RELATIONSHIPS BETWEEN SPRUCE BUDWORM (LEPIDOPTERA: TORTRICIDAE) EGG MASS DENSITY AND RESULTANT DEFOLIATION OF BALSAM FIR AND WHITE SPRUCE[1]

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Abstract

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Annual spruce budworm, *Choristoneura fumiferana* (Clemens), survey data were subjected to multiple and logistic regression analyses to examine the relationship between egg mass density in the fall and resultant defoliation the next season. Egg mass density was the most important variable associated with resultant defoliation, followed by current defoliation, regional population trends, host species, and sprays. Together, these accounted for 60% of the variation in resultant defoliation. Balsam fir [*Abies balsamea* (L.) Miller] suffered greater levels of defoliation than white spruce [*Picea glauca* (Moench) Voss] at a given egg mass density. Resultant defoliation of balsam fir also showed a steeper response to egg mass density than resultant defoliation of white spruce. Levels of current defoliation increased susceptibility to defoliation in a similar manner between species, as did regional population trends. Sprays were more effective at reducing resultant defoliation on balsam fir than on white spruce but, overall, did not confer a high level of foliage protection. Predictions of resultant defoliation using the multiple regression models had confidence limits averaging 75%, which are too large to be useful for predictive purposes. The logistic regression equations could be used to predict the probability of a stand receiving light or severe defoliation.

Résumé

Des données de relevés annuels des populations de la tordeuse des bourgeons de l'épinette, *Choristoneura fumiferana* (Clemens), ont été soumises à des analyses de régressions multiple et logistique afin d'examiner la relation entre la densité des masses d'oeufs à l'automne et la défeuillaison qui en résulte l'année suivante. La densité des masses d'oeufs a été la plus importante variable associée à la défeuillaison, suivie par la défeuillaison de l'année courante, les tendances régionales des niveaux de population, l'espèce de plante hôte et les arrosages. Mises ensemble, ces variables ont expliqué 60% de la variation dans la défeuillaison. Le sapin baumier [*Abies balsamea* (L.) Miller] a subi des niveaux de défeuillaison plus élevés que l'épinette blanche [*Picea glauca* (Moench) Voss] à une densité d'oeufs donnée. Le sapin baumier a répondu de façon plus abrupte, en terme de défeuillaison, à la densité des masses d'oeufs, que l'épinette blanche. Les niveaux de défeuillaison de l'années courante, ainsi que les tendances régionales des niveaux de population, ont augmenté la susceptibilité à la défeuillaison de façon semblable pour les deux espèces. Les arrosages ont été plus efficaces dans la réduction de la défeuillaison du sapin baumier que de l'épinette blanche, mais dans l'ensemble, n'ont pas offert un haut niveau de protection au feuillage. Les prédictions des défeuillaisons, utilisant des models de régression multiple, avaient des intervalles de confiance d'en moyenne 75%, ce qui est trop élevé pour rendre ce type de prédiction utile. Les équations de régression logistique pourraient être utilisées pour prédire la probabilité qu'un peuplement sera sujet à une défeuillaison légère ou sévère.

Introduction

Annual surveys of spruce budworm, *Choristoneura fumiferana* (Clemens), are conducted during summer to determine population levels, monitor damage, and forecast the intensity of next year's infestations. The egg mass population is surveyed because these are retained on the foliage for about a month (Morris 1955) and are a stable indicator of density. This allows sufficient time to survey large areas, forecast next year's damage, and plan spray programs.

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Spruce budworm lays eggs in the summer and overwinters as unfed second-instar larvae in silk hibernacula on branches. After emergence the next spring, larvae mine buds and needles during the second and third instars then feed on expanding foliage during the fourth, fifth, and sixth instars. Most defoliation occurs as a result of feeding by large larvae. The disadvantage of surveying egg masses to predict next year's damage is that defoliation is affected by factors such as the degree of mortality between oviposition and the feeding stages, as well as by previous defoliation (Morris 1955), although the effect of these factors on resultant defoliation has not been quantified. Population declines of spruce budworm are associated with decreases in larval survival during the feeding stages (Royama 1984). The relationship between density and resultant defoliation may therefore be affected by population trends in the area.

Egg mass densities are used to forecast infestations in terms of broad categories such as light, moderate, and severe infestations (Morris 1954; Webb *et al.* 1956). These categories give little indication of the actual levels of defoliation expected. The original classification schemes were based on data collected from balsam fir, *Abies balsamea* (L.) Miller, and are presently applied to both balsam fir and white spruce, *Picea glauca* Moench (Voss), with the assumption that the relationship between density and defoliation is the same for both hosts (Sanders 1980).

The purpose of this paper is to use historical data to determine the relationship between egg mass density and resultant defoliation, the effect of previous defoliation and population trends on the relationship, and to compare the relationship between the two principal hosts of spruce budworm in Ontario. Logistic regression equations are used to determine the probability of light or severe defoliation as a function of egg mass density.

Materials and Methods

Source of Data. Data were collected by the Forest Insect and Disease Survey (FIDS) Unit, Great Lakes Forestry Centre, for the annual spruce budworm infestation surveys. Data consisted of the geographic location of each sample, spruce budworm egg mass density (egg masses per 9.29 m^2 foliage), the percentage defoliation of current year's growth, the host species, and the type of insecticidal control measure used, if any.

Data were available for the years 1968–1988. The number of sites surveyed ranged from 130 in 1968 to 655 in 1976. Survey methods are outlined in Dorais and Kettela (1982) and Sanders (1980). Six branches per site were collected at mid-crown from host trees following oviposition and samples were examined in the laboratory. The actual number of branches per site examined varied and was determined using a sequential rule (Webb *et al.* 1956) to reduce processing time. Density was estimated by dividing the total number of egg masses (hatched + unhatched + <50% parasitized egg masses) by the total surface area of the branches examined (length × width at midpoint of the foliated portion of the branch). Density has been expressed as number per 100 $ft.^2$ of foliage since the 1940's. For consistency, this unit is still used, but is expressed as the metric equivalent, 9.29 m^2. The percentage defoliation of current year's growth was estimated concurrently with the egg mass sample using a visual rating method.

Data Analysis. Analysis was confined to sites surveyed for 2 or more consecutive years and was restricted to variables that are available after the sample is enumerated, namely, egg mass density, current defoliation, previous defoliation, population trend, spray, host species, and geographic region.

Numeric Variables. The following independent variables were used: egg mass density in year i, current defoliation in year i (which results from eggs masses laid in year $i-1$), and the rate of change from year $i-1$ to year i within each administrative region of Ontario as an index of regional population trend. The dependent variable, resultant defoliation, is defoliation measured at the same site in year $i+1$. Egg mass density was transformed

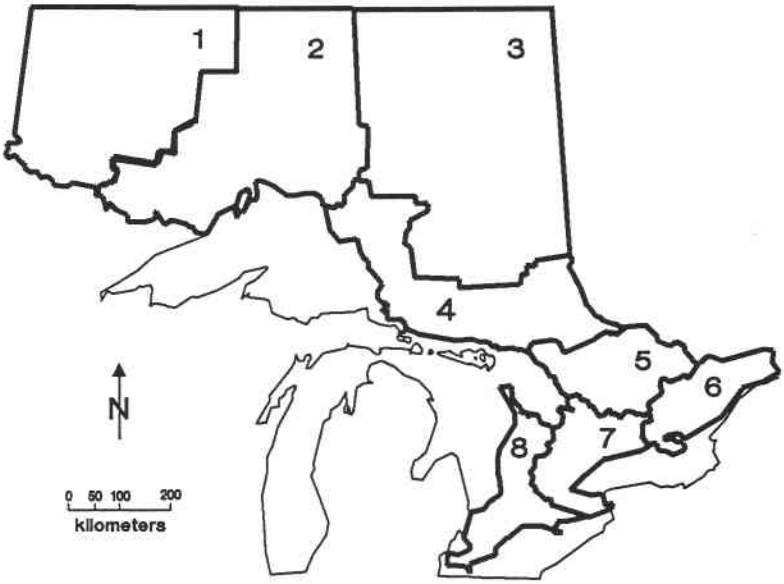

FIG. 1. Administrative regions used by Ontario Ministry of Natural Resources: 1, Northwestern; 2, North Central; 3, Northern; 4, Northeastern; 5, Algonquin; 6, Eastern; 7, Central; 8, Southwestern.

using ln $(x+1)$ and the defoliation variables were transformed using arcsine $(\sqrt{x})$ in order to linearize relationships. The regional population trend from year $i-1$ to year i was calculated for each of the administrative regions of Ontario (Fig. 1) as $\ln R = \ln(x_i) - \ln(x_{i-1})$ where R = regional population trend and x_i = the mean egg mass density for all samples taken within a region in year i. Positive values indicate that the population increased in the area prior to sample collection, negative values indicate a population decrease, and 0 indicates no change.

Categorical Variables. Effects due to host, sprays, and administrative regions were evaluated using categorical variables (Gujarati 1970*a*, 1970*b*). The variable H was set to 0 if the host was balsam fir, $H = 1$ if the host was white spruce. Similarly, if the site was sprayed between egg mass sampling and measurement of resultant defoliation, $S = 1$, otherwise $S = 0$. Seven variables were created to evaluate differences due to geographic location, i.e. the eight administrative regions in Ontario. These are (Fig. 1) Algonquin ($R1 = 1$, 0 otherwise), Central ($R2 = 1$, 0 otherwise), Eastern ($R3 = 1$, 0 otherwise), Southwestern ($R4 = 1$, 0 otherwise), North Central ($R5 = 1$, 0 otherwise), Northeastern ($R6 = 1$, 0 otherwise), Northern ($R7 = 1$, 0 otherwise), and Northwestern ($R1$ to $R7 = 0$) regions.

Stepwise multiple regression (PROC STEPWISE, SAS Institute 1985) was used to identify which numeric and categorical variables had a significant effect on the relationship between egg mass density and resultant defoliation. Significance tests were conducted by determining if the error sum of squares of a model without the variable was significantly lower than the error sum of squares of a model containing all variables entered previously. Once an appropriate model was determined, separate models were developed for white spruce and balsam fir in order to evaluate host-related differences.

Following identification of important variables, logistic regression was used to develop equations for relating the probability of resultant defoliation being light or severe to the predictor variables determined from the multiple regression analysis. Resultant defoliation was classified as light if less than or equal to 30% and severe if greater than or equal to

65%. Two binary variables were created to describe this, $Y1 = 1$ if resultant defoliation was light, 0 otherwise, and $Y2 = 1$ if resultant defoliation was severe, 0 otherwise. Parameters for the logistic models $P(Y1 = 1) = 1/[1 + \exp(-A_1 - B_1X)]$ and $P(Y2 = 1) = 1/[1 + \exp(-A_2 - B_2X)]$ were determined using logistic regression (PROC LOGIST, SAS Institute 1986). $P(Y1 = 1)$ and $P(Y2 = 1)$ are the respective probabilities of a site having light or severe resultant defoliation, A_1 and A_2 are the respective intercept parameters, B_1 and B_2 are vectors of regression parameters and X is a vector of initial conditions determined from the egg mass sample.

Results and Discussion

Initial stepwise multiple regression analysis revealed that egg mass density accounted for 48.5% of the variation in resultant defoliation and was the single most important variable associated with it using data from both hosts combined. The second most important variable was current year's defoliation, which alone accounted for 44.8% of the variation in resultant defoliation. Previous defoliation was correlated with egg mass density ($r = 0.76$), but added an additional 5.6% to the variation accounted for when included in a model containing egg mass density. Population trend by itself accounted for 7.2% of the variation in resultant defoliation, but increased the variation accounted for by 4.5% over a model already containing egg mass density and current defoliation. Correlation of population trend with egg mass density was low ($r = 0.15$). Inclusion of categorical variables for host species and spray raised the total variation accounted for to 60%.

The only categorical variables for regional effects that were statistically significant were $R5$ (North Central region) ($F = 12.4$; df = 1, 6717; $P < 0.0001$) and $R6$ (Northern region) ($F = 15.9$; df = 1, 6717; $P < 0.0001$). However, these only increased the total variation accounted for by 0.07%. There was no significant difference between the effects of both regions ($F = 0.029$; df = 1, 6717; $P > 0.50$). The combined effect of both regions in the model was to increase predicted defoliation by only 3% over a model that did not contain any regional effects. This amount is considered small in relation to the error associated with measurement of defoliation and is not considered biologically significant. The final variables included in the model were egg mass density, current defoliation, population trend, host, and spray.

Host species had a significant effect on the relationship between egg mass density and resultant defoliation and also a significant interaction with regional population trends ($F = 9.04$; df = 1, 7200; $P < 0.005$), which justifies development of separate models for each host. The results of the multiple and logistic regressions relating resultant defoliation to egg mass density, current defoliation, regional population trends, and sprays are shown in Table 1. In all cases, model fit was higher for balsam fir than for white spruce. This probably reflects more uncertainty in accurately estimating egg mass density on spruce than on balsam fir, because densities were expressed per unit area, not per unit weight as has been recommended recently (Régnière *et al.* 1989). The logistic regressions had consistently lower R^2 than the multiple regressions because the independent variables were reduced to two values, 0 and 1.

The effects of current defoliation, regional population trends and spraying on the relationship between egg mass density and resultant defoliation are shown in Figures 2, 3, and 4, respectively. Defoliation of balsam fir was higher than observed for white spruce at any given egg mass density. Also, resultant defoliation of balsam fir increased by a greater amount per unit egg mass density, as evidenced by the higher slope for egg mass density for balsam fir than for white spruce ($t = 16.32$; df = 1, 7209; $P < 0.0001$). The probability of light defoliation was greater for white spruce than for balsam fir at a given egg mass density (Fig. 2*c*,*d*) and the probability of severe defoliation was higher for balsam fir than for white spruce at a given egg mass density. White spruce therefore appears more resistant to defoliation by spruce budworm. Percentage defoliation is a relative measure

Table 1. Parameter estimates for final models* relating spruce budworm egg mass density estimates to resultant defoliation

Host	n	B_0	B_1	B_2	B_3	B_4	R^2
Multiple regression							
Balsam fir	5660	1.16	5.51	0.36	7.90	−10.89	0.62
		(0.46)	(0.16)	(0.01)	(0.34)	(1.42)	
White spruce	1553	0.94	3.70	0.37	5.84	−5.00	0.48
		(1.09)	(0.28)	(0.02)	(0.58)	(1.73)	
Logistic regression — light defoliation							
Balsam fir	5712	4.540	−0.800	−0.023	−0.832	1.133	0.47
		(0.138)	(0.034)	(0.002)	(0.057)	(0.201)	
White spruce	1591	5.343	−0.753	−0.024	−0.627	0.347	0.35
		(0.346)	(0.069)	(0.004)	(0.092)	(0.239)	
Logistic regression — severe defoliation							
Balsam fir	5712	−5.627	0.790	0.023	0.941	−1.177	0.44
		(0.182)	(0.039)	(0.002)	(0.059)	(0.229)	
White spruce	1591	−6.143	0.673	0.024	0.668	−0.665	0.29
		(0.455)	(0.084)	(0.004)	(0.103)	(0.294)	

*Multiple regression equation is: $Y = B_0 + B_1X_1 + B_2X_2 + B_3X_3 + B_4X_4$

where B_0 = intercept, X_1 = ln (egg masses/9.29 m^2), X_2 = arcsine ($\sqrt{\text{current year defoliation}}$), X_3 = ln (population trend), X_4 = 1 if sprayed, 0 otherwise.

The logistic regression equations are:

$P(Y1 = 1) = 1/\{1 + \exp[-B_0 - (B_1X_1 + B_2X_2 + B_3X_3 + B_4X_4)]\}$

and

$P(Y2 = 1) = 1/\{1 + \exp[-B_0 - (B_1X_1 + B_2X_2 + B_3X_3 + B_4X_4)]\}$

where $Y1$ = 1 if resultant defoliation was light, 0 otherwise, $Y2$ = 1 if resultant defoliation was severe, 0 otherwise.

of damage. Developing budworms eat the same amount of balsam fir and white spruce foliage on a dry weight basis (Koller and Leonard 1981). Because white spruce produces more foliage per unit area than balsam fir (Régnière *et al.* 1989), the percentage defoliation will be lower on white spruce at a given density of spruce budworm. Also, although balsam fir shoots flush sooner than white spruce, shoot expansion may be slower and insect grazing able to overtake foliage production on balsam fir (Koller and Leonard 1981).

The effect of current year defoliation on the relationship between egg mass density and resultant defoliation is shown in Figure 2*a*, *b* for balsam fir and white spruce, respectively. The slope, with respect to current year defoliation, is nearly identical for both species. As current year defoliation increased, so did the severity of resultant defoliation at a given egg mass density. Changes in current defoliation from 0 to 100% could potentially lead to an increase in resultant defoliation of 60% (Fig. 2*a*,*b*). This is reflected in the logistic regression (Fig. 2*c*–*f*). Stands with 0% current defoliation had up to a 50% higher chance of having light defoliation at a given egg mass density than did stands with 100% current year's defoliation. Stands with 0% current defoliation had up to 50% lower chance of suffering severe defoliation than stands that had 100% current defoliation.

The relationship between current year defoliation and resultant defoliation probably has two components. First, current year defoliation and egg mass density were correlated for both hosts (r = 0.76 and 0.67, respectively). Both variables are indicators of population density in an area, so the first component of the relationship between current year defoliation and resultant defoliation reflects this. However, addition of current defoliation to models already containing egg mass density raised the variation in resultant defoliation accounted for by 4 and 6% for balsam fir and white spruce over models containing egg mass density alone. Therefore, a second component to this relationship may be that stands vary in their susceptibility to budworm defoliation depending on previous defoliation histories, as suggested by Morris (1954), and that susceptibility to defoliation increases

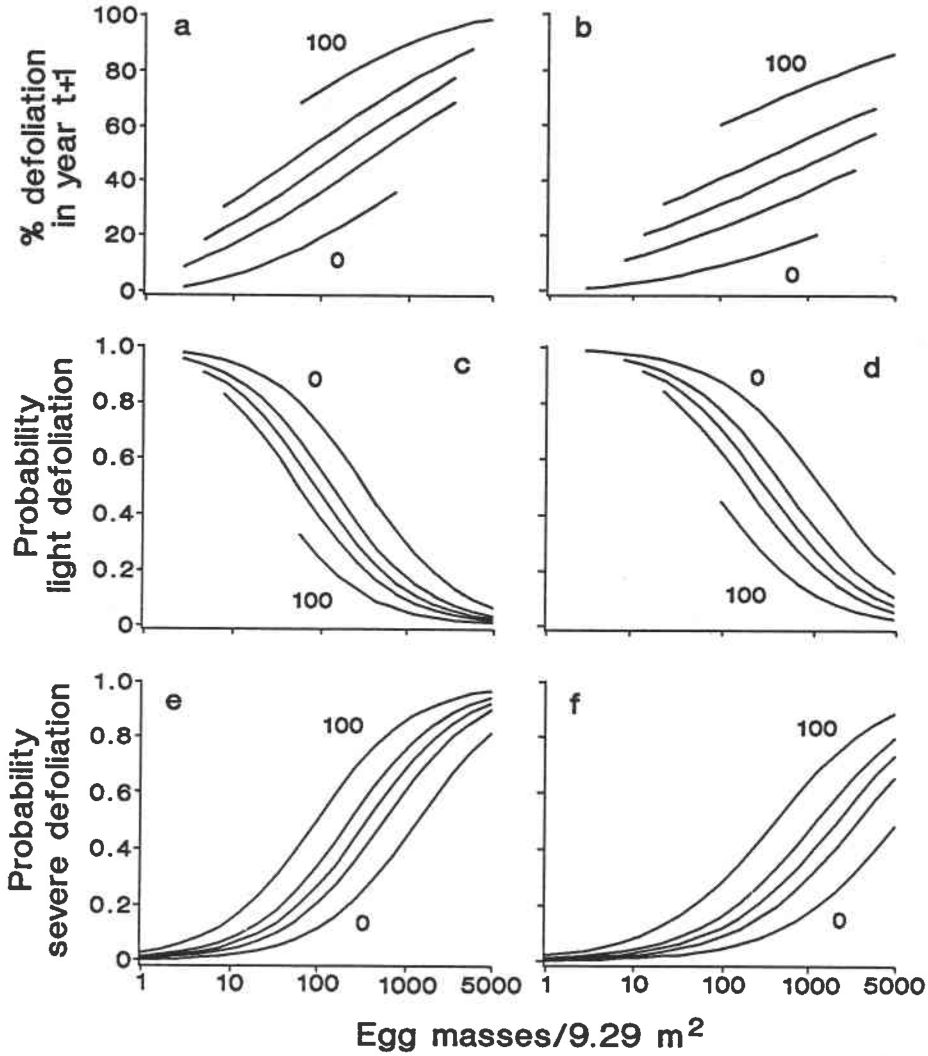

FIG. 2. Effect of current defoliation on the relationship between egg mass density and resultant defoliation. (*a*,*b*) Multiple regression results for balsam fir and white spruce, respectively. (*c*,*d*) Logistic regression results for probability of light defoliation on balsam fir and white spruce, respectively. (*e*,*f*) Logistic regression results for probability of severe defoliation on balsam fir and white spruce, respectively. Lines are equations (Table 1) solved at 0, 25, 50, 75, and 100% current defoliation, spray = 0 and population trend = 0.

throughout an infestation. Unfortunately, no analytical method can separate the importance of these two effects. This could only be resolved by experimentation.

The effect of regional population trends on the relationship between egg mass density and resultant defoliation is shown in Figure 3. Higher levels of defoliation resulted for a given density when populations had increased. The effect was slightly higher on balsam fir than on white spruce, again a reflection of spruce's greater resistance to relative measures of defoliation. The logistic regressions also indicate that stands in areas in which populations increased had a higher chance of severe defoliation and a lower chance of light resultant defoliation than stands in areas in which populations decreased.

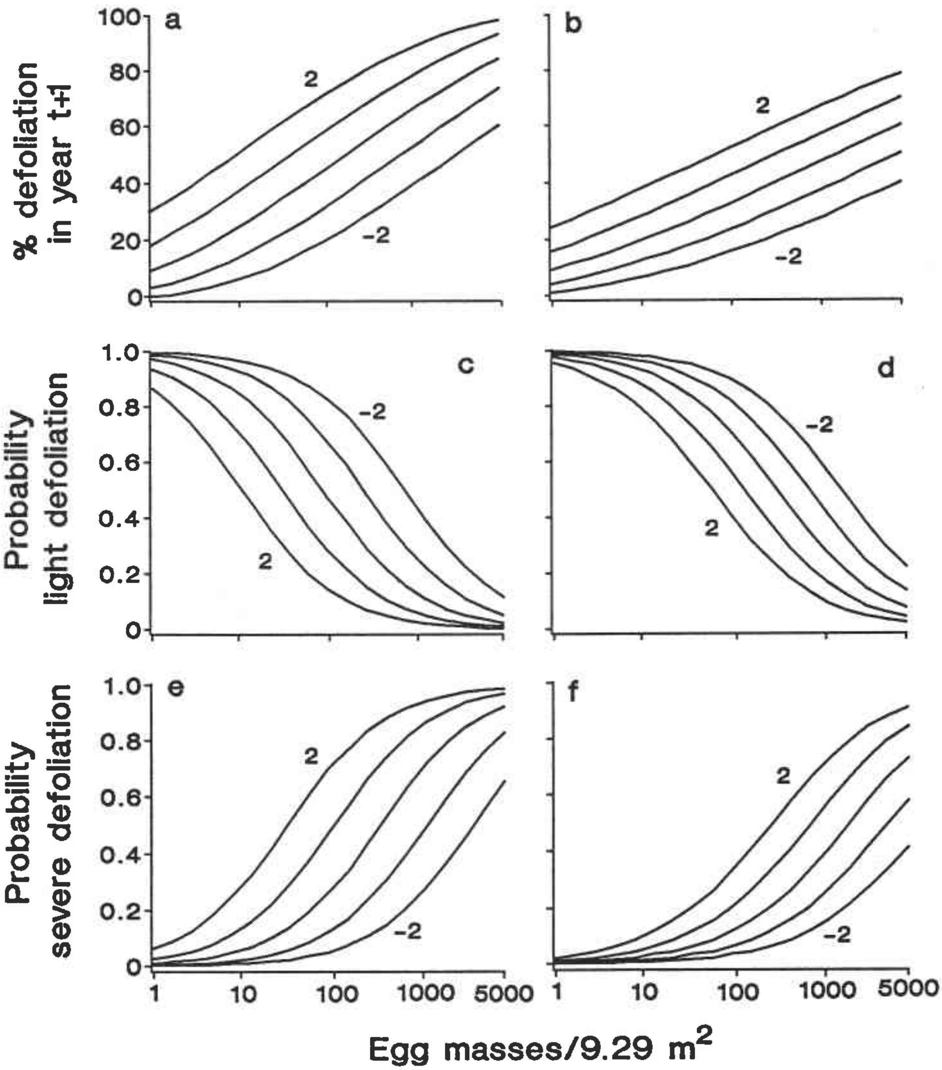

FIG. 3. Effect of regional population trend on the relationship between egg mass density and resultant defoliation. (*a*,*b*) Multiple regression results for balsam fir and white spruce, respectively. (*c*,*d*) Logistic regression results for probability of light defoliation on balsam fir and white spruce, respectively. (*e*,*f*) Logistic regression results for probability of severe defoliation on balsam fir and white spruce, respectively. Lines are equations (Table 1) solved with regional population trend = −2.0, −1.0, 0, 1.0, and 2.0, spray = 0 and current defoliation = 50%.

Most feeding occurs during the sixth instar of spruce budworm larvae (Koller and Leonard 1981). Survival during the sixth instar is the major determinant of population trends for spruce budworm larvae (Royama 1984). Low large larvae survival is associated with declining populations and high survival is associated with increasing populations. Starting with a fixed egg mass density in the fall, populations with high survival will have more budworm during the damaging stage than a population with low survival and greater foliage consumption. This effect will be most important during population collapse. Although the measure of population trend used precedes by 1 year the population trend

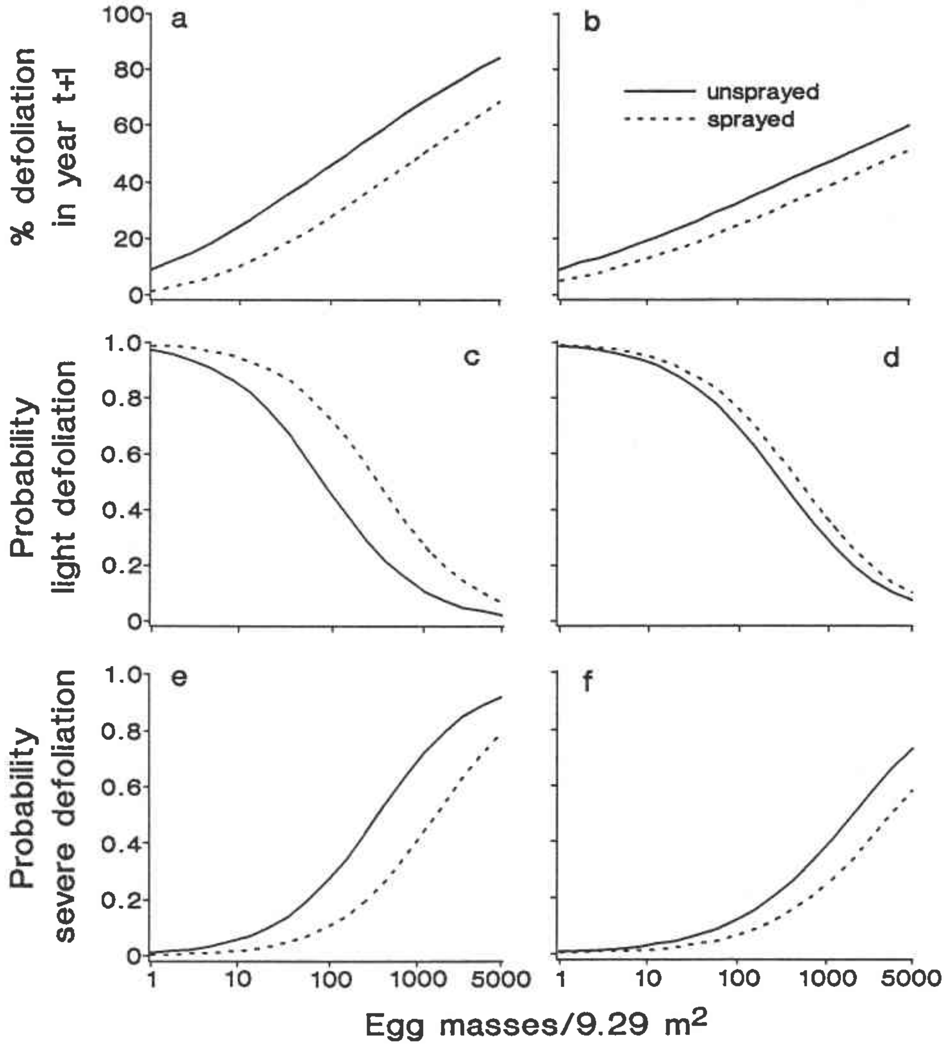

FIG. 4. Effect of spraying on the relationship between egg mass density and resultant defoliation. (*a*,*b*) Multiple regression results for balsam fir and white spruce, respectively. (*c*,*d*) Logistic regression results for probability of light defoliation on balsam fir and white spruce, respectively. (*e*,*f*) Logistic regression results for probability of severe defoliation on balsam fir and white spruce, respectively. Lines are equations (Table 1) solved for sprayed and unsprayed stands, 50% current defoliation, and regional population trend = 0.

between oviposition and damage, its use is justified because populations collapse over a period of several years (Royama 1984). Also, the measure used here is the only one the manager will be able to calculate at the time the forecasts are made.

The effect of spraying on the relationship between egg mass defoliation and resultant defoliation is shown in Figure 4. At a given egg mass density, sprayed balsam fir had approximately 25% lower resultant defoliation than unsprayed balsam fir. The effect of sprays on reducing defoliation of white spruce was much less, ca. 10%, possibly because the greater foliage density of white spruce inhibits droplet penetration. Spraying increased the probability of balsam fir having light defoliation by 0.3 at moderate densities, but this protection diminishes as density increased. Stands with greater than 1000 egg masses per 9.29 m^2 are unlikely to receive any benefit from spraying. Spraying did not significantly increase the probability of white spruce having light defoliation ($\chi^2 = 2.11$; df = 1; $P > 0.14$). The probability of severe defoliation was decreased by 0.3 and 0.2 when sprays were applied to balsam fir and white spruce, respectively (Fig. 4*e*,*f*). These results agree with previous studies, which indicated that spraying did not confer a very high degree of foliage protection (Fleming *et al.* 1984). Whether or not the cost of spraying is worth the small level of protection achieved needs to be evaluated and will depend on the value of the forest and its likelihood of dying because of budworm attack.

The multiple regression and logistic analyses yielded conclusions that were generally consistent with each other. Egg mass density as measured by FIDS was related to resultant defoliation, and was therefore adequate for forecasting. The relationship varied between hosts, which should be considered when forecasts are made. Also, previous defoliation and regional population trends had an effect above that of egg mass density, which should also be considered when forecasting. The variables used accounted for only 62 and 48% of resultant defoliation of balsam fir and white spruce. The unexplained variation could have resulted from other factors, but also might be related to the manner in which the data were collected. The number of samples used to determine egg mass density at a site is quite low, up to six branches maximum. This would result in density estimates with a relatively high variance and, at low densities, questionable accuracy due to stochastic sampling biases (Lysyk and Sanders 1987). Unfortunately, FIDS data are not presented in a manner that allows weighting of observations according to the number of branches counted. Estimates of egg mass density and current year defoliation were measured concurrently on the same branches. Estimates of resultant defoliation were taken in the same site the next year, but there is no guarantee that they were taken from the same tree. Some of the unaccounted variation may be due to spatial variation within a site.

The multiple regression equations could be used to predict an exact value for resultant defoliation given the information in the egg mass sample; however, the length of confidence intervals around predictions of resultant defoliation averaged 75% using the multiple regression equations. Therefore, predicting an exact level of resultant defoliation will be of limited value. Although subject to similar errors, the logistic regressions make a less exact prediction, for example, that there would be a high (or low) probability of estimated resultant defoliation in the stand being light (or severe). They merely assign a probability that estimated resultant defoliation will be light or severe. This is more satisfying as it recognizes the variability of the data used in forecasting, as well as the stochastic nature of insect plant interactions. The forest manager then has the opportunity to decide what level of risk to accept for a stand.

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