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SPATIAL DISTRIBUTION OF EGG CLUSTERS OF THE EUROPEAN PINE SAWFLY *NEODIPRION SERTIFER* (GEOFF.), IN YOUNG PINE PLANTATIONS IN MICHIGAN

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The European pine sawfly, *Neodiprion sertifer* (Geoffroy), is a perennial problem in young pine plantations in Eastern North America. Scotch pine, *Pinus sylvestris* L., and red pine, *P. resinosa* Ait., are its principal hosts. During recent behavioral studies of this sawfly in Michigan, spatial distribution patterns were determined in order to rapidly survey population levels in young pine plantations (Wilson and Gerrard, 1971). Earlier, Lyons (1964b) presented some distributional data on *N. sertifer* in regard to population sampling. Wright *et al.* (1967) and Hattemer *et al.* (1969) discussed *N. sertifer* distributions in Scotch pine and mixed pine species provenance plantings.

Presented here are the spatial distribution patterns for *N. sertifer* egg clusters in several Scotch pine and red pine plantations in Michigan and some implications for survey procedures. Because *N. sertifer* is still a pest of young plantings in Michigan, the whole tree provides a useful survey unit of population. As trees age and increase in size and sawfly populations change, part of the tree or a portion of the planting may be more useful in future surveys.

METHODS AND MATERIALS

Five Scotch pine and two red pine plantations of sapling size, encompassing a wide range of infestation levels over the geographic range of the insect in Michigan, were chosen for study (Table 1). The plantations, designated A to G, were located in Ingham, Ottawa, Lapeer, and Livingston Counties. The number of trees per plot varied from 296 to 1,325; plots C and F were the entire plantations. Plantations D and G were less than 200 feet apart. The trees were originally planted 5-6 ft apart, but tree mortality from

Table 1. Data from European pine sawfly infested plantations in Michigan.

Plantations (plot)	Year at census (spring)	No. of trees in plot	Percent of original stocking	No. whorls of branches	Mean no. egg clusters per tree
A	1962	1,325	98	3	0.93
A	1963	1,325	98	4	8.14
A	1964	569	98	5	19.53
B	1962	581	50	6	1.57
B	1963	581	50	7	2.90
C	1962	300[a]	57	3	1.76
C	1963	296[a]	56	4	2.42
D	1962	352	59	4	14.36
D	1963	352	59	5	2.45
E	1962	314	71	4	0.85
E	1963	314	71	5	0.14
F	1962	352[a]	29	3	0.23
F	1963	352[a]	29	4	0.38
G	1962	348	55	4	13.89

[a]Entire plantation censused.

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various causes reduced the stocking levels to 29-98 per cent of the original and thus provided both sparse and dense conditions.

Sawfly egg clusters, or freshly eclosed sawfly colonies, were counted on every tree in each plot in the spring. Egg clusters were counted by tree and by whorls each year for three years in plantation A.

THE DATA

Populations varied from 0.14 to 19.53 egg clusters per tree during the study (Table 1). The layout for trees in Plantation A and typical infestation patterns for three different years at increasing population levels are illustrated in Figure 1. Black discs in Figure 1 indicate infested trees; 11 per cent were infested in 1961, 48 per cent in 1962, and 95 per cent in 1963. Frequency distributions of egg cluster populations in Plantation A at 0.93, 8.14, and 19.53 egg clusters per tree for years 1962, 1963, and 1964 are given in Figure 2. These latter represent low, medium, and high populations, respectively.

DISTRIBUTIONAL PATTERNS

DISPERSION.–Mean and variance were calculated for egg cluster counts, and then the Poisson and negative binomial series and Taylor's power law were fitted to these data to determine dispersive patterns within plots. The statistics for these have been outlined by several authors (Anscombe, 1948, 1949; Bliss and Fisher, 1953; Fisher, 1941; Taylor, 1961).

If egg clusters are distributed among the trees at random, the distribution will approximate a Poisson series in which the variance (s^2) of the population sample is equal to its mean (m). Most populations, however, depart from randomness in such a way that there are more zeros and higher values than expected, with the results that the variance exceeds the mean (Waters, 1959; Bliss, 1941). When this occurs, the degree of overdispersion can be determined by calculating the parameter k of the negative binomial series in the formula ($s^2 = m + m^2/k$) using a common k value (Anscombe, 1949). Also, overdispersion can be determined from Taylor's power law (Taylor, 1961) by calculating the parameter b of the equation ($s^2 = am^b$) which is more conveniently illustrated and fitted as the regression equation $\log s^2 = \log a + b \log m$ where b is the slope and $\log a$ the intercept.

As expected, the data as a whole depart noticeably from Poisson expectation ($s^2 = m$) and fit both the negative binomial and Taylor's power law reasonably well (Fig. 3). However, only egg cluster population means above 1.0 cluster per tree tend not to differ from random expectation. Values of k for the negative binomial varied from 0.89-4.05 with a common k of 1.37 (Wilson and Gerrard, 1971) which was used in fitting the data. The index of aggregation b of Taylor's power law was calculated to be 1.49 (Fig. 3) and accounted for 98 per cent of the variation among the individual variances.

TREE SIZE EFFECT.–Egg cluster density in plantation A is directly related to tree height, especially at medium (1963 and high (1964) population levels (Fig. 4). This also was the case for all other plantations studied which had a mean population greater than 1.0 egg cluster per tree in any year. Plantations E and F, which averaged 0.85 egg clusters or less, showed no correlation with tree size as all tree sizes (by 1-ft height classes) on the average had about the same number of clusters per class. Lyons (1964a) found a similar relationship between larval colonies and tree height for three years of attack in a red pine stand. Wright *et al.* (1967) and Hattemer *et al.* (1969) found high correlations between sawfly density and tree size in pine provenance study plantings. In the latter case several varieties of Scotch pine, pine hybrids, and pine species were involved.

Distribution of egg clusters by individual tree height classes (i.e., 6 ft, 8 ft, etc.) for all plots or plantations does not differ significantly from distribution of egg clusters for entire plots. This fact is indicated by the two aggregation indices (k) and Taylor's law from variance-mean relationships on 4-, 6-, and 8-ft trees from all study plantings (Fig. 5). Trees of all sizes with population means of less than 1.0 egg cluster per tree show nearly random distribution whereas those with more than 1.0 egg cluster per tree become more aggregated as population increases.

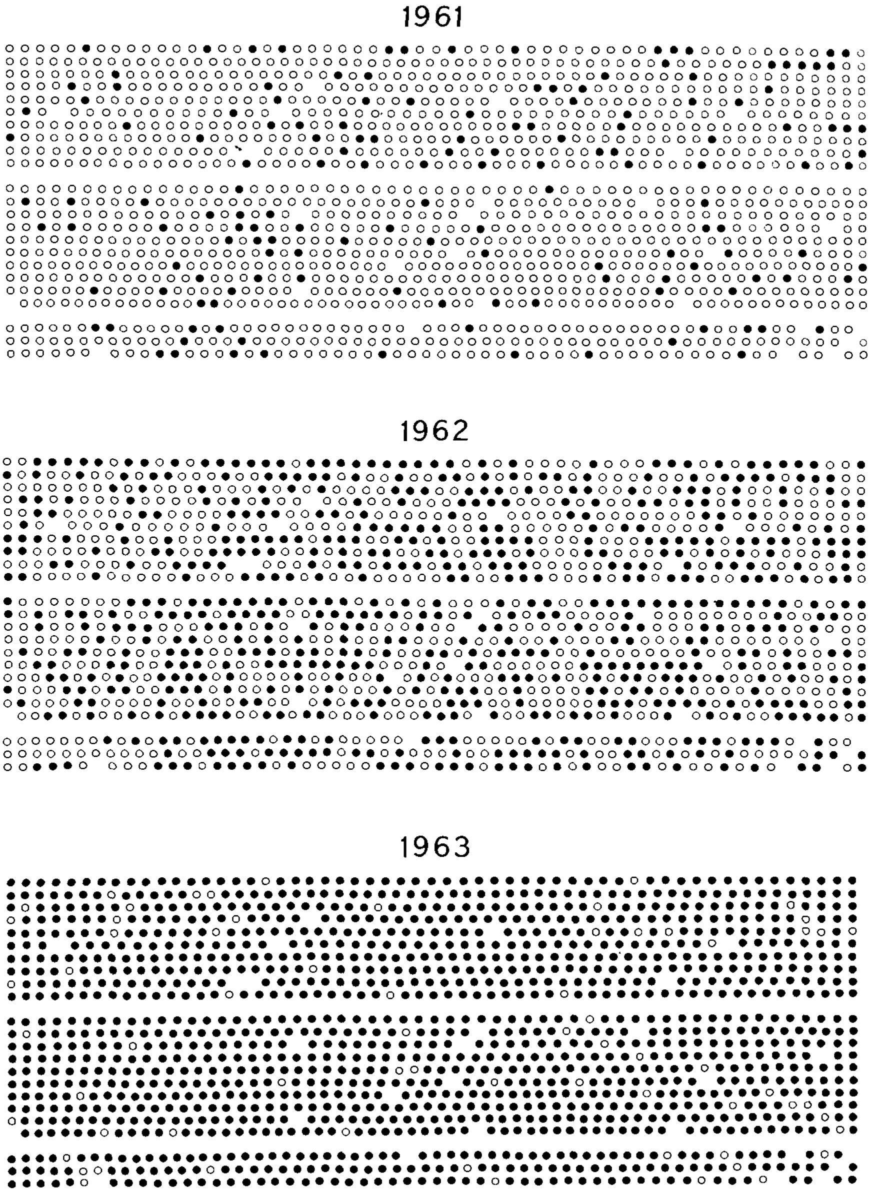

Fig. 1. Scotch pine plantation A showing distribution pattern of pines infested with sawfly egg clusters (black discs) for three years of increasing population levels. Upper edge (row 1 trees) adjoins an open grassy field; spaces between rows 10 and 11 and 20 and 21 are 10-foot wide firebreaks.

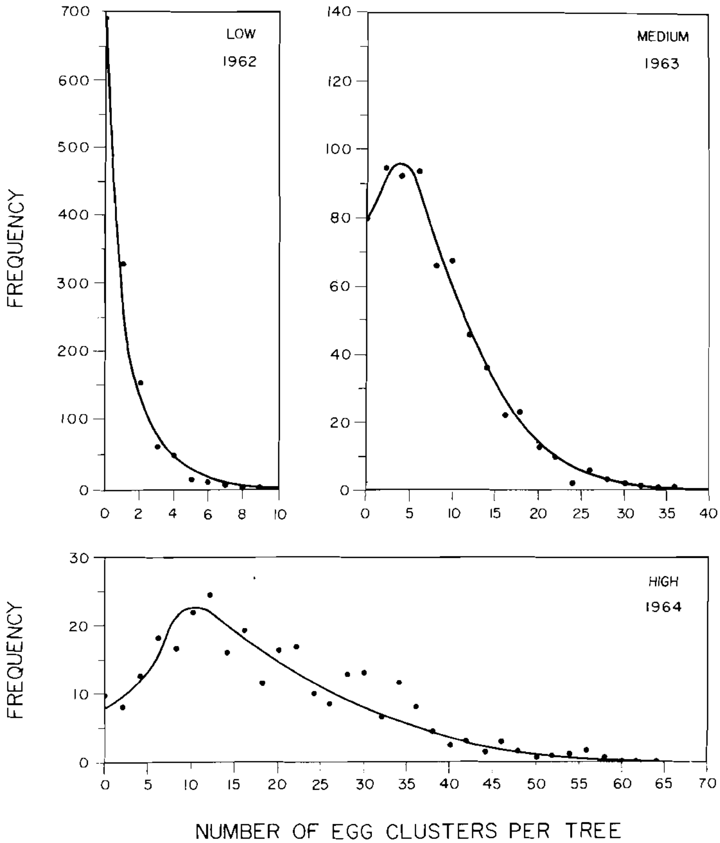

Fig. 2. Frequency distributions of number of egg clusters per tree in Scotch pine plantation A for low (1962), medium (1963), and high (1964) sawfly population levels.

EDGE EFFECT.–Organisms tend to increase in population at community junctions or ecotones. Such a phenomenon is called an edge effect (Odum, 1959). Under certain conditions the European pine sawfly exhibits a forest edge effect where the ecotone consists of pine and grass or other low-growing vegetation. I first noticed this edge effect in plantation A which had 98 per cent of full stocking, trees spaced 5.5 ft apart, and 10 ft-wide firebreaks at 10-row intervals–thus providing "solid" blocks of trees with a major edge at the pine-grass community junction, and several minor edges at the firebreaks. The edge effect at the major edge was barely detectable in 1962 when the population was 0.93 egg clusters per tree (Fig. 6). However, it became noticeable in 1963 when the population rose to 8.14 egg clusters per tree, and this first or edge row of trees adjacent to the grassy field (row 1, Fig. 6) had significantly higher (X^2_{95} test) egg clusters than any other interior row (rows 2-9 and 12-19, Fig. 6). The effect became even more pronounced and more highly significant in 1964 when the population increased to a mean of 19.5 colonies per tree. The edge row that year averaged 29.5 colonies per tree. In either year, the population on the major edge was 1½ to 2 times that of any other interior row.

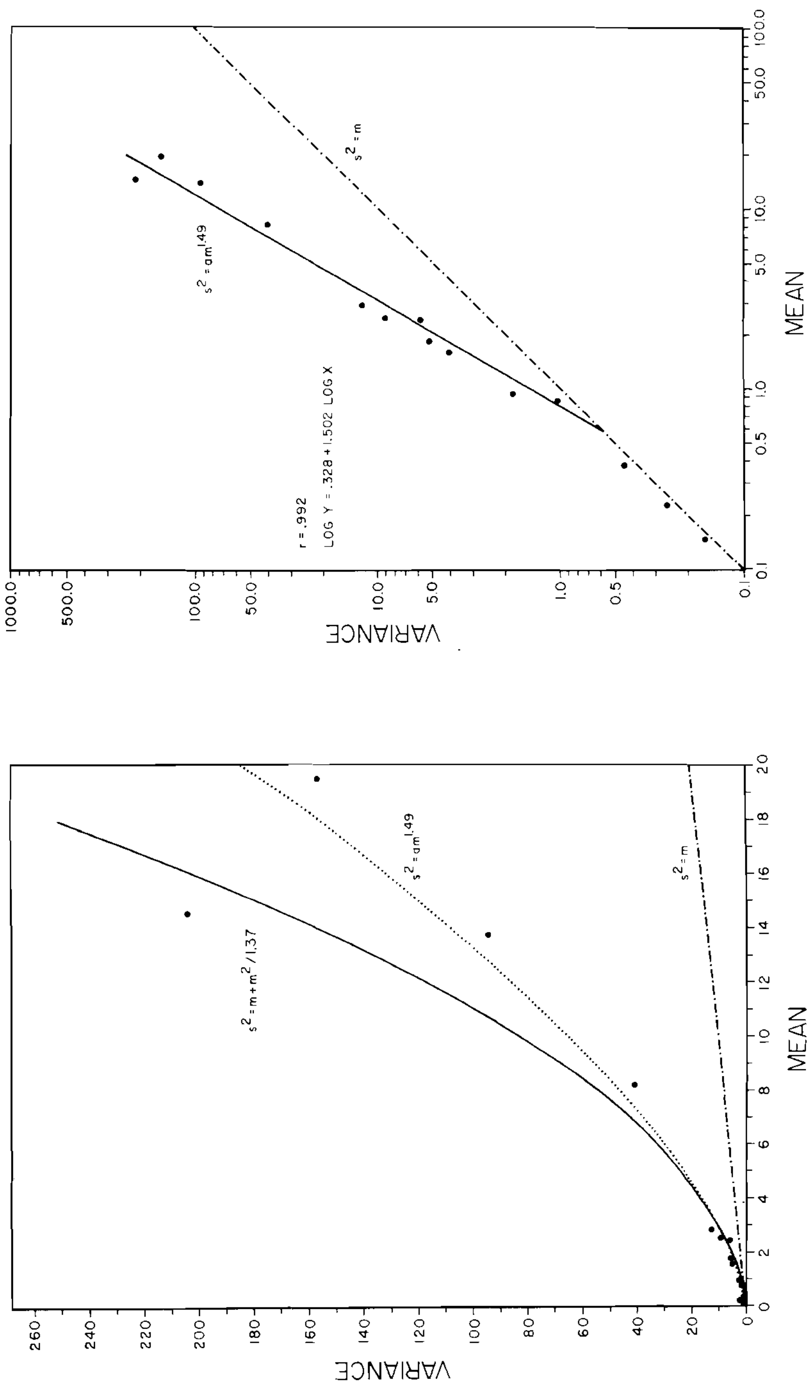

Fig. 3. Relation between intertree variance (s^2) and the mean number of sawfly egg clusters (m) per tree for all plots and years.

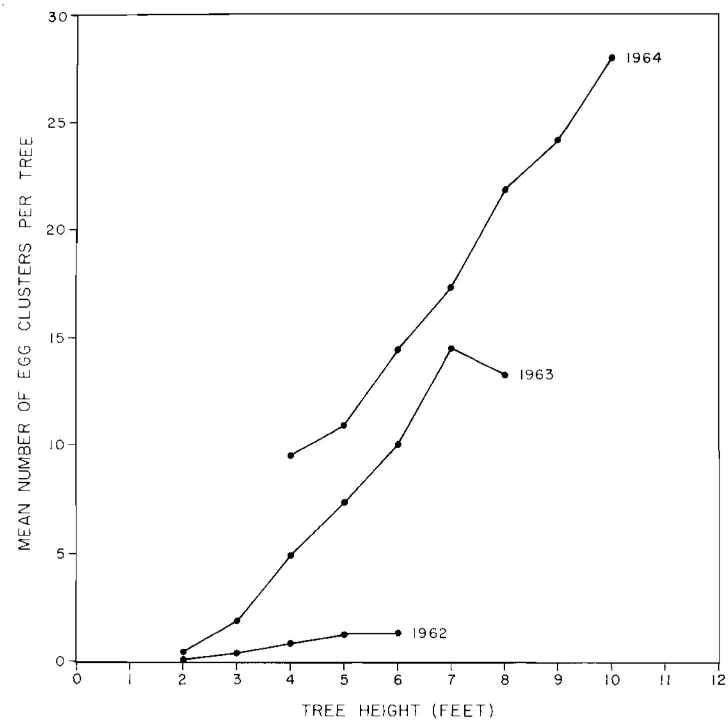

Fig. 4. Density of sawfly egg clusters in relation to tree height in Scotch pine plantation A for low (1962), medium (1963), and high (1964) population levels.

The firebreak edge rows (rows 10, 11, and 20, Fig. 6) tended to have slightly higher population than nonedge rows in 1963 but the differences were not significant until 1964. Unfortunately the data were not taken beyond row 10 that year so there was only one edge row along the firebreak to show the difference. Mean tree height between rows did not differ significantly so size adjustments were not deemed necessary in the analyses. Interestingly, edge effect is not as readily discernible when only the proportion of trees infested is compared between edge and interior row trees (see Fig. 1).

Edge effect was also examined in plantation B which had 50 per cent of full stocking and thus had many spaces scattered throughout the planting. Although population levels averaged only 1.6 and 2.9 egg clusters per tree for 1962, a distinct and significant edge effect was evident. The major difference, however, was that the first two rows together, instead of just the outer row, acted as an edge due to the greater number of missing trees in both rows. The data (±SE) were as follows:

	1962	1963
Mean egg clusters per row 1	3.0 ± 0.8	9.4 ± 1.3
Mean egg clusters per row 2	3.3 ± 0.5	8.5 ± 1.3
Mean egg clusters per row 3-23	1.5 ± 0.1	2.5 ± 0.1

Besides this, the third and fourth rows of the 1963 population had about twice as many egg clusters as the remaining rows, suggesting that they, too, were a part of the "edges."

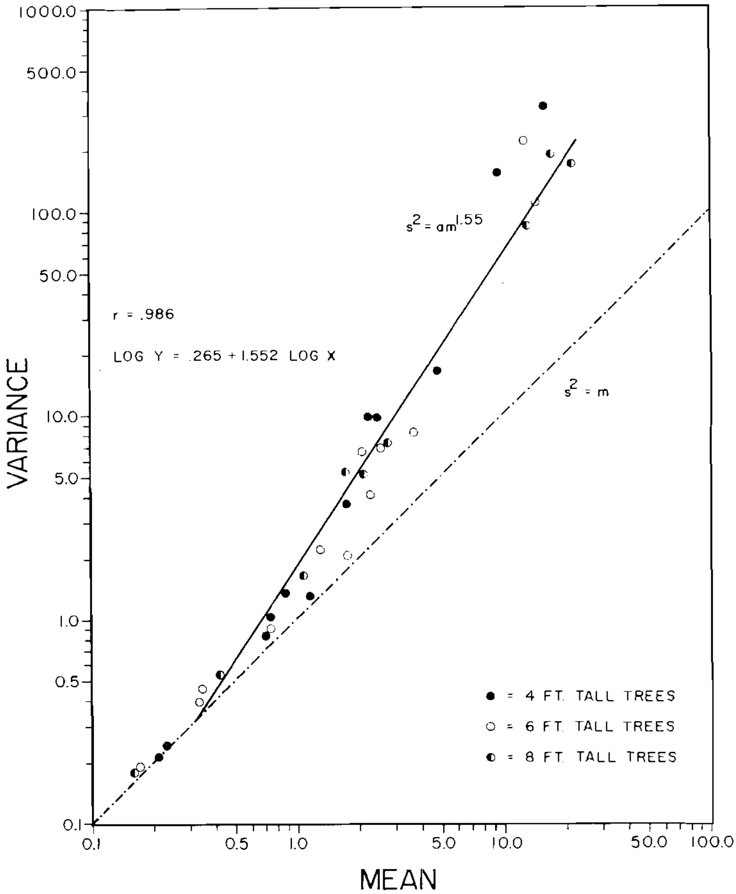

Fig. 5. Relation between intertree variance (s^2) and the mean number of sawfly egg clusters (m) per tree for 4-foot, 6-foot, and 8-foot trees for all plots and years.

VERTICAL DISTRIBUTION.—Egg cluster distribution by whorls was recorded for all trees in Plantation A in 1963 when the population mean was 8.14 egg clusters per tree. All trees had four whorls of branches but on some the bottom whorl was stunted or dead. The order of egg-cluster density by whorls was 2 > 3 > 1 > 4, with over 50 per cent on the second whorl (Table 2). Adjusting the data by the number of shoot tips, however, gives the order as 1 > 2 > 3 > 4 with over 50 per cent on the first whorl (Table 2). Considering the amount of foliage (linear inches) on each whorl the order is 2 > 1 > 3 > 4 with over 45 per cent on the second whorl (Table 2).

Egg cluster location on the edge row differed somewhat from inner rows (2-9, Fig. 1) in plantation A. There were not only more egg clusters on the edge row, but they were spread out more on the crown so that whorls 3 and 4 had proportionately more of them (Table 3).

Table 2. Number of sawfly egg clusters per tree, shoot tip, and amount of foliage by whorls for Scotch pine trees in plantation A, 1963.

Whorl	Egg clusters/tree No.	Egg clusters/tree Per cent	Number of shoot tips	Egg clusters/tip No.	Egg clusters/tip Per cent	Foliage amount (linear inches)	Egg clusters per 100 inches foliage No.	Egg clusters per 100 inches foliage Per cent
1	0.84	10.0	10.8	0.078	50.6	136	0.628	37.1
2	4.95	58.8	80.0	.062	40.3	645	.767	45.3
3	2.28	27.1	189.4	.012	7.8	940	.243	14.3
4	.35	4.1	174.7	.002	1.3	626	.056	3.3
1-4	8.14	100.0	454.9	.154	100.0	2,350	1.694	100.0

Table 3. Distribution of sawfly egg clusters by branch whorls for edge and nonedge Scotch pine trees in Plantation A, 1963.

Whorl	Mean no. egg clusters (+ SE)[a] Row 1 (edge)	Mean no. egg clusters (+ SE)[a] Rows 2-9	Percentage Row 1 (edge)	Percentage Rows 2-9	Ratio row 1 : rows 2-9
1	1.09 ± .16	0.80 ± .05	7.0	9.4	1.4 : 1.0
2	7.77 ± .64	5.17 ± .20	49.5	60.8	1.5 : 1.0
3	5.34 ± .60	2.45 ± .12	34.1	28.9	2.2 : 1.0
4	1.48 ± .49	0.25 ± .06	9.4	2.9	5.9 : 1.0
1-4	14.96 ± 1.18	8.51 ± .31	100.0	100.0	1.8 : 1.0

[a]Standard error.

Table 4. The mean, variance, and k values of counts of egg clusters of the European pine sawfly, 1962-1964.

	Original counts (x)			Transformed, log (x + 1)		Transformed, log (x + k/2)		Transformed $x^{.26}$		Transformed log ($x^{.26}$ + 1)	
Plot/yr	Mean	Variance	k	Mean	Variance	Mean	Variance	Mean	Variance	Mean	Variance
A-62	0.925	1.805	0.973	0.207	0.060	−0.004	0.123	0.547	0.343	0.158	0.028
A-63	8.140	40.309	2.060	.843	.121	.846	.119	1.572	.242	.399	.012
A-64	19.480	157.880	2.742	1.208	.115	1.222	.104	2.045	.221	.477	.007
B-62	1.583	4.200	.957	.299	.092	.114	.176	.547	.343	.158	.028
B-63	2.895	12.156	.905	.443	.126	.292	.223	.973	.422	.256	.029
C-62	1.760	5.233	.892	.320	.099	.124	.197	.744	.424	.207	.032
C-63	2.339	6.051	1.575	.429	.090	.382	.110	.995	.322	.277	.023
D-62	14.363	202.726	1.095	1.001	.186	.963	.228	1.776	.373	.429	.014
D-63	2.446	9.085	.901	.397	.120	.229	.222	.881	.441	.242	.031
E-62	.847	1.024	4.047	.208	.048	.434	.020	.575	.320	.167	.027
E-63	.147	.165	1.193	.042	.013	− .166	.024	.131	.119	.039	.011
F-62	.228	.262	1.516	.064	.019	− .044	.027	.196	.167	.058	.015
F-63	.378	.447	2.077	.102	.028	.116	.026	.310	.233	.092	.020
G-62	13.786	82.667	2.759	1.071	.106	1.090	.095	1.864	.195	.450	.007
	r = 0.92 ($P < 0.01$)			r = 0.76 ($P < 0.01$)		r = 0.18 ($P > 0.05$)		r = 0.06 ($P > 0.05$)		r = −0.40 ($P > 0.05$)	

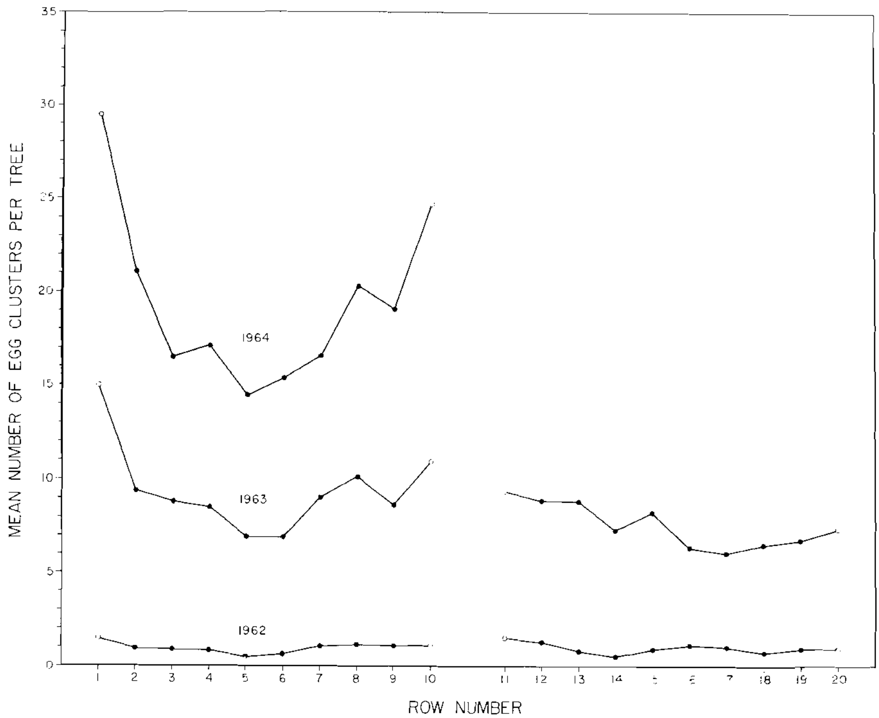

Fig. 6. Density of sawfly egg clusters by row in plantation A for low (1962), medium (1963), and high (1964) population levels. Row 1 adjoins an open grassy field; rows 10, 11, and 20 adjoin narrow firebreaks. Number of trees per row varies from 52-62. Rows 11-20 were not censused in 1964.

DISCUSSION

Spatial distribution of European pine sawfly egg clusters is influenced by many factors including the behavior of the sawflies, the interactions among themselves and other organisms, and especially the distribution of the essential elements of their habitat. Although pine plantations (if monocultures) are relatively uniform, there is still some variability in gene pool, spacing, height, and physiology which influences insect attraction. Appropriately then, the European pine sawfly—as with most other organisms—tends to be overdispersed in particular parts of the habitat rather than in a random or regular pattern.

The negative binomial series and Taylor's power law both provide useful indices of overdispersion which are constants, but by either index, the spatial pattern between trees is not detectably different from random at population levels below approximately 1.0 egg cluster per tree. Above this level overdispersion is clearly apparent.

Tree size, density, and location modify spatial distribution. There is a direct relationship between tree size and egg population. Overdispersion of egg clusters occurs within all height classes indicating that trees are not equally attractive to ovipositing female sawflies once the egg-cluster density reaches a certain level in a stand; or at least an overdispersed pattern is not discernible until this occurs. Using variance-mean ratios, Lyons (1964b) noted that distribution of *N. sertifer* larval colonies per tree (for 2- to 20-ft tall trees) was nearly random for some height classes. Intermediate level classes, however, showed the colonies to be moderately aggregated. Thus he surmised that trees of the same height were not equally exposed to attack in some cases. Larval colonies and egg clusters of this insect should have approximately the same pattern of distribution between trees—unless heavy predation occurs or starvation forces larval migration. Why Lyon's larval colony data appeared random and my egg colony data were not is not certain. His plantation trees ranged from 2-21 ft in height whereas most of mine varied from 2-8 or 2-10 ft; this may or may not be important.

Several authors state that *N. sertifer* prefers isolated or border trees and that the degree of exposure within a stand is also directly related to aggregation (Hein, 1956; Kangas, 1941; Nicklas and Franz, 1957; Breny, 1957; Lyons, 1964a; Hattemer *et al.*, 1969). Lyons (1964a) reports this is due to the tendency of adult females to oviposit on well-illuminated zones of their habitat, and exposed trees, wherever they are, may be expected to have more acceptable sites than shaded or crowded ones. My studies indicate the females do oviposit more heavily on border trees especially along an ecotone and especially as the population increases. In well-stocked plantings the border or edge consists generally of one row of trees, whereas in poorly stocked plantings more than one row may constitute the border because of the gaps between trees. At all densities the sawflies prefer the upper crown, but on exposed trees they tend to lay more eggs lower on the tree. As the female oviposits on the shoot tip, she probably chooses the location by the tip rather than by the amount of foliage. Borodin (1973) recently determined that the distribution of eggs in the trees by height is cubic parabolic. He provides a method for making quantitative estimates of the egg population.

The distribution pattern of *N. sertifer* should be considered in sampling for the eggs or larval colonies, especially if surveys are performed systematically rather than at random. Care should then be taken to sample all tree sizes and edge trees in proportion to their numbers in the stand. This seems to be unnecessary, however, if the rapid sampling technique devised by Wilson and Gerrard (1971) is used randomly or systematically. This technique involves sampling the proportion of trees infested. There appears to be no difference by tree size or location (edges) when proportion of trees infested is considered. Edge rows, for instance, had no more infested trees than interior rows even though the population may have been twice as large on the edge rows.

Analysis of variance and other statistical methods used in assessing sampling variation presuppose a normal distribution with variance independent of the mean. Thus it is necessary to transform overdispersed-type data to stabilize the variance. Because the sawfly egg cluster data were highly aggregated, they were transformed using: $(x + 1)$ (Wadley, 1950); $\log(x + K/2)$ (Anscombe, 1948); x^y (Healy and Taylor, 1962); and $\log(x^y + 1)$, in order to find a means of stabilizing variance. The correlation coefficient between mean and variance was highly significant when original counts and counts transformed to $\log(x + 1)$ were used, and not significant with the other transformations (Table 4). Taylor's power law transformation (x^y) was the most powerful of those tested and the most satisfactory for statistical purposes.

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