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RELATIONSHIPS BETWEEN OVERSTORY COMPOSITION AND GYPSY MOTH EGG-MASS DENSITY

Abstract.—Most of the silvicultural recommendations for reducing the hazard of gypsy moth outbreaks have been based in part on the premise that gypsy moth density levels are related closely to the proportion of favored food trees in the overstory. This premise did not prove to be true for a series of plots observed in eastern New England between 1911 and 1931.

Most of the silvicultural recommendations for reducing the hazard of gypsy moth outbreaks have been based on the premise that both gypsy moth density and defoliation level are determined by the proportion of favored food trees in the stand *(Baker and Cline 1936; Behre et al 1936; Behre 1939; and Behre and Reineke 1943)*.

Later Bess et al *(1947)* based their recommendations on the premise that a number of other ecological factors are related closely to gypsy moth abundance. They disputed the favored-food theory, arguing that "the history of this insect in the oak forests of Connecticut and western Massachusetts shows that food supply does not normally limit the abundance of the moth in these areas."

The objective of my recent study was to evaluate the relationship between overstory composition and subsequent gypsy moth population density.

Procedures

The data used were collected between 1911 and 1931 from an area in eastern New England by personnel of the Gypsy Moth Laboratory at Melrose Highlands, Massachusetts.

First the plots were stratified to represent two kinds of forest stands: (1) *favored food* stands, in which at least one-half of the overstory was made up of white oak, red oak, scarlet oak, and black oak; and (2) *poor food* stands, in which less than one-half of the overstory was made up of oaks, gray birch, paper birch, river birch, quaking aspen, large-toothed aspen, willow, apple, and larch.

Second, the data were stratified according to zone density (ZD) *(Campbell 1973a)*.

These included ZD $\leq$ 40, where not more than 40 percent of the acres examined within a given zone contained more than 500 egg masses per acre at the start of year (n); and ZD $>$ 40, where more than 40 percent of the acres contained more than 500 egg masses per acre.

Finally the data were stratified according to M(n − 1), density within each specific plot at the start of year n − 1; M(n), density within each plot at the start of year n; and M(n + 1), density within each plot at the start of year n + 1. Density was stratified five ways for each of these successive years as follows:

1. Not more than 50 egg masses per acre.
2. Between 51 and 500 egg masses per acre.
3. Between 501 and 2,500 egg masses per acre.
4. Between 2,501 and 5,000 egg masses per acre.
5. More than 5,000 egg masses per acre.

Results

Observed frequencies of gypsy moth egg-mass densities in each of five categories in year n + 1, from specified density categories in years n − 1 and n, are shown for both favored food stands and poor food stands when zone densities were low (ZD $\leq$ 40) (tables 1 and 2) and for both these food categories when zone densities were high (ZD $>$ 40) (tables 3 and 4).

Comparison of frequencies observed in tables 1 and 2 with those in tables 3 and 4 showed that low densities could be expected to be maintained when zone densities were

Table 1.—Observed frequency of gypsy moth egg-mass densities in each of five categories in year (n + 1), from specified density categories in years (n — 1) and (n)

[Stratified on FAVORED FOOD stands when zone density was low (ZD $\leq$ 40).]

Year (n − 1)[1]	Year (n)[1]	Year (n + 1)[1] I	II	III	IV	V	Total observations
I	I	0.841	0.159	0.0	0.0	0.0	69
	II	.294	.588	.118	.0	.0	17
	III	—	—	—	—	—	0
	IV	—	—	—	—	—	0
	V	—	—	—	—	—	0
II	I	.889	.111	.0	.0	.0	27
	II	.429	.476	.095	.0	.0	42
	III	.100	.500	.300	.100	.0	10
	IV	—	—	—	—	—	0
	V	—	—	—	—	—	0
III	I	.600	.400	.0	.0	.0	5
	II	.500	.500	.0	.0	.0	16
	III	.500	.250	.0	.250	.0	4
	IV	.0	.0	1.0	.0	.0	1
	V	—	—	—	—	—	0
IV	I	—	—	—	—	—	0
	II	—	—	—	—	—	0
	III	.0	1.0	.0	.0	.0	1
	IV	—	—	—	—	—	0
	V	—	—	—	—	—	0
V	I	—	—	—	—	—	0
	II	1.0	.0	.0	.0	.0	2
	III	.0	1.0	.0	.0	.0	1
	IV	—	—	—	—	—	0
	V	—	—	—	—	—	0

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II = Between 51 and 500 egg masses per acre.
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V = More than 5,000 egg masses per acre.

Table 2.—*Observed frequency of gypsy moth egg-mass densities in each of five categories in year (n + 1), from specified density categories in years (n — 1) and (n)*

[Stratified on POOR FOOD stands when zone density was low (ZD ≤ 40).]

Year (n − 1)[1]	Year (n)[1]	Year (n + 1)[1] I	II	III	IV	V	Total observations
I	I	0.816	0.184	0.0	0.0	0.0	152
	II	.273	.576	.061	.090	.0	33
	III	—	—	—	—	—	0
	IV	—	—	—	—	—	0
	V	—	—	—	—	—	0
II	I	.893	.107	.0	.0	.0	58
	II	.452	.512	.036	.0	.0	84
	III	.167	.666	.167	.0	.0	6
	IV	.250	.750	.0	.0	.0	4
	V	—	—	—	—	—	0
III	I	.667	.333	.0	.0	.0	3
	II	.556	.444	.0	.0	.0	18
	III	.0	1.0	.0	.0	.0	6
	IV	—	—	—	—	—	0
	V	—	—	—	—	—	0
IV	I	.500	.500	.0	.0	.0	2
	II	.714	.286	.0	.0	.0	7
	III	—	—	—	—	—	0
	IV	—	—	—	—	—	0
	V	—	—	—	—	—	0
V	I	—	—	—	—	—	0
	II	—	—	—	—	—	0
	III	.0	1.0	.0	.0	.0	1
	IV	1.0	.0	.0	.0	.0	1
	V	—	—	—	—	—	0

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low, and high densities tended to be maintained when zone densities were high *(Campbell 1973a and 1973b)*. The question is whether and to what extent egg-mass density was related to food quality within each zone density stratum. The following scheme was adopted to answer this question.

This system was, and is, in a constant state of flux. Population densities ebb and flow from year to year in response to factors that are reflected only in part by the specific independent variables used. Thus the frequency matrices (tables 1 to 4) can be viewed as reflections of four transient states.

But suppose the system were to follow the observed frequency distributions year after year, as shown in tables 1 to 4. In each case it would then rapidly reach a stable state, in which the number of populations leaving any category from year n to year n + 1 would be identically equal to the number of populations entering that category.

Assume that 1,000 populations meet the following criteria:

1. All populations are in favored food stands.
2. Zone density is low (ZD ≤ 40).
3. Densities in all populations have been less than 50 egg masses per acre in both years n − 1 and n.
4. Each of these 1,000 populations follows the frequency distributions in table 1.

Clearly, 841 of these populations will maintain fewer than 50 egg masses per acre in year n + 1, while 159 will reach densities between 51 and 500 egg masses per acre (table 1). By the end of the following year, 84.1 percent of the 841 former populations, plus 29.4 percent of the 159 latter populations, will have fewer than 50 egg masses per acre; 15.9 percent of the 841 former populations, plus 58.8 percent

Table 3.—*Observed frequency of gypsy moth egg-mass densities in each of five categories in year (n + 1), from specified density categories in years (n — 1) and (n)*

[Stratified on FAVORED FOOD stands when zone density was high (ZD > 40).]

Year (n – 1)[1]	Year (n)[1]	Year (n + 1)[1] I	II	III	IV	V	Total observations
I	I	0.500	0.500	0.0	0.0	0.0	2
	II	.0	.500	.286	.214	.0	14
	III	.200	.200	.400	.0	.200	5
	IV	—	—	—	—	—	0
	V	—	—	—	—	—	0
II	I	.333	.667	.0	.0	.0	3
	II	.278	.500	.194	.0	.028	36
	III	.114	.341	.250	.136	.159	44
	IV	.0	.0	.0	.500	.500	4
	V	.0	.0	.0	1.0	.0	2
III	I	.0	1.0	.0	.0	.0	1
	II	.080	.520	.240	.080	.080	25
	III	.019	.192	.442	.250	.047	52
	IV	.0	.0	.375	.125	.500	16
	V	.053	.158	.263	.368	.158	19
IV	I	1.0	.0	.0	.0	.0	1
	II	.100	.200	.400	.100	.200	10
	III	.0	.118	.412	.235	.235	17
	IV	.0	.125	.500	.125	.250	8
	V	.0	.080	.240	.320	.360	25
V	I	.0	.333	.667	.0	.0	3
	II	.0	.333	.500	.167	.0	6
	III	.038	.231	.346	.231	.154	26
	IV	.0	.174	.217	.217	.392	23
	V	.0	.167	.167	.389	.277	18

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V = More than 5,000 egg masses per acre.

Table 4.—Observed frequency of gypsy moth egg-mass densities in each of five categories in year (n + 1), from specified density categories in years (n — 1) and (n)

[Stratified on POOR FOOD stands when zone density was high (ZD > 40).]

Year (n − 1)[1]	Year (n)[1]	Year (n + 1)[1] I	II	III	IV	V	Total observations
I	I	0.750	0.167	0.083	0.0	0.0	12
	II	.063	.374	.500	.063	.0	16
	III	.0	.667	.333	.0	.0	3
	IV	—	—	—	—	—	0
	V	—	—	—	—	—	0
II	I	.750	.250	.0	.0	.0	4
	II	.081	.595	.257	.054	.013	74
	III	.018	.218	.545	.127	.092	55
	IV	.0	.375	.375	.125	.125	8
	V	.0	.333	.334	.333	.0	3
III	I	1.0	.0	.0	.0	.0	1
	II	.054	.571	.321	.054	.0	56
	III	.013	.227	.455	.143	.162	154
	IV	.0	.220	.488	.146	.146	41
	V	.061	.121	.394	.242	.182	33
IV	I	—	—	—	—	—	0
	II	.111	.500	.333	.0	.056	18
	III	.027	.103	.718	.076	.076	39
	IV	.0	.250	.350	.150	.250	20
	V	.0	.038	.385	.308	.269	26
V	I	.0	1.0	.0	.0	.0	1
	II	.0	.400	.400	.200	.0	5
	III	.0	.212	.545	.152	.091	33
	IV	.0	.129	.323	.258	.290	31
	V	.0	.0	.179	.393	.428	28

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Table 5.—Percentage of hypothetical cohort of gypsy moth populations in each of five density categories after specified number of generations

[All members of this cohort, which obeys frequency distributions in table 1, contained not more than 50 egg masses per acre in years (n − 1) and (n).]

Year	Percent in each density category[1] I	II	III	IV	V
n + 1	84.1	15.9	0.0	0.0	0
n + 2	75.4	22.7	1.9	.0	0
n + 3	71.8	25.0	3.0	.2	0
n + 4	70.4	25.7	3.5	.4	0
n + 5	69.8	26.1	3.7	.4	0
n + 6	69.5	26.3	3.8	.4	0
n + 7	69.3	26.4	3.8	.5	0

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V = More than 5,000 egg masses per acre.

Table 6.—*Percentage of four hypothetical cohorts of gypsy moth populations in each of five density categories at stable state*
[All members of each cohort follow frequency distributions of table 1, 2, 3, or 4 respectively.]

Zone density	Food quality	Percent in each density category[1]				
		I	II	III	IV	V
ZD > 40	Favored	69.3	26.4	3.8	0.5	0.0
	Poor	68.4	29.1	1.5	1.0	.0
ZD ≤ 40	Favored	8.9	29.2	26.3	18.3	17.3
	Poor	11.9	30.7	36.6	11.2	9.6

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of the 159 latter populations, will have between 51 and 500 egg masses per acre; and 11.8 percent of the 159 latter populations will have between 501 and 2,500 egg masses per acre. This process was summarized through eight successive generations (table 5).

The 1,000 hypothetical populations described above assumed a virtually stable-state condition after four generations, and this same state is approached with equal rapidity regardless of the original state of the system as long as it obeys the rules as shown in table 1.

Stable-state population density distributions (tables 1 to 4) are shown for each stratum in table 6. This is the basis for most of the following discussion of relationships between overstory composition and gypsy moth egg-mass density.

Discussion

There was virtually no difference between the stable-state distribution of gypsy moth egg-mass densities in favored food stands and in poor food stands when zone densities were low, and there was surprisingly little difference when they were high. About 17 percent of the favored food stands could be expected to support more than 5,000 egg masses per acre when zone density was high, as compared with only about 10 percent of the poor food stands. An almost identical proportion of the stands in each cover type could be expected to support fewer than 500 egg masses per acre at high zone densities.

These results indicate that the favored food theory had little merit at the time it was propounded, at least with respect to relationships between overstory composition and subsequent gypsy moth population density. A similar study is also being conducted in relationships between overstory composition and subsequent defoliation by this insect, using these same data.

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