. data). Estimates of egg or mid-instar larval density from the tip of a branch in each of whorls 2 and 4 provide the best predictions of subsequent densities of late-instar larvae in the upper crown (i.e., whorls 1 and 2) of black spruce (Johns et al., 2006) and may, therefore, be similarly useful for predicting upper crown defoliation. Preliminary studies examining relationships between *P. alaskensis* density and defoliation in white spruce in Minnesota (Cook and Hastings, 1976) and in black spruce in New Brunswick (Lavigne, 1996) also indicate that such relationships are feasible. However, to our knowledge no studies have established these relationships for *P. alaskensis* using tested sampling units for density or defoliation, which is critical if subsequent relationships between defoliation and categories of damage, such as growth loss or top-kill, are to be established.

This study employs previously established defoliation and *P. alaskensis* sampling methods, described in Johns et al. (2006), to establish relationships between the density of adults, eggs, and larvae and resultant defoliation in black spruce, in both field surveys and manipulative experiments. The effect of previous defoliation on relationships between density and defoliation was also evaluated because *P. alaskensis* may have an affinity for trees that have sustained defoliation in the past (Pointing, 1957).

2. Methods

2.1. Description of study insect

Pikonema alaskensis is a major pest of juvenile, open-grown spruce throughout central and northeastern North America (Katovich et al., 1995). Black spruce is the primary host of *P. alaskensis* in central Newfoundland, however white spruce (*P. glauca* [Moench] Voss) and blue spruce (*P. pungens* Engelm.) are also susceptible (Forbes, 1949). Detailed descriptions of the life history of *P. alaskensis* are available in Pointing (1957), Houseweart and Kulman (1976a), and Katovich et al. (1995). Briefly, adults eclose soon after bud burst and oviposit eggs at the base of needles in new flushing shoots. Offspring of unmated females are all male, whereas those from mated females may be either male or female (Houseweart and Kulman, 1976b). Young larvae feed mainly on current-year foliage through five (male) or six (female) instars, then drop to the ground and spin a cocoon in the upper duff layer, where they overwinter as prepupae (Rau et al., 1979).

2.2. Study areas

This study was conducted in intensively managed black spruce stands located approximately 50 km (five stands; N 48°40′11.3″, W 55°30′27.5″) and 100 km (four stands; N 48°17′07.3″, W 55°29′01.4″) south of Grand Falls-Windsor, Newfoundland. Trees were planted at densities of approximately 2500 stems/ha and ranged in height from 1.5 to 2.5 m with 10 to 14 whorls of branches. The branches of adjacent trees did not overlap. Needle loss was due primarily to feeding by *P. alaskensis* and/or natural needle fall. Densities of *Pikonema dimmockii* (Cress.) (Hymenoptera: Tenthredinidae), a solitary non-outbreaking herbivore (Pointing, 1957) and the only other defoliator observed, were less than one larva per tree. A few balsam fir (*Abies balsamea* [L.] Mill.), eastern larch (*Larix laricina* [Du Roi] K. Koch), and white birch (*Betula papyrifera* Marsh) trees were interspersed within each stand. Ground vegetation was dominated by sheep laurel (*Kalmia angustifolia* L.), blueberry (*Vaccinium* sp.), and haircap mosses (*Polytrichium* sp.).

2.3. Sleeve-cage experiments: larval density–defoliation relationships

In 2000 and 2001, relationships between *P. alaskensis* density and resultant defoliation were evaluated in four sleeve-cage experiments where we controlled the number of larvae on mid-crown branches or leaders and excluded potential mortality associated with dispersal and natural enemies. In each experiment, prior to bud burst, 15 or 20 trees were selected haphazardly and east- or west-facing branches in whorl 3 or 4 (Fig. 1) were selected and marked with flagging tape. Trees in this and other experiments discussed in this paper were selected within a 100 m × 100 m area to minimize differences in soil and site characteristics. Neither the densities of eggs and mid-instar larvae of *P. alaskensis*, nor defoliation attributable to sawfly larvae, are influenced by cardinal direction in black spruce (Johns et al., 2006). Branch defoliation was estimated visually before (i.e., mid-June) and again after larval feeding (i.e., late-August) using defoliation classes of 0, 1–5, 6–20, 21–40, 41–60, 61–80, 81–99, or 100% for shoots located along the first- and second-order branch axes, as described in Piene (1989). For consistency, only the first five age-classes of foliage (i.e., current-year, 1-, 2-, 3-, and 4-year old) were evaluated on each branch. Mean percent defoliation per shoot per branch attributable to *P. alaskensis* was calculated by subtracting defoliation estimates obtained prior to larval feeding, which were also used as an estimate of previous defoliation, from those obtained after larval feeding was completed. Estimates of previous defoliation included the combined effects of past feeding by *P. alaskensis* as well as natural needle fall.

A range of sawfly densities among branches was obtained in experiments either by utilizing the natural densities of larvae on selected branches, or by collecting larvae from adjacent stands and placing them on selected branches. To ensure that all *P. alaskensis* were counted, a dissecting needle was used to carefully spread the needles on current-year shoots to expose

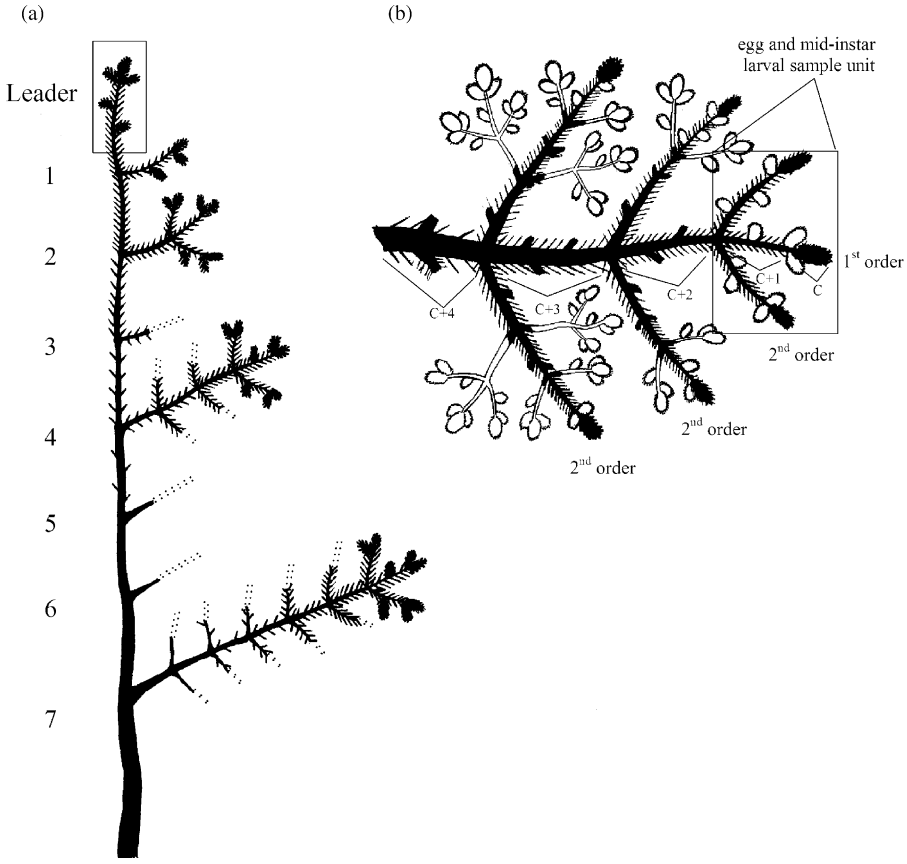

Fig. 1. (a) Schematic representation of a juvenile black spruce crown with seven whorls. For the purposes of this study, whorl 1 includes both the leader and a whorl 1 branch. (b) Schematic representation of within branch sample units for measurements of defoliation and *P. alaskensis* density. Defoliation was visually estimated for all age-classes along the first- and second-order branch axes (solid shoots and buds). Eggs and larvae were counted on all current-year shoots on the terminal and distal-lateral 1-year old shoots. C, C+1, C+2, C+3, and C+4 refer, respectively to current-year, and 1-, 2-, 3-, and 4-year old shoots.

the relatively cryptic early instar larvae. Withered needles were also often indicative of sawfly oviposition and/or larval feeding and provided a useful search image when trying to locate young larvae. Oviposition by female sawfly and feeding by young larvae occurs exclusively on current-year foliage and even older larvae only exploit older age-classes when current-year foliage became scarce (Pointing, 1957). Thus, throughout this paper egg and larval densities are expressed as the number of *P. alaskensis* per current-year shoot per branch. Sawflies were generally first or second instars (i.e., early instar) at the initiation of each experiment. To verify this, additional larvae were collected either from within the study stand (for studies using existing natural densities) or from the stand from which larvae were collected, and preserved in 70% ethanol. The mean instar of 25 larvae was determined based on head-capsule widths, which were similar to those observed for *P. alaskensis* by Vanderwerker and Kulman (1974) in Minnesota. After larval feeding was completed in each experiment, sleeve cages were removed from branches and examined, and cocoons counted to provide estimates of larval survival and the density of late-instar larvae per branch.

In the first sleeve-cage experiment, conducted in 2000, 15 trees were selected and 5 branches per tree were marked with flagging tape in a stand with 0.03–0.86 *P. alaskensis* larvae per current-year shoot and with 1–39% defoliation per shoot per branch. Hereafter, this will be referred to as the ''natural density'' experiment. After egg hatch, early instar larvae were counted on four of the five selected branches in each tree. These branches were enclosed in fine-mesh cloth sleeve cages (0.50 m × 0.75 m) filled with approximately 500 ml of sifted peat to facilitate cocoon formation. Sleeve cages only covered the portion of the four branches that were evaluated previously for defoliation and were secured to branches using a twist tie. All larvae were removed from the remaining (fifth) branch, which was then covered with a sleeve cage and used as a control to determine the effects of the sleeve cage on defoliation.

Similar sleeve-cage experiments were conducted in 2000 and 2001 on 20 trees in two stands (one different stand each year) with no *P. alaskensis* present and no previous defoliation, referred to hereafter as the ''manipulated density'' experiments. For these studies early instar larvae were collected from a stand (N 48°40′11.3″, W 55°30′27.5″) with relatively high *P. alaskensis* densities in both years (0.22 ± 0.02 larvae per current-year shoot). Fifty additional larvae were collected and preserved so that the mean instar of *P. alaskensis* could be verified. Larvae were collected by clipping individual shoots occupied by larvae and placing them in an open tub for transport to the study site. Five or six mid-crown branches were selected in each tree and randomly assigned a density treatment ranging from 0 to 0.53 larvae per current-year shoot in 2000

(originally applied as 0, 2, 4, 8, 12, or 18 larvae per branch), or of 0, 0.1, 0.35, or 0.70 larvae per current-year shoot in 2001. In 2001, a control branch was also selected and left with no larvae and no cage so that natural needle fall, in the absence of *P. alaskensis* and a sleeve cage, could be evaluated. To minimize injury to larvae during transfer, forceps were used to gently remove the needles occupied by larvae from shoots and to move them onto the study branches or leaders. Needles with larvae were placed between the flaring needles of current-year shoots. After placement, larvae moved almost immediately from the transferred needle onto adjacent shoots.

In 2001, a third ''manipulated density'' sleeve-cage experiment was conducted to establish density–defoliation relationships for black spruce leaders (Fig. 1a). Prior to bud burst, 75 trees with no *P. alaskensis* or previous defoliation were selected haphazardly in one stand. The leader of each tree was evaluated for previous needle fall and randomly assigned a treatment of 0 (no sleeve cage), 0, 0.1, 0.35, and 0.7 larvae per current-year shoot. Early instar larvae were collected, placed onto leaders, and enclosed in sleeve cages using the same methods described for the two ''manipulated density'' mid-crown branch experiments.

Stepwise multiple regression analysis (SAS Institute Inc., 1999) was utilized to evaluate the relationship between mean percent defoliation at the end of the ''natural density'' experiment and previous defoliation (as determined by spring estimates of defoliation) and early or late-instar (i.e., initial or final) larval density. However, in ''manipulated density'' experiments, where there was no previous defoliation associated with feeding by *P. alaskensis*, linear regression analyses were employed to evaluate relationships between the number of early or late-instar *P. alaskensis* larvae per current-year shoot and mean percent defoliation. In experiments with multiple defoliation estimates for each larval density class (i.e., Figs. 2c and 3a), raw data rather than mean estimates of defoliation were used in analyses (Zar, 1999). Prior to analyses, defoliation data were arcsine square-root transformed to meet model assumptions of normality and homogeneity of variance (Zar, 1999).

2.4. Field survey: eggs or larval density–defoliation relationships

Complementary field surveys were conducted to establish density–defoliation relationships in unmanipulated field conditions, where larvae were allowed to disperse and were subjected to mortality from natural enemies. In 2001, four stands with 12–21% defoliation per shoot per tree were selected. Trees were selected within this defoliation range to minimize potential differences in relationships caused by excessive variation in previous defoliation or defoliation history. In each stand, prior to bud burst, 25 trees with 1–2 years of previous defoliation and no top-kill were haphazardly selected. On each tree, the leader and one west-facing branch in each of whorls 1, 2, and 4 (Fig. 1a) were selected and marked with flagging tape and all age-classes evaluated for previous defoliation/needle fall using the method described above. At egg (i.e., $\leq$3% egg hatch), mid- (i.e., mean instar 3.3 $\pm$ 0.18, where egg = 0 and sixth instar = 6), and late-instar (i.e., mean instar 5.1 $\pm$ 0.05) stages, all shoots on each of the selected branches were carefully examined and all *P. alaskensis* counted. Fifty larvae were collected from each stand during each larval sampling period and the mean instar determined by measuring head-capsules.

The number of *P. alaskensis* eggs or mid-instar larvae per current-year shoot on the tip of a branch in each of whorls 2 and 4 provide the best estimates of subsequent late-instar larval density in whorls 1 and 2, where most *P. alaskensis* feed before dropping from the tree (Johns et al., 2006). Thus, analyses of covariance were carried out to evaluate stand-related differences in relationships between mean percent defoliation in whorls 1 and 2 or just on the leader of black spruce, and the density of *P. alaskensis* eggs or mid-instar larvae in whorls 2 and 4, and of late-instar larvae in whorls 1 and 2. In this study defoliation generally increased asymptotically with *P. alaskensis* density up to a threshold near 100% (Figs. 4 and 5). However, since any economic or action threshold derived from this study will most likely be far below 100% defoliation, linear regression was employed to analyze relationships, and one outlier that was well beyond the linear line was removed from both the graph and analyses. Analyses were conducted with and without including the influence of previous defoliation. All defoliation data were subjected to an arcsine square-root transformation prior to analyses.

2.5. Field survey: adult density–defoliation relationships

In 2001 and 2003, we evaluated relationships between spring densities of *P. alaskensis* adults and subsequent upper crown defoliation in black spruce within and among stands. In each of four (2001) and six (2003) stands, with previous mean defoliation ranging from 2 to 74% per shoot per tree, two parallel transects 10 m apart were set up beginning 10 m from the edge of the stand. Along each transect, a tree was selected haphazardly at each 10 m interval for a total of twelve trees per stand. Each spring, prior to *P. alaskensis* eclosion, a yellow sticky trap (10 cm $\times$ 15 cm) (Pherocon AM) was tied between west-facing whorl 2 and 3 branches in the trees selected along transects. In 2001, 25 trees located between the two transects were selected haphazardly within each stand and a west-facing whorl 1 branch, which provides a good estimate of upper crown defoliation (Johns et al., 2006) was evaluated for defoliation in the spring and fall using the methods described above. In contrast to 2001, defoliation estimates in 2003 were conducted on the 12 trees containing sticky traps that were selected along transects.

Pheromone traps (white delta) were also placed in three of the stands used to test sticky traps in 2001. In each stand, two 40 m transects were set up parallel to those established for sticky traps and one tree was selected along each transect every 10 m (i.e. 10 trees per stand). The minimum distance between pheromone and sticky traps was 5 m. A pheromone trap was tied to a whorl 2 branch in each selected tree. In an alternating fashion, half the traps were baited and the other half were left empty to serve as controls. Traps were baited with a synthetic

lure based on a previously identified (Bartelt et al., 1982), isolated and synthesized (Bartelt and Jones, 1983; Bartelt et al., 1983) multi-component sex pheromone. Sticky and pheromone traps were checked every three days until the end of egg lay (approximately 2 weeks).

Relationships between defoliation at the end of the season and the number of adult males and females per trap, as well as previous defoliation, were evaluated using stepwise multiple regression analysis. Prior to analysis, defoliation data were transformed using the arcsine square-root transformation to correct problems with heterogeneity of variance and normality.

3. Results

3.1. Sleeve-cage experiments: larval density–defoliation relationships

Survival of larvae in sleeve-cages was 93% in the 'natural density', and 78% (2000) and 53% (2001) in the 'manipulative density' experiments on branches in whorl 3 or 4. Defoliation increased linearly with the number of early and late-instar larvae per current-year shoot in each of these three experiments (Fig. 2). In the "natural density" experiment, accounting for previous defoliation in the model only marginally increased r^2 values (~7%) for both early and late-instar larvae ($F_{2,72} \geq 32.94$, $P < 0.01$) and was, therefore, discarded in subsequent analysis. Overall, early and late-instar larval density explained ≥73% of variation in defoliation among mid-crown branches ($F_{1,72-117} \geq 204.86$, $P < 0.01$) (Fig. 2). In general, relationships established in 2000 using early or late-instar larvae were very similar (Fig. 2a, b, d, and e), whereas the slope of relationships in the 2001 'manipulated density' experiment were much higher for late- than for early instar larvae (Fig. 2c and f).

For the "manipulated density" sleeve-cage experiment conducted on leaders, where larval survival was only 34%, the number of early and late-instar larvae per current-year shoot explained 35 and 75%, respectively, of the variation in defoliation ($F_{1,73} \geq 232.52$, $P < 0.01$) (Fig. 3).

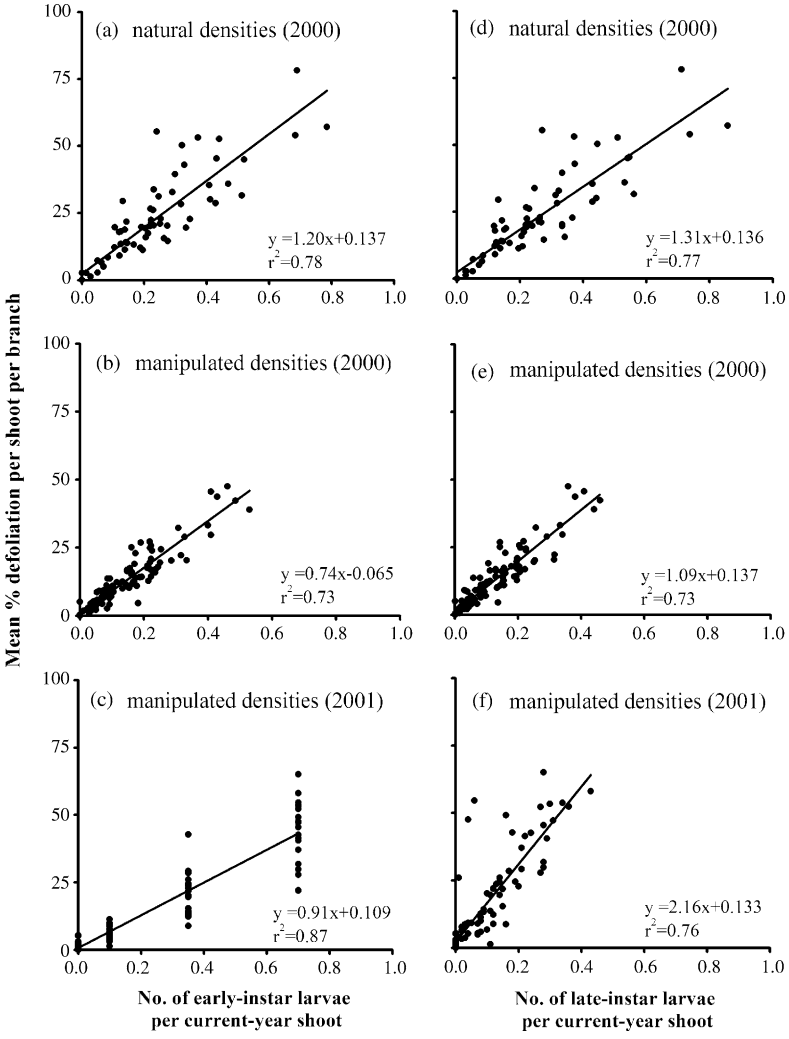

Fig. 2. Relationships between the number of early or late-instar larvae of *P. alaskensis* per current-year shoot in sleeve cages and mean percent defoliation per shoot on a whorl 3 or 4 branch of black spruce. Sleeve cages were placed over branches with naturally occurring (i.e., unmanipulated) densities in 2000 (a and d) and over branches on which pre-selected densities were placed in 2000 (b and e) and 2001 (c and f). Raw defoliation data are illustrated but regressions were carried out with arcsine square-root transformed data.

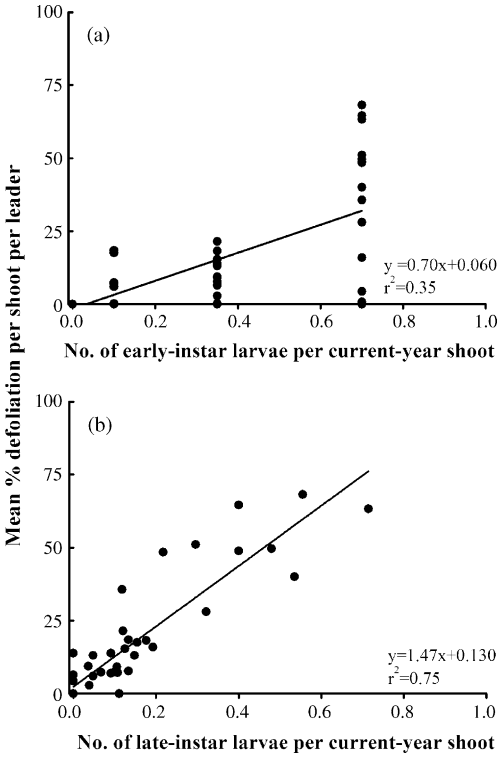

Fig. 3. Relationships between the number of early instar (a) and late-instar (b) larvae of *P. alaskensis* per current-year shoot in sleeve cages and mean percent defoliation on black spruce leaders. Raw defoliation data are illustrated but regressions were carried out with arcsine square-root transformed data.

3.2. Field survey: egg or larval density–defoliation relationships

Relationships between the density of sawfly eggs, mid-, and late-instar larvae and defoliation at the end of the season generally varied significantly among stands, whether or not the influence of previous defoliation was included in the model (Table 1). However, to provide robust density–defoliation relationships that were applicable over a range of conditions, data from stands were pooled for subsequent stepwise multiple regression analyses.

Despite differences among stands, all relationships established between *P. alaskensis* density and subsequent defoliation, both with and without using previous defoliation as a covariate, were highly significant ($F_{1,96} \geq 43.24$, $P < 0.01$). The number of eggs and mid-instar larvae per current-year shoot explained 31–40% of the variation in defoliation among leaders (Fig. 4a and b) and ≥40% of variation in defoliation in whorls 1 and 2 (Fig. 4c and d). Incorporating previous defoliation into the model slightly improved the r^2 values for relationships between defoliation on the leader or in whorls 1 and 2 combined, and densities of eggs (11 and 15%) and mid-instar larvae (9 and 11%).

The density of late-instar larvae in whorls 1 and 2 explained ≥67% of variation in defoliation on the leader and in whorls 1 and 2 ($F_{1,96} \geq 195.92$, $P < 0.01$) (Fig. 5). Using previous defoliation in the model only improved the r^2 values of relationships by approximately 3%.

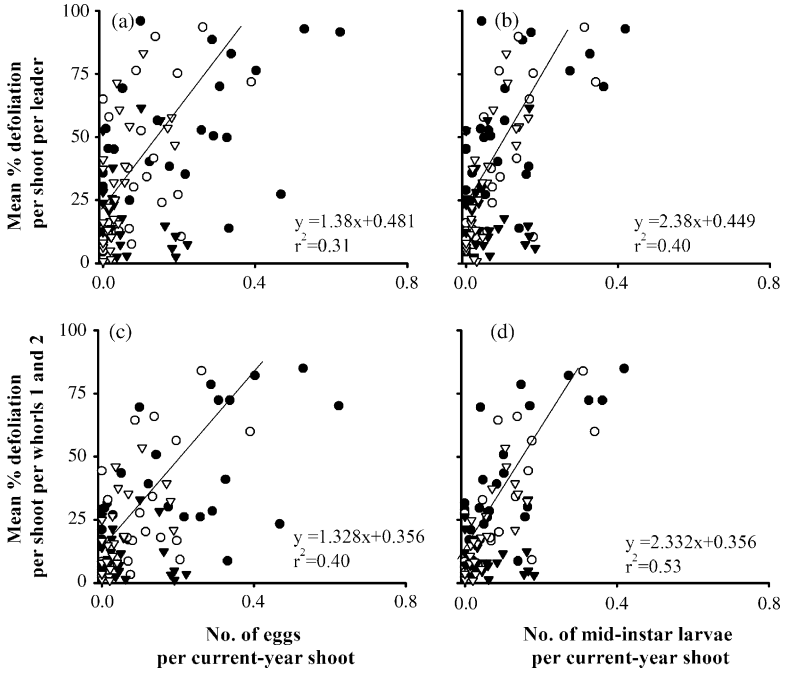

Fig. 4. Relationships in field surveys between the number of eggs and mid-instar larvae of *P. alaskensis* per current-year shoot and mean percent defoliation on the leader (a and b) or in whorls 1 and 2 (c and d) of black spruce. Density estimates were obtained from combining estimates from the distal portion of a whorl 2 and 4 branch. Each of the 4 stands are represented by a different symbol, however data were pooled prior to analyses. Raw defoliation data are illustrated but regressions were carried out with arcsine square-root transformed data.

Table 1
Summary of covariance analyses evaluating stand-related differences in relationships established in field surveys between mean percent defoliation on the leader or in whorls 1 and 2 of black spruce and the number of *P. alaskensis* eggs, mid-, or late-instar larvae per current-year shoot, performed both with and without taking previous defoliation into account

Location of defoliation	Predictor	Model statistics							
		With previous defoliation				Without previous defoliation			
		Coefficient	d.f.	F	r^2	Coefficient	d.f.	F	r^2
Leader	Model		5, 92	15.15	0.45		4, 93	12.18	0.34
	Stand		3, 92	1.44[a]			3, 93	1.57[a]	
	Eggs	1.3667	1, 92	21.88		0.4810	1, 93	18.17	
	Previous defoliation	0.4273	1, 92	18.07					
	Intercept	0.3633				1.3811			
	Model		5, 92	22.88	0.55		4, 93	19.87	0.46
	Stand		3, 92	3.78			3, 93	3.42	
	Mid-instar larvae	2.3150	1, 92	48.13		2.3825	1, 93	42.30	
	Previous defoliation	0.3949	1, 92	19.28					
	Intercept	0.3429				0.4486			
	Model		5, 92	64.73	0.78		4, 93	71.42	0.75
	Stand		3, 92	9.77			3, 93	8.68	
	Late-instar larvae	0.8828	1, 92	190.19		0.9253	1, 93	204.04	
	Previous defoliation	0.1949	1, 92	10.08					
	Intercept	0.3144				0.3577			
Whorls 1 and 2	Model		5, 92	26.32	0.59		4, 93	18.23	0.44
	Stand		3, 92	3.14			3, 93	2.24[a]	
	Eggs	1.1624	1, 92	25.30		1.3287	1, 93	27.48	
	Previous defoliation	0.4642	1, 92	33.32					
	Intercept	0.1762				0.3562			
	Model		5, 92	47.62	0.72		4, 93	36.24	0.61
	Stand		3, 92	8.58			3, 93	5.99	
	Mid-instar larvae	2.0587	1, 92	81.20		2.3317	1, 93	79.78	
	Previous defoliation	0.4052	1, 92	37.02					
	Intercept	0.1702				0.3225			
	Model		5, 92	80.21	0.81		4, 93	81.49	0.78
	Stand		3, 92	17.57			3, 93	14.93	
	Late-instar larvae	0.6980	1, 92	166.68		0.7769	1, 93	211.20	
	Previous defoliation	0.2435	1, 92	17.45					
	Intercept	0.1856				0.2670			

[a] Not significant at $P < 0.05$. All other variables are significant.

3.3. Field survey: adult density–defoliation relationships

The densities of male and female adults captured in sticky traps explained ≥88% of the variation in mean defoliation among stands in both 2001 and 2003 ($F_{1,2–4} \geq 29.15$, $P < 0.01$) (Fig. 6a and b). However, while relationships between female density and defoliation remained relatively consistent among years, densities of males captured in 2003 predicted much less defoliation than that estimated from similar densities in 2001. In 2003, the relationships between sawfly density per sticky trap and resultant defoliation *per tree* were highly significant for both males and females ($F_{1,70} \geq 46.27$, $P < 0.01$) (Fig. 6c and d), although the proportion of variation explained was less than for stand-level comparisons (i.e., compare r^2 values in Fig. 6a and b–c and d).

Only male adults were captured in baited pheromone traps and mean male density per trap per stand was positively but not significantly related to the mean defoliation per stand ($F_{1,2} = 0.567$, $P = 0.541$, $r^2 = 0.44$). No adults were captured in the non-baited control traps.

4. Discussion

Robust relationships between *P. alaskensis* density and resultant defoliation, established using sleeve-cage experiments and field surveys, indicate that adult, egg, and larval densities may all provide useful predictors of future defoliation in black spruce.

Although density–defoliation relationships were usually better for late instars than for early instars and eggs, relationships established with eggs and early instar larvae are still probably the most useful for monitoring as they provide the most time for planning and implementing suppression tactics. Despite high variability, all relationships were significant and the quality of relationships is due primarily to relatively high levels of survival of eggs and early instars and

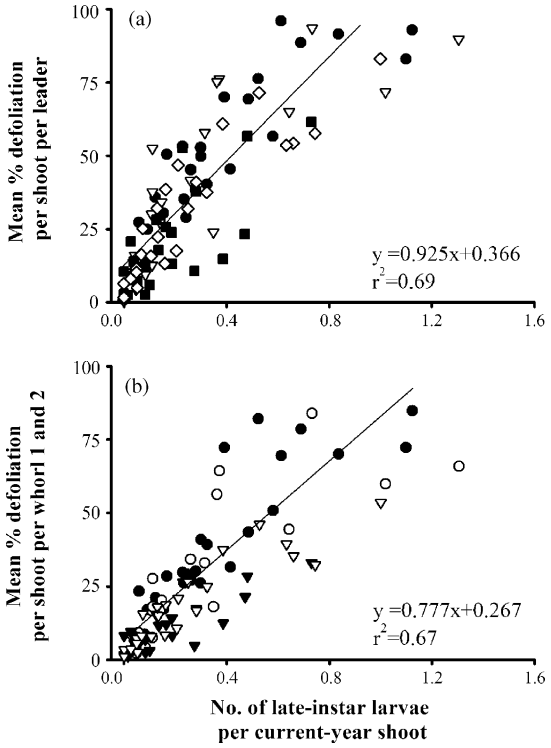

Fig. 5. Relationships in field surveys between the number of late-instar larvae of *P. alaskensis* per current-year shoot and mean percent defoliation on the leader (a) or in whorls 1 and 2 (b) of black spruce. Late-instar larval density estimates were obtained from whorls 1 and 2. Each of the 4 stands are represented by a different symbol, however data were pooled prior to analyses. Raw defoliation data are illustrated but regressions were carried out with arcsine square-root transformed data.

our sampling regime's ability to account for acropetal dispersal by considering the density of sawflies in two whorls. High survival in field surveys may be slightly exaggerated due to the difficulty of locating the cryptic eggs and first-instars relative to later larval stages (pers. obs.). Such underestimates of these early life-stages were particularly evident when using leader defoliation as the dependant variable, as there were several instances where no sawflies were detected in whorls 2 and 4 yet defoliation was still high at the end of the season (i.e., Fig. 4a and b). However, similar population trends have been noted for *P. alaskensis* feeding on black spruce in New Brunswick (Lavigne, 1996) and on white spruce in Minnesota (Houseweart and Kulman, 1976a), where destructive methods were used to ensure careful examination of branches for juvenile sawflies. Most *P. alaskensis* mortality occurs during the cocoon stage, long after feeding has been completed, as a result of small mammal and insect predation, as well as parasitism (Houseweart and Kulman, 1976a). Consequently, at least during the first couple of years of an outbreak, estimates of egg or mid-instar larval density may provide reliable predictions of future damage in black spruce stands, provided they are combined with additional information from sticky traps and previous defoliation.

Differences in relationships established for whorl 3 and 4 branches using sleeve-cage experiments in 2000 versus 2001 were probably attributable to differences in larval survival and/or differences in branch size among stands. Similarly, relationships established for leaders were also much better for late than early instars (compare Fig. 3a and b), due presumably to differences in survival between these stages.

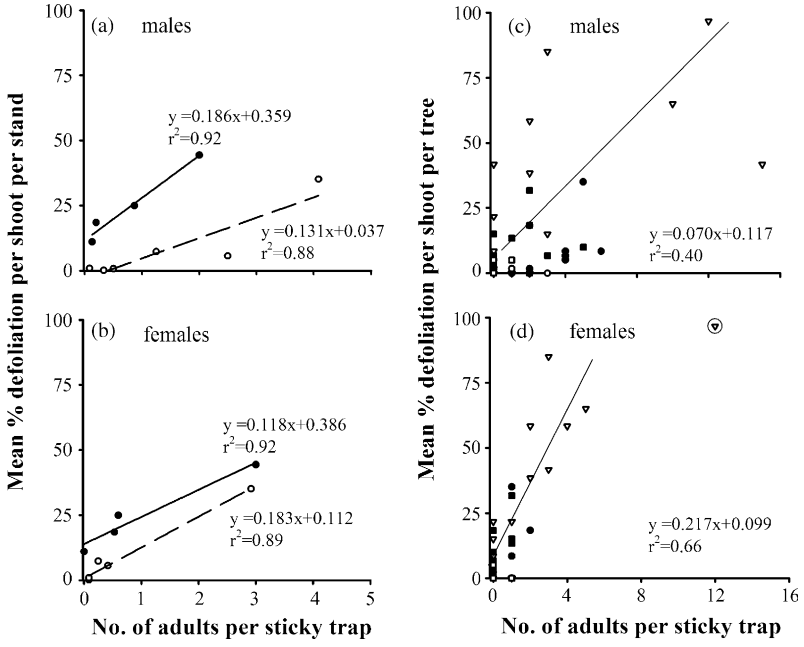

Fig. 6. Relationships between the number of *P. alaskensis* adult males (a) and females (b) per sticky trap and mean percent defoliation per plantation in 2001 ((●), solid line) and 2003 ((○), dashed line). Relationships between adult density and defoliation among trees (all stands pooled) were also established in 2003 for male (c) and female (d) adults. The circled data point represents a tree subjected to extremely high densities of *P. alaskensis* relative to all the other trees used in this study and was not included in analyses. Raw defoliation data are illustrated but regressions were carried out with arcsine square-root transformed data.

In general, relationships established in field surveys between late-instar larval density and defoliation in whorls 1 and 2 of black spruce were most similar to those established in sleeve-cage experiments (compare Figs. 2 and 3 to Figs. 4 and 5). This is probably due in part to some mortality during larval development and because older sawfly larvae consume significantly more foliage than younger larvae (e.g., Parsons et al., 2003). Thus, even though they prevented the natural foraging behavior of *P. alaskensis*, sleeve-cage experiments may provide baseline information useful for evaluating the amount of foliage consumed by this sawfly.

Estimates of adult density based on sticky traps may provide a useful predictor of subsequent defoliation in black spruce. Female density estimates from sticky traps were much better than male densities for predicting subsequent defoliation, both within and among stands. Female density may be much more closely related to subsequent defoliation than male density because within a given year it is the density of females that determines egg abundance and because the relative number of males may vary significantly from year to year (Houseweart and Kulman, 1976b). The relatively close proximity of pheromone traps to sticky traps in 2001 may have interfered with the effectiveness of the sticky traps for capturing males and could explain the resulting differences in relationships established for males in 2001 and 2003. Furthermore, the placement of sticky traps on trees that were later assessed for defoliation could have negatively influenced relationships by removing females from the population whose offspring would have contributed to defoliation of the trees.

Relationships were improved marginally by incorporating estimates of previous defoliation into the model with adult, egg, mid-instar, and to a lesser extent, late-instar larval densities of *P. alaskensis*. This may be due, in part, to the apparent preference of *P. alaskensis* to feed on trees that sustained defoliation in the past (Pointing, 1957). The slight improvement in density–defoliation relationships obtained by the inclusion of previous defoliation in analyses probably does not justify the additional work required to obtain this information. Even so, annual assessments of defoliation by *P. alaskensis* may still be useful in a monitoring program for this sawfly. Preliminary studies in New Brunswick (Lavigne, 1996) and central Newfoundland (unpubl. data) indicate that black spruce may sustain several years of severe defoliation before succumbing to top-kill. Thus, information about the defoliation history of trees within a stand, provided by annual surveys of defoliation, may be important for determining whether trees will be able to tolerate further defoliation or whether immediate suppression of *P. alaskensis* populations is required to prevent extensive top-kill.

Results from this study suggest that adult, egg, and larval densities of *P. alaskensis* can all provide good forecasts of defoliation at the end of the season, at least during the first few years of an outbreak. Although they may provide the most precise predictions of subsequent defoliation, measurements of late-instar larvae are not practical as they do not allow time to apply suppression tactics. Nevertheless, sampling methods used to establish relationships using eggs or mid-instar larvae, although significant, still occasionally underestimated defoliation. Consequently, it may be necessary to apply a multi-level approach that utilizes annual assessments of defoliation, sticky traps in locations where high levels of defoliation are expected, and subsequent egg and/or larval density assessments in areas where adult sampling results are inconclusive. Results from this study will be combined with the results of studies currently underway to establish relationships between upper crown and leader defoliation and height and stem growth loss, shoot production, and top-kill to produce sawfly density–damage relationships.

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