The Great Lakes Entomologist

Volume 8 Number 3 - Fall 1975 *Number 3 - Fall 1975*

Article 5

October 1975

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Recommended Citation

Wilson, Louis F. 1975. "Spatial and Seasonal Distribution of Pine Root Collar Weevil Eggs in Young Red Pine Plantations," *The Great Lakes Entomologist*, vol 8 (3) DOI: https://doi.org/10.22543/0090-0222.1253 Available at: https://scholar.valpo.edu/tgle/vol8/iss3/5

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SPATIAL AND SEASONAL DISTRIBUTION OF PINE ROOT COLLAR WEEVIL EGGS IN YOUNG RED PINE PLANTATIONS

Louis F. Wilson¹

The pine root collar weevil (Hylobius radicis Buchanan) is a continuous threat to young pine plantations in the northeastern United States and the adjacent Canadian Provinces. The female weevil oviposits during the daytime (Wilson, 1968a) near the root collars of red pine (Pinus resinosa Aiton), Scotch pine (P. sylvestris L.), and jack pine (P. banksiana Lambert), and occasionally other pines. During recent studies on the weevil (Wilson 1968a, 1968b) in Michigan, egg data were taken for use in population and sampling research. Presented here are distribution patterns of eggs within and between trees and throughout the oviposition period, and some implications for assessing populations.

METHODS

Seven red pine plantations were selected for study in Kalkaska, Grand Traverse, and Newaygo Counties, Michigan. In 1963, at the beginning of the study, four plantations were heavily infested (some trees were dying in each), two were moderately infested, and one was lightly infested. The trees varied from 5-12 ft tall. All plantations were sampled repeatedly at about three week intervals for four years during the summers from 1963 to 1966. Plantations were designated J, K, L, M, N, P, and R. In all, nearly 2,000 trees were sampled in the study.

Each collection consisted of egg and adult weevil counts in the root collar area from each of 20 randomly selected living trees. The procedure at each tree was to: (1) collect all adults in the vicinity of the root collar; (2) collect soil from around the root collar; and (3) dig up the root collar. The sex, location, and behavior of adult weevils were recorded (Wilson, 1968a). Specially partitioned samples of soil were taken around 100 trees in order to assess egg distribution in the soil. These were collected at the peak of oviposition in the two most heavily infested areas. The regular soil sample consisted of surface soil 1 cm deep surrounding the tree out to 9 cm, and a narrow (1-2 cm) band of subsoil 2-3 cm deep adjacent to the root collar. The partition sample was the same quality of soil as the regular sample except soil from four (or five) locations from around the tree were bagged separately. The partition samples consisted of concentric rings of soil from: (1) the first 3 cm; (2) the second 3 cm; and (3) the third 3 cm out from the root collar. The other two sample locations were: (1) the narrow band of subsoil 2-3 cm deep adjacent to and surrounding the root collar; and (2) the soil directly under branches in contact with the ground (if applicable) (Fig. 1).

In the laboratory, the soil was carefully broken into small particles and sifted through sieves to locate and count the eggs. Soil, dried pitch nodules, and bark were carefully removed from the root collars and examined for eggs whose location was noted.

SPATIAL DISTRIBUTION AT THE TREE

Egg samples were taken from 100 red pine trees in two plantations during the main portion of the ovipositional period in order to determine egg distribution at the tree. Eggs were counted from the root collar, the soil, and the litter at the locations shown in Figure 1; cardinal direction was not considered.

The samples yielded 327 eggs-271 (83 per cent) in the soil and 56 (17 per cent) in the root collar tissues. Eggs were not found in the litter. The locations of the eggs in the soil were as follows:

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Locations (Fig. 1)	Egg nos.	Per cent of total		
1	103	38.0		
2	12	4.4		
3	1	0.4		
4	136	50.2		
5	19	7.0		
Total	271	100.0		

Eggs were rare (0.4 per cent) but present in location 3 (6-9 cm from the trunk, but most (88 per cent) were in zoncs 1 and 4 nearest the tree. Schaffner and McIntyre (1944) reported that the female oviposits some of her eggs in the soil close to the tree, and Finnegan (1962) noted that eggs are often as far as 5 cm from the tree. We found 4.4 per cent of the eggs this distance from the tree (location 2). Nineteen eggs were collected in soil beneath branches touching the ground. Only 16 trees sampled had one or more such branches and this represented 19 percent of the eggs on those trees. This suggests eggs tend to be aggregated under branches because the surface area of soil under a branch is far less than 19 percent of the surface area around the root collar. Also, eggs were occasionally found embedded in the underside of branches touching the ground.

The vertical distribution of eggs in the bark, xylem, or pitchy soil attached to the bark was as follows:

	Distance from ground surface	Egg nos.	Per cent of total
Above ground	2	1	1.8
	1	1	1.8
Ground level	0	29	51.8
Below ground	1	10	17.8
	2	8	14.3
	4	2	3.6
	6	1	1.8
	8	3	5.3
	16	_1	1.8
Total		56	100.0

The majority of eggs are laid at the ground line, but some are found at least 16 cm below the ground. Millers (1960) observed eggs at depths of 18 cm. Eggs tend to be deeper around trees that have considerable injury.

Eggs are usually oviposited singly in bark cavities, but four double egg batches were collected. Some eggs were embedded in the xylem or in the pitch adhering to the bark. Schaffner and McIntyre (1944) and Finnegan (1962) reported eggs oviposited in adult feeding wounds in the inner bark of the root collar. Millers (1960, 1965) noted the egg cavities were covered with tightly packed frass.

Ninety-three per cent of all eggs, then, were found in the cylindrical zone 3 cm out from the root collar and 3 cm down from the ground line. About 2 per cent were found under a branch, and 5 per cent were in the remaining locations.

SPATIAL DISTRIBUTION THROUGHOUT THE PLANTATION

Dispersion of weevil eggs was estimated from 94 collections, taken from all 20 trees in all years throughout the egg laying period each year. Mean and variance were calculated for the egg counts and then the Poisson series and Taylor's power law were fitted to these data to determine dispersive patterns.

If the eggs are distributed among the trees at random, the distribution will approximate the 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 high values than expected, with the result that the variance

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Fig. 1. Locations of partitioned-soil-samples taken for distribution of pine root collar weevil eggs.

exceeds the mean. When this occurs, the degree of overdispersion can be determined by various methods including Taylor's power law (Taylor, 1961) by calculating the parameter b of the equation $(s^2 = am^b)$.

The relationship between mean and variance for the egg counts, as expected, departed noticeably from Poisson expectation $(s^2 = m)$ and fit Taylor's power law reasonably well indicating overdispersion (Fig. 2). The index of aggregation (b) was calculated to be 1.25 and accounted for 95 per cent of the variation among the individual variances. Low egg populations, below a mean of 0.5 eggs per tree, tend not to differ from random expectation, whereas populations above this are recognizably aggregated (i.e., they fall above the Poisson line in Fig. 2).

SEASONAL DISTRIBUTION

Male and female weevils emerge during the period from mid-July to early September, but the females do not oviposit until the following spring. If the females survive, eggs are also laid the second spring. Finnegan (1962) reported an average of 17.5 eggs the first egg-laying season and 14.2 the second. He found that female weevils lay from one to a maximum of four per day. Schaffner and McIntyre (1944) counted 40-64 eggs per female in one season; one female laid 64 the first season and 10 the next. Millers (1965) obtained an average of 32 eggs per female with a maximum of 67.

Most investigators have recorded that eggs first appear in early to late May and disappear in September (Finnegan, 1962, Millers, 1965, Schaffner and McIntyre, 1944). In Michigan we determined the time and date of oviposition in two heavily infested plantations during two growing seasons. In all 610 eggs were studied. Eggs were first detected in mid-May, increased in numbers in early June, and reached a peak in mid-June. Numbers declined after that but rose again to a small peak in late July, then declined steadily and finally vanished in early September (Fig. 3). Finnegan (1962) reported the oviposition peak in early July in Ontario, Canada. Curiously, in our data the frequency of matching behavior paralleled the egg distribution even to a slight rise in sexual activity in late July (Fig. 3).

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Fig. 2. Relation between intertree variance (s^2) and the mean number of weevil eggs (m) per tree for all plots and years.

Sex ratios of adults, despite special care in collection, differed somewhat from sex ratios in pupae. Eighty-three pupae collected in their underground cells yielded 44 females (54 per cent) and 39 males (46 per cent)-a reasonable 1:1 sex ratio. However, 908 adults collected throughout the study showed 501 (62 per cent) males. Finnegan (1962) in Ontario reported 48 per cent males in his studies. The reason for the preponderance of males in our studies was not apparent.

DISCUSSION

The female pine root collar weevil in Michigan oviposits from mid-May to early September with the peak egg laying in mid-June, mostly in the bark of the root collar or in the soil within 3 cm of the root collar. When the bottom-most branches are lying on or partially buried in the soil, the females tend to lay more eggs under these branches than the soil nearby. Adults commonly feed under such branches during the day (Wilson

https://scholar.valpo.edu/tgle/vol8/iss3/5 DOI: 10.22543/0090-0222.1253

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Fig. 3. Seasonal distribution of eggs and paired weevils.

1968a) so this is a likely site for oviposition. Eggs may be rarely found I8 cm underground (Millers, 1960) but only on trees that have had considerable injury from larval weevils. The lack of good oviposition sites due to heavy larval feeding may cause the insect to dig for good sites. In dry weather the insect may not have to dig to reach the root region below the root collar. The pitch-drenched soil adjacent to the tree often cracks and separates from the collar leaving an open crevice. Both sexes commonly inhabit these crevices on warm days.

Weevil eggs are aggregated or overdispersed as are most insect populations. Yet, with a dispersion index of 1.25 according to Taylor's power law (1.00 is random), the egg population is not strongly aggregated. This can be partially explained by behavior of the female. In well-stocked pine plantations, each insect disperses by walking from one tree to another almost every night (Wilson, 1968b). Its movements are nearly random, thus each tree has almost an equal opportunity of receiving a female each day. Once at a new tree a female may lay only a single egg per day or sometimes a pair (rarely more). This means that only a few trees will receive many eggs and only a few trees will have no eggs, a situation not encountered in highly overdispersed populations where many zeros and high values would be expected.

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 data to stabilize the variance. Because the pine root collar weevil data were aggregated, the data (x) were transformed using: $\log (x + 1)$ (Wadley, 1950); $\log (x + k/2)$ (Anscombe, 1948) using a common k of 1.782; x^y (Healy and Taylor, 1962); and $\log (x^y + 1)$ in order to find a means of stabilizing variance. Correlation coefficients between mean and variance were highly significant when original counts (Table 1) and all transformed counts were used:

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Original counts (x), r = 0.86 Transformed log (x + 1), r = 0.77 Transformed log (x + k/2), r = 0.83 Transformed log (x \cdot ²⁸ + 1), 4 = 0.63 Transformed x \cdot ²⁸, r = 0.71

Thus, none of the transformations tested were sufficiently powerful to stabilize variance for statistical purposes. Perhaps a transformation more sensitive to the limited range of x-values would be more appropriate.

Table 1. The mean and variance of original counts of eggs of the pine root collar weevil, 1963-1966.

Location ^a	$\overline{\mathbf{x}}$	s ²	Location	x	s ²	Location	x	\$ ²
JC1	3.00	9.857	RD3	0.27	0.210	R4	0.03	0.030
NC1	1.00	1.857	RS3	0.07	0.070	K6	0.23	0.359
PC1	2.80	4.600	JC4	0.95	1.313	K7	0.10	0.200
RC1	2.20	1.733	JP4	1.20	1.642	К9	0.05	0.050
JC2	2.40	6.686	JD4	1.25	1.776	K14	0.25	0.303
NC2	1.27	3.495	JS4	1.00	1.579	K15	0.20	0.274
PC2	4.13	16.695	RC4	3.05	4.997	K16	0.05	0.050
RC2	4.47	30.124	RP4	3.30	7.274	K20	0.15	0.239
JC3	1.21	4.489	RD4	2.60	4.463	K21	0.15	0.239
NC3	0.20	0.171	RS4	4.95	19.418	K22	0.10	0.095
PC3	3.47	4.267	N1	0.75	1.987	K23	0.05	0.050
RC3	1.27	2.924	N2	3.40	24.568	L3	0.03	0.030
JP1	1.87	3.981	N3	1.25	1.776	L4	0.03	0.030
NP1	0.80	1.171	N4	0.65	0.776	L5	0.08	0.160
PP1	2.87	6.838	N5	0.25	0.303	L7	0.05	0.050
RP1	2.07	3.067	N9	2.00	2.737	L8	0.45	1.208
JD1	0.73	0.781	N10	1.35	4.871	L9	0.10	0.200
ND1	0.20	0.314	N11	0.90	1.884	L10	0.20	0.274
PD1	1.00	2.286	N12	0.15	0.239	L14	0.19	0.262
RD1	1.27	0.781	N16	0.10	0.100	L15	0.05	0.050
JS1	0.60	0.971	N17	0.70	0.747	L16	0.05	0.050
NS1	0.07	0.070	N18	0.40	0.989	L17	0.05	0.050
PS1	0.13	0.124	N19	0.30	0.432	L21	0.32	0.339
RS1	0.29	0.220	J4	0.40	0.358	L22	0.15	0.134
JP2	0.43	0.418	J5	1.15	4.555	L23	0.05	0.050
NP2	0.87	1.267	J6	0.25	0.408	M1	0.10	0.095
PP2	1.43	1.956	J10	2.60	6.568	M2	0.25	0.303
RP2	0.67	1.095	J 11	6.40	20.779	M3	0.25	0.303
ND2	0.27	1.067	J12	1.40	5.726	M4	0.05	0.050
PD2	0.80	1.314	J13	2.20	5.958	M7	0.40	0.489
RD2	0.33	0.381	J14	0.30	0.326	M8	0.35	0.661
NS2	0.13	0.124	J18	2.95	5.103	M9	0.52	0.862
PS2	0.13	0.124	J19	2.85	4.871	M10	0.25	0.303
RS2	0.07	0.070	J20	0.95	2.155	M14	0.15	0.134
JP3	0.47	0.410	J21	0.65	1.082	M15	0.05	0.050
JD3	0.20	0.314	J25	0.10	0.100	M16	0.10	0.095
ND3	0.07	0.070	J26	1.45	3.839	M20	0.10	0.200
NS3	0.67	0.070	J27	0.85	1.292	M21	0.30	1.274
PP3	1.87	6.552	J28	0.05	0.050	M22	0.15	0.239
PD3	0.20	0.314	K1	0.05	0.050	M23	0.05	0.050

aCode letters refer to plantation and plot; numbers refer to collection.

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