Predicting defoliation by *Choristoneura biennis* (Lepidoptera: Tortricidae)

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The Canadian Entomologist **135**: 903 – 907 (2003)

Abstract—The 2-year-cycle spruce budworm, *Choristoneura biennis* Free. (Lepidoptera: Tortricidae), causes defoliation of spruce – subalpine fir forests in British Columbia, Canada. Historical and newly obtained data were used to develop a linear regression relating percent defoliation in the 2nd feeding year of the life cycle to the percentage of shoots damaged in the previous, 1st feeding year of the life cycle. The resulting regression was tested with independent data and correctly predicted (95% prediction intervals) defoliation in 14 of 15 stands. Patterns of defoliation were similar on white spruce, *Picea glauca* (Moench) Voss (Pinaceae), and subalpine fir, *Abies lasiocarpa* (Hook.) Nutt. (Pinaceae), and hence the regression can be used for either mixed or pure stands of either species.

Nealis VG, Turnquist R. 2003. Prédiction de la défoliation par *Choristoneura biennis* (Lepidoptera : Tortricidae). *The Canadian Entomologist* **135** : 903–907.

Résumé—La tordeuse bisannuelle de l'épinette, *Choristoneura biennis* Free. (Lepidoptera: Tortricidae), est responsable de la défoliation de forêts d'épinettes et de sapins subalpins en Colombie Britannique, Canada. Des données anciennes et nouvelles nous ont servi à mettre au point une régression linéaire qui relie le pourcentage de défoliation durant la seconde année d'alimentation du cycle biologique et le pourcentage de pousses endommagées l'année précédente, la première année d'alimentation du cycle. Cette régression a pu être évaluée avec des données indépendantes et elle prédit avec justesse (dans les intervalles de prédiction de 95 %) la défoliation dans 14 boisés sur 15. Les patterns de défoliation sont les mêmes sur l'épinette blanche, *Picea glauca* (Moench) Voss (Pinaceae), et le sapin subalpin, *Abies lasiocarpa* (Hook.) Nutt. (Pinaceae); la régression peut donc être utilisée pour des boisés purs ou mixtes des deux espèces.

[Traduit par la Rédaction]

Introduction

The 2-year-cycle spruce budworm, *Choristoneura biennis* Free. (Lepidoptera: Tortricidae), defoliates spruce–fir forests in central and northern British Columbia, Canada, and in the subalpine zones in the southeastern part of the province (Shepherd *et al.* 1995). As its name indicates, the 2-year-cycle spruce budworm requires two feeding seasons to complete its life cycle. Eggs are laid in the summer. Neonate larvae hatch the same season and seek sheltered locations where they moult and enter diapause to overwinter. Second-stage larvae emerge the following spring, feed on current-year foliage for a brief period, and then enter a second diapause for the remainder of the summer and the next winter. Following this second overwintering period, larvae emerge, resume feeding on current-year foliage, and complete development to adult (Shepherd 1961). During an outbreak of 2-year-cycle spruce budworm, the life cycle creates

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alternating years of apparent light and then more severe defoliation, which has an impact on tree growth (Unger 1984; Zhang and Alfaro 2002).

Most survey and prediction methods for spruce budworms rely on sampling budworm populations directly (Morris 1955). Predictions of defoliation by 1-year-cycle spruce budworms are commonly made from estimates of the density of egg masses and, to a lesser extent, overwintering larvae (Miller *et al.* 1971). Historical records of 2-year-cycle spruce budworm, however, show a weak relationship between egg-mass density and subsequent density of the large larval stages and defoliation (Silver *et al.* 1961).[2] Data collected during the present study confirmed this observation.

This paper develops a stand-level method of predicting defoliation by the 2-year-cycle spruce budworm on white spruce, *Picea glauca* (Moench) Voss (Pinaceae), and subalpine fir, *Abies lasiocarpa* (Hook.) Nutt. (Pinaceae), from estimates of feeding damage in the 1st feeding year of the insect's 2-year life cycle. Data are drawn from historical survey records (Silver *et al.* 1961)[2] and from new measurements obtained between 1998 and 2000. The method is tested using independent data collected between 1999 and 2002.

Materials and methods

An outbreak of the 2-year-cycle spruce budworm in central British Columbia during the 1950s led to surveys in the Prince George Forest District by the Forest Insect and Disease Survey of the Canadian Forest Service (Silver *et al.* 1961).[2] Ten trees were sampled in nine survey plots in successive years. In most cases, it appears that only subalpine fir was sampled. Most plots provided information for two or three generations of the spruce budworm so that a total of 19 plot- or stand-level damage estimates were compiled based on a single generation of the spruce budworm. In the 1st year of feeding by the 2-year-cycle spruce budworm, the percentage of current-year shoots damaged on branch samples was recorded. In the 2nd year, the percentage of defoliation was estimated.

Between 1998 and 2000, 15 sample plots were established in mature spruce – fir forests in two areas of British Columbia. Budworm populations north to northwest of Prince George (Area 1) mature in odd-numbered years (*e.g.*, 1999, 2001) and populations southeast of Prince George (Area 2) mature in even-numbered years. Within these two areas, the life stages of the respective populations are largely synchronized. Collectively, these plots represent sub-boreal to montane spruce/subalpine fir forests as far north as 56°53′N, 124°24′W on the eastern shore of Williston Lake, as far south and east as 52°47′N, 119°20′W near Valemont, and as far west as 55°08′N, 125°24′W near Takla Lake. All plots were established when the local budworm population was in its 2nd year of feeding and damage was most severe.

Plots were in the shape of a square, 50 m on a side and at least 50 m from the forest edge. A cluster of co-dominant host trees (*sensu* Morris 1955) was located at each corner of the square. A total of 10 white spruce and 10 subalpine fir per plot were identified to sample within these clusters. All sample trees were mature, co-dominant individuals with an overall diameter at breast height (1.3 m above ground) of 21.5 ± 2.59 cm (mean ± SE) and height of 23.5 ± 5.76 m (mean ± SE). One or two 45-cm living branch tips were removed from the mid-crown (10–15 m from ground) of each sample tree using extendable pole-pruners. Branches were bagged and returned to the

[2] GT Silver, J Grant, DA Ross. 1961. Review of infestations of the two-year-cycle spruce budworm in British Columbia. Unpublished report from the Canadian Forest Service, Forest Entomology and Pathology Laboratory, Victoria, British Columbia.

laboratory for measurement of defoliation. Budworm life stages found on the branches were removed and counted.

At plot establishment, an estimate of the severity of defoliation in the current, 2nd year of budworm feeding was obtained by assessing defoliation on all current-year shoots on each branch using the method of Fettes (1950) in which each shoot is assigned to a defoliation severity class from 0 (no defoliation) to 6 (100% defoliation) by 25% increments. This value was converted to percent defoliation using the mid-point of the defoliation class as the mean. A stand-level estimate was calculated for all branches combined for each tree species. Similarly, the estimate of defoliation in the previous, 1st year of feeding was measured on the same branch and expressed as the percentage of the total shoots damaged in that year, and a mean percent damage computed for each host tree species in each plot for each calendar year.

Differences in rates of defoliation on the two host-tree species in a given year were tested with a plot-level, paired-difference t test following an arcsine transformation. A regression model was developed using historical data (Silver *et al.* 1961),[2] and 11 of the new plots for which estimates of 1st- and 2nd-year damage were measured on the same branches. Prediction intervals of 95% were calculated (SPSS Inc 1997). Independent observations to test this model were obtained from the 15 new plots in separate feeding years and therefore were based on different branches from the same trees.

Results

There was a small difference between the mean percentage of damaged shoots on white spruce and subalpine fir in the 1st year of feeding of the 2-year-cycle spruce budworm (paired t test = 2.98, $P < 0.01$, $n = 30$). The actual mean difference between tree species in percent damaged shoots in that 1st year, however, was less than 9% on an overall mean of 60% and the correlation in damage between the two tree species at the plot and year level was high ($r = 0.93$, $P < 0.01$, $n = 30$). More critically, there was no difference between the severity of defoliation on white spruce and subalpine fir in the 2nd year of feeding of the 2-year-cycle spruce budworm's generation (paired t test = –1.12, $P = 0.27$, $n = 37$); there was also no difference between tree species when no distinction was made between the 1st and 2nd year of feeding (*i.e.*, damage over the entire budworm's generation (paired t test = 0.70, $P = 0.49$, $n = 66$). These results are consistent with observations of Harris (1964). Given these results and the primary interest in prediction at the stand level, defoliation data from both host trees were pooled for each plot and year combination to provide a more precise estimate of the mean level of defoliation.

Data from the outbreak of the 2-year-cycle spruce budworm in the 1950s indicate a linear relationship between the percentage of shoots damaged by small larvae in the 1st year of the generation and the severity of defoliation caused by large larvae in the 2nd year of the generation. New data collected between 1999 and 2001 augment this relationship (Fig. 1*a*). The resulting regression model is as follows:

$$d = -4.24 + 1.053x \ (F_{1,28} = 104.6,\ P < 0.001,\ R^2 = 0.78) \quad [1]$$

where d is percent defoliation in the 2nd year of feeding and x is the percentage of shoots damaged in the 1st year of feeding. The slope of this regression is greater than 0 ($t = 10.2$, $P < 0.001$), but the intercept is not ($t = -0.8$, $P > 0.1$). Note that both d and x in this regression are arcsine-transformed. Parameters for the untransformed relationship were nearly identical:

$$D = -5.57 + 1.092X \ (F_{1,28} = 130.7,\ P < 0.001,\ R^2 = 0.83) \quad [2]$$

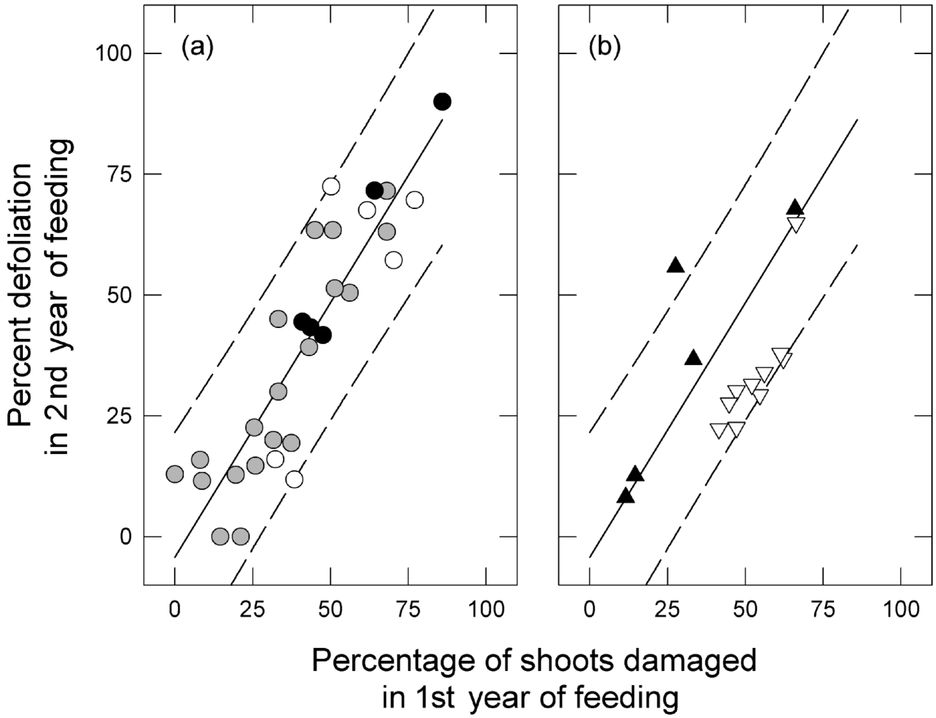

FIGURE 1. Regression and 95% prediction intervals for the relationship between the percent defoliation in the 2nd year of feeding and the percentage of shoots damaged in the 1st year of feeding of *Choristoneura biennis*. (*a*) Data used to develop regression model from historical data (shaded circle) (Silver *et al.* 1961),[2] Area 1 (open circle), and Area 2 (solid circles). (*b*) Test data superimposed on regression and prediction intervals from the regression model with data from Area 1 (open triangle) and Area 2 (solid triangle). See Equation 1 in text for regression parameters.

where D is the untransformed percent defoliation in the 2nd year of feeding and X is the untransformed percentage of shoots damaged in the 1st year of feeding. In practical terms, there is essentially a one-to-one relationship between the percentage of shoots damaged in the 1st year and the percent defoliation in the 2nd year of feeding.

Fourteen of 15 data points (93%) tested with Equation 1 fell within the 95% prediction intervals (Fig. 1*b*). The cluster of points along the lower prediction boundary (Fig. 1*b*) underestimate the percent defoliation (d) in those sites because there were still some feeding spruce budworms on the branches at the time of measurement. Actual defoliation was undoubtedly closer to the regression line in this figure. The 99% prediction intervals from Equation 1 enclose all of the points (Fig. 1*b*).

Conclusion

Annual damage from conifer-feeding budworms is predicted frequently from estimates of the density of the early developmental stages of the insect. Measurement of the density of these stages is time-sensitive and underestimates the true density because even experienced observers fail to find all insects on a branch (Morris 1955). Moreover, several measurements may be required from the same branch to make an adequate forecast (Nealis and Lysyk 1988; Nealis *et al.* 1997). The method described here does not rely on the measurement of the 2-year-cycle spruce budworm density but on the damage caused in the 1st year of feeding. This damage can be evaluated by sampling branches anytime after the brief feeding period of the 1st-year larvae (*e.g.*, July and later) and does not require searching the foliage for small, cryptic insect stages or making additional measures of branch characteristics. Use of damage and not the insect as the measure takes advantage of the 2-year life cycle of *C. biennis* to provide predictions 1 year in advance of severe damage with a flexible sampling schedule, no special processing techniques, and fewer sources of observer error.

Acknowledgements

We thank T Gray, L Sutherland, and V Waring for technical assistance and R Alfaro for advice on plot layout and review of the manuscript. S Bower and S Taylor of the British Columbia Ministry of Forests provided local support. Financial support was obtained from Canadian Forest Products, Finlay Forest Industries, British Columbia Ministry of Forests, and the Robson Valley Enhanced Forest Management Pilot Project.

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(Received: 20 March 2003; accepted: 17 July 2003)