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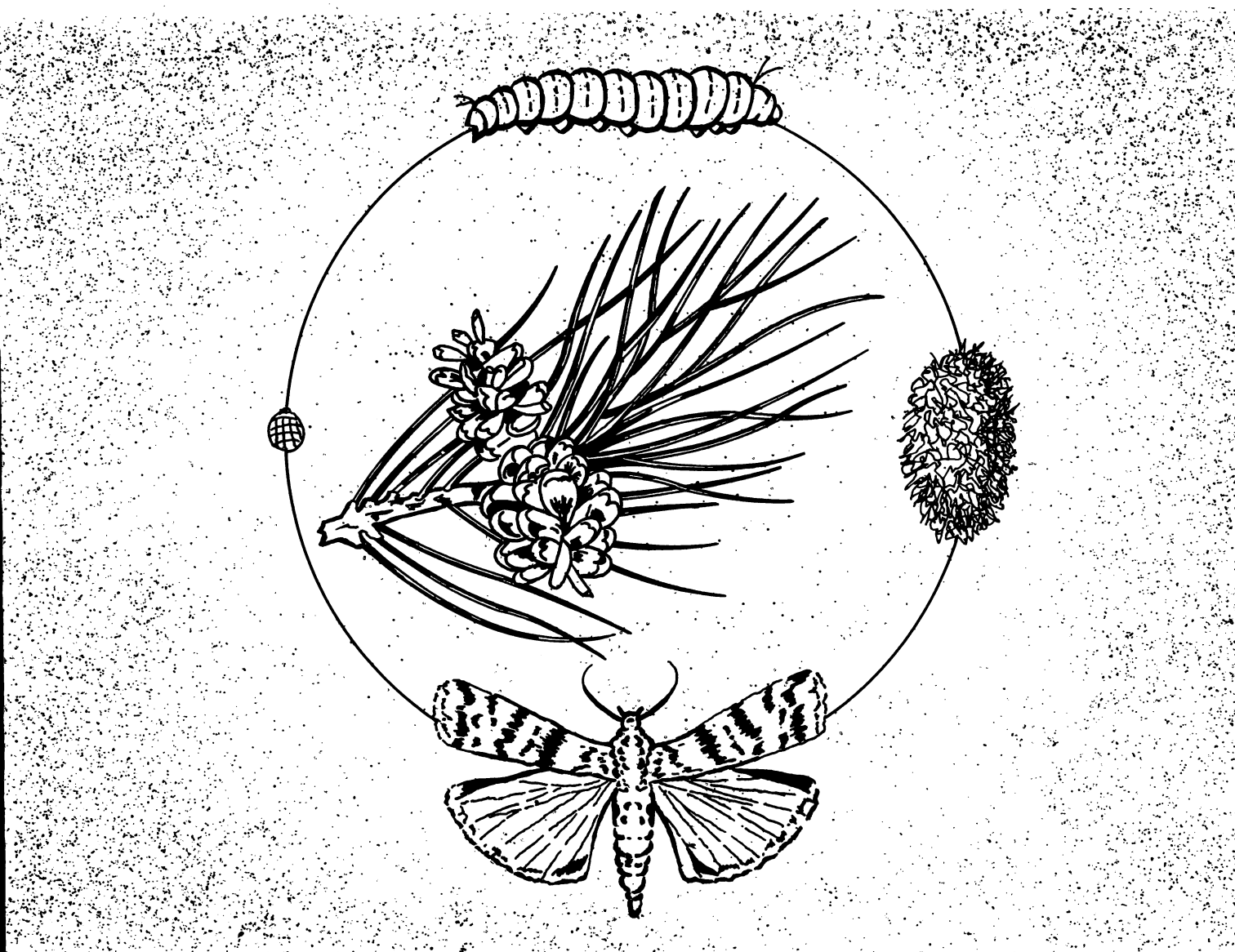
DISTRIBUTION OF THE CONE INSECT, *Dioryctria disclusa*, IN RED PINE TREES

WILLIAM J. MATTSON



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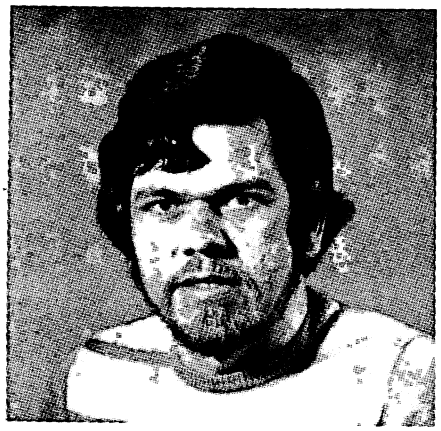

THE AUTHOR

William J. Mattson has been employed at the North Central Station as an insect ecologist since 1967. He received his B.S. in wildlife biology and M.S. in forest entomology from the University of Michigan and his Ph.D. in insect ecology from the University of Minnesota. His research has involved insect impact on cone production and forest productivity, insect population dynamics, insect behavior, and the role of phytophagous insects in forest ecosystems.

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DISTRIBUTION OF THE CONE INSECT, DIORYCTRIA DISCLUSA, IN RED PINE

William J. Mattson

In North and Central America, at least 12 species of *Dioryctria* moths attack the reproductive structures of conifers, especially the diploxylon or "hard" pines (Barcia and Merkel 1972, Mutuura and Munroe 1972, Coulson *et al.* 1972). Many are notorious for their destruction of cones in seed orchards and seed production areas (Mattson 1968, Sartor and Neel 1971, Coulson and Franklin 1970).

The general biology and ecology of cone feeding *Dioryctria* species are fairly well established (Barcia and Merkel 1972). However, detailed information is lacking about their host selection processes and spatial distributions. The distributions of insects both within and among trees are assumed to follow the distributions of their foods, which in addition to cones, may include buds, shoots, cankers, and male strobili.

In red pine, *Pinus resinosa* Ait., early-stage larvae of *D. disclusa* Heinrich feed in male strobili for about two weeks, i.e. until the strobili have begun to desiccate severely after dissemination of pollen (Lyons 1957a) after which, the larvae search for year-old cones. Each late-stage larva needs at least 2 cones to complete development in species (which have small cones) such as red, jack, *P. banksiana* Lamb., and Scots, *P. sylvestris* L., pines. Rarely do larvae share cones except when feeding is virtually completed and they have begun to pupate.

If *D. disclusa* larvae follow their food, a question arises about which food is followed because male and female strobili have different spatial distributions. For example, male strobili occur predominantly in the lower one-half; female strobili in the upper one-half crown (Matthews 1963, Hard 1964). Trees also vary greatly in their capacities to produce each type of strobili. Nonvigorous or shaded trees can often produce an abundance of male but not many female strobili (Matthews 1963, 1969). Whereas, open-grown trees can usually produce large crops of both kinds of strobili (Matthews 1969, Puritch 1972). Furthermore, there is a temporal distribution problem in trees that are capable of producing both kinds of strobili: How often is the abundance of male strobili correlated with the abundance of year-old female strobili? This is not known.

The cues females respond to when selecting trees for oviposition are unknown. One would expect them to select trees with an abundance of future food because competition for food among red pine cone insects can be severe (Lyons 1957b, Mattson 1968, 1971). Asher (1970) provided evidence that *Dioryctria* moths may be able to detect trees bearing potentially large cone crops when he discovered that electroantennograms of *D. abietella* (D.&S.) are highly responsive to certain volatile extractants from conelets of slash pine, *P. elliotii* Engelmann.

At the time of oviposition (late July for *D. disclusa* in the northern Great Lakes region), there are both cones and conelets on the trees but only few desiccated male strobili. Therefore, if females orient to food per se when seeking oviposition sites, it must be to either cones, conelets, or both.

The objectives of this study were threefold: (1) to compare the distribution of larvae with that of their food both within and among trees, and (2) to determine the significant sources of variation in insect densities in order to facilitate future insect sampling, and (3) to relate cone damage among trees to food and insect abundance.

METHODS

In 1967, I studied the within-tree distributions of early and late larvae and male and year-old female strobili at the Birch Hill seed production area (SPA) (64 years, 65 ft., 63 stems/acre) in Itasca Co., Minn. During 1968-1970 I studied the between-tree distributions of these same variables (excluding small larvae) at the Birch Hill and Portage Lake SPA (57 yrs, 63 ft., 113 stems/acre) about 8 miles away. In 1973 and 1974 I measured only cone damage and cone abundance/tree at the Birch Hill SPA.

Each year, I systematically selected 10 sample trees on a transect through the center of the SPAs. I divided the crown of each tree on the basis of crown thirds (upper, middle, lower) and directional quadrants (N, E, S, W) into 12 cells. Within each cell I selected a branch at random for counting larvae and strobili. I sampled early larvae and male strobili during the first week of June, and late larvae and female strobili (cones) in mid July. To estimate the total number of larvae and strobili/tree, I multiplied the mean number of items/branch in each level by the total number of branches in that level and then summed levels.

To detect differences in the densities of larvae and strobili among crown levels and directions, I performed analyses of variances on the 1967 data. All data were transformed to their log counterparts to stabilize variances. Next I pooled the raw data and segregated it by crown levels to compare the observed frequency distributions of insect counts/branch with the calculated negative binomial distribution of same. To relate the distribution of insects among trees to food abundance, I used scatter diagrams and various regression analyses where insects were the dependent variable and food was the independent variable. Similar methods were used to relate the distribution of cone damage among trees to food and insect abundance.

RESULTS

Within Tree Distributions: Early and Late Larvae, Male Strobili and Cones

Differences in the densities of both early larvae and male strobili per branch were significant ($p \leq 0.01$) among upper and middle and upper and lower crown levels ($Upper_a < Middle_b = Lower_b$)[1] (table 1). In contrast, differences in the densities of late larvae were significant among lower and middle and lower and upper crown levels ($Upper_a \leq Middle_a > Lower_b$). Cone densities were different only between lower and middle levels, and had the same density pattern among levels as late larvae.

[1] *Variables with the same subletter are not significantly different. ($p \leq 0.05$).*

Table 1.--*Mean number of* D. disclusa *larvae and reproductive structures per branch by direction in different crown levels at the Birch Hill Seed Production Area in 1967, n= 10 trees*

Items per branch	Upper					Middle					Lower				
	N	E	S	W	$\bar{X}$	N	E	S	W	$\bar{X}$	N	E	S	W	$\bar{X}$
Male strobili (MS)	4.5	1.6	3.9	1.5	2.9	29.9	30.3	30.5	36.5	31.8	44.4	26.5	35.9	35.6	36.5
Early-stage larvae (L_1)	0.8	0.5	0.9	0.7	0.7	4.8	4.1	6.4	6.4	5.4	3.0	2.4	4.3	2.8	3.1
Second-year cones (C)	7.0	6.5	9.1	6.0	7.1	11.2	8.3	15.6	4.6	10.5	4.8	3.4	6.9	3.0	4.5
Late-stage larvae and pupae (L_2)	1.1	1.3	1.4	0.9	1.2	2.8	0.6	3.1	1.5	2.0	0.5	0.4	0.5	0.5	0.5
Cones attacked by *D. disclusa* (Y)	3.5	4.3	4.7	2.3	3.7	6.4	4.3	8.1	3.3	5.5	2.1	1.8	2.7	1.9	2.1

Among directional quadrants, there were no significant differences in densities except for cones (Sa $\geq$ Nab $\geq$ Ebc $\geq$ Wc).

Frequency distributions of insect counts/branch conformed to the negative binomial (NB) distribution in all but one instance (large larvae in midcrown) (table 2). The exponent of k value of the NB was smallest for early larvae in the upper level and for late larvae in the lower level. This indicates that the larvae were aggregated most in these levels (Waters 1959).

Table 2.--*Statistics relating branch samples of* D. disclusa *in different crown levels to the negative binomial (N.B.) distribution. Chi-square values along with probability (p) of a larger value indicate the degree of correspondence between the observed frequency distribution of larvae/branch and the calculated N.B. distribution of same*

Sample statistics	Lower crown	Middle crown	Upper crown
SMALL LARVAE			
Variance	7.6	40.1	1.7
Mean[1]=	3.1	5.4	0.7
k values[2]	2.18	0.60	0.28
Chi-square	7.2 (p<.30)	8.0 (p<.50)	5.7 (p<.30)
LARGE LARVAE			
Variance	1.0	6.6	2.5
Mean[1]	0.5	2.0	1.2
k values	0.26	0.45	0.72
Chi-square	5.5 (p<.20)	19.5 (p<.03)	6.6 (p<.30)

[1]n=40 and n=56 for each crown level sample of small larvae and large larvae respectively.

[2]k values are the exponents of the negative binomial model and were calculated using method 1 or 2 of Anscombe (1949) whichever was appropriate.

Among Tree Distributions: Early and Late Larvae

Among trees, early larvae showed no relationship with cones (C) but did show a significant ($p \leq 0.05$) linear, positive correlation ($r = 0.62$) with male strobili (MS).

Late larvae (L2) were only weakly related to C (figure 1). In 1967, for example, L2 reached a peak at medium cone densities. In all other years, however, at both Birch Hill and Portage Lake there was no apparent relation between L2 and C. L2 was related to MS in only 2 of 5 sample years as shown in the following regressions:

1967 $\log(L2) = a + b(CxMS) + c(MS) + d(C)$---$R^2=0.74$

1968 $L2 = a + b(CxMS) + c(MS)$---$R^2=0.81$

The importance of a variable is indicated by its order in the equation (i.e. CxMS > MS > C). C and MS were not correlated in 4 of 5 years.

Cone Damage in Relation to Food Abundance/Tree

Numbers of cones attacked/tree (Y) exhibited a significant ($p \leq 0.05$) positive, linear correlation with cone abundance (C) in 6 of 9 years (figure 2). In 3 years (1969, 1973, 1974) at Birch Hill, the correlations were clearly positive but only approached significance. The highest correlations occurred (in 1970 at Portage Lake and Birch Hill) when population intensities (numbers relative to food) were highest and second highest respectively. The weakest (nonsignificant) correlations occurred in those years when population intensities were low (1969, 1973, 1974).

Merkel *et al.* (1965) as well as Coulson and Franklin (1968, 1970) also reported positive, linear correlations between Y and C for various species of *Dioryctria* in slash and short leaf pines. Stiell's (1971) data likewise showed a positive, linear correlation between Y and C for *D. disclusa* in red pine plantations.

Consequently, the evidence indicates that Y often shows a positive linear relationship to C: $Y = \pm a + b(C)$. Therefore, percentage cone damage/tree (Y/C) will either increase or decrease to an asymptote (b) depending on the sign of the intercept (a). Theoretically, the sign of a should be negative because Y becomes zero before C does. Therefore, percentage damage should increase slightly with increasing C and eventually approach an asymptote, as Stiell's (1971) data showed for red pine. On the other hand this conflicts with a report by Merkel *et al.* (1965) which showed that percentage damage declined with C. However, the correlations between percentage damage and C in Merkel *et al.* (1965) were significant in only 1 of 3 years. Percentage damage and C, in this study, showed slight negative correlations in 7 of 9 years and slight positive correlations in the other 2 years.

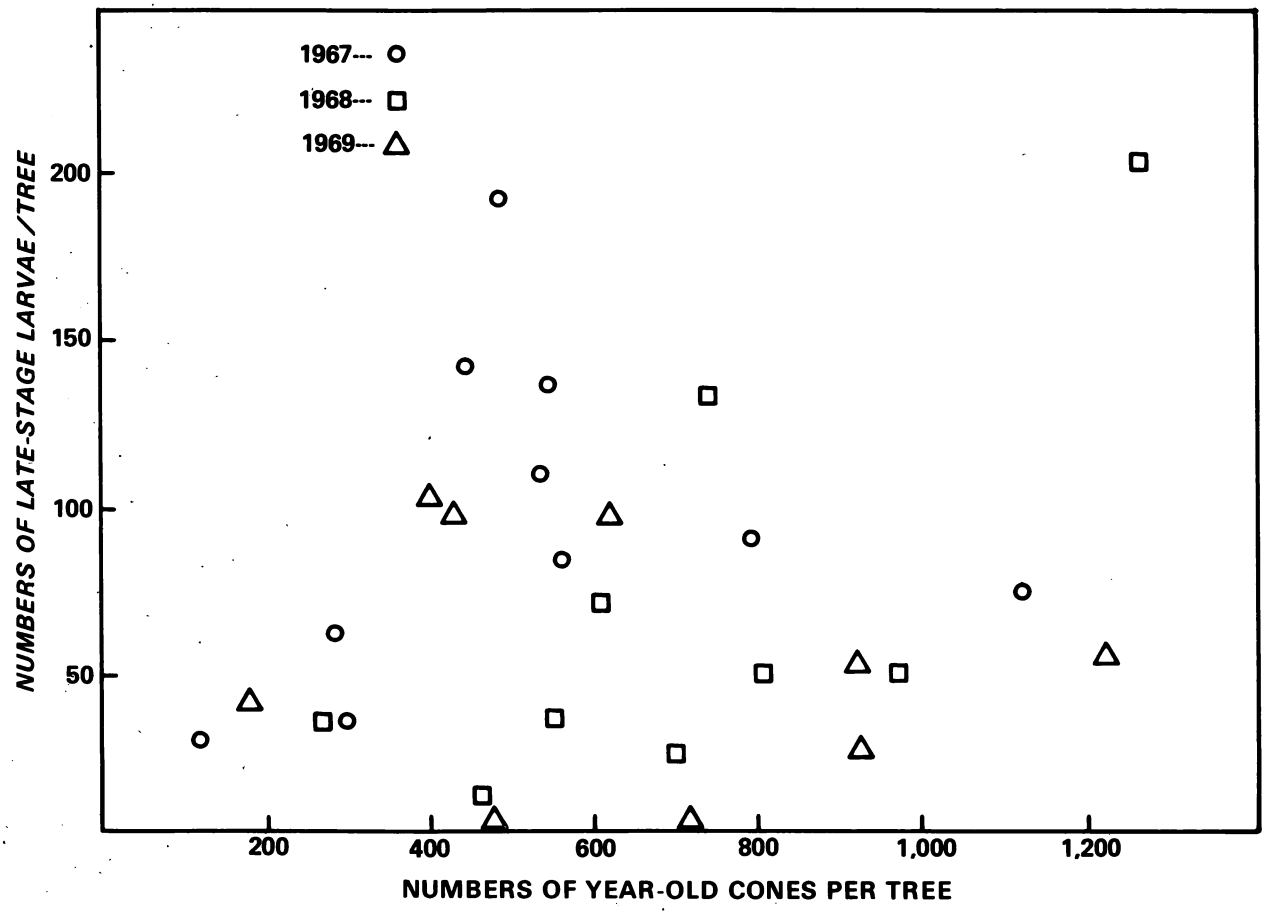

Figure 1.--*Numbers of late-stage* Dioryctria disclusa *larvae per tree in relation to numbers of cones per trees in three different years at the Birch Hill seed production area.*

However, none were statistically significant. This agrees with the data of Coulson and Franklin (1970). Consequently, the bulk of evidence suggests that percentage damage varies only slightly with C once cone crops exceed the very nominal levels.

Because MS was important in explaining the distribution of early and late larvae among trees in some years, I incorporated it along with C in a regression on Y. The best equation took the form: $Y = a + b(C) + c \log(MS)$. However, log(MS) made a significant contribution to the regression in only 2 of 5 years data (1967, 1969 at Birch Hill). This suggests that Y varies from tree to tree in a linear relationship to C and a logarithmic relationship to MS. MS is probably most important when it is small (<1000/tree).

Cone Damage in Relationship to Cone and Early Larval Abundance/Tree

Based upon Holling (1966), Y's increase relative to C's could be either (1) linear up to a plateau or (2) negatively accelerated up to a plateau, if numbers of larvae/tree were constant. Y, however, is not only a function of C but also of L (the number of early larvae/tree). In turn, L appears to be related to MS.

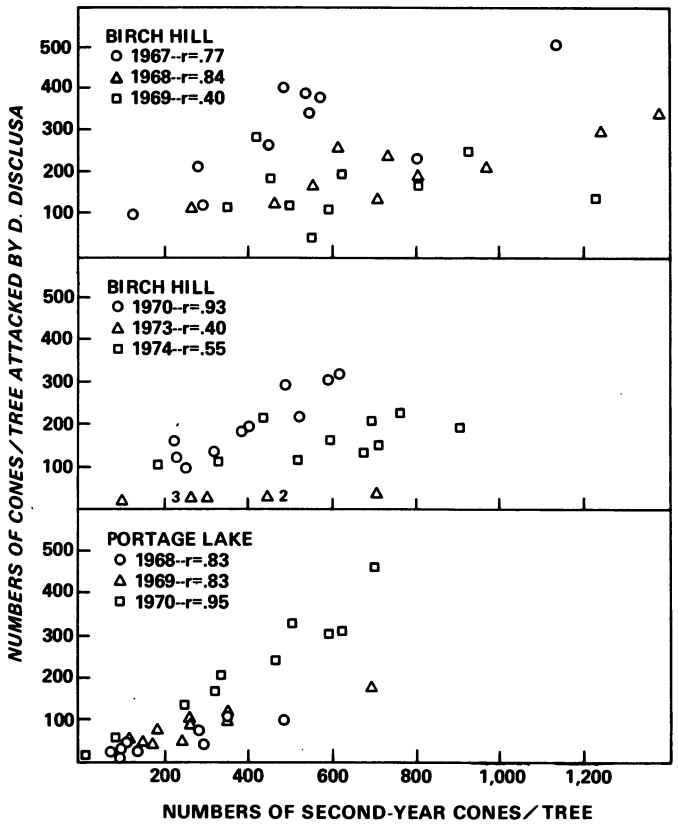

Figure 2.--*Numbers of cones per tree attacked by* Dioryctria disclusa *in relationship to total cones available per tree in different years at the Birch Hill and Portage Lake seed production areas.*

Watt (1959) formulated a general, mathematical model to characterize the relationship between the number of prey attacked and the densities of both prey and predators. His model can be applied to cones and cone insects as follows:

$$Y = kL\ (1-\exp(-aCL^{1-b}))$$

Where Y is the number of attacked cones; C, total cones; and L, total early larvae/tree. k is the maximum number of cones that each larva can attack, and a and b are parameters for the specific case. The model says that Y increases along with C and/or L and eventually plateaus. Increases in C alone cause Y to approach the maximum (the asymptote) defined by kL. Increases in L alone, raise the maximum potential damage (i.e. the asymptote defined by kL) and allows Y to approach the limit determined by C. The parameter, b, has a depressing effect on Y as it increases, and theoretically reflects the interference or competition that results as L increases. For example, as L increases, the probability of each larva attacking k cones decreases. Watt's model can probably account for some of the observed variation in the simple relationship between Y and C (figure 2). When L is large relative to C (i.e. population intensity is high), for example, Y appears to be a linear function of C because most cones are attacked. When L is small relative to C, Y becomes a function of kL; thus Y shows little relationship to C.

My attempts to fit the 1967 Birch Hill data to Watt's model were not successful, so I modified the model by replacing L^{1-b} with exp(-mL):

$$Y = kL(1-\exp(-aC\ \exp(-mL)))$$

In general, the consequence of such a change will be a more severe depression of the predation potential per predator for any given predator density. It implies greater interference among predators. This model accounted for 84 percent of the variation in Y. Parameters were as follows:

k=4, a=0.00138, m=0.00232. The fact that the modified model fit the data (even though it was only for a single year) suggests that it or the Watt model may be generally applicable to cone predation by insects. This, of course, remains to be tested.

DISCUSSION

Survival of *D. disclusa* appears to be particularly sensitive to the proper spatial and temporal distribution of food. They depend on a fortuitous combination of events: adequate crops of male strobili and year-old cones both in the same tree at the same time. The abundance of male strobili and cones are seldom correlated, however. Thus it is probably common for one food or the other to be a limiting factor. I speculate that highest insect survival and population densities will occur in open grown forests and at forest edges where (1) a greater proportion of trees are capable of producing both types of strobili, and (2) the annual production of strobili/tree is greater and more consistent. Within trees, I speculate the highest insect survival and densities will occur in the midcrown regions where (1) a greater proportion of individual branches will bear both kinds of strobili, and (2) the annual production of strobili is greater and more consistent.

This study revealed that *D. disclusa* and its foods can be sampled simultaneously using the same sources of stratification (levels, directions and trees). Crown levels proved to be an important source of variation for all variables. Directional quadrants were an important source of variation for cones and probably late larvae, but not for male strobili or early larvae.

Insect counts per branch and per tree were overdispersed, not random distributions as evidenced by the fact that the variance of counts tended to increase with insect density. For example, for large larvae per tree, the standard deviation (SD) of counts = 12.1 + .46(mean number larvae/tree) where r^2=.86. To estimate the number of sample trees (n) needed to achieve a desired level of sampling precision ((S.E./mean)=k) in estimating the mean number of late-larvae/tree, the following formula can be used:

$$n = \frac{[12.1 + .46(\text{mean})]^2}{k^2\ \text{mean}^2}$$

When densities are low (about 20/tree), to achieve a population estimate with a standard error (S.E.) roughly 15 percent of the mean (k=.15), one would need to sample about 50 trees. To achieve the same precision when densities average about 100/tree, one would need to sample about 15 trees.

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OXFORD: 416.2:453.--145.718. KEY WORDS: negative binomial, sampling, cone damage, male strobili, model.

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