

# Forecasting Defoliation Caused by the Gypsy Moth from Field Measurements

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**ABSTRACT** The correlation of various preseason field measurements with subsequent defoliation by the gypsy moth, *Lymantria dispar* (L.), was examined from a series of forest stands in central Pennsylvania. These measurements included preseason egg-mass density, density of old egg masses (residual egg masses from previous generations), fecundity, number of larvae hatching per mass, egg-mass length, and host-tree basal area. Egg density (product of fecundity and egg-mass density) was the best single variable for predicting defoliation. The product of egg-mass density and mean egg-mass length provided predictions of defoliation nearly as well as egg density, reflecting the previously observed linear relationship between egg-mass length and fecundity. The addition of the ratio of new-old egg masses to the model significantly increased the model fit. Parameters of these and other parameters in linear and nonlinear (Weibull) models are provided. These results indicate that recording one or two additional field measurements (egg-mass length or counts of old egg masses) increases the precision in the prediction of defoliation when densities range from 100 to 10,000 egg masses per acre (250 to 25,000 egg masses per ha).

**KEY WORDS** Lymantriidae, sampling, egg mass

THE AMOUNT OF forested land defoliated by the gypsy moth, *Lymantria dispar* (L.), continues to increase as this insect expands its range; in 1990 alone, >15 million ha were defoliated in the United States. This defoliation can have substantial effects on timber values through tree growth loss and mortality (Campbell & Sloan 1977, Gansner & Herrick 1982), as well as indirect effects on recreation and scenic values (Payne et al. 1973, Twery 1991). Large areas of forest land are sprayed every year to prevent this defoliation; >12 million ha were aerially treated as part of the USDA Forest Service Cooperative Suppression Program over the last 5 yr.

One of the major impediments to implementation of an effective integrated gypsy moth management program is the lack of an precise yet economical procedure for forecasting defoliation. Most gypsy moth management programs use one of several methods for censusing egg mass populations (Ravlin et al. 1987). These methods are often too costly to replicate at a level necessary to achieve sufficient accuracy (Ravlin et al. 1987, Liebhold et al. 1992).

Several studies (Campbell 1966, Campbell & Standaert 1974, Gansner et al. 1985, Williams et

al. 1991) have focused on predicting defoliation from gypsy moth egg-mass density, estimated either from fixed-radius plots (Kolodny-Hirsch 1986) or fixed- and variable-radius plots (Wilson & Fontaine 1978). Unfortunately, egg-mass density alone may not predict subsequent defoliation with a useful level of precision; variability in fecundity, egg survival, first-instar dispersal, and larval survival may all contribute to variance in the relationship between egg-mass density and defoliation (Campbell & Standaert 1974, Williams et al. 1991). In this study, we attempted to evaluate a variety of field measurements, along with egg-mass density, that may increase the precision of defoliation predictions.

## Materials and Methods

In 1989, twelve 60-ha study areas were located in forests in central Pennsylvania. Stands were chosen such that at least 50% of the host basal area was represented by species preferred by the gypsy moth (Mosher 1915). Sites were also selected based upon egg-mass density; preference was given to sites with egg mass densities ranging from  $\approx$ 250 to 25,000 egg masses per ha (100 to 10,000 egg masses/ac). In 1990, measurements were repeated at all study areas used in 1989 and five new areas were established. In 1991, measurements were repeated at nine of the 1990 sites (seven of the 1990 sites were also measured in 1989 and two were established in 1990), and

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**Table 1.** Results of stepwise regression on percentage defoliation ( $n = 40$ )

Variable 1	Variable 2	Intercept	Slope 1	Slope 2	R <sup>2</sup>
Egg density	—	-7.64	1.36	—	0.332
Length * egg mass density	—	-5.65	1.25	—	0.303
Larval density	—	-6.41	1.13	—	0.275
Egg mass density	—	-3.58	1.15	—	0.260
New/old egg masses	—	-0.80	0.748	—	0.259
Egg masses/host basal area	—	-0.18	0.496	—	0.110
Length	—	-6.23	4.23	—	0.068
Eggs per mass	—	-4.25	1.57	—	0.028
Host basal area	—	-0.46	0.00303	—	0.002
New/old egg masses	Egg density	-6.02	0.417	1.01	0.389
New/old egg masses	Length * egg mass density	-4.53	0.476	0.913	0.385
New/old egg masses	Egg mass density	-3.09	0.547	0.845	0.380

two new study areas were established. Thus, data were collected from a total of 40 site-years.

At each study area, a  $4 \times 5$  grid of sampling points (200 m between each point) was marked with wooden stakes. At each point, a count was made of all new (current year) and old (cumulative from previous years) egg masses within a 0.01 ha (1/40th acre) circular plot. In 1989, the length of the two egg masses closest to the plot center were measured, then collected just before spring hatch. These masses were taken to the laboratory, and one of the two was allowed to hatch and the number of first instars emerging was counted. The other egg mass was dehaired and dissected, and the total number of eggs per mass was counted (Tardif & Secret 1970). In 1990 and 1991, the length of one egg mass from each point was measured and taken to the laboratory. Eggs were individually counted after dehairing. A random sample of 100 eggs from each site was allowed to hatch in a covered petri dish containing a moistened piece of filter paper and maintained at 24°C and 14:10 (L:D)h. The number of larvae hatching per mass was estimated as the product of the proportion of these 100 eggs that hatched times the mean number of eggs per mass. In each of the 3 yr, hatch was monitored in a chamber of constant temperature, light, and moisture.

During peak defoliation, each plot was visited and defoliation estimates were taken. Trees were selected using a 10 BAF prism, and the species and defoliation condition of each tree (to the closest 10%) were visually estimated. At each woodlot, percentage defoliation was estimated as the average of all trees of highly susceptible species (Mosher 1915), weighted by their basal area.

Models that predicted defoliation from one or more pre-season variables were developed. These variables were: egg-mass density, egg density (egg density was computed as the product of egg-mass density and the woodlot mean number of eggs per mass), the product of egg-mass density and mean egg-mass length, the ratio of new egg masses to old egg masses, egg-mass density divided by basal area of highly favored species (Mosher 1915), mean egg-mass

length, number of eggs per mass, number of larvae hatching per mass, larval density (the product of number of larvae hatching per mass and egg-mass density), and host basal area. A stepwise regression procedure (SAS Institute 1988) was used to evaluate the contribution of each of these variables to the prediction of defoliation in simple and multiple linear regression models. Defoliation estimates were transformed as probits and a  $\log_{10}(X)$  transformation was used for all other variables (Sokal & Rohlf 1981). Nonlinear models provide a better fit to defoliation prediction models (Williams et al. 1991), but the relationship between egg-mass density and defoliation is nearly linear through the ranges in density present in our data. Therefore, we used stepwise linear regressions to select combinations of one or two variables that were most closely related to defoliation, then parameterized nonlinear models using these selected variables. Weibull functions,

$$y = a - b \cdot e^{-e^{-c} \cdot x^d},$$

where  $a-d$  are parameters, were fit iteratively to the data using the multivariate secant method (SAS Institute 1988). The upper asymptote ( $a$  in equation (1)) was set at 100% and the lower asymptote ( $a-b$ ) was set at 0%.

## Results and Discussion

Stepwise simple linear regression indicated that all of the field measurement variables except egg-mass length, number of eggs per mass, and oak basal area were significantly ( $\alpha = 0.05$ ) related to defoliation, but egg density was the best single predictor of defoliation (Table 1). Egg density is more closely related to defoliation than egg-mass density because gypsy moth fecundity varies considerably among populations and among years (Campbell 1967). Campbell & Standaert (1974) and Williams et al. (1991) found that egg density more precisely predicted defoliation than egg-mass density. However, the use of egg density measurements in gypsy moth management has been prevented largely by the

complexity of estimating fecundity (egg density is estimated as the product of fecundity and egg-mass density). In contrast, mean egg-mass length is very easy to estimate in the field, and the product of egg-mass density and egg-mass length was nearly as good a predictor of defoliation (Table 1). This reflects the previously observed linear relationship between egg-mass length and fecundity (Moore & Jones 1987). Thus, the product of egg-mass length and density should be approximately linearly related to egg density and therefore performs nearly as adequately as egg density in predicting defoliation.

Larval density was the third best predictor of defoliation (Table 1). That it is not the best predictor of defoliation is surprising because it incorporates among-year and among-site variation in egg mass viability. It was also surprising that egg-mass density, expressed as numbers per unit host basal area (Table 1), yielded a low  $R^2$  (0.110), much smaller than the 0.260 from egg-mass density expressed as numbers per unit ground area. Theoretically, one would expect that incorporation of host basal area would increase the correlation with defoliation because the ratio of insects to foliage, rather than the ratio of insects to ground area, should determine defoliation levels (Montgomery 1990), and basal area is positively related to foliage area (Rogers and Hinckley 1979). It is possible that the variation in oak basal area at the stands used in this study was so low that this effect was not pronounced (basal area ranged from 8.4 to 24.4 m<sup>2</sup>/ha).

Stepwise multiple linear regression indicated that the ratio of new-old egg masses, along with either egg density, egg-mass density, or the product of egg-mass length and egg-mass density, explained much more of the variation in defoliation than was explained by any of these variables alone (Table 1). Population replacement rate,  $N_t/N_{t-1}$ , has previously been recognized as contributing significantly to the prediction of defoliation (Campbell 1966, Campbell & Standaert 1974, Williams et al. 1991); however, its usefulness to gypsy moth managers has been precluded by the usual lack of data on densities in the previous generation in most stands. Counts of old egg masses are not estimates of egg masses in the previous generation because some egg masses disintegrate within 1 yr and others persist for many seasons. Nevertheless, results presented here indicate that the ratio of new-old egg masses apparently approximates the change in densities sufficient to contribute to the forecasting of defoliation.

The parameters given in Table 1 are for linear models; the relationship between these variables and defoliation may not always be linear, although the relationships between defoliation and both egg-mass density and egg density were approximately linear through most of the range

**Table 2.** Results of maximum likelihood procedure to fit nonlinear (Weibull) models

Independent variable	<i>c</i>	<i>d</i>	<i>r</i> <sup>2</sup>
Egg mass density	4.65 ± 1.09	0.602 ± 0.152	0.777
Log <sub>10</sub> egg mass density	4.88 ± 1.22	4.02 ± 1.08	0.774
Egg density	9.11 ± 2.03	0.67 ± 0.156	0.801
Log <sub>10</sub> egg density	15.1 ± 3.46	8.53 ± 2.00	0.799
Egg mass density × length	7.69 ± 1.83	0.70 ± 0.185	0.762
Log <sub>10</sub> (egg mass density × length)	11.2 ± 2.62	7.18 ± 1.73	0.803

Values are means ± SE. See equation 1 for explanation of parameters.

of densities in these data. However, the relationship between gypsy moth density and defoliation must ultimately be a sigmoidal curve (Williams et al. 1991). Therefore, we fit these data to a sigmoidal Weibull function in which the lower asymptote was set at 0% and the upper asymptote was set at 100%. The parameters for these models are given in Table 2 and are shown graphically in Figs. 1–3. Egg density, log<sub>10</sub> egg density, and log<sub>10</sub> (length × density) were the best predictors of defoliation. Weibull models that used length × density, egg-mass density, and log<sub>10</sub> egg-mass density to predict defoliation yielded poorer fits to the data (Table 2). The superiority of egg density and length × density was similar to the pattern seen in the linear models (Table 1), although there was generally not a great deal of difference among any of the Weibull models.

The Weibull model (equation 1) of defoliation as a function of gypsy moth egg-mass density, reported in Table 2, is shown in contrast to the Weibull model developed by Williams et al. (1991) from data collected in New Jersey and in contrast to a Weibull model fit to data collected by Gansner et al. (1985) from plots in central Pennsylvania (Fig. 4). The models yield very similar defoliation predictions for densities <1,000 and >10,000 egg masses per acre (≈2,500 and 25,000 egg masses/ha). In the range of 1,000 to 10,000 egg masses per acre (≈2,500 to 25,000 egg masses/ha), the Gansner et al. (1985) model predicts only slightly higher defoliation levels and the Williams et al. (1991) model predicts much lower defoliation levels. The high degree of congruence between our model and that developed from the Gansner et al. (1985) data may be because in both studies, data were collected in south-central Pennsylvania. The more marked difference in the form of the Williams et al. (1991) model may reflect some unknown difference in the forest types in New Jersey where Williams et al. (1991) collected their data. The differences among the models at densities of >1,000 egg masses per acre (≈2,500 egg masses/ha) are probably unimportant to management applications because all of the models predict sub-

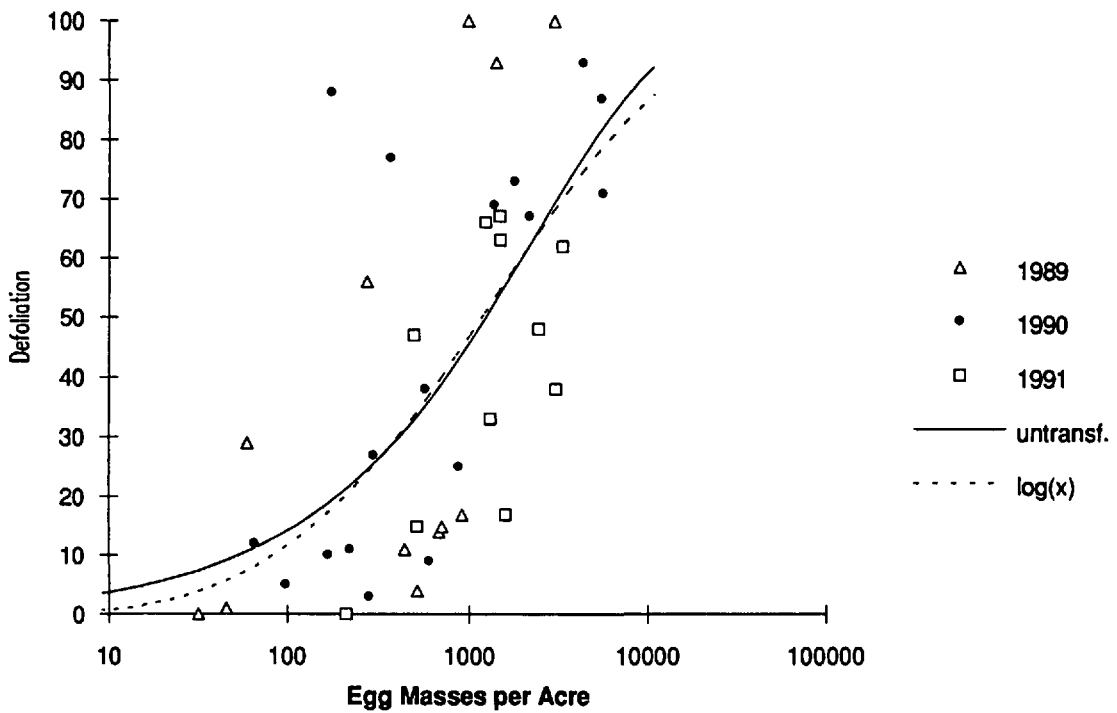


Fig. 1. Scatter plot of mean egg-mass density versus mean defoliation at 40 woodlots. Line represent fitted Weibull model; parameters are given in Table 2 (1 ac = 0.4047 ha.).

stantial (>30%) defoliation at these densities. Thus, for most management purposes all three models are essentially equivalent.

Some caution should be exercised in extrapolating the functions reported here either below

or above densities where data were collected. At densities of <50 egg masses per acre ( $\approx 125$  egg masses/ha), it is extremely unlikely that defoliation will occur unless there is a rare mass immigration of first instars from adjoining stands

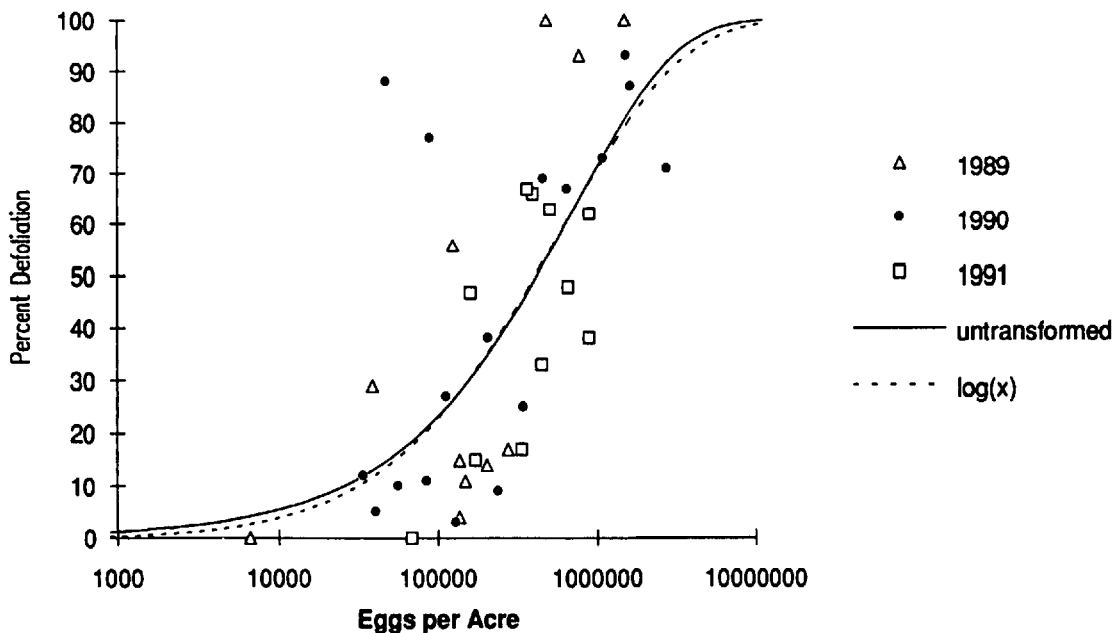


Fig. 2. Scatter plot of mean egg density (product of egg-mass density and fecundity) versus mean defoliation at 40 woodlots. Line represents fitted Weibull model; parameters are given in Table 2 (1 ac = 0.4047 ha.).

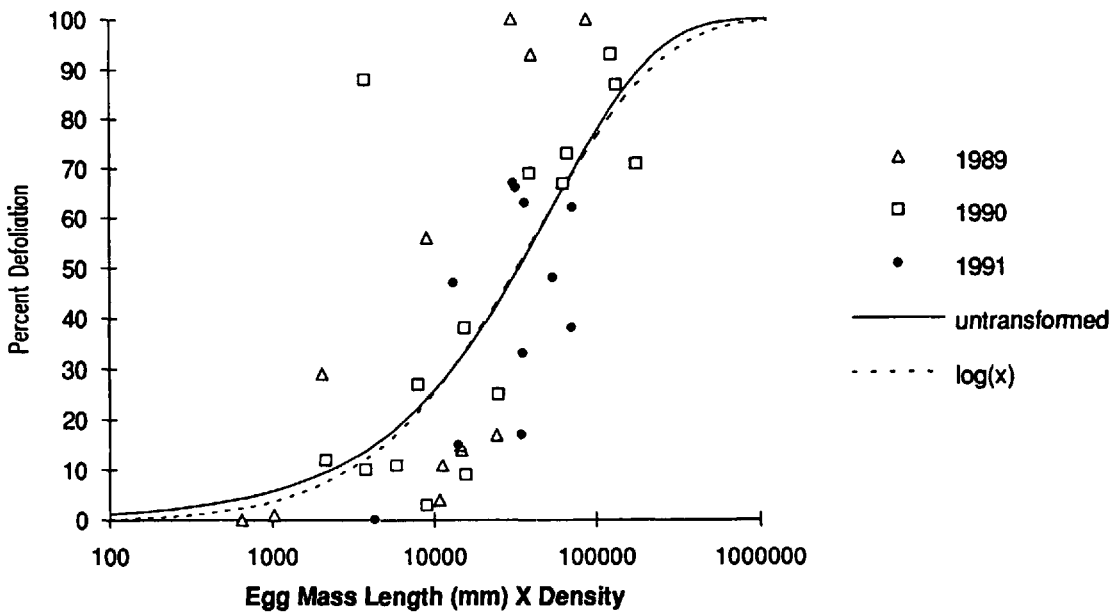


Fig. 3. Scatter plot of the product of mean egg-mass length times mean egg-mass density versus mean defoliation at 40 woodlots. Line represents fitted Weibull model; parameters are given in Table 2 (1 ac = 0.4047 ha.).

(Liebhold & McManus 1991). When densities are >10,000 egg masses per acre ( $\approx 25,000$  egg masses/ha; such densities are rare), defoliation is almost a certainty unless there is a violent population crash (Elkinton & Liebhold 1990). When egg mass densities range between 100 and 1,000 egg masses per acre ( $\approx 250$  to 2,500 egg masses/

ha), it is much more difficult to predict defoliation from egg-mass density alone. Data in Fig. 1 and similar data reported by Williams et al. (1991) demonstrate that, through this range of egg-mass density, defoliation can range from 0 to 100% with a weak correlation between density and defoliation. This is a major problem in the

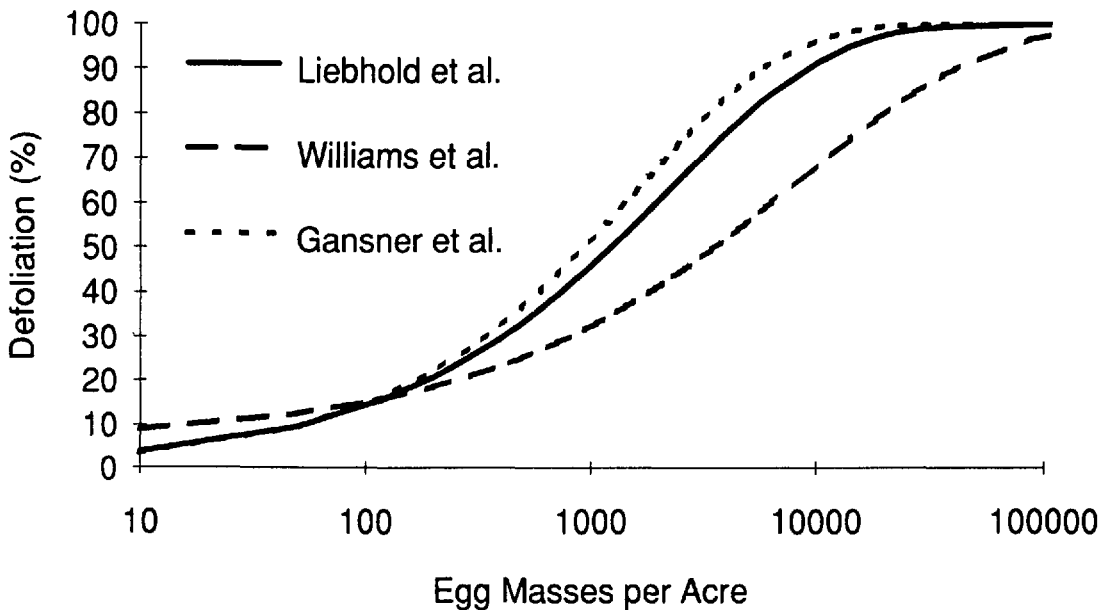


Fig. 4. Comparison of the Weibull models that predict defoliation from egg-mass density. "Liebhold et al." is the model reported here (equation 1; Table 2). "Williams et al." is the model reported by Williams et al. (1991). "Gansner et al." is the data presented in Gansner et al. (1985) fitted to the Weibull function given in equation 1 ( $c = 4.892, d = 0.661$ )(1 ac = 0.4047 ha.).

implementation of an integrated approach to gypsy moth management because incorrect decisions to suppress populations may result in a failure to protect timber and nontimber resources from defoliation effects or it may result in an unnecessary use of pesticides. With increasing budgetary constraints and environmental concerns, these problems can be substantial. The results presented here may alleviate these problems somewhat; collection of one or more additional measurements will increase the precision of defoliation predictions. Measurement of egg-mass length or counting old egg masses are relatively simple tasks, requiring little additional time when stands are visited for fixed-radius sampling. Webb et al. (1991) provided an example of how egg-mass length measurements might be included in the decision-making process of a gypsy moth management program. These measurements will slightly increase the precision of defoliation forecasts, but prediction of defoliation in areas where egg mass densities range from 100 to 1,000 egg masses per acre ( $\approx 250$  to 2,500 egg masses/ha) remains relatively imprecise.

All of the variables that were tested here as predictors of defoliation, as well as the actual defoliation values, were not true population values but were instead estimates based upon limited subsamples of the populations. Therefore, the variation about the relationship between any one of these variables and defoliation is caused both by the inherent variation in the relationship between true population values and by sampling error in estimates. Separation of these two components of variation is not a simple problem, but this work should be done in the future. A statistically based understanding of how variation in estimates of field variables affects error and uncertainty of defoliation predictions would be useful for making decisions based upon these predictions. Such risk-based forecasts may ultimately be more sound than traditional deterministic models for making pest management decisions (Anderson et al. 1977).

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