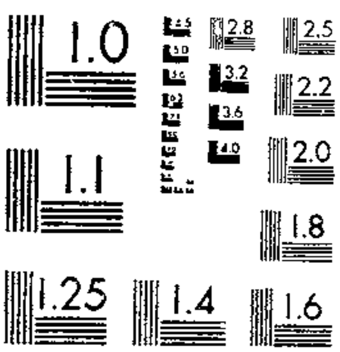
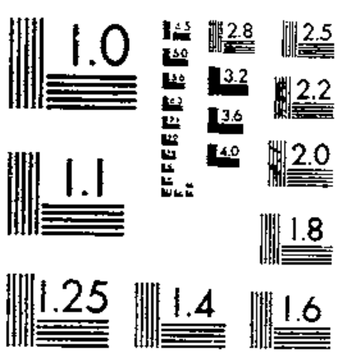
START



MICROCOPY RESOLUTION TEST CHART
NATIONAL BUREAU OF STANDARDS-1963-A



MICROCOPY RESOLUTION TEST CHART
NATIONAL BUREAU OF STANDARDS-1963-A

The *Biology* and *Ecology* of the *Red-Headed Pine Sawfly*

Technical Bulletin No. 1118

By Daniel M. Benjamin
Forest Service
U. S. DEPARTMENT OF AGRICULTURE

CONTENTS

Washington, D. C. August 1955

The Biology and Ecology of the *Red-Headed Pine Sawfly*[1]

By Daniel M. Benjamin,[2] Entomologist, Division of Forest Insect Research, Forest Service

INTRODUCTION

The red-headed pine sawfly (*Neodiprion lecontei* (Fitch)) is one of the most important native forest insects defoliating young hard pines in the eastern half of the United States and Canada. Recent outbreaks have resulted in the death or deformity of young pines on several thousand acres of plantations and the destruction of vast numbers of roadside and park hard pines. Often eastern and western white pine, tamarack, deodar cedar, and Norway spruce are severely defoliated by larvae that have left their pine host.

Although the red-headed pine sawfly has been recognized since 1858, few studies of its ecology have been conducted. Middleton's biological investigations (*21*) [3] with notes on its ecology are comprehensive; Brown and Daviault (*7*), and Schaffner (*27*, *28*) have also contributed ecological and biological information.

Because of the paucity of current information concerning the biology, ecology, and control of this insect on large forest plantations in the Lake States, the studies reported here were undertaken in 1947. Investigations were conducted on the Shawnee National Forest in southern Illinois in 1947, 1948, and 1949, and on the Manistee National Forest in the Lower Peninsula of Michigan in 1948 and 1949. Sawfly infestations on national forests in Michigan, Minne-

---

[1] Submitted for publication January 18, 1955; a condensation of a thesis in partial fulfillment of the requirements for the Doctor of Philosophy, University of Minnesota. The studies reported were undertaken by the Bureau of Entomology and Plant Quarantine in cooperation with the U. S. Forest Service and the University of Minnesota.

[2] The writer, now with the University of Wisconsin, expresses his sincere gratitude to F. C. Craighead, formerly in charge of the Division of Forest Insect Investigations, Bureau of Entomology and Plant Quarantine, for making these studies possible; to H. A. Bess, formerly in charge of the Milwaukee Forest Insect Laboratory, for guidance during the early phases of the studies; to C. E. Eaton, formerly in charge of the Milwaukee Forest Insect Laboratory, for valuable suggestions during the latter phases of the investigations, and for his critical examination of the manuscript; to A. C. Hodson, of the University of Minnesota, for suggestions and criticisms throughout the study. Without the interest, encouragement, and assistance of many members of the Forest Service, these studies would have been impossible.

Sincere appreciation is expressed for unpublished data made available by many Canadian and American entomologists; the writer is in particular indebted to the Canadian entomologists A. W. A. Brown and L. Daviault, and to the American entomologist J. V. Schaffner, Jr., of the New Haven Forest Insect Laboratory.

[3] Italic numbers in parentheses refer to Literature Cited, p. 55.

sota, Missouri, and Wisconsin were also examined. Information concerning the sawfly in other areas was obtained from literature and through correspondence with Canadian and American entomologists. This bulletin brings together widely scattered information concerning the sawfly and summarizes the biological, ecological, and control studies.

The red-headed pine sawfly has been reported from practically every State east of the Mississippi River and also from Arkansas, Louisiana, Minnesota, Missouri, and Texas west of the Mississippi River. Collections have been made as far south as Manatee County, Fla., at latitude approximately 27° N., and Jasper County, Tex., at 30° N., and as far north as Albanel, Quebec, 49° N., and Kindiogami Lake, Ontario, 46° N. The known distribution is presented in figure 1.

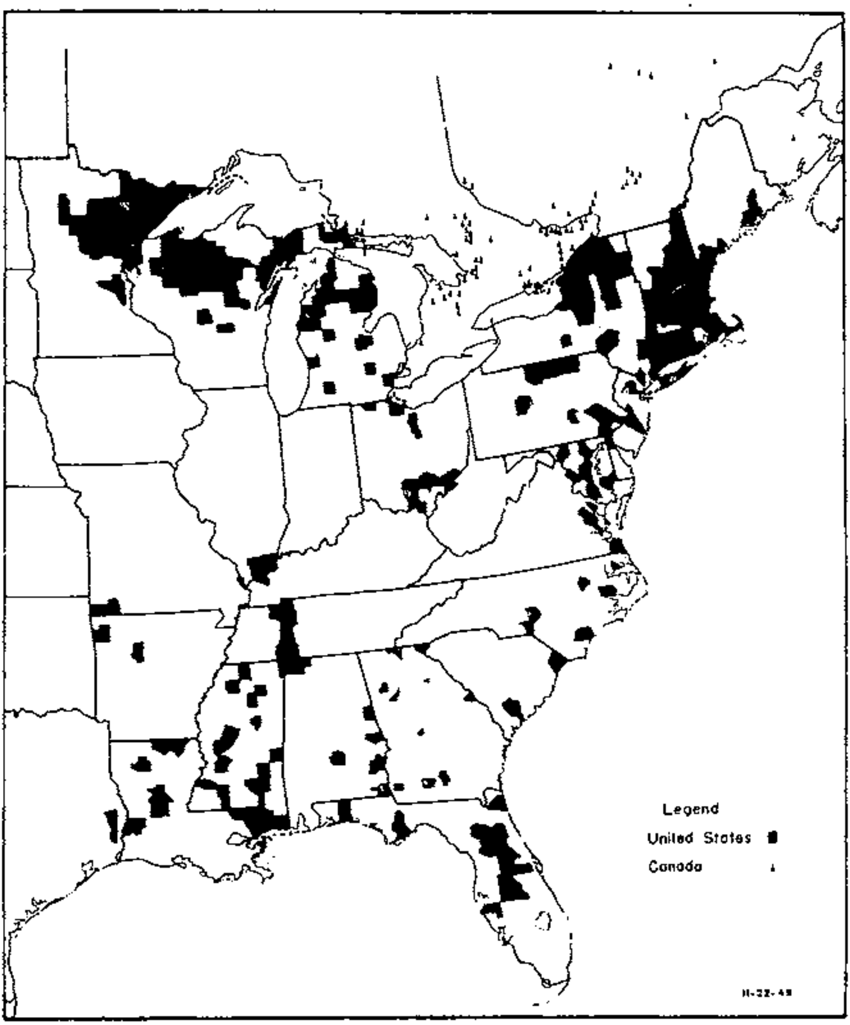


Figure 1.—North American distribution of the red-headed pine sawfly.

OUTBREAKS OF THE SAWFLY IN EASTERN NORTH AMERICA

Few reports of widespread defoliation by the red-headed pine sawfly were published during the 19th century. In general, these early writings referred to only defoliation of park and shade pines. With the extensive planting of stands of pure pine throughout the eastern half of the United States in the early part of the 20th century, local and widespread sawfly oubreaks began to occur. During the 1930's there were severe infestations in the Lake, Southern, and Northeastern States, and during the 1940's outbreaks were general in Illinois, Michigan, New York, and Wisconsin. A summary of the sawfly outbreaks in eastern North America during the past 19 years is presented in table 1.

TABLE 1.—*Red-headed pine sawfly outbreaks*[1] *in eastern North America, 1935–53*

Area	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953
Atlantic States:																			
North Carolina					o														
Virginia						o													
Lake States:																			
Michigan	o	x	x	x	x	x				o	o	x	x	x	o	o	o	o	o
Minnesota										o	o	o	o	o	o				
Wisconsin	o		o									o	x	x	x			o	o
North Central States:																			
Illinois											o	x	x	o					
Missouri					o		o							o	o			o	
Ohio	x	x																	
Northeastern States:																			
Connecticut												o							
New York			x	x	x	x	x	x	x	x	x	x	x						
Vermont					o	o	o	o									o		
Southern States:																			
Alabama			x	x	x	x	x												
Florida															o				
Tennessee			x	x	x	x	x												
Texas												o	o						
Canada:																			
New Brunswick[2]																			
Northern Ontario		o															o		
Quebec			o	o	o		o			o									
Southern Ontario		x			o	o	o		o	o	o	o	o	o	o		o		

[1] x = Widespread outbreak; o = local outbreak.
[2] Widespread outbreaks occurred in 1922–25.

NATIVE AND EXOTIC HOSTS, AND SAWFLY PREFERENCE

Defoliation by the red-headed pine sawfly is generally restricted to hard pines. The females rarely oviposit on soft pines or on other coniferous species. However, the larvae frequently migrate from completely defoliated trees to adjacent hard pines, eastern and western white pine, tamarack, deodar cedar, and Norway spruce, where they are able to complete their development.

Within the eastern half of North America the following nine native hard pines have been attacked by the sawfly:

Jack pine	(*Pinus banksiana* Lamb.)
Sand pine	(*P. clausa* (Chapm.) Vasey)
Shortleaf pine	(*P. echinata* Mill.)
Slash pine	(*P. elliottii* Engelm.)
Longleaf pine	(*P. palustris* Mill.)
Red pine	(*P. resinosa* Ait.)
Pitch pine	(*P. rigida* Mill.)
Loblolly pine	(*P. taeda* L.)
Virginia pine	(*P. virginiana* Mill.)

In addition, the following native and exotic species, successfully established in the eastern half of the continent, have been attacked:

Lodgepole pine	(*Pinus contorta* Dougl.)
Japanese red pine	(*P. densiflora* Sieb. and Zucc.)
Western white pine	(*P. monticola* Dougl.)
Swiss mountain pine	(*P. mugo* Turra)
Austrian pine	(*P. nigra* Arn.)
Ponderosa pine	(*P. ponderosa* Laws.)
Eastern white pine	(*P. strobus* L.)
Scotch pine	(*P. sylvestris* L.)
Japanese black pine	(*P. thunbergii* Parl.)
Deodar cedar	(*Cedrus deodara* (Roxb.) Loud.)
Tamarack	(*Larix laricina* (Du Roi) K. Koch)
Norway spruce	(*Picea abies* (L.) Karst.)
Northern white-cedar	(*Thuja occidentalis* L.)

The following data give the host preference of the sawfly in eastern North America:

Area	*Preferred host*	*Secondary host*	*Observer* [1]
Atlantic States:			
North Carolina	Shortleaf pine		Beal (3).
	Loblolly pine	Eastern arborvitae	Beal.
	Shortleaf pine	Cedar (unspecified)	Do.
	Slash pine	Spruce (unspecified)	Do.
Virginia		Loblolly pine	Schoene.
		Longleaf pine	Do.
		Slash pine	Do.
Lake States:			
Michigan	Jack pine	Eastern white pine	Benjamin.
	Red pine	Scotch pine	Do.
		Austrian pine	McDaniel (*20*).
		Jack pine	Do.
		Red pine	Do.
		Scotch pine	Do.
		Swiss mountain pine	Do.
Minnesota	Jack pine	Red pine	Hodson.
		Scotch pine	Do.
	Jack pine	Red pine	Eyre and Zehngraff (*13*).
Wisconsin	Jack pine	Tamarack	Benjamin.
	Red pine		Do.
North Central States:			
Arkansas	Swiss mountain pine.		Baerg.
Illinois	Pitch pine	Jack pine	Benjamin.
	Shortleaf pine	Loblolly pine	Do.
		Virginia pine	Do.

[1] See footnote on page 6.

Area	*Preferred host*	*Secondary host*	*Observer* [1]
North Central States—Continued			
Missouri	Shortleaf pine		Benjamin.
	do		MacAloney.
Ohio	Shortleaf pine	Loblolly pine	Polivka (23).
	do	Austrian pine	Polivka.
		Eastern white pine	Do.
		Jack pine	Do.
		Loblolly pine	Do.
		Lodgepole pine	Do.
		Scotch pine	Do.
Northeastern States:			
Connecticut		Austrian pine	Britton and Zappe (6).
		Eastern white pine	
		Jack pine	Do.
		Pitch pine	Do.
		Scotch pine	Do.
		Swiss mountain pine.	Do.
New Jersey	Swiss mountain pine.	Pitch pine	Boyd (5).
New York	Red pine	Austrian pine	McAndrews.
	Jack pine	Eastern white pine	Do.
		Japanese black pine	Do.
		Japanese red pine	Do.
		Lodgepole pine	Do.
		Pitch pine	Do.
		Ponderosa pine	Do.
		Red pine	Do.
		Scotch pine	Do.
		Swiss mountain pine.	Do.
		Eastern tamarack	Do.
	Red pine	Jack pine	Schaffner (27).
Pennsylvania		Eastern white pine	Will (33).
		Scotch pine	Do.
		Swiss mountain pine.	Do.
Southern States:			
Alabama	Longleaf pine	Loblolly pine	Kowal.
	Slash pine	Shortleaf pine	Do.
	Loblolly pine		Lund.
	Shortleaf pine		Do.
	Slash pine		Do.
Florida	Longleaf pine	Sand pine	Tissot.
		Slash pine	Do.
	Loblolly pine		Hetrick.
Georgia	Longleaf pine	Loblolly pine	Kowal.
	Slash pine	Shortleaf pine	Do.
	Loblolly pine		Lund.
Louisiana	Longleaf pine	Loblolly pine	Kowal.
	Slash pine	Shortleaf pine	Do.
	Loblolly pine		McCrory.
Mississippi	Longleaf pine	Loblolly pine	Kowal.
	Slash pine	Shortleaf pine	Do.
	Slash pine	Deodar cedar	Lyle.
		Norway spruce	Do.
Tennessee	Loblolly pine		Johnston.
	Slash pine		Do.
	Shortleaf pine	Loblolly pine	Zimmerman.
		Virginia pine	Do.
Texas	Loblolly pine	Shortleaf pine	Anderson.

[1] See footnote on page 6.

Area	*Preferred host*	*Secondary host*	*Observer* [1]
Canada:			
Ontario	Red pine	Jack pine	Atwood and Peck (*2*).
	Red pine	Jack pine	Watson.
		Scotch pine	Do.
	Red pine	Jack pine	West (*34*).
		Eastern white pine	Do.
Quebec	Red pine	Jack pine	Atwood and Peck (*2*).
	Red pine	Jack pine	Daviault.
		Eastern white pine	Do.
		Scotch pine	Do.
	Red pine	Jack pine	Daviault (*12*).

[1] Information credited to observers whose names are not followed by literature citations was taken from records in the files of the Division of Forest Insect Research, Lake States Forest Experiment Station, St. Paul, Minn.

In Michigan, Minnesota, and Wisconsin mixed roadside plantings, jack pine is generally completely defoliated before adjacent red pine is attacked (*16*). Isolated jack pine accidentally planted within solid blocks of red pine is also commonly defoliated before the red pine is attacked. This preference for jack pine in the Lake States is likewise manifest during intense outbreaks when both jack and red pine are infested. For example, in 1948 in central Michigan where a pure jack pine planting adjoined a pure red pine planting, an average of 6.5, 2.0, and 2.7 sawfly colonies were present per jack pine in the first, second, and third rows as compared with 1.5, 1.2, and no sawfly colonies per red pine in corresponding rows.

In southern Illinois, shortleaf pine is the preferred host of the sawfly. Seldom are other hard pines attacked when it is present. In its absence, loblolly, pitch, and Virginia pines are infested. This preference for shortleaf pine was well illustrated at Glendale, Ill., where the sawfly failed to attack a pitch pine clump growing within a heavily infested shortleaf pine planting (fig. 2).

SYNONOMY

The red-headed pine sawfly was described by Fitch (*14*) as *Lophyrus lecontei*, and de Dalla Torre (*10*) listed it under the genus *Lophyrus*. Rohwer (*26*) revised the Diprionidae, and erected the genus *Neodiprion* using the species *L. lecontei* Fitch as the genotype. Atwood and Peck (*2*), in a taxonomic treatment of the Canadian sawflies of the genus *Neodiprion*, list *N. lecontei* (Fitch). *N. lecontei* (Fitch) is also cited in a recently published check list of the family Diprionidae (Muesebeck, et al (*22*)).

DESCRIPTION OF LIFE STAGES

Descriptions of the larvae and adults of the red-headed pine sawfly have been published by Fitch (*14*), Middleton (*21*), and Atwood and Peck (*2*). For this reason only brief treatment of these stages will be given here.

Figure 2.—Group of pitch pine that escaped red-headed pine sawfly attack during an epidemic in the surrounding shortleaf pine plantation, Glendale, Ill., 1947.

ADULTS

The adult female is rather robust and from 6.0 to 9.5 mm. in length (fig. 3, *A*). The head and dorsum of the thorax are rufoferruginous. The abdomen is black with the ventral aspects of the tergites whitish. The legs are ferruginous with part of the femurs and bases of the coxae blackish. The wings are vitreous and subhyaline with dark venation. The antennae are serrate, 19 jointed, and black. The adult male is smaller than the female, measuring from 5.0 to 6.5 mm. in length, is entirely black, and has 19 jointed bipectinate antennae.

EGGS

The eggs are oval, 0.50 mm. long and 0.25 mm. wide, with a thin, whitish, smooth, shining, translucent shell (*27*). They are laid individually in a row of slits cut in the edge of the needles (fig. 3, *B*). The shoe-shaped egg pockets are cut rather close together, being separated from each other by one-third to one-half their length. All eggs laid by one female are generally grouped on needles of a single twig.

LARVAE

The sawfly hatches as a small larva, 2 to 5 mm. long, with a brownish transparent head capsule. As it feeds and molts, its body length increases, and becomes spotted, and the head capsule becomes gradually larger and more orange red. The fourth and fifth instars, the most frequently encountered stages, have a rufoferruginous head capsule with black spots surrounding the eyes (fig. 3, *C*). In these stages the thorax and abdomen are deep yellow to pale whitish yellow, marked as follows:

1. Prothorax and abdomen immaculate above with a double row of black spots extending from the mesothorax to the ninth abdominal segment.
2. Second row of supraspiracular black spots extending from the mesothorax to the ninth abdominal segment.
3. Third row of spots on the dorsal aspect of the spiracular area extending from the mesothorax to the ninth abdominal segment.
4. Fourth row of spots frequently present on the epipleural area on abdominal segments 1 through 8.
5. Black patch on the epiproct divided by a light median line.

Cocoons

The red-brown cylindrical cocoon is tough, single-walled, and papery with rounded ends (fig. 3, *D*). Female cocoons are larger than male cocoons in the following dimensions (*21*):

	Female cocoon	*Male cocoon*
Length (mm.):		
Average	10. 3	7. 5
Range	9. 5–11. 0	7. 0–7. 8
Diameter (mm.):		
Average	4. 6	3. 4
Range	4. 5–5. 0	3. 2–3. 5

LIFE HISTORY AND BIOLOGY

The sawfly overwinters in the prepupal stage encased in a cocoon spun in the litter or soil beneath the infested trees. Pupation occurs soon after the onset of warm spring weather, and emergence of the adults follows in a few weeks.

To escape from its cocoon the adult sawfly thrusts one mandible through it and, while using the other mandible as an extended anchor, makes a short slit by bringing the two mandibles together in a pliers-like action. The sawfly rotates itself as it cuts a circular hole, and escapes when the hole is of sufficient size. Figure 4 illustrates the emergence holes cut in the end of female cocoons by the adult sawfly and those of two common parasites.

Mating takes place immediately after emergence, and oviposition begins a short time later. The eggs hatch in 3 to 5 weeks, depending upon the temperature of the particular area. Five feeding instars and one nonfeeding instar are passed through prior to spinning of the cocoon.

A single generation per year occurs in Canada and in the northern part of the United States. In New York and lower Michigan one generation is completed and a few second-generation adults may also emerge. At East Falls Church, Va., a rather complex life cycle included two generations in which the life of a single colony varied from 12 to 14 months, depending on the time of egg deposition (*21*). In Ohio two generations were reported by Polivka (*23*). In south-

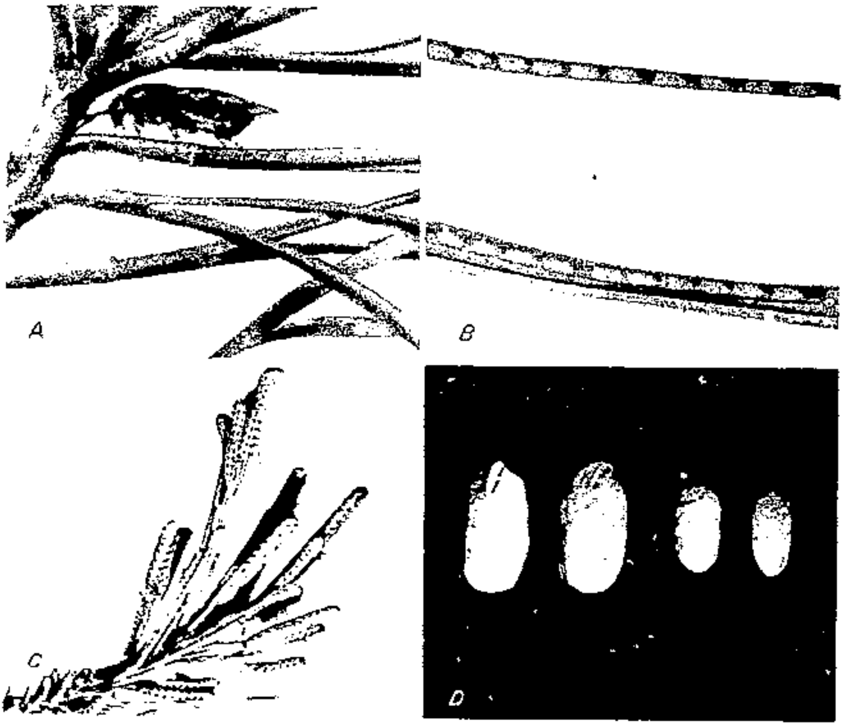


Figure 3.—Red-headed pine sawfly. A, Adult female; B, eggs; C, larvae; and D, cocoons—female on left and male on right.

Figure 4.—Cocoons from which adult red-headed pine sawfly and their parasites have emerged: *Phorocera hamata* A. & W. on left, *Spathimeigenia spinigera* Tns. in the center, and female sawfly on right.

ern Illinois two and a partial third generation per year occurred in 1917 and 1918. Four to five generations per year were reported for the southeastern part of the United States by Herrick,[3] and three plus generations by Kowal.

[3] Information from correspondence and unpublished records in the files of the Division of Forest Insect Research, Lake States Forest Experiment Station, St. Paul, Minn.

Varying periods of diapause often carry the prepupal sawflies over several years. Diapause up to 5 years was reported in Canada by Daviault.[5] Among larvae whose cocoons were spun during the first week of August, 17 percent went into diapause, and among larvae whose cocoons were spun in late September, 77 percent were in diapause. In the 15 larval collections reared in Illinois in 1947, 4.2 percent of the sawfly larvae went into diapause during the first generation and 90.4 percent during the second generation. Only 1.3 percent of the second-generation 1947 sawflies failed to emerge in 1948.

The period of adult activity varies throughout the range of this insect. Although the overall length of the emergence period for the adult differs from year to year, the peak of emergence did not vary more than 10 to 16 days in northeastern United States (Schaffner and Youngs).[5] In Quebec the emergence period was relatively short and the dates of adult appearance did not vary much from year to year according to Daviault.[5] In southern Illinois first-generation adults appeared the first week of May in 1947 and 1948, and the peak of emergence occurred the middle of the month. Second-generation adult emergence began around mid-July and continued into the third week of August. Third-generation adults were observed about the 15th of September; stragglers continued to appear throughout the last part of October. The life cycle in southern Illinois is presented in figure 5. Emergence of adults in lower Michigan began the first week of June from 1946 through 1949 as illustrated in figure 5. The peak was passed the middle of the month and emergence was completed by the end of June.

Mating

Mating generally occurs quite soon after the adults escape from the cocoons and emerge from the soil beneath the pine host. Females are monogamous; males will mate a second time when offered the opportunity. The following information concerning the mating habits was obtained by observation of reared sawflies released in southern Illinois in 1947 and 1948.

Virgin females released on pines during the adult sawfly flight period attracted large numbers of males. If mating did not occur immediately, the female took a position near the end of a pine needle with her abdomen toward the needle tip. Males actively searched the immediate vicinity, approaching from the lee side. The female generally remained quiet, often within sight of the male, cleaning her antennae, legs, and wings. No attempt was made by her to capture a mate. If several males encountered her simultaneously, she fluttered her wings, then flew to a nearby tree; the males invariably followed.

Mating occurred without courtship; the male approached from the anterior end. Copulation was accomplished essentially as described by Rohwer (*24*). In this study in southern Illinois, copulation averaged 24 minutes with a range of 10 to 45 minutes for 8 observations.

[5] See footnote 4, p. 9.

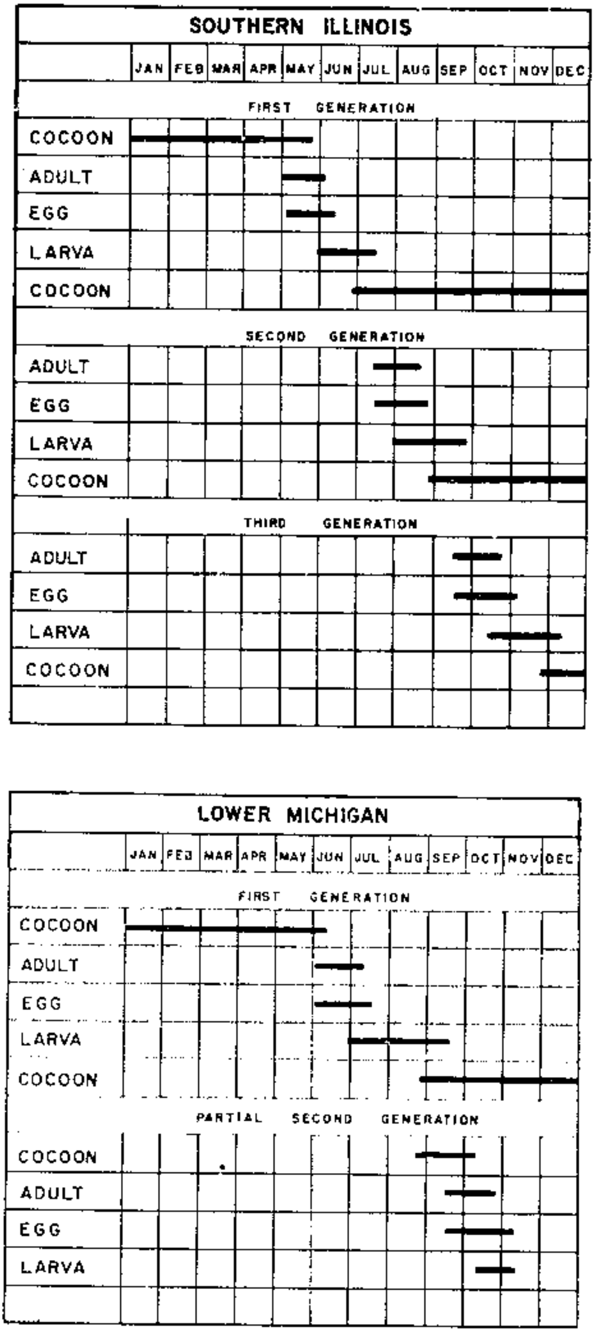


Figure 5.—Life cycle of red-headed pine sawfly in southern Illinois (1947–48), and in lower Michigan (1946–49).

Oviposition

Oviposition often begins within 5 minutes after mating has been accomplished. Needles of the current and previous years are selected, and in one instance a needle bract was used. Needle selection, after a suitable site has been chosen (see page 32), follows a regular pattern. The female examines the needles from base to tip until an acceptable one is found. This needle is palpated to about its midpoint where she stops and backs to its base. Next an incision is made with her ovipositor slightly in from the edge on the flat inner side of the needle. After a few cuts have been made and the needle appears satisfactory, the lancets are withdrawn from the small slit and one step is taken toward the tip of the needle. Here the egg pocket is cut by inserting the lancets to their maximum depth, and enlarging the egg pocket parallel to the round face of the needle (fig. 6, *A*). Immediately following the completion of the egg pocket, the lancets are slowly moved back through the egg pocket and the egg is deposited (fig. 6, *B*).

After an egg is deposited, the female lowers her abdomen to contact the needle, folds her ovipositor into place, and raises her abdomen before taking a step forward to begin cutting the next egg slit. Irregularities in spacing of egg pockets are due to her slipping during initial sawing and when she cleans debris from her antennae and legs. Acceptance of the second and subsequent needles follows the foregoing pattern; always the initial cut is made at the needle base and abandoned before cutting is undertaken for the first and subsequent eggs.

When the egg supply is exhausted, the female walks to the base of the needle in which her last eggs were laid. As if to guard her egg batch, she remains there in the shelter of the small twig until she dies or is captured by ants or some other predator. Females live an average of 4.5 days, with a range of 2 to 17 days, and males live an average of 3.2 days, with a range of 1 to 17 days (Daviault).[5]

Fecundity and Size of Egg Batch

Females emerge from their cocoons with their complement of eggs ready for fertilization; additional eggs are not matured.

Middleton (*21*) reported that an unspecified number of caged females laid an average of 82 eggs per batch with a range of 25 to 178, and that 6 virgin females had an average of 139 eggs in their ovaries, with a range of 58 to 218. Thus, 57 eggs on an average were not laid by these female sawflies. According to Daviault[5] 80 eggs on an average were laid per mated female with a maximum of 123 eggs, and 95 eggs per batch laid by virgin females, with a maximum of 244 eggs.

Eggs per batch for wild female sawflies collected in southern Illinois averaged between 108 and 137 on shortleaf pine, 102 and 138 on pitch pine, and 141 on jack pine (table 2). Four virgin females laid an average of 137 eggs per batch on shortleaf pine during the third generation in 1947 and an average of 121 during the first generation in 1948. Collections in Michigan averaged 116 eggs per batch on red pine and 108 on jack pine.

---

[5] See footnote 4, p. 9.

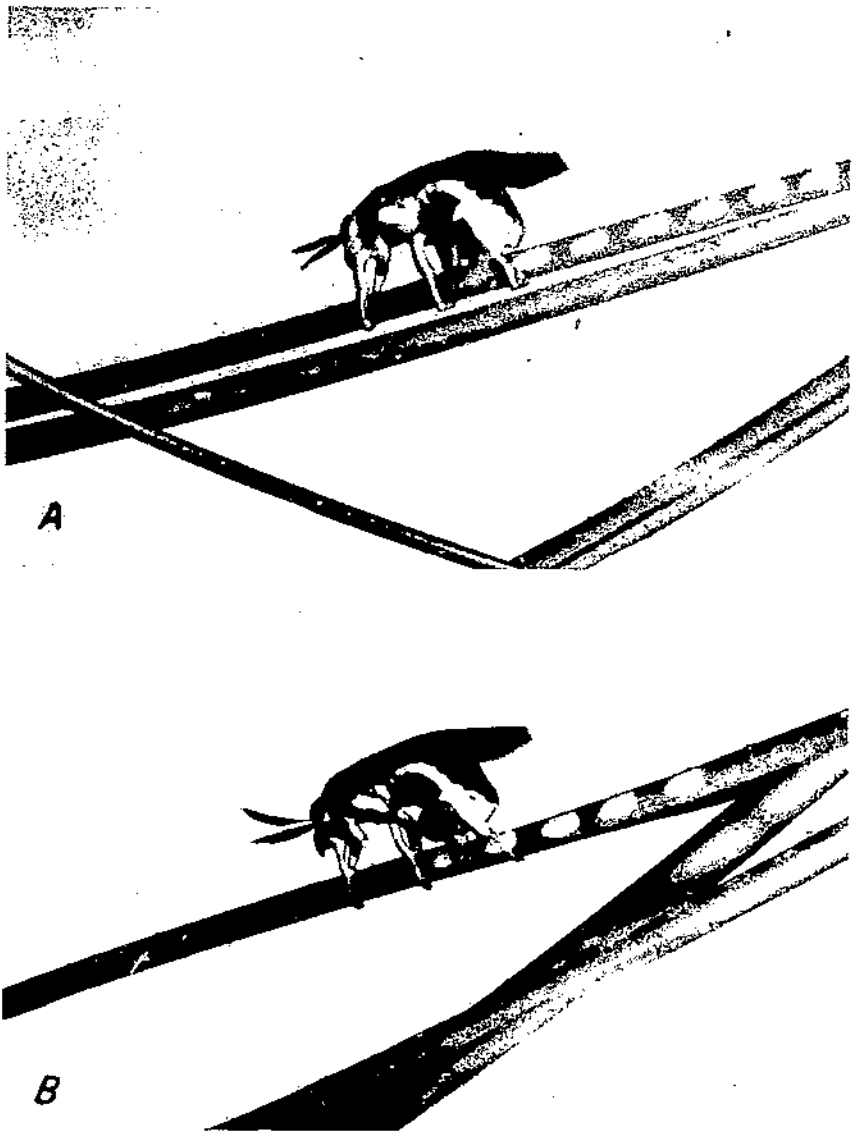


Figure 6.—Female red-headed pine sawfly: *A*, Cutting egg pocket in shortleaf pine needle prior to oviposition; *B*, returning saw through egg pocket and depositing egg.

In Illinois 21 female sawflies collected during the cage and field studies had an average of 3 eggs in their abdomens after the completion of oviposition. In Michigan 2 eggs per female on an average were dissected from 5 females after oviposition. These studies indicate a more complete egg discharge than the 57 unlaid eggs reported by Middleton (*21*). Possibly his collections were made prior to the completion of oviposition.

TABLE 2.—*Average number of red-headed pine sawfly eggs per batch on three host species, Shawnee National Forest, Ill.*

Host species and year	Generation	Egg batches	Eggs	Average eggs per batch
		Number	*Number*	*Number*
Shortleaf pine:				
1947	3	101	13,900	137.6 ± 1.9
1948	1	86	9,311	108.3 ± 2.6
	2	7	804	114.8 ± 11.7
	3	11	1,481	134.6 ± 6.3
Pitch pine:				
1947	2	138	14,178	102.7 ± 2.7
	3	2	276	138.0
1948	1	11	1,484	134.9 ± 21.5
	2–3	1	103	103.0
1949	2–3	2	224	112.0
Jack pine:				
1947	2	10	1,410	141.0 ± 13.3

NUMBER OF EGGS PER NEEDLE

In Canada the red-headed pine sawfly laid an average of 4.7 eggs per jack pine needle, with a maximum of 12, and 8.3 per red pine needle, with a maximum of 36 (Daviault).[5] Atwood and Peck (2) report the range of eggs per red pine needle as from 10 to 30. Table 3 presents similar statistics for southern Illinois and lower Michigan.

TABLE 3.—*Average number of red-headed pine sawfly eggs per needle on various host species, Illinois and Michigan, 1947–48*

Region and host species	Egg batches	Eggs	Needles	Average of eggs per needle	Range
Shawnee National Forest, Ill.	*Number*	*Number*	*Number*	*Number*	*Number*
Jack pine	10	1,410	222	6.4	2–14
Pitch pine	138	14,178	1,245	11.4	4–27
Shortleaf pine	71	9,065	1,035	8.8	2–31
Virginia pine	4	224	40	5.6	1–10
Manistee National Forest, Mich.					
Jack pine	13	2,065	276	7.5	2–19
Red pine	13	1,515	139	10.9	4–35

EGG DEVELOPMENT

Sawfly eggs develop within the pine needle, gradually swelling and forcing the edges of the egg pocket apart. The length of the incubation period depends upon the temperature of the particular region. In Quebec incubation averaged between 23 and 26 days (Daviault);[5] whereas at East Falls Church, Va., it averaged 21 days at a mean

[5] See footnote 4, p. 9.

temperature of 71° F., 18 days at 74°, and 13 days at 78° (*21*). In Illinois incubation averaged 20 days with a range of 13 to 27 days during the first generation, 15 days with a range of 13 to 21 days during the second generation, and 24 days with a range of 21 to 36 days during the third generation. Eggs laid in November did not hatch during the third generation period or the next season.

Larval Feeding Habits

The first-instar larvae escape from the egg and needle by wriggling out between the edges of the egg pocket. Practically all larvae from eggs laid on a single needle hatch within a short time. The egg laid first generally hatches first and the larvae appear in approximately the order in which the eggs were laid. Five feeding instars and one nonfeeding instar are passed through by the sawfly larvae. The duration of these instars varies according to the temperature.

First-instar larvae feed on the needles from which they hatch or on adjacent needles. They chew small ragged notches in the edges, generally taking but a few pieces from any one. The progeny of each female feed as a gregarious colony, staying for the most part in the vicinity of the oviposition site in an unexposed location. After the larvae molt, the colony either moves a short distance from the egg site and continues to feed on the lower side of the branch, or it moves to a sheltered position directly above its egg site. The second-instar larvae do noticeable damage when they strip the edges of the needles, leaving only the central vascular tissue which soon dries and appears as reddish, strawlike masses (fig. 7). These strawlike flags are visible from a considerable distance and are therefore useful during prespray population surveys.

Figure 7.—Strawlike remains of shortleaf pine needles resulting from the feeding of second-instar larvae of red-headed pine sawfly.

337588—55——3

After molting a second time, the larvae generally ascend the tree to feed on the needles of the leader and branch tips. Third, fourth, and fifth instars feed voraciously in well-exposed positions on the tree, often in groups of 3 to 5 per needle. They consume the entire needle and frequently chew cupshaped holes in the tender bark. As a colony, they move from the leader to a branch (fig. 3, *C* and 8). No apparent pattern is followed in the choice of this next branch. Often a colony will pass over several undefoliated branches to select some well-exposed distant branch for its feeding site.

Figure 8.—Red-headed pine sawfly colony feeding on red pine.

Injury to hard pines resulting from sawfly defoliation is often severe during epidemics. This is true especially when young pine plantations are attacked. If the larvae consume all of the needles before they complete their feeding, they may leave their stripped host to seek adjacent pines or other coniferous species. Before this occurs, much tender bark may be consumed by the starving larvae. Defoliation of secondary hosts is frequently severe, thus greatly increasing the injury attributable to a single sawfly generation.

Larval Migration Habits

Little information is available concerning the migration habits of red-headed pine sawflies, the distance they can travel successfully, or how they avoid unfavorable conditions encountered enroute. To determine their migration habits and the damage they are capable of inflicting on their new hosts, studies were initiated in lower Michigan in 1949. In these studies, known numbers of colonies of second-instar larvae were introduced on jack and red pines, and daily observations made. The smallest trees artificially infested with the largest numbers of colonies were stripped of their foliage first. Examination of each artificially infested tree and its neighbors indicated that larval migration did not begin until defoliation of the host trees was complete and a considerable amount of tender bark was also destroyed.

For convenience of orientation and to maintain orderly records of the rate of defoliation and larval migration, the study areas were plotted to scale (fig. 9, *A* and *B*).

Each tree was indicated by a number corresponding to the number of colonies introduced, and a letter indicated the replicate. For example, tree 4–c was a four-colony tree in the third replicate. Noninfested trees in the plantation were located in their appropriate row (indicated by capital letter) and at their measured distance from an established baseline indicated at each side of the plantation study area. Thus, a tree located in the fourth row 42 feet from the baseline was referred to as tree D–42.

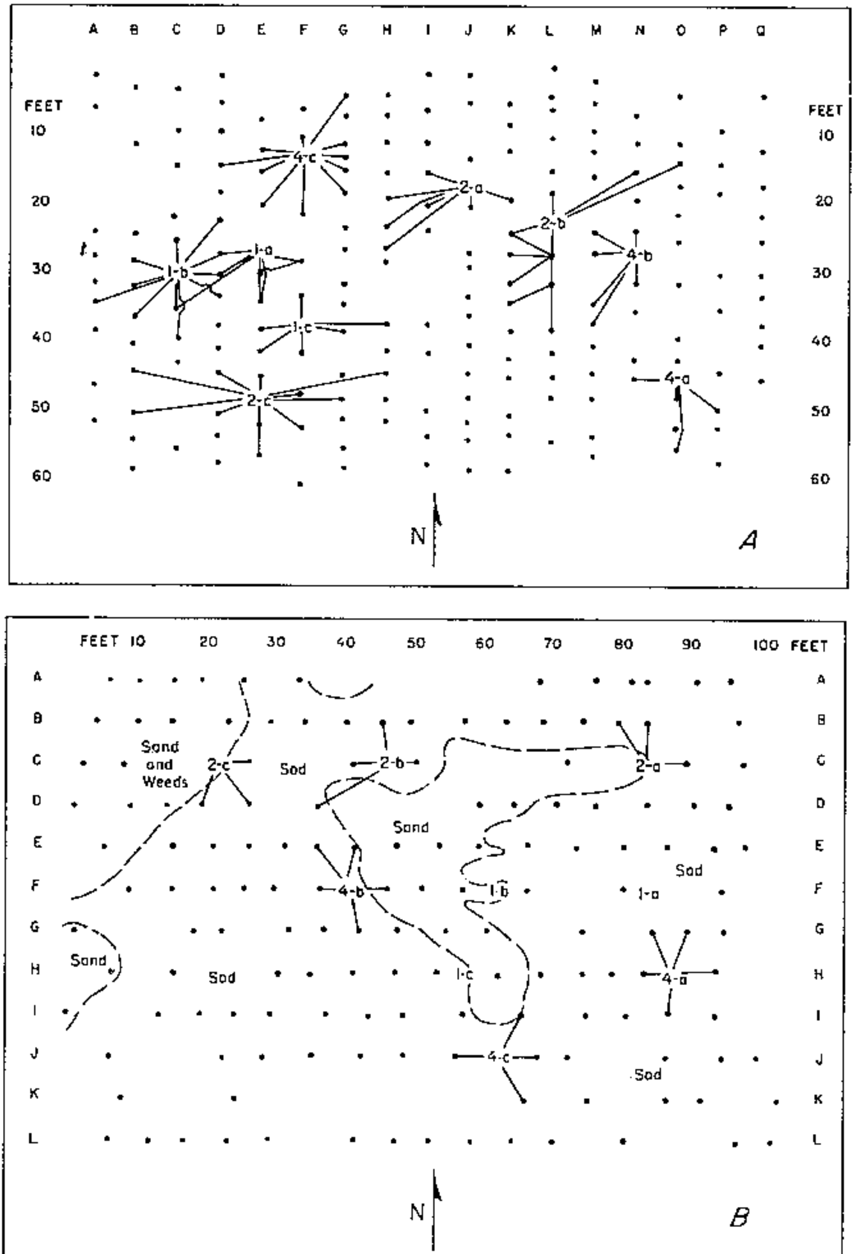
In the sand-blow study area of 1-foot jack pine (fig. 9, *A* and 10) 21 colonies of second-instar larvae were liberated: 1, 2, and 4 colonies each on 3 trees of comparable foliage characteristics.

Soon after the initial host pines were stripped of their foliage, the larvae migrated to nearby trees to continue feeding. Larvae established themselves on 72 nearby pines where they caused varying degrees of defoliation, depending on the size of the larval population reaching the tree. Eighteen of the secondary host pines sustained defoliation in excess of 25 percent; 4 of the 18 were completely stripped of their foliage. Distances as great as 19 feet were traversed across the sand. Although no apparent time or migration pattern was evident, the larvae did tend to follow one another as evidenced by the appearance of 150 larvae on a single nearby tree. Heavy mortality among migrating larvae occurred when a sudden clearing of the cloudy sky resulted in the elevation of sand-surface temperatures to approximately 105° F. which is above the critical level (fig. 11).

Larval migrants from 2 naturally infested sand-blow areas of 1-foot jack pine successfully established themselves up to 13 feet from their host tree. On a nearby study area 1 larva reached a pine 5 feet from its initial host; 42 larvae succumbed in a sand depression when direct sunlight broke through a dense cloud cover and sand-surface temperatures rose to 127° F.

After defoliation of the 2-foot red pine was completed in the sodded areas, larval migrants from the 2- and 4-colony trees successfully established themselves on 24 nearby trees up to a maximum of 11 feet from their host (fig. 9, *B*). Defoliation in excess of 25 percent was observed on 6 trees, 2 of which were completely stripped of their foliage. Larval feeding on the 1-colony trees was finished prior to complete host defoliation, and the larvae did not migrate. A few larval migrants from the 2- and 4-colony trees were attacked by ants; the significance of this factor was not assessed. No mortality due to high soil-surface temperatures was observed.

The rapidity with which these small jack and red pines were stripped by large larval populations, and the magnitude of the defoliation injury to adjacent pines by the migrants, present a clear



4-a ORIGINAL HOST TREE • RED PINE TREE —— LARVAL MIGRATION PATH

Figure 9.—Migration pattern of red-headed pine sawfly larvae: *A*, From 1-foot jack pine planted in sand-blow area; *B*, from 2-foot red pine planted in sod area.

Figure 10.—Sand-blow plantation of 1-foot pine in which migration studies of red-headed pine sawfly larvae were conducted.

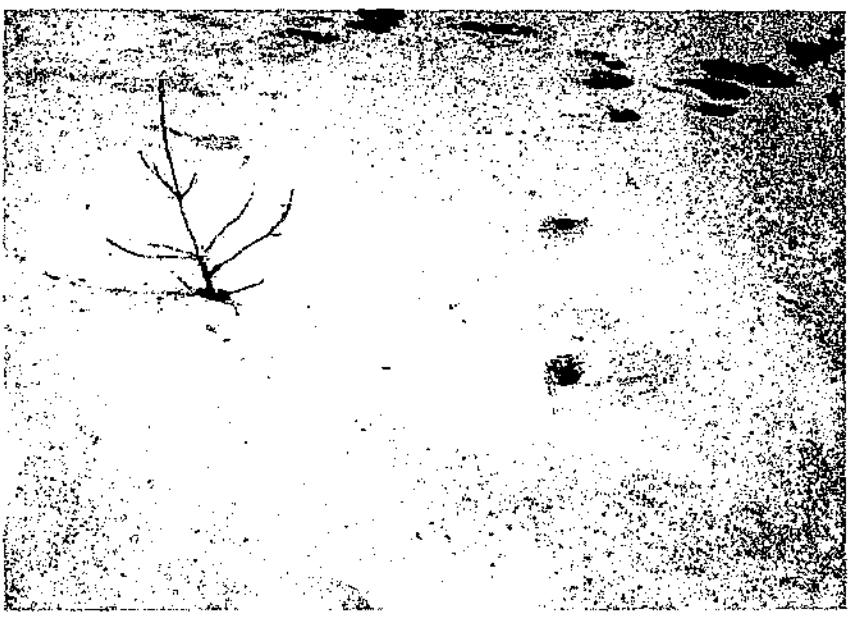


Figure 11.—Dead red-headed pine sawfly larvae in sand-blow depression. Mortality was caused by exposure to high sand-surface temperatures during migrations from defoliated jack pine.

example of the intraspecific self-limiting tendency of high insect populations under conditions of limited food supply. If the foregoing plantations had been infested throughout at the 2-colony level or above, intraspecific competition would certainly have resulted in a drastic population reduction through starvation.

PARTHENOGENETIC REPRODUCTION AND SEX RATIO

As arrhenotoky is the rule in the genus *Neodiprion*, only males have been reared from virgin red-headed pine sawflies. The sex ratio for field collections is as follows:

Location	*Females*	*Males*	*Observer* [1]
Quebec	44	56	Daviault.
Ontario	69	31	Brown.
East Falls Church, Va	75	25	Middleton (*21*).
Southern Illinois:			
First generation	84	16	Benjamin.[2]
Second generation	82	18	Do.
Third generation	81	19	Do.

[1] Information credited to observers whose names are not followed by literature citations was taken from correspondence and unpublished records in the files of the Division of Forest Insect Research, Lake States Forest Experiment Station, St. Paul, Minn.

[2] Data obtained in 1947.

NATURAL CONTROL FACTORS

Little is known concerning the influence of natural control factors on the population dynamics of the red-headed pine sawfly. Consequently, the employment of biological control agents in the management of populations of this sawfly has not been emphasized. In eastern North America the following 58 species of parasitic and predatory insects have been reported associated with the red-headed pine sawfly. Of these insects, 20 have been collected in the United States, 23 in Canada, and 15 in both countries.

PARASITES

Order and species [1]	*Country*	*Observer* [2]
DIPTERA:		
Bessa harveyi (Tns.)	Canada	Brown.
Hylotomoyia hylotomae (Coq.)	United States	Greene (*15*). Schaffner.
Megaselia proboscidea (Mall.)	Canada	Brown. Daviault.
Megaselia pulicaria (Fall.)	do	Brown.
Muscina assimilis (Fall.)	do	Daviault.
Pelecotheca macra (Van der Wulp)	United States	Middleton (*21*). Muesebeck.
Phorocera claripennis Macq	do	Greene (*15*). Muesebeck. Schaffner.
Phorocera hamata A. & W	do	Benjamin. Schaffner.
	Canada	Bradley. Brown. Daviault (*11*).

See footnotes on page 23.

PARASITES—Continued

Order and species [1]	Country	Observer [2]
DIPTERA—continued		
Spathimeigenia aurifrons Curran	United States	Schaffner.
	Canada	Bradley. Brown. Daviault.
Spathimeigenia erecta Ald.	Canada	Bradley. Brown. Daviault.
Spathimeigenia spinigera Tns.	United States	Aldrich (*1*). Benjamin. Bentley (*4*). Greene (*15*). Middleton (*21*). Muesebeck. Orr. Polivka. Schaffner. Sellers (*29*). Zimmerman.
	Canada	Bradley.
Spathimeigenia sp.	United States	Benjamin.
Villa sinuosa Wied.	do	Blair.
Zenillia sp.	Canada	Daviault.
HYMENOPTERA:		
Agrothereutes lophyri (Nort.)	United States	Benjamin. Bentley (*4*). Zimmerman.
	Canada	Daviault.
Amblymerus verditer (Nort.)	do	Daviault.
Aptesis indistincta (Prov.)	United States	Schaffner.
	Canada	Brown.
Bracon pygmaeus Prov.	United States	Polivka.
Closterocerus cinctipennis Ashm.	do	Benjamin.
Dahlbominus fuscipennis (Zett.)	do	Blair.
	Canada	Wilkes (*32*).
Delomerista diprionis Cush.	do	Daviault.
Dibrachys cavus (Walk.)	United States	Benjamin.
	Canada	Daviault.
Endasys subclavatus (Say)	United States	Benjamin. Bentley (*4*). Schaffner. Zimmerman.
	Canada	Daviault.
Exenterus amictorius (Panzer)	United States	Sellers (*29*).
Exenterus canadensis Prov.	do	Benjamin. Muesebeck. Townes (*30*).
	Canada	Brown. Daviault (*11*). Walley (*31*).
Exenterus diprionis Rohw.	United States	Benjamin. Cushman (*9*). Middleton (*21*). Muesebeck. Orr. Schaffner.
	Canada	Bradley. Hutchings (*17*). Townes (*30*).

See footnotes on page 23.

PARASITES—Continued

Order and species[1]	Country	Observer[2]
HYMENOPTERA—continued		
Lamachus contortionis Davis	United States	Benjamin. Champlain (*8*). Middleton (*21*). Muesebeck. Polivka. Rohwer (*25*). Schaffner.
	Canada	Bradley. Brown. Daviault (*11*). Townes (*30*).
Lamachus lophyri (Ashm.)	do	Brown.
Lamachus virginianus (Rohw.)	United States	Middleton (*21*). Muesebeck. Polivka. Rohwer (*25*). Schaffner.
	Canada	Brown. Townes (*30*).
Mastrus aciculatus (Prov.)	do	Brown.
Melittobia acasta (Walk.)	United States	Benjamin.
Mesoleius submarginatus (Cress.)	do	Schaffner.
	Canada	Brown.
Mnesidacus nigricoxus (Prov.)	do	Daviault (*11*).
Olesicampe lophyri (Riley)	United States	Benjamin. Schaffner.
	Canada	Brown. Daviault (*11*).
Otacustes crassus (Prov.)	do	Daviault.
Perilampus hyalinus Say	United States	Benjamin. Middleton (*21*). Muesebeck. Orr. Schaffner.
	Canada	Bradley. Brown. Daviault.
Plectiscidea carinata (Prov.)	do	Daviault.
Psychophagus omnivorus (Walk.)	do	Daviault.
Gelis sp	do	Daviault.
Hemiteles sp	do	Daviault.
Mastrus sp	do	Daviault.
Mesochorus sp	do	Daviault.
Orthostigma sp	do	Brown. Daviault.
UNDESCRIBED SPECIES:		
Agrothereutes sp	United States	Benjamin.
Tetrastichus sp	do	Benjamin.
Trichopria n. sp	do	Benjamin.

PREDATORS

Order and species[1]	Country	Observer[2]
DIPTERA:		
Erax aestuans (L.)	United States	Benjamin.
HEMIPTERA:		
Apateticus bracteatus (Fitch)	United States	Benjamin.
Apiomerus crassipes (F.)	do	Benjamin.
Arilus cristatus (L.)	do	Benjamin. Polivka.

See footnotes on page 23.

PREDATORS—Continued

Order and species [1]	Country	Observer [2]
HEMIPTERA—continued		
Nabis ferus (L.)	Canada	Daviault.
Podisus serieventris Uhler	United States	Benjamin.
Pselliopus cinctus (F.)	do	Polivka.
Sinea diadema (F.)	Canada	Daviault.
Zelus socius Uhler	United States	Benjamin.
Apateticus sp	Canada	Daviault.
Podius sp	do	Daviault.
HYMENOPTERA:		
Vespula maculifrons (Buysson)	United States	Benjamin.

[1] The writer is indebted to C. F. W. Muesebeck of the Bureau and to members of his staff for identifying parasites and predators of the sawfly collected in the Lake States region.

[2] Information credited to observers whose names are not followed by literature citations was taken from correspondence and unpublished records in the files of the Division of Forest Insect Research, Lake States Forest Experiment Station, St. Paul, Minn.

LARVAL PARASITES

Among the entomophagous insects attacking the sawfly, larval parasites have received most attention. Evaluation of their effectiveness is generally lacking, however, and most published reports cite only species reared or collected. In the United States Greene (*15*), Middleton (*21*), Bentley (*4*), Sellers (*29*), Polivka,[5] and Schaffner[5] have listed larval parasites of the sawfly. In Canada, Brown[5] reported "cocoon parasitism" intensities of 15, 16, 21, 30, and 18 percent from 1937 through 1941, but did not indicate the relative importance of the 16 species concerned.

In Quebec, Canada, Daviault[5] reported, in unpublished studies, 24 species of parasitic and predatory insects attacking the sawfly. *Spathimeigenia aurifrons* and *Phorocera hamata* were the most important; the former was reared from 13.9 percent of the sawfly cocoons in 1937, and from 38.0 and 14.7 percent in 1938 and 1941, respectively; *P. hamata* was reared from 16.2, 5.2, and 24.3 percent of the cocoons in these respective years. The effectiveness of these two species was markedly reduced by the hyperparasite *Perilampus hyalinus* which constituted 68.3, 52.1, and 53.9 percent of the nonsawfly emergents during these years. Hymenopterous parasites were of little significance in reducing sawfly populations. Among those most commonly reared were *Exenterus canadensis*, *Lamachus contortionis*, and *Olesicampe lophyri*. The effectiveness of the predators was not indicated.

In southern Illinois during 1947 and 1948, six species of parasites were reared from sawfly larvae. Parasitization averaged 42.2 percent during the first generation in 1947 and 40.5 percent among the 1947 emergents from the second-generation collections. Among the 1948 emergents from the 1947 second-generation group, parasitization averaged 28.1 percent. Parasitization determinations were not made during the third generation in 1947 or 1948.

[5] See footnote 4, p. 9.

337588 55 4

The dipterous parasite, *Spathimeigenia spinigera*, constituted 76.2 percent of the first-generation and 78.9 percent of the second-generation larval parasites during 1947. The dipteron *Phorocera hamata* constituted 13.3 percent of the first generation and 18.9 percent of the second-generation larval parasites. Hymenopterous parasites *Agrothereutes lophyri*, *Endasys subclavatus*, *Lamachus contortionis*, and *Olesicampe lophyri* were recovered during 1947. Hyperparasites *Dibrachys cavus*, *Melittobia acasta*, *Perilampus hyalinus* and *Trichopria* sp. were also collected but were of little significance.

In lower Michigan during 1948, among the eight parasitic species reared and collected, *Phorocera hamata* appeared to be the most important of the Diptera, and *Exenterus canadensis*, *E. diprioni*, and *Lamachus contortionis* the most important of the Hymenoptera. The hyperparasite *Perilampus hyalinus* was very common throughout 1948 and 1949.

EGG PARASITES

The egg parasite *Closterocerus cinctipennis* was one of the most significant biotic factors limiting sawfly populations on the Shawnee National Forest during 1947, 1948, and 1949. Its importance was initially revealed during prespray surveys conducted in shortleaf pine plantations in 1947 when, as a result of reduced larval hatch in the first generation, 1,900 acres of heavily infested plantations were omitted from a 6,000-acre spray program. Eggs collected on 4 of the 13 plantations where this reduced hatch occurred were heavily parasitized by *C. cinctipennis;* parasitization averaged 88.7 percent with a range of 70.3 to 93.1 percent: 4 of the 20 egg batches were 100 percent parasitized (table 4).

TABLE 4.—*Egg parasitization of the red-headed pine sawfly by Closterocerus cinctipennis in shortleaf pine plantations, Shawnee National Forest, Ill.*

Year and generation	Plantations examined	Egg batches collected	Eggs	Average parasitization
	Number	*Number*	*Number*	*Percent*
1947:				
1	4	20	4,154	88.7 ± 1.7
3	8	[1] 80	10,475	87.1 ± 1.5
1948:				
1	13	86	9,311	79.3 ± 2.8
2	4	7	804	80.6 ± 10.4
3	3	11	1,481	81.4 ± 6.7

[1] Includes 10 egg batches collected on jack pine plantations.

Egg parasitization during the second generation was not assessed owing to the urgency of experimental and commercial control activities. Third-generation sawfly activity in 1947 was markedly reduced when a high percentage of the second-generation larvae entered diapause. Third-generation adult emergence averaged only 5.6 percent on 7 shortleaf pine plantations sampled. Egg parasitization on 8 plantations examined throughout the forest averaged 87.1 percent and ranged from 58.5 to 99.7 percent; 25 of the 80 egg batches were 100 percent parasitized.

Sawfly populations were very low throughout the shortleaf pine plantations in 1948. Parasitization averaged 79.3 percent and ranged from 25.4 to 97.1 percent; 30 of the 86 egg batches examined were 100 percent parasitized and 3.8 percent of the eggs were destroyed by an unidentified predator.

Second-generation sawfly activity was observed on only four plantations in 1948. Parasitization averaged 80.6 percent. Destruction of 11.2 percent of the eggs by some unknown predator occurred and included many parasitized eggs.

In the third generation in 1948 parasitization averaged 81.4 percent. The unidentified predator accounted for an average of 16.5 percent of the eggs, increasing the total egg destruction to 97.9 percent.

Egg parasitization was not determined on the shortleaf pine plantations during early 1949 owing to the exceedingly low level of the sawfly population. Twenty-eight shortleaf pine plantations examined were practically free of sawfly activity. Ovipositing sawflies were observed on two plantations within the "pine hills" native shortleaf range. *Closterocerus* adults were seen ovipositing in the newly laid sawfly eggs.

In a pitch pine plantation in the Shawnee National Forest in 1947, second-generation egg parasitization was determined on 5 trees on 1 small isolated roadside planting containing approximately 40 heavily infested trees. Parasitization averaged 95.7 percent with a range of 91.1 to 99.4 percent: 72 of the 138 egg batches were 100 percent parasitized (table 5).

These five pitch pines were examined periodically for sawfly eggs during the remainder of 1947 and during 1948–49. Two egg batches collected after the third-generation flight in 1947 were 94.9 percent parasitized. Four of the five pines were oviposited on during the first-generation flight in 1948. Parasitization of the 9 batches averaged 88.5 percent. The single egg batch laid during the second-generation flight was 98.0 percent parasitized, and all 224 of the eggs laid during the second- and third-generation flights in 1949 were parasitized.

TABLE 5.—*Influence of egg parasite Closterocerus cinctipennis on red-headed pine sawfly population in roadside pitch pine plantation, Shawnee National Forest, Ill.*

Year and generation	Trees	Egg batches	Eggs	Average parasitization
	Number	*Number*	*Number*	*Percent*
1947:				
2	5	138	14, 178	95. 7
3	1	2	276	94. 9
1948:				
1	4	9	1, 280	88. 5
2	1	1	103	98. 0
1949:				
2–3	1	2	224	100. 0
Total	(1)	152	16, 061	95. 2

[1] Total number of trees examined, 5; for example, in 1947 second-generation sawfly eggs were observed on all 5 trees and third-generation sawfly eggs on 1 of the 5.

No attempt was made to determine sawfly or parasite egg fertility, larval or cocoon parasitism, or predator activity on this pitch pine plantation. In such a limited population more could be learned about the potentialities of the egg parasite if the sawfly infestation were allowed to progress with a minimum of disturbance. Egg parasitization determinations were delayed, therefore, until adult egg parasites had emerged and attacked the next generation of sawfly eggs. Third-generation sawfly eggs were collected in late fall after the sawfly hatch had taken place.

During the 2¾ years the sawfly population was under observation on the roadside pitch pine plantation, 152 egg batches containing 16,061 eggs were laid on 5 pines. Parasitization averaged 95.2 percent and reduced the sawfly potential to 771 eggs; the remaining 4.8 percent of the original population was accounted for by diapause and mortality factors. That severe defoliation did not result is evidence of the critical role of *Closterocerus cinctipennis* in controlling the sawfly population.

Closterocerus cinctipennis adults have been reared from red-headed pine sawfly eggs in the ranger districts of Park Falls in the Chequamegon National Forest in north-central Wisconsin and Cadillac in the Manistee National Forest in central Michigan.

A few specimens of an egg parasite in the genus *Tetrastichus* were reared from red-headed pine sawfly eggs in southern Illinois during 1947, 1948, and 1949. The significance of this species appeared negligible.

Introduced Parasites

Colonization of introduced parasites for control of the red-headed pine sawfly was started in Ontario in 1937 (*32*). Of the species released there during the next 9 years, only *Dahlbominus fuscipennis* has shown promise. The other species can be propagated successfully in the laboratory but their effectiveness in the field has not been evaluated. They include: *Aptesis basizonia* (Grav.), *A. subguttatus* (Grav.), *Exenterus abruptorius* (Thunb.), *Lamachus eques* (Htg.), *Lophyroplectus luteator* (Thunb.), and *Sturmia* sp.

Four attempts to establish the chalcid prepupal parasite *Dahlbominus fuscipennis* in populations of the sawfly in the United States have been made. In 1940, 300,000 adults were released in northern Alabama, and in 1941, 280,000 in western Tennessee on pine plantings along the Tennessee Valley Authority reservoir (Zimmerman).[5] During 1941, an unknown number of adult parasites were released on the Manistee National Forest. Nothing is known concerning the success of these liberations. The fourth attempt to establish *D. Fuscipennis* was made on the Manistee National Forest in 1946, when 100,000 adults were liberated in 7 red and jack pine plantations. Adults of this parasite were reared from cocoon collections in 1947; subsequent collections were negative.

Predators

Twelve species of predatory insects have been reported attacking the sawfly in eastern North America. Eight of these species were collected in the United States and two in Canada. Daviault[5] listed

[5] See footnote 4, p. 9.

two additional unidentified predators attacking the sawfly in Canada. No birds have been reported feeding on the sawfly larvae or adults. The importance of rodent predators has not been determined.

Diseases

Casual observations have been made by entomologists of large numbers of dead sawfly larvae hanging limp on their pine host. Unfortunately, the identity of the causal organism, the extent of the epizootic, and quantitative information concerning its effect on the sawfly population are in most instances not published.

Climatic Factors

Climatic factors play an important role in the population dynamics of insects. Temperature and moisture extremes often have been cited as responsible for the decline of outbreaks of many forest insects. Little information is available, however, concerning the influence of climatic factors on populations of the red-headed pine sawfly.

In unpublished records, Orr[5] reported heavy mortality among first-instar larvae apparently due to high temperatures on the Manistee National Forest in 1936, and also mortality among first- and second-instar larvae during driving rains. Unpublished records of MacAloney[5] mention extremely heavy larval mortality in a blizzard in late October 1938 during a sawfly outbreak in northern Michigan. This blizzard, with its accompanying low temperatures and deep snow, apparently reduced populations to an endemic status as "after the snow melted . . . literally millions of dead *Neodiprion lecontei* larvae were found under the trees."

Heavy mortality among first-instar larvae was observed in southern Illinois in 1947, when air temperatures remained above 100° F. for protracted periods. Mortality among migrating larvae occurred in Michigan in 1949 when sand-surface temperatures rose above 105°. Temperatures above this were common on clear days, and larval survival was less than 3 minutes under these conditions. Heavy egg mortality, possibly due to low temperatures, occurred in Michigan in 1949 when early June temperature fell to 18°. Third- and fourth-instar larvae survived temperatures as low as 22° in Illinois in 1947 and resumed feeding when the air temperatures again rose above 60°.

ECOLOGY

Investigations of most forest insects of economic importance are generally initiated during outbreaks or after serious economic losses have been sustained. Major emphasis is first on the curtailment of further losses through the application of insecticides or empirical cultural practices. Studies of the ecology of the pest may begin when the pressure of these activities has eased. Evaluation of low populations, possibly the key to prediction and successful avoidance of future outbreaks, is frequently deferred indefinitely or not undertaken.

[5] See footnote 4, p. 9.

Investigations of the red-headed pine sawfly were begun after the sawfly had been in outbreak for some time. Although major emphasis was initially on control, the ecology of the population on the Shawnee National Forest in Illinois was studied during the decline to an endemic status in 1947 and the endemic period in 1948 and 1949, and on the Manistee National Forest in Michigan during the 1948 outbreak and the endemic stage in 1949. National-forest areas heavily infested in northern Michigan, Minnesota, Missouri, and Wisconsin were visited to obtain a region-wide picture of the insect.

The ecology of the sawfly will be treated from two aspects: its behavior under high population or epidemic conditions, and its behavior under endemic conditions. Host-site preference will be examined and the influence of climatic factors on the sawfly discussed.

High Population Relationships

Infestation *vs.* Defoliation

Spraying on the Shawnee National Forest was initiated when 10 percent of the shortleaf pines in plantations averaging 6 feet and under and 20 percent in plantations averaging 7 feet and over were infested with sawflies. To test the validity of these economic levels and to determine the relationship between the intensity of infestation and severity of defoliation, the intensity of a single sawfly defoliation occurring during the third generation in 1946 in unsprayed shortleaf pine plantations was estimated in early 1947. Thirty-five plantations were examined at the rate of 4 plots containing 22 trees each per 40 acres. The height of each tree was estimated to the nearest foot and the defoliation estimated on a geometric progression basis. The defoliation classes used were percentages of 0, 1, 4, 7, 13, 25, 50, 75, 87, 93, 96, 99, and 100.[9]

The average height of each plantation was calculated and the plantations assigned to one of the following height classes: 2.0 to 3.9 feet, 4.0 to 6.9 feet, and 7.0 feet and over. The percentages of infestation and defoliation of the attacked trees were computed. Coefficient-of-correlation analysis indicated a linear relationship between the percent infestation and the percent defoliation in the first two classes. The data in the third class were too few for adequate statistical treatment.

---

[9] In estimating the percent defoliation, a tree was assigned first to a broad classification, that is, above or below 50 percent and next to its proper class through mental comparison with the next lower or higher defoliation category. The following example explains the procedure: Assume a tree 87 percent defoliated. It is obvious immediately that defoliation is in excess of 50 percent. The next decision places the tree between the 75- and 100-percent classes. The remaining decision is to judge how much greater the defoliation is than 75 percent; that is, whether the tree is closer to 87 percent than to 75 or 100 percent. This tree appears to fall approximately between the two categories and is assigned, therefore, to the 87-percent defoliation class. The same procedure is followed in assigning trees to classes below the 50-percent level. Naturally a small amount of indecision occurs in assigning trees to classes between the 87- and 99-percent and between the 13- and 1-percent categories when this method is first employed. After the initial period of introduction the writer and several associates have found estimates based on the geometric progression more consistent than with the more popular 10-percent interval system.

The infestation-defoliation relationship on the plantations in the 4.0- to 6.9-foot class was demonstrated by fitting a straight-line curve through the data by the coefficient-of-correlation method (fig. 12, *A*). At the 10-percent infestation level, there was a defoliation average of 29 percent, and at the 50- and 75-percent infestation levels, 48 to 59 percent defoliation. respectively. Slightly more severe defoliation occurred on the plantations in the smaller class (fig. 12, *B*). At the 10-percent infestation level 32 percent defoliation occurred and at the 50- and 75-percent levels 57 and 73 percent defoliation respectively. Because of shortleaf pine's remarkable ability to recover from severe defoliation, it was advisable to revise upward the 10-percent and 20-percent economic infestation levels in the shorter height classes.

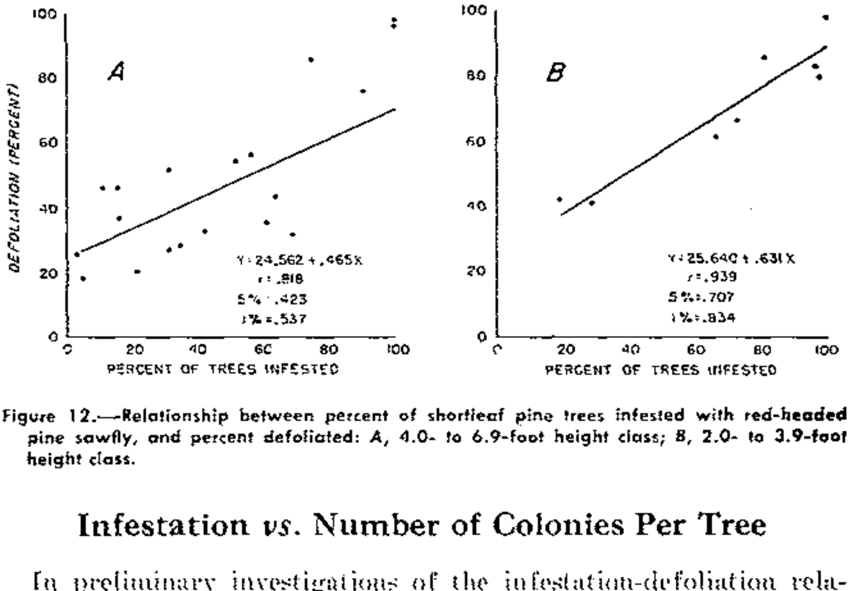


Figure 12.—Relationship between percent of shortleaf pine trees infested with red-headed pine sawfly, and percent defoliated: *A*, 4.0- to 6.9-foot height class; *B*, 2.0- to 3.9-foot height class.

Infestation *vs.* Number of Colonies Per Tree

In preliminary investigations of the infestation-defoliation relationship in jack pine plantations conducted on the Manistee National Forest in 1948, the number of colonies per infested tree was determined on a plantation block averaging 6 feet in height. Thirty plots containing 25 trees each were included in this study. The average number of colonies per infested tree increased as the percentage of infestation increased, as illustrated in figure 13.

In the 1- to 9-percent infestation class, 0.8 percent of the trees were infested with 2 colonies; no trees were attacked by more than 2 colonies. In the 20- to 29-percent infestation class, 3.6 percent of the trees contained 2 colonies, and 0.7 and 0.4 percent contained 3 and 4 colonies respectively. In the 60- to 69-percent infestation category, 20 percent of the trees were infested with 2 colonies, and 12.0, 8.0, 4.0, and 4.0 percent with 3, 4, 6, and 8 colonies respectively. What the maximum number of colonies per tree could become cannot be predicted from these limited data.

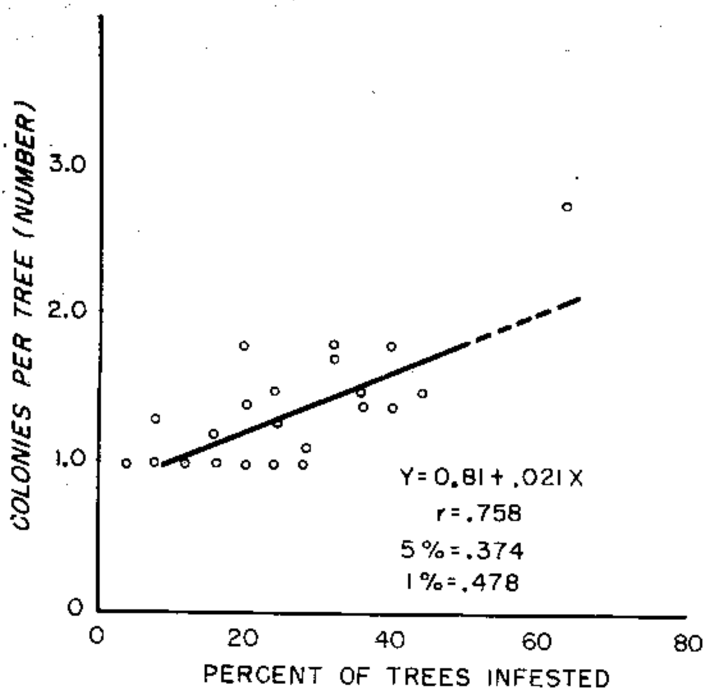


Figure 13.—Relationship between percent of jack pines infested with red-headed pine sawfly larvae and the average number of colonies per tree.

Number of Colonies Per Tree *vs.* Defoliation

Early in 1949 red-headed pine sawfly colonies were introduced on red and jack pine trees of different heights to resolve the problem of feeding intensities at various colony levels on the Manistee National Forest. Populations containing 1, 2, 4, and 8 second instar sawfly colonies were placed on 3 replicates of 1-, 2-, 4-, and 6-foot high trees. Daily observations were made of the rate and intensity of defoliation and the behavior of the larvae. Although disease caused high mortality during the latter part of these studies on the larger trees and markedly influenced the intensity of feeding, general feeding trends were evident on some of the plots.

Red Pine.—Plots for red pine defoliation studies were selected in sand-blow plantations representative of areas highly susceptible to sawfly attack in central Michigan. On the 1-foot tree plots 4 colonies per tree completely defoliated the red pines by the end of the 6th day, 2 colonies caused complete defoliation by the 11th day, and 1 colony by the 18th day (fig. 14, *A*). On the 2-foot red pine complete defoliation was accomplished by 4 and 2 colonies by the 16th and 22d days, respectively (fig. 14, *B*). One-colony defoliation reached the 50-percent level by the 25th day; apparently disease influenced the rate of larval feeding on this plot. Feeding was interrupted completely on the 4- and 6-foot red pine plots.

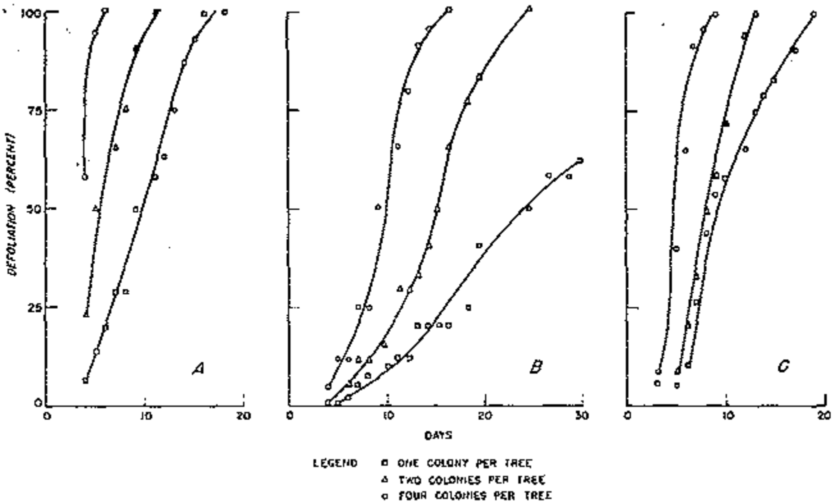


Figure 14.—Rate of defoliation by 1, 2, and 4 red-headed pine sawfly colonies: A, 1-foot red pine; B, 2-foot red pine; C, 1-foot pack pine.

In addition to defoliating the trees on which they were introduced, the larvae migrated to adjacent red pines, where they continued to feed. In the study area of 2-foot red pine, migrants from the 4-colony hosts established themselves on 14 trees; 2 trees were completely defoliated. One of 10 pines attacked by 2-colony migrants was 50 percent defoliated. In the study area of 1-foot red pine 29 pines were attacked by larval migrants from the three 4-colony host trees. Twelve were defoliated in excess of 50 percent, 8 were completely defoliated. Migrants from the 2-colony trees established themselves on 18 adjacent pines. Six of the pines were defoliated in excess of 50 percent, 2 being completely stripped. Migrants from the 1-colony red pines reached 5 nearby pines where they caused only minor injury.

Jack Pine.—The jack pine defoliation plots were located on sandblow areas representative of forest plantings most susceptible to sawfly attack (fig. 10, p. 19). Defoliation of the 1-foot jack pines was completed within an average of 19, 13, and 9 days by 1, 2, and 4 colonies of sawflies, respectively (fig. 14, *C*). Disease curtailed feeding on the remaining plots. Larval migrants from the 1-foot jack pines suffered rather high mortality after leaving their host pines owing to high sand-surface temperatures. Despite these losses larvae from the 4-colony trees established themselves on 21 nearby pines, where they caused defoliation in excess of 50 percent on 4 trees. Migrants from the 2-colony trees attacked 28 nearby pines; 2 of the pines sustained defoliation in excess of 50 percent and 3 were completely defoliated. One-colony migrants reached 23 nearby pines, completely defoliating 1 and severely defoliating 2 others.

These intensity data have practical application in predicting the rate of defoliation of forest plantations and the time limits within which control operations must be completed to avoid severe defoliation. For example, control applications must be completed within 10 days after larval hatch to prevent 50-percent defoliation of 1-foot red pines by 1-colony infestations per tree, and by the 5th day to prevent 50 percent defoliation by 2-colony infestations. To avoid complete stripping of 1-foot red pine, control must be applied before the 18th day after hatching on 1-colony infestations and by the 11th and 6th day on 2- and 4-colony infestations, respectively. On the 1-foot jack pine plantations, 50-percent defoliation would result by the 9th day on 1-colony infestations, by the 7th and 6th days from 2- and 4-colony attacks.

Site Preference

During the outbreaks on the Shawnee National Forest, areas supporting exceptionally high sawfly populations were kept under observation to gain an insight into the ecology of the sawfly. When shaded and open-growing pines were present in the same plantation, the former were preferred. When the latter were infested, most of the nearby shaded pines were also infested. When the sawfly population declined in 1947 and 1948, pines growing in the open were first to become free of sawflies. In areas of low populations, only pines growing in the shade of overtopping hardwoods were infested.

This is not in accord with the findings of Brown and Daviault (*7*) and Atwood and Peck (*2*), who reported infestations in only young pines growing in the open; nor is it in accord with the report that shaded-pine areas were relatively free from sawfly attack (MacAloney and Secrest *19*). Beal (*3*), however, reported 23 percent of open-growing shortleaf pines infested as compared to 53 percent overtopped pines infested with the sawfly.

To determine more accurately the trees or parts of trees most frequently attacked, the site of egg deposition was investigated. The presence of sawfly eggs is a better criterion of site selection than the presence of larvae because the latter may be absent as a result of egg parasitization. In shaded areas, oviposition did not follow a specific pattern; eggs were laid on needles on all parts of shortleaf pines. Under partial shade, however, eggs were concentrated in the most densely shaded needles. In endemic populations oviposition was restricted to shaded areas of plantations.

On open-growing shortleaf, sawfly eggs were concentrated in the dense needle clusters on the lower branches. Of 70 egg batches laid on 20 open-growing trees, during the second generation in 1947, 43 were laid on the south and east sides, 9 on the north side, 6 on the west, and the remaining 12 on the leader. With the exception of eggs laid on the leader, all were laid in the dense needle clusters on the underside of the lower branches. During the endemic period in 1948–49 eggs laid on pines in poor-survival areas were also concentrated in dense needle clusters on the lower branches (fig. 15).

It appears, therefore, that on the Shawnee National Forest the sawfly selected shaded pines and the most densely shaded parts of partially shaded or open-growing pines for oviposition. The attack on roadside and recreational-site pines was one of availability. Confronted with but one choice, the sawfly oviposited on whatever pine species was present and suitable.

Figure 15.—Poor survival of a shortleaf pine plantation that was highly susceptible to red-headed pine sawfly attack. Pine in foreground had large concentration of sawfly eggs on densely shaded needles on lower branches.

On the Manistee National Forest, large concentrations of sawfly larvae were observed on jack and red pine plantations overtopped by hardwoods. In addition, pines growing in poor-survival areas, on sand blows, and along the edges of closed plantations were severely infested. The infestation patterns and the severity of attack on the foregoing sites are discussed here separately.

Shaded Plantations. Defoliation resulting from the 1946–48 outbreak on the Manistee Ranger District was more severe on underplanted jack pine than on jack pine growing in the open. The infestation was more intense, both from the standpoint of number attacked and the degree of defoliation of individual trees. To evaluate the influence of hardwood cover on sawfly site selection, 25 one-tenth of an acre plots containing 1,159 trees were examined in an area of 560 acres of underplanted jack pine. The amount of shade was roughly estimated with ⅛ hardwood overstory closure categories, and the number of trees killed, the number partially defoliated but not killed in 1946 and 1947, and the uninjured were tallied.

Although a progressive increase in attack was evident as hardwood crown closure became more complete, the relationship was not statistically significant (coefficient of correlation $r = 0.698$, 1 percent = 0.917, 5 percent = 0.811). Possibly under less severe conditions, the relationship might have been more pronounced. On the area surveyed 88.3 percent of the trees examined had been attacked by the sawfly.

The accumulative 1946–48 sawfly infestation in an adjacent 80-acre understory jack pine plantation was determined after the completion of the 1948 defoliation. Nine plots of 26 trees each were examined along a 2-tree strip. The presence or absence of hardwood overstory was noted but no attempt was made to estimate the degree of overstory closure. In the shaded parts of the plantation 98.4 percent of the pines had been attacked: in the open, 75.7 percent. Among trees in the shade 74.8 percent had been completely defoliated and were dead: in the nonshaded areas only 22.5 percent had been killed. These differences were statistically significant. Sawfly activity was at low ebb on this plantation during 1949. A few sawfly colonies were found feeding on the surviving understory jack pines, where severe mortality had occurred; pines growing in the open were practically free of larvae.

Plantation Edges.—Defoliation of older jack pine plantations is often more severe along the edges than within these closed stands. This pattern occurred on national forests scattered throughout the Lake States. On these plantation edges the branches of jack pine extended to the ground, and the foliage of the trees was more dense than on trees growing within the closed stand. On the Cadillac Ranger District in 1948 and 1949, the majority of the sawfly eggs laid on border trees were on the protected needles well under the lower branches and near the ground.

Plantations With Associated Border Hardwoods.—Throughout the sawfly outbreak on the Cadillac Ranger District from 1946 to 1948 exceedingly heavy defoliation of jack pine occurred along the edges of plantations where the crowns of border hardwoods extended over the trees. The majority of the overtopped pines were completely stripped of their foliage. The relationship between hardwood presence and sawfly attack was studied along the south boundary of one jack pine plantation and the east boundary of two other plantations where residual hardwoods shaded the outer rows of jack pine. The distance of each jack pine tree from an established baseline was measured, and the percent of defoliation was estimated with the geometric-progression procedure previously outlined. Hardwood stems and crowns were located and plotted as crown projections. Sawfly defoliation was identified by evidence of previous bark feeding, remains of chewed needles and needle sheaths, and by the presence of large quantities of larval frass.

Pine mortality was closely associated with the hardwood crowns on the south and east boundaries of the study areas: the latter is illustrated in figure 16. The decrease in defoliation intensity that occurred as the distance from the south-boundary hardwood crowns increased is illustrated in figure 17. That this may have resulted from the presence of larger amounts of foliage on the pines growing in the open is questionable, in view of the striking decline in number of trees attacked as the distance from the hardwood crowns increased.

Plantations With Associated Internal Hardwoods.—The relationship between hardwoods and sawfly attack in the absence of the border influence was examined in three jack pine areas containing single overtopping hardwoods within plantations. Spacing of pines was 6 by 6 feet throughout, even under the residual hardwoods. The distances of each hardwood and of the pines from an established baseline were measured, the percent of defoliation of each pine estimated, and hardwood crown projection over the jack pine determined.

Figure 16.—Heavy red-headed pine sawfly infestation associated with shading by residual hardwoods of east border of jack pine plantation.

Trees directly beneath hardwood crowns, and in a band extending to the north were completely defoliated in every case (fig. 18). Again there was a decline in the number of trees attacked as the distance from the hardwood crown increased.

Plantations in Sand Blows and Poor Survival Areas. Severe sawfly attack also occurred in red and jack pine growing in sand blows and where survival was poor on the Cadillac Ranger District during 1946–48. It rarely extended beyond the first or second rows of pines growing in sodded or closed parts of stands (figs. 19, *A* and *B*, and 20). The majority of egg batches on pines in these areas were deposited on dense needle clusters on the lower branches. Initial invasion of new plantings by the sawfly occurred in sand blows.

Low Population Relationships

Areas ecologically favorable to the sawfly on the Shawnee and Manistee National Forests were examined periodically throughout the outbreaks to determine the status of the sawfly population. Practically every favorable site harbored reservoir populations long after the epidemic subsided. These persisting populations could conceivably be the loci of future outbreaks. Areas on the two forests will be discussed separately as they represent different geographic areas with different host species.

Shawnee National Forest

First to become free of sawfly activity when sawfly populations declined on the Shawnee National Forest in 1948 were open planta-

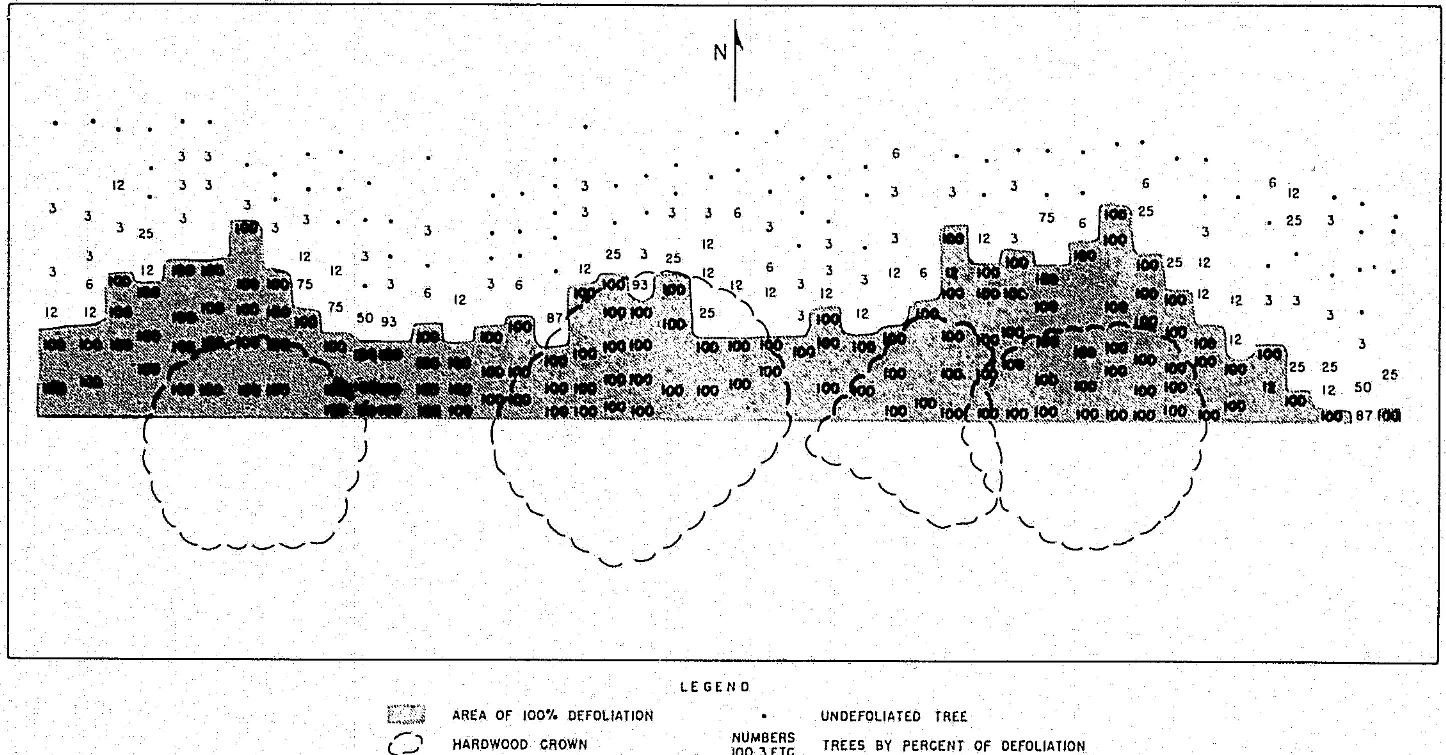


Figure 17.—Diagram of south edge of jack pine plantation, illustrating heavy red-headed pine sawfly attack in vicinity of hardwood crowns.

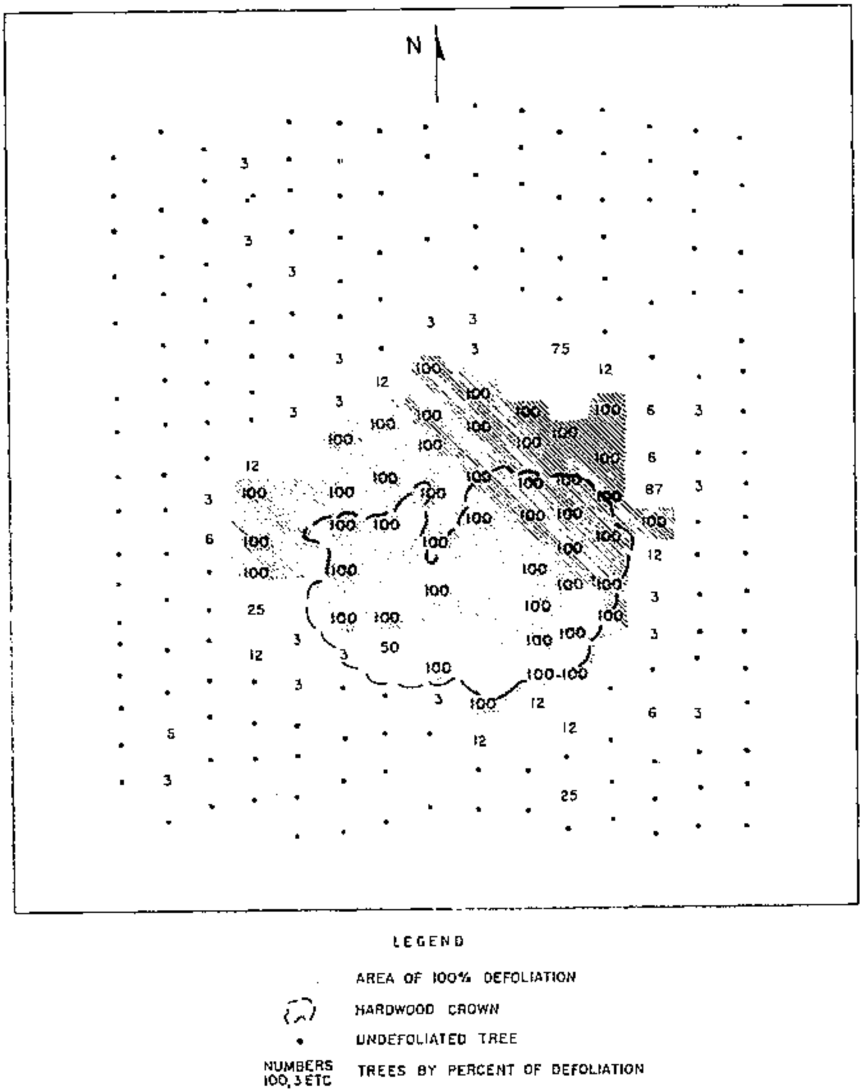


Figure 18.—Diagram of jack pine plantation, illustrating severe red-headed pine sawfly attack in vicinity of hardwood crown.

tions. Reservoir sawfly populations persisted in shortleaf pine plantations where sassafras and persimmon overtopped the pines and where hardwoods shaded plantation edges. No differences in egg parasitism between shaded and open plantations occurred which could account for the continued differential sawfly attack in the shaded areas. Defoliation in the shaded areas increased in the second generation in 1949, and in the third generation sawfly activity was markedly increased over the forest as a whole. Heaviest infestations were observed

Figure 19.—Sand-blow plantations severely defoliated by red-headed pine sawfly, Manistee National Forest, 1948: *A*, Jack pine; *B*, red pine

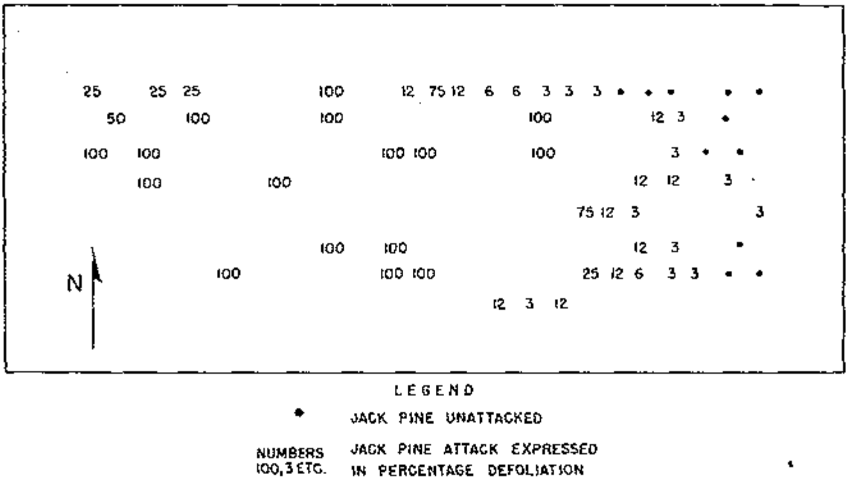


Figure 20.—Diagram of jack pine plantation, illustrating severity of red-headed pine sawfly attack in area of poor survival.

in the shaded areas; only scattered defoliation occurred in the open-growing plantations. Reservoir sawfly populations also persisted on the open, widely spaced, poor survival areas of shortleaf pine in 1948, and heavy defoliation of these lone trees occurred during the increased sawfly activity period in 1949.

Manistee National Forest

Small sawfly populations were present on all plantations on the Manistee Ranger District and on the shaded jack pine survivors of the 1946–48 outbreak. On the Cadillac Ranger District reservoir populations persisted on jack and red pine growing on the plantation edges, under hardwood shade, and in sand-blow areas. Open plantations and where the pine crowns had closed were practically free of sawflies. Volunteer pine seedlings established in areas where complete defoliation and mortality of jack pine had occurred were attacked by the sawfly during 1949 and 1950. On one area 7 of 34 volunteer seedlings and 6 of the jack pine survivors of the previous outbreak were attacked. Fourteen sawfly egg batches were present on the volunteer seedlings and 14 colonies on the original jack pine survivors in the vicinity of the hardwood crown. One of 10 volunteer seedlings in the shaded area between 2 east-border hardwoods was attacked.

Climatological Influences

The profound influence exerted by climatic factors on forest insect survival, distribution, and development is well recognized. Studies of the influence of climatic factors on the red-headed pine sawfly are few, however. With the exception of papers by Middleton (*21*) and Brown and Daviault (*7*), casual observations constitute the information available.

Temperature

Numerous workers have reported early emergence of sawflies from cocoons spun in sites exposed to maximal quantities of daily heat, and they report the early appearance of sawfly adults following abnormally mild springs. Daviault[7] recorded that the peak of abundance of adult emergence generally coincided with similar peaks on air-temperature curves, and that emergence was more rapid from cages well exposed to direct sunlight. A decrease in the number emerging and an increase in the time of emergence was observed as depth of cocooning increased. Females and males appeared in the morning as soon as the heat of day was felt, and practically all adults had emerged between 8 o'clock and noon.

Brown and Daviault (*7*) report that the red-headed pine sawfly had the highest theoretical threshold of development after hibernation in the cocoon of any of the 8 species of sawflies investigated in Canada. Females had a theoretical threshold of 49° F. and the males 47°, with thermal constants of 414 and 441 day degrees, respectively. Under field conditions, a 2.6-percent decrease in time was recorded for females and 2.0 percent for males.

The writer observed red-headed pine sawflies ovipositing at air temperatures as high as 106° F. and as low as 46°. Oviposition time—the time consumed in cutting the egg pocket in the needle, laying the egg, and moving to the next egg pocket site—varied according to temperature. At 90° it averaged 49 seconds per egg, and at 52° 143 seconds. Between 60° and 70°, oviposition averaged 90 seconds per egg.

Egg incubation time is closely associated with atmospheric temperature. Hatching occurs earlier during periods of high temperatures and is markedly delayed during periods of low temperatures. Middleton (*21*) reported egg incubation times of 21, 18, and 13 days at mean temperatures of 71.23° F., 74.59°, and 78.8°, respectively at East Falls Church, Va. Daviault[7] reported mean incubation periods of 25 days at 64°, and 23 days at 67° in Quebec, Canada. Egg incubation periods averaged 20, 15, and 24 days during the first-, second-, and third-generation activity periods in June, August, and September, respectively, on the Shawnee National Forest.

Larval feeding is retarded during cool, cloudy days and accelerated during warm days (*21*). The writer observed a decline in the feeding intensity when temperatures neared 100° F., and complete cessation below 55°.

The severe mortality among migrating larvae caused by high sand-surface temperatures has been discussed in a foregoing section. Larval survival was less than 3 minutes when sand temperatures above 105° F. were encountered. Sawfly larvae survived temperatures as low as 22° on several occasions on the Shawnee National Forest in 1947, and resumed feeding in the warmer parts of the day.

Moisture

Little is known concerning the influence of moisture on red-headed pine sawfly activity. Middleton (*21*), surmising that egg hatch was closely associated with humidity, mentioned that sawfly eggs hatched

---

[7] See footnote 4, p. 9.

in 21 days at an average relative humidity of 74 percent, in 18 days at 68 percent, and in 13 days at 65 percent. He added, however, that normal hatch was probably greatly influenced by a balance of the light and moisture with limits and optima existing. Brown and Daviault (7) observed greater sawfly survival in the cocoon stage between 40- and 45-percent relative humidity than between 90 and 95 percent. The threshold of development of female sawflies was 10.8° C. in the 90- to 95-percent relative humidity range and 9.5° in the 40- to 45-percent range. Male threshold temperatures were 9.4° and 8.4°, respectively.

Light

Sawfly emergence on the Manistee National Forest from 1946 through 1950 reached its peak during the first week of June, according to Forest Service personnel. Since oviposition generally begins soon after emergence and reaches its peak during this period, the shadow patterns cast by the hardwood crowns in the first week of June should closely coincide with the areas of severe infestation in the vicinity of the hardwoods if a valid shade-infestation relationship existed. In the absence of an "oviposition week" shadow pattern (the lateness of initiating field studies in 1948 and 1949 prevented the measurement of shadow patterns during the oviposition period) the shadow pattern cast during the week of July 10th, 19 days after the longest day of the year, was selected as most similar to that cast during the first week of June. The areas of heavy infestation coincided with the shadow patterns cast at 10:00 a. m., 12:00 m., and 2:00 p. m. (fig. 21): the 8:00 a. m. and 4:00 p. m. shadows were practically horizontal and therefore are not considered.

Although the sawfly selected shaded pines for oviposition and the densest needle clusters on the open-growing pines, the absence of light may not be designated as the only factor influencing egg site selection. Other physical factors commonly associated with decreased sunlight may also be acting. Differences in needle characteristics which conceivably influence site selection may occur under these conditions. Final needle selection or rejection was undoubtedly based primarily on needle characteristics.

Predicted Number of Generations Per Year

The available information concerning the number of generations per year of the sawfly has been superimposed on a map of eastern United States showing the average length of growing season, based on the average number of frost-free days per year (*18*, fig. 22). Predictions of the number of generations of the sawfly are based on average growing seasons, and deviations in number of generations can be expected during exceptionally long or short growing seasons.

INFLUENCE OF DEFOLIATION ON HOST

In northern United States and in Canada, jack and red pines succumb to a single, complete defoliation. Single branches generally die, although partially defoliated branches frequently survive if a few needles or living needle stubs remain. Among the southern

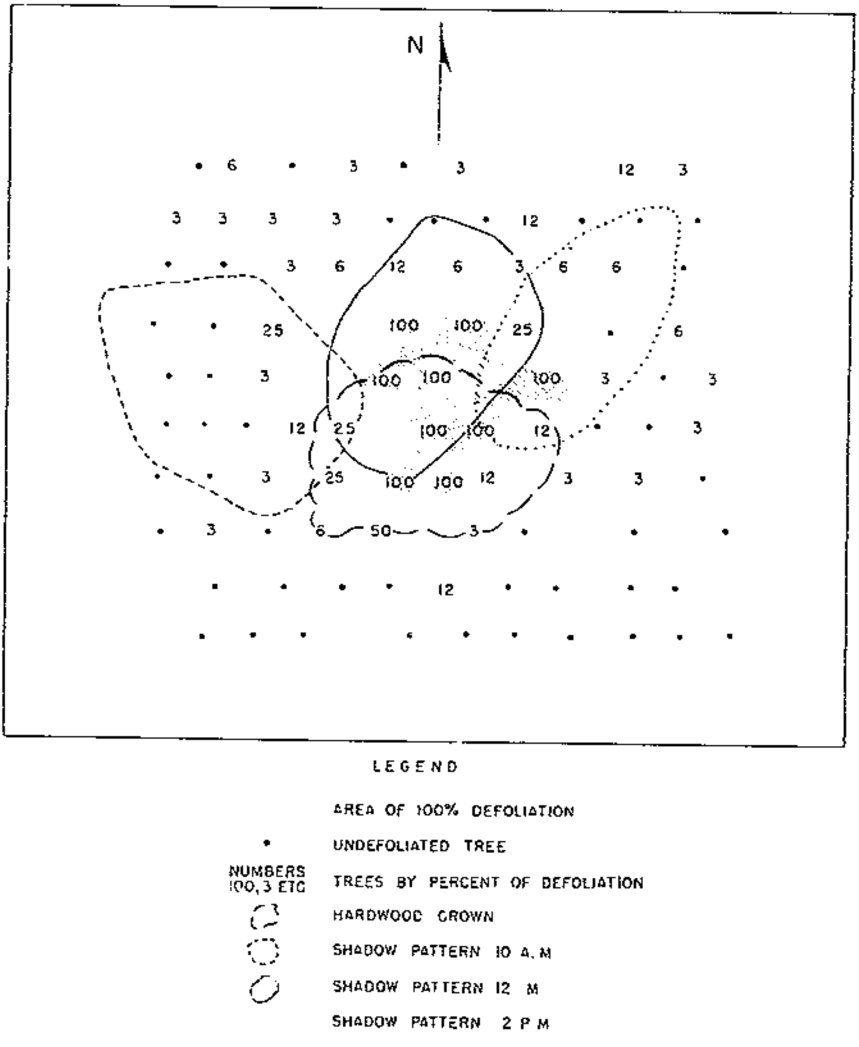


Figure 21.—Diagram of jack pine plantation illustrating relationship between hardwood shadow cast during red-headed pine sawfly oviposition period and heavy sawfly attack.

hard pines loblolly, longleaf, shortleaf, and slash pines often survive complete defoliation.

Beal (*3*) reported shortleaf and loblolly pines better able to withstand red-headed pine sawfly defoliation when growing in the open than when growing in competition with overtopping hardwoods. Mortality among open-growing trees resulted only when 75 percent or more of the foliage was destroyed; 84.2-percent mortality resulted when 76- to 100-percent defoliation occurred. Among trees growing in competition with overtopping hardwoods, 33.3 percent died when 26 to 50 percent of the foliage was destroyed, 55.0 percent died from

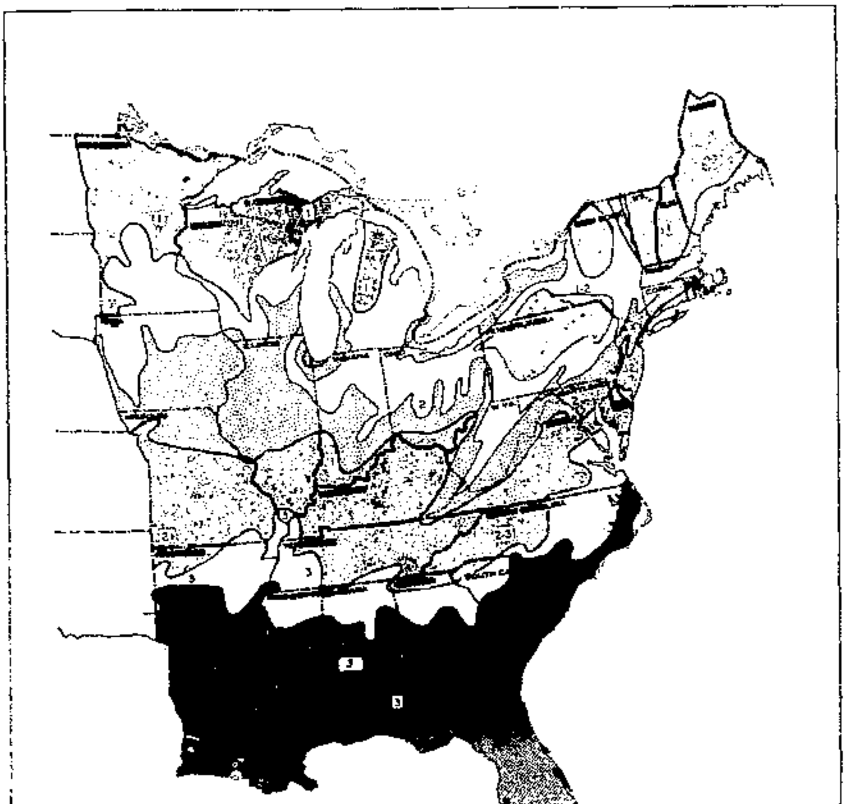


Figure 22.—Predicted number of generations per year of the red-headed pine sawfly, based on length of growing season.

51- to 75-percent defoliation, and 96.5 percent died when 76- to 100-percent defoliation occurred. Severe root competition and larval bark feeding were possible additional factors influencing survival.

The effects of defoliation on shortleaf pine survival on the Shawnee National Forest was evaluated on 125 trees sustaining varying degrees of sawfly feeding in 1947 in an open 6-year-old plantation. Tree heights were measured to the nearest foot and defoliation estimated. In November 1949 all trees were reexamined, tree vigor noted, and tree heights remeasured. Although the initial purpose was to determine shortleaf pine survival following defoliation of various intensities, the gross effects of partial and complete defoliation on radial increment were also demonstrable.

Host Survival and Vigor

Shortleaf pine mortality resulting from defoliation was negligible. Only 3 of 44 pines completely defoliated by third-generation larvae in 1946 died as a result of the attack. All trees partially to completely defoliated during the first- or second-generation period in 1947 survived and regained their former vigor (fig. 23). Height-growth expression of defoliation injury was masked by leader destruction by the Nantucket pine tip moth (*Rhyacionia frustrana* (Comst.)), during 1947 and 1948. Despite the combined sawfly and pine tip moth injury, height growth for the 3-year period averaged 4.3 feet on 41 trees completely stripped by third-generation larvae in 1946, 4.6 feet on 16 trees denuded during the first generation in 1947, and 3.3 feet on 20 trees completely defoliated by the second generation in 1947.

Radial Increment

The effects of partial and complete defoliation on radial increment were determined by equating the average annual radial increment of defoliated trees with that of comparable nondefoliated trees in the same plantations. Two pines from each defoliation category were cut 6 inches above the ground in November 1949 and the annual radial increment measured under a binocular microscope along 4 radial surfaces; average radial increment for all trees through 1946 was computed as a single average.

The effects of first-generation sawfly defoliation in 1947 were reflected in a reduction in annual increment in the year of injury and a rapid recovery during 1948 and 1949 (fig. 24, *A*). The reduction in annual radial increment associated with sawfly defoliation was approximately in the order of the severity of the injury: below 50-percent defoliation, reductions in annual increment were not detectible. When compared on an accumulative annual increment basis the temporary nature of the increment loss was revealed (fig. 24, *B*).

The effects of complete second-generation sawfly defoliation were determined by comparing the average annual radial increment of 4 pines completely stripped of their foliage during the second generation in 1947 with a like number of trees completely defoliated during the first generation. The late defoliation was reflected in a reduction in the following season's increment (fig. 24, *A*). The delayed effects of defoliation in the second generation resulted because most of the wood had been laid down prior to the initiation of defoliation in contrast to the former situation in which defoliation began prior to the completion of radial growth. The reduction in annual increment during the year following defoliation was minimized by an acceleration in radial growth during the second growing season which regained the previous losses (fig. 24, *B*).

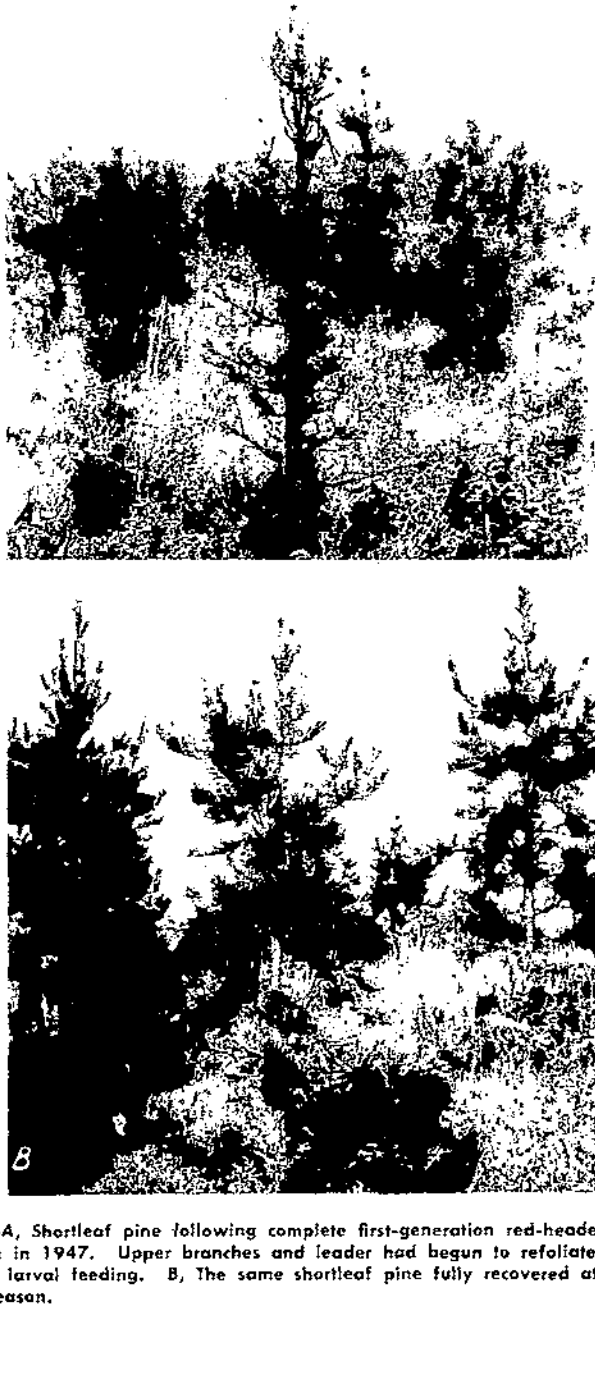


Figure 23.—A, Shortleaf pine following complete first-generation red-headed pine sawfly defoliation in 1947. Upper branches and leader had begun to refoliate prior to completion of larval feeding. B, The same shortleaf pine fully recovered at end of 1949 growing season.

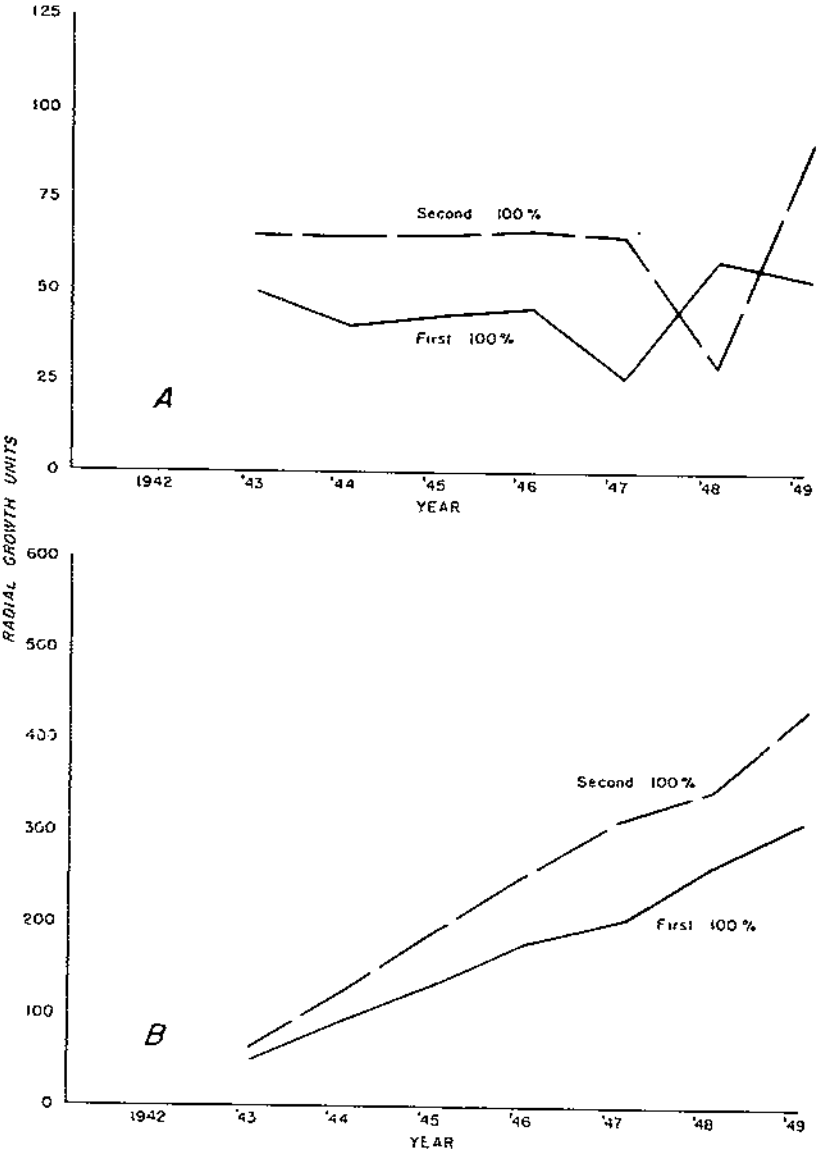


Figure 24.—Comparison of effects of complete first and second generation sawfly defoliation: A, On annual shortleaf pine increment; B, on accumulative annual shortleaf pine increment.

The effects of a single third-generation defoliation were not determined. However, in a plantation where complete third-generation defoliation was coupled with previous severe defoliation in 1946, 2 plots of 22 trees each were selected and a small square of phloem removed from the base of each tree on June 6, 1947, to wound the growing tissue so that subsequent growth could be identified. Five trees from each plot were cut in November 1949 for radial increment determinations.

Complete third-generation defoliation combined with the previous severe defoliation during 1946 resulted in a reduction in annual increment during 1946 followed by a greater reduction in increment in 1947. Recovery was rapid and the injured trees appeared to be regaining their losses by 1949.

POPULATION SURVEY METHODS

The development of reliable sampling methods for determining forest insect population levels is often difficult. The methods of approach differ from those used for evaluating agricultural insect populations. Particularly is this true when the large physical size of forest trees, the vast acreages involved, and the value of the crop are considered. In addition, forest insect surveys are complicated by variations in stand composition and density, and tree age and shape. The habits of the insect species and the facility with which its various life stages can be detected and examined influence the methods employed. Finally, the ultimate application of the insect population density information has a marked influence on the survey method selected. Control activities, for example, may require a survey method sufficiently rapid and thorough enough that examination of the infested forest area can be completed before economic injury has occurred.

SURVEY CRITERIA

Adult Stage

Adult sawflies have not proved satisfactory survey criteria. Although readily observed, the flight period is short and the peak of emergence seldom extends over more than a week. Following emergence the majority of each female's eggs are laid within 2 or 3 days. Timing considerations and the difficulty of obtaining an adequate supply of virgin females during the critical adult flight period practically rule out the use of virgin female baited traps in routine population determinations. Adult sawflies are not attracted to lights.

Egg Stage

Sawfly egg population estimates are theoretically the most reliable criterion of initial sawfly populations. Several obstacles preclude their use in routine surveys however. The size of the host tree influences somewhat the reliability of this stage as a useful criterion. For example, on trees less than 4 feet in height, egg counts have proved satisfactory, while on larger trees observation difficulties reduced the efficiency of estimating the population. The presence of a large egg parasite population practically precluded the use of sawfly eggs in precontrol surveys on the Shawnee National Forest. On the northern forests, widespread egg parasitism has not occurred and egg surveys have proved more reliable.

Larval Stage

The larval stage has proved the most reliable sawfly population criterion for control programs. Once larval hatch is complete, defoliation progresses at a rapid rate. Although drastic population reductions caused by extremes of weather, and predation and disease occur, the former are rather infrequent and the latter relatively uncommon.

On the Shawnee National Forest the first- and early second-instar larvae habitually feed well back in the sheltered, densely shaded parts of shortleaf pine. Their small size, combined with their secretive feeding habits, limits the use of these early instars. Second-instar larvae move onto exposed branches and leaders to continue feeding. The strawlike flags left as a result of their early needle-edge feeding habits (fig. 7, p. 15) are also useful criteria of sawfly presence.

On the northern forest areas, where complete defoliation results in mortality, surveys must begin early. Jack and red pines seldom produce dense foliage and the early larval instars are readily detected. Precontrol operation surveys can generally be undertaken as soon as larval hatch is completed.

Frass Collections

Frass collections have been used successfully in population investigations of several forest insects attacking large trees. Because the sawfly seldom attacks trees that are more than 12 feet to 15 feet in height, this criterion was not tested by the writer. It was more feasible to examine the tree for larvae. The principal value of frass collections was in the identification of larval feeding 2 or 3 years after injury.

Cocoon Stage

Time and space cocoon counts have been used successfully in evaluating spruce, pine, and larch sawfly populations. Unfortunately, the cocoons of the red-headed pine sawfly are often difficult to collect. The last instar larvae migrate considerable distances before spinning their cocoons, presenting such a wide distribution that it is impractical to search for them. On sandy soils where a large quantity of surface debris (twigs and sticks) exists, cocoons can be found with little difficulty; in loamy soil, cocoon search is futile.

Injured Host Tree

Current and past sawfly defoliation are excellent survey criteria. Current injury, in the form of denuded branches or early instar feeding flags, can be used where time limitations do not require immediate completion of a survey. Previous season's sawfly defoliation can be employed when it is necessary to predict control needs several months in advance.

Ecologically Favorable Sites

Periodic examination of plantation sites ecologically favorable to the sawfly will reveal the relative population status and indicate increases or decreases in the population. The criterion employed may be the condition of the host tree or any of the active insect stages.

POPULATION SURVEY PROCEDURES

The intensity of the survey, or the acreage of the infested area to be examined, is based upon several factors. Of prime importance are the overall acreages known or suspected to be infested, the severity of the outbreak, the time available, and the manpower that can be devoted to the project. The purpose of the survey, i. e., whether the information is to be used in formulating plans for control activities or for studies of population trends, will also influence the intensity of the survey and the type of information to be collected. The selection of the survey criterion will depend, in addition, upon the stage of the insect or host condition available.

The following survey procedure has proved practicable for estimating population levels to determine the need for applying control measures against the red-headed pine sawfly: A one-half percent cruise is made of the infested plantations, taking a series of 10, 1/50-acre two-tree row plots, each 1 chain long, per 40 acres examined. These plots may be examined along a single line or along a series of offsets arranged as staggered steps through the plantation. In poor survival areas, 22 trees may be substituted for the 1/50-acre plots. The following information should be collected together with a plantation map of the area:

1. Location of plantation, township, range, section, subsection, ownership.
2. Date of survey.
3. Survey party.
4. Percent cruise, plot location, and procedure followed.
5. Rough sketch of plantation block indicating parts examined and infested area.
6. Average plantation height.
7. Species of pine examined.
8. Entomological information.
   a. Number of infested and noninfested trees (current and past) per plot by species.
   b. Stage of insect pest—instars, etc.
   c. Estimate of previous and current injury.
9. Outstanding topographic features—rivers, lakes, hills, and also telephone lines.
10. Estimated overstory.
    a. Height.
    b. Species.
    c. Sky cover estimates.
11. Soil type and ground cover.
12. Recommendation for method of control: aerial or ground equipment.

The plantation sequences to be followed should be left to the discretion of the survey leader. In general, the youngest, most heavily infested areas, and areas of high aesthetic value should be examined early. Plantations of the preferred host growing in ecologically favorable sites should be high on the examination list.

ECONOMICS OF RED-HEADED PINE SAWFLY CONTROL

The ultimate decision concerning the initiation of artificial control measures to reduce insect populations must be based on sound economic and entomological considerations. This obviously requires close cooperation of the forester and the forest entomologist. Briefly, an estimate of population suppression expenditures must be compared with the predicted losses that would result if control measures were not applied. It should be emphasized, however, that it is not generally entomologically sound to attempt eradication of widespread native forest defoliators. Also, it is not sound to attempt further population reductions under endemic conditions. Artifical control applications should be considered temporary measures designed to bring the trees through a particularly susceptible stage of their rotation.

The determination of economic sawfly population levels at which artifical control measures must be initiated is difficult. During the 1947 sawfly outbreak on the Shawnee National Forest 10-percent infestation levels in shortleaf pine plantations averaging 6 feet in height and less, and 20 percent in shortleaf pine plantations averaging more than 7 feet in height were arbitrarily selected. Subsequent studies revealed shortleaf pine able to survive severe defoliation with relatively low permanent increment losses. Control applications are, therefore, delayed through at least one defoliation period. The need for control activities on recreational areas is left to the discretion of the forest official.

Because both jack and red pine are extremely susceptible to defoliation injury, controls should be applied when outbreak sawfly populations are found. The 10- and 20-percent economic damage levels previously cited for shortleaf pine are being used on the pine plantations in the Lake States and are recommended for the North Central States hard pine areas.

CONTROL PRACTICES

Control of the sawfly may be accomplished easiest by destroying the larval stage during the feeding period. Attempts to destroy the adult, egg, or cocoon stages will probably be unsuccessful, both from the standpoint of actual population reduction accomplished as well as from the economic standpoint. Most successful larval kills obtained during routine control programs on national-forest plantations have been accomplished by delaying spraying until the majority of the larvae have passed the second instar and moved to exposed feeding sites.

INSECTICIDES

Satisfactory control of the sawfly has been reported for practically every stomach poison tested against the larvae. Among the more recently developed organic insecticides, DDT is the most economical and good kills have been obtained with most formulations. The equipment employed will dictate the formulation and dosage to be applied. Equipment limitations and recommendations for specific operations are discussed in the following section.

For aerial applications a solution containing 1 pound of technical grade DDT dissolved in an auxiliary solvent and diluted to make 1 gallon of insecticide, should be applied at the rate of 1 gallon per acre. This application rate is also recommended for truck-mounted mist blowers. Oil solutions containing 3 percent DDT have given good results when dispensed with knapsack sprayers equipped with mist-producing nozzles (2.5 gallons per *hour* capacity) at the rate of approximately 1 gallon per acre. Care must be exercised to avoid overdosing since foliage burning is possible when oil solutions are used. By allowing the insecticide mist to drift through the pine foliage, sufficient insecticide is applied to kill the larvae. For garden- or orchard-type knapsack sprayers, 3 percent water suspension of wettable DDT powder or 3 percent water emulsions should be substituted for the oil solutions. When applied at the rate of 20 to 25 gallons of insecticide per acre, good kills have resulted.

CAUTION.—DDT is poisonous. Store in plainly labeled containers away from all food products.

Recommendations for insecticides and various types of equipment for use on ornamentals, small plantations, and nursery rows are outlined by Schaffner (*28*).

EQUIPMENT

The size of the infested area, the period during which the insect is susceptible to insecticides, and the physical characteristics of the area, such as the amount of hardwood overstory, accessibility, and shape will largely dictate the choice of equipment. For aerial applications to be economically feasible, the control program should include at least 500 acres. Individual areas less than approximately 20 acres should not be treated from the air and it is doubtful whether satisfactory kills can be obtained in plantations growing under greater than 50-percent hardwood canopy cover. Control applications from the ground, using hand equipment, will be governed by the total acreage infested, the accessibility of the area, and the size of the infested trees.

SUMMARY OF CONTROL COSTS

The cost of applying control measures on national forests throughout the north central region has varied considerably. This is to be expected since the total size of the program and the size and distribution of the individual forest plantations materially affect the efficiency of the operation. For control jobs of 500 acres or over, the average cost per acre treated with oil solutions of DDT by airplane is $1.75 to $2.00, by mist blower $1.50 to $2.50, and by hand, $2.50 to $5.00.

SILVICULTURAL CONTROL

The avoidance of sawfly defoliation injury through sound silvicultural practices and planting methods lies primarily in the selection of situations ecologically unfavorable to the sawfly. In many instances, this is not always possible. Sand-blow areas and partially shaded sites ultimately will be planted. Often these sites may be unfavorable to substitute pine species comparatively resistant to sawfly attack. Under these conditions, artificial control measures may have to be applied to bring these plantations through their most hazardous period. When areas highly susceptible to sawfly attack are planted, they should be kept under surveillance and control undertaken if economic sawfly populations develop.

To reduce the risk of red-headed pine sawfly attack, the following recommendations are presented.

1. South Central States.
   a. Avoid planting hard pines under hardwoods.
   b. Avoid planting hard pines within approximately 25 feet of all hardwood borders, or remove or girdle residual hardwoods.
   c. Undertake early release of hard pine plantations from hardwood overstory.
   d. Replant areas of poor survival to prevent widely spaced, open plantations.
   e. Promote early closing of plantations by planting at no greater than 6- by 6-feet spacing.
   f. Maintain surveillance over susceptible plantings.
2. North Central States.
   a. Avoid planting hard pines under hardwood overstories, particularly with jack pine plantings.
   b. Avoid planting hard pines within approximately 25 feet of hardwood borders or residual hardwood crowns. Remove or girdle residual hardwoods prior to planting hard pines.
   c. Replant areas of poor survival to prevent development of widely spaced open plantations.
   d. Substitute red pine for jack pine wherever possible.
   e. Maintain surveillance over susceptible plantings.

SUMMARY

Biological and ecological studies of the red-headed pine sawfly (*Neodiprion lecontei* (Fitch)) and its control through the application of DDT sprays from aircraft were undertaken as a cooperative project by the former Bureau of Entomology and Plant Quarantine, the Forest Service, and the University of Minnesota. These studies were conducted on the Shawnee National Forest in southern Illinois during 1947, 1948, and 1949, and on the Manistee National Forest in central Michigan in 1948 and 1949. Sawfly infestations on national forests in Michigan, Minnestota, Missouri, and Wisconsin were also examined.

This sawfly is one of the most important native forest insects defoliating young hard pines in eastern North America. Since its description by Fitch in 1858, it has been reported from practically every State east of the tier of States bounding the west banks of the Mississippi River from Jasper County, Tex., and Manatee County, Fla., to Kindiogami Lake, Ontario, and Albanal, Quebec.

Outbreaks of sawfly from 1922 through 1953 occurred in Alabama, Massachusetts, Michigan, New York, Ohio, and Tennessee during the 1930's, and in Illinois, Michigan, New York, and Wisconsin during the 1940's.

Nine native hard pines and seven introduced species are hosts of the sawfly. In addition, migrating larvae attack two species of white pine, tamarack, deodar cedar, and Norway spruce. In the Lake States the sawfly prefers jack pine; red, Scotch, Austrian, and Swiss mountain pines are also attacked but less frequently. In the southern part of the United States, shortleaf pine is preferred; south of the range of shortleaf pine, loblolly, longleaf, and slash pines are infested. In the northeastern part of the United States and Canada, red pine is preferred. In all regions the available species of hard pine is attacked in the absence of the preferred host.

The sawfly overwinters as a prepupa in a cocoon spun in the soil. In the spring, pupation occurs and emergence of the adults, mating, and oviposition soon follow. Females lay an average of 102 to 141 eggs per batch in a series of shoe-shaped pockets cut in the pine needle. The number of eggs per needle varies from an average of 5.6 eggs on Virginia pine to 12.2 eggs on red pine. Practically the entire complement of eggs is laid; an average of from 2 to 3 eggs remains following the completion of oviposition.

The progeny of each female sawfly feed as a gregarious colony throughout the larval period. Newly hatched larvae chew cup-shaped notches in the needles in which the oviposition occurs. In the second instar, they feed on the mesodermal parts of the pine needles, leaving the central vascular tissue as strawlike flags. In the third instar, they feed on the leader and branch tip needles. Defoliation progresses from the top of the tree toward the base. Larvae readily leave completely defoliated hard pines and migrate up to 19 feet across bare sand to establish themselves on nearby pines where they often cause severe defoliation. Heavy mortality among migrating larvae occurs when they encounter soil-surface temperatures above 105° F. Migration across sodded areas is more successful than across sand.

From 3 to 5 generations of the sawfly per year have been reported in southern United States, 2 to 3 generations per year in the mid-central areas, and 1 generation per year in the northern sections and in Canada. Diapause up to 5 years duration has been reported.

Fifty-eight species of parasites and predators attack the sawfly. Twenty were exclusively in the United States, 23 exclusively in Canada, and 15 in both the United States and Canada. The egg parasite (*Closterocerus cinctipennis*) was a prime factor in reducing the sawfly population on the Shawnee National Forest in 1947 and 1948. The most important larval parasites were *Spathimeigenia spinigera* and *Phorocera hamata*.

On the Shawnee National Forest a linear relationship exists between the number of trees infested and the severity of defoliation of the attacked trees. On shortleaf pine plantations ranging from 4.0 to 6.9 feet in height defoliation injury increased from 29 percent at the 10-percent infestation level to 59 percent at the 75-percent infestation level. On plantations ranging from 2.0 to 3.9 feet, 32-percent defoliation was sustained at the 10-percent infestation level and 73-percent defoliation at the 75-percent infestation level.

On the Manistee National Forest a relationship between the intensity of the infestation and the number of sawfly colonies per jack pine tree exists. As the percentage infestation increased greater numbers of trees suffered multiple attack.

Studies of the rate of defoliation by 1, 2, 4, and 8 colonies per tree for 4 height classes of jack and red pine were undertaken. Although disease killed many of the larvae before defoliation was complete on some plots, general trends indicated the influence of time and population concentration limitations. Migration habits of the sawfly were studied.

On the Shawnee National Forest defoliation was more severe and the number of trees attacked greater in the shaded areas than in the open areas. Oviposition by female sawflies was concentrated on pines in the shaded parts of the plantations and on the shaded parts of open-growing pines. The same situation existed on the Manistee National Forest. Heavy attacks were also common on (1) the edges of pine plantations shaded by bordering hardwoods, (2) pine plantations shaded by single residual hardwoods within the stand, (3) sand-blow plantations, and (4) nonclosed, poor-survival plantations. In most instances, sawfly egg concentrations were observed in the shaded parts of the pines. A survey of a 560-acre jack pine plantation suggested a linear relationship between the amount of hardwood cover and the number of trees attacked by the sawfly.

On the Shawnee National Forest, reservoir populations persisted on the shaded pines and on poor-survival areas during the endemic phase of the sawfly gradation. On the Manistee National Forest reservoir populations were also surviving on the shaded pines and on the sand-blow and poor-survival areas. In several instances, reproduction coming in under hardwoods shading previously killed jack pine was heavily attacked by the sawfly.

Of the meteorological factors affecting the sawfly, light was of prime importance in determining the oviposition site. Shadow patterns of single hardwoods cast during the oviposition period between 10:00 a. m., 12:00 m., and 2:00 p. m. showed a close agreement with severe sawfly attack. The length of growing season is closely correlated with the number of generations per year of the sawfly in the United States.

In the northern part of the United States and Canada, jack and red pines succumbed to a single complete defoliation. Single branches normally died when they were completely stripped of their foliage. Incompletely defoliated branches frequently survived when a few needles or partially consumed needles remained.

Shortleaf pines survived complete defoliation by first- and second-generation sawfly feeding on the Shawnee National Forest. Only 7 percent of the trees succumbed following complete third-generation sawfly defoliation (1946) coupled with possible previous severe attack.

Height growth was good on all trees despite leader injury resulting from Nantucket pine tip moth infestations that masked differences in height growth caused by sawfly defoliation. First-generation defoliation effects below 50 percent were not evident. Defoliation of 50 to 100 percent caused increasingly greater immediate reduction in annual increment. These losses were temporary and the trees recovered their losses with an increased annual increment the following 2 years. Complete second-generation defoliation did not result in immediate radial increment reduction as the pines had about completed their growth by the time defoliation occurred. Defoliation injury was reflected in a reduced annual increment the next year. The increment loss was regained during the second year following defoliation. Complete third generation preceded by previous severe defoliation was reflected in a decreased annual increment the following year. Increased increment the next 2 years compensated for the losses.

Among the several criteria available for population surveys, the adult, egg, and cocoon stages are not recommended. The larval stages and the presence or absence of host injury show the most promise.

Control of the red-headed pine sawfly larvae is readily accomplished using either ground or aerial equipment to dispense insecticides. DDT is the most practical insecticide to use. For aerial applications, oil solutions containing 1 pound of DDT per gallon and applied at the rate of 1 gallon per acre have been satisfactory. Three percent DDT solutions are recommended for use with hand equipment. A summary of application costs for the past 4 seasons indicates that current aerial applications ranged from $1.75 to $2.00 per acre and ground applications from $2.50 to $5.00 per acre depending upon the acreages involved.

The possibility of reducing red-headed pine sawfly populations through silvicultural practices is discussed. Planting of susceptible pines on sites ecologically favorable to sawfly attack should be avoided. If these species must be planted on these areas, it is recommended that they be kept under surveillance for evidence of injury.

LITERATURE CITED

(1) ALDRICH, J. M.
1931. NORTH AMERICAN TWO-WINGED FLIES OF THE GENUS *Spathimeigenia* WITH DESCRIPTIONS OF FIVE NEW SPECIES. U. S. Natl. Mus. Proc. 80 (11): 1-10.

(2) ATWOOD, C. E., AND PECK, O.
1943. SOME NATIVE SAWFLIES OF THE GENUS *Neodiprion* ATTACKING PINES IN EASTERN CANADA. Canad. Jour. Res. Sect. D, Zool. Sci. 21: 109-144, illus.

(3) BEAL, J. A.
1942. MORTALITY OF REPRODUCTION DEFOLIATED BY THE RED-HEADED PINE SAWFLY (*Neodiprion lecontei* FITCH). Jour. Forestry 40: 562-563.

(4) BENTLEY, G. M.
1940. INSECT PEST SURVEY. U. S. Dept. Agr., Bur. Ent. & Plant Quar. 20: 191.

(5) BOYD, W. M.
1945. INJURIOUS INSECTS OF NEW JERSEY NURSERIES. N. J. Dept. Agr. Cir. 355: 65-66, illus.

(6) Britton, W. E., and Zappe, M. P.
1927. some insect pests of nursery stock in connecticut. Conn. Agr. Expt. Sta. Bul. 292: 161.
(7) Brown, A. W. A., and Daviault, L.
1942. a comparative study of the influence of temperature on the development of certain sawflies after hibernation in the cocoon. Sci. Agr. 22: 298–306, illus.
(8) Champlain, A. B.
1922. records of hymenopterous parasites in pennsylvania. Psyche 29: 95–100.
(9) Cushman, R. A.
1940. a review of the parasitic wasps of the ichneumonid genus *Exenterus* hartig. U. S. Dept. Agr. Mis. Pub. 354: 4, illus.
(10) Dalla Torre, C. O. de
1894. catalogue hymenopterum. vol. 1. tenthredinidae including uroceridae. p. 295.
(11) Daviault, L.
1942. l'organization et les travaux du laboratoire d'entomologie forestiere de berthierville. Foret Quebecoise 4: 387–406, illus.
(12) ———
1947. le tenthrede de leconte (*N. lecontei*). Foret Quebecoise 12: 573–575, illus.
(13) Eyre, F. H., and Zehngraff, P.
1948. red pine management in minnesota. U. S. Dept. Agr. Cir. 778, 70 pp., illus.
(14) Fitch, Asa.
1858. leconte's saw-fly, *Lophyrus lecontei* new species. Insects of New York. 4th Rpt. pp. 58–59.
(15) Greene, C. T.
1921. dipterous parasites of sawflies. Ent. Soc. Wash. Proc. 23: 41–43.
(16) Hodson, A. C., and Christensen, C. H.
1945. minnesota forest insect and disease survey for 1944–1945. Minn. Agr. Expt. Sta. Sci. Jour. Ser. Paper 2296: 1–4.
(17) Hutchings, C. B.
1926. the shade tree insects of eastern canada for the year 1925, with remarks on their activities and prevalence. Quebec Soc. Protect. Plants Ann. Rpt. 1925–26: 112–117.
(18) Kincer, J. B.
1941. climate and weather data for the united states. U. S. Dept. Agr. Yearbook 1941: 658–747, illus.
(19) MacAloney, H. J. and Secrest, H. C.
1944. the more common insects attacking young coniferous plantations and natural stands on the national forests in the lake states and suggestions for preventing or controlling injury. U. S. Dept. Agri. Bur. Ent. & Plant Quar., Forest Insect Invest., Milwaukee, Wis. 15 pp. [Processed.]
(20) McDaniel, E. I.
1938. some chewing insects infesting michigan evergreens. Mich. Agr. Expt. Sta. Cir. Bul. 141: 48–49.
(21) Middleton, W.
1921. leconte's sawfly (*Neodiprion lecontei* fitch) an enemy of young pines. Jour. Agr. Res. 20: 741–760, illus.
(22) Muesebeck, C. F. W., et al.
1951. hymenoptera of america north of mexico. synoptic catalog. U. S. Dept. Agr., Agr. Monog. 2. 12–89.
(23) Polivka, J. B.
1938. forest insect survey. Ohio Agr. Expt. Sta. Bul. 592: 129–130.
(24) Rohwer, S. A.
1915. the mating habits of some sawflies. Ent. Soc. Wash. Proc. 17: 196–198.
(25) ———
1915. descriptions of new species of hymenoptera. U. S. Natl. Mus. Proc. 49: 205–249.

(26) ROHWER, S. A.
1918. NEW SAWFLIES OF THE SUBFAMILY DIPRIONIDAE. Ent. Soc. Wash. Proc. 20: 79–90.
(27) SCHAFFNER, J. V.
1943. SAWFLIES INJURIOUS TO CONIFERS IN THE NORTHEASTERN STATES. Jour. Forestry 41: 580–588, illus.
(28) ———
1951. THE REDHEADED PINE SAWFLY. U. S. Dept. Agr. Leaflet 296, 4 pp. illus.
(29) SELLERS, W. F.
1940. *Exenterus marginatorius* AS A PARASITE OF PINE SAWFLIES. U. S. Dept. Agr. Bur. Ent. & Plant Quar. News Letter. 7 (11): 12. [Processed.]
(30) TOWNES, H. K., JR.
1944. A CATALOGUE AND RECLASSIFICATION OF THE NEARTIC *Ichneumonidae*. Amer. Ent. Soc. Mem. 2 (1): 799.
(31) WALLEY, G. S.
1933. NEW AND LITTLE KNOWN CANADIAN PARASITIC HYMENOPTERA (ICHNEUMONOIDAE). Canad. Ent. 65: 253–261.
(32) WILKES, A.
1947. CONTROL OF FOREST INSECTS IN THE PROVINCE OF ONTARIO BY INTRODUCTION OF INSECT PARASITES. LECONTE'S SAWFLY. *Neodiprion lecontei* (FITCH). Canad. Dept. Agr. Ent. Branch, Parasite Invest. Unit, Ottawa. 83 pp., illus.
(33) WILL, H. C.
1944. NOTES AND NEWS ON SAWFLY LARVAE IN PENNSYLVANIA. Pa. Acad. Sci. Proc. 18: 48–49.
(34) WEST, A. S.
1952. NOTES ON LECONTE'S SAWFLY. Canad. Ent. 84: 59–61, illus.

U. S. GOVERNMENT PRINTING OFFICE, 1955

For sale by the Superintendent of Documents, U. S. Government Printing Office
Washington 25, D. C. - Price 20 cents

END