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DISTRIBUTION OF OVIPOSITION SLITS CONSTRUCTED BY OBEREA SCHAUMII LECONTE AND SAPERDA CONCOLOR LECONTE (COLEOPTERA: CERAMBYCIDAE) ON ASPEN SUCKERS (POPULUS TREMULOIDES MICHAUX).

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DISTRIBUTION OF OVIPOSITION SLITS CONSTRUCTED BY *OBEREA SCHAUMII* LECONTE AND *SAPERDA CONCOLOR* LECONTE (COLEOPTERA: CERAMBYCIDAE) ON ASPEN SUCKERS (*POPULUS TREMULOIDES* MICHAUX)

by

Wayne Lawrence Myers

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy at the
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1967

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DISTRIBUTION OF OVIPOSITION SLITS CONSTRUCTED BY OBEREA SCHAUMII LECONTE AND SAPERDA CONCOLOR LECONTE (COLEOPTERA: CERAMBYCIDAE) ON ASPEN SUCKERS (POPULUS TREMULOIDES MICHAUX)

by Wayne L. Myers

Host density and other environmental factors influencing the distribution of oviposition slits constructed by Oberea schaumii Lec. and Saperda concolor Lec. were studied in aspen sucker stands located in western upper Michigan. Interest in these beetles arises from two sources: 1) the damage they cause by excavating larval feeding galleries in suckers and small branches of aspen; and 2) very similar nutrition and habits which suggest the possibility of the two species occupying a common ecological niche, such joint niche occupation being an exception to the competitive exclusion principle. Results of this study are valuable in two respects: 1) they obviate the possibility of joint niche occupation; and 2) they aid in formulating silvicultural treatments to minimize damage from O. schaumii and S. concolor.

This research was conducted during the summers of 1964, 1965, and 1966 in the Upper Peninsula of Michigan. Six sample areas were established; four located in Iron County, one in Gogebic County, and one in Dickinson County. Seventy-five sampling units of 30 suckers each were established in each area. Soils in all the sample areas were light and infertile, but moisture availability varied between areas. Aspen suckers on the sample areas were 7 to 10 feet in height and averaged 5 to 6 years old in 1965. Average stand density varied from 1000 suckers per acre in sample area 1 to 5300 suckers per acre in sample area 5.

Experimental method consisted of counting new O. schaumii and S. concolor oviposition slits on the sampling units in August of each year. Ecological data recorded from each sampling unit in 1965 provided the independent variables for the analysis.

Differences between sample areas with respect to observed O. schaumii infestations were declared significant at the 1% level by a nonparametric randomization test. Significant differences between sample areas were not demonstrated for S. concolor infestations.

Data from the sampling units were analyzed by both graphical and multivariate regression techniques. For both O. schaumii and S. concolor, multivariate regression analysis revealed a decrease in oviposition frequency per sucker with increasing sucker density. This correlation was much stronger for O. schaumii than for S. concolor, but in neither case was precision sufficient for predictive purposes. For both species, the total number of attacks per acre was maximum at a stand density of about 6000 suckers per acre. O. schaumii oviposition slits were consistently less frequent in the presence of brush, while S. concolor oviposition showed no consistent tendencies with respect to presence or absence of brush. Correlation with infestation was observed only for the components of stand density. Attacks of both species followed the negative binomial distribution as fitted by the maximum likelihood method.

General conclusions were: 1) interspecific differences in the relationship of oviposition to stand density indicate that O. schaumii and S. concolor do not occupy a common ecological niche; and 2) silvicultural treatments designed to produce dense, vigorous aspen regeneration should minimize damage from O. schaumii and S. concolor.

Acknowledgements

Special thanks are due Prof. Fred B. Knight, committee chairman and Principal Investigator of the National Science Foundation sponsored project[1] under which the research for this dissertation was performed. His guidance has been invaluable.

My appreciation goes to the Canada Department of Forestry and Rural Development under whose employ preparation of this thesis was completed, and also to the University of Michigan for providing computer time and facilities.

Finally, I wish to thank all members of my doctoral committee for the time and effort which they have contributed so freely.

1. National Science Foundation Sponsored Research Project GB-2149, entitled: "Population regulation in Oberea schaumii Lec. and Saperda concolor Lec. infesting trembling aspen (Populus tremuloides Michx.)"

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INTRODUCTION

Oberea schaumii Lec. and Saperda concolor Lec. (Coleoptera: Cerambycidae) are significant to practicing foresters as well as ecologists. To the forester they are pests which damage aspen by excavating larval feeding galleries in small branches and sucker stems. To the ecologist they furnish a test case for the competitive exclusion principle which states that two ecologically equivalent species cannot survive indefinitely in competition with each other. O. schaumii galleries are found in such close proximity to S. concolor galleries that the two species appear to share a common microhabitat. Furthermore, an apparent preference for open, sunny oviposition sites has been noted for both species (Harrison, 1959; Graham, Westell, and Harrison, 1963). Joint niche occupation, if it exists, constitutes an exception to the principle.

Any consistent difference between O. schaumii and S. concolor in their selection of oviposition sites would provide proof that these two species do not occupy identical niches. This thesis seeks to resolve the following questions by analyzing the distribution of their oviposition slits in aspen sucker stands:

1. What are the relationships between host density and oviposition by O. schaumii and S. concolor?
2. What factors other than host density affect O. schaumii and S. concolor oviposition in sucker stands?

Answers to these questions will clarify the nature of ecological interactions between the two species and aid in formulating silvicultural treatments to minimize their damage.

Prior to 1960 publications concerning these species consisted of

taxonomic studies (Felt and Joutel, 1904), and notes on the damage which they cause (Harrison, 1959). Since that time John Nord at the University of Michigan has studied their biology and distribution in mature trees. His results will be published shortly (pers. comm.). Oviposition and egg viability were studied by Grimble (1966). None of these studies provide satisfactory answers to the questions posed.

This research was conducted during the summers of 1964, 1965, and 1966 in the western portion of Michigan's Upper Peninsula. Experimental method consisted of counting O. schaumii and S. concolor oviposition slits on 30-sucker sampling units of 5 and 6 year old (as of 1965) aspen suckers. Ecological data recorded from each sampling unit in 1965 provided the independent variables for the analysis.

BIOLOGY AND ECONOMIC IMPORTANCE OF THE INSECTS AND THEIR HOST

Both O. schaumii and S. concolor infest bigtooth aspen, Populus grandidentata Michaux, as well as P. tremuloides; however, this study was restricted to their activities in P. tremuloides sucker stands.

a) Life History of Oberea schaumii

Oberea schaumii, the poplar branch borer, is an orange-bodied cerambycid with dark elytra. The orange prothorax is marked by four black spots. Adults range from 1/2 to 3/4 inch in length, the males being slightly smaller than females. The yellow larva has the typical Cerambycidae form, and when fully developed it is between 1 and 1 1/2 inches in length.

The life cycle requires a three year period. Adults emerge in late June, and they remain active for about two months. Adult food is aspen foliage. The female constructs an oviposition slit about 1/2 inch long in the bark of aspen branches or suckers less than one inch in diameter. The ovipositor is inserted at one end of the slit, and the egg is deposited beneath the center of the slit. An oviposition slit usually contains a single egg. Only one oviposition slit is constructed at an oviposition site.

A female deposits from 75 to 150 eggs during the summer (Grimble, 1966). These hatch in about two weeks, and after a short period of feeding in the phloem the young larva bores into the xylem and burrows a gallery down the stem. Nutrition is derived from carbohydrates in the wood, but cellulose is not metabolized. The gallery is from 1 1/2 to 2 1/2 inches long by the end of the first summer depending upon the date of oviposition. As it grows the larva widens the tunnel and continues lengthening its

gallery during the second and third summer. Late in the second summer or early in the third summer an auxiliary hole is cut to the outside through which frass is ejected. Until this second hole is cut, frass is ejected through the oviposition slit. The auxiliary hole usually marks the lower extremity of the gallery. Total gallery length varies from 6 to 10 inches depending partly on the diameter of the stem. Late in the third summer the larva moves back up the gallery and cuts an emergence hole nearly to the surface, often about 1 inch above the original egg slit. The pupal chamber is constructed in the gallery 1 to 2 inches below the emergence hole.

Salient differences between the life cycle of O. schaumii and that of S. concolor as described in the next section are: (1) S. concolor requires only two years to complete a generation; (2) oviposition slits of S. concolor are grouped in a ring around the stem; and (3) S. concolor lays twice as many eggs as O. schaumii.

b) Life History of Saperda concolor

Saperda concolor, the poplar gall saperda, is a uniformly gray cerambycid. The adults are approximately 1/2 inch in length, the males being somewhat smaller than females. The larva is white with the typical form of the Cerambycidae. When fully developed it is slightly less than 1 inch long.

The life cycle usually requires a two year period, but eggs laid very early in the season occasionally emerge as adults the following year. Emergence of adults occurs in early June and the beetles live for about two months during which they feed on aspen foliage. The female constructs 1 to 5 horseshoe-shaped oviposition slits in a ring around the stem of a

small branch or sucker. The number of slits in a ring is directly correlated with stem diameter, the most common number being three. Each oviposition slit measures about 1/4 inch in width by 5/16 inch in length, the arms of the horseshoe opening upward. A single egg is inserted under the bark flap from the bottom of the horseshoe. The maximum number of eggs per beetle is 300 (Grimble, 1966). The eggs hatch in about two weeks and the larvae tunnel horizontally through the phloem. This girdling effect by several larvae causes growth of callus tissue in the form of a globose gall. After boring about 1/2 inch around the stem, a larva enters the xylem where it passes the remainder of its larval stage. Frass is ejected through the oviposition slits. Galleries extend upward or downward as much as 1 1/2 inches. Pupation takes place in the gallery during the spring two years after oviposition.

Usually only one insect per gall survives, but occasionally two reach maturity. The occurrence of more than one adult from a gall is so rare that cannibalism is the only possible explanation. Cannibalism occurs frequently among wood boring beetles so this is not illogical.

Until 1965 these beetles were incorrectly identified as Saperda populnea var. moesta Lec. because of confusion with regard to shape of oviposition slits. Early reports indicated that S. concolor constructed only longitudinal oviposition slits (Felt and Joutel, 1904). Confusion was understandable due to a lack of host, morphological, and distributional data coupled with difficulty in determining the exact shape of egg slits in older galls. Comparative studies by John Nord at the University of Michigan have clarified this situation.[2]

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2. Knight, Fred B. 1965. Annual progress report: National Science Foundation sponsored research project GB-2149. "Population regulation in Oberea schaumii Lec. and Saperda concolor Lec. infesting trembling aspen (Populus tremuloides Michx.)". The Univ. of Mich., Ann Arbor, Mich.

c) Biology of Trembling Aspen

Populus tremuloides is one of the more widely distributed trees in North America, its range covering most of the northern and western portions of this continent. This tree grows rapidly, but is very intolerant of shade. It is short-lived, becoming decadent between 45 and 60 years of age in Michigan. Normal dimensions are 50 to 60 feet in height and 1 to 2 feet in diameter. Seeds are produced abundantly, but require continuously moist mineral soil to germinate and survive. The root system is shallow and extensive. Root suckers sprout profusely when the main stem is severed, and this is the most common means of regeneration in trembling aspen. Repeated suckering in successive generations produces extensive clones. These clones vary widely in morphology and in physiological characteristics such as suckering capacity (Garrett and Zahner, 1964). Clonal differences in suckering capacity are largely responsible for the uneven density of some stands sampled in this study.

d) Economic Importance of Damage to Aspen Caused by O. schaumii and S. concolor

Aspens occupy 1/3 or more of the forested land in the Great Lakes region (Graham, Westell, and Harrison, 1963). Nearly 1.5 million cords of aspen pulpwood were harvested from the Lake States in 1961 (Horn, 1962). This is a significant contribution to the regional economy and justifies research on pests of aspen. Although O. schaumii and S. concolor do not kill trees directly, they damage stands in several ways. Their galleries mechanically weaken stems to such a degree that they are easily broken by wind and other natural agencies. This produces stem deformities which may render the trees unusable. In addition, Harrison (1959) found that wounds caused by these species often serve as infection courts for the

stem canker fungi Hypoxylon pruinatum (Klotsche)(Che.) and Cytospora chrysosperma (Pers.)(Fries). Cankers caused by these fungi are among the more serious stem defects of aspens. Even if galleries are not infected by canker, they are likely to have stain which increases bleaching cost in pulping.

PROCEDURE

a) Establishment of Sample Areas

Four sample areas were established in the spring of 1964. In each area 50 sampling locations were marked by 3 ft. wooden stakes with painted tops. The stakes were positioned by running 10 parallel compass lines along which stakes were spaced 1 chain apart. Each compass line was 5 chains in length and contained 5 stakes. The perpendicular distance between compass lines was 1 chain. Occasionally this spacing was modified in order to stay within the boundaries of the sucker stand. At each sampling location the 30 suckers nearest the stake were marked with paint. The 30 marked suckers around each stake constituted a sampling unit. Thus all sampling units contained 30 suckers, but the area occupied by a sampling unit varied with sucker density. The compass lines were lettered A to J, and the stakes on a line were numbered 1 to 5. This system uniquely identified each 30-sucker sampling unit by a letter and a number.

The scarcity of S. concolor galls recorded in 1964 indicated that a sample size of 200 sampling units was entirely inadequate for studying this species, although it appeared adequate for O. schaumii. Accordingly, the sample size was increased from 200 to 450 sampling units in the spring of 1965. This was accomplished by adding 25, thirty-sucker sampling units to each of the four existing sample areas and establishing two entirely new areas of 75 sampling units each. The two additional areas were numbered 5 and 6. Procedure for locating the new 30-sucker sampling units was the same as that followed in 1964. The final set of samples, then, consisted of 6 sample areas each containing 75 sampling units of 30 suckers.

b) Description of Sample Areas

During July, 1965, a survey was conducted to determine the ecological characteristics of each sampling unit. This was accomplished by establishing a .01 acre quadrat around each center stake and recording information on sucker density, character of brush[3], overstory, sucker height, sucker age, soil texture, drainage, local topography, and cover distribution. This information was coded and punched onto data cards (Table I), each card representing a sampling unit. Data gathered in this survey are summarized by sample area in Table II and Table III. The summary in Table II includes data from all 75 sampling units in each sample area, while the summary in Table III includes data from only those sampling units established in 1964. A separate summary of 1964 sampling units gives an indication of the variability in plant cover on each sample area.

The summaries presented in Table II and Table III are very general. A more detailed description of each sample area is given below.

i) Sample area 1

Sample area 1 was located in Section 33, T. 45 N., R. 36 W., Iron County, Michigan, in the Ottawa National Forest. The soil was a podzol, fine sandy loam in texture. The A horizon was leached sand. Sand pits had formed where roadcuts removed the vegetative cover from this layer. The B horizon was fine sandy loam, and the C horizon was sand. Drainage was poor, the topography sloping gently to a swamp at one side. Pools of stagnant water were prevalent in the spring. The water table was near the surface judging by presence of the swamp. Site quality was medium for aspen.

3. The term "brush" includes all woody, understory vegetation other than aspen suckers.

Table I. Data card format and units of measurement for site variables. (Quadrat size = .01 acre)

Column #	Variable	Units
1	Sample area No.	
2-3	Sampling unit No.	
5	Density class of 5 to 6 year old aspen suckers	0 = 0-9 Suckers; 1 = 10-19; 2 = 20-29; 3 = 30-39; 4 = 40-49; 5 = 50-59; 6 = 60-69; 7 = 70-79; 8 = 80-89; 9 = 90-99
7	Density class of aspen suckers more than 6 years old	0 = 0-4 Suckers; 1 = 5-9; 2 = 10-14; 3 = 15-19; 4 = 20-24; 5 = 25-29; 6 = 30-34; 7 = 35-39; 8 = 40-45; 9 = 46-50
9-10	Number of mature trees	
12	Brush index*	0 = none 1 = sparse, low 2 = medium, low 3 = dense, low 4 = sparse, high 5 = medium, high 6 = dense, high
14-15	Approximate ht. of 5 to 6 year old suckers	measured to nearest foot
17-18	Approximate ht. of older suckers	measured to nearest foot
20	Average age of sucker stand in the sample area	

*Index includes all woody vegetation in the understory other than aspen suckers. The division between high and low brush was placed at 3 1/2 feet.

Table I. (continued)

Column #	Variable	Units
23	Texture of topsoil	1 = sand 2 = loamy sand 3 = sandy loam 4 = loam 5 = silt loam 6 = clay loam 7 = clay
25	Local topography	0 = level 1 = hill or hummocks
27	Drainage	1 = wet 2 = moist 3 = average 4 = dry 5 = very dry
29	Aspect	0 = level 1 = north 2 = northeast 3 = east 4 = southeast 5 = south 6 = southwest 7 = west 8 = northwest
31-32	Last two digits of the year in which the sampling unit was established	
34	Distribution of the cover on the survey quadrat	0 = uniform 1 = 25% or more of the quadrat open
36-37	Number of mature aspen trees	

Table II. Summary of data on plant cover from all sampling units (1965)

	Sample Area Number					
	1	2	3	4	5	6
Mean age of suckers (years)	5	5	5	6	5	5
Mean ht. of suckers (feet)	9.5	9.0	7.5	8.5	8.0	9.0
Mean no. of aspen suckers per acre	2987	980	5313	2867	5287	1700
Mean no. of mature trees per acre	251	148	8	8	37	171
No. of survey quadrats with brush present	75	27	60	75	70	73
No. of survey quadrats with 25% or more of area open	19	36	46	42	40	52

Table III. Summary of data on plant cover from sampling units established in 1964

	Sample Area Number			
	1	2	3	4
Mean age of suckers (years)	5	5	5	6
Mean ht. of suckers (feet)	9.0	8.5	7.0	8.5
Mean no. of aspen suckers per acre	2910	820	4940	3150
Mean no. of mature trees per acre	238	146	10	12
No. of survey quadrats with brush present	50	11	40	50
No. of survey quadrats with 25% or more of area open	11	24	12	30

Overstory consisted primarily of intolerant to mid-tolerant hardwoods (P. tremuloides, Betula papyrifera Marsh., Betula lutea Michx., and Acer rubrum L.). Scattered Pinus strobus L., Picea glauca (Moench) Voss, and Abies balsamea L. were also present. Overstory trees averaged 251 stems per acre.

The aspen sucker stand arose after a pulpwood cutting and averaged 5 years of age in 1965. Mean height of the sucker stand was 9.5 feet. Average density was 2987 suckers per acre. There were more than 25 clones in sample area 1, but a 30-sucker sampling unit was usually restricted to a single clone. The aspen sucker stand in combination with logging slash, Corylus spp., and reproduction of more tolerant hardwoods created a thick and tangled understory (Figure 1).

In the swampy portion the herbaceous vegetation consisted of sphagnum moss. In more open places the ground was covered by bracken fern (Pteridium aquilinum (L.) Kuhn.) and Rubus spp. Various other herbaceous species were also present.

ii) Sample area 2

Sample area 2 was located in Section 20, T. 46 N., R. 35 W., Iron County, Michigan, on land owned by the Kimberly-Clark Corporation. Soil type was the same as that in sample area 1, Hiawatha fine sandy loam. Drainage was good, the topography being level to slightly rolling. The depth to water table was not great since this area was bordered on two sides by spruce swamp and Kidney Creek was only 1/4 mile distant.

The sparse overstory consisted of scattered P. tremuloides, B. papyrifera, Picea glauca, and Abies balsamea. Average overstory density was 148 stems per acre. The aspen in this overstory were overmature

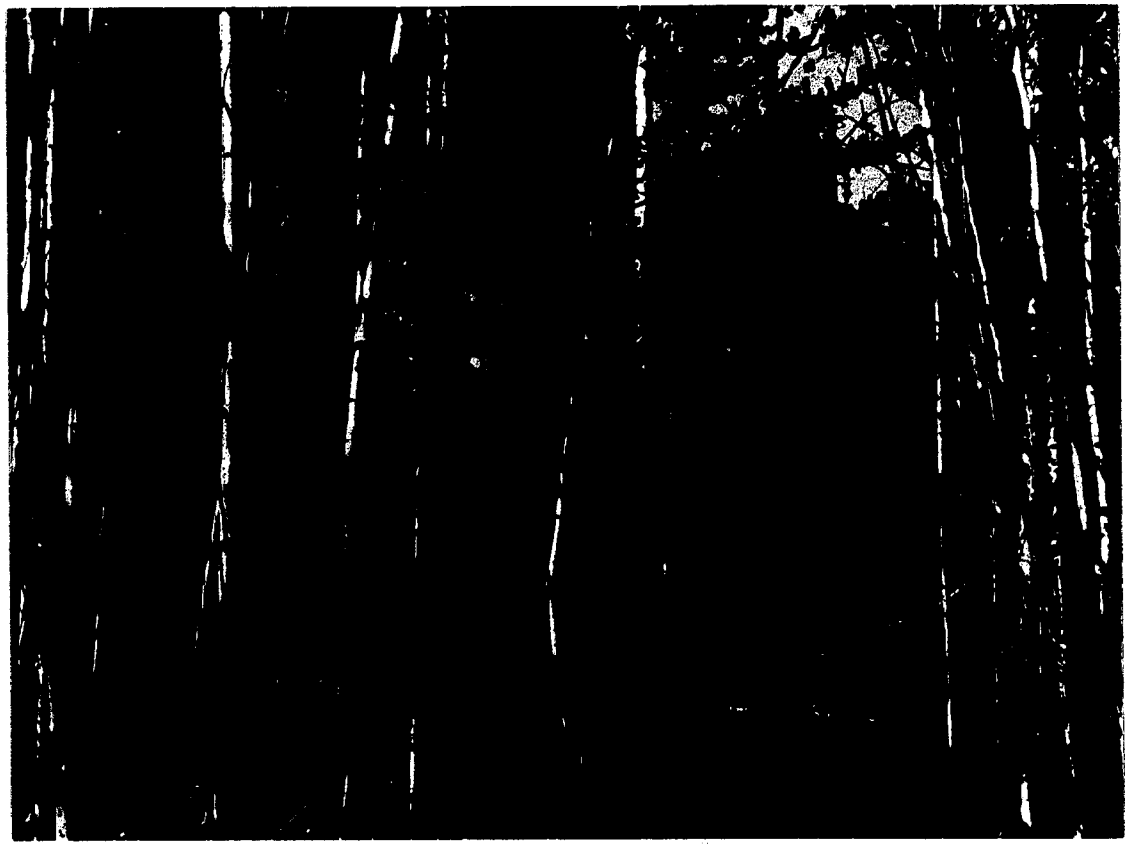


Figure 1. Regeneration of aspen and other hardwoods, sample area 1. May, 1966.

and badly rotted by Fomes ignarius (L. ex Fr.) Gill.

The aspen sucker stand contained numerous clones which were often not contiguous. Sprouting vigor was low with the exception of a few clones. Density averaged 980 suckers per acre. These suckers averaged 5 years old and 9 feet tall in 1965. Scattered clumps of Corylus spp. constituted the only other woody understory. The area was very open (Figure 2). A dense mat of bracken fern about 3 feet in height covered the ground.

iii) Sample area 3

Sample area 3 was located in Section 19, T. 44 N., R. 29 W., Dickinson County, Michigan, in the Sturgeon River State Forest. A borrow pit was located in the center of this area. The A soil horizon was leached sand, the B horizon was fine sandy loam, and the C horizon was gravel. The water table was 10 to 15 feet below ground surface as evidenced by water remaining throughout the summer in the borrow pit. A small stream flowed at a distance of about 1/4 mile.

Charred stumps indicated that early vegetation was pine, the aspens invading as a fire type. The current stand of aspen suckers arose after a clearcutting for pulpwood. There was no overstory, the mature trees shown in Table II and Table III being on the border of the sucker stand. Suckers averaged 5 years of age in 1965. Mean height of the sucker stand was 7.5 feet. Density averaged 5313 suckers per acre; however, some clones had less than 1/4 of the average density (Figure 3 and Figure 4). There were about 10 clones in sample area 3; a single clone covered approximately 25% of the area. Brush was primarily scattered patches of Corylus spp., Vaccinium spp. also being present. Grasses and lichens



Figure 2. Sparse aspen regeneration, sample area 2. May, 1966.



Figure 3. Dense aspen clone, sample area 3. May, 1966.

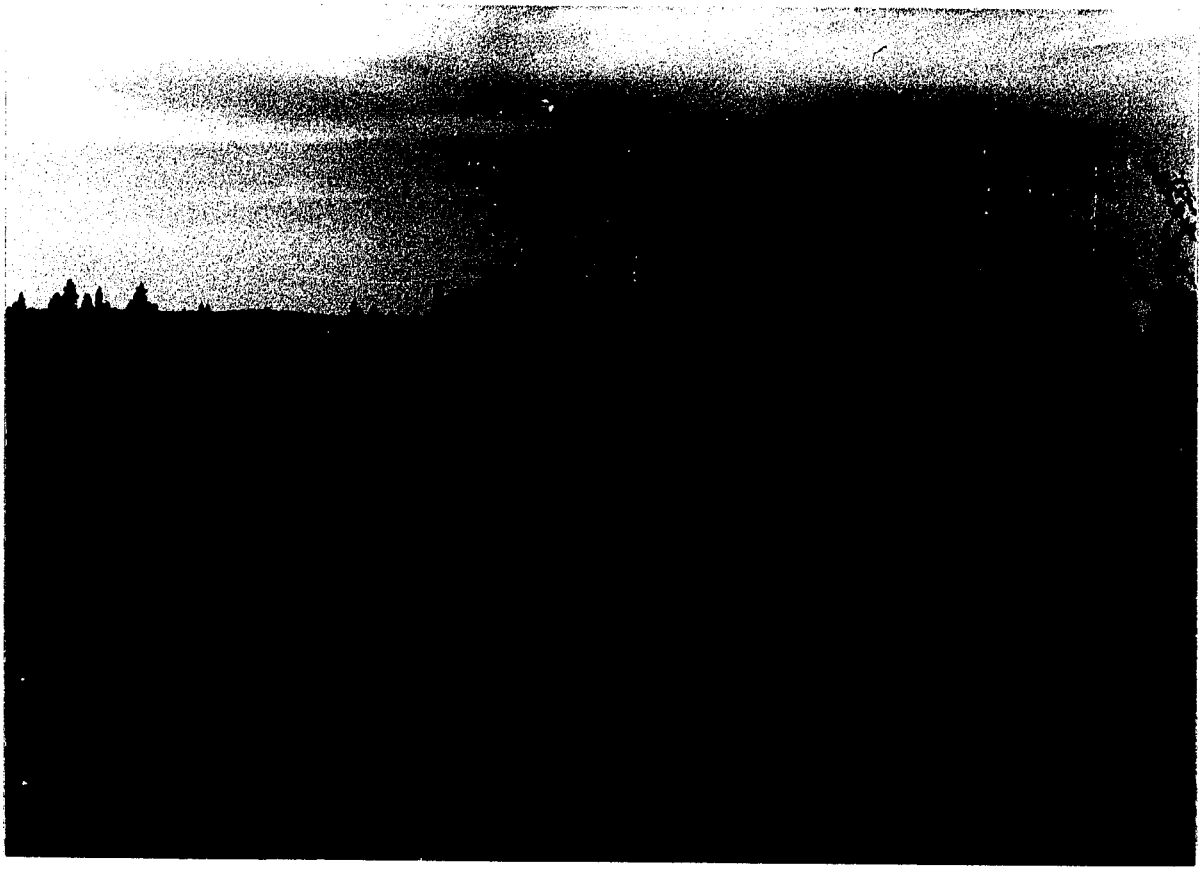


Figure 4. Sparse aspen clone, sample area 3. May, 1966.

sparsely covered the ground surface.

iv) Sample area 4

Sample area 4 was located in Section 7, T. 43 N., R. 35 W., Iron County, Michigan, in the Ottawa National Forest. A gravel pit was located immediately to the northeast of this sample area. The A horizon of the soil profile was loamy sand containing many large and small rocks, the B horizon was fine sandy loam, and the C horizon was gravel. Drainage was good except for an alder (Alnus rugosa (Du Roi) Spreng.) swamp at the northwest corner. Part of the area was on a hillside with a northerly aspect.

The area formerly supported a red pine (Pinus resinosa Ait.) plantation. The current stand of aspen suckers arose in the wake of a fire which escaped from a nearby dump and destroyed the plantation in 1957. There was no overstory save for a few scattered aspens which survived the fire (Figure 5). The aspen sucker stand averaged 6 years of age and 8.5 feet high in 1965. Average density was 2867 suckers per acre. There were more than 25 clones in this sucker stand.

Brushy species included Corylus spp., Alnus rugosa, Salix spp., and Amelanchier spp. Regeneration of fire cherry, (Prunus pensylvanica L.) was scattered over the area. A variety of grasses and herbaceous dicots were present.

v) Sample area 5

Sample area 5 was located in Section 10, T. 42 N., R. 32 W., Iron County, Michigan, in the Iron Range State Forest. This site was situated on an outwash sand plain. The A horizon of the soil profile was loamy

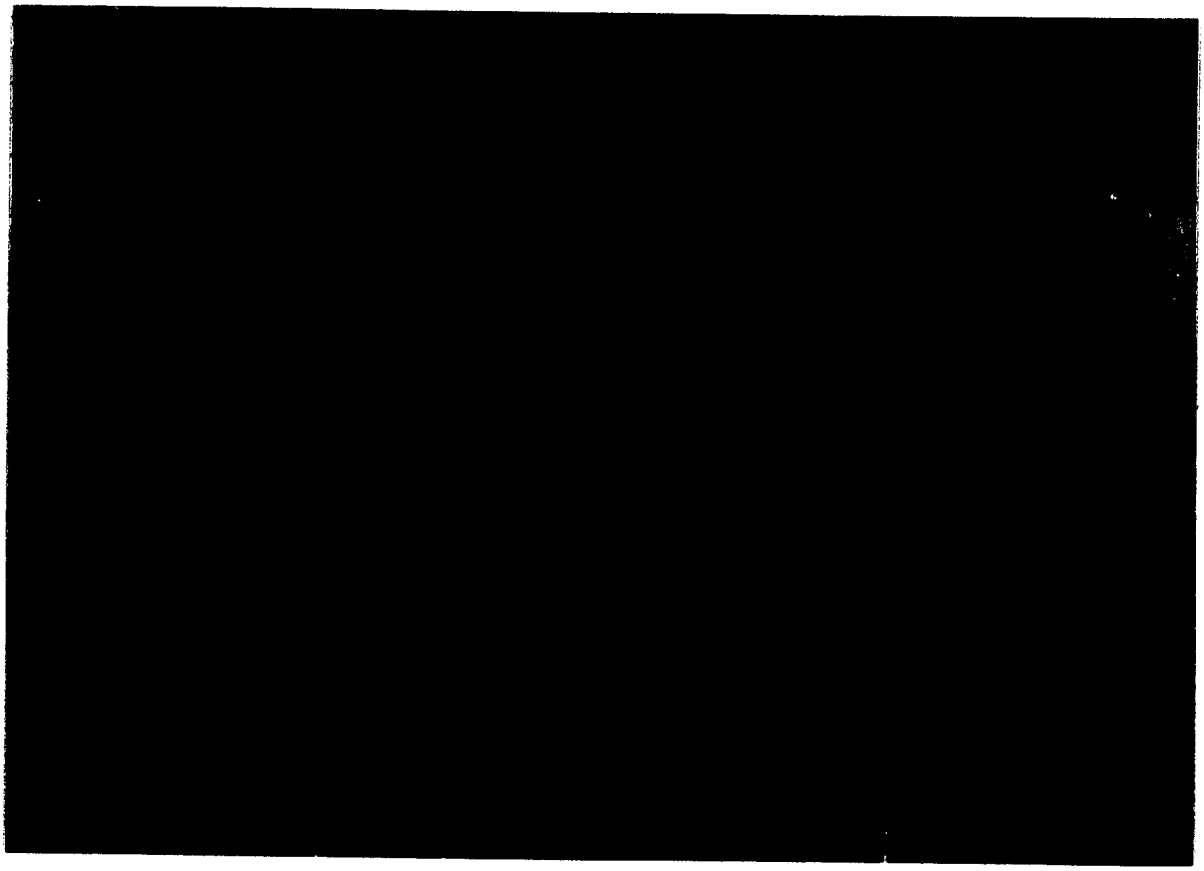


Figure 5. Aspen regeneration, sample area 4. May, 1966.

sand, the B horizon was fine sandy loam, and the C horizon was fine sand typical of the plain. Drainage was good, the sample area being situated on a hillside. Sample area 5 was consistently hotter and drier than any other. This site has been burned repeatedly since logging of the old pine forest.

There was no overstory (Figure 6), mature trees recorded in Table II and Table III being on the stand border. The sucker stand averaged 5 years of age and 8 feet high in 1965. Average density was 5287 suckers per acre, but sampling units on the stand periphery averaged less than 1/2 of this figure. There were less than 20 clones in the sample area. Other low, woody vegetation included Corylus spp., Amelanchier spp., Salix spp., and Vaccinium spp. Foliose lichens were abundant.

vi) Sample area 6

Sample area 6 was located in Section 23, T. 44 N., R. 39 W., Gogebic County, Michigan, in the Ottawa National Forest. The topsoil was loamy sand, whereas the subsoil was fine sandy loam. Topography was level except at the extreme east end. Drainage was moderate, and the water table was near the surface since Dinner Lake was only 1/2 mile distant. The site remained moist throughout the year.

The overstory was composed of intolerant to midtolerant hardwoods (P. tremuloides, B. papyrifera, B. lutea, and Acer rubrum) in mixture with Picea glauca, Pinus resinosa, and Abies balsamea. Overstory density averaged 171 stems per acre; however, its distribution was uneven (Figure 7).

The current stand of aspen suckers sprouted after a pulpwood cutting. The sucker stand averaged 5 years of age and 9 feet high in 1965. Average

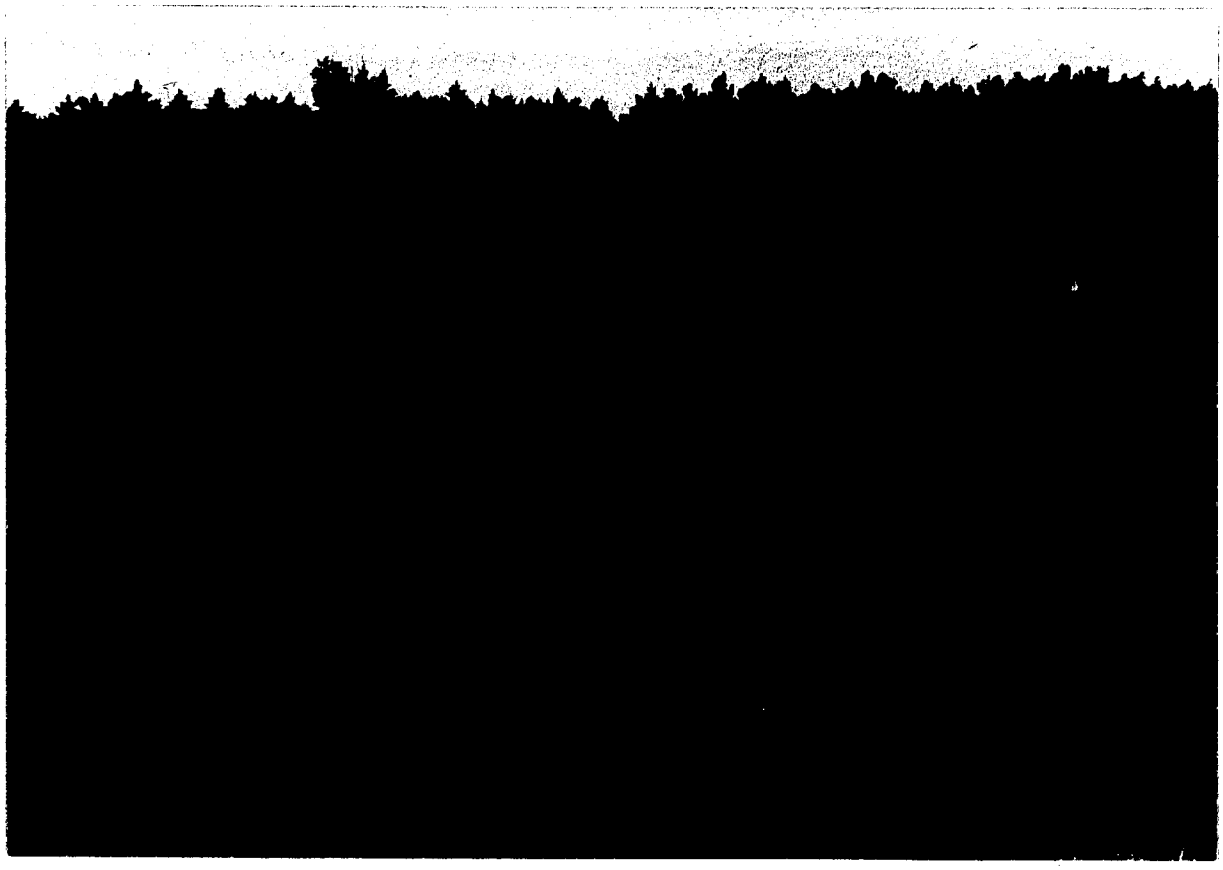


Figure 6. Dense aspen regeneration, sample area 5. May, 1966.

density was 1700 suckers per acre. The sucker stand included more than 25 clones which varied widely in density and area. Other low woody vegetation included Corylus spp., Salix spp., Rubus spp., and hardwood regeneration. Bracken fern covered most of the area.

In summary, the sample areas all had light sandy soils. Sample area 1 was a moist site with dense cover. Sample area 2 was moderately dry with sparse cover. Sample area 3 was moderately dry with uneven cover. Sample area 4 was mesic with uniform cover. Sample area 5 was dry with dense cover. Sample area 6 was moist with uneven cover. Average age of all sucker stands was 5 or 6 years in 1965. The sucker stands ranged from 7 to 10 feet in height. The maximum distance between sample areas was 80 miles.

c) Recording the Number of Oviposition Slits

In August, 1964, the 30 suckers in each sampling unit were examined, and the numbers of new O. schaumii oviposition slits and S. concolor galls were recorded for each sampling unit. Each oviposition slit, or gall, was marked with a numbered aluminum tag for later observation.

In August, 1965, the numbers of new oviposition slits and galls were again recorded for each 30-sucker sampling unit. In this second examination suckers which had been attacked in 1964 were replaced with another sucker.

A third set of data on new oviposition slits and galls was collected in August, 1966. The rule of excluding previously attacked suckers was abandoned in the 1966 counts because it had biased the 1965 counts downward disproportionately for sample area 2 where the scarcity of suckers was of real significance. Had the rule been continued, it would have been

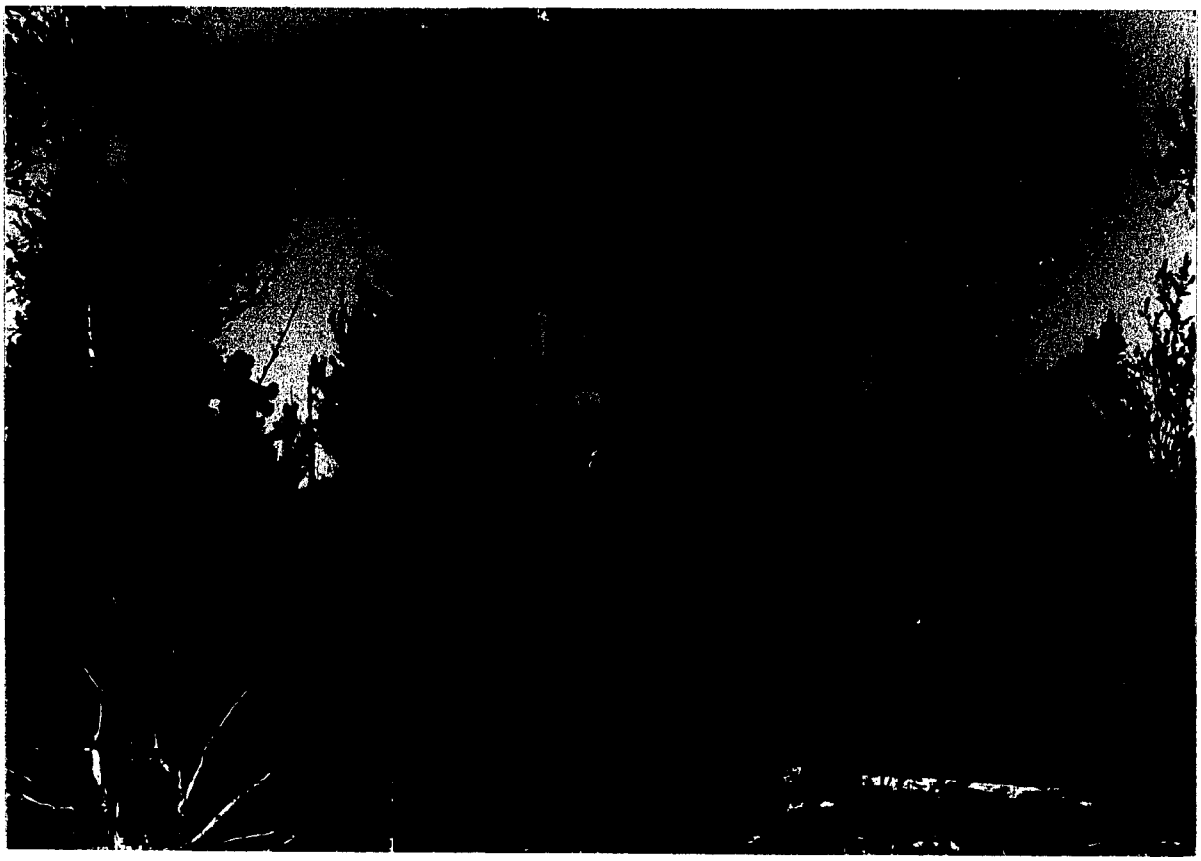


Figure 7. Aspen regeneration, sample area 6. May, 1966.

necessary to drop sample area 2 from the study because it would have been impossible to find 30 unattacked suckers for many sampling units.

The data obtained from these 1964, 1965, and 1966 counts are analyzed in the next section.

RESULTS

a) Differences in Infestations Between Sample Areas

The purpose of this thesis is to determine which environmental factors affect the distribution of O. schaumii and S. concolor oviposition slits in aspen sucker stands. If the ecological differences between sample areas were relevant to selection of oviposition sites, observed numbers of oviposition slits should differ consistently between areas. In this section histograms are used to compare sample areas with respect to observed number of oviposition slits.

The original 50 sampling units in areas 1 - 4 maintained the same order with respect to O. schaumii attacks in all 3 years, despite lower population levels in 1965 (Figure 8). Sample area numbers ranked in order of decreasing infestation were 2, 3, 4, and 1. Under a null hypothesis of no difference in infestation between sample areas, the probability that ranking in order of decreasing infestation would produce the same permutation of sample area numbers in 3 successive years is less than 1%. Unless these samples were very unusual, O. schaumii infestations differ significantly between sample areas.

The ranking of areas 1 - 4 with respect to 1965 O. schaumii infestations did not change when the data from sampling units established in 1965 were included (Figure 9). Similar pooling in 1966 reversed the ranks of areas 3 and 4.

The S. concolor data were inconsistent (Figure 10 and Figure 11). The observed rankings could occur by chance with a probability greater than 5%. Therefore, differences between sample areas with respect to S. concolor infestation cannot be declared significant. However, this

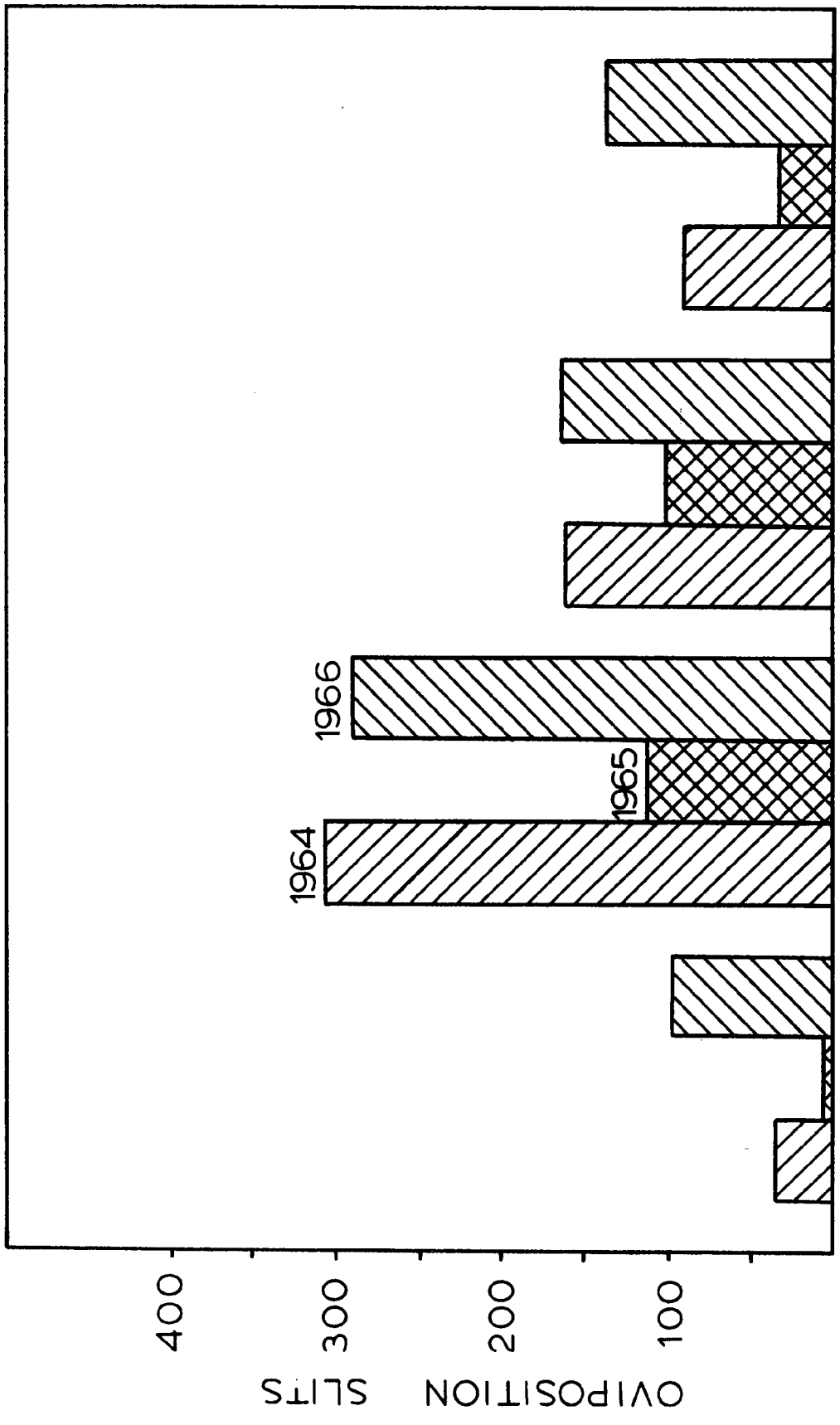


Figure 8. Number of O. schaumii oviposition slits on 1500 suckers in each sample area. (Numerical data in Appendix A)

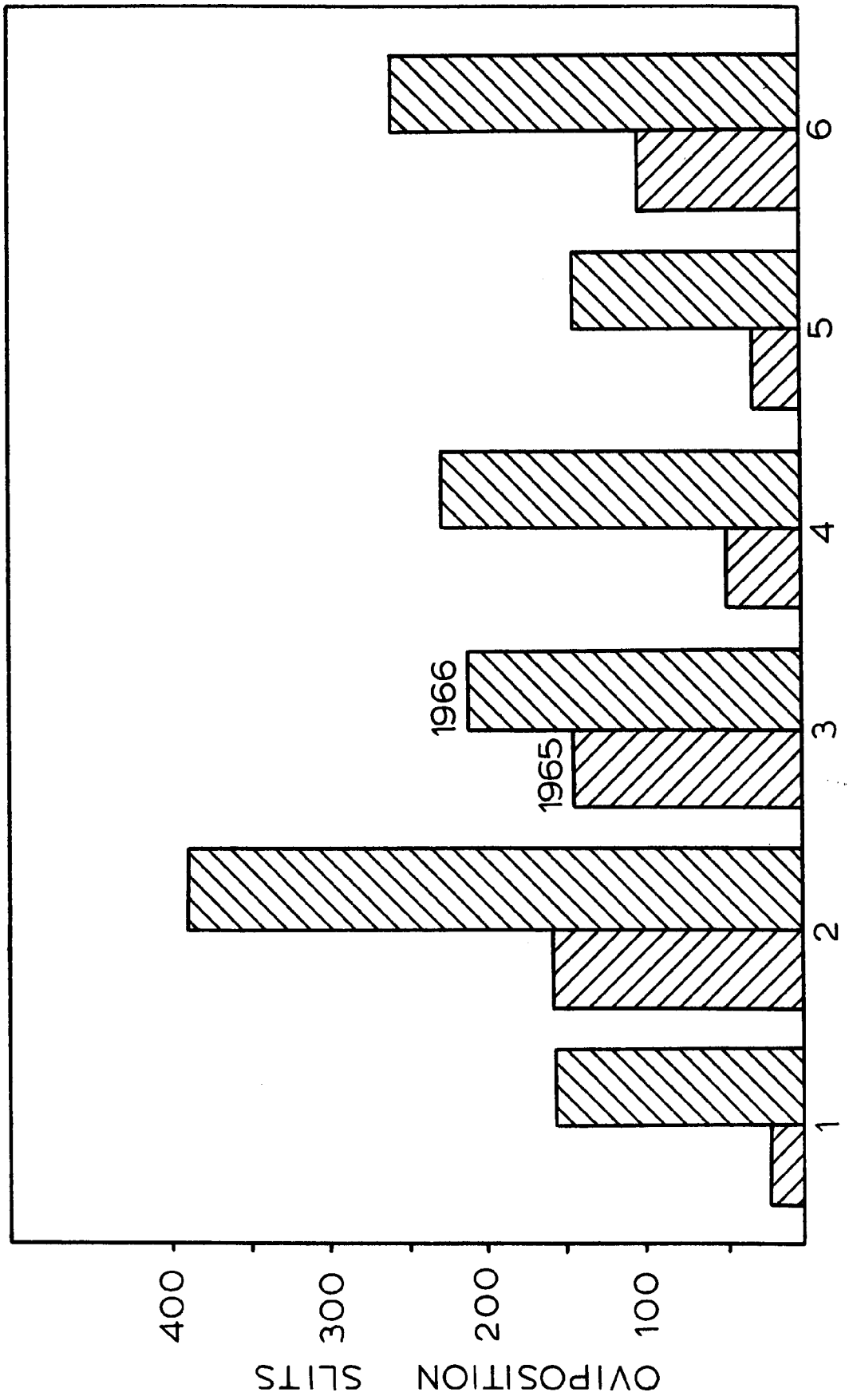


Figure 9. Number of O. schaumii oviposition slits on 2250 suckers in each sample area. (Numerical data in Appendix A)

does not preclude relationships which might be masked by the variability within sample areas. The possible existence of such relationships is best explored by reducing the level of comparison to the 30-sucker sampling unit.

b) Single Variable Analysis of Data from Sampling Units

Direct comparison of 30-sucker sampling units reduces difficulties caused by environmental variations within a sample area, and prevents possible effects of geographic separation from obscuring relationships. However, such comparisons involve the following disadvantages:

1. Large sampling error associated with the small size of a 30-sucker sampling unit.
2. Each sampling unit being strongly affected by conditions in the surrounding stand, especially near clonal or stand boundaries.
3. Unequal numbers of sampling units representing alternative environmental conditions.

Due to these three factors, high correlations are not to be expected and equations will have little predictive value.

To determine which factors were responsible for the observed variation in numbers of O. schaumii oviposition slits, and to test the possible effect of these factors on S. concolor, an IBM 709/7090 computer was used to construct contingency tables for the 1964 and 1965 data. One of these tables is shown in Appendix B. Number of attacks per 30 suckers was shown on the left side of these tables, and the classes appropriate to the variable of interest were shown across the bottom. Numbers in the matrix showed the frequency of sampling units

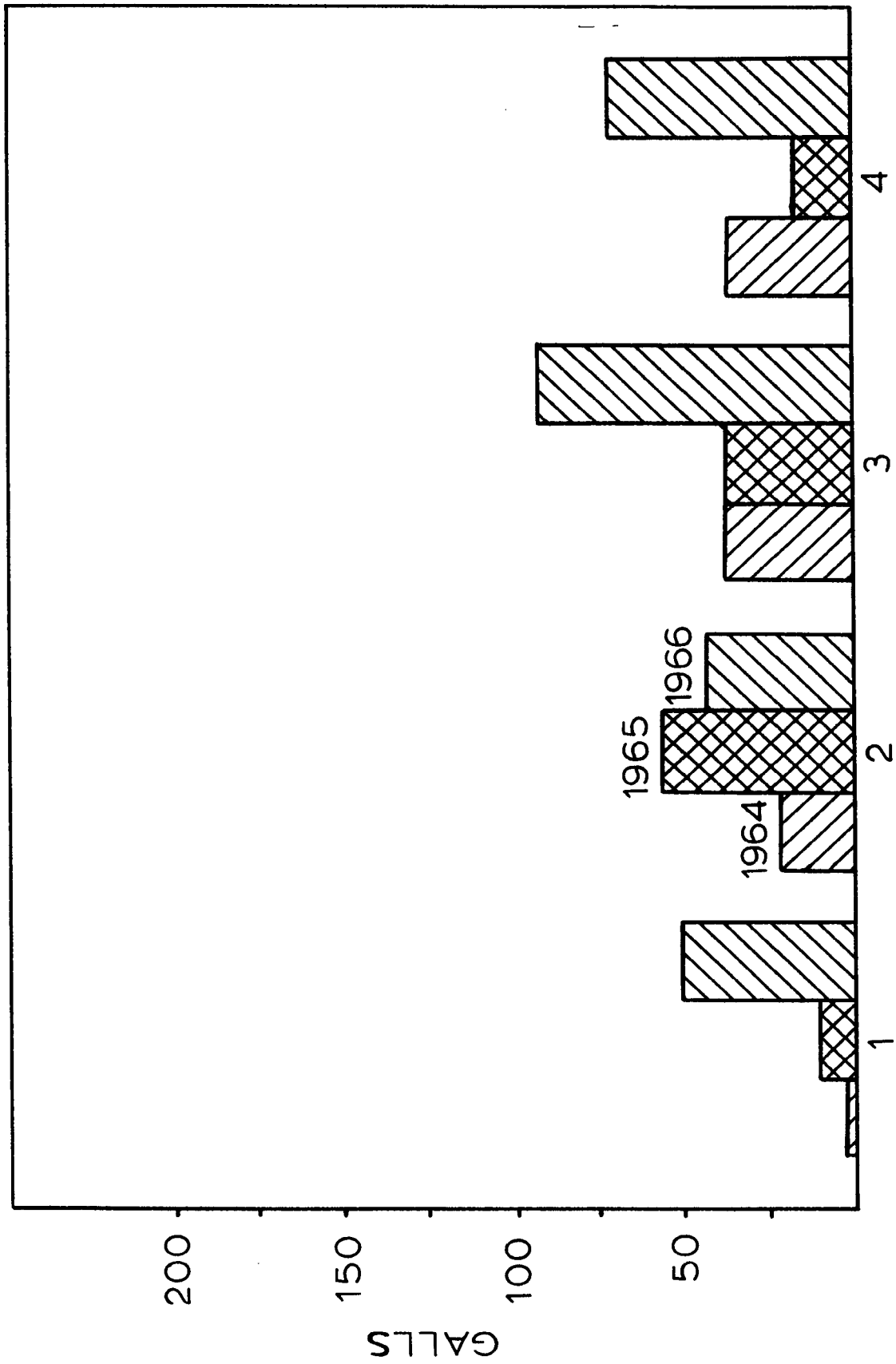


Figure 10. Number of S. concolor galls on 1500 suckers in each sample area. (Numerical data in Appendix A)

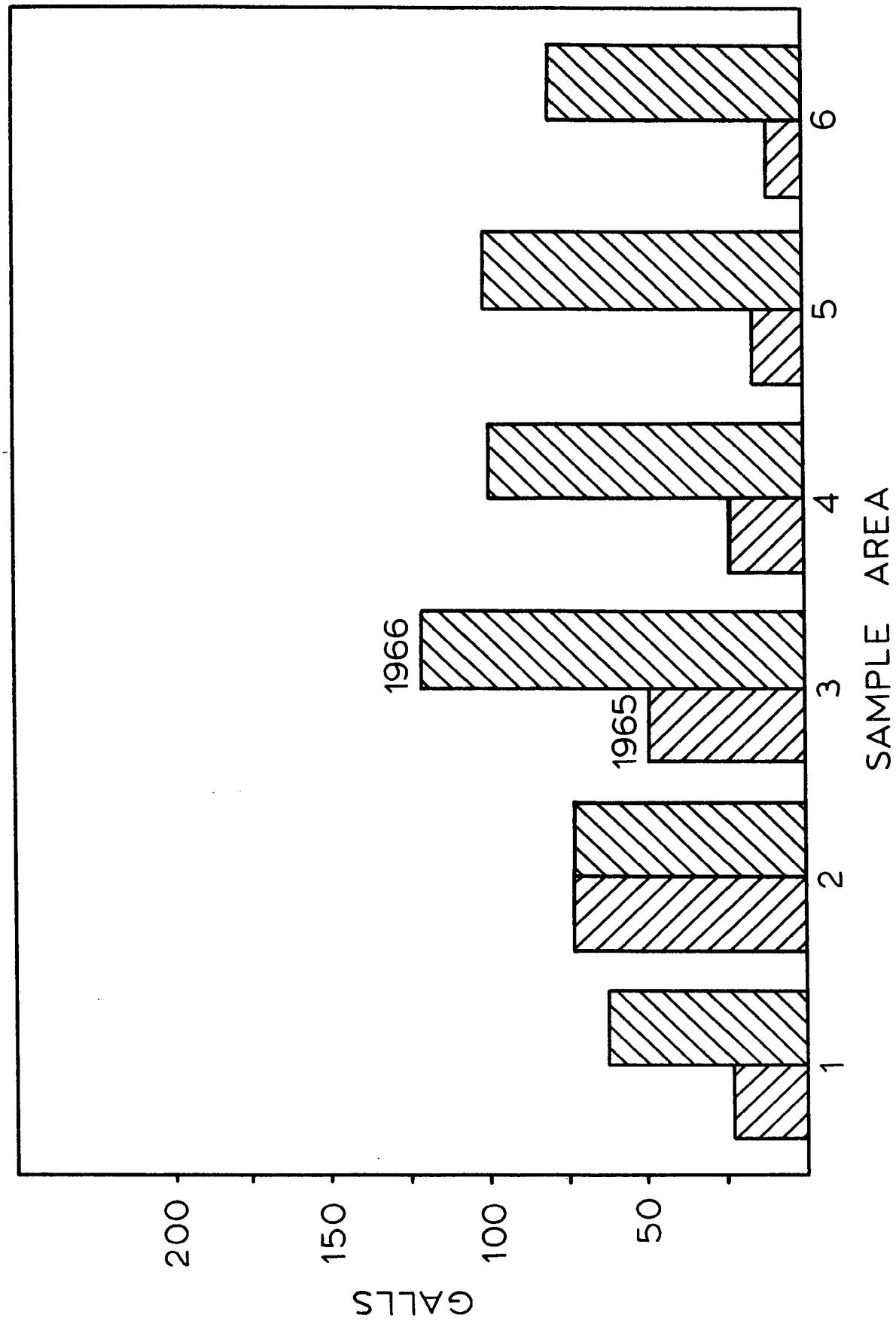


Figure 11. Number of S. concolor galls on 2250 suckers in each sample area. (Numerical data in Appendix A)

on which the given coincidence was realized. Such tables were constructed for all of the variables shown in Table I. Summarization and visual inspection of these tables indicated that only variables associated with stand density were consistently correlated with infestation.

For stand density variables measured on an interval scale, means were calculated for each interval represented by 10 or more sampling units. These means were plotted and a least squares line fitted to them. The resulting graphs are shown on the following pages. The r shown on these graphs is only an ordinal measure of fit; its presence does not imply a t test since all assumptions of the Pearson r are not met. Such simple graphs have more intuitive appeal than the multivariate regressions which are used to test significance in the next section of this paper.

For density variables measured in binary classes, i.e. brush and openings, a t test was used which incorporated unequal replication. The data in these tests were not normally distributed and should theoretically be transformed by $\log(X + k)$, where k refers to the negative binomial exponent. In view of the large sampling error, however, the complication of logarithms does not seem justified; especially since Snedecor (1956) indicates that non-normality does not greatly affect the test. To compensate for the added uncertainty, t values which barely reach the 5% level should not be regarded as significant.

Average number of O. schaumii oviposition slits per 30 suckers was inversely correlated with density of 5 to 6 year old suckers (Figure 12). The steeper slope in 1964 apparently arose from the lack of data points representing sucker densities greater than 5500 suckers per acre. Attacks did occur at densities greater than 6000 suckers per acre, but these densities were not adequately sampled until the number of sampling

units was increased in 1965. This effect and the scatter of 1966 data points suggest that a downward sloping curve with upward concavity would have given a better approximation. However, the linear formulation is satisfactory for the present purpose, with the reservation that the 1964 graph is not directly comparable with those for 1965 and 1966. The 1965 and 1966 graphs are completely comparable since they are based on the same sampling units. The more gentle slope in 1965 was apparently the result of populations being so low that many sampling units were not visited by females; this having more effect on means of low density sampling units than on means of high density units.

Multiplying the equations in Figure 12 by (3.333 X) gives equations for total number of attacks per acre in the respective years as follows:

$$Y'_{64} = 14.465X - .140X^2$$

$$Y'_{65} = 4.700X - .037X^2$$

$$Y'_{66} = 17.665X - .303X^2$$

where: Y'_i = attacks per acre

X = suckers per .01 acre

Based on these equations, mean number of attacks per acre was maximum at 2915 suckers per acre in 1964, 6351 suckers per acre in 1965, and 5166 suckers per acre in 1966. The 1964 estimate was too low for the reasons given above.

The presence of older suckers correlated with reduced O. schaumii infestation on the sample suckers (Figure 13). These older suckers were 3 to 8 feet taller than the main sucker stand. Such suckers occurred on relatively few plots, and were essentially absent from the 1964 plots.

Only in 1965 was a correlation evident between O. schaumii

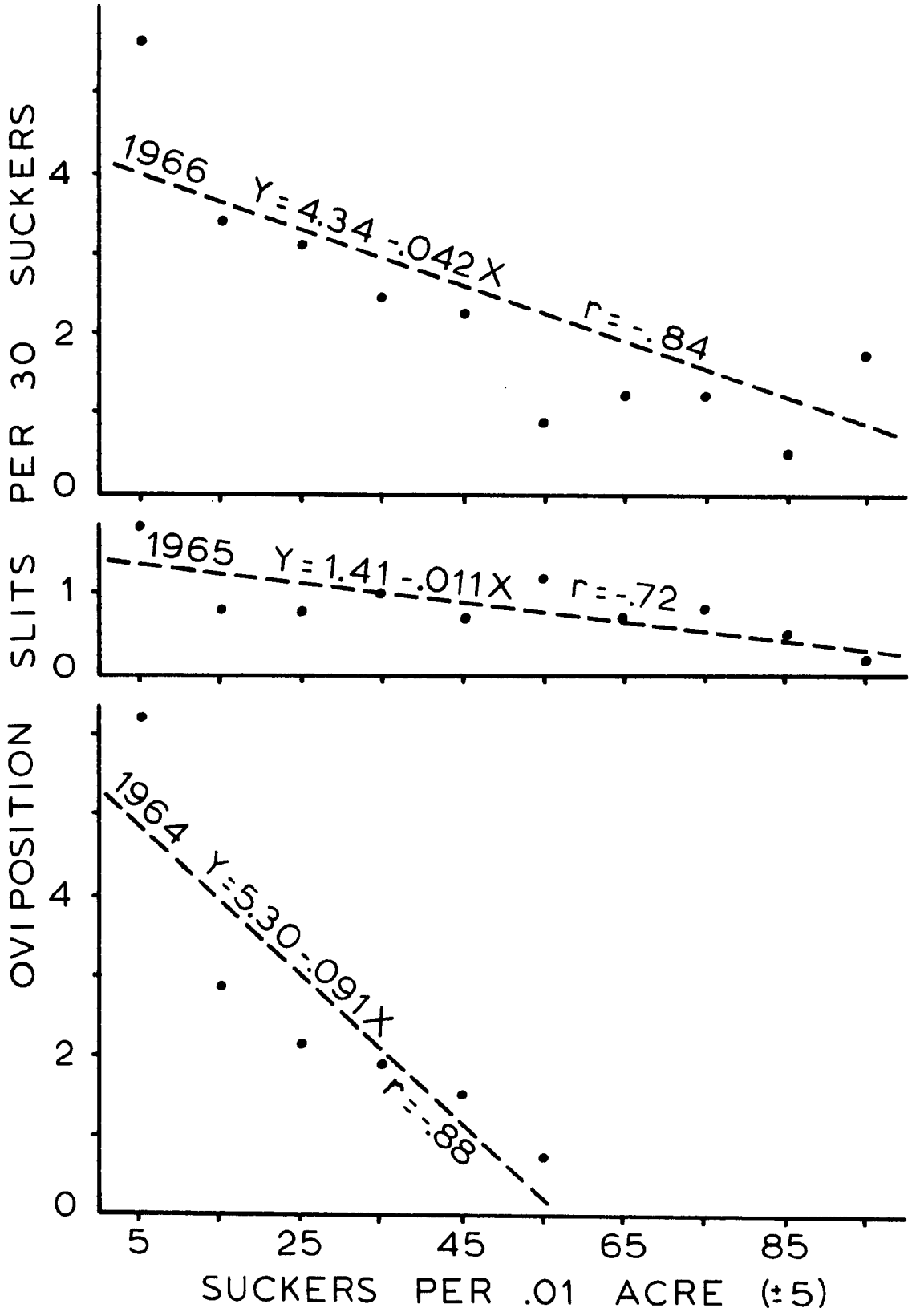


Figure 12. Comparison of O. schaumii attacks with density of suckers 5 to 6 years old (as of 1965).

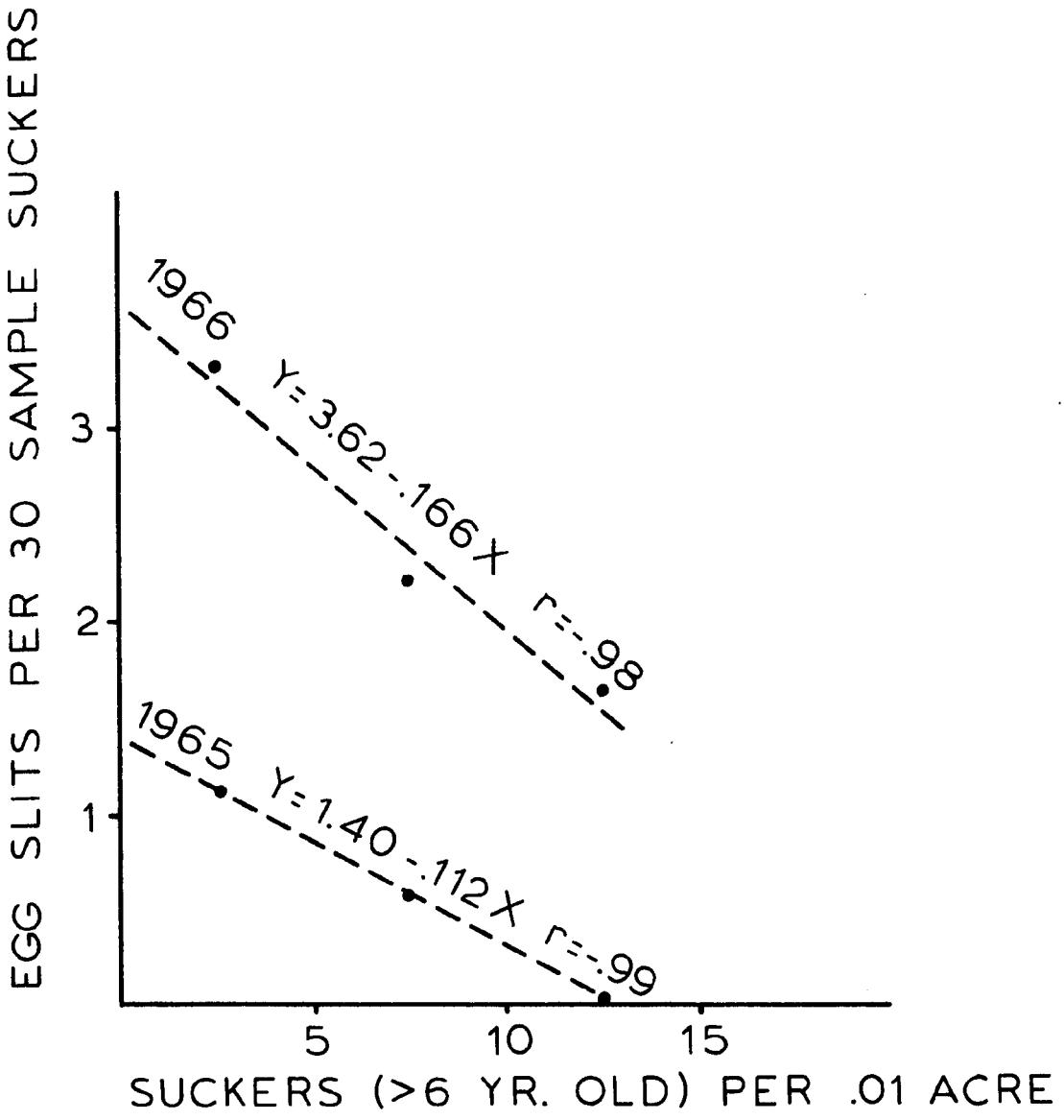


Figure 13. Comparison of O. schaumii attacks with density of suckers more than 6 years old.

infestation and density of the overstory (Figure 14).

In all three years O. schaumii infestations were more severe on sampling units lacking brush than on units containing brush (Table IV).

Table IV. Comparison of O. schaumii infestations in the presence and absence of brush

Statistic	1964	1965	1966
Mean number of egg slits per 30 suckers on sampling units lacking brush	5.90	2.14	4.73
Mean number of egg slits per 30 suckers on sampling units containing brush	2.07	.80	2.81
Mean difference	3.83	1.34	1.92
Std. error of the mean difference	.61	.16	.39
t value	6.24***	8.48***	4.92***

***Significance level = .001 (t = 3.29+)

In all three years O. schaumii infestations were more severe on sampling units with an opening than on units with uniform cover (Table V). Many of these openings occurred along clonal boundaries.

Response of S. concolor infestation to conditions of increasing host density was similar to that of O. schaumii. Mean number of galls per 30 suckers decreased with increasing density of the aspen sucker stand in all three years (Figure 15).

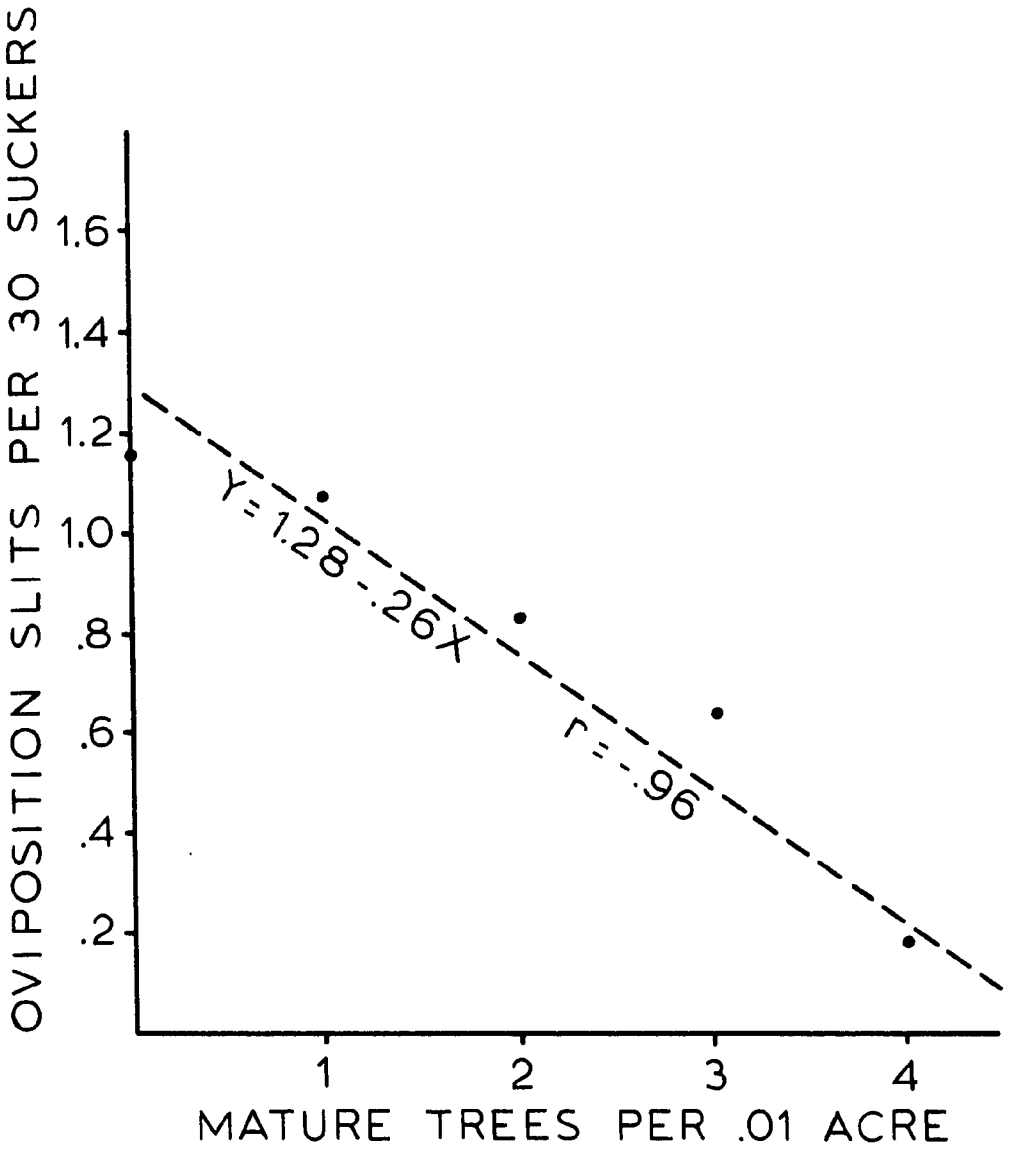


Figure 14. Comparison of 1965 O. schaumii attacks with density of mature trees.

Table V. Comparison of O. schaumii infestations in the presence and absence of an opening

Statistic	1964	1965	1966
Mean number of egg slits per 30 suckers on sampling units with 25% or more of area open	4.10	1.37	3.80
Mean number of egg slits per 30 suckers on sampling units with uniform cover	1.93	.62	2.36
Mean difference	2.17	.75	1.44
Std. error of the mean difference	.51	.15	.27
t value	4.25***	5.00***	5.33***

***Significance level = .001 (t = 3.29+)

Multiplying the equations in Figure 15 by (3.333 X) gives the following equations for total number of S. concolor galls per acre:

$$Y'_{64} = 2.300X - .027X^2$$

$$Y'_{65} = 2.166X - .020X^2$$

$$Y'_{66} = 5.000X - .033X^2$$

where: Y'_i = galls per acre

X = suckers per .01 acre

Maximum infestation occurred at 4259 suckers per acre in 1964, 5414 suckers per acre in 1965, and 7576 suckers per acre in 1966.

As with O. schaumii, the presence of older suckers correlated with reduced S. concolor infestation on the sample suckers (Figure 16).

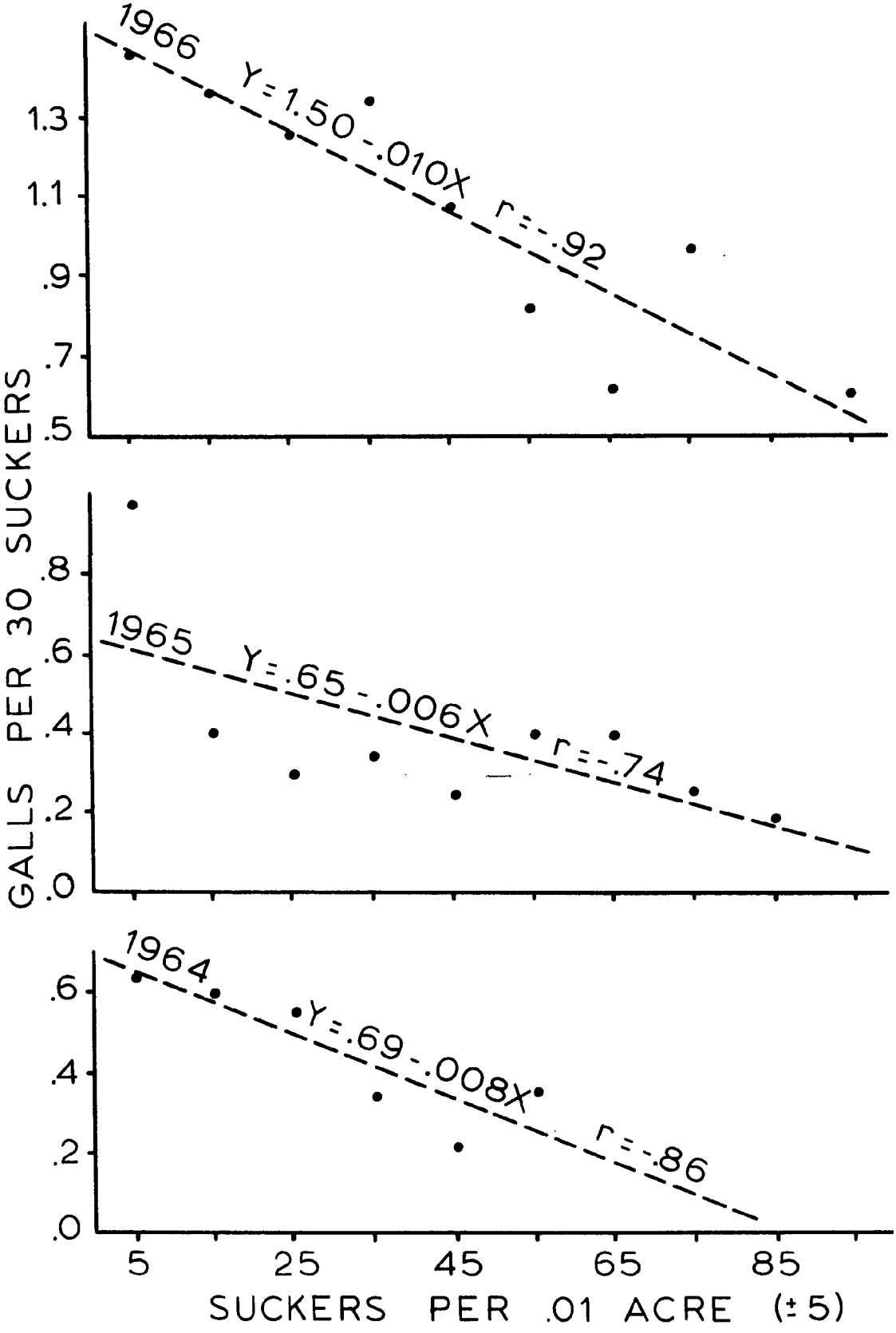


Figure 15. Comparison of S. concolor attacks with density of suckers 5 to 6 years old (as of 1965).

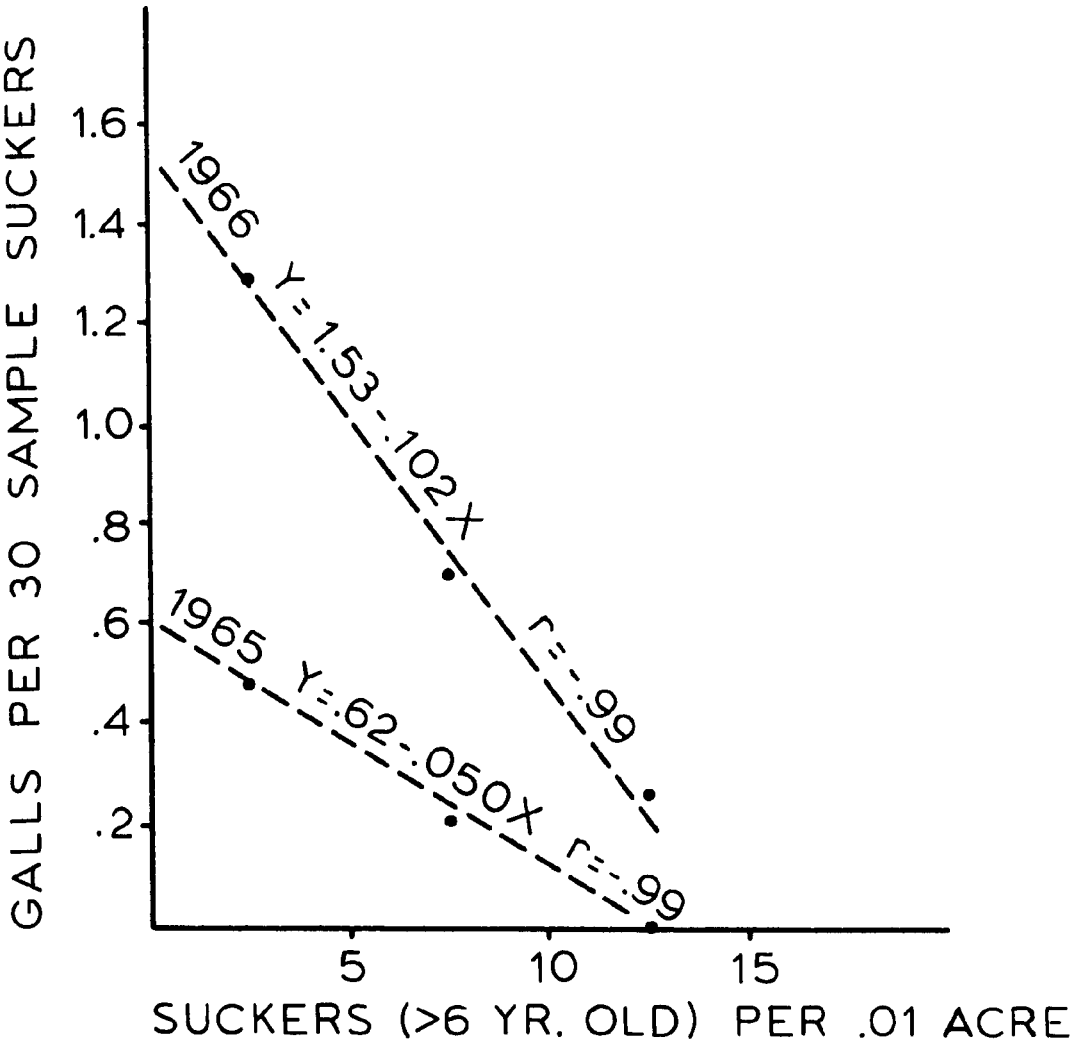


Figure 16. Comparison of S. concolor attacks with density of suckers more than 6 years old.

Again, no equation is given for 1964 since such suckers were almost nil on the 1964 sampling units.

Only in 1966 was S. concolor infestation correlated with overstory density (Figure 17).

The presence of brush did not have a consistent effect on S. concolor infestation (Table VI).

Table VI. Comparison of S. concolor infestations in the presence and absence of brush

Statistic	1964	1965	1966
Mean number of galls per 30 suckers on sampling units lacking brush	.45	.87	1.03
Mean number of galls per 30 suckers on sampling units containing brush	.52	.37	1.23
Mean difference	.07	.50	.20
Std. error of the mean difference	.17	.21	.21
t value	$.41^{NS}$	2.38*	$.95^{NS}$

NS not significant
* significance level = .05 (t = 1.96+)

In all three years S. concolor infestations were more severe on sampling units with an opening than on sampling units with uniform cover (Table VII).

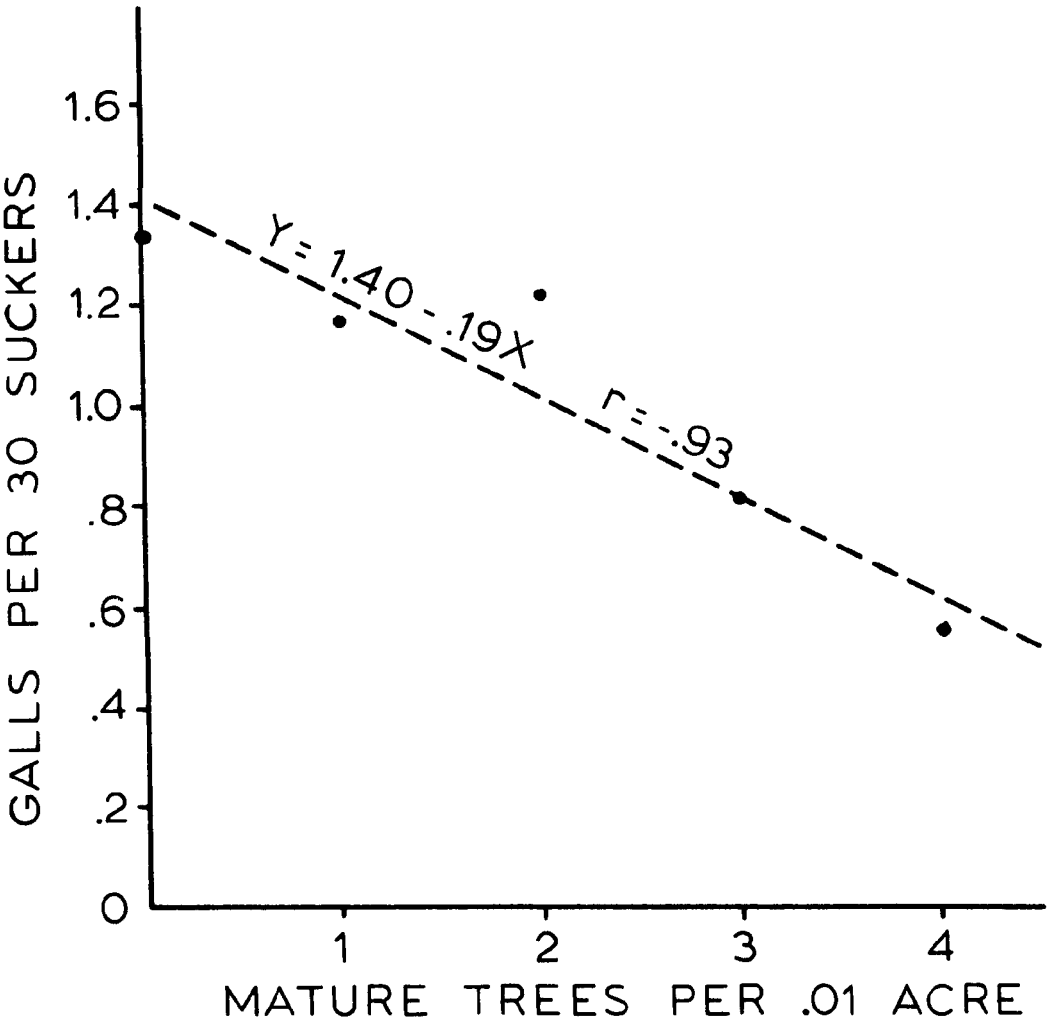


Figure 17. Comparison of 1966 S. concolor attacks with density of mature trees.

Table VII. Comparison of S. concolor infestations in the presence and absence of an opening

Statistic	1964	1965	1966
Mean number of galls on sampling units with 25% or more of open area	.69	.57	1.52
Mean number of galls on sampling units with uniform cover	.32	.31	.85
Mean difference	.37	.26	.67
Std. error of the mean difference	.15	.09	.15
t value	2.47*	2.89**	4.47***

* significance level = .05 (t = 1.96+)
** significance level = .01 (t = 2.58+)
*** significance level = .001 (t = 3.29+)

These comparisons of sampling units indicate that both Q. schaumii and S. concolor attacks per sucker decrease with increasing aspen density. Q. schaumii reacts more strongly to factors associated with stand density since even the presence of brush shows a significant effect. Multivariate regression analysis provides significance tests for all variables examined in this section and is more appropriate for evaluating the sporadic correlation of infestations with overstory density.

c) Multivariate Regression Analysis of Data from Sampling Units

A final step in testing these relationships between attacks per sucker

and stand density was to use multivariate regression analysis. In this approach, the method of least squares is used to generate an equation of the form:

$$Y = b_0 + b_1X_1 + b_2X_2 + \ldots + b_nX_n$$

where Y is the dependent variable and the X_i are the independent variables. A "t" test for significance of a variable is given by the formula:

$$t = \frac{b_i}{s_{b_i}}$$

where: b_i = partial regression coefficient of X_i

s_{b_i} = standard error of b_i

The primary purpose of Figures 12 - 17 was graphic presentation. In those graphs, unequal weighting and deletion of points with low replication precluded statistical tests of the fitted lines. The multivariate regressions described in Appendices C - H provided statistical tests of significance. In the multivariate regressions each sampling unit of 30 suckers was treated as an observation and all units were included.

Attacks per 30-sucker sampling unit are shown in the next section to follow the negative binomial distribution rather than the normal distribution. Therefore, the multivariate regressions were subject to error arising from this source. Transformations were not used because the sampling error was large relative to errors introduced by non-normality.

Six regressions, one for each species in each year, were calculated according to the Gauss - Doolittle method (Steel and Torrie, 1960). The dependent variable was again attacks per 30 suckers. In these regressions

there seemed no further reason for separately treating suckers of different ages. All aspen suckers were combined into a single variable which was expressed as number per .01 acre. Mature trees were also entered as number per .01 acre. Both brush and openings were represented by 0 when absent and 1 when present.

Multivariate regressions pertaining to O. schaumii confirmed the results of graphical analysis. Sucker density and brush were significant in every case, often at extremely high levels (Table VIII). Mature trees showed correlation at the 5% level only in 1965, and therefore should not be regarded as significant. Presence of an opening was significant at the 5% level in all cases, but the t values were much smaller than those in Table V due to the correlation of openings with sucker density.

The 1964 S. concolor regression confirmed the inadequacy of the original number of sampling units. None of the variables showed significance in this regression. Only sucker density was consistently correlated in the 1965 and 1966 S. concolor regressions.

R^2 values for O. schaumii were twice as high as those for S. concolor; however, none of the regressions were sufficiently precise for predictive purposes.

d) Frequency Distribution of Data from Sampling Units

In population studies it is often important to know the statistical distribution which the attacks follow. Such knowledge is a prerequisite for designing more efficient sampling schemes.

The distributions of attacks per 30 suckers observed here were obviously non-normal, being highly skewed toward the smaller values.

Table VIII. Results of multivariate regression analysis relating attacks per 30 suckers to stand density

Species	Year	R^2	t levels of independent variables			
			Sucker density	Presence of brush	Mature trees	Presence of opening
O. schaumii	1964	.289	3.39***	5.34***	1.47 N.S.	2.60**
O. schaumii	1965	.155	2.52*	6.01***	2.52*	3.22**
O. schaumii	1966	.209	7.76***	3.62***	.76 N.S.	2.05*
S. concolor	1964	.051	1.37 N.S.	1.14 N.S.	1.74 N.S.	1.69 N.S.
S. concolor	1965	.079	3.26**	3.64***	.75 N.S.	1.39 N.S.
S. concolor	1966	.062	2.77**	1.85 N.S.	2.22*	2.88**

N.S. not significant
* significance level = .05 (t = 1.96+)
** significance level = .01 (t = 2.58+)
*** significance level = .001 (t = 3.29+)

A distribution with its mode in the low end of the range commonly arises in one of two ways.

The first situation prevails when there are many sample plots of a given size, each having the same probability of occurrence. In this case the first attack in no way influences the probability of further attacks on the same plot, i.e. the distribution is random. The Poisson series describes such a distribution. Under this system each unit has the population mean as its expected frequency, and the variance should equal the mean. The mean, the parameter of the Poisson series, describes the distribution according to the following formula:

$$P(X = k) = \frac{e^{-m} m^k}{k!}$$

where: P( ) is read "the probability that"

m = mean

k = current value being considered

e = base of the Naperian logarithms

Applicability of the Poisson series may be easily determined by ascertaining whether the mean is equal to the variance within the limits of chance. Chi-square is a valid test for this purpose, and the test criterion is:

$$\chi^2_{n-1} = \frac{n s^2}{m}$$

where: n = number of observations in the distribution

s^2 = variance

m = mean

For the 1964 O. schaumii distribution:

$$\chi^2_{199} = \frac{(200)\ (14.15)}{3.00} = 943$$

which is far larger than would be expected due to chance alone. Therefore, the variance was significantly larger than the mean, and the observed distribution did not fit the Poisson series. Since the 1964 O. schaumii distribution departed so widely from the Poisson, there was no need to test the others in that respect.

The second situation prevails when the population exhibits "clumping". This is the case when the first attack upon a plot increases the probability that this plot will receive additional attacks. Such a distribution is non-random, and the variance is significantly larger than the mean.

The most common clumped distribution is the negative binomial. The negative binomial is an extension of the Poisson series in which the population mean is not constant but varies continuously in a distribution proportional to that of chi-square. As the variance approaches the mean, this distribution approaches the Poisson. On the other hand, if the clumping increases and the zero plots are ignored, it approaches Fisher's logarithmic series. The negative binomial is defined by the mean and a positive exponent k. The theoretical distribution is obtained by expansion of the expression $(q-p)^{-k}$ where $p = m/k$ and $q = 1 + p$. The probability that a plot will contain x individuals is given by the following formula:

$$P_x = \frac{(k + x - 1)!}{x!\ (k - 1)!} \cdot \frac{R^x}{q^k}$$

where: $R = p/q = m/(k+m)$

m = mean

The above chi-square test for fit of the Poisson showed that the observed data exhibited clumping. Therefore, the negative binomial distribution should be appropriate. However, test of fit was not as simple as for the Poisson. There are three methods for estimating the coefficient k. The efficiency of these methods varies directly with the difficulty involved in computing them.

According to the first and second moment solution:

$$k = \frac{m^2}{s^2 - m}$$

where m = mean

s^2 = variance

However, this method gives an efficiency of 90% in only the following three cases: (1) $k/m > 6$ with small values of m, (2) $k > 13$ with large values of m, and (3) $(k + m)(k + 2)/m \geq 15$ with intermediate values of k.

The second method of estimating k is based on the proportion of zero samples and requires an iterative solution to balance the equation:

$$\hat{k}_2 \log(1 + m/\hat{k}_2) = \log(N/f_0)$$

where: m = mean

N = number of observations

f_0 = frequency of zero samples

To estimate k with 90% efficiency by this method, at least 1/3 of the units must be empty; but if $m < 10$, enough more empty units are required

to satisfy the inequality $(m + .17)(f_0/N - .32) > .20$.

The third method of estimating k is Fisher's maximum likelihood procedure (Bliss and Fisher, 1953). This requires iterative interpolation for z = 0 in the equation:

$$z_i = \sum\left(\frac{Ax}{k_i' + X}\right) - N \ln\left(1 + \frac{m}{k_i'}\right)$$

where: Ax = the accumulated frequency in all units containing more than X organisms.

k_i' = ith estimate of k

X = observational value (1, 2, 3, ..., n)

N = number of observations

m = mean

ln = Naperian logarithm

This method is fully efficient for most combinations of the mean and k; and is therefore the most desirable. Its primary disadvantage is the large amount of calculation involved. This can be overcome by expressing the procedure as a computer program. I have done so using the Michigan Algorithm Decoder programing language. This program together with an explanation of its use is given in Appendix I. The program includes a chi-square test. Chi-square is valid for this purpose once k has been efficiently estimated.

All six observed distributions were tested for conformity to the negative binomial distribution according to the algorithm in Appendix 9. Chi-square calculations are presented in Appendices J - O. The distributions observed for both species in all three years conformed very well to the negative binomial distribution since there was a 25% probability

that the greatest deviation would arise from chance alone (Table IX). The exponent k was small and quite stable for 1964 and 1965, but doubled for both species in 1966. The observed k values of .5 to 1.5 indicated a high degree of clumping. These results agree with those of Waters (1955) and Knight (1960) who found the negative binomial distribution effective in describing insect populations.

Table IX. Summary of tests for fit of the negative binomial distribution

Species	Year	Mean	k	χ^2	DF	Probability
O. schaumii	1964	3.005	.949	3.685	6	72%
O. schaumii	1965	1.011	.696	4.426	5	50%
O. schaumii	1966	3.111	1.655	10.241	8	25%
S. concolor	1964	.500	.624	1.802	2	42%
S. concolor	1965	.447	.618	.766	2	70%
S. concolor	1966	1.202	1.202	4.488	4	30%

DISCUSSION

a) Weather During the Oviposition Period

Only 256 O. schaumii attacks were recorded in 1965 on the same 200 sampling units which produced 601 and 698 attacks in 1964 and 1966 respectively. The observations of Grimble (1966) suggest that this difference may be due to the summer of 1965 being cold and wet, while the summers of 1964 and 1966 were warm and dry. He reported 1965 weather data recorded in sample area 4 where O. schaumii and S. concolor adults were kept on caged suckers. Nighttime minimum temperatures in sample area 4 were 19°F and 25°F on June 29 and June 30, 1965, respectively. These low temperatures caused heavy mortality among the caged beetles. Similar mortality in wild populations might help to explain reduced O. schaumii infestation in 1965. This factor does not, however, account for S. concolor attacks being least prevalent in 1964.

b) Influence of Stand Density on Infestation

The inverse correlation of O. schaumii oviposition with increasing sucker density was stronger than that for S. concolor. Furthermore, O. schaumii oviposition slits were consistently less numerous in the presence of brush; this not being true of S. concolor galls. These differences indicate that O. schaumii and S. concolor do not occupy a common ecological niche.

Selection pressures generating such a behavioral response in O. schaumii are easily conceived. Host resistance is greater in vigorous clones. In fact, many O. schaumii larvae appear to be overgrown before they can enter the xylem. Natural selection should thus favor progeny

of adults ovipositing in low vigor stands on poor sites. Both low vigor and poor site quality give rise to sparsely stocked sucker stands. Stimuli associated with sparse sucker stands are therefore appropriate for discrimination between favorable and unfavorable oviposition sites.

The girdling effect of S. concolor galls interferes with translocation and growth of the host, thus increasing the probability of larval survival. Selection of low vigor hosts would therefore not seem so crucial to S. concolor.

Sensory and behavioral analyses would be required to define the primary stimulus responsible for the observed behavior of O. schaumii. High temperatures did not make the dense stand in sample area 5 more attractive, so temperature is probably not the primary stimulus. Heavily attacked, sparse clone(s) adjacent to the lightly attacked, dense clone(s) in sample area 3 suggest that relative light intensity may be important. There are several possibilities with respect to stimuli; but in any case, the basic conditions exist.

c) Implications for Management

Graham, Harrison, and Westell (1963) recommend complete clearcutting and soil scarification as a means of regenerating aspen stands. This results in maximum density of suckers in the new stand. They also recommend that management efforts be concentrated on the better sites. These recommendations will clearly minimize the damage caused by O. schaumii and S. concolor. Dense stands offer the best insurance of obtaining an adequate number of crop trees which have not been severely attacked. On good sites growth will be rapid and the main stem of the suckers will be susceptible to attack for a shorter period of time.

O. schaumii is likely to be most troublesome in sparse sucker stands on poor sites. In such stands every sucker may be heavily infested. This will accentuate the poor stocking, and the only crop trees grown may contain stain or canker following the boring activities.

In some cases sparse stocking may be unavoidable and use of sprays necessary to prevent undue damage; a case in point being a severely attacked outplanting of aspen hybrids near Marenisco, Michigan.

SUMMARY AND CONCLUSIONS

This study was conducted to determine the influence of environmental factors, especially host density, upon the distribution of O. schaumii and S. concolor oviposition slits in aspen sucker stands. The results obviate any possibility of these two species occupying a common ecological niche, and are valuable in formulating silvicultural treatments to minimize damage from these two species.

The research was performed during the summers of 1964, 1965, and 1966 in the Upper Peninsula of Michigan. Six sample areas were established; four located in Iron County, one in Gogebic County, and one in Dickinson County. Aspen suckers on the sample areas ranged from 7 to 10 feet in height and averaged 5 to 6 years old in 1965. Seventy-five sampling units of 30 suckers each were established in each area.

Experimental method consisted of counting new O. schaumii and S. concolor oviposition slits on the sampling units in August of each year. Ecological data recorded from each sampling unit in 1965 provided the independent variables for the analysis.

For both O. schaumii and S. concolor, multivariate regression analysis revealed a decrease in oviposition frequency per sucker with increasing sucker density; however, the correlation was much stronger for O. schaumii than for S. concolor. For both species, the total number of attacks per acre was maximum at stand densities of about 6000 suckers per acre. O. schaumii oviposition slits were consistently less frequent in the presence of brush, while S. concolor oviposition showed no consistent tendencies with respect to presence or absence of brush. Correlation with infestation was observed only for the components of stand density.

Attacks of both species followed the negative binomial frequency distribution.

Interspecific differences in the relationship of oviposition to stand density indicate that O. schaumii and S. concolor do not occupy a common ecological niche.

Silvicultural treatments designed to produce dense, vigorous aspen regeneration should minimize damage from O. schaumii and S. concolor.

Appendix A. Number of O. schaumii oviposition slits and S. concolor galls in each sample area

Species	Year	Area 1		Area 2		Area 3		Area 4		Area 5	Area 6
		# of suckers		# of suckers		# of suckers		# of suckers		# of suckers	# of suckers
		1500	2250	1500	2250	1500	2250	1500	2250	2250	2250
O. schaumii	1964	38	--	308	--	163	--	92	--	--	--
O. schaumii	1965	4	12	114	159	103	146	35	50	33	55
O. schaumii	1966	99	158	292	390	167	212	140	230	148	262
S. concolor	1964	2	--	22	--	39	--	37	--	--	--
S. concolor	1965	11	24	57	73	38	50	18	24	18	12
S. concolor	1966	51	63	43	73	92	122	72	100	102	81

Appendix B. Sample contingency table. Number of 1964 S. concolor galls vs. aspect of sampling unit

SAPERDA 1964

ATTACKS									
10	1								
9									
8									
7									
6									
5									
4	1				1			1	
3	2					1	1		
2	5	1	1	2	1				1
1	26	3	2	2	4	3	1		3
0	185	43	7	27	26	20	22	13	44
ASPECT	0	1	2	3	4	5	6	7	8

Appendix C. Multivariate regression relating 1964 *O. schaumii* infestations to stand density

Variables	Coded variables
Y = number of oviposition slits per 30 suckers	$Y' = .1 \times Y$
X_1 = number of suckers per 1/100 acre	$X_1' = .01 \times X_1$
X_2 = 0 when brush absent, 1 when brush present	$X_2' = X_2$
X_3 = number of mature trees per 1/100 acre	$X_3' = .1 \times X_3$
X_4 = 0 when cover uniform, 1 when 25% or more of sampling unit open	$X_4' = X_4$

Degrees of freedom = 195

$R^2 = .288884$

$R = .537479$

$s^2_{y.1234} = .102728$

Coded variable	Coefficient	Std. error	t value
X_1'	-.413108	.121825	3.390995
X_2'	-.298195	.055822	5.341890
X_3'	-.244013	.166313	1.467191
X_4'	.128189	.049366	2.596706

Decoded equation:

$$Y = 3.313521 - .004131 X_1 - .298195 X_2 - .024401 X_3 + .128189 X_4$$

Appendix C. (continued)

Forward solution

	A matrix				G matrix
	X_1'	X_2'	X_3'	X_4'	Y'
X_1'	9.265950	5.429500	-2.048650	-4.154500	-5.479550
X_2'		36.995000	.673500	-5.745000	-14.175500
X_3'			4.769550	-4.148500	-1.050150
X_4'				49.995000	10.850500
A_{1j}	9.265950	5.429500	-2.048650	-4.154500	-5.479550
B_{1j}	1.000000	.585962	-.221094	-.448362	-.591364
A_{2j}		33.813519	1.873930	-3.310619	-10.964689
B_{2j}		1.000000	.055419	-.097908	-.324269
A_{3j}			4.212754	-4.883564	-1.653990
B_{3j}			1.000000	-1.159233	-.392614
A_{4j}				42.146955	5.402792
B_{4j}				1.000000	.128189

Backward solution

	C matrix			
	C_{i1}	C_{i2}	C_{i3}	C_{i4}
C_{1j}	.144469	-.020117	.079029	.016251
C_{2j}		.030329	-.012229	.000799
C_{3j}			.269258	.027504
C_{4j}				.023726

Appendix D. Multivariate regression relating 1965 *O. schaumii* infestations to stand density

Variables	Coded variables
Y = number of oviposition slits per 30 suckers	$Y' = .1 \times Y$
X_1 = number of suckers per 1/100 acre	$X_1' = .01 \times X_1$
X_2 = 0 when brush absent, 1 when brush present	$X_2' = X_2$
X_3 = number of mature trees per 1/100 acre	$X_3' = .1 \times X_3$
X_4 = 0 when cover uniform, 1 when 25% or more of sampling unit open	$X_4' = X_4$

Degrees of freedom = 445

$R^2 = .154974$

$R = .393668$

$s^2_{y.1234} = .021285$

Coded variable	Coefficient	Std. error	t value
X_1'	-.082371	.032635	2.524007
X_2'	-.116136	.019315	6.012736
X_3'	-.123938	.049235	2.517274
X_4'	.048381	.015035	3.217891

Decoded equation:

$$Y = 1.123022 - .000823\, X_1 - .116136\, X_2 - .012394\, X_3 + .048381\, X_4$$

Appendix D. (continued)

Forward solution

	A matrix				G matrix
	X_1'	X_2'	X_3'	X_4'	Y'
X_1'	26.234445	5.672223	-5.192111	-16.188888	-2.959444
X_2'		59.111112	1.464445	-8.444444	-7.922222
X_3'			10.643578	-5.587777	-1.331888
X_4'				112.277778	8.438889
A_{1j}	26.234445	5.672223	-5.192111	-16.188888	-2.959444
B_{1j}	1.000000	.216212	-.197911	-.617085	-.112807
A_{2j}		57.884709	2.587040	-4.944200	-7.282356
B_{2j}		1.000000	.044692	-.085414	-.125807
A_{3j}			9.500382	-8.570781	-1.592127
B_{3j}			1.000000	-.902151	-.167585
A_{4j}				94.133415	4.554320
B_{4j}				1.000000	.048381

Backward solution

	C matrix			
	C_{i1}	C_{i2}	C_{i3}	C_{i4}
C_{ij}	.050021	-.004335	.029381	.008349
C_{2j}		.017507	-.004272	.000479
C_{3j}			.113904	.009584
C_{4j}				.010623

Appendix E. Multivariate regression relating 1966 *O. schaumii* infestations to stand density

Variables	Coded variables
Y = number of oviposition slits per 30 suckers	$Y' = .1 \times Y$
X_1 = number of suckers per 1/100 acre	$X_1' = .01 \times X_1$
X_2 = 0 when brush absent, 1 when brush present	$X_2' = X_2$
X_3 = number of mature trees per 1/100 acre	$X_3' = .1 \times X_3$
X_4 = 0 when cover uniform, 1 when 25% or more of sampling unit open	$X_4' = X_4$

Degrees of freedom = 445

$R^2 = .209117$

$R = .457294$

$s^2_{y.1234} = .078847$

Coded variable	Coefficient	Std. error	t value
X_1'	-.487455	.062802	7.761775
X_2'	-.134500	.037149	3.620555
X_3'	-.072490	.094769	.764912
X_4'	.059287	.028949	2.047980

Decoded equation:

$$Y = 3.356709 - .004875 X_1 - .134500 X_2 - .007249 X_3 + .059287 X_4$$

Appendix E. (continued)

Forward solution

	A matrix				G matrix
	X_1'	X_2'	X_3'	X_4'	Y'
X_1'	26.234445	5.672223	-5.192111	-16.188888	-14.134444
X_2'		59.111112	1.464445	-8.444444	-11.322222
X_3'			10.643578	-5.587777	1.231112
X_4'				112.277778	16.088889
A_{1j}	26.234445	5.672223	-5.192111	-16.188888	-14.134444
B_{1j}	1.000000	.216212	-.197911	-.617085	-.538774
A_{2j}		57.884709	2.587040	-4.944200	-8.266176
B_{2j}		1.000000	.044692	-.085414	-.142804
A_{3j}			9.500382	-8.570781	-1.196823
B_{3j}			1.000000	-.902151	-.125976
A_{4j}				94.133415	5.580973
B_{4j}				1.000000	.059287

Backward solution

	C matrix			
	C_{i1}	C_{i2}	C_{i3}	C_{i4}
C_{1j}	.050021	-.004335	.029381	.008349
C_{2j}		.017507	-.004272	.000479
C_{3j}			.113904	.009584
C_{4j}				.010623

Appendix F. Multivariate regression relating 1964 S. concolor infestations to stand density

Variables	Coded variables
Y = number of galls per 30 suckers	$Y' = Y$
X_1 = number of suckers per 1/100 acre	$X_1' = .01 \times X_1$
X_2 = 0 when brush absent, 1 when brush present	$X_2' = X_2$
X_3 = number of mature trees per 1/100 acre	$X_3' = .1 \times X_3$
X_4 = 0 when cover uniform, 1 when 25% or more of sampling unit open	$X_4' = X_4$

Degrees of freedom = 195

$R^2 = .050836$

$R = .225469$

$s^2_{y.1234} = 1.080586$

Coded variable	Coefficient	Std. error	t value
X_1'	-.541282	.395111	1.369949
X_2'	.206163	.181033	1.138814
X_3'	-.938006	.539403	1.738970
X_4'	.270913	.160119	1.691947

Decoded equation:

$$Y = .465407 - .005413 X_1 + .206163 X_2 - .093801 X_3 + .270913 X_4$$

Appendix F. (continued)

Forward solution

	A matrix				G matrix
	X_1'	X_2'	X_3'	X_4'	Y'
X_1'	9.265950	5.429500	-2.048650	-4.154500	-3.100000
X_2'		36.995000	.673500	-5.745000	2.500000
X_3'			4.769550	-4.148500	-4.350000
X_4'				49.995000	18.500000
A_{1j}	9.265950	5.429500	-2.048650	-4.154500	-3.100000
B_{1j}	1.000000	.585962	-.221094	-.448362	-.334558
A_{2j}		33.813519	1.873930	-3.310619	4.316483
B_{2j}		1.000000	.055419	-.097908	.127655
A_{3j}			4.212754	-4.883564	-5.274609
B_{3j}			1.000000	-1.159233	-1.252057
A_{4j}				42.146955	11.418195
B_{4j}				1.000000	.270913

Backward solution

	C matrix			
	C_{i1}	C_{i2}	C_{i3}	C_{i4}
C_{1j}	.144469	-.020117	.079029	.016251
C_{2j}		.030329	-.012229	.000799
C_{3j}			.269257	.027504
C_{4j}				.023726

Appendix G. Multivariate regression relating 1965 *S. concolor* infestations to stand density

Variables	Coded variables
Y = number of galls per 30 suckers	$Y' = Y$
X_1 = number of suckers per 1/100 acre	$X_1' = .01 \times X_1$
X_2 = 0 when brush absent, 1 when brush present	$X_2' = X_2$
X_3 = number of mature trees per 1/100 acre	$X_3' = .1 \times X_3$
X_4 = 0 when cover uniform, 1 when 25% or more of sampling unit open	$X_4' = X_4$

Degrees of freedom = 445

$R^2 = .078792$

$R = .280700$

$s^2_{y.1234} = .756052$

Coded variable	Coefficient	Std. error	t value
X_1'	-.634535	.194469	3.262910
X_2'	-.418858	.115048	3.640723
X_3'	-.220237	.293457	.750491
X_4'	.124630	.089622	1.390618

Decoded equation:

$$Y = .940474 - .006345\ X_1 - .418858\ X_2 - .022024\ X_3 + .124630\ X_4$$

Appendix G. (continued)

Forward solution

	A matrix				G matrix
	X_1'	X_2'	X_3'	X_4'	Y'
X_1'	26.234445	5.672223	-5.192111	-16.188888	-19.896666
X_2'		59.111112	1.464445	-8.444444	-29.733333
X_3'			10.643578	-5.587777	-.359333
X_4'				112.277778	29.033334
A_{1j}	26.234445	5.672223	-5.192111	-16.188888	-19.896666
B_{1j}	1.000000	.216212	-.197911	-.617085	-.758417
A_{2j}		57.884709	2.587040	-4.944200	-25.431423
B_{2j}		1.000000	.044692	-.085414	-.439346
A_{3j}			9.500382	-8.570781	-3.160513
B_{3j}			1.000000	-.902151	-.332672
A_{4j}				94.133415	11.731933
B_{4j}				1.000000	.124630

Backward solution

	C matrix			
	C_{i1}	C_{i2}	C_{i3}	C_{iv}
C_{1j}	.050021	-.004335	.029381	.008349
C_{2j}		.017507	-.004272	.000479
C_{3j}			.113904	.009584
C_{4j}				.010623

Appendix H. Multivariate regression relating 1966 S. concolor infestations to stand density

Variables	Coded variables
Y = number of galls per 30 suckers	$Y' = .1 \times Y$
X_1 = number of suckers per 1/100 acre	$X_1' = .01 \times X_1$
X_2 = 0 when brush absent, 1 when brush present	$X_2' = X_2$
X_3 = number of mature trees per 1/100 acre	$X_3' = .1 \times X_3$
X_4 = 0 when cover uniform, 1 when 25% or more of sampling unit open	$X_4' = X_4$

Degrees of freedom = 445

$R^2 = .062428$

$R = .249856$

$s^2_{y.1234} = .027528$

Coded variable	Coefficient	Std. error	t value
X_1'	-.102916	.037109	2.773343
X_2'	.040553	.021955	1.847096
X_3'	-.124293	.056000	2.219517
X_4'	.049249	.017090	2.881743

Decoded equation:

$$Y = 1.187971 - .001029 X_1 + .040553 X_2 - .012429 X_3 + .049249 X_4$$

Appendix H. (continued)

Forward solution

	A matrix				G matrix
	X_1'	X_2'	X_3'	X_4'	Y'
X_1'	26.234445	5.672223	-5.192111	-16.188888	-2.621888
X_2'		59.111112	1.464445	-8.444444	1.215516
X_3'			10.643578	-5.587777	-1.004377
X_4'				112.277778	7.547778
A_{1j}	26.234445	5.672223	-5.192111	-16.188888	-2.621888
B_{1j}	1.000000	.216212	-.197911	-.617085	-.099940
A_{2j}		57.884709	2.587040	-4.944200	1.782398
B_{2j}		1.000000	.044692	-.085414	.030792
A_{3j}			9.500382	-8.570781	-1.602937
B_{3j}			1.000000	-.902151	-.168723
A_{4j}				94.133415	4.636014
B_{4j}				1.000000	.049249

Backward solution

	C matrix			
	C_{i1}	C_{i2}	C_{i3}	C_{i4}
C_{1j}	.050021	-.004335	.029381	.008349
C_{2j}		.017507	-.004272	.000479
C_{3j}			.113904	.009584
C_{4j}				.010623

Appendix I. Program to fit negative binomial frequency distribution

1) Input and output

This program requires the following items as input:

(a) The observed frequency distribution in the form specified below.

(b) MAXOBS, which is the largest value observed on any sampling unit.

(c) ERRLIM, which is an upper bound on the allowable error in the iterative solution for k. This is the largest allowable absolute value of z. The lowest practical limit is 1.0×10^{-6}.

(d) POOL: In chi-square tests the very small observed frequencies are customarily pooled. All frequencies less than or equal to the specified value of POOL are grouped in the calculations.

Output of the program is as follows:

(a) The observed frequency distribution.

(b) The expected frequency distribution.

(c) A_x values for the maximum likelihood solution.

(d) The values of $(o - e)^2/e$.

(e) Chi-square with its associated degrees of freedom.

(f) Calculated values of $\bar{x}$ and k with their associated standard errors.

2) Use of the program at the University of Michigan

Makeup of the card deck is as follows:

(a) Identification cards.

(b) EXECUTE specification card.

(c) "Binary" program deck.

Appendix I. (continued)

(d) DATA specification card.

(e) First and second data cards.

The last two cards in the deck contain the user's data. The following frequency distribution of 1965 S. concolor galls per plot will be used to illustrate the formats of these two cards:

Observed frequency distribution

Observed value	Frequency
0	321
1	84
2	31
3	9
4	1
5	2
6	1
7	0
8	1

MAXOBS = 8

ERRLIM = .0001

POOL = 5.

First data card - starting with column #1 and proceeding to the right. Spacing is immaterial as long as the punched information does not extend beyond column #72. The decimal point must be punched for ERRLIM and POOL, but must not be punched for MAXOBS. Example:

MAXOBS = 8, ERRLIM = .0001, POOL = 5.,

Second data card - starting with column #1 and proceeding to right. If the frequency distribution is too large to be punched in columns 1-72, extra cards may be used. An asterisk, rather than a comma, must follow the last value in the distribution. Even though they are integers, each value in the distribution must have a decimal point punched after it.

Appendix I. (continued)

Example:

FREQ (0) = 321., 84., 31., 9., 1., 2., 1., 0., 1. *

The "FREQ (0) =" is a fixed expression and must precede the distribution no matter what values it contains. The observed frequencies, starting with the 0 class and proceeding upward in order, are listed in the form shown after the fixed expression.

Any number of distributions may be processed by simply adding another data set (two cards described above) to the end of the deck for each distribution.

3) Definitions of program variables

FREQ - this is an array in which the observed frequency distribution is stored.

EXPECT - this is an array in which the expected frequency distribution is stored as its elements are calculated.

AX - this array contains the A_x values calculated during the maximum likelihood solution for k.

CHISQ - this array contains the $(o - e)^2/e$ elements which are summed to obtain chi-square.

MEAN - arithmetic mean.

KHIGH - current upper estimate of k.

KLOW - current lower estimate of k.

ZHIGH - current high value of z.

ZLOW - current low value of z.

KEST - most recent estimate of k.

Appendix I. (continued)

VAR - variance

VXBAR - variance of the mean.

SEMEAN - std. error of the mean.

VHATK - variance of the estimated k.

SEHATK - std. error of the estimated k.

DF - degrees of freedom.

SCHISQ - sum of chi-square.

MAD program

```
                INTEGER I, J, DF, MAXOBS., PLOCUS
                DIMENSION FREQ(1000), EXPECT(1000), AX(1000), CHISQ(1000)
START           THROUGH LOOP1, FOR I = 0,1, I .G. 1000
                FREQ(I) = 0.
                EXPECT(I) = 0.
                AX(I) = 0.
LOOP1           CHISQ(I) = 0.
                READ DATA
                N = 0.
                SUM = 0.
                THROUGH LOOP2, FOR I = 0,1, I .G. MAXOBS
                N = N + FREQ(I)
LOOP2           SUM = SUM + ( I * FREQ(I))
                MEAN = SUM / N
                THROUGH LOOP3, FOR I = 0, 1, I .G. MAXOBS
                ASUM = 0.
                THROUGH LOOP4, FOR J = I + 1, 1, J .G. MAXOBS
LOOP4           ASUM = ASUM + FREQ(J)
```

Appendix I. (continued)

```
LOOP3       AX(I) = ASUM
            ZHIGH = 0
            ZLOW = 0.
            SFXSQ = 0.
            THROUGH LOOP5, FOR I = 0, 1, I .G. MAXOBS
LOOP5       SFXSQ = SFXSQ + (FREQ(I) * I * I)
            VAR = (SFXSQ - ((SUM * SUM) / N)) / (N - 1)
            KEST = (MEAN * MEAN) / (VAR - MEAN)
REPEAT      SUMTRM = 0.
            THROUGH LOOP6, FOR I = 0, 1, I .G. MAXOBS
LOOP6       SUMTRM = SUMTRM + (AX(I) / (KEST + I))
            Z = SUMTRM - (N * ELOG. (1 + MEAN / KEST))
            WHENEVER ZHIGH .NE. 0. .AND. ZLOW .NE. 0., TRANSFER TO
            CONT WHENEVER Z .LE. 0.
               KHIGH = KEST
               ZLOW = Z
               KEST = KEST - .01
            OTHERWISE
               KLOW = KEST
               ZHIGH = Z
               KEST = KEST + .01
            END OF CONDITIONAL
            TRANSFER TO REPEAT
CONT        CONTINUE
CIRCLE      KEST = KLOW + (ZHIGH * (KHIGH - KLOW)) / (ZHIGH - ZLOW)
```

Appendix I. (continued)

```
                SUMTRM = 0.
                THROUGH LOOP7, FOR I = 0, 1, I .G. MAXOBS
LOOP7           SUMTRM = SUMTRM + (AX(I) / (KEST + I))
                Z = SUMTRM - (N * ELOG. (1 + MEAN / KEST))
                WHENEVER .ABS. Z .LE. ERRLIM
                   K = KEST
                   TRANSFER TO ITREND
                OR WHENEVER Z .LE. 0.
                   KHIGH = KEST
                   ZLOW = Z
                OTHERWISE
                   KLOW = KEST
                   ZHIGH = Z
                END OF CONDITIONAL
                TRANSFER TO CIRCLE
ITREND          CONTINUE
                VXBAR = (MEAN + MEAN * MEAN/K) / N
                SEMEAN = SQRT. (VXBAR)
                VHATK = (KHIGH - KLOW) / (ZHIGH - ZLOW)
                SEHATK = SQRT. (VHATK)
                THROUGH LOOP8, FOR I = MAXOBS, -1, I .E. 0
LOOP8           WHENEVER FREQ(I) .LE. POOL, PLOCUS = I
                Q = 1 + MEAN / K
                EXPECT (0) = N / (Q .P. K)
                R = MEAN / (K + MEAN)
                THROUGH LOOP9, FOR I = 1, 1, I .E. PLOCUS
```

Appendix I. (continued)

```
LOOP9           EXPECT(I) = (((K + I - 1) * R) / I) * EXPECT(I - 1)
                SUMEX = 0.
                THROUGH LOOP10, FOR I = 0, 1, I .E. PLOCUS
LOOP10          SUMEX = SUMEX + EXPECT(I)
                EXPECT(PLOCUS) = N - SUMEX
                DF = PLOCUS - 2
                THROUGH LOOP11, FOR I = 0, 1, I .E. PLOCUS
LOOP11          CHISQ(I) = ((FREQ(I) - EXPECT(I)) .P. 2) / EXPECT(I)
                POOLF = 0.
                THROUGH LOOP12, FOR I = PLOCUS, 1, I .G. MAXOBS
LOOP12          POOLF = POOLF + FREQ(I)
                CHISQ(PLOCUS) = ((POOLF - EXPECT(PLOCUS) ) .P. 2) /
               1 EXPECT(PLOCUS)
                SCHISQ = 0.
                THROUGH LOOP13, FOR I = 0, 1, I .G. PLOCUS
LOOP13          SCHISQ = SCHISQ + CHISQ(I)
                PRINT FORMAT HEAD
                VECTOR VALUES HEAD = $1H1 ,H+NO.  PER SAMPLE +, S10,
               1 H+OBS. FREQ,+,S10,  H+EXPECTED FREQ. +, S15, H+  AX +,S10,
               2 H+(O-E) (O-E) / E+*$
                VECTOR VALUES LINE =$1H-,S10,I5,S10,F10.0,S10,F15.6,S10,
               1 F10.6,S10,F15.6*$
                THROUGH LOOP14, FOR I = 0, 1, I .G. MAXOBS
LOOP14          PRINT FORMAT LINE, I,FREQ(I),EXPECT(I),AX(I),CHISQ(I)
                PRINT FORMAT OUT1, SCHISQ, DF
```

Appendix I. (continued)

```
      VECTOR VALUES OUT1 =$1HO, H/CHI SQUARE = /, F10.6,H/ WITH /,
     1 13, H/ DEGREES OF FREEDOM/*$
      PRINT FORMAT OUT2, MEAN, SEMEAN
      VECTOR VALUES OUT2 =$1HO,H/MEAN = /, F10.6,H/ WITH STANDARD ER
     1 ROR OF /, F10.6*$
      PRINT FORMAT OUT3, K,SEHATK
      VECTOR VALUES OUT3 =$1HO,H/K = /, F10.6,H/ WITH STANDARD ERRO
     1 R OF /, F10.6*$
      TRANSFER TO START
      END OF PROGRAM
```

Appendix J. The negative binomial frequency distribution fitted to 1964 *O. schaumii* oviposition data

Oviposition slits per 30 suckers	Observed frequency	Expected frequency	$\frac{(o-e)^2}{e}$
0	47	51.6195	.4134
1	43	37.2351	.8925
2	33	27.5780	1.0659
3	20	20.6030	.0176
4	16	15.4584	.0189
5	9	11.6283	.5940
6	7	8.7621	.3543
7	7	6.6105	.0229
7+	18	20.5047	.3059
	200	Chi-square =	3.6854

mean = 3.0050 with standard error of .2501

k = .9491 with standard error of .1334

degrees of freedom = 6

probability = 72%

Appendix K. The negative binomial frequency distribution fitted to 1965 O. schaumii oviposition data

Oviposition slits per 30 suckers	Observed frequency	Expected frequency	$\frac{(o-e)^2}{e}$
0	241	241.0268	.0000
1	98	99.3274	.0177
2	54	49.8886	.3388
3	26	26.5566	.0116
4	9	14.5356	2.1081
5	10	8.0870	.4524
6	7	4.5479	1.3220
6+	5	6.0297	.1758
	450	Chi-square =	4.4264

mean = 1.0111 with standard error of .0742

k = .6956 with standard error of .0995

degrees of freedom = 5

probability = 50%

Appendix L. The negative binomial frequency distribution fitted to 1966 O. schaumii oviposition data

Oviposition slits per 30 suckers	Observed frequency	Expected frequency	$\frac{(o-e)^2}{e}$
0	69	78.1470	1.0706
1	96	84.4324	1.5847
2	74	73.1670	.0094
3	70	58.1889	2.3973
4	41	44.2030	.2321
5	24	32.6334	2.2840
6	20	23.6267	.5567
7	14	16.8652	.4867
8	12	11.9099	.0006
9	12	8.3398	1.6063
9+	18	18.4862	.0127
	450	Chi-square =	10.2411

mean = 3.1111 with standard error of .1410

k = 1.6552 with standard error of .1776

degrees of freedom = 8

probability = 25%

Appendix M. The negative binomial frequency distribution fitted to 1964 S. concolor oviposition data

Galls per 30 suckers	Observed frequency	Expected frequency	$\frac{(o-e)^2}{e}$
0	137	138.5239	.0167
1	44	38.4612	.7976
2	11	13.8912	.6017
3	4	5.4039	.3647
3+	4	3.7196	.0211
	200	Chi-square =	1.8018

mean = .5000 with standard error of .0670

k = .6243 with standard error of .1866

degrees of freedom = 2

probability = 42%

Appendix N. The negative binomial frequency distribution fitted to 1965 *S. concolor* oviposition data

Galls per 30 suckers	Observed frequency	Expected frequency	$\frac{(o-e)^2}{e}$
0	321	321.5203	.0008
1	84	83.3794	.0046
2	31	28.2965	.2582
3	9	10.3580	.1780
3+	5	6.4456	.3242
	450	Chi-square =	.7658

mean = .4466 with standard error of .0413

k = .6183 with standard error of .1376

degrees of freedom = 2

probability = 70%

Appendix O. The negative binomial frequency distribution fitted to 1966 *S. concolor* oviposition data

Galls per 30 suckers	Observed frequency	Expected frequency	$\frac{(o-e)^2}{e}$
0	187	192.1275	.1368
1	127	119.9593	.4132
2	69	66.2790	.1117
3	40	35.0323	.7044
4	11	18.0970	2.7832
5	8	9.2185	.1610
5+	8	9.2862	.1781
	450	Chi-square =	4.4884

mean = 1.2022 with standard error of .0717

k = 1.2990 with standard error of .2048

degrees of freedom = 4

probability = 30%

LITERATURE CITED

Bliss, C. I., and R. A. Fisher. 1953. Fitting the negative binomial distribution to biological data; and, note on the efficient fitting of the negative binomial. Biometrics 9: 176 - 200.

Felt, E. P., and L. H. Joutel. 1904. Monograph of the genus Saperda. New York State Museum Bull. 74. 86 p.

Garrett, P. W., and R. Zahner. 1964. Clonal variation in suckering of aspen obscures effect of various clearcutting treatments. Jour. Forestry 62: 749 - 750.

Graham, S. A., C. E. Westell, Jr., and R. P. Harrison, Jr. 1963. Aspens: Phoenix trees of the Great Lakes region. Univ. of Michigan Press, Ann Arbor, Mich. 272 p.

Grimble, D. G. 1966. An oviposition and egg viability study of Oberea schaumii Lec. and Saperda concolor Lec. infesting trembling aspen (Populus tremuloides Michx.). M. F. Thesis, Univ. of Michigan, Ann Arbor, Mich. 49 p.

Harrison, R. P., Jr. 1959. Insects and diseases of aspen. Ph.D. Thesis, Univ. of Michigan, Univ. Microfilms, Ann Arbor, Mich. 259 p.

Horn, A. G. 1962. Production and imports of pulpwood decline in the Lake States, 1961. Lake States For. Exp. Sta. Tech. Note 624. 2 p.

Knight, F. B. 1960. Measurement of Engelmann spruce beetle populations. Ecology 41: 249 - 252.

Snedecor, G. W., and W. G. Cochran. 1956. Statistical methods: applied to experiments in agriculture and biology. Iowa State Univ. Press, Ames, Iowa. 534 p.

Steel, R. G. D., and J. H. Torrie. 1960. Principles and procedures of statistics: with special reference to the biological sciences. McGraw-Hill Book Co., New York. 481 p.

Waters, W. E. 1955. Sequential sampling in forest insect surveys. Forest Sci. 1: 68 - 79.