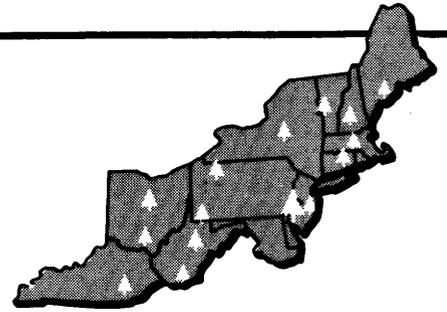


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Northeastern Forest Experiment Station



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FORECASTING DEFOLIATION BY THE GYPSY MOTH IN OAK STANDS

Abstract.—A multiple-regression model is presented that reflects statistically significant correlations between defoliation by the gypsy moth, the dependent variable, and a series of biotic and physical independent variables. Both possible uses and shortcomings of this model are discussed.

THE GYPSY MOTH, *Porthetria dispar* (L.), is one of the most destructive pests of hardwood forests in the northeastern United States. Populations of this insect have sometimes achieved densities of more than 5,000 egg masses per acre and have maintained these high densities for several years running (Campbell 1973a). Such populations are capable of killing a high proportion of the overstory trees through repeated and heavy defoliations (Kegg 1971).

On the other hand, the proportion of the foliage that will be removed by gypsy moth larvae in any given place and year depends not only on the number of insects that are present, but also on other variables. A particular insect density does not determine a particular defoliation level. Rather, an array of defoliation levels may result from that density (Campbell 1966). And before we can predict defoliation for any given time and place with reasonable accuracy, it is clear that relationships between defoliation and other heretofore unidentified or at least unquantified variables must be accounted for.

OBJECTIVE

Our objective is to describe a multiple-regression model that reflects statistically significant correlations between defoliation by the gypsy moth, the dependent variable, and a series of biotic and physical independent variables. Although the data used to develop this model were collected from an area in northeastern New England between 1911 and 1931, it seems reasonable to suppose that most of the underlying mechanisms through which a particular defoliation regime is determined today are not much different from those in 1911–31. On the other hand, the system may have changed since that time to the point where the model presented is of little or no practical immediate value. In any case, this model will be tested for predictive accuracy in the near future.

PROCEDURES

The biological data used here were accumulated by personnel of the old Melrose Highlands Gypsy Moth Laboratory in Massa-

chusetts. Procedures used to process these data, and a complete list of the independent variables tested, have been described (*Campbell 1973b*).

Processed data included an estimate of each of the following variables for each plot in the Melrose system during each year the plot was examined.

Significant independent variables:

- ZDL = Percentage of the plots examined in a zone in the fall of year (n) that contained more than 500 egg masses per acre.
- ZDH = Percentage of the plots examined in a zone in the fall of year (n) that contained more than 5,000 egg masses per acre.
- MLSTYR = Egg masses per acre in the fall of year (n-1).*
- MNOW = Egg masses per acre in the fall of year (n).*
- Trend = $\frac{MNOW}{MLSTYR}$
- DOM = Percentage of the dominant trees in the stand that were favored as food by the gypsy moth (FCA).
- TFOL = An index of total foliage per acre.
- DCA_n = Percentage defoliation of favored food trees (FCA) during year (n).
- PM = Precipitation in May of year (n), in inches.

Dependent Variable:

DEF_(n+1) = Percentage defoliation of the whole stand during year (n+1).

First, the above data were stratified to represent only stands where more than one-half of the overstory was composed of oaks, because defoliation in this stratum is of great concern to many people. Other strata were set aside for examination later.

Second, the dependent variable, defoliation

(*One egg mass was always added to observed egg-mass density per acre because no egg masses were observed in some of the Melrose plots during some years.)

in year (n+1) (DEF_(n+1)), was transformed to $\ln(101-DEF_{(n+1)})$. Although defoliation in most of the plots ranged between zero and 25 percent during most of the years they were observed, this insect is likely to damage trees only when defoliation is greater than 50 percent; and the above transformation seemed a reasonable way to increase the accuracy of the model for forecasting these higher defoliation levels. By the same token, of course, the model is probably less accurate than another transformation—for example $\ln(DEF_{(n+1)})$ —would have been for forecasting situations where little or no defoliation might be expected.

A few relationships were known to exist between defoliation and the independent variables. Others were merely suspected. Non-linear relationships were presumed to be common. Similarly, interactions were suspected between combinations of the independent variables and subsequent defoliation. So a variety of multiple-regression models were tested, having the general form $Y = b_0 + b_1 \times_1 + b_2 \times_2 + \dots + b_n \times_n$; and due provision was made for testing for both non-linearity and interactions.

RESULTS

The equation presented in table 1 represents our best prediction model for defoliation, using the criteria of least squares. Statistical relationships between defoliation and independent variables cannot be visualized just by inspection of the separate terms in the model because both the dependent variable, DEF_(n+1), and current egg-mass density, MNOW, were transformed to $\ln(101-DEF_{(n+1)})$ and $\ln(MNOW)$, before the model was developed. On the other hand, the contribution of each term in the model to expected $\ln(101-DEF_{(n+1)})$ can be examined separately, and the expected value of defoliation itself can be determined by simply transforming the expected value of $\ln(101-DEF_{(n+1)})$ back to DEF_(n+1). This procedure has been followed in developing figures 1 to 5. Since these figures were all derived by using the mean value of each independent variable

Table 1.—Analysis of variance in defoliation in year $(n + 1)$ 1_n ($101 - DEF$ $(n + 1)$) as a function of the specified independent variables ($N = 533$)

Intercept = 4.5315 Variable	Regression coefficient	Standard error of coefficient	t ratio on 524 d.f.
(DOM) • (1nMNOW)	0.00098977	0.00030319	3.3*
(DMO) • (1nMNOW) ²	-.00019212	.00003268	-5.9*
(ZDL) • (ZDH) ²	-.00000219	.00000056	-3.9*
(DCA(n)) • (PM) • (1nMNOW)	.00009470	.00002394	4.0*
(TREND) • (1nMNOW)	-.05556634	.01332184	-4.2*
(TREND) • (1nMNOW) ²	.01473679	.00329108	4.5*
(TREND) • (1nMNOW) ³	-.00097398	.00019814	-4.9*
(TFOL)	.00091184	.00034688	2.6*

*Significant at 0.01 probability level.
R² = 0.41.

that was not otherwise specified, these mean values are shown below:

Variable	Mean value
Low zone density (ZDL)	53 percent
High zone density (ZDH)	14 percent
Prior egg-mass density (MLSTYR)	2,705 egg masses per acre
Current egg-mass density (MNOW)	2,488 egg masses per acre
Dominance of class-A trees (DOM)	86 percent
Index of total foliage (TFOL)	61
Prior defoliation (DCA(n))	22 percent
Precipitation in May of year (n) (PM)	3.17 inches

Zone densities (ZDL and ZDH).—Defoliation in any particular place within a zone could be expected to increase in year $(n+1)$ as the percentage of the acres examined within that zone in the fall of year (n) that contained high egg-mass densities increased. This relationship is examined in figure 1 for zones where at least 40 percent of the acres examined in the fall of year (n) contained more than 500 egg masses per acre, ZDL, and where at least 10 percent of these same acres contained more than 5,000 egg masses per acre, ZDH.

Presumably, the relationships in figure 1 reflect primarily on an abundant supply of newly hatched larvae within the zone, and on the tendency of these larvae to disperse to other locations. In addition, Leonard (1967) has suggested that newly hatched larvae are more likely to disperse when they are crowded than when they are not, and has indicated a mechanism through which this might be determined. These relationships may also reflect a tendency by mobile predators—such as

flocking birds—to concentrate on high-level host populations when they are available, thus allowing lower-density populations to survive in larger numbers than they otherwise might, and consequently to subject the stand to more defoliation.

Egg-mass densities (MLSTYR and MNOW).—The relationship between current egg-mass density, MNOW, and defoliation, $DEF_{(n+1)}$, was straightforward as long as the difference in density between last year's density, MLSTYR, and the current level, MNOW, was not great (fig. 2). Although defoliation clearly increased as current density increased, the figure simply does not support a long-held concept of gypsy moth population management, which is that heavy defoliation can be expected at or above 500 egg masses per acre. Indeed, even when current density was about 5,000 egg masses per acre, the model indicates that only about 38 percent defoliation could be expected if the population had been stable at 5,000 egg masses per acre for 2 years running.

Thus, unless the model is greatly in error for this density range, either most egg-mass surveys for proposed control work greatly underestimate actual current egg-mass density, or the usual decision to exercise population control at 500 egg masses per acre should be re-evaluated.

On the other hand, the model indicates that egg-mass populations as low as 500 current egg masses per acre might result in heavy defoliation of the stand following explosive increases in population densities between

Figure 1.—Relationship between defoliation during year ($n + 1$), and the percentages of acres in the zone in the fall of the year (n) containing more than (a) 500 egg masses per acre (ZDL), and (b) 5,000 egg masses per acre (ZDH). All other independent variables have been held constant at their mean values.

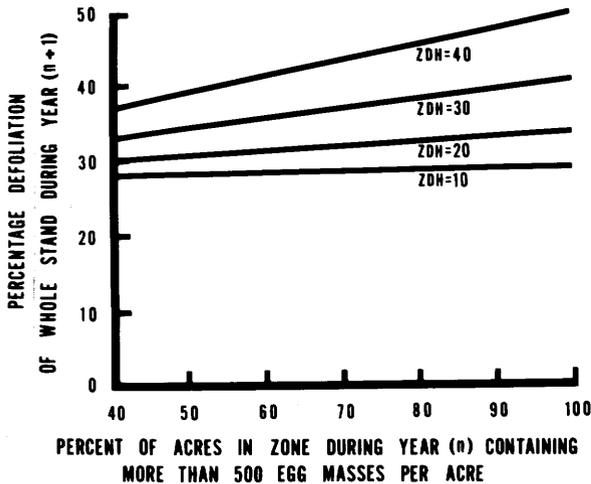


Figure 2.—Relationship between defoliation during year ($n + 1$) and egg-mass densities in the fall of year (n) and ($n - 1$), (MNOW and MLSTYR). Outbreak conditions.

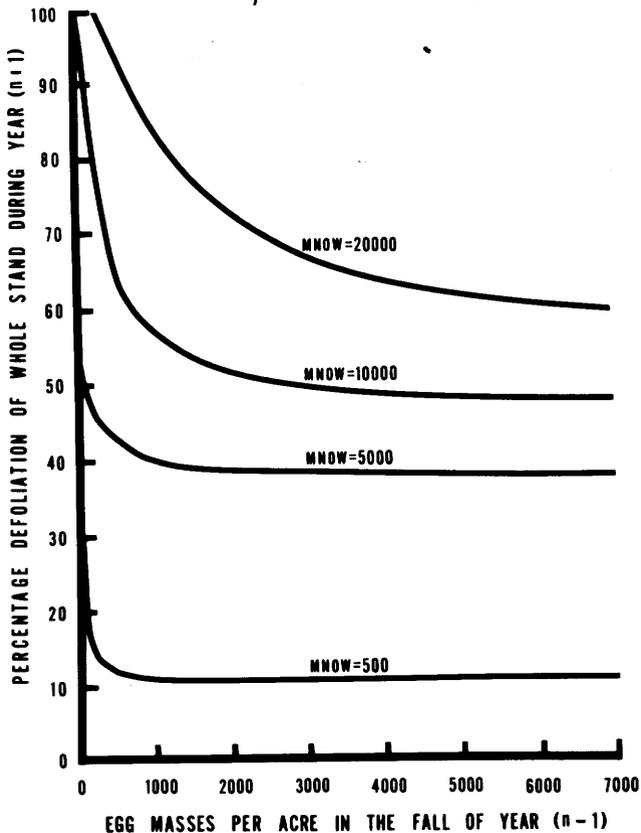


Figure 3.—Relationship between defoliation during year ($n + 1$), egg-mass density in the fall of the year (n), (MNOW), and the percentage of the dominant trees in the stand that were in food class A (FCA). Outbreak conditions.

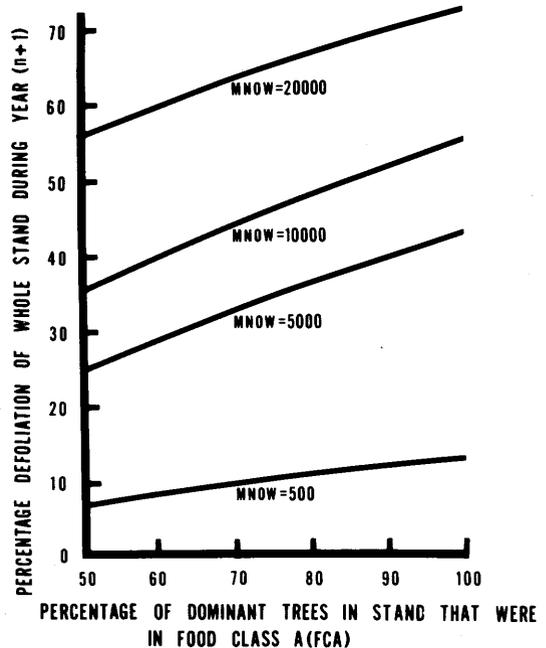


Figure 4.—Relationships between defoliation during year ($n + 1$), egg-mass density in the fall of year (n) (MNOW), and an index of total foliage per acre (TFOL). Outbreak conditions.

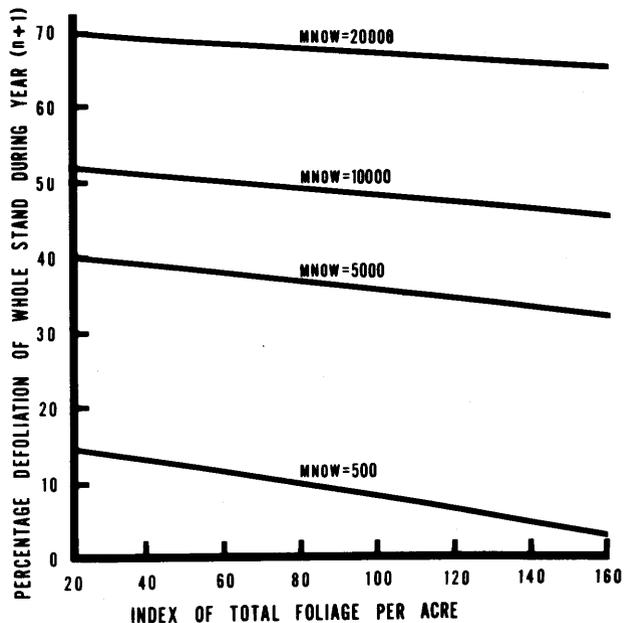
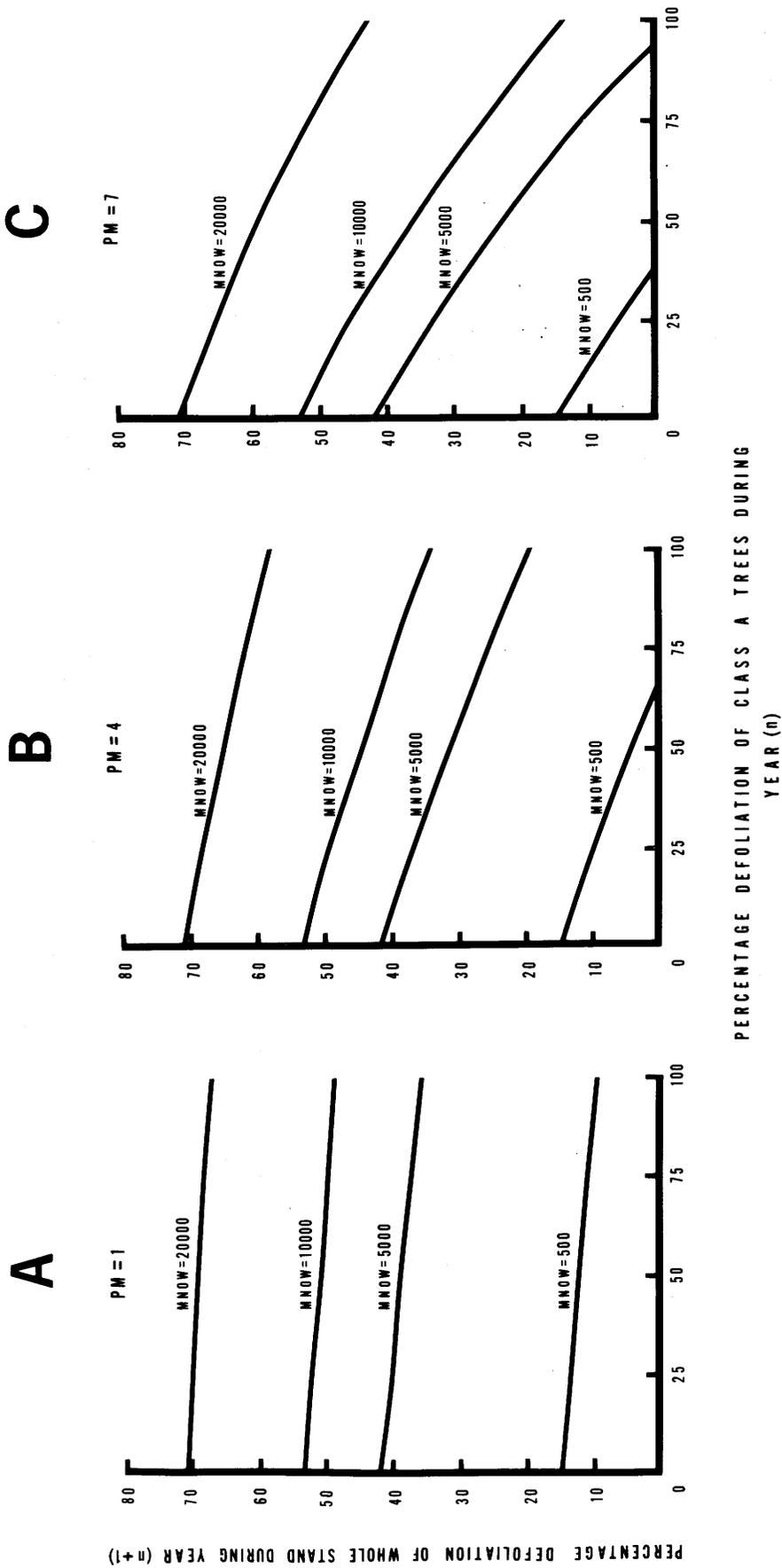


Figure 5.—Relationships between defoliation during year $(n + 1)$, $(DEF_{(n+1)})$, percentage defoliation of food class A trees during year (n) , (DCA_n) , and egg-mass density in the fall of year (n) , $(MNOW)$. A. Relationships between $DEF_{(n+1)}$, DCA_n , and $MNOW$ when precipitation in May of year (n) , (PM) , is held constant at 1 inch. B. Relationships between $DEF_{(n+1)}$, DCA_n , and $MNOW$ when PM is held constant at 4 inches. C. Relationships between $DEF_{(n+1)}$, DCA_n , and $MNOW$ when PM is held constant at 7 inches. Outbreak conditions.



years ($n-1$) and (n). Since many control operations have been aimed at just such populations, it seems reasonable to suppose that current population management philosophy for this insect may have been dominated by this latter fact. In any case, though we have observed the tendency of rapidly increasing populations to cause much heavier defoliation than their relatively stable, but equally dense, counterparts, we cannot propose a specific mechanism to account for it. Perhaps it is determined primarily by a time lag for the establishment and/or build-up of the natural enemies of the insect; or it may reflect primarily on the physiological state of the insect itself. Possibly mechanisms of both sorts are involved.

Dominance of class A trees (DOM).—Relationships between the percentage of the dominant trees in the overstory that were favored as food by gypsy moth larvae, DOM, current egg-mass density, MNOW, and subsequent defoliation, $DEF_{(n+1)}$, are somewhat puzzling at first glance (fig. 3), because the dominance of class A trees was more closely related to defoliation when current density was high than when it was low. This difference may reflect the imposition of a food limitation on the insect as density increased.

Foliage index (TFOL).—Defoliation tended to decrease as the total amount of foliage available to the larvae hatching from a given egg-mass density increased (fig. 4). This is only logical because the proportion of the total foliage consumed per larva was certain to decrease as the total amount of that foliage increased. However, defoliation only decreased by about 3 to 5 percent as the index of total foliage doubled, which may indicate either that dispersal losses among the newly hatched larvae tended to be greater within poorly stocked stands, or that much more foliage was consumed per larva as the total amount of available foliage increased, or both.

Prior defoliation ($DCA_{(n)}$) and precipitation (PM).—Defoliation in year ($n+1$) was reduced as a function of prior defoliation of the class A trees during the preceding summer, $DCA_{(n)}$; and more defoliation could be ex-

pected in year ($n+1$) when precipitation in May of year (n) was low than when it was high (fig. 5). Probably this latter relationship reflects a greater tendency, in part, for a disease epizootic to develop in the insect population issuing in year ($n+1$) as a consequence of the higher humidity conditions present during the larval stage in year (n).

In fact, neither mechanisms that are associated with heavy prior defoliation, such as reduced fecundity, nor those that may be associated with high May precipitation levels in year (n), such as increased disease incidence in year ($n+1$), offer a completely plausible rationale for the results shown in figure 5. Another rationale might suggest that mechanisms similar to those described by several authors (Wellington 1965; Morris 1969) may alter the physiology of the insect in generation ($n+1$) through directly influencing the maternal parent during generation (n). This possibility should be explored.

DISCUSSION

These results, in our opinion, emphasize two immediate needs:

First, the model accounted for only 41 percent of the variation in $\ln(101-DEF_{(n+1)})$, the variable chosen to reflect defoliation in OAK stands. This may imply that we either do not have, or have not used, a truly relevant index of a fundamentally important—but currently unknown—process in determining a defoliation level. Thus, although our primary purpose was to produce a prediction model for defoliation by this insect, our results emphasize the need for specific studies to identify and understand the processes through which particular levels of defoliation by this insect are determined.

Second, agencies charged with the management of this population system should review their criteria for control. Unless the population system is now behaving quite differently from what is indicated by this model, current criteria for control may sometimes lead to the treatment of populations that would have caused little defoliation if they had been left untreated.

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