J. Acad. Entomol. Soc. 2: 1-12 (2006)

Sampling methods for evaluating yellowheaded spruce sawfly density and defoliation in juvenile black spruce stands

Rob C. Johns, Don P. Ostaff, and Dan T. Quiring

Abstract: Field surveys were carried out in central Newfoundland to establish sampling procedures for evaluating the density of yellowheaded spruce sawfly, *Pikonema alaskensis* (Roh.) (Hymenoptera: Tenthredinidae), and associated defoliation in black spruce, *Picea mariana* (Mill.) BSP (Pinaceae), stands. Sampling defoliation only for shoots on the main branch axis and second-order branches in whorls 1, 2, and 4 explained more than 71% of the variation in estimates obtained by sampling all shoots on the branches. Sampling defoliation on a branch in whorls 1 and 2 (i.e., the leader and one branch in each of whorls 1 and 2) to evaluate tree-level defoliation explained more than 74% of the variation in defoliation in the two whorls combined. Cardinal direction influenced neither defoliation nor *P. alaskensis* density. Sampling the three most distally located one-year-old shoots of branches in whorls 2 and 4 accounted for more than 88% of the variation in *P. alaskensis* densities when all shoots on the branch were examined. Due to prolific dispersal by late-instar larvae from mid- and lower- to apical upper-crown branches, the leader, one whorl 1, and one whorl 2 branch were selected as the most appropriate sample unit for these instars. Relationships between the density of eggs and mid-instar larvae in whorls 2, 4, or both whorls combined, explained 21 to 49% of the variation in the density of late-instar larvae in whorls 1 and 2. Sampling branches in both whorls 2 and 4 may be necessary to account for seasonal variations in the distribution of eggs and/or mid-instar larvae within the crown of black spruce. Sampling methods provided by this study should facilitate the establishment of monitoring programs for *P. alaskensis* and associated defoliation in black spruce stands.

Résumé: Des relevés de terrain ont été effectués dans le centre de Terre-Neuve afin d'établir les procédures d'échantillonnage pour l'évaluation de la densité de la tenthrède à tête jaune de l'épinette, *Pikonema alaskensis* (Roh.) (Hymenoptera : Tenthredinidae) et de la défoliation de peuplements d'épinette noire, *Picea mariana* (Mill.) BSP (Pinaceae), qu'elle cause aux niveaux des branches et de l'arbre. L'estimation de la défoliation par l'échantillonnage des pousses sur l'axe de la branche principale et sur les branches de deuxième ordre des verticilles 1, 2 et 4 seulement a expliqué plus de71 % de la variation dans les estimations faites en échantillonnant toutes les pousses sur les branches. L'échantillonnage d'une seule branche des verticilles 1 et 2 (c.-à-d. la flèche et une branche des verticilles 1 et 2) pour évaluer la défoliation au niveau de l'arbre a expliqué plus de 74 % de la variation l'importante dispersion des derniers stades larvaires à partir des branches de la couronne, on a déterminé que la meilleure unité d'échantillonnage de ces stades larvaires est composé de la flèche, d'une branche du verticille 1 et d'une branche du verticille 2. Les relations entre la densité des oeufs et celle des stades larvaires intermédiaires sur les verticilles 2, 4 ou les deux ont expliqué de 21 à 49 % de la variation dans la densité des derniers stades larvaires sur les verticilles 1 et 2. Il pourrait être nécessaire d'échantillonner des branches sur les verticilles 2 et 4 pour tenir compte des variations saisonnières dans la répartition des oeufs ou des stades larvaires intermédiaires dans la couronne de l'épinette noire. Les méthodes d'échantillonnage établies par cette étude devraient faciliter l'élaboration de programmes de surveillance de *P. alaskensis* et de la défoliation que cet insecte cause dans des peuplements d'épinette noire.

Received 8 August 2005. Accepted 8 December 2005. **Published on the Acadian Entomological Society Web site at acadianes.org/journal on 28 February 2006.**

Rob C. Johns: Population Ecology Group, Department of Biology, University of New Brunswick, Fredericton, New Brunswick, E3B 6E1, Canada.

Don P. Ostaff: Population Ecology Group, Faculty of Forestry and Environmental Management, University of New Brunswick, Fredericton, New Brunswick, E3B 6C2, Canada and Natural Resources Canada, Canadian Forest Service, Atlantic Forestry Center, PO Box 4000, Regent Street, Fredericton, New Brunswick, E3B 5P7, Canada.

Dan T. Quiring[1]: Faculty of Forestry and Environmental Management, University of New Brunswick, Fredericton, New Brunswick, E3B 6C2, Canada.

[1]Corresponding author (email: quiring@unb.ca)

INTRODUCTION

Obtaining precise estimates of insect density and of the defoliation they cause is critical for establishing efficient sampling plans and robust density-damage relationships in integrated pest management. In general, the amount of sampling required to obtain a certain level of precision should be directly proportional to the complexity of the pest foraging behavior and/or host-plant architecture (Southwood 1978). However, the foraging behavior of insects within and among their host plants can be significantly influenced by host-plant architecture (Neuvonen 1999) and associated heterogeneity in the temporal and spatial availability of quality resources (Hassell and Southwood 1978; Stamp and Bowers 1990; Carroll and Quiring 1994; Williams et al. 2001), and/or physical environment (Knapp and Casey 1986; Stamp and Bowers 1990; Alonso 1997; Bryant et al. 2002). Thus, for large plants such as trees, the necessary effort required to evaluate insect density and associated defoliation may far exceed that required to obtain similar levels of precision for insects feeding on relatively smaller and less complex plants, such as those in agriculture. Sampling methods designed in accordance with insect foraging behavior, both within and among their host plants, may aid in reducing sampling costs as well as providing the foundation to establish decision-making rules in pest management programs.

The yellowheaded spruce sawfly, *Pikonema alaskensis* (Roh.) (Hymenoptera: Tenthredinidae), is a univoltine defoliator of most species of young open-grown *Picea* throughout Atlantic Canada and the Northeastern USA (Nash 1939). Many aspects of *P. alaskensis* ecology have been studied in white spruce (*Picea glauca* (Moench) Voss.) (Pinaceae) stands (reviewed in Katovich et al. 1995). Briefly, adult eclosion is synchronized with bud burst, after which females oviposit their eggs individually at the base of needles of current-year shoots (Pointing 1957). Early-instar larvae feed on current-year shoots but older larvae can feed on several foliar age classes (Pointing 1957). Fifth- (male) or sixth- (female) instar larvae usually complete development in mid-August, then drop to the ground, spin cocoons in the upper duff layer and overwinter as prepupae (Rau et al. 1979).

Severe and/or repeated outbreaks of *P. alaskensis* have occurred in intensively managed stands of juvenile black spruce (*P. mariana* (Mill.) BSP) (Pinaceae)) in isolated regions of central Newfoundland (Hall et al. 1998) and New Brunswick (Lavigne 1996). Reports of extensive top kill (upper-crown branch mortality) (R.C Johns, University of New Brunswick (UNB), unpublished data), and associated losses in height and volume growth have generated concern for the future supply of black spruce in Newfoundland. Preliminary studies indicate that patterns of injury in black spruce are related to the tendency of late-instar larvae to disperse acropetally (sensu Quiring 1993) from mid and lower (i.e., whorls 3 to 7) to the upper (i.e., whorls 1 and 2) crown, where the majority of feeding occurs (R.C. Johns, UNB, unpublished data). High densities of *P. alaskensis* in the upper third of the crown in white spruce have also been noted previously (Houseweart and Kulman 1976). This foraging behavior and associated pattern of defoliation were documented concurrently with this study and will be discussed in subsequent papers.

Outbreaks of this insect may be difficult to predict from year to year due to the tendency of some *P. alaskensis* prepupae to remain in diapause for more than one year (Bartelt et al. 1981). Instead, eggs to mid-instar larvae, within the year of outbreak, are the most common stages sampled. This leaves limited time for decision-making and the application of suppression tactics. Before an integrated pest management plan can be established for this pest, simple and precise methodologies accounting for acropetal dispersal, determining the densities of *P. alaskensis* eggs and larvae within the crown of black spruce, and, evaluating defoliation at the branch and tree levels, must be established. These methodologies, combined with knowledge of the relationship between defoliation and subsequent damage, would be useful for annual monitoring programs to rate stands based on their susceptibility to injury from outbreaks of the sawfly.

Thus, the objectives of this study were to: (1) establish a general sampling method for evaluating defoliation of black spruce; (2) establish a sample unit for evaluating defoliation in the upper crown of black spruce; (3) establish a sample unit for eggs and larvae of *P. alaskensis*; and, (4) determine the relationship between the density of eggs and mid-instar larvae in whorls 2 and 4 (i.e., before dispersal) and subsequent densities of late-instar larvae in whorls 1 and 2 (i.e., during and after dispersal).

METHODS AND MATERIALS

Study Areas

This study was conducted in intensively managed black spruce stands located approximately 50 km (N48°40'11.3", W55°30'27.5") and 100 km (N48°17'07.3", W55°29'01.4") south of Grand Falls-Windsor, Newfoundland where *P. alaskensis* has historically been a problem. All field surveys were conducted in stands that had sustained 1–3 years of defoliation due to previous outbreaks of *P. alaskensis*. Trees

were planted at densities of ca. 2500 stems per hectare and ranged in height from 1.5–2.5 m with 10–14 whorls. The branches of adjacent trees did not overlap. Needle loss was primarily due to *P. alaskensis* feeding and/or natural needle fall. *Pikonema dimmockii* (Cress.) (Hymenoptera: Tenthredinidae), a solitary non-outbreaking herbivore (Pointing 1957), was the only other defoliator observed and occurred in densities of less than one larva per tree. A few balsam fir (*Abies balsamea* (L.) Mill.) (Pinaceae), eastern larch (*Larix laricina* (Du Roi) K. Koch) (Pinaceae), and white birch (*Betula papyrifera* Marsh) (Betulaceae) trees were interspersed within each stand. Ground vegetation was dominated by sheep laurel (*Kalmia angustifolia* L.) (Ericaceae), blueberry (*Vaccinium* sp.) (Ericaceae), and haircap mosses (*Polytrichum* sp.) (Polytrichaceae).

1. Estimating defoliation

1.1 A general method for estimating defoliation

A general sampling method for evaluating defoliation caused by feeding *P. alaskensis* in black spruce was evaluated in two different stands where previous defoliation ranged from 1%–94% per shoot per branch. In each stand in late-August, after all larvae had dropped from trees, 15 trees were selected haphazardly within a 100 m x 100 m area and marked with flagging tape. In 2000, five east- or west-facing branches in whorls 4 and 5 were selected in each tree, whereas in 2004 one west-facing branch was selected in each of whorls 1, 2, and 4 (Fig. 1a). Defoliation was visually assessed for all shoots less than three-years old on all branches using classes of 0, 1–5, 6–20, 21–40, 41–60, 61–80, 81–99, or 100%. Next, defoliation was evaluated again for a subset of shoots on the same branches using sampling methods employed previously for balsam fir (Piene 1989). In this sampling method, defoliation was evaluated only for shoots along the main axis of first- and second-order branches (Fig. 1b). However, due to relatively low numbers of developing shoots in whorl 1, defoliation was estimated for three current-year shoots (i.e., one terminal, distal-lateral, and medial-lateral shoot) when examining either the leader or a whorl 1 branch. By evaluating defoliation for only the subset of shoots designated by this sampling method, the mean numbers of shoots sampled for branches in each whorl were reduced by approximately 67%–76%.

The effect of cardinal direction on defoliation among whorls was also evaluated in 2000 (2 cardinal directions) and 2004 (all 4 cardinal directions). In 2000, 20 trees were selected haphazardly in each of two stands with 1%–43% previous defoliation. In each tree, one north- and one south-facing branch in each of whorls 2, 4, and 7 were selected and marked with flagging tape. Selected branches were evaluated for defoliation at the beginning and end of the season using the sampling methods described above. To verify that branches in all cardinal directions sustained similar levels of defoliation when fed upon by *P. alaskensis*, 15 trees in a different stand were selected haphazardly in 2004 and defoliation was evaluated at the end of the season for north-, south-, east-, and west-facing branches in whorls 1, 2, and 4.

1.2 Estimating defoliation in the upper crown

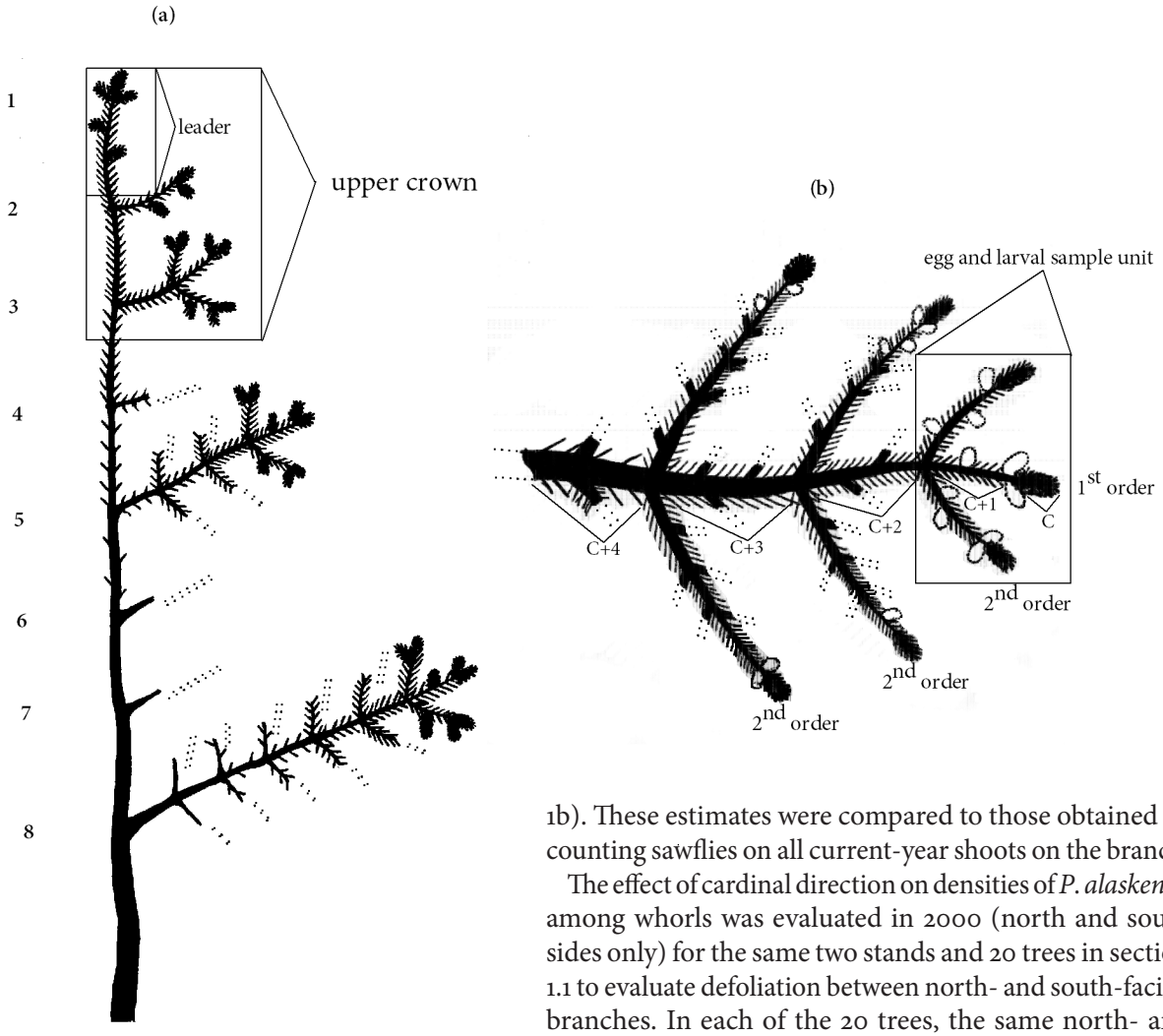
Using the general defoliation sampling methods from section 1.1, a simple method for assessing defoliation was evaluated in each of four stands in 2001. Feeding by *P. alaskensis* is generally concentrated on the leader, although at extremely high densities feeding damage may extend into lower adjacent whorls (R.C. Johns, UNB, unpublished data). Thus, the defoliation estimation method employed in this study focused on estimating defoliation on the leader and for a branch in whorls 1 and 2. In each stand, prior to bud burst, 25 trees that had defoliation in the upper two whorls ranging from 1% to nearly 100% were selected haphazardly. On each tree, the leader and one west-facing branch in whorls 1 and 2 (Fig. 1a) were marked with flagging tape. Defoliation was evaluated for the leader and each branch at the end of the season, after all larvae had dropped from the trees.

2. Estimating the density of *P. alaskensis*

2.1 Estimating the density of eggs and mid-instar larvae

In 2001, sampling methods for measuring the density of eggs and mid-instar larvae on branches were evaluated on the same 25 trees in each of the four stands used in section 1.2. In each tree, *P. alaskensis* were counted on one west-facing branch in each of whorls 2 and 4 at mean egg (i.e., ≤ 3% egg hatch) and mid-instar (i.e., mean developmental stage of 3.3 ± 0.18) larval stages. The mean instar of these larvae was determined by measuring their head-capsule widths under a calibrated dissecting scope (Vanderwerker and Kulman 1974). To ensure that all larvae were counted, needles of current-year shoots were spread with a dissecting needle to expose the relatively small and inconspicuous early life-stages. Withered needles were also usually indicative of oviposition and/or larval feeding and provided a useful search image when trying to locate eggs or young larvae (R.C. Johns, UNB, personal observation). Oviposition and larval feeding occur exclusively on current-year foliage, except that late-instar larvae may

Fig. 1. Schematic representations of (a) a juvenile black spruce, and (b) within-branch sample units for measurements of defoliation and P. alaskensis density. For the purposes of this study, whorl 1 includes both the leader and a whorl 1 branch. 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 one-year old shoots. C, C+1, C+2, C+3, and C+4 refer, respectively, to current-year, and one-, two-, three-, and four-year-old shoots.



feed on older foliage when current-year foliage becomes scarce (Pointing 1957). Thus, for simplicity, egg and larval densities throughout this paper are expressed in terms of the number of *P. alaskensis* per current-year shoot per branch. Although the density of *P. alaskensis* in whorl 7 is often similar to that in whorls 2 and/or 4 (R.C. Johns, UNB, unpublished data), there are significantly more shoots in whorl 7, making it impractical for a sampling unit. In each of whorls 2 and 4 we counted only the *P. alaskensis* on current-year shoots growing from one terminal and two distal-lateral, one-year-old shoots of each branch (Fig. 1b). These estimates were compared to those obtained by counting sawflies on all current-year shoots on the branch.

The effect of cardinal direction on densities of *P. alaskensis* among whorls was evaluated in 2000 (north and south sides only) for the same two stands and 20 trees in section 1.1 to evaluate defoliation between north- and south-facing branches. In each of the 20 trees, the same north- and south-facing branches in whorls 2, 4, and 7 were examined and sawflies counted at mean egg (i.e., ≤ 60% egg hatch) and mid-instar (i.e., mean 3.8 ± 0.12, where egg = 0 and sixth instar = 6) larval stages. To verify the developmental stage of larvae for the mid-instar larval collection, 10 additional larvae were collected from each of five trees adjacent to those used in this study and preserved in 70% ethanol.

2.2 Predicting the density of late-instar larvae in upper crown

Sampling methods used in this study were based on some of our previous work, where we demonstrated that *P. alaskensis* eggs and mid-instar larvae are most

concentrated in whorls below whorl 2, while late-instar larvae, following a period of prolific upwards dispersal, are most concentrated in whorls 1 and 2 (R.C. Johns, UNB, unpublished data). Thus, using the stands and trees from the study described in section 2.1, mean late-instar larvae (i.e., mean developmental stage of 5.1 ± 0.05) were counted for all shoots in whorls 1 and 2 so that we could evaluate relationships between densities of eggs or mid-instar larvae in whorls 2, 4, or both whorls combined, and subsequent densities of late-instar larvae in whorls 1 and 2.

3. Statistical analysis

Relationships between defoliation (i.e., section 1.1 and 1.2) or *P. alaskensis* density (i.e., section 2.1) estimates obtained using sampling methods and those obtained from all shoots on the branch are the most relevant to this study and have been represented in figures along with associated r^2 values. However, direct statistical analysis of these relationships using linear regression was not possible because estimates from the sampling method were also used to obtain estimates for the total branch and thus, the assumption of independence among variables is violated (Zar 1984). To overcome this problem in section 1.1, linear regression analysis (SAS Institute Inc. 1999) was conducted for defoliation estimates obtained from shoots evaluated in the sampling method and estimates obtained for the rest of the shoots on the branch. In section 1.2, *P* values were derived from linear regression analyses of relationships between defoliation on the leader or individual branches in whorls 1 and 2, and defoliation estimates for the other branches evaluated in the upper crown (i.e., leader vs. whorls 1 and 2 branches; whorl 1 vs. the leader and whorl 2 branch; whorl 2 vs. the leader and a whorl 1 branch). In this case, relationships differed significantly among stands ($F_{3,99} \geq 14.01$, $P \leq 0.01$, Analysis of Covariance (ANCOVA)). However, to provide robust relationships that were applicable over a range of conditions, data from stands were pooled for subsequent regression analyses. All defoliation data were arcsine square-root transformed prior to analyses. In section 1.1, we present branch level relationships between the total number of eggs or mid-instar larvae per current-year shoot on a branch in whorls 2 or 4, or both whorls combined, and estimates obtained from sampling only the distal portion of branches. *P* values were derived from linear regression analyses of relationships between the density of *P. alaskensis* at the distal portion of branches and those on the rest of the branch. All relationships presented in figures have associated *P* values of < 0.01.

In sections 1.1 and 2.1, analysis of variance (ANOVA) was employed to evaluate the influence of stand (random), cardinal direction (fixed), and whorl (fixed) on defoliation and the number of sawflies per current-year shoot (i.e., eggs and mid-instar larvae), respectively, with the effects of tree (random) nested in stand. Prior to analyses, defoliation data were arcsine square-root transformed to meet model assumptions of homogeneity of variance and normality (Zar 1984) and the residuals tested for goodness of fit using the Shapiro-Wilk test (SAS Institute Inc. 1999).

For section 2.2, preliminary analyses indicated that stand did not influence relationships between the density of eggs or mid-instar larvae in whorls 2 and 4 and that of late-instar larvae in whorls 1 and 2 ($F_{3,98} \leq 1.61$, $P \geq 0.19$, ANCOVA). Thus, these data were pooled for subsequent analyses. At low and moderate population densities the relationship between the density of eggs or mid-instar larvae in whorls 2 and/or 4 and that of late-instar larvae in whorls 1 and 2 should be linear. However, when population densities are extremely high, relationships should become logistic due to the relatively low number of shoots available in the upper compared to lower whorls. In this study only one tree with extremely high densities of sawflies was observed and was identified as an outlier using the modified Thompson tau technique. Thus, this datum was removed from subsequent linear regression analyses.

RESULTS

1. Estimating defoliation

1.1 A general method for estimating defoliation

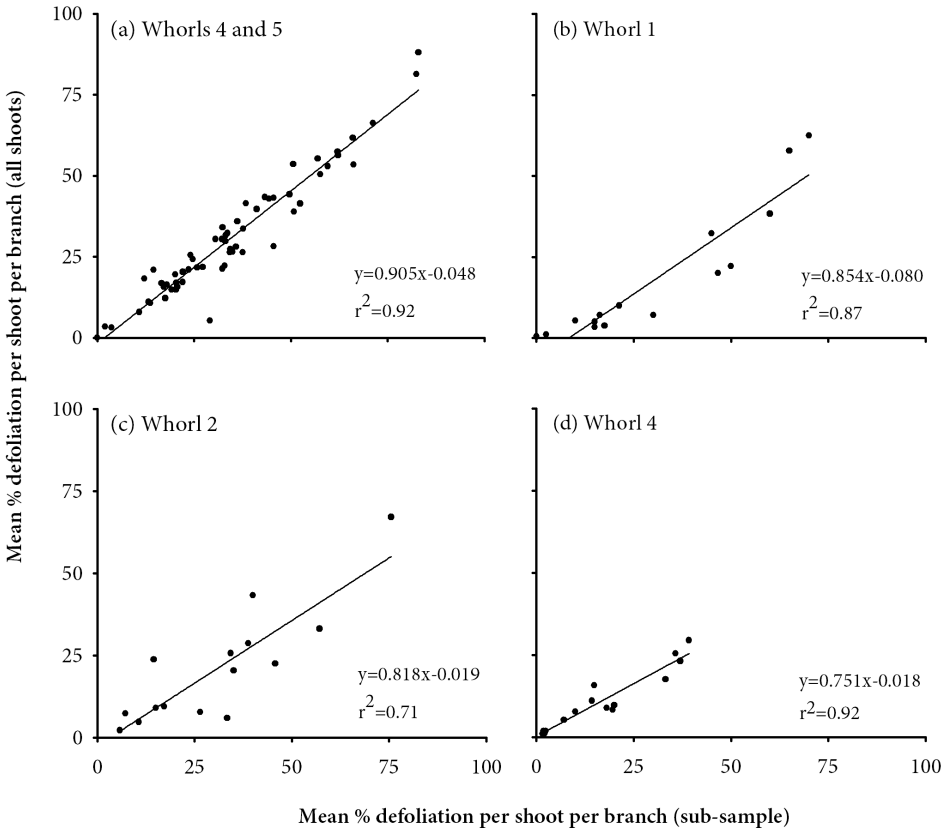
Sampling all shoots on branches in whorls 4 and 5 in 2000 (Fig. 2a) and on branches in whorls 1, 2, and 4 in 2004 (Fig. 2b-d) provided good predictions of defoliation.

In 2000, defoliation did not significantly differ between stands ($F_{1,192} = 2.49$, $P = 0.12$), between north- and south-facing branches ($F_{1,192} = 0.12$, $P = 0.72$), nor were there any significant interactions ($F_{1\text{-}2,192} \leq 1.80$, $P \geq 0.17$). However, there was a significant difference in defoliation among whorls ($F_{2,192} = 26.47$, $P < 0.01$) (Fig. 3a, b). Similarly, in 2004 defoliation increased in a non-linear fashion from lower to upper whorls ($F_{1,228} = 6.81$, $P < 0.01$) but did not differ in relation to cardinal direction ($F_{3,228} = 0.37$, $P = 0.78$) (Fig. 4). There were no significant interactions ($F_{6,228} = 0.40$, $P = 0.87$).

1.2 Estimating defoliation in the upper crown

Defoliation in whorls 1 and 2 was significantly related to defoliation estimates obtained using only the leader, a whorl 1 branch, or a whorl 2 branch (Fig. 5).

Fig. 2. Relationships between defoliation estimates obtained using sampling methods and by evaluating defoliation for all shoots on the branch for black spruce branches in (a) whorls 3 or 4 in 2000, and (b) whorl 1, (c) whorl 2, and (d) whorl 4 in 2004. For simplicity, raw data are presented here although data were arcsine square-root transformed prior to analyses.



2. Estimating the density of *P. alaskensis*

2.1 Estimating the density of eggs and mid-instar larvae

The number of eggs or mid-instar larvae per current shoot located on the distal portion (Fig. 1b) of a branch in whorls 2, 4, or both whorls combined, explained more than 88% of the variation in the total number of *P. alaskensis* on the branch (Fig. 6).

The mean number of *P. alaskensis* eggs per current-year shoot differed marginally between stands ($F_{1,192} = 3.52$, $P = 0.07$) but not between north- and south-facing branches in either stand ($F_{1,192} = 1.87$, $P = 0.17$) (Fig. 7a,b). There were no significant interactions between stand and cardinal direction ($F_{1\text{-}2,192} = 2.47$, $P = 0.09$) although there was a significant interaction between stand and whorl ($F_{2,192} = 3.04$, $P = 0.04$). The density of mid-instar larvae per current-year shoot differed significantly between stands ($F_{1,192} = 5.10$, $P = 0.02$) and marginally among whorls ($F_{2,192} = 2.69$, $P = 0.07$), but did not differ between north- and south-facing branches ($F_{2,192} = 0.27$, $P = 0.60$) (Fig. 6c,d). There was no interaction between stand and cardinal direction ($F_{2,192} = 0.78$, $P = 0.38$) and only a marginal interaction between stand and whorl ($F_{2,192} = 2.69$, $P = 0.07$).

2.2 Predicting the density of late-instar larvae in upper crown

The number of eggs and mid-instar larvae per current-year shoot in whorls 2, 4, and both whorls combined were positively related to the densities of late-instar larvae per current-year shoot in whorls 1 and 2 ($F_{1,98} \geq 25.33$, $P < 0.01$) (Fig. 8). The slopes of regressions were typically higher for relationships established using mid-instar larvae compared to eggs. The coefficient of determination for relationships established using branches from both whorls were more than 15% and 8% higher, respectively, than those established for eggs and larvae using only a whorl 2 or whorl 4 branch.

Fig. 3. Seasonal mean (±SE) percent defoliation per shoot attributable to feeding by *P. alaskensis* for north- and south-facing branches in whorls 2, 4, and 7 in each of two black spruce stands in central Newfoundland (a, b) in 2000.

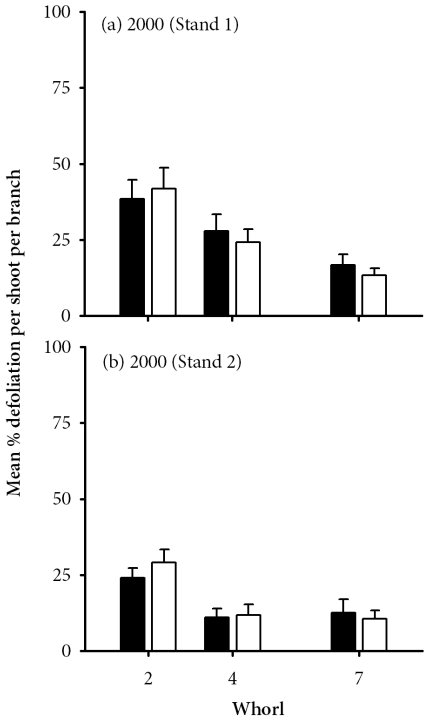
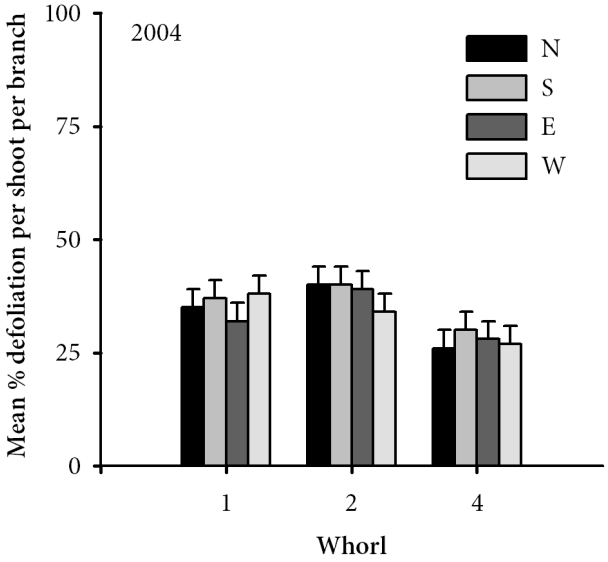


Fig. 4. Seasonal mean (±SE) percent defoliation per shoot attributable to feeding by *P. alaskensis* for north-, south-, east-, and west-facing black spruce branches in whorls 1, 2, and 4 in 2004.



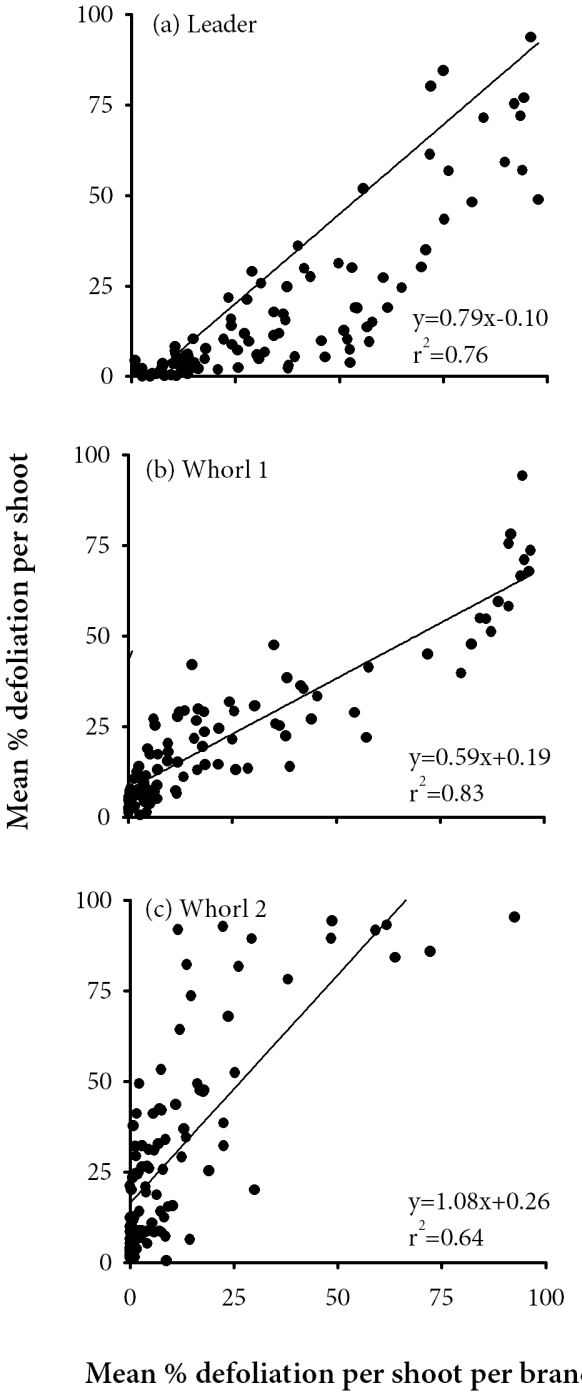
DISCUSSION

This study provides simple and precise sampling methods for evaluating the densities of eggs and larvae, as well as defoliation caused by *P. alaskensis* on black spruce. In summary, visually estimating defoliation on branches for a subset of shoots along the first- and second-order branch axes (Fig. 1b) was very precise, while defoliation in the upper crown caused by P. *alaskensis* after they disperse acropetally can be estimated using only the leader or a single branch in whorls 1 or 2. Egg and mid-instar larval densities in whorls 2 and 4 can be estimated for an entire branch by simply examining the current-year shoots located at the branch tip and on the most distally located one-year-old shoots (Fig. 1b). Furthermore, the density of late-instar larvae in the upper crown is best predicted from densities of eggs and mid-instar larvae in whorls 2 and 4 combined. It is unknown whether the relationships established will hold for smaller or larger trees than those used in this study. However, tall trees that are approaching crown closure are less likely to be attacked by *P. alaskensis* as their numbers tend to decline significantly as shading increases (Morse and Kulman 1984). Furthermore, the utility of these methods for other closely related species of insects is unknown. However, if other insects possess foraging behaviors similar to *P. alaskensis*, then variations of the methods provided by this paper may be appropriate.

Predictions of branch defoliation provided by sampling methods used in this study were consistent among whorls and cardinal direction, suggesting that these methods may be applicable for branches located anywhere in the crown. Similar sampling methods have been used to evaluate defoliation for a variety of insect pests that feed on both current and old balsam fir (Fettes 1950; Piene 1989; Moreau et al. 2003) and white spruce (Piene 1991) foliage. When evaluating defoliation caused by this sawfly, emphasis needs to be placed on damage that occurs in whorls 1 and 2. Thus, we recommend sampling a whorl 1 branch as it gives almost as good an estimate of defoliation as the leader and removal of a whorl 1 branch does not disrupt apical dominance (Powell 1982).

Sampling methods proposed here for evaluating the density of eggs and mid-instar larvae within branches were very precise and are similar to those established previously for *P. alaskensis* in white spruce (Houseweart et al. 1974). However, in this study branch-level estimates of sawfly density were used to predict densities of late-instar larvae in the upper crown following acropetal dispersal, thereby accounting for acropetal dispersal.

Fig. 5. Relationships between mean upper crown defoliation (i.e., mean of whorls 1 and 2 combined) and mean defoliation for (a) the leader, or for one branch in (b) whorl 1 or (c) whorl 2 from black spruce. Raw data are presented here but data were arcsine square-root transformed prior to analyses.



Cardinal direction did not influence the density of *P. alaskensis* in this study, probably because trees used were relatively small and no one direction was subjected to high levels of shading. Thus, although the sampling methods established in this study focused on west-facing branches, branches facing any direction would probably provide suitable estimates of egg or larval density.

Most of the difficulty in establishing robust relationships for estimating the density of late-instar larvae from earlier life stages of this insect was related to the propensity of late-instar larvae to disperse acropetally (R.C. Johns, UNB, unpublished data), and concentrate in the upper crown of trees. To account for this foraging behavior, densities of *P. alaskensis* eggs and mid-instar larvae were evaluated in whorls 2 and 4, whereas late-instar larvae were sampled in whorls 1 and 2. Densities of late-instar larvae appeared to be much higher than those of eggs or mid-instar larvae (Fig. 8), due to aggregation of late-instar larvae on the relatively few shoots of the upper two whorls following acropetal dispersal.

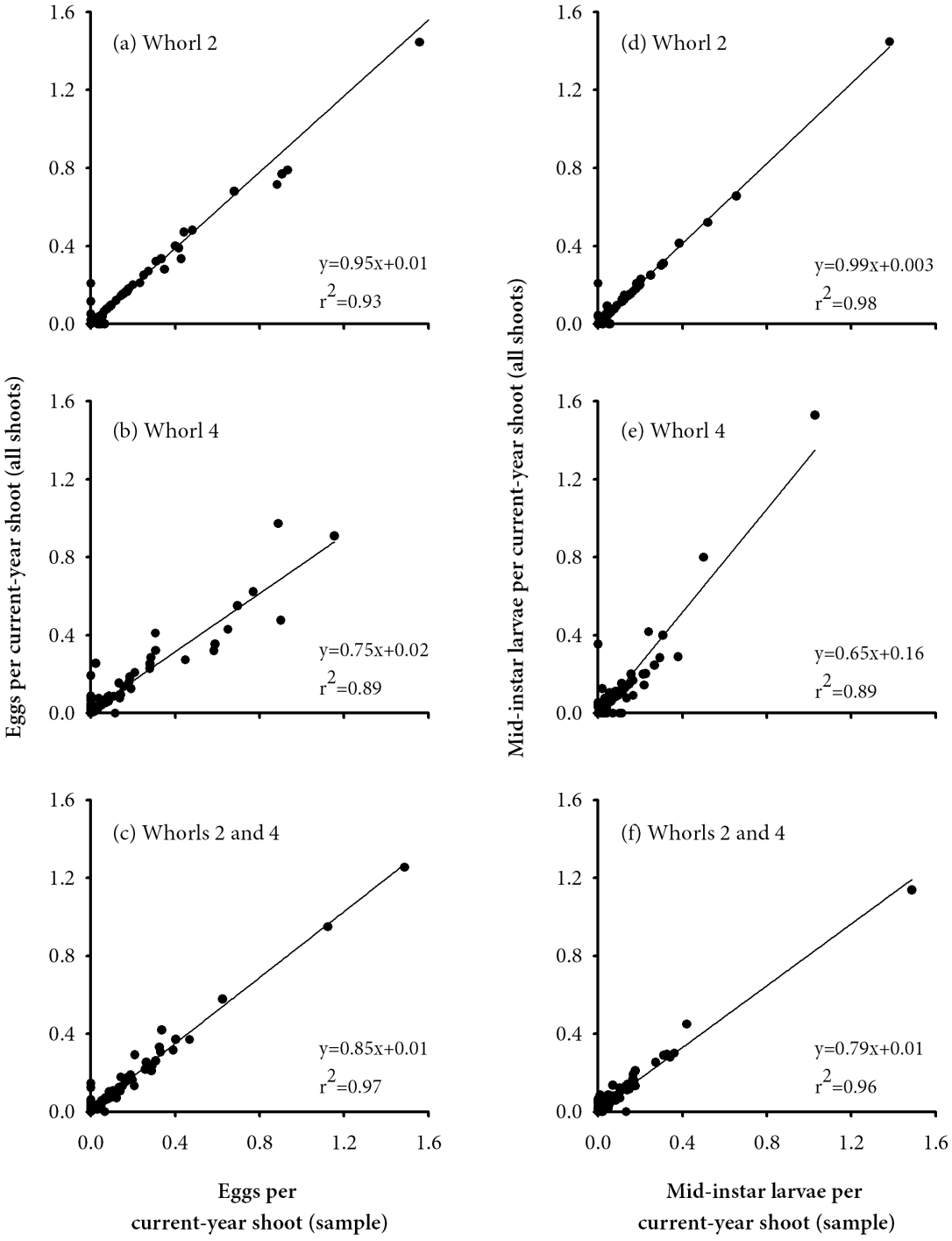
In 2001, sampling eggs and mid-instar larvae on a branch in both whorls 2 and 4 to predict densities of late-instar larvae in whorls 1 and 2, only marginally increased r^2 values relative to sampling just a whorl 2 branch (compare Fig. 8 a,d to c,f). However, as our surveys of sawfly density from 2000 suggest, egg and mid-instar larval density are not always high in whorl 2 (Fig. 6a,c), and sampling a branch in each of whorls 2 and 4 may be necessary to more accurately estimate the density of eggs and mid-instar larvae. A similar approach was used with spruce bud moth, *Zieraphera canadensis* (Mutt. & Free.) (Lepidoptera: Tortricidae) (Ostaff and Quiring 2000), which is the only other insect for which acropetal dispersal has been documented (Quiring 1993).

Sampling methods provided by this study should facilitate the establishment of monitoring programs for *P. alaskensis* and the prediction of defoliation in juvenile black spruce stands. Furthermore, studies currently underway have successfully employed these methods to establish relationships between *P. alaskensis* density and defoliation, and between defoliation and growth loss, relationships that can be incorporated into a pest management program for this insect.

ACKNOWLEDGMENTS

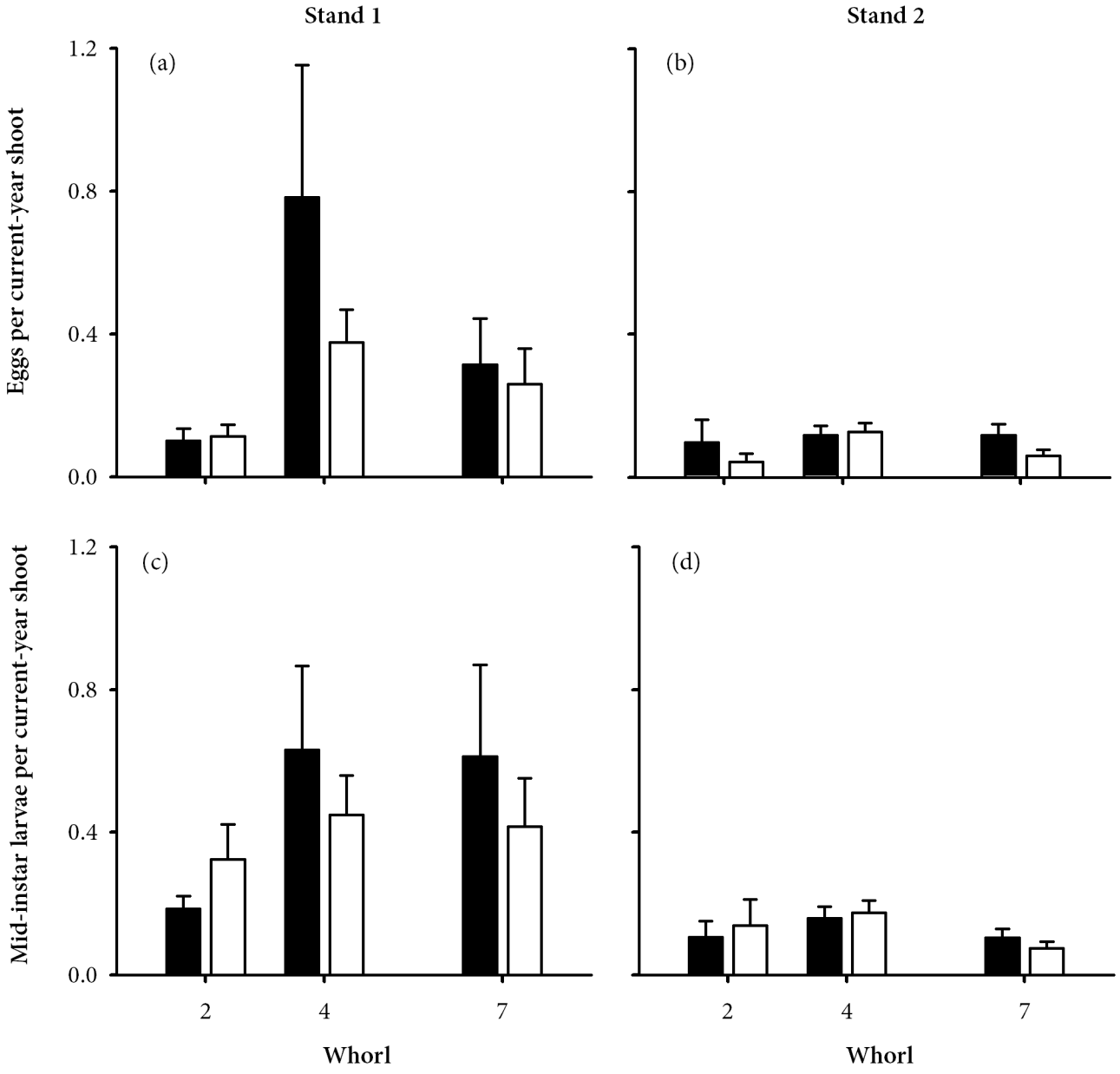
We thank H. Crummey, G. Flemming, B. Gregory, V. Howell, T. Johns, E. Kettela, D. Lavigne, J. Park, and A. Sharpe for technical assistance and J. Boone, J. Evans, R. Graves, C. Griffin, B. Johns, J. Leggo, J. Luff, J. Marshall, H. Piene, K. Ryall, J. Sweeney, and S. Woods for comments

Fig. 6. Relationships between *P. alaskensis* density at (a-c) mean egg, and (d-f) mean mid-instar larval stages estimated either by examining all shoots on a black spruce branch in whorls 2, 4, or both whorls combined, or by sampling current-year shoots located on the terminal and first distal-lateral one-year old shoots of the same branches.



on an earlier version of the manuscript. Financial support was provided by an IPS NSERC scholarship

Fig. 7. Mean (±SE) number of *P. alaskensis* per current-year shoot at (a, b) mean egg, and (c, d) mean mid-instar larval stages on north- and south-facing branches in whorls 2, 4, and 7 of black spruce in two different black spruce stands in central Newfoundland.



with Abitibi-Consolidated and Corner Brook Pulp and Paper Ltd., a NSERC Discovery grant, the Spray Efficacy Research Group, and BIOCAP/NCE. The Canadian Forest Service contributed additional logistical support.

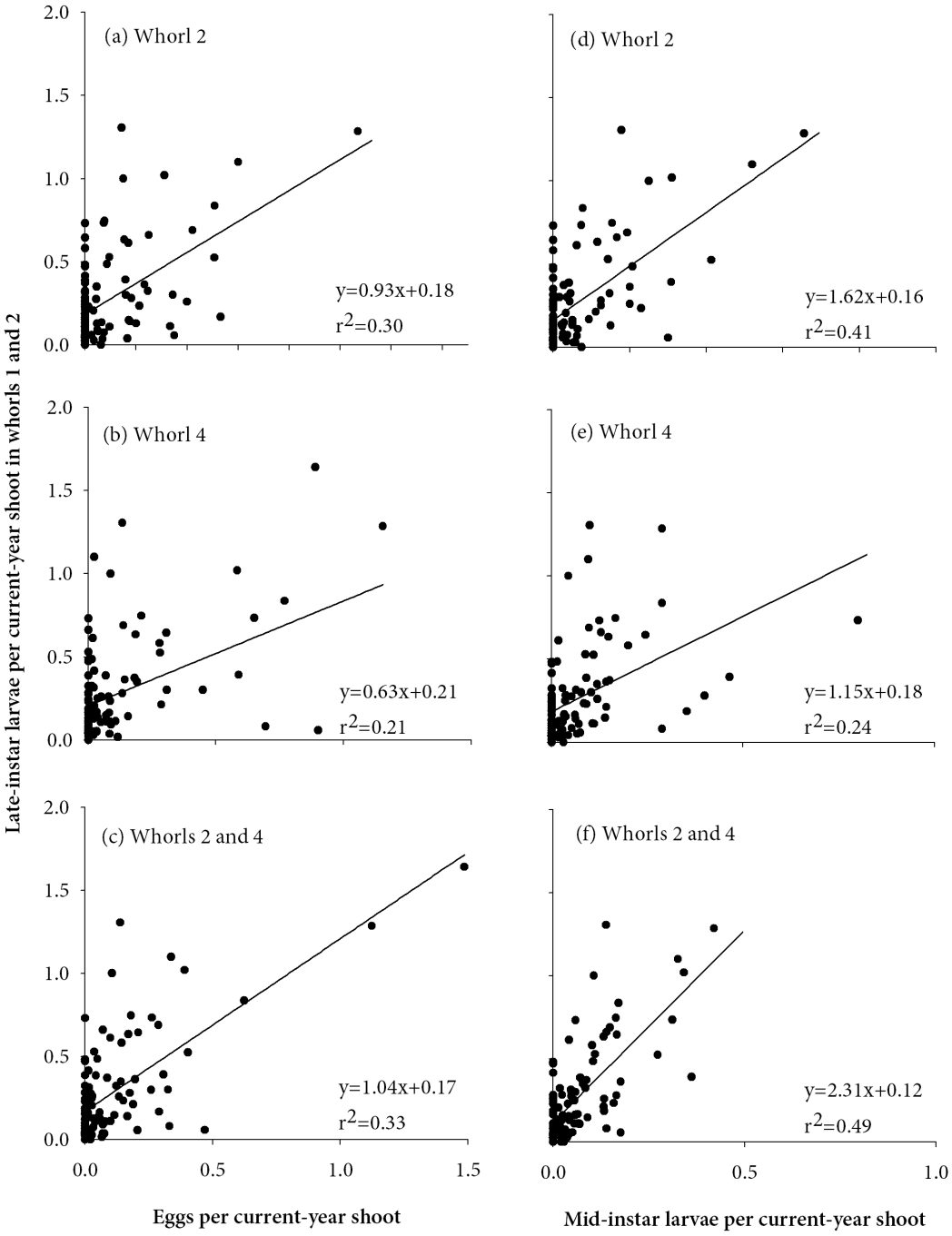
REFERENCES

Alonso, C. 1997. Choosing a place to grow. Importance of within-plant microenvironment for *Yponomeuta mahalebella*. Entomol. Exp. Appl. **83**: 171-180.

Bartelt, R.J., Kulman, H.M., and Jones, R.L. 1981. Effects of temperature on diapausing cocoons of yellowheaded spruce sawfly, *Pikonema alaskensis*. Ann. Entomol. Soc. Am. **74**: 472-477.

Bryant, S.R., Thomas, C.D., and Bale, J.S. 2002. The influence of thermal ecology on the distribution of three nymphalid butterflies. J. Appl. Ecol. **39**: 43-55.

Fig. 8. Relationships between the mean number of late-instar larvae per current-year shoot in the upper crown of black spruce (mean of whorls 1 and 2) and (a-c) mean egg density, and (d-f) mean mid-instar larval density estimates for one branch in whorl 2, whorl 4, and of both whorls combined.



Carroll, A.L., and Quiring, D.T. 1994. Intratree variation in foliage development influences the foraging strategy of a caterpillar. Ecology, **75**: 1978-1990.

Fettes, J.J. 1950. Investigations of sampling techniques for population studies of the spruce budworm on balsam fir in Ontario. For. Ins. Lab. Sault Ste. Marie Ont. Ann. Tech. Rep. 4 pp. 163-401.

Hall, J.P., Bowers, W.W., and Hirvonen, H. 1998. Forest insect and disease conditions in Canada in 1995. For. Ins. Dis. Surv. Nat. Res. Can. Can. For. Serv. Ottawa Ont.

Hassell, M.P., and Southwood, T.R. 1978. Foraging Strategies of Insects. Ann. Rev. Ecol. Syst. **9**: 75-78.

Houseweart, M.W., Vanderwerker, G.K., Weisberg, S., and Kulman, H.M. 1974. Use of regression on egg and first-instar samples of yellowheaded spruce sawfly, *Pikonema alaskensis*, on white spruce. Ann. Entomol. Soc. Amer. **67**: 887-890.

Houseweart, M.W., and Kulman, H.M. 1976. Life tables of the yellowheaded spruce sawfly, *Pikonema alaskensis* (Rohwer) (Hymenoptera: Tenthredinidae) in Minnesota. Environ. Entomol. **5**: 859-867.

Katovich, S.A., McCullough, D.G., and Haack, R.A. 1995. Yellowheaded Spruce Sawfly-Its Ecology and Management. USDA For. Serv. North Cent. Res. Sta. CTR NC-179.

Knapp, R., and Casey, T.M. 1986. Thermal ecology, behavior, and growth of gypsy moth and eastern tent caterpillars. Ecology, **63**: 598-608.

Lavigne, D. 1996. Yellowheaded spruce sawfly in New Brunswick. New Brunswick Dep. Nat. Res. Energy.

Moreau, G., Quiring, D.T., Eveleigh, E.S., and Bauce, É. 2003. Advantages of a mixed diet: feeding on several foliar age-classes increases the performance of a specialist herbivore. Oecologia, **135**: 391-399.

Morse, B.W., and Kulman, H.M. 1984. Effects of white spruce release on subsequent defoliation by the yellowheaded spruce sawfly, *Pikonema alaskensis* (Hymenoptera: Tenthredinidae). Great Lakes Entomol. **17**: 235-237.

Nash, R.W. 1939. The yellowheaded spruce sawfly in Maine. J. Econ. Entomol. **32**: 330-334.

Neuvonen, S. 1999. Random foraging by herbivores: complex patterns may be due to plant architecture. J. Ecol. **87**: 526-528.

Ostaff, D.P., and Quiring, D.T. 2000. Role of the host plant in the decline of a specialist herbivore, the spruce bud moth. J. Anim. Ecol. **69**: 263-273.

Piene, H. 1989. Spruce bud worm defoliation and growth loss in young balsam fir: defoliation in spaced and unspaced stands and individual tree survival. Can. J. For. Res. **14**: 811-817.

Piene, H. 1991. The sensitivity of white spruce to spruce budworm defoliation. North. J. Appl. For. **8**: 168-171.

Pointing, P.J. 1957. Studies on the comparative ecology of two sawflies *Pikonema alaskensis* Roh. and *Pikonema dimmockii* Cress. (Tenthredinidae, Hymenoptera). Ph.D. thesis, University of Toronto, Toronto, Ontario. pp. 148.

Powell, G.R. 1982. Shoot and bud development in balsam fir: Implications for pruning of Christmas trees. For. Chron. **58**: 168-172.

Quiring, D.T. 1993. Influence of intra-tree variation in the timing of budburst on herbivory and the behaviour and survivorship of *Zeiraphera canadensis*. Ecol. Entomol. **18**: 353-364.

Rau, D.E., Houseweart, M.W., and Kulman, H.M. 1979. Distribution of cocoons of the yellowheaded spruce sawfly. Environ. Entomol. **8**: 340-343.

SAS Institute Inc. 1999. The SAS system version 8 for Windows. SAS Institute. Cary, NC.

Southwood, T.R.E. 1978. Ecological Methods. 2nd Edition. Chapman and Hall, London.

Stamp, N.E., and Bowers, M.D. 1990. Variation in food quality and temperature constrains the foraging of gregarious caterpillars. Ecology, **7**: 1031-1039.

Vanderwerker, G.K., and Kulman, H.M. 1974. Stadium and sex-determination of yellowheaded spruce sawfly larvae, *Pikonema alaskensis*. Ann. Entomol. Soc. Am. **67**: 29-31.

Williams, I.S., Jones, T.H., and Hartley, S.E. 2001. The role of resources and natural enemies in determining the distribution of an insect herbivore population. Ecol. Entomol. **26**: 204-211.

Zar, J.H. 1984. Biostatistical Analysis. 2nd Edition. Prentice-Hall Inc., Englewood Cliffs, NJ.