

Some Factors in the Distribution of European Pine Sawfly Egg Clusters in an Experimental Plantation of Hard Pines¹

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Summary. 1. During three successive years the frequencies of oviposition by *Neodiprion sertifer* (Hymenoptera: Diprionidae) were observed in 546 pines (provenances of various hard pine species, hybrids between such species, and some white pines). The insects were able to discriminate between 30 host genotypes since in this preference test average oviposition frequency varied between genotypes.

2. Oviposition frequencies had to be inferred to from groups of feeding larvae.

3. Besides genotype, four other groups of variables had an effect on the number of larval colonies: position of a tree in the plantation (in terms of rows and columns), its dimensions, the dimensions of its neighbors, and the number of colonies in the neighbors.

4. Apparently different crown portions were preferred oviposition sites in the various genotypes.

5. Water potentials of a sample of host trees during the hatching period showed no relations to susceptibility.

Introduction

Since its introduction into North America, the European pine sawfly *Neodiprion sertifer* (GEOFF.) (Hymenoptera: Diprionidae) has attacked its native host, the Scots pine, *Pinus silvestris* L., and various other indigenous or introduced species of pine. The females of this insect deposit egg clusters on the foliage during late summer. In April or May of the following year the larvae hatch and feed in more or less distinct groups. They devour large masses of foliage and crawl to other parts of the host tree or even a neighbor tree when their food source is depleted. If infestations occur in successive years, death of the tree may result.

In the present report field observations made by HENSON, O'NEILL, and MERGEN (1969, cf. chap. I) were further statistically analysed. The objective of the present analyses was to study some of the factors involved in the selection of the site of oviposition by the insect. The paper by HENSON et al. contains both a comprehensive survey of the present status of knowledge of the insect and reports on numerous experiments on the insect-host plant relationship.

Field design and data collection

Hard pine progenies were planted in one-tree plots in three adjacent plantations at a 4 m spacing.

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Progenies were randomized within blocks and these blocks within plantations. The numbers of trees per progeny were widely different and therefore not every progeny was represented in each block. In 1965 most of the trees were 12 to 14 years old.

The progenies in many instances were combined for easier analysis to represent the 30 types of table 1, the numbers of trees in types ranging from 1 to 73. It will be noted that genetic diversity of the same type was presumably lowest in the 12 geographic sources of Scots pine in which fewer original lots were bulked, and highest in the species hybrids. Reciprocal hybrids were classified as different types. As a rule the first five types ('species') were each represented by various seed origins which were bulked for the statistical analysis.

Trees were located by rectangular coordinates for row and column. The mean row and column values were very similar for each of the types which were represented by large numbers of trees. Naturally types with smaller numbers of trees (often belonging to only one progeny) were variable in average position. The type numbers of table 1 were not entered in fig. 1 which is the transcript of a computer-produced map showing the location of trees belonging to any of the 30 types (plus and multiplication signs). The triangles refer to trees that were either 1) interplanted white pines, 2) hard pines of doubtful identity, or 3) trees that died during the three-year observation period. There were few trees belonging to the last class and they were not used in the actual analysis in order to maintain identical samples for three successive years. Heavy initial mortality amounting to almost 30% is obvious from fig. 1, to which further reference will be made later. (The average position of the 30 types formed is illustrated in fig. 2.)

Table 1. "Types" of hard pines evaluated in regression analysis

Type	no. of trees	Species
1	49	<i>P. thunbergii</i>
2	8	<i>P. thunbergii</i> (2 selfed progenies)
3	73	<i>P. densiflora</i>
4	5	<i>P. tabulaeformis</i>
5	49	<i>P. nigra</i>
<i>Species hybrids</i>		
6	2	<i>P. thunbergii</i> × <i>P. yunnanensis</i>
7	16	<i>P. thunbergii</i> × <i>P. sinensis</i>
8	69	<i>P. thunbergii</i> × <i>P. tabulaeformis</i>
9	5	<i>P. thunbergii</i> × <i>P. taiwanensis</i>
10	1	<i>P. thunbergii</i> × <i>P. nigra</i>
11	33	<i>P. thunbergii</i> × <i>P. densiflora</i>
12	15	<i>P. densiflora</i> × <i>P. thunbergii</i>
13	4	<i>P. densiflora</i> × <i>P. nigra</i>
14	4	<i>P. nigra</i> × <i>P. densiflora</i>
15	5	<i>P. densiflora</i> × (<i>P. densiflora</i> × <i>P. thunbergii</i>)
16	38	<i>P. thunbergii</i> × (<i>P. densiflora</i> × <i>P. thunbergii</i>)
17	8	<i>P. densiflora</i> × (<i>P. densiflora</i> × <i>P. sylvestris</i>)
18	32	<i>P. banksiana</i> × (<i>P. contorta</i> × <i>P. banksiana</i>)
<i>P. sylvestris</i> origins		
19	3	Turkey
20	5	Czechoslovakia
21	22	Austria
22	2	Spain
23	9	Spain
24	3	France
25	1	France
26	16	England
27	11	Scotland
28	4	Finland
29	4	Sweden
30	2	unknown ex Morris Arboretum

In 1965, 1966, and 1967 the larval colonies of *Neodiprion sertifer* were counted to obtain a measure of the egg population. Observations were made early in the season to assure that these early instar counts in fact did represent the originating egg clusters. It was necessary to assume that the number of larvae hatching from a given egg cluster was of sufficient size that they could establish themselves and start feeding.

In 1966 colony counts were recorded for three crown portions (upper, medium and lower third of total tree height) and for 8 compass directions. In 1966 tree height and crown diameter (average of two measurements taken 90° apart) were also assessed in order to calculate the lateral crown surface area, assuming the shape of a cone.

Statistical analyses

Multiple regression was used to test the influence of 1) environmental features and 2) the genotypes of the trees as represented by their type classification

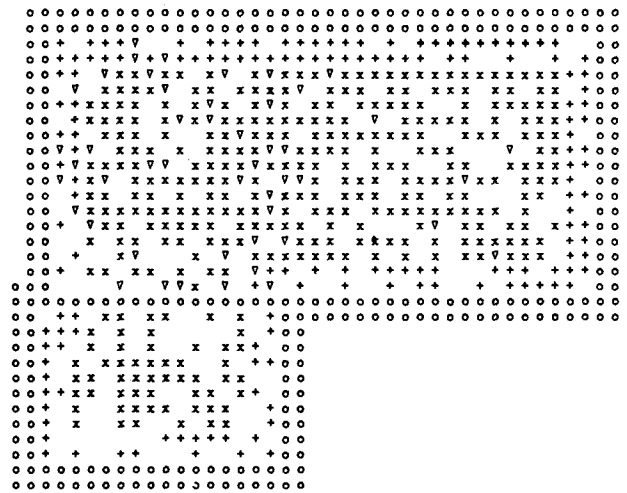


Fig. 1. Plantation map with 1063 tree positions; 291 dummy trees in surround (○); 226 dead trees (blanks); 48 trees used in computing neighborhood averages only (▽); 498 trees used in regression analyses (+ and ×); 346 innermost trees unaffected by dummy trees in surround (×)

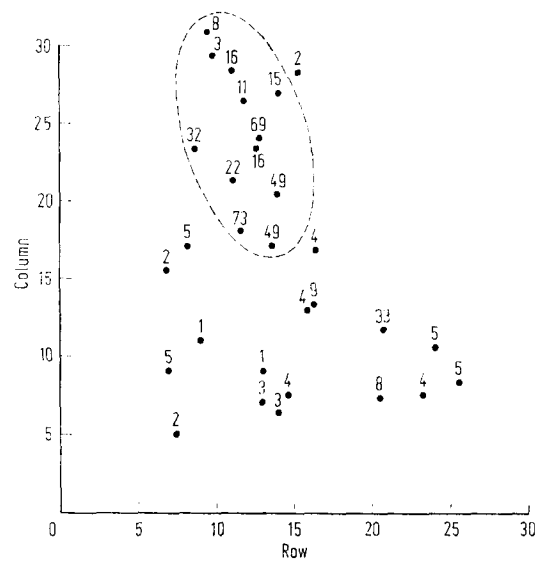


Fig. 2. Average position of trees belonging to the 30 types that were kept separate; numbers denote the numbers of trees in types

on oviposition. These regressions made use of the colony counts (N) as the dependent variable (Y) and were run for each of the three years separately. In each of the two models evaluated there were four groups of variables.

The row (R) and column (C) numbers were to express differences in the exposure to attack from outside the plantation and differences in the general attractiveness of trees due to their position on a moderately steep northern slope. In one instance the product of the two, representing the linear interaction term, was included as a variable.

Tree height (H), crown diameter (D) and crown surface area (A) were tested in both linear and qua-

dratic terms since larger crowns may be more likely to arrest the insects. In addition, large trees not only can support larger numbers of arrested insects, but they may also function as visual stimuli and thus receive some positive response from the fecund females.

The third group of variables consisted of the average dimensions and average colony counts of the neighbors of a given tree. Each neighbor was assigned a weight according to its distance to the tree under question (see fig. 3; identical letters denote equal weights). Due to heavy initial mortality some of the experimental trees were nearly solitary while others were still surrounded by a close group of neighbors as seen in fig. 1. The plantations were not surrounded by border trees and this might affect the pattern of infestation in the plantation. In addition a double-spaced lane ran through the plantation. Therefore, these vacant positions were included in the analysis as trees with zero dimensions and zero colony counts. This should account for the variation in exposure of a tree's foliage to light, for the direct exposure to insect attack (some short trees must have been virtually hidden in a group of tall neighbors while others considerably exceeded the dimensions of adjacent trees and may have formed a more likely target), for the usually positive environmental covariance between a tree and its group of neighbors in vigor and growth (STERN 1968), and perhaps other factors.

The inclusion of the average colony counts on the neighbors of a tree was primarily to account for non-randomness of initial attack. The plantation was invaded primarily from the margins but some tall trees in the interior were also attacked in the first year. This, as well as secondary spread of the female insects with sometimes limited distance of flight from these focuses (HENSON, 1965 a), required the assumption of patches of high and low exposure to attack

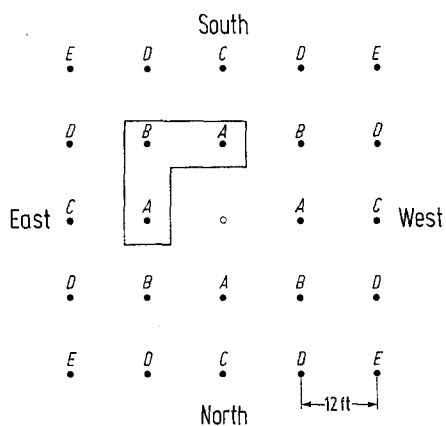


Fig. 3. Position of a given tree (O) among its group of neighbors; equal letters denote equal weights. Spacing was 4 x 4 m; the three trees in the frame received fourfold weights. For further explanation see text

that were not sufficiently corrected for by R and C. The distance to the nearest tree with high colony counts in the same year or the year before could also be used as an independent variable. However, we used the counts of all the surrounding trees in the two nearest rows around a tree in question and weighted them by their inverse distances from the tree.

Two methods of computing such averages were used. In the first model H, D, A, and N of the eight immediate neighbors were weighted by their linear distances to a given tree, leading to variables H1, D1, A1, and N1. The sixteen trees in the outer ring of neighbors entered the variables H2, etc. Trees in either ring thus were given differential weights, but in the analysis ring 1 as such received the same weight as ring 2.

In model (2) some modifications were made. For H, D, and A the distances to the neighbor trees were squared to put more weight on the dimensions of immediate neighbors; in this model H1, etc. were the average dimensions of the eight immediate neighbors, H2, etc. the averages of all 24 of them. Furthermore, some of the 1966 observations suggested that there were more colonies feeding on the southern, south-eastern and eastern aspects of the trees. Therefore, neighbors standing in these directions (framed in fig. 3) were tentatively given double and fourfold weights to account for their more significant role in light interception and temperature variation. HENSON et al. (1969), however, in the analysis of all of the 1966 data, found a concentration of colonies in the southern and western aspects in only two of the three initial plantings that made up the bulked plantation and in the southern and eastern aspects in only one of the plantings. Inspection of the simple correlations of these regressors with the dependent variable led to assigning them fourfold weights. N1 and N2 in model (2) were however computed so that only those trees which had a non-zero count entered the average; a neighbor may have been unacceptable simply because it belonged to a non-host species or for other genetic reasons. Also this flexibility was introduced on the basis of closer simple correlations between N and N1 (and N2, respectively).

The fourth group of predictors in either model were dummy variables standing for membership to one of the 30 types. One of these had to be omitted to avoid a linear dependence in the input matrix; this condition may have affected the partial regression coefficients also of some of the quantitative variables.

The small progeny-wise variation in age of the experimental trees was neglected since it was believed that this was expressed by their dimensions.

The method of accounting for regression in contingency tables was adapted from COCHRAN (1954).

Results

1. Regression analyses

For the full models using either N or $\log(N + 1)$ as input, predictions and residuals were uncorrelated. Therefore only the results obtained with untransformed data were used. In residual plots against R and C an increase was expected in the spread of the deviations towards low and high values and in the center of the distributions where there was a concentration of dummy trees (fig. 1). However, only very slight increases in the width of the band at the indicated positions were found. In addition, separate analyses (model 1 only) run for the 346 trees unaffected by non-existing neighbors (denoted by x in fig. 1) were about as efficient and gave very much the same results as the complete sample of 498 trees. Table 2 shows a summary of these degrees of multiple determination (R^2).

Table 2. Degrees of multiple determination of the complete models

	1965	1966	1967
Model (1)			
346 trees	.52	.61	.52
498 trees	.47	.57	.51
Model (2)			
498 trees	.48	.57	.50

Variables fitted to the models were:
 Model (1): $R, C; H, D, A; H^2, D^2, A^2; H_1, D_1, A_1; H_2, D_2, A_2; N_1, N_2; 29$ types.
 Model (2): $R, C; H, H^2, D, A; H_1, H_1^2, D_1, A_1; H_2, H_2^2, D_2, A_2; N_1, N_2; 29$ types.

Unless otherwise stated, the significance tests of certain variables were always based on the full model, i.e. after adjustment for all of the other variables. Therefore, test statistics of single variables tended to be non-significant if they were closely correlated with other regressors.

In both models one of the plantation coordinates had a significant influence as did the position of a tree as such if expressed by the joint effect of R and C ; but the adjustment for the interaction term increased the fraction of explained variance by only 1%. Bearing in mind that these variables varied also between types, correcting for position in the plantation was actually required.

Among the dimensions of the tree itself, tree height, H , and H^2 , had the most pronounced single effects as concluded from the size of the F -ratio. The test statistics for tree dimensions were consistently highest for the 1966 analyses since this was the year of measurement and the year-to-year correlations in tree dimensions may have been far from complete. The same is also suggested by the slightly higher

values of R^2 in table 2. The joint linear effect of H , D , and A was naturally highly significant in any years under any model and even more so if the squares of these variables were added. In a replicated provenance trial WRIGHT et al. (1967) found the percentages of trees attacked in 10-tree plots almost completely explained by their average tree height alone.

Due to non-zero environmental correlations between the dimensions of the two rings of neighbors neither such variable had a significant effect if tested separately. But when all of these highly intercorrelated variables were jointly tested, they increased the efficiency of the model considerably. An inspection of the simple correlations revealed negative coefficients between N and the average dimensions of neighbors. This result looks reasonable in that either the insects did not oviposit in shaded trees or crown portions or they were filtered out or distracted by taller neighbors and/or big masses of foliage in the neighborhood. But this is not necessarily so. The significance tests were unchanged in the sample of 346 trees; hence the influence of the size of adjacent trees was not an artifact attributable to simulation of dummy trees in the surround.

In all years the correlations between N and N_1 (and N_2) were around .30 in model (2) and only slightly less in model (1). These simple correlations to N were almost as close as the ones for H , D , and A . The test for the joint effect of N_1 and N_2 can be looked at as a test for non-randomness of infestation regarding the areal pattern and for the apparent or even implied location effect on N if a tree happened to stand in a part of the plantation that was severely hit. It showed significance in all years with any model also in the sample of 346 trees. This effect was still significant in 1967 but there was a consistent though slight decrease. From the first through the third year the insect population as estimated from the colony counts was increasing, the ratio of the total counts being 1.5:6:11 (in thousands). The effect of N_1 and N_2 may also partly reflect local concentrations of host progenies displaying differential intensity of attack. It must be remembered that forming 30 types did not possibly account for all of the genetic variation between various progenies. Another interpretation may be attractance of more and more insects to a tree and its neighborhood by the odor of resin exuded from the slits made during oviposition (cf. PLANK and GERHOLD 1965).

The contrast between the 12 Scots pine provenances and the other 18 types was not significant. The Scots pine types deserved primary interest since they represent the original host species of *Neodiprion sertifer*. With a weighted overall mean of 19 colonies per tree (table 3) they are apparently most severely attacked but *P. densiflora* and *P. tabulaeformis* have about as many colonies. The conclusion drawn by HENSON et al. (1969) that the insect, which supposedly was introduced into North America from central

Table 3. *Adjusted type means in three years (Model 1)*

Type	No. of Trees	1965	1966	1967	Mean
1	49	1.2	3.2	7.8	4.1
2	8	.5	3.0	5.5	3.0
3	73	4.0	17.6	25.0	15.5
4	5	3.2	20.0	50.4	24.5
5	49	2.2	10.3	16.7	9.7
	184				10.6
6	2	1.0	3.5	2.5	2.5
7	16	1.6	3.4	13.3	6.1
8	69	4.1	12.3	34.5	17.0
9	5	1.2	6.2	14.0	7.1
10	1	6.0	16.0	24.0	15.3
11	33	2.9	17.5	28.2	16.2
12	15	2.3	10.3	19.8	10.8
13	4	1.0	8.3	9.3	6.2
14	4	2.5	11.0	15.3	9.6
15	5	3.2	10.6	15.2	9.7
16	38	1.8	4.1	8.8	4.9
17	8	2.1	7.1	19.1	9.4
18	32	1.7	6.6	11.4	6.6
	232				11.2
19	3	5.0	25.7	53.0	27.9
20	5	5.6	23.6	34.0	21.0
21	22	6.1	19.0	31.3	18.8
22	2	11.0	20.5	17.5	16.3
23	9	16.3	41.4	43.8	33.8
24	3	7.7	29.7	49.3	28.9
25	1	15.0	32.0	36.0	27.6
26	16	4.4	16.8	28.9	16.7
27	11	1.9	8.1	22.0	10.7
28	4	2.3	10.0	18.5	10.3
29	4	0	2.0	7.3	3.1
30	2	3.0	25.0	45.5	24.5
	82				18.8

Europe, was better adapted to or simply more attracted by sources from the center of the European distribution range of Scots pine still holds. Exceptions are the Turkish and one of the Spanish sources, but the samples are of rather small size. The species hybrids do not show any clear pattern with regard to intermediacy between the parent species. This may be due to the bulking of progenies into types, but informations on the individual parentages are not available. It was obvious that the females could clearly discriminate between host genotypes even after adjustment for the many environmental variables.

The type means of table 3 are highly intercorrelated between years as measured by both the product moment correlations and the unweighted rank correlations; the concordance of the estimates in the three successive years amounts to $W = .91^{***}$. This suggests absence of interaction between types and years, the latter representing very different population densities in the insect as well as different climatic conditions. Also WRIGHT et al. (1967) report non-significant estimates of interaction with time. The incidence of attack increased greatly without accompanying changes in the ranks of the types. The

overall correlations between the 498 predictions according to regression model (1) were .73 for immediately successive years and .56 between 1965 and 1967. On the other hand, the residuals showed correlations of .48 between immediately successive years and .36 between 1965 and 1967. Keeping in mind that the bulk of the independent variables were the same in the analyses of the three years, the latter coefficients still represent close year-to-year correlations between trees of the same type and relevant environmental variables that were unknown and thus not corrected for.

2. Crown positions

Separate regression analyses for the 1966 counts in the upper (U), medium (M) and lower (L) crown portions gave the same overall results except that there appeared to be some variation in the tests of the neighborhood data. This was further pursued by first comparing the counts with the fractions of A in the three crown portions, the ratio U:M:L being 1:3:5. The detailed assessment of colony numbers in the field is of course difficult and misclassifications are not completely unavoidable as HENSON et al. (1969) concluded with regard to the results on compass directions. Crown forms also

Table 4. *Numbers of feeding larval colonies in the three crown portions; key to type numbers see table 1*

Type	Upper	Medium	Lower	Sum	Total Height(m)
1	72	72	21	166	2.17
2	6	16	6	28	1.97
3	358	608	319	1285	3.35
4	27	46	27	100	3.58
5	147	239	118	504	3.18
6	0	6	1	7	2.56
7	11	24	19	54	4.20
8	202	413	235	850	4.00
9	11	16	4	31	3.35
10	3	12	1	16	3.77
11	170	249	157	576	3.18
12	50	66	37	153	2.99
13	5	11	17	33	1.84
14	19	14	11	44	2.07
15	29	17	7	53	3.54
16	51	71	33	155	3.12
17	14	27	16	57	3.41
18	62	115	33	210	4.82
19	14	39	24	77	4.69
20	37	53	28	118	5.74
21	81	224	112	417	5.05
22	10	22	9	41	4.10
23	93	195	85	373	4.82
24	22	50	17	89	5.05
25	10	16	6	32	5.91
26	61	149	58	268	5.48
27	16	58	15	89	4.46
28	5	27	8	40	2.43
29	1	5	2	8	1.71
30	15	26	9	50	3.58
Sum	1602	2887	1435	5924	

U, M, and L are all closely correlated to their sum, N, but the correlations between the amounts of infestation in the upper and lower crown portions are surprisingly low.

Factor analyses of the various data sets revealed nothing that could not be surmised from the correlations among the variables. The first three factors based on eigenvalues $\lambda \geq 1$ accounted for about 82% of the variance, the fourth for an additional 5%. However, the interpretation of the latter was not clear. All variables entered had communalities above .8 except U, M, and L with estimates about .6. These estimates indicate that the factors eliminated accounted for less variation in the colony counts as in other variables. Rotation according to Kaiser's varimax method (HARMAN 1967) with the three first factors retained suggested the same interpretation of factors; a sample of such analyses is presented in table 6. The first factor is bipolar and describes general physical growth in the neighbors as opposed by oviposition numbers in the trees themselves. The weights of the last three variables are rather small, but the distribution of the signs of the weights is most remarkable. Only the second factor can be interpreted as physical growth in the trees studied and its implied impact on oviposition frequencies. These frequencies have moderately high weights also in the third factor which reflects the impact of size-independent oviposition counts in the neighbors on oviposition in the trees that they surround. It therefore makes some difference whether or not a tree stands between neighbors that are for some reason acceptable to the ovipositing females. This effect of areal concentrations of oviposition on the intensity of attack in a given tree decreases from top to base of the tree crowns; this factor accounts for almost

three times more variation in the upper than in the lower third of the crowns.

Analyses of the sets of variables when the neighborhood averages were defined according to regression model (1) were different in that the coefficients in the first factor were always positive. Thus, redefinition of the weights assigned to neighbors yielded qualitatively different results.

When R and C were also included in the factor analyses, they had appreciable loadings only in one of the later factors, the coefficients of the other variables then being close to zero. They were finally omitted since they were also peculiar to this particular plantation. Squares of certain variables such as H, H1, and H2 followed the same pattern of factor loads as the original linear measures. Also the sum of the detailed 1966 counts showed no pattern of factor weights that essentially differed from the pattern that M displayed. The contribution of the first three factors were always much the same as in the sample analysis presented in table 6. The analysis also suggests that there was almost no point in either 1) keeping the averages of the immediate neighbors separate or 2) taking account of the outer ring of neighbors in addition to the inner ring.

4. Water potential in a sample of trees

The distribution of the early instar colonies may reflect the mechanism by which the fecund females find hosts, and chance. The development from eggs to prepupae however depends greatly on the ability of the females to select a suitable substrate for their offspring. HENSON (1965 b) observed decreasing hatching success with increasing storage time of pine branches carrying the egg clusters. He attributed this to water loss in the foliage and the reduced ability of the eggs to remove water from the surrounding tissue. Failure to imbibe water means that eclosion of larvae from the eggs embedded in the egg pocket cannot occur. If there existed consistent differences in the water potential of trees during the short hatching period, it might reasonably be related to hatching success.

Measurements with a thermocouple psychrometer of both sucrose solutions of known molarity and needle discs gave readings of low repeatability. Other methods do not allow sampling of a reasonable number of trees (KRAMER and BRIX 1965). Therefore, the pressure chamber technique (SCHOLANDER et al. 1965) was applied. Its use is discussed by BOYER (1967) and KAUFMANN (1968). With this technique cut branches are inserted upside down in a cylinder. High-pressure nitrogen is then introduced from a tank. Briefly, the rationale of the method is to obtain estimates of the plant water potential from the amount of pressure applied to the stomates required to force xylem water back to the cut surface of the branch. Nine trees representing four seed origins of

Table 6. Factor analysis of 14 variables assessed in 1966 (model 2); after varimax-rotation retaining 3 factors

Variable	Factors loads		
	1	2	3
H	.19	.88	-.11
D	.14	.92	-.09
A	.16	.93	-.09
H1	.94	.02	.05
D1	.97	0	-.03
A1	.97	.04	.01
H2	.94	.04	.05
D2	.98	.01	-.05
A2	.97	.06	0
N1	.12	-.07	.88
N2	.04	0	.92
U	-.09	.49	.52
M	-.20	.67	.42
L	-.20	.61	.33
eigen values	5.77	3.62	2.08
per cent of total variance	40.9	25.3	15.8

Table 7. Water potentials in at, multiplied by (-1), of 16 trees on four days during the 1968 hatching period; averages of four measurements each

		4/23	4/25	4/30	5/2
1) <i>P. sylvestris</i>	Turkey	9.7 8.1	8.4 9.0	8.6 8.1	7.0 8.6
2) dto.	Austria	12.6 10.3	10.0 9.2	9.8 9.2	8.4 7.6
3) dto.	France	10.4 11.0 9.8	8.8 9.3 8.6	9.8 10.4 11.5	7.8 8.0 8.6
4) dto.	Sweden	6.4 8.5	6.3 6.9	8.0 7.4	6.9 6.7
5) <i>P. densiflora</i>			9.6 8.5 9.4 10.4	9.8 9.4 9.1 10.1	7.4 8.6 8.3 8.3
6) <i>P. ayacahuite</i>			12.6 12.7 11.6	14.6 13.1 13.1	12.2 11.9 12.8

Pinus sylvestris with very different numbers of feeding larval colonies were measured on four dates (April 23, 25, and 30; May 2) during the hatching period observed in plantations near the one described above. From April 25 on, three trees of *P. ayacahuite*, a non-host species, and four trees of *P. densiflora* were also measured. Per tree and date two parallel samples were taken from the southern aspect at about breast height between 10 a.m. and 2 p.m. Because all four days were cloudless, sampling was done in two randomized blocks in time. Two successive readings were made from each sample once it was in the chamber. This required careful increase of the pressure in order to obtain a valid second reading. There was in fact no consistent difference between the first and second readings; in the 114 samples measured in the field at a precision of 5 lbs./sq.in. 30% gave higher first readings, 45% gave a higher second reading and in the remaining 25% the two readings were equal.

It is apparent from the 'cell means' of the 16 trees in table 7 that trees of the same lot did not change their rank as much as the progeny means. This can also be seen from a graphical presentation of the latter (fig. 5). The differences between progenies are rather pronounced and an analysis of variance showed them to be highly significant¹ (Table 8). However, this was due mainly to the difference between *P. ayacahuite* and the other progenies; this in turn may be attributable to a shortcoming of the method of measurement. After cutting off the sample branch-

¹ The authors are heavily indebted to Dr. George M. FURNIVAL for the design of the input matrix in terms of orthogonal comparisons of the cell sums.

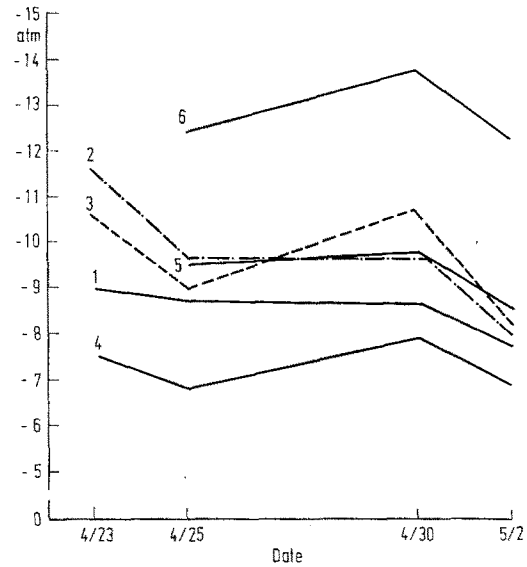


Fig. 5. Water relationships of six genotypes of the host plants during the hatching period of the sawfly: (1) *Pinus sylvestris* Turkey, (2) *P. sylvestris* Austria, (3) *P. sylvestris* France, (4) *P. sylvestris* Sweden, (5) *P. densiflora*, (6) *P. ayacahuite*. — Graph shows the weighted averages of tab. 7

Table 8. Analysis of variance of water potentials of 16 trees on 4 days. Asterisks refer to the .05 and .001 levels of significance

Source	d.f.	s.s.	m.s.
Total	227	198,265.07	
types	5	133,467.62	26,693.52**
trees/types	10	4,516.75	451.68
days	3	25,767.70	8,589.23**
types × days	13	11,541.81	887.83*
trees × days	25	10,347.85	413.91
samples/cells	56	18,318.75	327.12**
error	171	8,257.50	48.29

lets, resin had to be wiped off continually (cf. KAUFMANN 1968). Pressure readings were taken when there was a sudden increase in the rate of bubbling at the cut surface of the branchlet. Because of the peculiar viscosity of the resin of *P. ayacahuite* these readings may have been considerably biased downward (they were much more negative)¹. All the estimates were most likely modified by both the time of the day and the position in the tree but more rigid sampling was not possible.

¹ The variances between samples and readings in samples were included for completeness at the bottom of table 8 although they had no biological significance. The error of measurement was estimated by $s_E = .48$ at; the standard deviation of the variance between samples was $s_S = .80$ at. Hence the error of a cell mean was $s = .52$ at. This is about as large as in a comparable study on osmotic pressure of the needle cell sap (HATTEMER 1964) but may have been increased by the changes induced during the four hour sampling time.

The results showed no relation to any aspects of susceptibility against the sawfly.

Discussion

W. E. WATERS and G. NAMKOONG suggested the assumption of an underlying contagious distribution as a random attack effect, the influences of the other variables affecting the subsequent distribution of colony counts. A linear model is of course only one out of several approaches; its choice was mainly for simplicity. The same objections apply also to factor analysis. The distribution of oviposition points could be described with an efficiency of 50 to 60%. Considerable increase in R^2 was achieved by introducing features of neighbor trees as measures of the micro-site. Making reference to the close year-to-year correlations of means of genotypes it seems that under the present close environmental correlations this could hardly be increased more. It is assumed that dealing with the genetic variation in more detail was an alternative approach but required other computational facilities.

Correcting for features of the neighbors did not however allow to take account of their genotype since the 30 types could not be scaled by anything else than just dimensions and counts of the single trees. According to HENSON et al. (1969) the incidence of attack in a given tree reflects the result of a mechanism that consists of at least three stages: discernment of the host tree as such (which is to some extent guided by its neighbors), response to some olfactory stimulus (functioning either as attraction or repulsion), and some tactile stimulus displayed by the foliage. The second stage, however may be greatly modified by volatiles emanating from trees which the insect is unable to properly locate. Susceptibility may thus mean something very different depending on whether the available genotypes of host trees are growing in intimate mixture or tested separately. Results by GERHOLD and SOLES (1966) and GERHOLD (1968) with *Pissodes strobi* (Coleoptera: Curculionidae) seem to support this in that the association of a given species with certain others in test cages had most remarkable effects on both feeding and oviposition frequency. An observation in the present study seems to further support this conclusion; immediately around the interplanted non-host white pines there was clearly less oviposition than around host trees. The method applied in computing N_1 and N_2 could only approximate such conditions. The circumstances of testing hence may have been unique because it is most unlikely that these genotypes will again be grown in the same mixture.

One point needs discussion with regard to practical applications: The present study deals with only one aspect of host resistance. There exist various characteristics of the host trees that influence the probability of successful development and survival of the

later stages, and consequent damage to the tree. Consequently, there are as many aspects of resistance vs. susceptibility as there are critical stages in the life cycle of the insect. These are not necessarily closely correlated. Direct selection for resistance on a practicable basis requires an accounting for all elements of the insect's behavior that affect the probabilities of initial attack, subsequent survival and injury to the tree. The totality of these effects must be determined. SOEGAARD (1964) and GERHOLD (1966) discuss problems in the initiation of breeding projects. WRIGHT et al. (1967) and HENSON et al. (1969) present experimental results on the European pine sawfly.

Moreover, the wide variation of oviposition frequency among types of very different genetic make-up is not directly usable in selection since it cannot be interpreted. However, this study can demonstrate the influence of certain environmental variables and host genotypes under the conditions of natural infestation.

Zusammenfassung

1. Während dreier aufeinanderfolgender Jahre wurde die Eiablage durch *Neodiprion sertifer* (Hymenoptera: Diprionidae) an 546 Kiefern ausgezählt. Die Versuchsbäume gliederten sich in Herkünfte verschiedener Zweinadlerkiefern, Hybriden zwischen solchen Arten und einige Fünfnadler (Haploxyton). In diesem Wahltest wurden einige der 30 verschiedenen Genotypen des Wirts zur Eiablage bevorzugt.

2. Die Eiablagestellen mußten mittels Fraßkolonien der beiden ersten Larvenstadien lokalisiert werden.

3. Neben dem Genotyp waren vier andere Gruppen von Eigenschaften eines Baums von Einfluß auf die Eiablage: die Position (Koordinaten) in der Pflanzung, die Kronendimensionen und die seiner Nachbarn sowie die Häufigkeit der Eiablage bei den Nachbarbäumen.

4. Bei Bäumen verschiedenen Genotyps wurden offenbar verschiedene Kronenteile zur Eiablage bevorzugt.

5. Die Wasserverhältnisse einer Stichprobe von Versuchsbäumen während der Schlupfzeit des Insekts zeigten keinen Zusammenhang zur Anfälligkeit.

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