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Natural Variation in Susceptibility of Pinus to Neodiprion Sawflies as a Basis for the Development of a Breeding Scheme for Resistant Trees

Walter R. Henson

Louis C. O'Neil

Francois Mergen

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YALE UNIVERSITY : SCHOOL OF FORESTRY

BULLETIN No. 78

NATURAL VARIATION IN SUSCEPTIBILITY OF
PINUS TO *NEODIPRION* SAWFLIES AS A BASIS
FOR THE DEVELOPMENT OF A BREEDING
SCHEME FOR RESISTANT TREES

By

WALTER R. HENSON
LOUIS C. O'NEIL
FRANÇOIS MERGEN

NEW HAVEN : YALE UNIVERSITY

1970

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2012

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THE AUTHORS

Walter R. Henson was Professor of Forest Entomology at the Yale School of Forestry at the time of this study; he now serves as Chief of the Research Branch, Ontario Department of Lands and Forests, Canada.

Louis C. O'Neil is an Associate Professor on the Faculty of Sciences at the University of Sherbrooke, Province of Québec, Canada.

François Mergen is Dean and Pinchot Professor of Forestry at the Yale School of Forestry.

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A great deal of the work reported here was done on insects collected from an infestation of known history under the direction of Professor F. Knight of the University of Michigan. To him also our thanks are due.

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INTRODUCTION

DURING the past ten years there has been widespread interest in the general problem of the relationship of phytophagous insects to their hosts. A particularly interesting approach has been found in the study of polyphagous insects capable of subsisting on a great variety of host material but showing in nature a considerable degree of selectivity.

The most recent approaches to this problem probably have all been influenced by a review by Thorsteinson in 1960. Thorsteinson pointed out that the sensory response of insects to their host plants occurred at a series of levels. The identification of the host plants by the adult female is probably accomplished by a combination of more or less-random searching movements and short-distance perception of suitable hosts by olfactory signals. That the presence of the proper olfactory signal is apparently necessary for the release of egg laying has been shown by numerous laboratory investigations of rearing techniques. In a large number of cases, the presence of host material is necessary to initiate egg laying. In its absence the females simply retain their eggs and eventually die.

With respect to the feeding of the larval insect, the chemical environment must, apparently, provide a combination of chemical and tactile stimuli which release the feeding behavior of the larva. In addition, Thorsteinson maintained that olfactory stimuli are also required to prevent the wandering of the larva away from the food.

The study of specific attractants in host material and their behavioral impact on the insect have probably reached their highest development in the current very active investigations of bark beetle responses to the volatile materials in the host trees (Kangas and Perttunen, 1967; Wood, et al., 1967).

For the maintenance of feeding, once the feeding releaser mechanism has been invoked, the gustatory senses of the insects are reported to be related to the nutrient value of the foliage. In the review cited, Thorsteinson reported large numbers of investigations in which the nutrient value of various media is related directly to the amount of the material eaten. Thorsteinson does not suppose that the insects recognize directly the nutrient status of foliage. However, he sees no reason why some individual nutrient substances in the leaf cannot supply the appropriate feeding stimulus. These feeding stimuli are, apparently, sugars for the most part. In general, reports of insect response to mineral nutrients have been lacking.

SUSCEPTIBILITY OF *PINUS*

Thus with the field of insect host relationships centered on the study of the chemical environment of the insects, the relevance of the study of artificial media to the general study of host relationships becomes apparent. Artificial media have been developed for the support of a large number of economically important insects and, in almost all cases, these media have included a specific feeding attractant either in the form of a host extract or in the form of the pure chemical.

An alternate approach to the study of host-insect relationships is afforded by the observation of the behavior of insects on a variety of host materials. This latter approach is better adapted to the requirements of studying the phenomenon of host resistance and the very practical requirements of developing lines of host material which will show a useful degree of resistance to insect attack. The present study stems from such an interest.

Sawflies of the genus *Neodiprion* infest many species of North American conifers. A sub-group of the genus is confined to species of *Pinus* and these are referred to as the "pine sawflies." Insects such as *Neodiprion sertifer* are perennial and difficult problems in plantations of a number of species of pine throughout the Northeast. Large-scale plantings of conifers in blocks of single species have materially favored increased activity and damaged by sawflies.

Some native members of the genus, such as *Neodiprion swaini banksianae*, are recurrent problems in the jack pine forests of the North. This insect has caused extensive defoliation over a large section of northcentral Quebec. It is also a serious problem in jack pine forests of Michigan, Wisconsin and Minnesota. Other members of the genus are frequently serious problems on pines in the South, on ponderosa pine in the West, on lodgepole pine in the Intermountain region, and on white pines in the Northeast.

Currently control of sawflies in outbreak proportions requires repeated topical applications of chlorinated hydrocarbons like DDT. These procedures are effective in plantations, but they present serious biological and economic difficulties in forest practice, coupled with serious ecological implications. Ordinary insecticide control is difficult because of the habits of the insects requiring repeated spraying.

Planting genetic strains of pines inherently resistant to sawflies would be one means of exerting long-term control of these destructive defoliators. The sawflies are oligophagous or polyphagous, but each does not attack certain pine species. Inherently resistant species, or hybrids of these species with susceptible species, might be useful in controlling damage. Certain varieties or individual trees of susceptible species also may demonstrate an acceptable level of resistance to infestation. Selecting a breed for resistance within and among species

TO *NEODIPRION* SAWFLIES

of pines deserves considerable emphasis in multilateral efforts to control damage to pines by *Neodiprion* sawflies.

The European pine sawfly *Neodiprion fertifer* (Geoff.) is an introduced insect widely distributed throughout Eastern North America and an important defoliator of the two- and three-needled pines in plantations, as well as in natural stands. The insect has attracted considerable attention from economic entomologists, foresters, and students of insect behavior. The literature on this insect has recently been reviewed by Lyons (1967). Because of its polyphagy and the fact that its behavior is relatively well known, the European pine sawfly appeared to be an admirable insect for the study of host relationships. Wright, Wilson and Randall (1967) have reported remarkable differences among scotch pine varieties in susceptibility to this insect. Similar differences have been suggested by Coppel and Benjamin (1965) and Benjamin, Larson and Drooz (1955). This host selectivity is not unique to *Neodiprion fertifer* as is suggested by the study of Tsao and Hodson (1956) working on the allied form, *Diprion simile*.

We shall report field studies on host selection by adult females, laboratory studies of larvae on various hosts and field studies of larvae on various hosts. On the basis of the experimental work we shall attempt to suggest the nature of variability with respect to the impact of the insect on various types of host material.

SUSCEPTIBILITY OF *PINUS*

HOST SELECTION BY ADULT FEMALES: FIELD METHODS

The observations were carried out in the Yale Forestry School genetics plantation of pine types on the Great Mountain Forest in Norfolk, Connecticut. This plantation was established by one of us (F. M.) in 1958 by the transfer of plantation seedlings from Valhalla, New York. The plantations are on an open, old field site with a gentle slope. All plantations were established with a uniform 12 x 12 ft. spacing, the columns running north-south. The rows of the adjacent units of the plantation are contiguous so that the overall spacing is uniform even at the internal boundaries.

The surrounding Great Mountain Forest includes a large area of plantation red and scott's pine most of which is chronically infested with *Neodiprion sertifer*. The trees of the experimental plantation have been kept relatively clear of sawfly up to the beginning of the present observations by insecticidal treatment.

The experimental plantations include a large variety of pine types, a listing of which is presented in Table 1. We hope that it will be apparent from this description of the plant material that the immigrant females of *Neodiprion sertifer* did encounter in the experimental plantations a range of hard pine types widely representative of the *Jylvestris* group as well as a less concentrated sampling of allied forms. It is important to note that the placing of the various pine types in the plantation was accomplished by randomized blocks with tree randomization in the blocks, 1 source per block. This arrangement provides a random association of adjacent trees but does not provide a latin square array in which all types are equally represented in all rows and all columns. The importance of this feature of the plantation lies in the fact that one cannot assume that all equal small portions of the plantation area contain an equivalent number and variety of the various pine types. Because of this, there is implicit in the physical layout of the experimental area the possibility of an interaction between the effect of host type and rate of infestation and the effect of position in the plantation on the same measurement.

The first field measurements (1965) consisted of an examination of each tree in the plantations during the early part of the season following the hatching of the overwintering eggs. At this time of year, the location of each egg cluster can be obtained by observing flagged needles which originally contained the egg cluster and which are partly eaten by the newly emerged larvae. By making the counts early in the season one may be assured that the number of

TABLE I. PINE TYPES STUDIED FOR SUSCEPTIBILITY TO *NEODIPRION*

Groupings	Species	M#	Source	SERTIFER GEOFF.		Hybrid Identity
				♀ parent	♂ parent	
1	<i>sylvestris</i>	96,144	Scotland			
		98,145	East England			
		95,146	Australia			
		89	Spain (Segovia)			
		90	France (Auvergne)			
		91	Finland			
		92	France (Alsace)			
		93	Sweden (66° 19' N 20° 31' E, alt. 600')			
		94		<i>sylvestris</i> M405, Morris Arbor	Mixture of sylv. pollen	
		97 99 303	Czechoslovakia Turkey Spain			
2	<i>banksiana</i>	111		<i>banksiana</i> M7374, Morris Arbor	o.p.	
		112		<i>banksiana</i> M7375, Morris Arbor	murr. x banks.	
	<i>contorta</i> x <i>banksiana</i>	110				

TABLE 1. PINE TYPES STUDIED FOR SUSCEPTIBILITY TO *NEODIPRION*
SERTIFER GEOFF. (Continued.)

Groupings	Species	M#	Source	♀ parent	♂ parent	Hybrid Identity
3	<i>densiflora</i>	61	Japan?			
		62,142	Korea, 35km.N of Seoul			
		63,64,141	Japan?			
		B6		densiflora G1651 Andorra Nursery		o.p.
		87		densiflora G1937 Andorra Nursery		o.p.
		88		densiflora G1060		o.p.
		304		Haverford College		
		134		densiflora 1940 Andorra Nursery		o.p.
		138		densiflora 2188 Andorra Nursery		o.p.
		206		densiflora 2154 (Wright's neighbor)		o.p.
207		densiflora 2154 (Wright's neighbor)				
4	<i>densiflora</i> x <i>thunbergii</i>	135		densiflora 1938 Andorra Nursery	Thunbergii E. J. Schreiner F1	F2
		136		densiflora x thun. 1938— Andorra Nursery	o.p.	
		291		densiflora 2153	mixture of	

TABLE 1. PINE TYPES STUDIED FOR SUSCEPTIBILITY TO *NEODIPRION*
SERTIFER GEOFF. (*Continued.*)

Groupings	Species	M#	Source	♀ parent	♂ parent	Hybrid Identity
5	<i>thunbergii</i> x <i>densiflora</i>	68		thunbergii 1608 Morris Arbor		
		69		" "		mixture of densi. pollen. dens. M347 Morris Arbor.
		202		thunbergii 2 169 (Wright's neighbor)		mixture of dens. pollen.
		283		thunbergii 2013 (Wright's yard)		mixture of dens. pollen.
		285		thunbergii 1769 ?		mixture of dens. pollen.
		284		thunbergii 3013, 1775,1767		mixture of dens. pollen.
6	<i>densiflora</i> x (<i>dens. x th.</i>)	84		<i>densiflora</i> 2154 (Wright's neighbor)		dens. x thun. I438?
7	<i>thunbergii</i> x (<i>dens. x th.</i>)	115		thunbergii 2 169 2017, Haverford Coll.		+ dens. x thun. F1 E. J. Schreiner, Yale
		120		thunbergii 2169 Haverford Coll.		dens. x thun. + not pure o.p.
		124		thunbergii 2 167 Haverford Coll.		dens. x thun.
		130		" "		dens. x thun. not pure o.p.
		132		thunbergii 2013 Haverford Coll.		dens. x thun., E. J. Schreiner, Beltsville
		133		thunbergii 2015 Haverford Coll.		dens. x thun.

TABLE 1. PINE TYPES STUDIED FOR SUSCEPTIBILITY TO *NEODIPRION*
SERTIFER GEOFF. (Continued.)

Groupings	Species	M #	Source	♀ parent	♂ parent	Hybrid Identity
8	<i>nigra</i> x <i>densiflora</i>	307	No further information on this.			
9	<i>densiflora</i> x (<i>dens. x sylv.</i>)	137		<i>densiflora</i> 2188 Andorra Nurs.	<i>dens. x sylv.</i> F ₁ E. J. Schreiner	
10	<i>thunbergii</i>	67		<i>thunbergii</i> 2169 (Wright's neighbor)	mixture of thun. pollen.	
		74		<i>thunbergii</i> G2013 (Wright's neighbor)	<i>thunbergii</i> 1608 Morris Arbor.	
	<i>thunbergii</i>	118		<i>thunbergii</i> 2169	Morris Arbor.	
		126		<i>thunbergii</i> 2167	<i>thunbergii</i>	
		128		<i>thunbergii</i> 2167	<i>thunbergii</i> 1608 Morris Arbor.	
		147	Japan			
		148	Korea			
		200		<i>thunbergii</i> 2013 (Wright's yard)	o.p.	
		277		<i>thunbergii</i> 2014 (Wright's yard)	o.p.	
		278		<i>thunbergii</i> 2167 (Wright's neighbor)	o.p.	
		279		<i>thunbergii</i> 2169 (Wright's neighbor)	o.p.	
		280		<i>thunbergii</i> 1769	o.p.	
11	<i>thunbergii</i> x <i>yunnanensis</i>	113		<i>thunbergii</i> 2169 2015, 2013	<i>sin. yunn.</i> IFG	
		122		<i>thunbergii</i> 2167	<i>sin. yunn.</i> IFG	

TABLE I. PINE TYPES STUDIED FOR SUSCEPTIBILITY TO *NEODIPRION*
SERTIFER GEOFF. (Continued.)

Groupings	Species	M#	Source	♀ parent	♂ parent	Hybrid Identity
12	<i>thunbergii</i>	114		thunbergii 2169	sin. IFG	
	x <i>sinensis</i>	123		2015, 2013 thunbergii 2167	sin. IFG	
13	<i>thunbergii</i>	116		thunbergii 2169	tabulaeformis	
	x			2017	1527, Morris. Arb.	
	<i>tabulaeformis</i>	117		thunbergii 2169	tabulaeformis	
		119		thunbergii 2169	1528, Morris Arb.	not pure
		125		thunbergii 2167	tabulaeformis	
		127		thunbergii 2167	1527 + o.p.	
		129		thunbergii 2167	tabulaeformis	
		201 282 72		thunbergii 2169 thunbergii 2014 thunbergii 2169	1527 tabulae. 1528 tabulae. 1527 + o.p. tabulae. 1527 tabulae. 1527 mix. of tab. pollen	not pure
14	<i>thunbergii</i>	203		thunbergii 2014	do	
	selfed	73		(Wright's yard) thunbergii 2169 (Wright's neighbor)	do	
15	<i>thunbergii</i> x <i>taiwanensis</i>	289		thunbergii 2169 (Wright's neighbor)	taiwanensis IFG	

TABLE I. PINE TYPES STUDIED FOR SUSCEPTIBILITY TO *NEODIPRION*
SERTIFER GEOFF. (Continued.)

Groupings	Species	M #	Source	♀ parent	♂ parent	Hybrid Identity
16	<i>thunbergii</i> x <i>nigra</i>	77		<i>thunbergii</i> 1608 Morris Arbor	mixture of <i>nigra</i> pollen	
17	<i>nigra</i>	75	Italy (Calabria)			var. <i>calabriae</i>
		76		<i>nigra</i> M349 Morris Arbor	o.p.	
		78	France (Arboretum des Barres)			var. <i>calabriae</i>
		79	England (Norfolk)			var. <i>calabriae</i>
		80	Corsica			var. <i>corsicana</i>
		81	Corsica			var. <i>calabriae</i>
		82	Greece (Thessaly)			var. <i>austriaca</i>
		83 + 143	Italy (Vallombrosa, Firenze)			var. <i>calabriae</i>
		139		<i>nigra</i> 1766	o.p.	
		205	no information on this			
18	<i>tabulaeformis</i>	204		<i>tabulaeformis</i> 1528 Morris Arb.	o.p.	
19	<i>densiflora</i> x <i>nigra</i>	290		<i>densiflora</i> 2154 (Wright's neighbor)	mixture of <i>nigra</i> pollen	

TO *NEODIPRION* SAWFLIES

Age of Stock: 4 yrs.
 Spacing: 12' x 12'
 Date outplanted: May 1958

IBM Code
 Tree Identification
 20A—N
 21A—I
 23A—K
 24A—N
 22A—L
 N



M20 B	M21 C	M24 G	M20 I		M20 N
M22 B	M21 B	M23 F	M24 J	M24 L	M21 I
M20 A	M22 D	M24 F	M22 H	M23 I	M20 M
M23 B	M23 D	M20 F	M22 G	M20 K	M24 N
M24 C	M20 D	M20 E	M20 H		M23 K
M22 A	M23 C	M23 E	M24 I	M24 K	M24 M
M24 B	M24 E	M21 E	M24 H	M20 J	M22 L
M21 A	M24 D	M22 F	M20 G	M21 G	M22 K
M24 A	M22 C	M21 D	M23 G	M23 H	M20 L
M23 A	M20 C	M22 E	M21 F	M22 I	M23 J

FIGURE 1. Plantation #1. Jack Pine Geographic Seed Sources.

colonies of feeding larvae seen are closely approximate to the number of initiating egg clusters and this assumption can be checked by comparing these numbers.

For each tree in each of three succeeding years, the number and size of the sawfly colonies was recorded by height and direction in the crown. The height of the tree, the height of the tree crown, and the diameter of the tree crown were recorded (the latter in the north-south and east-west directions). The individual trees were identified by means of metal tags at their base and the data were recorded on mimeographed schematic maps of the plantations in which tree-type index numbers were entered in each location. The importance of this double identification of the tree type lies in the fact that there was considerable mortality within some pine types in the plantation and a consequent possibility that the data would be misrecorded as a result of gaps in the original planting sequence. From time to time during the field observations

Age of Stock: Variable 4-8 years
 Spacing: 12'x12'
 Date Outplanted: Spring 1958

N →

Row # 1 →

73 A		67 A	69 A	110 A	98 A			62 A		62 B	61 A	83 A	62 C		62 D
95 A	67 B	67 C	98 B	69 B	66 A	110 B	54 A	63 A	97 A	61 B	64 A	62 E	62 F	62 G	64 B
97 B	87 A		66 B	67 D	95 B	66 C	64 C	72 A		98 C	66 D		94 A	66 E	83 B
	302 A		110 C	95 C	97 C	62 H	19 A		63 B	72 B		62 I	84 A	83 C	68 A
89 A	73 B	98 D	86 A	67 E	86 B	33 A	72 C		61 C	66 F	98 E		95 D	66 G	83 D
	97 D	89 B	67 F	88 A	95 E		110 D	66 H	72 D	34 A	110 E	84 B	68 B	76 A	84 C
88 B	88 C		72 E	86 C	110 F	34 B	92 A			94 B	69 C	66 I	68 C	84 D	76 B
500 A	86 D	302 B		96 A	86 E	110 G		79 A		79 B	84 E	96 B	69 D		66 J
304 A	302 C	304 B	110 H	72 F	303 A	79 C	279 A		110 J	97 E	76 C	79 D	66 K	72 G	79 E
66 L	304 C	90 A	306 A		78 A	86 F	86 G	78 B	76 D	76 E	79 F	66 M	75 A		66 N
	99 A	93 A	90 B		77 A	82 A		303 B		76 F	68 D		79 G	66 O	76 G
106 A	72 H	72 I	99 B	90 C	82 B	93 B	86 H	78 C	76 H	110 K	75 B	145 A	303 C	66 P	74 A
95 F			99 C	80 A		82 C	110 L	76 I	78 D	307 A		75 C	74 B	79 H	76 J
		93 C		93 D	82 D		91 A	91 B		91 C	91 D	307 B	66 Q		105 A
	95 G			81 A	93 E					303 D		109 A	75 D	74 C	307 C
95 H	106 B	95 I	81 B		81 C	303 E		303 F		206 A	303 G		66 R	307 D	145 B
							280 A		303 H				303 I	101 A	

Row # 17 →

↑
Column

FIGURE 2. Plantation #2. Conifers and Pine Hybrids.

↑
Column

Age of stock: 4 yrs.

Date Outplanted: April 1950

	117 A	119 A	114 A	136 A	143 A		112 A	126 A		137 A		144 A	146 A	146 B	127 A		Column # 37
		146 C		117 B	144 B	127 B	112 B	137 B	141 A	115 A	114 B	119 B	134 A	129 A	123 A	132 A	
N	112 C	146 D	141 B	146 E	137 C	117 C	136 B	112 D	132 B	144 C		119 C			114 C	143 B	
	130 A		116 A	142 A	143 C	128 A	135 A	133 A	147 A	111 A	118 A		113 A	135 B		145 A	
	111 B		120 A		118 B	116 B	115 B		147 B	135 C	145 B	138 A	142 B	125 A	130 B	133 B	124 A
	111 C	128 B	130 C	135 D	118 C			116 C	142 C				125 B	139 A	143 D	147 C	145 C
	116 D		130 D	128 C	111 D	115 C	125 C			138 B		142 D		145 D	147 D	133 C	
	135 E		133 D				125 D			116 E		143 E	128 D	145 E	111 E		142 E
	112 E	146 F	117 D	141 C	132 C	141 D	136 C		146 G	126 B	137 D	127 C	119 D	112 F	143 F		
	130 E	124 B	133 E	128 E		145 F		142 F	111 F	143 G	118 D	125 E					
	130 F		111 G	125 F		120 B		118 E		133 F		138 C	128 F	116 F	145 G	142 G	147 E
	112 G	115 D	117 E		119 E	144 D	146 H	141 E		114 D	136 D	132 D	123 B			127 D	126 C
		126 D	114 E	119 F	137 E	117 F	134 B		123 C	141 F	146 I	129 B		115 E	127 E	144 E	
	119 G	146 J	123 D	127 F	144 F		117 G		114 F			137 F		132 E		112 H	141 G
		137 G	148 A		123 E	142 H	127 G	132 F	117 H	112 I	115 F	141 H		114 G	146 K	144 G	
	111 H	116 G	130 G	147 F	145 H		135 F			138 D	125 G		142 I	133 G			
	134 C	117 I	127 H	146 L		141 I	137 H	123 F	144 H	126 E	132 G	119 H			114 H	129 C	112 J
	111 I	138 E	135 G	133 H	120 C	142 J	147 G	125 H				130 H	118 F	116 H	145 I		
	112 K	119 I	123 G		115 G	117 J	147 H	125 I	114 I	129 D	134 D	148 B		141 J	144 I	146 M	
	118 G	120 D	142 K	143 H		147 I		111 J	115 H	118 H	135 H		122 A	130 I	145 J		Column # 18

Row
1

FIGURE 3. Plantation #5. Hard Pine Hybrids.

Row
17

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Age of Stock: 3 yrs.
 Spacing: 12' x 12'
 Date Outplanted: May 1958

N ↑	M204 A	M200 A		M202 A			M291 A	M284 A		M201 A	← Colu # 1	
			M282 A	M278 A		M205 A			M206 A			
	M285 A	M201 B	M283 A		M207 A	M202 B		M203 A		M289 A		
			M202 C	M201 C	M283 B		M203 B	M200 B	M207 B			
	M202 D					M284 B	M201 D	M283 C	M291 B			
			M207 C		M200 C	M202 E	M201 E		M291 C	M283 D		
				M282 B	M279 A			M206 B	M204 B			
	M282 C			M204 C	M277 A		M205 B		M279 B			
	M284 C	M285 B	M290 A	M200 D	M203 C	M283 E	M207 D					
				M202 F	M289 B	M203 D	M201 F	M207 E		M200 E		
	M202 G	M290 B	M200 F	M283 F	M203 E	M285 C	M289 C	M207 F		M201 G		
	M204 D			M205 C								
		M290 C	M200 G		M282 D	M290 D						
	M289 D	M207 G		M203 F	M285 D	M202 H	M201 H	M283 G		M200 H		
	M277 B	M206 C	M205 D			M204 E						
		M291 D	M200 I	M202 I	M289 E	M207 H	M284 D	M203 G	M283 H	M201 I	← Colu #	
	Row # 18	FIGURE 4. Plantation #7. Hard Pine Hybrids.										Row # 27

the various observers repeated the observations on individual trees to permit a comparison of the interpretation of colony size numbers and locations between observers. A high degree of uniformity was found so that the counting data may be considered to be comparatively reliable. It is our impression, however, that the reliability of the counts in heavily infested trees would be somewhat reduced by the difficulty of distinguishing the numbers of colonies when the entire tree was infested and largely stripped of the foliage.

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OBSERVATIONS AND ANALYSIS

Because the experimental plantation had been treated with insecticide during the period of larval growth over a number of years preceding the present study, it was assumed that the population observed in the first year of the study was largely the result of infestation by females dispersed from the surrounding infested forest. It is known (Henson, 1965a) that the dispersal of this species is accomplished by two distinct behavioral types of females. The vast majority of females are unable to make extended free flights and their mean flight distance is in the order of less than 10 meters per flight. On the other hand a small proportion (probably about 3 percent) of the females in an established population are able to make extensive free flights in the order of some kilometers in length.

If the infestation observed during the first year of this study was the result of dispersal from surrounding forests it might be suspected that the immigrant females would not be uniformly distributed through the experimental plantation and that differences in rate of infestation within the plantation might be simply a function of the distance to the nearest source of hosts from which the immigrants could fly. The numbers of colonies per tree were summed by rows and by columns for each plantation. These totals were used to develop linear regression expressions none of which showed a significant difference from a slope of zero. This implies that there was no systematic difference in the rate of infestation that arose simply from the differences in proximity of the surrounding infested forests. The data for all three years of study were examined in the same manner with the same results. In the second and third years, however, it should be pointed out that the source of infestation could be assumed to include both immigrant and indigenous females since no control was applied. The finding that there was no systematic pattern within the infested plantations permits us to examine the number of colonies per tree as it relates to the tree type without considering the position of individual trees or the pattern of planting of single types.

SEASONAL CHANGES IN POPULATION

The observations reported in this paper were taken during the field seasons of 1965, 1966 and 1967. During this period the population of *Neodiprion sertifer* changed markedly with the overall increase ranging between threefold and twelvefold. A summary of the gross colony counts is presented in Table 2.

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TABLE 2. SUMMARY OF *N. SERTIFER* POPULATION SURVEY DATA IN PLANTATIONS 1, 3, 5 AND 7—NORFOLK, CONNECTICUT. 1965, 1966 AND 1967.

		1965	1966	1967
Plantation # 1 Pinus Banksiana	Total Colonies	49	98	129
	Total Trees	58	58	58
	Trees Infested	29	37	39
	Colonies / tree	0.84	1.70	2.22
	% Trees Infested	50.0	63.8	67.2
Plantation # 3 Hard Pine Hybrids	Total Colonies	783	3331	4122
	Total Trees	207	210	205
	Trees Infested	129	188	182
	Colonies / Tree	3.78	15.86	20.11
	% Trees Infested	61.7	89.5	88.8
Plantation # 5 Hard Pine Hybrids	Total Colonies	654	1980	5183
	Total Trees	246	247	243
	Trees Infested	192	233	230
	Colonies / Tree	2.66	8.02	21.33
	% Trees Infested	78.0	94.3	94.6
Plantation # 7 Hard Pine Hybrids	Total Colonies	182	968	2081
	Total Trees	93	92	91
	Trees Infested	56	78	76
	Colonies / Tree	1.96	10.50	22.87
	% Trees Infested	60.2	84.8	83.5

A formal analysis of the position effects to detect the possibility that the differences between rows would show an interaction with the population differences between the years was done by means of a standard analysis of variance. A summary of this analysis is presented in Table 3. It will be noted that the interaction is not significant. The significance of the mean squares for rows reflects the differing distributions of host types between rows as noted earlier. The significance of this term therefore does not express a position effect.

TABLE 3. VARIANCE ANALYSIS OF COLONY NUMBERS BY PLANTATION, ROW AND YEAR.

Source	DF	MSS	F
Years	2	2523.103	213.932**
Rows	26	24.383	2.067**
Interaction	52	6.145	0.521 N.S.
Error	1447	11.794	
Plantations	1	8.598	0.729 N.S.
Total	1528		

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EFFECT OF TREE AND CROWN HEIGHT

The various pine types in the experimental plantations showed quite different degrees of success in the climate of Norfolk, Connecticut. As a consequence there was a considerable difference between pine types in the size of the experimental trees. Because it was considered important to distinguish the effect of varying degrees of attractiveness of the host foliage and the effect of varying amounts of available foliage, the data on tree size were examined in some detail. The distribution of tree heights was examined for normality by dividing the total range of observed heights into 20 classes and erecting a frequency distribution of heights within these classes. This distribution was compared with the normal by means of Chi-Square, and the sum Chi-Square value of 32.25 with 21° of freedom established the normality of the size distribution.

Our impression that the rate of infestation would bear a general relationship to the size of the tree was confirmed by means of an analysis of variance of colony numbers on trees of the various height classes over the three years of observation. A summary of this analysis is presented in Table 4.

TABLE 4. VARIANCE ANALYSIS OF MEAN COLONY NUMBERS PER TREE BY HEIGHT CLASSES AND YEARS.

Source	DF	MSS	F
Years	2	1709.821	91.277**
Height	19	144.794	7.730**
Interaction	38	34.983	1.868**
Error	1466	18.732	
Total	1525		

It will be noticed that the significance of the years term in this analysis reflects the overall increase in the rate of infestation. The significance of the heights term reflects the fact that in general larger trees support greater numbers of colonies. The significance of the interaction term is the result of the enhanced concentration of colonies on the larger trees as the overall infestation rate increased.

EFFECT OF LATERAL CROWN AREA

Since it was obvious that the number of colonies per tree was a function of tree height and that the tree height was confounded with pine type, an expression of the amount of foliage presented by each individual tree was sought. For simplicity the crown of the tree was considered to display a conical form

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and an expression of the amount of foliage in each individual crown was developed from the simple geometrical expression for the area of the cone. Because the crown diameter at the base did not show a good linear relation to tree height the expression for the conical surface area had to be developed individually for each tree on the basis of the field measurements of crown height and crown diameter. The surface areas of the crowns were individually computed on this basis and the range of crown surface area was divided into 26 equal classes. The distribution of frequencies of trees falling into each of these crown surface area classes was computed and shown to be normal. The mean number of colonies per tree in each of the crown classes was then computed and the analysis recorded above was repeated. The results of this analysis are given in Table 5.

TABLE 5. VARIANCE ANALYSIS OF MEAN NUMBER OF COLONIES PER TREE BY CROWN SURFACE AREA AND YEAR.

Source	DF	MSS	F
Years	2	3545.5	123.915**
Surface Area	25	325.08	11.362**
Interaction	50	75.529	2.640**
Error	1448	28.612	
Total	1525		

Here again the significance of the years term reflects the change in the overall infestation level. The significance of the surface area term reflects the response of insects to the larger trees and also the confounding of tree size with tree type. The significance of the interaction reflects the enhanced concentration of insects on the larger trees as the infestation level increased.

The relationship between the numbers of colonies observed and the lateral crown area was further investigated by means of regression analysis with a separate analysis being performed for the data of each of the three years. For this analysis the \log_{10} of the colonies per tree was used, a device which normalized the distribution of colony counts. A summary of this analysis is presented in Table 6.

It will be noted that in the data for each of the three years the regression of the logarithm of colony numbers on crown surface area was significant. The individual regression coefficients for the different years were slightly but significantly different as suggested by the significance of the interaction term in Table 5. The distribution of the residuals against the lateral crown area were examined and found to show no significant regression. It will be noted that

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TABLE 6. ANALYSIS OF THE REGRESSION OF LOG₁₀ COLONIES PER TREE ON LATERAL SURFACE AREAS.

1965.			
Regression coefficient = 0.0015172		Standard error = 0.0001482	
T (507 df) = 10.23967**			
Source	DF	Mean Squares	F ratio
Regression	1	11.29991	104.8509**
Deviation	507	0.1077713	
Total	511		
Multiple correlation coefficient = 0.4139**		Intercept = 0.2317962	

1966.			
Regression coefficient = 0.0022221		Standard error = 0.00016787	
T (510 df) = 13.23694**			
Source	DF	Mean Squares	F ratio
Regression	1	24.47614	175.2166**
Deviation	510	0.1396907	
Total	511		
Multiple Regression coefficient = 0.505678**		Intercept = 0.5817691	

1967.			
Regression coefficient = 0.0025612		Standard error = 0.0001965	
T (503 df) = 13.03225**			
Source	DF	Mean Squares	F ratio
Regression	1	31.37413	169.8396**
Deviation	503	0.1847315	
Total	504		
Multiple Regression coefficient = 0.502416**		Intercept = 0.760827	

here again all the regressions of the logarithms of colony counts on ground surface area were significant with respect to the total variance of the data. This finding makes it absolutely necessary to take into account differences in tree size when one is attempting to isolate the effect of foliage quality on colony numbers. The changing population from year to year in this analysis is reflected in the change in the intercept.

COMPASS DIRECTION OF COLONIES IN TREES

As a clue to insect behavior and also to the origin of the egg-laying females, the direction in the crown within which the larval colonies were found was examined. In the field observations, this was recorded in the eight secondary compass directions (north, northwest, west, etc.). The segment totals for all

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eight segments of the crowns were obtained and these totals were compared against the null expectation of equal distribution in all directions. The pooled Chi-square for this comparison was 40.517 for 7 degrees of freedom which indicates heterogeneity. It was noticed that the segment totals for the prime compass directions (north, east, south, west) were considerably higher than those for the secondary compass directions (northeast, southeast, southwest, northwest). This difference suggested an involuntary unwillingness on the part of the observers to assign colonies to the secondary compass points. This unfortunate observer error was met by lumping the compass direction totals into 4 primary directions (north, east, south, and west) and taking the total for the primary direction plus one half of the totals for the adjoining directions, ($N = N + \frac{1}{2}NW + \frac{1}{2}NE$). This lumping was done for all the direction data. It

was found that in plantation number 3 there was a preponderance of colonies in the south and west segments (Chi-square = 23.403 DF 3). In plantation 5 a preponderance in the south and west segments (Chi-square = 40.817 DF 3) and in plantation 7 a possible preponderance in the south and east segments (Chi-square = 6.048 DF 3). This suggests that the females prefer the sunlit and hotter sides of the trees.

EFFECTS OF CROWN CLOSURE

A further possible source of confounding between host type and the number of sawfly colonies on the tree is to be expected from the fact that in a limited number of cases there was partial crown closure in the plantation. There are two obvious effects of such closure, the first being the possibility that the attractiveness of an individual tree is changed by the extent of exposure of foliage and the second being the possibility that the close proximity of an attractive tree with foliage interlacing that of a less attractive tree would result in an increase in the degree of attack on the less attractive tree. The physical effect of exposure was investigated by a computer sorting scheme which systematically searched the entire plantation and **isolated** those trees where the sum of one half the maximum crown diameter of the tree of interest plus one half the maximum crown diameter of an adjacent tree exceeded 12 feet. Both members of each of these pairs of trees could be considered to have experienced at least some degree of crown closure. The sorting was done for the 1967 data where maximum numbers of insects were found and for only two of the subplantations (3 and 5). The mean number of insect colonies per unit surface area of crown was computed separately for those trees that were touch-

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ing and for those trees which **were** not touching. These mean numbers were found not to be significantly different. The level of the colonies in the crowns of these two groups of trees (touching and not touching) was then computed. The results are given in Table 7. The discrepancies in tree numbers within the cells of Table 7 reflect the fact that a number of the trees in the various categories did not support any colonies in some of their segments.

TABLE 7. EFFECT OF CROWN CLOSURE ON POSITION OF COLONIES IN THE CROWNS.

(1967, Plantations 3 and 5)				
Plantation 3 Crown level	Total	# Trees	Colony Numbers	# Trees
	Trees touching		Trees not touching	
Upper	104	12	809	133
Middle	161	12	1282	141
Lower	85	12	568	115
Plantation 5				
Upper	21	7	443	164
Middle	72	11	948	198
Lower	35	9	483	149

It will be noticed that the colonies in the trees with some closure were somewhat higher in the crowns than that in the trees showing no closure. This observation is interesting when considered in conjunction with the observation that the compass direction of the infestation seems slightly biased toward the sunlit side of the trees. Closure apparently causes the insects to avoid the lower, protected foliage.

COLONY SIZE

During the field observations in 1966 an attempt was made to examine the distribution of numbers of larvae per colony. It was not possible to make individual counts of all colonies and so three categories of colony size were arbitrarily set up: large colonies consisting of more than 50 larvae, medium size colonies consisting of 16 to 50 larvae, and small colonies of less than 15 larvae. These are given in Table 8. It will be noted that there is suggestion of heterogeneity in the distribution of colony sizes in the three plantations for the 1966 data.

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TABLE 8. χ^2 TEST OF HOMOGENEITY OR INTERACTION AS TO COLONY SIZE
IN VARIOUS PLANTATIONS-1966.

Plantations	Numbers of Colonies		
	Large	Medium	Small
3	916	1862	254
5	563	1194	223
7	269	638	61

Chi-square = 25.700 DF4

The source of this heterogeneity appears to be an excessive number of small colonies in plantation 5 and an excessive number of medium and small colonies in plantation 7. It is purely speculative but still interesting to note the fact that plantations 5 and 7 are increasingly distant from the putative source of infestation in the direction of the prevailing wind. It seems at least possible that the increasing proportions of medium size and small size colonies reflect the movement of females with the wind through the plantations and their deposition of successive clutches of eggs.

Complete counts of numbers of larvae on a considerable number of colonies were made in each of the three years to determine whether the overall level of infestation was related to the size of the colonies as well as the numbers. The results of these counts are given graphically in Figures 5, 6 and 7. These figures give frequency distribution by ten-larvae intervals from single counts to the largest colonies encountered. It is apparent that as the overall level of infestation increased the size of the colonies similarly increased. The obvious arithmetic conversion of the counts of numbers of colonies and the sampling of colony size into an estimate of the absolute numbers of larvae is not performed because these counts display rather different aspects of the female adult behavior. The numbers of colonies per tree represent the number of times an adult female was able to lay eggs whether her clutch was large or small. On the other hand, the numbers of larvae per colony reflect not only the attractive characteristics of the tree but also the fecundity and perhaps the vigor of the attacking female. It is for this reason that we have used colony numbers in the *Cut-*rent investigations.

The assumptions implicit in the analysis reported to this point are that the insect shows a selective response to the various host types and, secondly, that this selective response is in part a direct expression of preference for certain types of host tissue and also in part a response to the physical conformation of the host trees. Because the physical conformation of the host trees is to a large extent a function of host type we have proceeded in a manner which is designed to **reduce** the confounding of the various types of response. To this

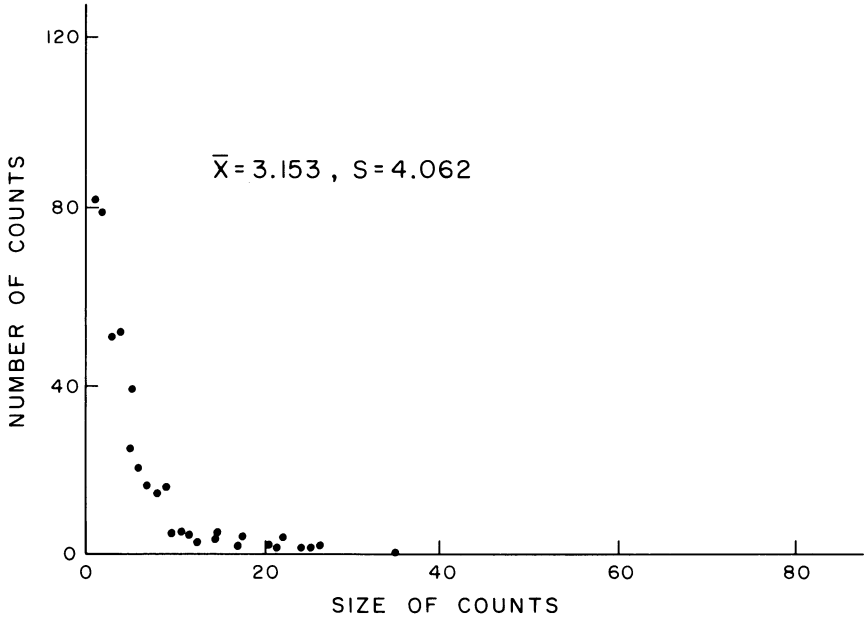


FIGURE 5. 1965 Colony Counts.

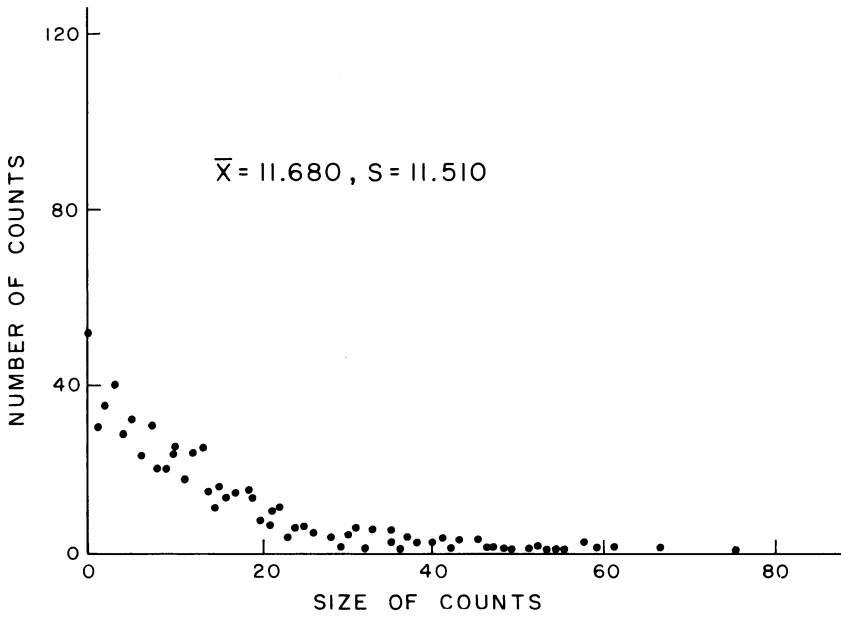


FIGURE 6. 1966 Colony Counts.

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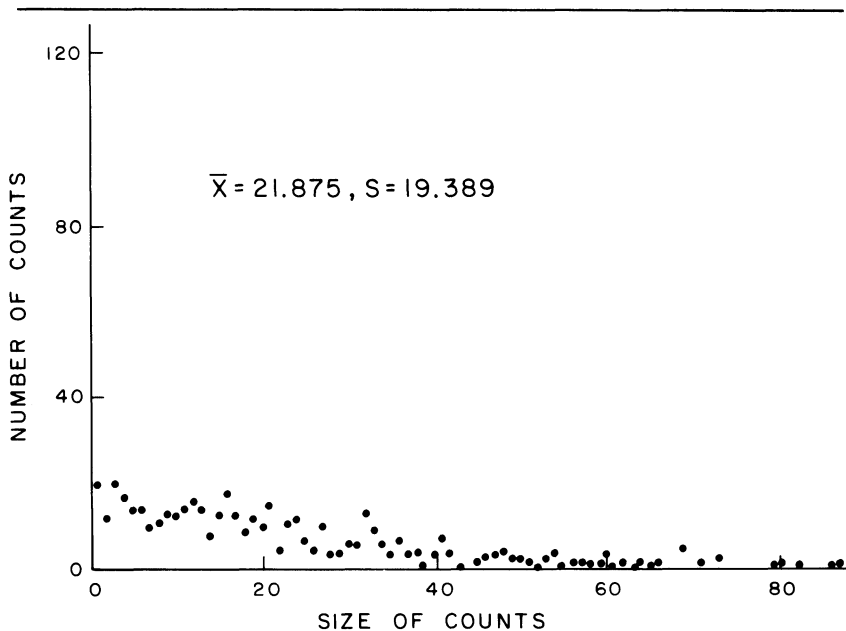


FIGURE 7. 1967 Colony Counts.

point we have seen that there is a relationship between the number of colonies per tree and the size of the trees. There is also a bias in the position of the colonies on the tree which is related to exposure to the sun. There is little or no effect of position in the plantation. We have seen further that the positive relationships displayed tend to be intensified with increasing levels of infestation. The selective behavior of the female has two components: the response to the size and other physical properties of the trees and response to foliage quality. The lateral crown area was the best overall expression of tree size. The correlation coefficient between the log to the base 10 of colonies per tree and lateral surface area was 0.4139 in 1965, 0.5056 in 1966, and 0.5024 in 1967. These correlations were highly significant. On this basis it is appropriate to consider differences between numbers of colonies per tree on the various hosts when this count is corrected at least for the effect of crown area.

To determine whether lateral crown area of the trees was the only physical variable for which correction has to be made, the data were subjected to an analysis of variance and simultaneously to multiple regression analysis considering the colony count per tree and the $\log_{10} + 1$ as the dependent variables.

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Independent variables representing the tree age, height, crown area, crown area squared, row and column address, and tree type were included. Because of the numbers of types of trees (see Table 1), the very large number of sources were grouped into nineteen groups as listed in the first column of Table 1. For convenience in this discussion these groups will be referred to by the species named as set forth in the second column of Table 1.

To assess the effects of the various independent variables, the multiple correlation coefficient for the entire array was derived and compared with the multiple correlation coefficient when the variance due to a single independent variable was pooled with the error term. In this way it was possible to assess the significance of each independent variable. In Table 9, a summary of the significance of the various independent variables, with the variation due to tree type pooled, is given.

The significance of the various independent variables was assessed by an independent technique which consisted in a computation of the mean squares for regression in the entire array of data and by subtraction, a calculation of the mean squares for deviation. Using the mean squares for deviation as an error term, it was possible to determine the significance of each of the independent variables separately or in any combination. This compilation was repeated using as the dependent variable the $\log_{10} + 1$. Because the distribution of the raw colony counts was far from normal, a log transformation of the data seemed to be a conservative precaution in the use of the standard tables for the distribution of F ratios. The computation with the transformed data gave F ratios uniformly higher than those derived from the raw colony counts. In this case then, the departures of the data from normality do not present a hazard in their interpretation.

It will be noticed that of the variables measured, only tree age was com-

TABLE 9. SIGNIFICANCE OF INDEPENDENT VARIABLES IN
REGRESSION ANALYSIS OF COLONIES PER TREE

Dependent Variable	Independent Variable	Significance of Ind. Variables		
		1965	1966	1967
Colonies per tree				
	Tree age in years	n.s.	n.s.	n.s.
	Tree height in feet	n.s.	n.s.	n.s.
	Crown area (ft ²)	H.sig.	H.sig.	H.sig.
	Crown area squared	H.sig.	H.sig.	n.s.
	Row location	sig.	sig.	H.sig.
	Column location	H.sig.	H.sig.	n.s.
	Tree type	H.sig.	H.sig.	H.sig.

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pletely non-significant. This is, of course, the result of the lack of variability in age; there being only two age classes in the entire array of trees.

Because the object of the analysis was to separate that portion of the variance in the number of colonies per tree which could be attributed to tree type without respect to the confounding variation in size and other physical characteristics, the regression analysis was pursued. Partial regression coefficients were derived for all the independent variables listed with the exception of tree type. The colony counts for each tree type could then be adjusted by application of the regression coefficients for the combined independent variables other than type. This calculation was performed on mean colony count numbers for all the trees falling in each of the groupings listed in Table 1. The corrected colony counts per tree for each year are given in Table 10 for each group of tree types.

Because these colony counts are corrected by regression for tree height, age, crown surface area, and geographical address within the plantation, the ranking of the corrected colony numbers may be considered as the equivalent of the comparative attractiveness of the foliage to the adult sawfly without respect to the influence of the other factors in the tree. The overall ranking of the various groups as abstracted from Table 12 and 1 are given in Table 11. The comparative attractiveness of the various groups constitutes the core of the findings on susceptibility to egg depositing.

The two groups included in this study which represent the most usual North

TABLE 10. MEANS ADJUSTED BY REGRESSION OF COLONY NUMBERS, TREE TYPES (1-19) IN MULTIPLE REGRESSION ANALYSIS OF POPULATION DATA, WHEN $X_1 = \bar{X}_1, X_2 = \bar{X}_2, \text{ETC.}, \text{FOR EACH YEAR.}$

Dependent variable:	1965	1966	1967	Year Ranks			Sum Rank
	$y = \text{colonies/tree}$			'65	'66	'67	
I. 4.1723024	12.90993	23.81482	19	14	11	17	
2. 0.309483	2.02178	6.13853	2	2	1	2	
3. 3.8923234	16.89354	28.48789	16	19	16	19	
4. 3.44771776	15.15368	27.31287	11	16	14	15	
5. 2.5320045	16.28203	29.38264	7	17	17	16	
6. 2.671763	8.90271	19.15629	8	5	6	5	
7. 3.8093821	11.40267	20.32970	14	11	7	9	
8. 4.1649504	16.60030	28.12542	18	18	15	18	
9. 3.1166041	11.19029	25.49456	9	10	13	11	
10. 3.8302563	11.78327	24.21099	15	12	12	13	
11. 3.6202275	12.90724	16.22992	13	13	4	7	
12. 1.127805	2.24471	11.19979	3	3	3	3	
13. 3.454328	10.42679	33.91811	12	9	18	14	
14. 2.295380	8.04238	18.05074	6	4	5	4	
15. 0.393978	1.10280	8.65164	1	1	2	1	
16. 3.9260899	9.07540	21.27163	17	6	9	10	
17. 2.073114	10.00857	21.89366	5	7	10	6	
18. 1.907790	10.01415	45.72123	4	8	19	8	
19. 3.407554	12.96985	21.26179	10	15	8	12	

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TABLE 11. PINE TYPES IN ORDER OF INCREASING SUSCEPTIBILITY TO
NEO. SERTIFER EGG DEPOSITION.

Rank	Species Group	Genotype (M#)		
1	<i>thunbergii</i> <i>selfed</i>	203		
		73		
2	<i>banksiana</i>	111		
		112		
		110		
3	<i>contorta</i> <i>banksiana</i>	113		
		122		
4	<i>yunnanensis</i> <i>thunbergii</i> <i>tabulaeformis</i>	116		
		117		
		119		
		125		
		127		
		129		
		201		
		282		
		72		
		84		
5	<i>densiflora</i> (<i>dens. x th</i>)	84		
6	<i>nigra</i>	75		
		76		
		78		
		79		
		80		
		81		
		82		
		83-143		
		139		
		205		
		7	<i>thunbergii</i>	118
				126
				128
147				
148				
200				
277				
278				
279				
280				
8	Species Group	Genotype (M#)		
9	<i>tabulaeformis</i> <i>thunbergii</i> (<i>dens. x th</i>)	204		
		115		
		120		
		124		
		130		
10	<i>thunbergii</i> x <i>taiwanensis</i>	132		
		133		
		289		

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TABLE 11. PINE TYPES IN ORDER OF INCREASING SUSCEPTIBILITY TO *NEO. SERTIFER* EGG DEPOSITION. (Continued)

" 11	<i>densiflora</i> x (<i>dens. x sylv.</i>)	137
" 12	<i>densiflora</i> x <i>nigra</i>	290
" 13	<i>thunbergii</i>	67
" 14	<i>thunbergii</i> <i>sinensis</i>	74 114
" 15	<i>densiflora</i> x <i>thunbergii</i>	123 135
" 16	<i>thunbergii</i> x <i>densiflora</i> <i>thunbergii</i> x <i>densiflora</i>	136 291 68 69 202 283 285 284
" 17	<i>sylvestris</i>	96.144 98.145 95.146 89 90 91 92 93 94 97 99 303
" 18	<i>nigra</i> x <i>densiflora</i>	307

American hosts of *Neodiprion sertifer* are the *Pinus banksiana* group which was one of the most resistant and the *Pinus sylvestris* group which was one of the most susceptible.

Certain of the groups of trees provide special interest and invite a further examination. The most important of these is the group designated *sylvestris* which was the 17th in order of increasing attractiveness to the insect. This group was made up of a series of 15 sources of *sylvestris* material mostly from the old world. When the raw colony counts per tree were examined for the *sylvestris* group a considerable variation in the numbers was seen. The various sources of pine which made up this group, together with the infestation data, are given in Table 12.

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TABLE 12. *PINUS SYLVESTRIS* TYPES WITH MEAN NUMBERS OF COLONIES PER TREE:
IN ORDER OF INCREASING COLONY NUMBERS IN 1967.

Source	# cols./tree	# trees	# cols./tree	# trees	# cols./tree	# trees
	1965		1966		1967	
93 Sweden	0.	5	1.60	5	7.25	4
89 Spain	8.67	3	20.50	2	17.50	2
91 Finland	2.25	4	10.00	4	18.50	4
M94 Morris Arboretum <i>syvestris</i>	2.50	2	18.00	2	18.50	2
144 Scotland	1.78	9	5.89	9	22.77	9
146 Austria	3.62	13	10.31	13	24.31	13
145 East England	4.40	10	13.30	10	26.60	10
98 East England	3.40	5	21.40	5	33.50	4
97 Czechoslovakia	7.00	4	23.60	5	34.80	5
92 France (Alsace)	15.00	1	32.00	1	36.00	1
95 Austria	9.67	9	31.44	9	41.44	9
94 Morris Arboretum	3.00	2	25.00	2	45.50	2
303 Spain	16.33	9	41.44	9	47.22	9
90 France (Auvergne)	7.67	3	27.67	3	49.33	3
99 Turkey	5.00	3	25.70	3	53.00	3

There is a suggestion in these data that the most resistant trees are found in the very extreme portions of the range of this natural host of the insect and that the least resistant tend to be from the more central parts of the range. The exception to this would appear to be the occurrence of an exceedingly susceptible line of trees from Spain and another from Turkey. Neither of these locations could be considered central in the range of the host or of the pest.

In no other group was there such extreme variation between the most heavily and least heavily infested trees.

DISCUSSION

It is apparent that the numbers of colonies of *Neodiprion sertifer* to be seen on the various possible hosts in the field reflects a number of factors in the trees. At the very least, the ovipositing adults show a response to the size of the trees and also to the quality of their foliage. As we shall show, the ranking of genotypes with respect to susceptibility to egg deposition is not predictive with respect to the capacity of the foliage to support the larvae through various parts of their development. Again, survival of larvae and their speed of development are not predictive of fecundity.

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LABORATORY STUDIES OF LARVAE ON VARIOUS HOSTS

Neodiprion sawflies feed in a characteristic manner with the larvae arranged in a cluster at needle tip, their feeding surface being the end of the needle. Typically a group of larvae feeds simultaneously on the same needle with the needle supporting 5 to 7 newly emerged first-instar larvae and only 1 or 2 larvae in the penultimate instar. The feeding behavior has been studied in detail by Ghent (1958 and 1960).

It has been shown (Lyons, 1962; Henson 1965b) that the aggregative feeding habit of *Neodiprion* sawfly has a positive survival value. The nature of this advantage is not completely clear but Lyons showed (1962) that even though the larvae from small egg clusters feeding in small aggregations are less likely to be parasitized, the overall survival among larvae is directly related to the number of larvae per colony. There is a distinct suggestion that the advantage of aggregative behavior is a function of the need larvae have for relatively large quantities of water which they can obtain only from their food. The proportion of the time spent in searching for food and moving from an exhausted feeding site will be high when the larvae are feeding at low density. Only a small proportion of the larvae are capable of establishing new feeding sites. Feeding efficiency is thus dependent on aggregations being of a certain minimal size that will insure a reasonable number of active larvae capable of leading a movement from an exhausted site to a fresh one. Henson (1965b) has shown that survival increases in the laboratory directly with increasing numbers of larvae in the cluster up to a total of 8 larvae per cluster. In our present studies we have seen some evidence that clusters over 35 larvae tend to be inefficient because of the speed with which the site is exhausted. Such clusters usually break up into a series of smaller feeding aggregations at about the end of the third instar.

METHODS

The larvae used in the present study were field collected in Michigan on the lands of the University of Michigan from a plantation of *Pinus sylvestris* which has been infested for a considerable length of time. We are indebted for these collections to Professor F. B. Knight. Insects were collected as eggs during January and March; the twigs bearing the egg clusters were bagged in separate polyethylene bags with the cut ends wrapped in wet absorbent cotton. The egg-bearing foliage were stored at 4°C in the dark. Larvae were recovered by bringing the egg-bearing foliage directly to room temperature and supplying the foliage with water. The ends of the twigs were recut under the water

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at about 2-day intervals. Treated this way, eggs showed swelling within 1 or 2 days of coming to room temperature and the larvae hatched in about 7 days.

Because it had been shown (Henson, 1965a) that clonal differences in the vigor of the sawfly sometimes occurred, the larvae for the present study were taken in rotation from a series of twigs each taken from a different tree. In this way we were assured of a "pooled" supply of larvae within which clonal differences would be minimized.

Foliage for the present study was field collected in the Yale Forest Genetics plantation at Norfolk, Connecticut. The twig butts were wrapped in wet cotton. In the laboratory, the twig ends were cut under water and the foliage set up in beakers with the twigs held by burrett clamps. Foliage was arranged in random order following tables of random numbers. Each rearing was replicated three times.

The rearings were established by transferring newly emerged larvae from the stock cultures to the experimental rearings in sequence until the full number of larvae had been established on each experimental host. This very laborious method was used to insure that there was no confounding between the order of emergence of the stock larvae and their assignment to the experimental host. (It has been shown for a number of insects [Wellington, 1960] that in some insects there are individual differences between larvae, which are first expressed by the sequence in which the larvae hatched from the egg.) The individual rearings were examined daily or more often. The foliage being tested was changed for the entire experiment when the most advanced rearing required it. This insured that all the larvae were handled at the same time.

Preliminary field observations had suggested that the success of individual larvae in developing from eclosion to the adult was most frequently interrupted at a number of rather discrete stages. The data from our rearings were thus examined in such a way that the laboratory mortality at stages in the life history corresponding to the known peaks in field mortality could be separated.

The **first** rather frequent source of mortality in the field appears to be associated with the establishment of the newly emerged instar larvae on feeding sites on foliage. In practice it was impossible to measure this initial establishment in a meaningful way because the laboratory technique necessarily involved the transfer of new eclosed larvae from the foliage bearing the eggs to the foliage being assessed. The newly deposited larvae thus lacked the normal putative clues for aggregation and feeding.

It was arbitrarily decided that survival to the start of the third instar would be accepted as evidence of successful establishment on the foliage. The choice of this interval was made on the grounds that the first instar alone is too short

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a period to provide good evidence of establishment. For instance, starved first instar larvae occasionally undergo the first ecdysis spontaneously in the complete absence of food. Such larvae never survive long enough to confuse the issue if the end of the second instar is used as a reference point.

In Table 13 the rate of establishment of pooled larvae on various hosts is

Groupings	Host Type	Survival Egg to 3rd Instar %	Group Rank.
1	<i>sylvestris</i> MI144 MI146 M90 M93 M94	90% 5% 73.33% 50% 96.67% Average = 58.57%	5
2	<i>banksiana</i> MI110 MI111 MI112	26.67% 88.33% 43.33% Average = 58%	4
4	<i>densiflora</i> <i>x thunbergii</i> MI136	83.33%	9
7	<i>thunbergii</i> <i>x (dens. x thun.)</i> MI132	18.33%	1
9	<i>densiflora</i> <i>x (dens. x sylv.)</i> MI137	73.33%	6
10	<i>thunbergii</i> MI126 MI147 MI148	30% 31.67% 23.33% Average = 29.33%	2
11	<i>thunbergii</i> <i>x yunnanensis</i> MI113	30%	3
12	<i>thunbergii</i> <i>x sinensis</i> MI114	78.33%	8
13	<i>thunbergii</i> <i>x tabulaeformis</i> MI117 MI127	88.33% 55% Average = 78.18%	7

given. A very high rate of failure in these rearings was encountered. It is known from the field that all the types of foliage tested are capable of supporting at least a small proportion of the larvae which hatch from eggs directly. None of the foliage tested can therefore be considered as perfectly immune. It was found in the laboratory that even the most suitable sort of foliage could not support even the most vigorous larvae if that foliage was wilted or even slightly embarrassed for water. It was impossible to tell when the larvae were actually placed on the foliage whether each test piece of foliage was in good condition. Therefore the conservative procedure was followed. The cut foliage was regarded as being in suspect condition if there was not at least the minimal establishment of larvae on all three replicates. This very rigorous approach is necessary if we are to avoid the risk of confusing the effect of foliage quality on larval response and those of foliage condition.

Two groups of host material are of particular interest. The first of these is the *sylvestris* material where survival from egg to third instar ranges between 5 and 96 percent. It has already been shown that the *sylvestris* material was among the preferred hosts for the ovipositing females but that there was considerable variation between geographic sources within this group with respect to the amount of oviposition. The occurrence of the very low mortality in M144 and M94, moderate mortality in M90 and M93 and high mortality in M146 corresponds in general to the putative oviposition of the females to these same materials.

By contrast the *banksiana* group is in general among the most resistant material as suggested by the number of colonies of larvae it supports: that is, its comparative attractiveness to the females. At the same time, however, within the *banksiana* group, there was moderate success in establishment in the material designated M110 and M112 and very good rate of establishment demonstrated in the material designated M111. These results are rather unexpected in view of the apparent response of the females to these trees.

There is not sufficient evidence to comment on the variability of establishment rates within the other groups represented in the successful introductory rearings.

For convenience, the number of days from eclosion to the end of the third instar rather than the equivalent measurement to the beginning of the same instar was measured. This rather longer period was chosen as the first measurement of rate of growth because the error of observation of up to one day would be of much greater importance for any period shorter than the full three instars. The averages are given in Table 14.

It will be noted that there is an extreme range of developmental time from

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TABLE 14. AVERAGE TIME (IN DAYS) TO END OF 3RD INSTAR.

Groupings	Host Type		Days of growth to end of 3rd instar
1	<i>sylvestris</i>	M144	7.33
		M146	9.5
		M90	10.33
		M93	8.67
		M94	8.67
		$\bar{x} = 8.9$	
2	<i>banksiana</i>	M110	9.5
		M111	7
		M112	8.75
		$\bar{x} = 8.42$	
4	<i>densiflora</i> x <i>thunbergii</i>	M136	8.5
7	<i>thunbergii</i> x (<i>dens.</i> x <i>thun.</i>)	M132	10.67
9	<i>densiflora</i> x (<i>dens.</i> x <i>sylv.</i>)	M137	11.17
10	<i>thunbergii</i>	M126	10.33
		M147	10.5
		M148	10.5
		$\bar{x} = 10.5$	
11	<i>thunbergii</i> x <i>yunnanensis</i>	M113	8.8
12	<i>thunbergii</i> x <i>sinensis</i>	M114	8.5
13	<i>thunbergii</i> x <i>tabulaeformis</i>	M117	9
		M127	13
		$\bar{x} = 11$	

7-13 days for the first three instars of growth. It should be emphasized that these differences were displayed in laboratory rearings where the temperature, humidity, and light regime under which the larvae were growing were all controlled. In Table 15 the percentage survival through the third instar for the same range of host materials is given. It will be noticed that survival through the third instar alone ranged from only 3% in the *thunbergii* x *densiflora* back-

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TABLE 15. PERCENTAGE SURVIVAL THROUGH 3RD INSTAR.

Groupings	Host type		Survival percentages
1	<i>sylvestris</i>	M144	61.5%
		M146	8.3%
		M90	49%
		M93	1.7%
		M94	51.7%
		$\bar{x} = 34.44$	
2	<i>banksiana</i>	M110	4.46%
		M111	54.8%
		M112	10.15%
		$\bar{x} = 23.14\%$	
4	<i>densiflora</i> x <i>thunbergii</i>	M136	51.4%
7	<i>thunbergii</i> x (<i>dens.</i> x <i>thun.</i>)	M132	3.06%
9	<i>densiflora</i> x (<i>dens.</i> x <i>sylv.</i>)	M137	26.9%
10	<i>thunbergii</i>	M126	7.0%
		M147	8.46%
		M148	3.9%
		$\bar{x} = 6.45\%$	
11	<i>thunbergii</i> x <i>yunnanensis</i>	M113	15%
12	<i>thunbergii</i> x <i>sinensis</i>	M114	28.7%
13	<i>thunbergii</i> x <i>tabulaeformis</i>	M117	65.3%
		M127	22.5%
			$\bar{x} = 43.9\%$

cross material designated M132 to more than 65% in the *thunbergii* x *tabulaeformis* material designated M117. Here again, the *sylvestris* group and the *banksiana* group are of particular interest. In the *sylvestris* group survival through the third instar alone ranged from 1.7 percent in M93 to 61.5 percent in M144, and in spite of these extreme differences in survival the rate of growth for the first three instars was not notably different between the two materials.

In the *banksiana* group the survival through the third instar ranged from

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.46% to 54.8%. Here, however, there was a notable difference in the rate of growth with superior survival occurring in the material that permitted the most rapid growth.

In general there is rather a close relationship between the length of time

TABLE 16. THE TIME OF GROWTH TO SPINNING UP AND THE SURVIVAL PERCENTAGE TO SPINNING UP BY HOST TYPE 1965.

Groupings	Host type		Time of growth to spinning up	Survival percentage from end of 3rd instar to spinning up
	<i>sylvestris</i>	MI44	27	46.4%
		MI46	24	4.2%
		M90	29	44.5%
		M93	40	1.14%
		M94	24	28.5%
2	<i>banksiana</i>	MI10	31	2.79%
		MI11	26	38%
		MI12	31	6.2%
4	<i>densi/lora</i> x <i>thunbergii</i>	MI36	32.5	38.4%
7	<i>thunbergii</i> x (<i>dens.</i> x <i>thun.</i>)	MI32	31	2.77%
9	<i>densi/lora</i> x (<i>dens.</i> x <i>syl.</i>)	MI37	32.5	13.8%
10	<i>thunbergii</i>	MI26	4 ¹	5.4%
		MI47	30.5	7.34%
		MI48	27	28%
II	<i>thunbergii</i> x <i>yunnanensis</i>	MI13	31.5	14.2%
12	<i>thunbergii</i> x <i>sinensis</i>	MI14	28.5	12.5%
13	<i>thunbergii</i> x <i>tabulaeformis</i>	MI17	33	49.2%
		MI27	35	14.2%

from eclosion to the end of the third instar and the percentage of survival for the same period.

The total time required for development from eclosion to the spinning of the pre-pupa is perhaps the best overall indication of the suitability of the foliage for the support and nourishment of the larvae. However, as we have seen in the comparison of rate of growth and survival, for periods during early part of larval development, the survival is not always a linear negative function of the time required for this discrete portion of development. In Table 16 the time required for growth from eclosion to spinning up and percentage survival is given.

The most rapid development was seen in a *thunbergii* x *sinensis* hybrid designated MI14 where the total time required was 28.5 days. The slowest development was seen in a *thunbergii* x *tabulaeformis* array where the average rate of growth was 34 days. Individual host types, however, gave a much greater degree of variation. For instance, in the *sylvestris* group, MI46 permitted full development in 24 days and M93 in 40 days. Again, in the *thunbergii* group MI48 permitted full development in 27 days and MI26 required 41 days. In these data again, the most interesting groups are the *sylvestris* which is usually considered a favorable host and the *banksiana* which is considered to be rather unfavorable. In the criteria of measurement here considered among the *sylvestris* tested, M93 required the extreme period of 40 days for the completion of development and gave a very low survival rate of 1.14 percent. On the other hand MI46 permitted development in 24 days but still gave the very low survival rate of 4.2 percent.

The disappointing and great difficulty of obtaining complete data in laboratory rearings renders a complete comparison by all the suggested criteria of all the available host materials impossible. The implicit difficulties are of course most severe with respect to those criteria obtained by the behavior of the insect in the latter stages of its development. Mortality is obviously a cumulative phenomenon and there is no way in which a separate, and valid experimental approach could be made to the effect of host material on mature larvae and adults. It was in short physically impossible to grow sufficient numbers of larvae on the less favored hosts to provide adequate data late in the insect's development. Despite these difficulties, some data on pupal weight, sex ratio, and mean egg count were obtained. These data are given in Table 17.

In rather general terms the pupal weights are inversely related to development times as set forth in the table. It should be remembered, however, that female pupae weigh almost twice as much as male pupae and hence **mean** pupal weight must be interpreted only with regard for the sex ratio. The egg

TABLE 17. PUPAL WEIGHTS, SEX RATIO AND AVERAGE EGG COUNTS BY HOST TYPE IN 1965.

Groupings	Host type		Pupal weights (grams)		Sex ratio		Mean egg counts		
1st Series	1	<i>sylvestris</i>	M114	.0519	.0520	F/M 18/6 16/4 11/5	0.83	67.2	} 76.27
			M90	.0545				89.4	
			M94	.0496				72.1	
	2	<i>banksiana</i>	M110	.0477	.0526	2/3 13/7 12/2	.87	59	} 60.38
			M111	.0517				61.75	
			M112	.0584				—	
	4	<i>densiflora</i> x <i>thunbergii</i>	M136	.0573		15/2		74.3	
	7	<i>thunbergii</i> x (<i>dens.</i> x <i>thun.</i>)	M132	—		—		53.8	
	9	<i>densiflora</i> x (<i>dens.</i> x <i>sylv.</i>)	M137	.0546		7/1	.86	65.4	
	10	<i>thunbergii</i>	M126	.0491	.0474	9/5 7/2 1/2	.65	—	} 52.95
			M147	.0457				48.9	
			M148	—				56	
	11	<i>thunbergii</i> x <i>yunnanensis</i>	M113	.0530		13/1	.93	64.3	
12	<i>thunbergii</i> x <i>sinensis</i>	M114	.0508		15/4	.79	47.1		
13	<i>thunbergii</i> x <i>tabulaeformis</i>	M117	.0449	.0524	10/8 15/2	.71	58.55	} 67.28	
		M127	.0599				76		
2nd series.	1	<i>sylvestris</i>	M90	—		—		62.5	
	2	<i>banksiana</i>	M111	—		—		73.5	} 77.75
			M112	—		—		82	
	9	<i>densiflora</i> x (<i>dens.</i> x <i>sylv.</i>)	M137	—		—		68.3	
	12	<i>thunbergii</i> x <i>sinensis</i>	M114	—		—		57.5	

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counts reported refer only to mature and immature eggs counted by dissection and do not include precursors as described by Ghent (1959).

In 1965 when the rearings reported here were carried out, we attempted a second series of rearings immediately following the studies that have been discussed to this point. This series, designated FFC, was carried out approximately a month later and it was characterized by very high levels of mortality even among those larvae that became established. The initial establishment rates were uniformly low and the entire series was regarded as being so plagued by failure that its interpretation is very doubtful.

By the time FFC was undertaken, the larvae had been in storage for an extreme period and the egg-bearing needles were to some extent desiccated. There was widespread failure in the hatching of the stock material and the newly emerged larvae were in all probability of low vigor as a result of the exhaustion of their food reserves and perhaps embarrassment for water. Secondly, the foliage tested was gathered in the field at a time when normal field development of the insect is virtually complete. This means that there was throughout the entire FFC series a major phenological disjunction. A summary of the results of this rearing is given in Table 18.

It will be noted that for those few host types where development was possible at all, the time of growth and mortality was not unduly discrepant from the experience in the more successful series.

A number of rather distinct ways of examining the suitability of the test foliage for the support, growth and reproduction of European sawfly have been suggested to this point and they will now be discussed.

DISCUSSION

At this point in the study it is already abundantly clear that the relationship between insect attack and the success of that attack, as these relate to foliage qualities of trees, in an exceedingly complex relationship. We see evidence that there are differences between hosts with respect to frequency of female adult ovipositional strikes, establishment of the newly emerged larvae, mortality and rate of growth through the various portions of larval development, differential mortalities between sexes and fecundity of the resultant females. We have also seen that a host type may be eminently suitable as an oviposition site and relatively unsuitable as a substrate for the growth of the larvae. Similarly, some hosts have capacity to support rapid growth and large resultant egg complements but at the same time they subject the insects to very high rates of mortality. Other hosts permit only a low rate of establishment but at

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TABLE 18. THE TIME OF GROWTH TO SPINNING UP AND THE MORTALITY PERCENTAGE TO SPINNING UP BY HOST TYPE 1965.

Groupings	Host Type		Time of growth to spinning up	Survival to spinning up
1	<i>sylvestris</i>	M90	24	33.6%
		M93	—	—
		M94	—	—
		M144	38	66.5%
		M146	—	—
2	<i>banksiana</i>	M110	—	—
		M111	22	37.1%
		M112	26	62.9%
4	<i>densiflora</i> x <i>thunbergii</i>	M136	22	71.4%
7	<i>thunbergii</i> x (<i>dens.</i> x <i>thun.</i>)	M132	35	62.5%
9	<i>densiflora</i> x (<i>dens.</i> x <i>sylv.</i>)	M137	21	68.4%
10	<i>thunbergii</i>	M126	—	—
		M147	—	—
11	<i>thunbergii</i> x <i>yunnanensis</i>	M113	—	—
12	<i>thunbergii</i> x <i>sinensis</i>	M114	25.5	92.3%
13	<i>thunbergii</i> x <i>tabulaeformis</i>	M117	—	—
		M127	—	—
17	<i>nigra</i>	M82	23	50
18	<i>tabulaeformis</i>	M204	28	70

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the same time provide an admirable substance for the growth of the larvae once establishment has been achieved. A field investigation of this very complex relationship was indicated.

FIELD STUDIES OF LARVAL DEVELOPMENT

Stock from the Michigan infestation was reared to emergence in a field insectory at the field station of the Forest Genetics Plantation in Norfolk, Connecticut. Experimental colonies were established in the field on mid-crown laterals of the desired tree types. The establishment of the feeding colonies was done by severing the portion of the stock twig bearing the newly emerged larvae and placing this on the foliage of the tree in the field. The rapid wilting of the severed stock foliage prevented the establishment of the larvae on their original host and forced them to move to the foliage of the test tree. There was, however, a considerable loss of larvae during this process and it was found impossible to measure this loss accurately. The figures for survival therefore

TABLE 19. SUMMARY OF TIME FOR ESTABLISHMENT AND LARVAL SURVIVAL BY HOST TYPE.

Groupings	Host type	Time days of growth to establishment to beginning of 2nd instar	Survival percentage to pupation
1	<i>sylvestris</i> (M90; M91; M144; M146; M303)	Mean = 4.3	67.94%
2	<i>banksiana</i> (M110; M111; M112)	Mean = 4.9	69.20%
3	<i>densiflora</i> (M64; M207)	Mean = 4.35	99.62%
4	<i>densiflora</i> x <i>thunbergii</i> (M135; M136)	Mean = 4.85	20.92%
5	<i>thunbergii</i> x <i>densiflora</i> (M69; M202)	Mean = 4.8	58.13%

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TABLE 19. SUMMARY OF TIME FOR ESTABLISHMENT AND LARVAL SURVIVAL BY HOST TYPE. (Continued)

6	<i>densiflora</i> x (<i>dens.</i> x <i>th.</i>) (M84)	Mean = 6.3	71.66%
7	<i>thunbergii</i> x (<i>dens.</i> x <i>th.</i>) (M132)	Mean = 5.0	65.21%
8	<i>nigra</i> x <i>densiflora</i> (M307)	Mean = 6.0	85.00%
9	<i>densiflora</i> x (<i>dens.</i> x <i>sylv.</i>) (M137)	Mean = 5.0	65.67%
10	<i>thunbergii</i> (M118; M200)	Mean = 5.9	74.39%
12	<i>thunbergii</i> x <i>sinensis</i> (M114)	4.7	71.87%
13	<i>thunbergii</i> x <i>tabulaeformis</i> (M72; M117; M282)	Mean = 5.0	56.27%
15	<i>thunbergii</i> x <i>taiwanensis</i> (M289)	5.0	74.51%
17	<i>nigra</i> (M75; M76; M78)	Mean = 6.67	54.10%
18	<i>tabulaeformis</i> (M204)	5.3	54.71%

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refer only to the survival of the larvae from the commencement of feeding, at which point counting became easy, to spinning up of the pupae.

All rearings were replicated and data were not included in the analysis when at least some initial establishment of all replicates was not seen. The rationale for this rather rigorous decision was the fact that all host material tested in this study was known to be capable of supporting at least some degree of infestation when it was naturally established. Because the study was carried out on intact trees it was felt that the complete failure of a rearing had to be attributed to experimental failure rather than to the complete resistance of the host material.

The rearings were observed daily. On intuitive grounds, we felt that the length of time required for establishment as measured by time to the first ecdysis would be related to the overall experience of the larvae on the various hosts. These data are given in Table 19.

It will be noticed that the length of time to the beginning of the second instar ranged between 4.3 and 6.67 days. The most rapid establishment is seen on trees of the *sylvestris* group which is certainly one of the preferred hosts. The slowest establishment is seen on trees of the *nigra* group not generally considered a preferred host. The survival to pupation was not very different on these two groups of trees with the *nigra* group showing 54.1 percent survival and the *sylvestris* 67.94 percent.

It may be parenthetically observed that the numerical data in this study are open to considerable question. For instance, the survival on type M207 of the *densiflora* group is given as 157.14 percent. Obviously there was a considerable recruitment to the experimental rearings from naturally established larvae on the same host. The artificially established aggregations were held to an initial size lower than 35 or 40 larvae. Groups larger than this show considerable splitting during the later phases of their development. However, since the success of transfer from the stock foliage to the test foliage could not be controlled, the initial size of the test aggregation was very variable. For this reason it is considered that the speed of development is a more reliable and hence a more interesting measure of the suitability of the various host types. In Table 20 a detailed summary of the data on rate of development is given.

It will be noticed that the time in days to the second instar is relatively uniform with respect to the fastest development. Only in groups 5, 6, and 10 were there instances of notably retarded development where the larvae grew so slowly that more than five days were required for the first instar. In groups 10, 15, 17, and 18 there were hosts which permitted the first instar to be completed in four days. It is interesting to notice that in both cases where the instar

TABLE 20. ESTABLISHMENT TIME AND SURVIVAL
IN EXPERIMENTAL INNOCULATIONS.

Groupings	Host type		Time in days to:				Cocoon
			2nd. instar	3rd. instar	4th. instar	5th. instar	
1	<i>sylvestris</i>	M90	5-10	8-13	12-17	<i>Minimum time</i> 15	19-26
		M91	5-12	10-14	13-16	16	20-35
		M144	5-9	9-12	12-17	17	20-27
		M146	5-9	8-12	12-18	17	21-33
		M303	5-8	8-12	12-16	15	19-29
2	<i>banksiana</i>	M110	5-12	8-16	12-16?	16	19-43
		M111	5-9	7-12	11-16	15	18-42
		M112	5-11	9-13	12-17	19	20-31
3	<i>densiflora</i>	M64	5-9	9-13	14-18	19	33-38
		M207	5-8	8-13	13-20	19	27-28
4	<i>densiflora</i> x <i>thunbergii</i>	M135	5-12	9-13	13-17	19	22-38
		M136	5-10	9-12	12-21	19	21-31
5	<i>thunbergii</i> x <i>densiflora</i>	M69	5-9	10-13	14-21	19	21-38
		M202	6-10	11-14	14-24	18	30-40
6	<i>densiflora</i> x (<i>dens.</i> x <i>th.</i>)	M84	6-13	8-14	13-18	18	25-33
7	<i>thunbergii</i> x (<i>dens.</i> x <i>th.</i>)	M132	5-13	10-19	15-26	20	27-39
8	<i>nigra</i> x <i>densiflora</i>	M307	5-12	10-16	13-20	18	21-44
9	<i>densiflora</i> x (<i>dens.</i> x <i>sylv.</i>)	M137	5-11	8-14	14-20	20	21-35
10	<i>thunbergii</i>	M118	8-12	10-16	14-20	19	24-35
		M200	4-10	10-14	13-20	20	25-38
12	<i>thunbergii</i> x <i>sinensis</i>	M114	5-10	9-13	12-17	17	22-34
13	<i>thunbergii</i> x <i>tabulaeformis</i>	M72	5-8	10-12	13-18	18	21-39
		M117	5-10	10-14	13-20	19	26-35
		M282	5-10	10-14	12-20	19	21-38
15	<i>thunbergii</i> x <i>taiwanensis</i>	M289	4-10	10-17	14-24	19	25-43
17	<i>nigra</i>	M75	4-13	9-14	13-18	18	23-40
		M76	5-13	10-15	13-18	19	26-42
		M78	5-11	10-16	13-19	17	22-30
18	<i>tabulaeformis</i>	M204	4-12	8-15	12-15	17	20-40

TABLE 21. SEX RATIO, AND AVERAGE EGG COUNTS BY HOST TYPE
IN THE 1ST SERIES, 1966.

Groupings	Host type		Sex ratio	Mean egg count	
1	<i>sylvestris</i>	M90	♀ ♂ 2/1	.72	65.0
		M144	2/1		
		M146	3/0		
		M303	8/5		
2	<i>banksiana</i>	M110	4/1	.79	59.6
		M111	3/1		
		M112	4/1		
3	<i>densiflora</i>	M64	4/0	.83	46.4
		M207	1/1		
4	<i>densiflora</i> x <i>thunbergii</i>	M135	1/3	.44	11.0
		M136	3/2		
5	<i>thunbergii</i> x <i>densiflora</i>	M69	2/1	.63	36.4
		M202	3/2		
6	<i>densiflora</i> x (<i>dens.</i> x <i>th.</i>)	M84	3/1	.75	41.8
7	<i>thunbergii</i> x (<i>dens.</i> x <i>th.</i>)	M132	2/1	.67	27.4
8	<i>nigra</i> x <i>densiflora</i>	M307	10/7	.59	51.4
9	<i>densiflora</i> x (<i>dens.</i> x <i>sylv.</i>)	M137	5/1	.83	62.2
10	<i>thunbergii</i>	M118	2/1	.69	68.0
		M200	2.4/1		
12	<i>thunbergii</i> x <i>sinensis</i>	M114	.5/1	.33	70.0
13	<i>thunbergii</i> x <i>tabulaeformis</i>	M72	1/2	.67	—
		M117	—		
		M282	3/0		
15	<i>thunbergii</i> x <i>taiwanensis</i>	M289	2/1	.67	52.0
17	<i>nigra</i>	M75	6/1	.53	47.2
		M76	3/1		
		M78	1/1		
18	<i>tabulaeformis</i>	M204	2/1	.67	52.0

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was notably slow, the total time of development to the spinning of the cocoon was also slow. On the other hand, none of the groups that completed the first instar unusually fast were able to complete the entire larval period remarkably fast. No survival figures are given in connection with these data because of the uncertainty of the counts at the time of establishment. It is apparent that in general, the speed of development to the cocoon stage is most rapid and shows the smallest spread in those host types that are generally considered most favorable.

The sex ratio and average egg counts of this same material are given in Table 21.

Here it will be noticed that while the sex ratio varies quite widely in the various groups and at times **within** members of the same group, the egg counts are remarkably uniform within different host types assigned to a group. We have recovered a number of dead females in the plantations and in no case have we found a female that managed to deposit all of her complement of apparently mature eggs. On this basis we would suppose that the fecundity of the female is not either limiting or particularly responsive to the host type.

Pupae from the rearings just reported **were** placed in screen cages on the branches of the hosts on **which** they were reared. The adults were allowed to emerge, mate and lay eggs within these cages. Ten males and ten females were caged on each branch and after **egg** laying was complete in late fall the branches were brought into the laboratory and the eggs counted. The data are given in Table 22. In these data it is perfectly clear that there was a considerable variety in the egg laying response of the caged females to the various types of host foliage.

Very extreme numbers of eggs **were** deposited on host M90 in the *sylvestris* group, on host M144 in the *thunbergii* x *sinensis* group, and on M204 in the *tabulae/ormis* group. In general terms, the egg laying response of the caged females was equivalent to that of the naturally occurring females as evidenced by the colony census data for 1967 reported in the first part of this paper.

A limited series of laboratory rearings was carried out simultaneously with the field rearings in order to provide **Some** means of relating the results of the laboratory studies to those of the field studies herein reported. The number of days to each instar **by** host type is given in Table 23.

Here it will be noted that the **till** to accomplish the first ecdysis is rather longer than that in the field but that the overall development times are rather shorter than the field time. We would regard this as a suggestion that the initial establishment of the larvae on cut foliage is more difficult than on the intact tree and that the overall development in the field is somewhat retarded

TABLE 22. NUMBER OF EGGS DEPOSITED BY
CAGED FEMALES BY HOST TYPE.

Groupings	Host type		No. of trials	Mean no. of eggs/spray
1	<i>sylvestris</i>	M90	8	131.87
		M91	7	51.29
		M144	6	39.33
		M303	7	96.57
		Mean =	7	79.77
2	<i>banksiana</i>	M111	9	47.67
		M112	8	57.13
		Mean =	8.5	52.4
3	<i>densiflora</i>	M64	3	68.0
		M207	13	67.77
		Mean =	8	67.89
4	<i>densiflora</i> x <i>thunbergii</i>	M135	1	50.0
		M136	2	99.0
		Mean =	1.5	74.5
5	<i>thunbergii</i> x <i>densiflora</i>	M202	1	59.0
6	<i>densiflora</i> x (<i>dens.</i> x <i>th.</i>)	M84	9	99.56
7	<i>thunbergii</i> x (<i>dens.</i> x <i>th.</i>)	M132	3	23.33
8	<i>nigra</i> x <i>densiflora</i>	M307	7	70.71
9	<i>densiflora</i> (<i>dens.</i> x <i>sylv.</i>)	M137	1	29.0
10	<i>thunbergii</i>	M118	4	52.0
12	<i>thunbergii</i> x <i>sinensis</i>	M114	2	207.0
13	<i>thunbergii</i> x <i>tabulaeformis</i>	M72	4	34.5
		M117	6	48.5
		M282	5	33.6
		Mean =	5	38.87
15	<i>thunbergii</i> x <i>taiwanensis</i>	M289	1	19
17	<i>nigra</i>	M76	4	19
18	<i>tabulaeformis</i>	M204	3	162.33

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TABLE 23. THE NUMBER OF DAYS TO EACH INSTAR BY HOST TYPE IN LABORATORY SERIES, 1966.

Groupings	Host type		Time in days to:				Cocoon
			2nd. instar	3rd. instar	4th. instar	5th. instar	
1	<i>sylvestris</i>	M145	6-9	9-12	11-15	18	19-27
		M303	7-9	9-12	11-15	15	17-25
4	<i>densiflora</i> <i>x thunbergii</i>	M136	6-9	9-13	12-19	15	19-28
17	<i>nigra</i>	M78	6-8	10-22	14-22	20	32-37
18	<i>tabulaeformis</i>	M204	7-9	9-12	15-20	16	20-27

by periods of inclement weather which do not affect laboratory rearings to the same degree. In Table 24 the survival of these rearings, the sex ratio and mean egg counts are given. The survivals are rather similar to those found in the 1965 laboratory rearings.

The sex ratios, however, are notably low. Mean egg counts are not remarkable. The low sex ratio of course suggests differential mortality of females in the laboratory rearings. Because this differential mortality was not particularly evident in other laboratory rearings, we are at a loss to account for it.

Mass rearings of large numbers of larvae collected in the field during the third and fourth instar were brought into the laboratory and reared on the original host material. In Table 25 the cocoon weights, sex ratios, and mean

TABLE 24. SURVIVAL, SEX RATIO AND EGG COUNTS—FIELD REARINGS 1966.

Groupings	Host type		Survival to pupation, %	Sex ratio	Mean egg count	
1	<i>sylvestris</i>	M145	28.20%	$\left. \begin{array}{l} \text{♀ ♂} \\ 2/1 \end{array} \right\} .57$	26	
		M303	72.09%			.6/1
4	<i>densiflora</i> <i>x thunbergii</i>	M136	77.19%	.6/1	.38	41.5
17	<i>nigra</i>	M78	10.52%	—		66
18	<i>tabulaeformis</i>	M204	85.71%	.75/1	.43	44.8

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egg counts of this material are given. It will be noticed that the sex ratios are very high and that the mean egg counts are somewhat high in comparison with the data previously reported. On this basis, it is fairly evident that the critical time in the differential mortality between males and females is early in larval development. The females seem to succumb to a disproportionate degree during the first three instars and perhaps the males to a disproportionate degree during the latter three instars when the material is laboratory reared. We would expect, therefore, that host material or environmental conditions which gave rise to high mortality during the early part of larval development would result in an adult population with a low sex ratio and that the opposite would be true of environmental conditions producing late larval mortality. This point would be very important to settle in the course of any investigation on the population dynamics of the insect. The fact that the egg counts in this laboratory mass reared material are high, suggests that the automatic replacement of the food source before it is exhausted relieves the larvae of the necessity for repeated movement between feeding sites and improves to some extent the efficiency of their feeding. As Ghent (1959) has pointed out, adult females have in their ovaries during the pupal stage a considerably larger number of undeveloped eggs than will ever reach maturity in the adult ovary. The nutritional status of the insect may therefore be supposed to be critical in the determination of fecundity. The relative uniformity of the egg numbers in the field reared larvae without respect to host type and the lower number of eggs in these animals as compared with the laboratory rearings suggests that under conditions of field feeding this insect will never reach its physiological potential of fecundity. It would be interesting to rear insects from the third instar to maturity individually so that there would be no question of these insects having to move from an exhausted feeding site to a fresh one. Under these conditions we would expect that the mortality would be high but that the egg counts in those females that survive would be extraordinarily high, perhaps as great as the extreme count of 93.4 which was found in the mass rearing on M112 of the *banksiana* group.

As we have seen, there is abundant evidence that the most critical period in the mortality experience in the developing larvae occurs from hatch to the end of the second instar. During this period, the absolute mortality is high and also there appears to be a differential mortality between the sexes. It was of interest to approach the problem of whether the less severe mortality late in larval life was a phenomenon separate from the early mortality or whether it was the result of accumulative non-reversible effect that the relatively unfavorable host had on the insect early in its larval development. The most appropri-

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TABLE 25. COCOON WEIGHTS, SEX RATIOS AND MEAN EGG COUNTS,
LABORATORY MASS REARINGS.

Groupings	Host type		Cocoon weights (gr.)	Sex ratio		Mean egg count
	<i>sylvestris</i>	M90	.0776	♀ ♂ 19/1		
		M91	.0712	16/1		83.4
		MI44	.0726	9/1		71
		MI46	.0766	11.25/1		85.2
		M303	.0713	11.5/1		78.8
		Mean =	.0739	13.35/1	.93	79.6
2	<i>banksiana</i>	MII0	.0678	11.5/1		80.6
		MII1	.0808	49/1		80.2
		MII2	.0745	16/1		93.4
		Mean =	.0744	25.5/1	.96	84.73
3	<i>densiflora</i>	M64	.0637	49/1		75.6
		M207	.0660	11.5/1		69.4
		Mean =	.0649	30.25/1	.97	72.5
4	<i>densiflora</i> x <i>thunbergii</i>	M135	.0619	8/1		71.4
		M136	.0760	24.5/1		71.0
		Mean =	.069°	16.25/1	.99	71.2
5	<i>thunbergii</i> x <i>den.riflora</i>	M69	.0632	15.33/1		77.4
		M202	.0574	9/1		50.8
		Mean =	.0603	12/1	.92	64.1
6	<i>densiflora</i> x (<i>dens.</i> x <i>th.</i>)	M84	.0617	9/1	.90	71.0
7	<i>thunbergii</i> x (<i>dens.</i> x <i>th.</i>)	M132	.0662	15.7/1	.94	82.2
8	<i>nigra</i> x <i>densiflora</i>	M307	.0632	9/1	.90	79.2
9	<i>densiflora</i> x	M137	.0633	6.86/1	.88	79.8
10	<i>thunbergii</i>	MII8	.0699	24/1		81.8
		M200	.0680	11.5/1		66.4
		Mean =	.0690	17.75/1	.95	74.1

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TABLE 25. COCOON WEIGHTS, SEX RATIOS AND MEAN EGG COUNTS, LABORATORY MASS REARINGS. (Continued)

12	<i>thunbergii</i> x <i>sinensis</i>	M114	.0687	15.7/1	.94	81.2
13	<i>thunbergii</i> x <i>tabulaeformis</i>	M72	.0694	15.7/1		85.2
		M117	.0681	24/1		80.0
		M282	.0678	15.7/1		75.4
		Mean =	.0684	18.47/1	.95	80.2
15	<i>thunbergii</i> x <i>taiwanensis</i>	M289	.0601	9.2/1	.90	77.8
17	<i>nigra</i>	M75	.0611	9/1		75.8
		M76	.0758	12/1		94.0
		M78	.0680	15.7/1		88.2
		Mean =	.0683	12.2/1	.92	86.0
18	<i>tabulaeformis</i>	M204	.0659	24/1	.96	60.8

are experiment appeared to be the transfer of insects from relatively favorable hosts to relatively unfavorable hosts at a mid-point in their larval development.

The judgment as to which hosts were favorable or unfavorable for these purposes was made on the basis of the population survey 1965 and 1966. Seven preferred hosts and seven poor hosts were selected as sources and receivers respectively. These trees are listed in Table 26.

TABLE 26. SOURCES AND RECEIVERS OF LARVAL TRANSFERS.

The 7 "preferred" hosts: Sources	M64	<i>P. densiflora</i>
	M68	<i>P. thunbergii</i> x <i>P. densiflora</i>
	M78	<i>P. nigra</i> (France)
	M110	<i>P. contorta</i> x <i>P. banksiana</i>
	M129	<i>P. thunbergii</i> x <i>P. tabulaeformis</i>
	M204	<i>P. tabulaeformis</i>
	M303	<i>P. sylvestris</i> (Spain)
The 7 "poor" hosts: Receivers	M76	<i>P. nigra</i> x <i>P. thunbergii</i>
	M112	<i>P. banksiana</i> (mutant)
	M114	<i>P. thunbergii</i> x <i>P. sinensis</i>
	M115	<i>P. thunbergii</i> x (<i>P. densiflora</i>)
	M126	<i>P. thunb.</i> x <i>P. thunb.</i> x <i>P. thunb.</i>
	M200	<i>P. thunbergii</i>
	M289	<i>P. thunbergii</i> x <i>P. taiwanensis</i>

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It should be noted that this experiment was relatively small in scope and that one tree of each type only was used. This means that the results cannot be compared directly with the results of other rearings reported herein. In all the other rearings, replicate examples of each source were always used and in most cases a number of sources were combined within each group. For example, in the present experiment, the *Pinus sylvestris* used as a donor (M303 Spain) is not really representative of all the members of the *sylvestris* group. It is, in fact, one of the most susceptible. The transfers were made June 16th and 17th at which time the larvae on the donor or source trees were in the third, fourth, and fifth instars with the majority in the fourth instar. Seven larval colonies were taken from each of the source trees and distributed, one to each of the receiver trees. The transfer was made by cutting the shoot bearing the larval colony on the source, trimming it to remove all foliage not bearing insects, and attaching it to a branch of the receiver tree on one-year-old foliage. Thus a total of 499 transfers were made. A larval count was made at the time of transfer and the location of the colony on the receiver tree was made to conform as closely as possible to the location on the source tree. Daily counts were made of the larvae in each colony up to the point where the larvae were lost on dropping to the duff for pupation.

The results of these transfers were very difficult to interpret because the colonies, when established at this stage of development on a new host, moved very freely over the foliage of the new host. They merged with neighboring colonies and frequently split into small aggregations feeding briefly in a succession of sites.

Our best estimate of the overall survival of the transferred larvae is that the mortality was uniformly very low. This observation is consistent with the finding that even on the apparently most favorable hosts the survival after the third instar is rather good and that the pupal weights and fecundity of the surviving insects are normal. On this basis we conclude at mid-point in larval life when the colonies are in the third, fourth, and fifth instars that the critical period in the development of the larvae has passed. In brief, once the larvae have fed on a preferred host through the first three instars they appear to be able to thrive on virtually any host.

An attempt was made to determine the "natural" sex ratio of the insect for the purpose of interpreting the data on sex ratio obtained from the rearings on various hosts. Larvae in the second instar were collected from each of 30 types of hosts and reared in the insectory on red pine foliage. These rearings were done in large cardboard boxes fitted with screened covers. The insect bearing foliage was simply placed in the boxes and fresh foliage was added daily. The

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TABLE 27. SEX RATIO OF COCOONS FROM MASS LARVAL REARINGS.

Source	Total Cocoons	Sex Ratio
M64-L	50	.98
M69	50	.94
M72	50	.94
M75	50	.90
M76	52	.92
M78	50	.94
M84	50	.90
M90	40	.95
M91	50	.94
MI10	50	.92
MI11	50	.98
MI12	51	.94
MI14	50	.94
MI17	50	.96
MI18	50	.96
MI32	50	.94
MI35	54	.89
MI36	50	.96
MI37	54	.87
MI44	50	.90
MI46	50	.92
M200	50	.92
M202	50	.90
M204	50	.96
M207	50	.92
M282	50	.94
M289	51	.90
M303	51	.92
M307	50	.90
Mugho Pine	50	.80

rearings were cleaned periodically to remove the accumulation of denuded twigs. The bottoms of the boxes were covered with dried peat moss and at the conclusion of the rearings the cocoons were recovered from the moss. At least 100 larvae were included in each rearing. The survival through these rearings was uniformly high, always above 80%. Sex ratios were derived simply by sorting the cocoons, the female cocoons being almost twice the size of the male. The data are given in Table 27. The sex ratios are uniformly high. Because the survival in the rearings was high, we may conclude that these sex ratios are representative and that the departures from them in the experimental rearings reported above represent a differential mortality between the sexes.

It is interesting to note that in other studies of this insect, Henson (unpublished data) has found that the sex ratio of the insect varies remarkably between clones derived from high dispersive females and clones derived from a resident indigenous population, most of which are probably the progeny of

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non-dispersive females. The progeny of dispersive females uniformly had high sex ratios and those of non-dispersive females rather low sex ratios. Since the population studied in the Yale Forest Genetics plantations could not have been established before the dispersal period in the fall of 1964, the insects reared in the present experiment must have been the second generation progeny of dispersive females. The extremely high sex ratios are therefore predictable and a confirmation of the supposition that all the resident insects in the experimental plantations were the result of immigration starting the fall of 1965. In the study cited above, Henson has shown that in one case at least a clone of *Neodiprion sertifer* derived from a dispersive female reverted to sex ratios indistinguishable from those found in the progeny of non-dispersive females within three generations. This point was checked by a repetition of the present mass rearings on rather a small scale in 1967. The results of these rearings suggest that the 1967 infestation was again the result of egg laying by immigrant females because the sex ratios in 1967 were indistinguishable from those in 1966. We may therefore conclude that the individual quality of the various clones of insects used throughout the studies reported in this series are uniform.

CHROMATOGRAPHY OF NEEDLE TISSUE

Wright and his co-workers (1967) have recently reported the occurrence of an interesting polyphenol apparently confined to the favorite hosts of *Neodiprion sertifer*. This finding was partially confirmed by Thielges (1968) who found a compound of similar chromatographic properties to those reported by Wright only in trees with a history of heavy infestation.

The genotypes included in this study were therefore examined for the occurrence of this biochemical. The foliage sampled was one year branch tips which were collected in February and stored in polyethylene bags at 5° C in the dark for about a month. The needles were clipped above the fascicle sheath and dried for 48 hours at 60° C. 8 gm samples of the dried foliage were ground to powder and transferred to extracting vessels in 95% alcohol. The alcohol was then driven off at 60° C.

Extraction was accomplished in 250cc Erlenmyer flasks with 100 cc of anhydrous ethyl ether with 24 hours continuous shaking. The ether was removed by vacuum filtration in a Buchner funnel on No. 1 Watman paper. The needle tissue was repeatedly washed with successive 25 cc aliquots of ether until the filtrate was colorless.

The needle material was then extracted with 100 cc of bulk grade n-butanol. The butanol extract was recovered by filtration and the solid residue washed

three times with 25 cc allequots of n-butanol which was then added to the extract.

The butanol extract was transferred to a 200 cc volumetric flask and evaporated to dryness at 65° C under water pump vacuum.

The residue was taken up in 1 cc of n-butanol at about 55° C. 120 microliters of the resulting solution was spotted, 10 microliters at a time to Watman 3 MM chromatography paper and dried 24 hours.

Chromatography was by descending solvent system with first dimension utilizing the organic phase of an n-butanol acetic acid water solvent mixture (4:1:5) in 18 hours development time. The second phase used a sodium formate formic acid water mixture (10 gm to 2 ml to 200 ml) solvent system in a 4½ hour period. The papers were then oven-dried overnight at approximately 60° and developed with a mixture of sulphanilic acid, hydrochloric acid and sodium nitrate in water, followed immediately by 10% aqueous sodium carbonate, excess 10% sodium carbonate was wiped off with tissue paper and the chromatograms dried.

A very extensive investigation of the identity of polyphenols as displayed by this method of chromatography has been presented by Thielges (1968), and he discussed the variation and inheritability of these compounds. In the present instance we have made no attempt to assess the polyphenols other than the one expressly reported to be connected with the susceptibility to *Neodiprion sertifer*. This compound appears to be n-catechol on the basis of its chromatographic characteristics, although a positive identification has not been obtained.

The chromatograms were divided into four groups: those in which none of the interesting compound could be found plus those where there was a trace, the small, medium and large spot papers. The chromatograms were then identified as to source from the index numbers used during the analysis. A listing of the results is presented in Table 28. Some two-year-old foliage was included in this analysis. This is indicated in the Table. The replications are all individually indicated.

The data suggest that the occurrence of the compound presumed to be n-catechol is exceedingly sporadic throughout the genotypes tested. A high level of variation even within single trees is seen. Certainly, there is no obvious relationship between the compound and the various bioassays of susceptibility that we have reported.

One's first reaction to data of this type is to question the analytic procedure. A comparison of our chromatograms with those obtained by Thielges during his previously cited investigation suggests that the separations obtained in our work may have been less than complete. This would tend to give spurious

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TABLE 28. OCCURRENCE OF "N-CATECHOL" IN FOLIAGE BY GENOTYPE.

Groupings	Host type	Absent trace	Small	Medium	Large	
1	<i>sylvestris</i>	M89		IX IX IY IZ IZ'		
		M90		IX		
		M91	IX			IY IY
		M92			IX IY	IY
		M93	IX IY	IX IX IY		
		M97			IX	
		M99		IX IX		IY
		M144	2X 2X 2X	2X		IX
		M145	2X 2X		2X	2X IX
		M303	IX	IX		IY IY IZ
2	<i>banksiana</i>	M110	IX		IX	
		M112			IX	
3	<i>densiflora</i>	M64	IX	IX	IY	
4	<i>densiflora</i> x <i>thunbergii</i>	M135	IX IY	IX	2X	2Y
		M136	IX IX IX		IX IX IY 2X	
5	<i>thunbergii</i> x <i>densiflora</i>	M69	IX		IX IY	
8	<i>nigra</i> x <i>densiflora</i>	M307	IX	IX	IY	
9	<i>densiflora</i> x (<i>dens.</i> x <i>sylv.</i>)	M137		IX	IX	
10	<i>thunbergii</i>	M118	IX	IX		
		M147	IX	IX 2X	IX	IX 2X
11	<i>thunbergii</i> x <i>yunnanensis</i>	M113		IX	IX IY	
12	<i>thunbergii</i> x <i>sinensis</i>	M114		IX 2X 2X	IX	2X 2X

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TABLE 28. OCCURRENCE OF "N-CATECHOL" IN FOLIAGE BY GENOTYPE. (Continued)

13	<i>thunbergii</i> x <i>tabulaeformis</i>	M72	ix ix iy	iy iy iy iy	iy	iz iz	
		M117	2x 2y 2y	ix ix iy	ix iy 2y	2x	
		M127	ix ix	ix	2x		
15	<i>thunbergii</i> x <i>taiwanensis</i>	M289	ix	iy			
17	<i>nigra</i>	M75	ix ix iy		iy		
		M76	ix ix iy				
		M78	ix		iy	iy	
		M82		ix ix iy			iy
		M83			ix		
		M143	ix	ix		2x	
18	<i>tabulaeformis</i>	M204	ix		iy		

1 year foliage = 1. No. of trees x = 1, y = 2

z = 3, z' = 4

2 year foliage = 2. No. of trees = same as above.

"traces" and "small" readings. On this basis, we would regard all readings below the "medium" category as probably negative. With this clarification, the "within-tree" variation is considerably reduced. However, the best we can say is that, while our result for some *sylvestris* types are provocative, we are unable to confirm Wright's findings. It is clear from Thielges' very detailed and careful work that the polyphenols in pine foliage are very variable between genotypes. Another work which one of us (WRH) has attempted (unpublished) on the volatiles emitted by pine foliage has shown that there is a profound and confirmable variation in the heavy volatiles (probably terpenes) emitted by intact foliage at different times of day. This suggests that the biochemical status of pine foliage is a sensitive mechanism and that we should not be too surprised by evidence of variability in data such as the present which were obtained on material not rigidly under experimental control.

STUDIES OF THE NEEDLE TISSUE

Some aspects of the intimate relationship between the insect and its host tissue were investigated. The first of these was the microscopic anatomy and macroscopic dimensions of the foliage. For the microscopic examination needles were collected in the field at the time of larval hatch. These were fixed immediately in standard formalin-acetic acid alcohol for 48 hours and stored in

TABLE 29. ANATOMICAL CHARACTERISTICS OF NEEDLE TISSUE.

Groupings	Host type	No.	Vascular bundles						No.	Resin epi.	duct cell	Lumen	Stomata Total	Open	Cuticle thickness Corner
			xy		rays		width								
			1	2	1	2	1	2							
1	<i>sylvestris</i> M90 M146	2	9	7	2	2	.112	.092	14	Absent Absent		17 11	5 3	.0097 .0028	
		2	10	10	2	2	.092	.084	11						
2	<i>banksiana</i> M110 M111 M112	2	all sections squashed						2	.216 .224	.0444 .0673	.0326 .0524	16.5 12	5 5	.0075 .0133
		2	12	11	3.5	4.5	.14	.129	2						
		2	4	4	0	1	.031	.041	2						
4	<i>densiflora</i> M136 <i>x thunbergii</i>	2	9	8.5	2	1.5	.088	.088	6	Absent		9	3	.0055	
9	<i>densiflora</i> M137 <i>x (dens. x sylv.)</i>	2	6.3	8.3	1.3	2.3	.071	.088	6	.219	.0418	.0190	14.7	4	.0115
10	<i>thunbergii</i> M126 M147	2	12.3	7.8	4.3	4	.0157	.013	3	.3095	.0644	.0442	14	4.7	.0113
		2	11	13	4	5	.120	.161	2	.237	.0524	.0399	5	3	.0076
11	<i>thunbergii</i> M113 <i>x yunnanensis</i>	2	13	11	3	4	.122	.120	7	.246	.0604	.0354	12	3	.0127
12	<i>thunbergii</i> M114 <i>x sinensis</i>	2	6.5	7	2	2	.084	0.82	3	.276	.0547	.0308	14.5	5	.0124
13	<i>thunbergii</i> M117 <i>x tabulaeformis</i> M127	2	9.6	9.2	3.2	4.2	.122	.133	4	.250	.0620	.0360	11	4.5	.0085
		2	6	6	1	1	.061	.061	8	.252	.0558	.0422	16	6	.0112

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70% alcohol. Embedding was done by alcohol dehydration through chloroform to paraffin. The exposed needles in the paraffin blocks were soaked in 10% glycerin in alcohol to soften the tissue and sectioning was done at 10 μ . The sections were mounted and dried overnight, staining was done with safranin and fast green and destaining was done as required in 50% alcohol acidified with hydrochloric acid. The stained sections were passed through alcohol and Canada balsam. The sections were examined at 180 diameters magnification and various aspects of their morphology noted. The data from these examinations are given in Table 29.

FOLIAGE CONSUMPTION

An attempt was made to measure the amount of foliage required to support a given amount of larval growth so that a comparison could be suggested with respect to the nutrient qualities of the various sorts of foliage. The mean oven dry weight of 10 fascicles of each genotype of *Pinus* tested was determined from spring collected foliage. Small aggregations of larvae were reared and upon completion of development the oven dry weight of all foliage remaining on the twigs used to feed the larvae was determined. By subtraction, the amount of foliage actually eaten was calculated. The number of feeding larvae each day during the rearing was obtained although regrettably the records for ecdysis are not complete. However, from the known duration of the various instars, the number of larval days feeding for each instar was calculated. An expression of the amount of larval feeding was obtained by summing the numbers of larvae in each instar for the entire rearing and dividing by the number of days for the completion of development times the number of larvae completing development. This gave a comparative measure of the biomass of insects produced in each rearing. A summary of the foliage consumed, the "larval units" consuming it, and the foliage consumed per larval unit in milligrams is given in Table 30.

It may be seen that an astonishing degree of variability in the apparent amount of foliage required for the development of the insects appeared. It may further be seen that the genotype which give high survival and rapid development do not necessarily do so at the lowest cost in consumed foliage. Apparently a very great deal more is involved in the nourishment of the larvae than the provision of a certain number of "calories" per day. These observations evoke a comparison with the very extensive work which has been done by Auclair and Raulston (1966) and others on the nutrition of aphids. There

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TABLE 30. AMOUNT OF FOLIAGE (OVEN-DRY WEIGHT IN MILLIGRAMS) CONSUMED BY *N. SERTIFER* LARVAE, 1965.

Groupings	Host type		Foliage consumed (mg)	Larval units	Foliage per unit (mg)	Remarks
1 = x7	<i>sylvestris</i>	M95	9507	2.61	3643	Adults obtained
		or M146				" "
		M90 or M92 <i>sylv. x sylv.</i>	9029 119	1.67 1.69	5406 70	Dead in 4th instar
2 = x8	<i>banksiana</i>		10310	1.93	5342	Adults obtained
			3675	1.90	1934	" "
		M110 <i>contorta x banksiana</i>	120	1.53	78	Dead in 3rd instar
3 = x9	<i>densiflora</i>		12333	1.62	7613	Adults obtained
7 = x13	<i>thunbergii x (dens. x th.)</i>		7022	1.46	4810	Adults obtained
9 = x15	<i>densiflora x (dens. x sylv.)</i>	M137	12020	1.29	9318	Adults obtained
10 = x16	<i>thunbergii</i>	M148	30	0.80	38	Dead in 2nd instar
12 = x18	<i>thunbergii x sinensis</i>		3033	2.05	1480	Adults obtained
			9938	1.58	6290	" "
13 = x19	<i>thunbergii x tabulaeformis</i>		138	0.81	170	Dead in 3rd instar
17 = x23	<i>nigra</i>	M82	721	3.19	226	Adults obtained
18 = x24	<i>tabulaeformis</i>	M204	12487	1.63	7661	Adults obtained

is a distinct possibility that the amount of foliage required to support development of an insect is determined by the supply of some microcomponents such as an essential amino acid. The second possibility which should be investigated is that the amount of foliage required is determined by the insects' water requirements rather than the nutrient quality of the foliage. The various genotypes studied in this work differ tremendously in their degree of succulence and the present determinations are all done on the basis of oven dry weight. Both these possibilities should be investigated.

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EFFECT OF NEEDLE CONDITION ON EGG DEVELOPMENT

It has been known for some time that there is no true diapause in the egg stage of *Neodiprion sertifer*. The embryological development of the eggs proceeds after oviposition until it is stopped by cold weather. The further development of eggs can be initiated at any time during the winter, provided that the egg bearing foliage is in a flush condition.

The normal signal of the start of spring development is the swelling of the eggs within the needle tissue. This is a very marked event involving the substantial doubling of the egg volume. It is accomplished by the withdrawal of water into the egg from the needle tissue. This swelling commonly occurs within one to two days of the time when the material is raised from over-wintering temperatures to room temperature.

The experience we have had and that reported by other workers all suggests that the proper timing of larval hatch is an important requirement for larval success. Because it is known that there is no egg diapause, we became interested in the regulation of the time of spring development of the eggs and the manner in which this phenomenon is related to the phenology of the host.

Field collected needles bearing eggs were **fixed** in formalin acetic acid. The eggs were dissected out, embedded in paraffin and stained with fucsin after sectioning and mounting.

It was found that embryological development of the egg proceeded in fall to the fully segmented stage following inversion of the embryo within the egg. Considerable yoke remained in the egg throughout the winter.

In the spring the further development of the larvae did not occur, no matter what temperature the material was held at, until the egg had withdrawn water from the surrounding foliage and reached its final size.

The shape of the needles of *Pinus sylvestris* in cross section gives a direct means of assessing the succulence of the foliage. During the winter the proximal surface of the needles is concave and as the foliage reaches a condition of spring turgor, the cross section of the needle becomes semi-circular. In some cases the proximal surface becomes convex.

Intensive and repeated collection of egg bearing foliage during the spring showed that the swelling of the eggs never takes place before the needles assume the condition of spring turgor. This suggests that the water tension of the needle controls, or at least limits, the ability of the included egg to recover water. The embryo is in turn limited in its development to a stage just after inversion until the engorgement of the egg with water of host origin. After this event the development of the embryo proceeds directly at a rate apparently limited by the temperature alone.

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If eggs are held within their supporting foliage at normal room temperature but the foliage is prevented by high osmotic pressure of the watering solution from coming to a normal spring lush condition, the eggs will remain alive for some weeks but will not be able to continue development. Under these circumstances the death of the egg follows the exhaustion of the yolk.

It appears then that the phenological conjunction of egg development and host seasonal development depends on the water relationship between the egg and its host. The insect embryo is unable to develop in the spring until the host reaches a normal condition of spring lushness.

The accuracy and power of this coupling mechanism has been repeatedly confirmed in natural infestations where eggs on adjacent trees may hatch at quite different times in spite of a presumed similarity in their temperature experience. In each case the time of hatching is approximately equivalent to the ripening of microsporangiate strobili on the individual host. The observation of this effect was rendered direct and facile by the availability within the genetics plantation of a series of trees which differed in their photoperiodic response because of the variety of geographical origin.

NEEDLE LENGTH

As Ghent (1959) has shown, the spacing of the eggs on the needles is inversely related to the width of the needles. This relationship is a necessary function of the mechanism by which the adult female moves between the deposition of individual eggs. Because of this observation we felt that there might well be a relationship between needle size and the attractiveness of the foliage to gravid females. An extended series of measurements of needles in the genetics plantations was made and the data were analyzed with respect to the relationship between needle width and length and the number of colonies per unit of crown surface area. The analysis was done on the 1965 census data only. The technique of analysis was the same as that used for the examination of the surveyed data itself except that a further stratification of the descriptive data on the trees corresponding to needle characteristics was introduced.

Analysis was by a standard multivariate regression routine on the computer. The independent variables included the age of the trees, their height, their lateral crown area, their geographic position in the plantation, and their needle length as divided in three classes. The classes of needle length were 2 to 4.9 cm., 5 to 7.9 cm., and 8 cm. and longer. There was no significant correlation between the independent variables. The overall significance of the variance due to regression was examined by means of a standard analysis incorporated in the regression program. The outcome of this variance analysis is given in Table 31.

The variance due to regression was significant. The same analysis performed

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with the lumping of the variance due to needle size with the deviation was performed and the results are given in Table 32. When this was done the variance due to regression was still significant but the multiple correlation coefficient was reduced from 0.30609 to 0.27245. This suggests that needle length is a significant characteristic of the foliage. Needle width gave similar results.

TABLE 31. VARIANCE ANALYSIS OF NUMBER OF COLONIES PER UNIT CROWN AREA AND NEEDLE LENGTH, TREE POSITION AND SIZE.

Source	DF	Sum squares	Mean squares	F
Regression	8	141.828	17.728	2.222**
Deviation	172	1371.885	7.976	
Total	180	1513.713		
Multiple correlation coefficient		0.30609		
Standard error of residual		2.8241		

TABLE 32. VARIANCE ANALYSIS OF NUMBER OF COLONIES PER UNIT CROWN AREA WITH NEEDLE LENGTH VARIANCE LUMPED WITH RESIDUALS. REGRESSION DUE TO TREE POSITION AND SIZE ONLY ARE SEPARATED.

Source	DF	Sum squares	Mean squares	F
Regression	6	112.364	18.727	2.325**
Deviation	174	1401.348	8.053	
Total	180	1513.713		
Multiple correlation coefficient		0.27245		
Standard error of residual		2.838		

Because needle length and width are both surprisingly constant within genotype it has not been possible to separate the variance due to needle length from the variance due to genotype. Thus, needle length and presumably needle width must be considered as being of possible significance in the selection of the host but confounded with the other characteristics of host foliage which thus far have defied separation.

SUMMARY OF GENOTYPE-SAWFLY INTERACTIONS

Perhaps the most immediately striking feature of this investigation of the host relationships of *Neodiprion sertifer* is the complexity we have seen. For the investigations reported here some of the data are incomplete because of the frequent and usually completely unexplained failure of rearings, but also in many cases because of the critical shortage of some types of plant material which simply do not do well in their exotic surroundings at Norfolk, Con-

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necticut. It cannot be over-emphasized that many of the types of plant material we have used can be produced and grown in northern Connecticut only with very great difficulty. The opportunity to include them in these studies, even to a limited extent, thus represents a unique, and we hope valuable, contribution.

The second general point which should be made is that the various aspects of the plant-insect relationship which are displayed in our data are by no means representative of linear functions or even of simple functions. It would be quite invalid for us to imply that each of the bioassays we have used reflect mechanisms of equal importance in the overall determination of plant vulnerability. The assessment of the various interactions that we display will have to be made on the basis of an investigation of the population dynamics of the insects. This would involve the construction of detailed life tables which would permit the analysis of the numerical impact of each interaction on the dynamics of the insect population as they interact with different genotypes.

With these limitations in mind, however, it is interesting to examine the various genotypes in the light of the entire battery of tests to which they have been subjected. We feel that such an examination should permit the simultaneous attempt to select and breed trees of comparatively low susceptibility to insect damage. When this selection is coupled to a selection for desirable growth characteristics, a very considerable degree of promise may now be found in a program of selective breeding for hard pine tree improvement.

The characteristics of growth and form of the genotypes we have studied are outside the province of this work. They have been reported elsewhere (Mergen and Furnival, 1960).

PINUS SYLVESTRIS

Pinus sylvestris is usually considered to be one of the preferred hosts of *Neodiprion sertifer*. It receives one of the largest rates of adult strike and its differential in this respect is maximal at low insect densities. The variation within the genotype with respect to numbers of adult strikes is extreme and ranges from among the most susceptible to among the least susceptible genotypes we have tested. However, the overall performance of the group in this respect suggests a high degree of vulnerability. Survival from the springtime hatching of the eggs through the period of establishment is moderate. The growth rate of larvae is moderate, survival of the larvae is high, the sex ratio of the resulting adults is unexceptional and the egg counts are very high. On this basis we would assess *Pinus sylvestris* as being a group of genotypes very susceptible to the impact of the insect. However, the variation between geno-

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types within the group is extreme and this species or array of genotypes offers a very fruitful area for the attention of the selection breeder.

PINUS BANKSIANA

The group of genotypes we examined show a very low rate of adult strike and it is reasonable to suppose that in forests which contain a variety of potential hosts for *Neodiprion sertifer* the *Pinus banksiana* will tend to remain relatively undamaged. Interestingly enough, the group of genotypes we tested show moderate rates of larval establishment and very good rates of growth through the early part of the larval period. The survival early in the larval growth is moderate, the development through the latter period of growth is rather rapid and the survival moderate. Sex ratios tend to be rather high and the mean egg counts are moderate. We would expect therefore that *Pinus banksiana* would always be attacked only to a limited extent and that the rate of increase of the insect in extensive stands of pure *Pinus banksiana* would always be minimal. This expectation is based on the low rate of strike, the moderate but sustained mortality and the moderate fecundity from the viewpoint of the insect alone. Therefore, *Pinus banksiana* has a great deal to commend it. The variation between genotypes in our limited series is not great and the species does not therefore within itself offer a very interesting opportunity for selective breeding.

PINUS DENSIFLORA

Pinus densiflora received the highest overall rate of adult strikes of all the groups of genotypes studied. In this respect it was very similar to *Pinus sylvestris* but it received more eggs at high densities of the insect. Rate of establishment, rate of growth and survival are all moderate to high. In particular the insect shows an extraordinarily high rate of survival and in the field there is evidence that considerable numbers of insects moved to *Pinus densiflora* during their larval development, presumably leaving other hosts. Egg counts are moderate and sex ratio rather high. On this basis we feel that *Pinus densiflora* has a pattern of high susceptibility.

PINUS DENSIFLORA X THUNBERGII

The *densiflora* x *thunbergii* hybrid had a high rate of adult strikes, a high rate of establishment survival, rate of growth, sex ratio and egg counts. We would regard this hybrid as being very susceptible but as showing sufficient

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internal variability between the two genotypes making up the group as to be of interest to the selective breeder.

PINUS THUNBERGII X DENSIFLORA

The *thunbergii densiflora* hybrids are high in the ranking of adult strike rate. They show moderate rates of establishment and moderate to good survival through the larval period. The cocoon weights and sex ratios are high and we would regard these hybrids as being rather similar to the preceding group which result from the reciprocal cross.

PINUS DENSIFLORA X (DENSIFLORA X THUNBERGII)

This group consisted of a single genotype of *Pinus densiflora* pollinated with *densiflora x thunbergii* cross. Surprisingly the tree had a relative low rate of adult strike. The survival of the larvae was high but the rate of development only moderate. Sex ratios of the larvae reared on this hybrid were moderate and the egg counts were moderate. Because the performance of this hybrid is notably different from that of the preceding two groups we feel that the back cross represented here offers an interesting opportunity.

PINUS THUNBERGII X (DENSIFLORA X THUNBERGII)

This group represents an array of hybrids with a *Pinus thunbergii* female parent and a *densiflora x thunbergii* male parent. Its performance is rather close to that of the reciprocal cross in the preceding group.

PINUS NIGRA X DENSIFLORA

The single genotype in this group was the second highest receiver of adult egg strikes. The larvae were able to establish themselves and grow with good survival. The rate of growth was moderate, survival of the larvae was high, the sex ratio and egg count moderate and **we feel** that this hybrid is not a promising one from the viewpoint of selective breeders.

PINUS DENSIFLORA X (DENSIFLORA X SYLVESTRIS)

This hybrid, developed from a *densiflora* female parent and a *densiflora x sylvestris* male parent, received a moderate number of egg strikes, establishment was moderate, rate of growth moderate, initial survival rather high, sex ratio is very high and we feel the hybrid is not promising material.

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PINUS THUNBERGII

Pinus thunbergii as a group of genotypes received a moderate number of eggs, provided moderate larval establishment, very slow rate of growth during the early part of the larval life although the survival was moderate at that period. Growth was slow from the mid to the latter part of larval growth and survival moderately high during that period. Sex ratio is high and egg counts are moderate. From the viewpoint of the variability found in the array of genotypes we had within this group we feel that there is considerable interest in these trees. This is particularly so in view of the extended period of development and the moderate egg counts.

PINUS THUNBERGII X YUNNANENSIS

The adult strike on these hybrids was rather low. The rate of establishment and other growth and survival characteristics were rather low but we have relatively little information on this group.

PINUS THUNBERGII X SINENSIS

The rate of egg strike on these hybrids was very low. The establishment rate and other growth characteristics of the larvae, however, was high and survival was moderate. Sex ratios are low and the egg counts were moderate. The amount of variability between the two hybrids in this group was rather low and we regard this cross as being relatively susceptible to the insect.

PINUS THUNBERGII X TABULAEFORMIS

The rate of adult strike on this hybrid was high, establishment and other growth characteristics of the young larvae were moderate. However, there was moderate survival and the total rate of growth was rather rapid. The sex ratios are high and the egg counts are moderate to high. Because of the variability in this group we regard the cross as potentially interesting and worthy of further investigation.

PINUS THUNBERGII X THUNBERGII

The rate of adult strike on this selfed *Pinus thunbergii* is low. We do not have enough information on this hybrid to assess it realistically.

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PINUS THUNBERGII X *TAIWANENSIS*

The rate of egg strike on this material was the lowest we observed. Its establishment appeared moderate and its survival high, sex ratios are high and the egg counts moderate to rather high. This hybrid is interesting because it appears to be so exceedingly resistant to the egg laying of the adults. In the remainder of its characteristics it is not very promising.

PINUS THUNBERGII X *NIGRA*

The number of eggs received by this hybrid is moderate but we know very little else about it.

PINUS NIGRA

A considerable variety of genotypes in this species have been examined. The group as a whole received low numbers of eggs. At low densities, the egg numbers were very much on a low side, at moderate densities they were medial and at high densities they were again medial. Establishment was relatively slow and survival only modest. Sex ratios were high and the egg counts also high. The variability within this group of hybrids was comparatively high, and because of its relatively low rate of egg strike and its apparent variability together with the possibility of crosses with other species, we feel that this species is worthy of extended investigation.

PINUS TABULAEFORMIS

The rate of egg strike on this species was low at low densities but extremely high at high densities. Establishment appeared moderate and larval development and survival rather high. Sex ratios are apparently moderate and egg counts are moderate. It will already have been noted that hybrids of this species show a considerable degree of variability in their apparent susceptibility to the insect. On this basis we would like to see an investigation of the variability within the species if further genotypes could be obtained. A variety of crosses seems possible and even convenient so that largely on the basis of the performance of its hybrids we feel that *Pinus tabulaeformis* is of interest.

PINUS DENSIFLORA X *NIGRA*

The rate of adult strike on this hybrid was high at low densities and moderate at medium and high densities. Only one genotype was available, but inter-

TO *NEODIPRION* SAWFLIES

estingly enough in the limited ovi-positional experiments that genotype received a very high number of eggs. We would suppose that this high rate of ovi-position by caged females is equivalent to the performance of wild population at low density. On this basis of our limited work on the hybrid it is not possible to reach even tentative conclusions as to its overall susceptibility.

CONCLUSION

The relationship between *Neodiprion sertifer* and its hosts of genus *Pinus* are exceedingly complex. Considering the various genotypes with which we have worked as being all to varying degrees "suitable" hosts for the insect, we are presented with a great variety of responses on the part of the insect. For convenience we might attempt to distinguish between "vulnerability" and "susceptibility."

If the concept of "susceptibility" is an expression of the degree to which the tree will be attacked by the insect, and "vulnerability" is an expression of the degree to which the tree will be damaged by the insect, we may conclude that the most suitable host is vulnerable. Certainly we may say that the bioassay of "susceptibility" is most appropriately accomplished by an examination of the rate of adult strikes. This measure appears almost independent of the other bioassays which we have attempted. "Vulnerability" could be measured in a number of ways. The most important of these would be the rate of establishment of the newly emerged larvae and the survival of the larvae from emergence to pupation. This survival may be measured over the entire period of larval development or it may be measured during portions of that development. Because the majority of the foliage eaten by the larvae (probably about 90% by weight) is consumed by the last two feeding instars, the mortality during the early part of larval development may be considered to be of extreme importance. It is this process that determines the number of larvae having the major impact on the host. In general, the mortality during the later stages of larval development is moderate and during our investigations we have failed to detect a host or genotype on which the late larval mortality would be critical from the viewpoint of the population dynamics of the insect. From that viewpoint, a combination of the rate of adult strikes or egg-laying and the mortality during the period of larval establishment in spring appear to be the most critical measurements.

The sex ratios in this insect appear almost always to be sufficiently high and the egg counts of the females sufficiently high that it is difficult to envision an insect-pest-plant system within which the population would not be at least

SUSCEPTIBILITY OF *PINUS*

self-sustaining except in terms of relative avoidance of the host by the adult and/or disastrous establishment mortality of the young larvae.

We have examined a large number of genotypes of *Pinus* and found a number of trees which simply do not receive large numbers of eggs. We have found some trees where probably because of phenological disjunction the rate of establishment of the larvae is very low.

In any attempt to develop a genotype of pine resistant to *Neodiprion sertifer*, we feel that the most efficient method of procedure would be to bioassay the stock in small blocks surrounded by a stand of some favored host such as *Pinus sylvestris* which was chronically infested with the sawfly. Candidate stock for a breeding program should be selected on the basis of the rate of adult strike and the rate of initial establishment and survival of the larvae. Stock developed on the basis of these two criteria should perform well under moderate fluxes of adult insects from indigent populations, provided they were planted in sufficiently large blocks so that the indigenous insects could not transfer to the candidate plantation during larval development. In short, it appears that *Neodiprion sertifer* larvae after they have reached about the middle of the third instar can feed, grow, pupate, and produce fecund adults on virtually any host. The thrust of a program to produce resistant stock should therefore be toward the production of a type of tree unattractive to the adults and unsuitable for the establishment and survival of the young larvae. An examination of the data presented in this report will suggest specific genotypes which offer good hope of achieving this objective.

BIBLIOGRAPHY

- AUCLAIR, J. L. and J. R. RAULSTON. 1966. Feeding of *Lygus hesperus* (Hemiptera: Miridae) on a chemically defined diet. Ann. Ent. Soc. Amer. 59: 1016-1017.
- BENJAMIN, D. M., J. D. LARSON and A. T. DROOZ. 1955. The European pine sawfly on the Henderson State Forest, Illinois, with notes on its biology and control. J. Forestry 53(5): 359-362.
- COPPEL, H. C. and D. M. BENJAMIN. 1965. Bionomics of the nearctic pine-feeding Diprionids. Ann. Rev. Ent. X: 69-96.
- GHENT, A. W. 1959. Row-type oviposition in *Neodiprion* sawflies as exemplified by the European pine sawfly *N. sertifer* (Geoffrey). Can. Jour. Zoology 37: 267-281.
- — — . 1960. A study of the group-feeding behavior of larvae of the jack pine sawfly, *Neodiprion pratti-banksianne*. Behavior XVI(I-2): 100-148.
- HENSON, W. R. 1965a. Individual variation and the dispersive capacity of *Neodiprion sertifer* (Hymenoptera). Proc. XII. Int. Cong. Ent. London 1964 (1965).
- — — . 1965b. Individual rearing of the larvae of *Neodiprion sertifer* (Geoffrey) (Hymenoptera: Diprionidae). Can. Ent. 97: 773-778.
- KANGAS, E. and V. PERTTUNAN. 1967. Studies on the olfactory stimuli guiding the bark beetle *Blastophagus piniiperda* L. to its host tree. Ann. Ent. Fenn. 33(3): 181-211.
- LVONS, L. A. 1962. The effect of aggregation on egg and larval survival in *Neodiprion swainei* Midd. Can. Ent. 94: 49-58.
- — — . 1963. The European pine sawfly, *Neodiprion sertifer* (Geoffrey). A review with emphasis on studies in Ontario. Proc. Ent. Soc. Onto 94: 5-38.
- — — . 1967. Some recent population trends of *Neodiprion sertifer* in Ontario. Proc. Ent. Soc. Ont. 97: 124.
- MERGEN, F. and G. M. FURNIVAL. 1960. Discriminant analysis of *Pinus thunbergii* x *P. densiflora* hybrids. Proc. Soc. Am. For. Mtg. 1960: 36-40.
- THIELGES, B. A. 1967. Taxonomic and genetic significance of phenolic compounds in the foliage of *Pinus* (Subsection Sylvestres). Yale University Dept. of Forestry Ph.D. Thesis. 146 pp.
- THORSTEINSON, A. J. 1960. Host selection in phytophagous insects. Ann. Rev. Ent. 5: 193-218.
- TSAO, C. H. and A. C. HODSON. 1956. The effect of different host species on the oviposition and survival of the introduced pine sawfly. Jour. Econ. Ent. 49: 400-401.
- WRIGHT, J. W., L. F. WILSON and W. K. RANDALL. 1967. Differences among Scotch pine varieties in susceptibility to European pine sawfly. For. Sci. 13: 175-181.
- WELLINGTON, W. G. 1960. Qualitative changes in natural populations during changes in abundance. Can. J. Zool. 38: 289-314.
- WOOD, D. L., L. F. BROWNE, R. M. SILVERSTEIN and J. O. RODIN. 1966. Sex pheromones of Bark Beetles I. Mass production, bioassay, source and isolation of sex pheromone of *Ips conusus* (Le C). Jour. Ins. Physiology 12: 523-536.

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