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IMPACT OF THE REDHEADED PINE SAWFLY (HYMENOPTERA: DIPRIONIDAE) ON YOUNG RED PINE PLANTATIONS

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ABSTRACT

The ecology of the redheaded pine sawfly was studied relative to its impact on red pine plantations. An ecological model, which formed the basis for socioeconomic analysis, was constructed. Because the sawfly prefers trees under moisture stress, damage is most severe in stands growing on sand blows, where there is competition for moisture from bracken fern and hardwoods, and where soils are too moist, too shallow, or too compacted. Outbreaks also appear to be related to dry years. The sawfly has a variable impact on multiple-use values. Because it injures the least productive trees in a stand, timber is only indirectly affected. Small openings created by tree mortality after an outbreak may provide edge wildlife habitat. The sawfly has both negative and positive effects on recreationists, depending upon the type of recreation; it may be a nuisance to campers, but may positively influence hunting. Preventive sawfly management involves proper site selection for red pine.

The redheaded pine sawfly, *Neodiprion lecontei* (Fitch), is an important defoliator of young hard pines in eastern North America (Benjamin 1955). On National Forest lands it has been the third most important target insect for suppression, and over 25,500 ha (63,000 acres) of pine have been treated for the sawfly in the Eastern Region in the last 50 years. Additionally, this sawfly has been suppressed on many thousands of acres of pine on state-owned and private lands. It is particularly injurious to red pine, *Pinus resinosa* Ait., and jack pine, *P. banksiana* Lamb., in the Northeast, but it also feeds on Scots pine, *P. sylvestris* L., Austrian pine, *P. nigra* Arn., and other species of pines planted in the vicinity of the primary hosts. This sawfly, which usually occurs in colonies of more than 100 larvae, is a voracious feeder that readily strips small (1–5 m) trees of part or all of their foliage. Numerous young trees may be deformed or killed during an outbreak. Severe outbreaks did not occur until after the advent of the widespread reforestation projects in the early 1930's. Since then, the most notable Lake States outbreaks have occurred in the periods 1936–1940, 1946–1948, 1957–1960, and 1968–1973.

Current emphasis on the environment and the benefit-cost analyses of forest protection require that land managers have data on sawfly impact on which to base their management decisions. This study was conducted to help forest managers understand the impact of the redheaded pine sawfly in young red pine plantations. To accomplish this, data were recorded in red pine plantations infested with the sawfly during the 1968–1973 outbreak.

The primary objectives of this study were (1) to identify the major environmental factors that influence the behavior and survival of the redheaded pine sawfly and survival of its host: (2) to develop a basic ecological model of sawfly impact on red pine; (3) to identify various land management options based on socioeconomic criteria; and (4) to propose guidelines for managing this sawfly in red pine plantations.

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DEFINITION AND CONCEPT OF IMPACT

The impact of an insect population feeding on its host trees can be broadly defined as the cumulative net effect of the insect damage that results in modification of management activities for specified forest (land) resource uses and values (USDA Forest Service 1972). More specifically, impact has two components: (1) ecological, the cumulative net effects of the insect on the total forest site and areas off-site; and (2) socioeconomic, the value judgments and decision criteria established by land management objectives (Fig. 1). The ecological component is based on physical changes to the tree and site caused by insect activity (e.g., discolored branches, dead trees, density of ground cover). However, the on-site physical changes may be of such magnitude as to initiate off-site changes as well (e.g., erosion, water recharge). The socioeconomic component is essentially the user's reaction to these changes and is the most difficult component to appreciate and understand. What the ecological effects imply depends upon the management objectives and values at stake, and management goals differ by degree and change frequently. For example, suppose a land manager has a well-defined objective for a particular parcel of land. If that objective is primarily timber production, then insect injury might have a negative effect. The effect on wildlife, however, may be positive, and perhaps there will be no major effect on watershed protection. Also, widespread insect-caused tree mortality could be considered beneficial in an overmature forest, thus having a substantial positive effect, while one insect falling in a person's food at a campsite could have nearly as great a negative effect.

Impact, a dynamic variable, is a function both of change in forest stand condition and of the criteria established for particular management objectives. Both components are measurable, but the socioeconomic part of management objectives cannot be fully assessed until the ecological part is understood.

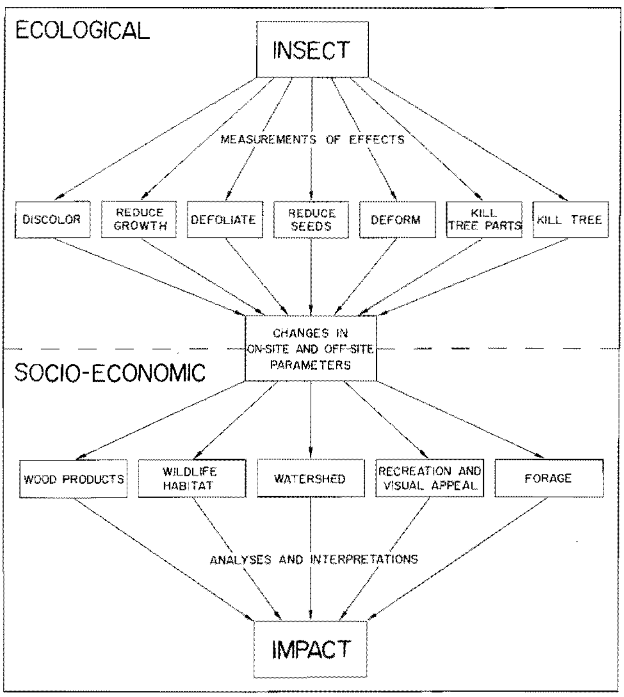

Fig. 1. Generalized model of impact from a forest insect (modified from USDA Forest Service [1972]).

The ecological component of impact for a forest insect consists of three major elements: the pest, the tree, and the physical environment they both occupy. Portions of each of these must be examined to identify the specific components that relate most to impact and to design a useful model. The approach of this study was to isolate major environmental elements of the ecosystem relative to impact, examine them and their interactions, and then, through a model, propose various impact interpretations based on land management goals.

BRIEF LIFE HISTORY OF THE SAWFLY

In most of Canada and the northern United States, the sawfly has a single generation per year (univoltine). A partial second generation sometimes occurs in portions of Michigan, Wisconsin, and New York. This study dealt with univoltine populations in the northern portion of its range.

The sawfly overwinters as a prepupa in a cocoon spun in the litter or topsoil beneath its host. Pupation occurs soon after the advent of warm weather, and emergence of the adult follows in a few weeks. Some prepupae may remain in diapause over several seasons before transforming to adults.

The female deposits about 120 eggs in the current or previous year's needles. They are laid individually in rows of slits or pockets cut in the edge of the needles of hard pines. All eggs laid by one female are generally clustered within needles of a single twig.

The larvae eclose in three to five weeks, depending on temperature and locality, and then feed gregariously in colonies that often contain over 100 insects. Univoltine populations of larvae feed in July or early August in most northern areas. At this time the new needles have fully expanded and the larvae then feed on both old and new foliage. Young larvae consume only the outer tissue of the needle. older larvae consume the entire needle; they generally strip a branch of all its foliage before migrating to another. When foliage becomes scarce, the larvae search for new hosts, and resume feeding until fully grown. Then they drop to the ground and spin their cocoons.

Moderate to heavy defoliation stunts height growth of infested trees and results in forking and bushing in the upper crown. Complete defoliation kills red pine and other northern pines.

STUDY AREAS

At the time this study began, the 1968–1973 outbreak of the redheaded pine sawfly was in progress. Three young (five to nine-year-old) red pine plantations (Table 1) in Michigan were selected for study in the spring of 1971 and 1972, based on a survey of sawfly-infested areas (Millers 1971). All plantations were on sandy soils with level to gently rolling topography. Edges were bordered by mixed hardwood stands or open fields. Tree spacing was about 1.8

Table 1. Description of redheaded pine sawfly study areas in Wexford County, Michigan (March 1971).

Plot	Location	Tree age (Years)	Mean height (m)	Plot size (ha)	No. of trees per Hectare	No. of trees per Acre
A1	T22N, R11W, S34NE	9	1.6	0.16	2,275	933
A2	T22N, R11W, S34NE	9	1.6	0.20	1,500	600
A3	T22N, R11W, S27SE	9	1.5	0.30	2,213	885
B1	T22N, R11W, S28NE	8	1.4	0.16	2,181	873
C1	T22N, R11W, S11SW	5	0.7	0.40	1,485	594
C2	T22N, R11W, S11SW	5	0.6	0.40	1,908	763

by 1.8 m (6 by 6 ft). Ground cover consisted mostly of grasses and intermittent patches of bracken fern, *Pteridium aquilinum* (L.) Kuhn, with a minor component of miscellaneous forbs, lichens, grasses, and sedges.

Six study plots, destined for intensive research, were established in the three plantations (Table 1). A large private planting (the Anderson plantation) contained three of the plots (designated A1, A2, and A3) because it had several infestation centers and diverse terrain. A second planting, located on USDA Forest Service land near the old Boon Fire Tower, contained one plot (designated B1). Two additional plots (C1 and C2) were established in a USDA Forest Service plantation begun by the Daughters of the American Revolution (DAR). The plots, which varied in size from 0.1 to 0.4 ha (0.2 to 1.0 acre), were set up specifically to include definite clusters of trees infested with sawflies, variable terrain, and different ground cover. Figures 2, 3, and 4 contain plot maps depicting the typical open-field conditions.

To broaden the scope and geographical area represented by this study, additional plantations with a history of redheaded pine sawfly outbreaks were examined in August of 1972. These were in Lower and Upper Michigan, Wisconsin, New York, and Ontario, Canada

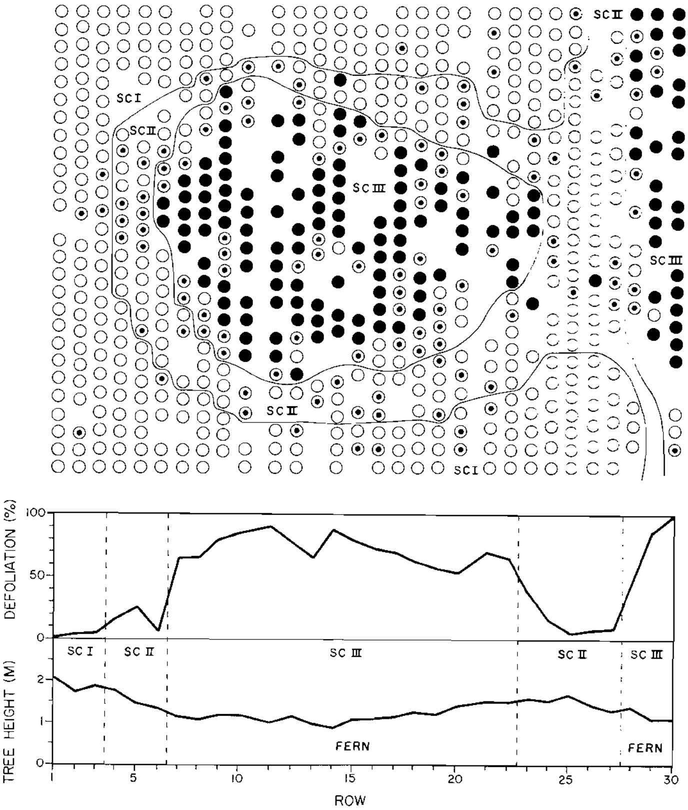

Fig. 2. Red pine plot A3 showing distribution pattern of trees defoliated by redheaded pine sawfly larvae from 1968 to 1971. Defoliation: white = 0–9%, spot = 10–90%; black = 91–100%; SC-I, SC-II, SC-III are site-class divisions. Right side of plot is the edge and along a dirt road. SC-I and SC-II areas had grasses and forbs, SC-III had bracken fern. North at top. Lower graph portrays a profile of defoliation pattern and tree heights by rows for a cross-section of trees through the mid-section of the plot. Fern refers to bracken fern occupying SC-III area.

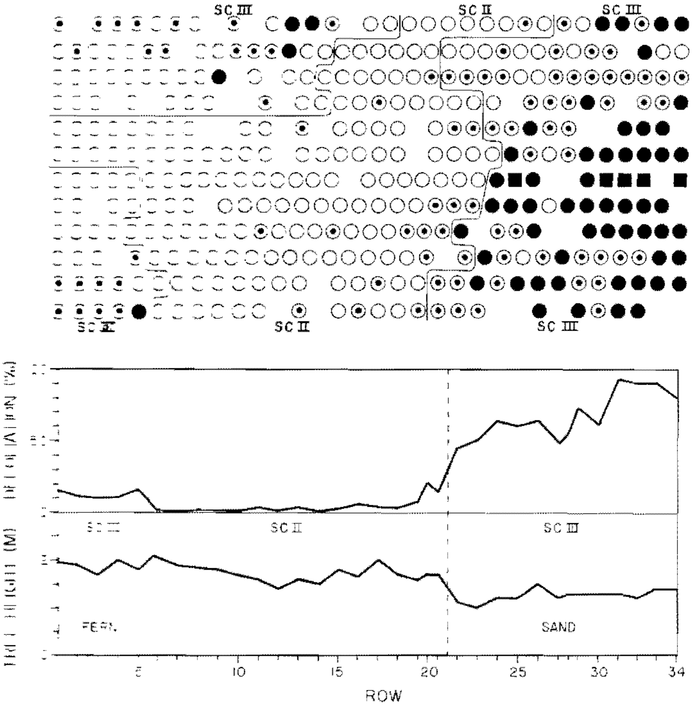

Fig. 3. Red pine plot A1 showing distribution pattern of trees defoliated by redheaded pine sawfly larvae from 1968 to 1971. Defoliation: white = 0–9%; spot = 10–90%; black = 91–100%. Right side of plot is the edge and along a dirt road. Squares represent jack pine trees. SC-I, SC-II, SC-III are site-class divisions. The SC-II area had grasses and forbs. North at top. Lower graph portrays a profile of defoliation pattern and tree heights by rows for a cross-section of trees through the mid-section of the plot. Fern refers to bracken fern occupying one SC-III area, and sand indicates a sand blow in the other SC-III area.

(Table 2). Insect populations, tree growth, diversity of terrain, and soil profiles were analyzed in these plantations.

SAWFLY ABUNDANCE AND DISTRIBUTION

Several investigators have reported that redheaded pine sawfly populations are associated with particular vegetation or particular sites. Early studies showed that the sawfly typically attacks isolated trees in the open, or at least prefers open-grown trees (Beal 1942, Brown and Daviault 1942, Atwood and Peck 1943). MacAloney and Secrest (1944) concurred that shaded pines are relatively free from attack. Griffiths (1958) further concluded that not only does the sawfly prefer open-grown trees over shaded ones, but attacks on open-grown trees are highly aggregated. Benjamin (1955), however, reported that the sawfly decidedly prefers pines associated with a hardwood overstory. When trees are attacked in the open, he concluded, the attacks are generally confined to areas with poor tree survival and where there is little or no associated vegetation, such as on sand blows.

Our initial observations of sawfly-infested stands also suggested that particular trees and sites are preferred habitat for the sawfly. Measurements were taken to determine the abundance and distribution of the sawfly within the study plots in order to learn the site conditions they prefer.

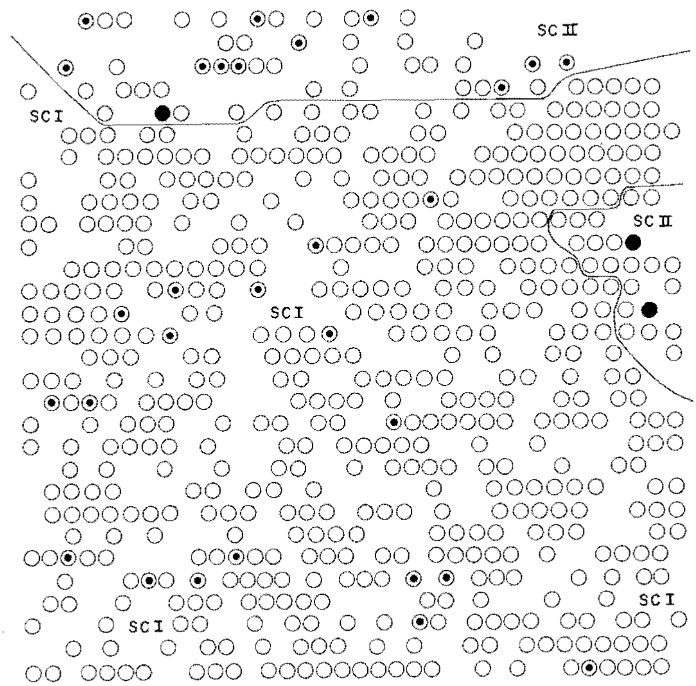

Fig. 4. Red pine plot C1 showing distribution pattern of trees defoliated by redheaded pine sawfly larvae from 1968 to 1971. Entire plot is surrounded by more pine trees. Defoliation: white = 0–9%; spot = 10–90%; black = 91–100%. SC-I and SC-II are site-class divisions. North at top.

Methods

Sawfly egg clusters were counted in June on all trees in five of the Michigan study plots from 1971 to 1973; counts were made in the sixth plot (B1) only in 1972 and 1973. In 1971 in plots A2 and A3, egg clusters were counted by first (top) branch whorl (including leader) and remaining branch whorls. Larval colonies were counted on all trees on all plots each year in July when the larvae were about half grown. Tree heights to the nearest 3 cm (0.1 ft) were measured each spring on all plots. General categories of dominant ground cover (e.g., forbs, grasses, bracken fern) and superficial edaphic factors (e.g., A horizon present or absent, sand blow) were recorded at about 2-m (6.5-ft) intervals between all rows of trees throughout each plot. Associated overstory trees were noted and the degree of overstory estimated. Small pits were dug to a depth of 0.3 to 0.6 m (1 to 2 ft) at 1.8-m (6-ft) intervals along transects perpendicular to the edge of hardwood stands for determination of root abundance.

Results and Discussion

The peak year of the sawfly outbreak in Michigan was 1971, and this was reflected in most plots. The Boon Tower (B1) population, however, peaked in 1972; except for this stand, there was a general collapse in the other plots in 1973 (Table 3). The Anderson plantation (plots A1, A2, A3) had the highest infestation, averaging more than one egg cluster per tree at the infestation peak (Table 3), with a range of 0 to 20 clusters per tree.

Table 2. Location of additional infested red pine plantations examined in the study.

Plantation number	State or province	County	Location
1	Michigan	Benzie	T27N, R12W, S16NE
2	Michigan	Benzie	T28N, R13W, S35SW
3	Michigan	Houghton	T47N, R36W, S31NE
4	Michigan	Houghton	T27N, R38W, S26
5	Michigan	Houghton	T47N, R38W, S26E1/2
6	Michigan	Mackinac	T43N, R1W, S35S1/2
7	Michigan	Mackinac	T41N, R4W, S14
8	Michigan	Mackinac	T42N, R4W, S31NW
9	Michigan	Mackinac	T43N, R5W, S3NE
10	Michigan	Mackinac	T43N, R3W, S20SW
11	Michigan	Mackinac	T43N, R3W, S20NE
12	Michigan	Mackinac	T43N, R3W, S18
13	Michigan	Wexford	T21N, R12W, S18
14	Michigan	Wexford	T21N, R11W, S3, 4, 9, & 10
15	Michigan	Wexford	T22N, R11W, S13SE
16	Wisconsin	Menominee	T30N, R16E, S26NW
17	Wisconsin	Menominee	T20N, R16E, S3, 4, 9, & 10
18	New York	St. Lawrence	Stockholm Towp. Block 33
19	New York	St. Lawrence	E of Canton
20	New York	St. Lawrence	S of Stockholm Center
21	Ontario	Simcoe	Vespra Twp, Conc. 1, Lots 34 & 35
22	Ontario	Simcoe	Flos Twp., Conc. 2, Lots 26 & 27
23	Ontario	Frontenac	Oso Twp., Conc. 3, Lot 26
24	Ontario	Frontenac	Hinchinbrooke Twp., Conc. 5, Lot 9
25	Ontario	Lanark	Bathurst Twp., Conc. 4, Lot 16

Table 3. Frequency of redheaded pine sawfly egg clusters in three Michigan study plantations from 1971 to 1973.

	Mean number of egg clusters per tree		
Plot	1971	1972	1973
A1	1.03	0.02	0
A2	1.29	0.02	0
A3	0.98	0.03	0
B1	—	0.60	0.15
C1	0.18	0.10	0
C2	0.08	0.04	0

In plots A2 and A3 combined, the first whorl (and leader) of the tree contained an average of 36.1% of the egg clusters, and the remaining whorls 63.9%. Since the trees averaged eight whorls per tree, this suggested a preference for oviposition in the upper crown. Tree size, however, affected egg cluster location; taller trees had more clusters on the first whorl (Fig. 5). The tallest trees in the plots (3.0–3.6 m) had all egg clusters on the top whorl. The canopies of these larger trees were beginning to close in, perhaps causing the sawflies to choose higher levels. Benjamin (1955), however, reported more oviposition in the lower crowns of jack pine.

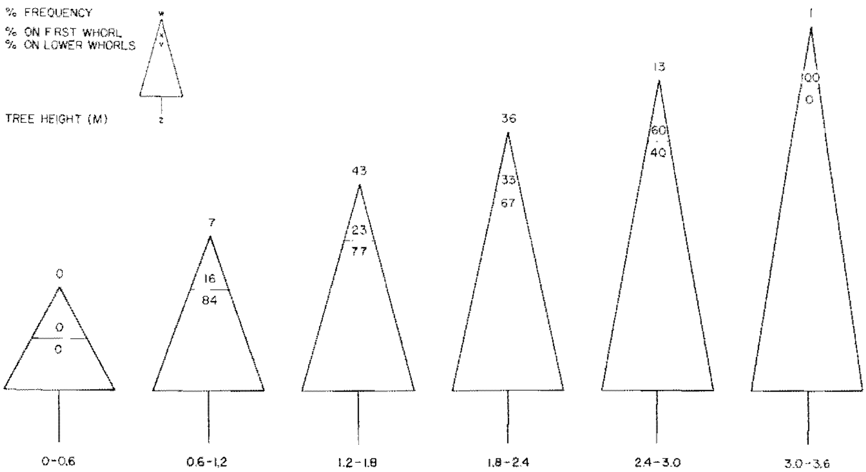

Fig. 5. Distribution of 775 sawfly egg clusters on red pine (frequency, first whorl [including leader], and lower whorls) by tree size class for plots A2 and A3 combined.

Egg clusters were most abundant on trees in the mid-height range. There were only a few living trees shorter than 0.6 m in plots A2 and A3, and these had no eggs. These trees had been heavily defoliated the year before the peak of the infestation and had little foliage available for oviposition. Trees 0.6 to 1.2 m tall contained 7% of the egg clusters, but most of these too were defoliated from the previous year and, therefore, had limited foliage available. Mid-size trees (1.2 to 1.8 , and 1.8 to 2.4 m) contained 79% of the total egg clusters, and trees 2.4 to 3.0 m tall contained 13%. The largest trees (3.0 to 3.6 m tall), which made up over one-third of each plot, had only 1% of the egg clusters (Fig. 5). Similar relations occurred in plots A1 and B1. Plots C1 and C2, which had small trees (0.3 to 1.2 m tall) and a light infestation, showed no relationship between number of egg clusters and tree size.

The sawfly population varied considerably between and within study plots. In some plots or locations within plots, sawfly egg clusters were few and widely scattered. Yet, in particular locations of some plots, egg clusters were numerous and aggregated in apparent epicenters. These different situations are directly comparable to the defoliation patterns shown in Figures 2, 3, and 4. For example, A3 (Fig. 2) had a heavy epicentric infestation at the plot center and east border; plot A1 (Fig. 3) had a major epicenter on the east and minor ones to the north and west. In contrast, C1 (Fig. 4) had a widely scattered and lighter infestation with no discernible epicenters. Infestation patterns in all plots remained relatively constant throughout the outbreak, and the epicenters seemed not to spread beyond certain limits.

In the plots where epicenters were obvious there were usually distinct edaphic and vegetational differences between the epicenters and their surroundings. For example, the epicenter in A3 (Fig. 2) was confined entirely to a large bracken fern patch. About 94% of the trees within the patch were attacked; less than 20% of those outside, where the infestation was scattered, were attacked. Similarly, in plot A1 (Fig. 3) the epicenter was located in a bare-sand area of the plot's east border. Plots C1 and C2, which did not have high sawfly populations, had what appeared to be uniform soil conditions with mixed grasses and forbs as ground cover with an occasional small patch of bracken fern. Plot B1 had an epicentric population in a moderately dense bracken fern patch adjacent to a hardwood stand. This plot was long, narrow, and only 12 rows wide. Established between two hardwood stands, it actually flanked both sides of a tertiary woods road. The hardwoods, mostly red maple, *Acer rubrum* L., extended over rows 1, 2, and 3 on the south border and rows 11 and 12 on the north (Fig. 6). The mean tree height for the plot was 2.04 m ± 0.46 SD, while the edge trees in rows 1, 2, and 12 were shorter by at least 1.00 SD. Root examinations showed that the

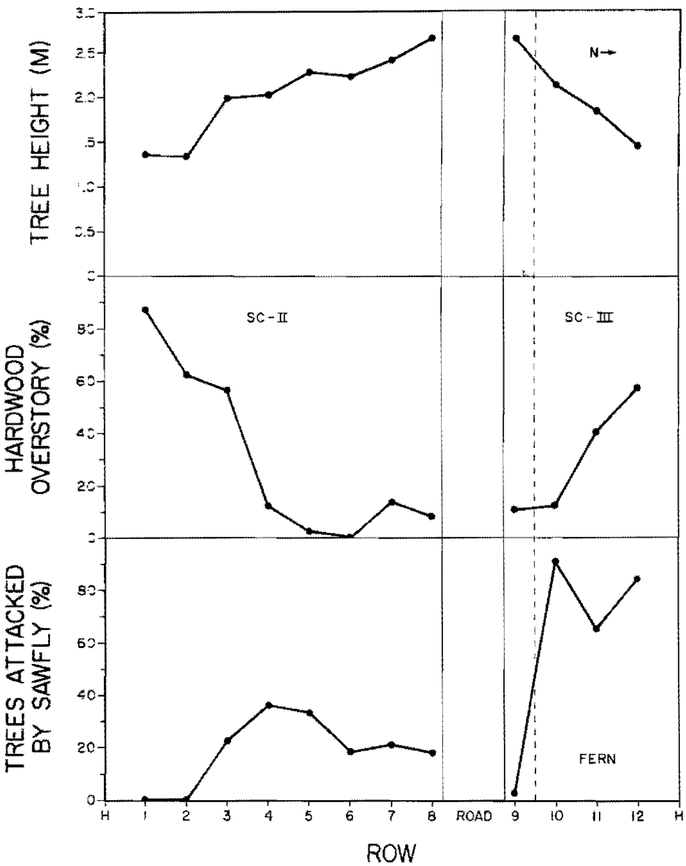

Fig. 6. Red pine plot B1 showing mean tree heights, hardwood overstory, and trees attacked by redheaded pine sawfly by rows in 1972. SC-II, SC-III are site-class divisions. Fern refers to bracken fern in SC-III.

maple roots occupied the same soil zone as the red pines and, similarly to the overstory, the root mats were most dense along the stand edges out to two or three rows of red pine.

In view of the above, that is, the presence of epicenters in some portions of plots and not in others, the variable population levels and patterns between and within plots, and the vegetational and edaphic variability, it appears that the sawfly chooses trees growing on particular sites. To investigate this further, three discernible "site classes" (SC) were identified:

SC-I: Ground cover composed principally of grasses, miscellaneous forbs, mosses, and lichens. Very little or no bracken fern present. Hardwoods, if present, at least 10 m distant. Soil with distinct upper organic matter layer. Sawfly population widely scattered and trees generally lightly infested.

SC-II: Ground cover composed mostly of grasses, forbs, lichens, and mosses with, at most, lightly scattered or small patches of bracken fern. Hardwoods at least 5 m distant. Soil with thin organic matter or patches of soil with upper organic matter layer present and interspersed with soil without organic matter. Sawfly population generally scattered with occasional clusters of trees moderately infested.

SC-III: Three subclasses were recognized: (1) ground cover mostly bracken fern, soils with or without distinct upper organic layer; (2) ground cover and soils variable but hardwoods less than 5 m distant; (3) ground cover sparse or absent and soil with very little or no organic matter layer. Typical case is pure sand or a sand-blow site. Sawfly population aggregated and trees generally heavily infested.

The SC-I and SC-III conditions were readily definable because they were most distinctive. SC-III areas had especially distinct boundaries because the bracken fern patches and sand blows had sharp perimeters. SC-II areas were difficult to classify and more arbitrary. For the most part, they occupy a transition zone between SC-I and SC-III when all three classes occur together.

Using the above "site class" criteria, boundaries for the different site conditions were established in each of the study plots (e.g., Figures 2, 3, 4, 6). The plots overall were sufficiently variable to contain one, two, or all three site classes. For example, plot C2 was totally SC-I, whereas A2 and A3 contained all three site classes. Plots A1, B1, and C1 each had two site classes.

Reevaluation of the number of egg clusters per tree by site class showed highly significant (*t* test, $P < 0.01$) differences within plots where more than one class occurred (Table 4). Egg clusters were considerably more numerous on trees in SC-III areas than in SC-I and SC-II areas in the heavily infested Anderson and Boon Tower plots. This direct correlation would be expected because the site classes were partially defined relative to the sawfly population.

To check the significance of site class further, 15 other sawfly-infested Michigan red pine plantations were examined for edaphic and vegetational differences relative to the sawfly population (plantations 1–15, Table 2). In stands with conditions similar to the study plots, the site class categories were supported. Where sawfly populations were highest, there were bracken fern patches or sand blows; hardwood edges were not encountered. The most striking area was plantation no. 1 in Benzie County, which covered 8 ha (20 acres) and had trees averaging about 1.5 m tall. Near the north edge was one large bracken fern patch covering 2.0 to 2.4 ha (5 to 6 acres). By the end of the sawfly outbreak, more than 98% of the trees had been killed within the bracken fern area. Tree mortality ended almost precisely at the boundary dividing the bracken fern from the forb and grass cover. Less than 15% of the trees outside the bracken were even attacked during the outbreak, and less than 1% died. In summary, the most obvious epicentric sawfly populations were on sites characterized by bracken fern or sand blows, or sites adjacent to hardwoods.

Also, casual observations of sawfly survival suggested that egg clusters on SC-I trees contained about 30% more dead eggs than those on SC-III trees. Egg survival from 100 clusters averaged 65% in 1972 and 36% in 1973. The egg parasite *Closterocerus cinctipennis* Ashemead destroyed less than 10% of the eggs each year on all site classes; unknown causes killed the rest. Hetrick (1959) suggested that copious resin flow from oviposition scars

Table 4. Redheaded pine sawfly egg populations on study plots for three site classes.

	Mean number of egg clusters per tree[a]		
Plot	SC-1	SC-II	SC-III
A1	n.a.[b]	0.73	1.25
A2	0.53	1.73	2.31
A3	0.34	0.92	2.38
B1	n.a.	0.31	2.10
C1	0.13	0.54	n.a.
C2	0.08	n.a.	n.a.

[a]Data taken in 1972 for plot B1, 1971 for other plots.
[b]Not applicable, site class not in plot.

greatly reduced viability of eggs in another sawfly, *Neodiprion hetrickii* Ross, when oviposited on vigorous slash pine. This may also be the case for *N. lecontei*, because the SC-I red pine trees are generally more vigorous than those on the other site classes and resin flow may be abundant.

Larval mortality was also higher on SC-I trees. Mean larval survival percentages (between the first and about the third instar) for the three site classes were: SC-I, 41.3%; SC-II, 56.4%; and SC-III, 52.3%. Survival on SC-I trees was significantly ($P < 0.05$) lower than on SC-II and SC-III trees. Knerer and Atwood (1973) reported that mortality of first-instar *Neodiprion nanulus nanulus* Schedl and *Neodiprion abietis* (Harris) on red pine was related to turgor of the foliage. The SC-I trees, being more vigorous, should have greater turgor than trees in SC-II and SC-III areas.

TREE GROWTH AND INJURY

Degree of injury to red pine from the redheaded pine sawfly depends on several variables, including tree size and amount of defoliation. In even-aged stands, red pine grows with little variation if site conditions are uniform, because its heritability of growth-variation is low (Yao et al. 1971). But soil variability and differences in available water greatly influence red pine growth in even-aged stands (Hannah 1967, Neary et al. 1972, White and Wood 1958). Tree size varied in some of our plots, with the shorter ones most susceptible to attack.

Benjamin (1955), in his studies of red pine defoliation, showed that one or two larval colonies could defoliate 0.3- and 0.6-m (1- and 2-ft) tall trees, respectively, and still be unsatiated. He found heavily defoliated trees up to 2 m (7 ft) tall. Many of the heavily attacked trees in the Michigan plots were shorter than 2 m (7 ft), and some trees had as many as 20 colonies.

Since tree growth and sawfly injury are essential components of impact, height growth, degree of defoliation, and tree mortality were recorded throughout the study.

Methods

Tree heights for each tree on each plot were measured to the nearest 3 cm (0.1 ft) each fall from 1971 to 1973. Heights for 1969–1970 were determined from internodal growth measurements. After larval feeding each year, percentage of defoliation of each tree and leader (terminal) shoot was estimated by two observers. The percentage of defoliation (to the nearest 5%) for each tree and leader was agreed upon by the observers through re-estimation or compromise. Dead trees were tallied at the end of each growing season or in the following spring. Seventy young larval colonies were selected on trees that had little previous defoliation and sufficient foliage for the larvae to complete feeding. Larvae were counted in each colony when they reached the third instar, and a few colonies were recounted in the fifth instar. Defoliation was measured as length of branch-foliage consumed upon completion of feeding. Average numbers of needles per centimeter of branch and needle lengths were recorded from several trees and several stands.

Results and Discussion

Each study area contained even-aged trees, but the ages of plantations ranged from five to nine years at the start of the study in 1971. Tree height in 1971 varied from 0.13 to 3.20 m (0.4 to 10.5 ft) among the six Michigan study plots. The plot trees were on two soil series and showed somewhat different growth rates. The trees on Kalkaska intergrading to Montcalm soil had a higher mean height in centimeters (Y) over age (X) relation ($Y = 62.2 + 25.9X$; $r^2 = 0.850$) than the trees on Kalkaska intergrading to Rubicon soil ($Y = -101.9 + 32.7X$; $r^2 = 0.990$). Both regressions showed highly significant ($P > 0.01$) relations.

Tree heights within plots varied by site class before, during, and after the sawfly outbreak. Trees on SC-I were the tallest throughout the study. SC-III trees, in contrast, were short or suppressed and those that survived larval attacks remained the shortest throughout the study (Fig. 7). SC-II trees, on the average, were intermediate in size and often occupied a zone between SC-I and SC-III trees.

Stocking level or tree density was highly variable in the heavily attacked Anderson plots, and stocking level decreased during the outbreak as sawfly populations decimated vulnerable trees. Tree stocking of plots A1, A2, A3, when tallied before and after the outbreak, demonstrated the following survival percentages: Pre-outbreak, SC-I, 94%; SC-II, 86%; SC-III, 68%; Post-outbreak, SC-I, 93%; SC-II, 83%; SC-III, 31%.

Pre-outbreak survival indicated that the stand was nearly fully stocked (94%) in the SC-I areas, marginally stocked in the SC-III areas, and intermediate in the SC-II areas. Pre-outbreak mortality was probably related to poor initial survival following planting, especially on the SC-III areas. All trees that died during the study were killed by sawflies. Tree survival, and density, were nearly unchanged by sawflies in SC-I areas; but survival on SC-III areas was reduced from a marginal 68% to a poor 31% in the Anderson plots.

Most tree mortality from sawflies occurred during the first years of the outbreaks (1968–1970) in most study areas, although populations in plot B1 didn't build up sufficiently to kill trees until 1971 (Table 5). Slightly more than 1% mortality occurred in the comparatively lightly infested DAR plantation (plots C1, C2), which contained mostly SC-I areas (Table 5). It appears that the size of the trees at the onset of the infestation as well as site location influenced mortality. The DAR stand contained the youngest trees in the study; had they been a few years older and hence larger, mortality most likely would have been negligible, assuming the sawfly population remained the same. Other plot data, such as from plots A2

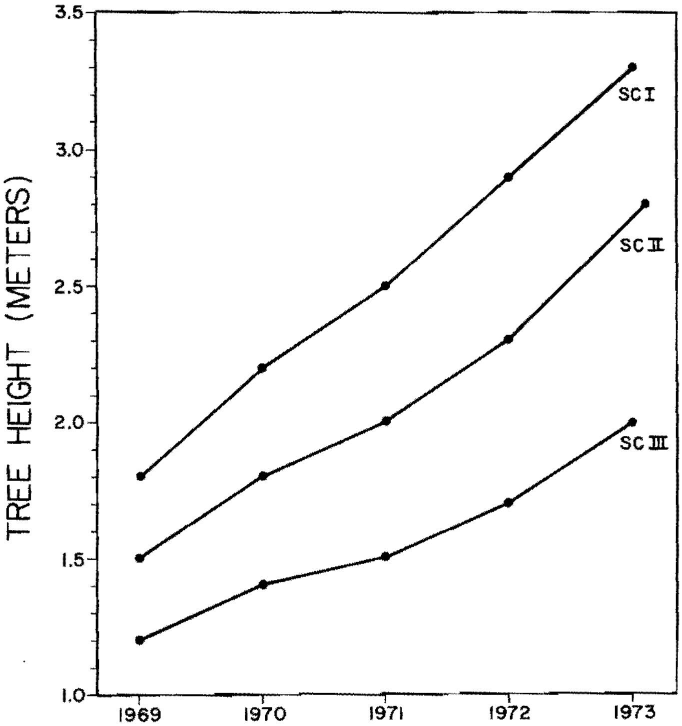

Fig. 7. Mean tree height for three site classes by year for plot A3.

Table 5. Red pine mortality during the redheaded pine sawfly outbreak in the Michigan study plots.

Plot	Live trees at pre-outbreak	Number of trees dead in: 1968–69	1970	1971	1972	1973	Lives trees at post-outbreak	Percent mortality
A1	364	43	10	3	0	0	308	15.4
A2	300	106	6	1	0	0	187	37.7
A3	664	107	3	8	0	0	546	17.8
B1	337	0	0	17	10	0	310	8.0
C1	595	1	3	1	1	0	589	1.0
C2	763	2	4	3	1	0	753	1.3

and A3 where SC-I trees were larger, seemed to suggest this also. Sawfly populations over all years were only slightly higher on the SC-I trees in the Anderson plots but, because of their size or the number of sawfly colonies, there was no mortality and the trees were never fully defoliated. This is clearly evident when defoliation and mortality in widely diverse plots such as C2 and A3 are compared (Table 6). Note that for SC-I areas, both plots have similar defoliation patterns except in the 90 to 100% defoliation class (which generally kills red pine). The SC-I areas on plot A3 did not have trees defoliated in the 90 to 100% class.

Degree of defoliation was distinctly related to site class; SC-III trees suffered the heaviest defoliation and SC-I trees the least (Figs. 2, 3). Also, more leaders in SC-III trees were attacked by the sawfly and heavily defoliated as the sawfly population increased and defoliation of the tree increased (Fig. 8). On SC-III areas of all plots, about half the trees suffered defoliation in excess of 90% (Figs. 2, 3), and nearly all of these had the leaders fully defoliated. Defoliation in excess of 90% rarely occurred on SC-I and SC-II areas. Most trees on these sites were defoliated less than 10%, an amount insignificant to height growth unless the leaders are heavily defoliated. Of the trees attacked on SC-I and SC-II areas, only 3 and 10% of the leaders, respectively, were injured sufficiently to cause temporary deformity and minor growth loss. A dead leader resulted in one or more lateral shoots taking over the next year.

Severe defoliation in one season or heavy partial defoliation over several seasons killed red pine. Two and sometimes three years were needed for some trees to reach a defoliation threshold for mortality. Mean amount of defoliation resulting in death of the tree was 96.5 ± 0.2%. Nearly all trees defoliated less than 90% survived the outbreak. Trees approaching 90% defoliation, however, nearly stopped growing and were severely distorted at the end of the outbreak.

The study showed that each larva was capable of defoliating 2.8 cm (1.1 in.) of foliated branch, or foliage consumed in centimeters of branch (Y) regressed on number of larvae (X) was $Y = 28.6 + 1.9X$ ($SE = 61.9$; $r^2 = 0.89$). Thus, a fully surviving colony of 120 larvae can defoliate 3.4 m (11 ft) of foliage, which is more than the foliage available on a 0.3-m- (1-ft) tall red pine, but probably a little less than that on a 0.6-m- (2-ft) tall red pine, based on Benjamin's (1955) defoliation studies.

Table 6. Sawfly-caused defoliation and mortality for various site classes, plots C2, A3.

Plot	Site class	Trees (No.)	Percent trees in defoliation class: 0–10%	11–89%	90–100%	Trees dead (%)
C2	I	763	93.1	5.6	1.3	1.3
A3	I	279	94.5	5.5	0	0
	II	166	71.7	26.5	1.8	1.8
	III	219	12.3	25.2	62.5	52.4

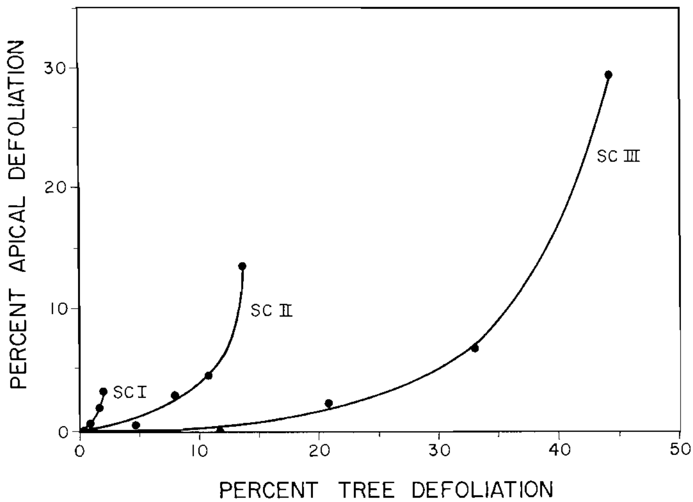

Fig. 8. Relation of red pine leader defoliation to whole tree defoliation by the redheaded pine sawfly.

SOIL-SITE CHARACTERISTICS

Gross site requirements for red pine are well documented. Wilde (1966) considered 10% silt plus clay to be the minimum fine particle ratio for adequate growth. On soils heavier than sandy loams, silt and clay have an adverse effect on red pine growth, since they tend to restrict permeability and aeration (Van Eck and Whiteside 1963). In Lower Michigan soils formed in deep sands, productivity is also related to soil profile development. Hannah (1967) found a positive correlation between site index and the depth of the A and B horizons. At least 45 to 50 cm (10 to 11 in.) of reasonably permeable, fairly well-aerated soil is necessary for normal red pine growth. Below this depth, if the soil is compacted, very coarse, or calcareous, growth decreases after 25 years (Van Eck and Whiteside 1963). On the other hand, if the soil below 45 cm (18 in.) is medium-to-fine textured, the growth rate is likely to be rapid (White and Wood 1958). The influence of soil moisture, according to Stoeckeler and Linstrom (1950), masks the influence of nutrients, possibly because higher nutrient levels are associated with finer-textured soils. Excessive soil compaction can restrict root development and stress trees (Armson and Williams 1960). Stone et al. (1954) noted that red pine grows poorly or dies on imperfectly and poorly drained soils. Best growth of red pine is associated with a soil pH of 4.5 to 6.0 (Wilde and Iyer 1962).

The soils and related site conditions were examined in the study plots and in other sawfly-infested plantations to see if soil characteristics were related to tree development and to degree of sawfly attack.

Methods

Two personnel from the Soil Conservation Service (Cadillac, Michigan) dug soil pits in sawfly-attacked and non-attacked portions of the six study plots and classified them as to soil series and, in plots A1 and C1, as to local soil type. We later determined the solum characteristics of sawfly-attacked and non-attacked sites in the other four study plots and in the locations visited during the extensive survey conducted in Michigan, Wisconsin, New York, and Ontario, Canada. Soil texture and depth were measured and examined for key differences using a 10-cm (4-in.) bucket soil auger. The soil pH was measured using a Hellige-Truog soil reaction test kit.

Results and Discussion

The Anderson and Boon Tower soils were classified as Kalkaska intergrading to Rubicon phases. The DAR plantation soils were Kalkaska intergrading to Montcalm phases. Interpreting from Hannah's (1967) soil classification system, the DAR plantation soils are more productive for red pine than the Anderson or Boon Tower soils. The tree growth data support this (see regression equations in "Tree Growth and Injury" section).

Soil characteristics varied somewhat within plots as well. For instance, the non-attacked SC-I area in plot A1 had an A2 horizon and a somewhat deeper soil with narrow texture and color bands than the severely attacked SC-III area. This SC-I area also had a more strongly developed B horizon, and portions of the upper B horizon of SC-III were irregularly and strongly cemented. These visible soil differences within plot A1, and similar conditions in plot A2, suggested that water and nutrients would be least available for red pine growth in the SC-III areas. The growth responses of trees on SC-I and SC-III areas generally reflected this (Fig. 7).

In plot A3 the soil differences between SC-I and SC-III areas were more subtle. Depth to the C horizon was 13 cm (4 in.) greater in the SC-III area, but both areas showed similar soil profiles, though less strongly developed than those in plot A1. The major apparent difference between the SC-I and SC-III areas in plot A3 was not the soil, but rather a dense patch of bracken fern throughout the SC-III area. The trees in the SC-III area, as noted before, were stunted and appeared to be competing with the bracken fern for moisture.

Plot B1 had a road through its center that had previously been a railroad grade. Hardwoods bordered both the north and south edges of the plot and the soils in the woods had a prominent A2 horizon. About 6 or 7 m (three rows of trees) in from the planting's south edge, the A2 horizon ceased and was replaced by an irregularly bordered Ap-like disturbed horizon. Near the center of the plot was an area of compacted soil which lacked an A2 horizon. Sawfly damage was somewhat aggregated within the compacted area (rows 4 and 5, Fig. 6), suggesting the sawfly preferred trees growing on strongly disturbed soil. North of the road the Ap horizon continued to the hardwood edge. There the sawfly population and tree injury (Fig. 6) was greatest, but bracken fern dominated much of the site.

Soil differences between SC-I and SC-II areas in plot C1 were slight. The SC-II area had some erosion of the topsoil and a coarser-textured and thinner Ap horizon. Plot C2, which was classified SC-I only, had soils similar to those of the SC-I area of plot C1.

Soil and other site conditions were also examined in the sawfly-infested areas of the other 25 plantations in an attempt to identify other characteristics that affect the sawfly population (Table 7). The observations yielded five general categories or site conditions where sawflies were abundant.

The first and most common site condition was shallow soil. Depth of parent material was significantly less (t test, $P < 0.01$) on attacked versus non-attacked sites (the means showed a 51 cm [20 in.] difference). Sometimes the topsoil was absent (sand blows), lacked fine-textured layers and color bands, or was predominantly sand and gravel or other coarse soil mixtures. In several stands, limestone and other rock outcroppings broke the soil surface or underlaid the shallow (10 to 75 cm [4 to 28 in.]) soil as bedrock. In the latter situation, there were few discrete pockets of sawfly attacks and distinct site classes were not evident. These soils had little water-holding capacity and in general were excessively well-drained for red pine.

The second condition consisted of sites that had medium-to-fine textured soils, but were imperfectly drained. Conditions varied from moist, heavy soils to those wet most of the time from a high water table. The pH was generally neutral or higher in these areas and somewhat unfavorable for good red pine growth.

The third condition was characterized by highly disturbed soils. Two plantings were heavily attacked on farmsteads near abandoned farm building foundations. The sawfly-infested trees occupied distinctly rectangular zones indicative of previously fenced-in areas.

The fourth condition consisted of lowland areas thought to be frost pockets. Soils were medium-textured and well-drained, and differed only slightly from those of adjacent areas with fewer sawfly attacks. Trees, however, were discernibly shorter in the frost-pocket areas.

Table 7. Some prominent site characteristics of redheaded pine sawfly-infested areas in red pine plantations.

Plantation number	Location	Moisture regime	Soil texture	Prominent site characteristics
1	Michigan	dry	coarse	Shallow soil (sand blow)
2	Michigan	dry	medium	Shallow topsoil
3	Michigan	moist	medium	Disturbed soil (old farmstead)
4	Michigan	dry	medium	Frost pocket
5	Michigan	moist	medium	Imperfectly drained, dense sod
6	Michigan	dry	coarse	Shallow topsoil
7	Michigan	dry	medium	Shallow soil, rock outcrop
8	Michigan	wet	fine	Imperfectly drained
9	Michigan	dry	fine	Shallow soil, rock outcrop, bracken fern
10	Michigan	wet	medium	Imperfectly drained
11	Michigan	dry	medium	Frost pocket
12	Michigan	moist	fine	Imperfectly drained, dense sod
13	Michigan	dry	coarse	Shallow soil
14	Michigan	dry	coarse	Shallow soil (sand blow)
15	Michigan	dry	coarse	Shallow soil (overburden)
16	Wisconsin	dry	coarse	Shallow soil (sand and gravel)
17	Wisconsin	moist	medium	Disturbed soil (old farmstead)
18	New York	wet	coarse	Imperfectly drained
19	New York	moist	coarse	Shallow soil, hardwood edge
20	New York	dry	coarse	Shallow soil
21	Ontario	moist	medium	Disturbed soil (compacted)
22	Ontario	moist	fine	Imperfectly drained
23	Ontario	dry	coarse	Shallow soil (overburden)
24	Ontario	wet	fine	Imperfectly drained
25	Ontario	dry	medium	Shallow soil, rock outcrop

The fifth condition consisted of variable soil characteristics, but the plantings were associated with such features as bracken fern, adjacent hardwood edges, or dense sod.

The edaphic conditions relative to tree growth and moisture-holding capacity of the soil and site classes are summarized in Figure 9. These data indicate that the sites most heavily attacked by the sawfly (SC-III areas) are characterized by one or more of the following conditions: (1) soils are shallow, coarsely textured, or have poorly developed banding; (2) soils are eroded, compacted, or covered with overburden; (3) soils are imperfectly or excessively drained; and (4) soil pH tends to be slightly acid to alkaline in the upper 23 cm (9 in.) of solum (mean pH is 7.0 but ranges from 6.5 to 8.0). Bell (1971) recommended that these same conditions are not suitable for planting red pine. In contrast, areas with the best tree growth and least sawfly injury (SC-I) tended toward loamy sands, or sands with moderate to deep subsoil development, pH in the range of 4.5 to 6.2, and moderate water-holding capacity.

PRECIPITATION AND OUTBREAKS

The sawfly has long been known to be somewhat cyclic; it has periods of abundance and then periods follow when it is only locally abundant or rarely found. This indicates that population outbreaks may be reacting to large-scale phenomena, such as changes in weather or precipitation patterns. Because local sawfly populations often appear to be related to excessively or imperfectly drained sites, we decided to compare precipitation patterns with population outbreaks. To do this, we compared weather records for Michigan with sawfly outbreaks from 1935 to 1973.

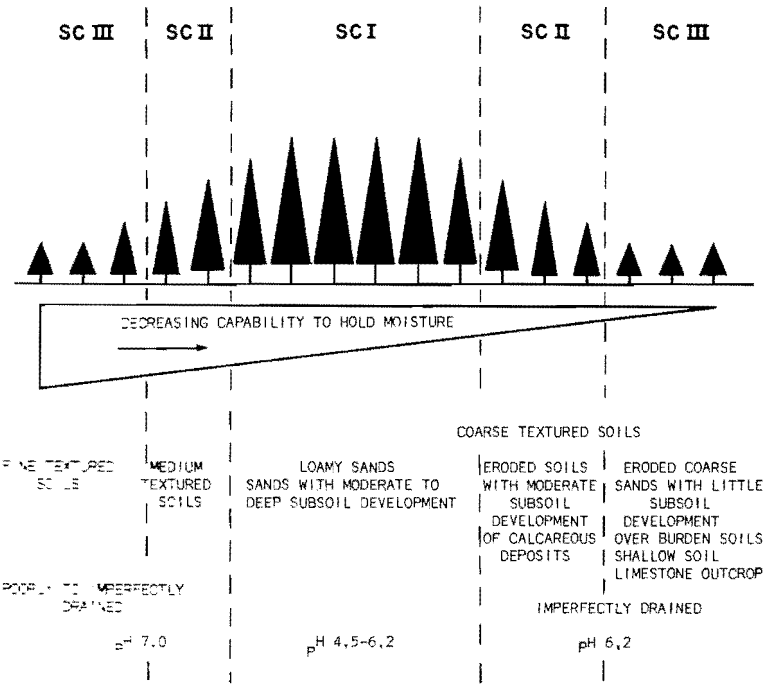

Fig. 9. Schematic red pine ecosystem showing relative tree growth, moisture-holding capacity, and soil characteristics in relation to site-class categories.

Methods

Information on pest outbreaks in Michigan was obtained from the literature (Fowler 1973, Benjamin 1955) and from supplemental file reports and suppression records from state and federal agencies. Sawfly populations, reported by year and location, were subjectively classified as "endemic," "local outbreaks," or "widespread outbreaks." When population levels were not specified in a report, the tone (i.e., sawfly decreasing, population static, etc.) helped to classify the population level. When no yearly reports were given, the population was considered endemic.

The U.S. Weather Bureau divides Michigan into 10 climatic divisions. The redheaded pine sawfly historically has been of concern in the four northern divisions: West Upper, East Upper, Northwest Lower, and Northeast Lower; an area covering all of the upper Peninsula of Michigan and that portion of the Lower Peninsula north of a line from Manistee to East Tawas. Weather data from these four divisions were used in the analyses to compare drought or excess moisture and sawfly population levels.

Palmer's Drought Index, which is based on monthly moisture departures from the monthly average, was chosen to represent wet or dry periods (Palmer 1965, Strommen et al. 1969). Drought is expressed in four classes by the U.S. Weather Bureau: mild, moderate, severe, and extreme. Palmer assigned −1.0 to −4.0 to these classes, and 1.0 to 4.0 to comparable wetter than normal classes. Palmer's Drought Index values were calculated for each climatic division for a given year by summarizing the average monthly precipitation for the period of April–June of that year and the July–September precipitation averages from the previous year. These values were used because they have the greatest influence on bud set and moisture uptake of the tree and are most closely related to tree growth (Neary et al.

1972); thus they have the greatest influence on stress within the tree. These values were then compared with the sawfly population data for the same year and one, two and three years following the index period.

Results and Discussion

Sawfly population records indicated four widespread outbreak periods for Michigan at about 10-year intervals: the late 1930's, 1940's, 1950's, and 1960's. Outbreaks were particularly evident during these periods in the West Upper and Northwest Lower divisions of Michigan, and less so in the East Upper division (Fig. 10). The Northeast Lower Michigan area showed generally parallel population increases but none reached outbreak status. Endemic populations, overall, occurred in the early 1940's, 1950's, and 1960's.

Palmer's Drought Index values indicated somewhat cyclic wet and dry periods during this period. Some of the dry periods seemed to be related to higher sawfly populations and, conversely, wetter than average years were related to endemic populations (Fig. 10). The Northeastern Lower Michigan area, which had no widespread outbreaks, was notably wetter than the other divisions over the 1935–1973 period of concern, suggesting that the abundant moisture may have prevented large population releases there.

When the average index values were plotted against the three sawfly population levels for the same year as the index (Fig. 11), all divisions showed a consistent trend: moist periods tended to be associated with endemic sawfly populations, normal years with local sawfly outbreaks, and drier years with widespread outbreaks (ANOVA, $P < 0.10$). This was particularly true for the West Upper Michigan division (Fig. 11) which had the most widely fluctuating moisture regimes. Indices plotted over sawfly populations for one, two or three years after the index period showed no significant correlation, indicating the population release occurred immediately after drought.

Very wet years did not appear to cause population releases, a condition which might be expected if overabundant water causes tree stress. Pine plantations on very wet sites are exceptions in these four divisions, as most are planted on upland sandy soils that drain rapidly. These are more susceptible to drought during dry periods than to excess water during wet periods, as the data indicate.

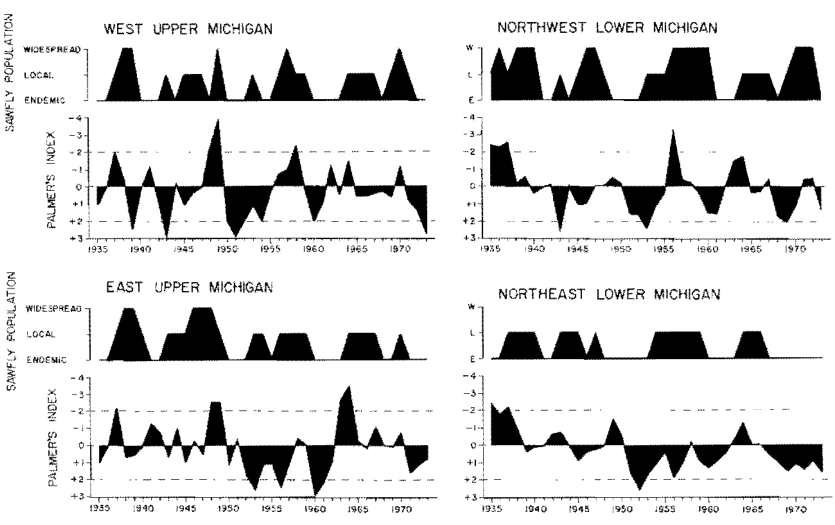

Fig. 10. Redheaded pine sawfly populations and Palmer's index values for the period 1935–1973 for Michigan's four northern divisions.

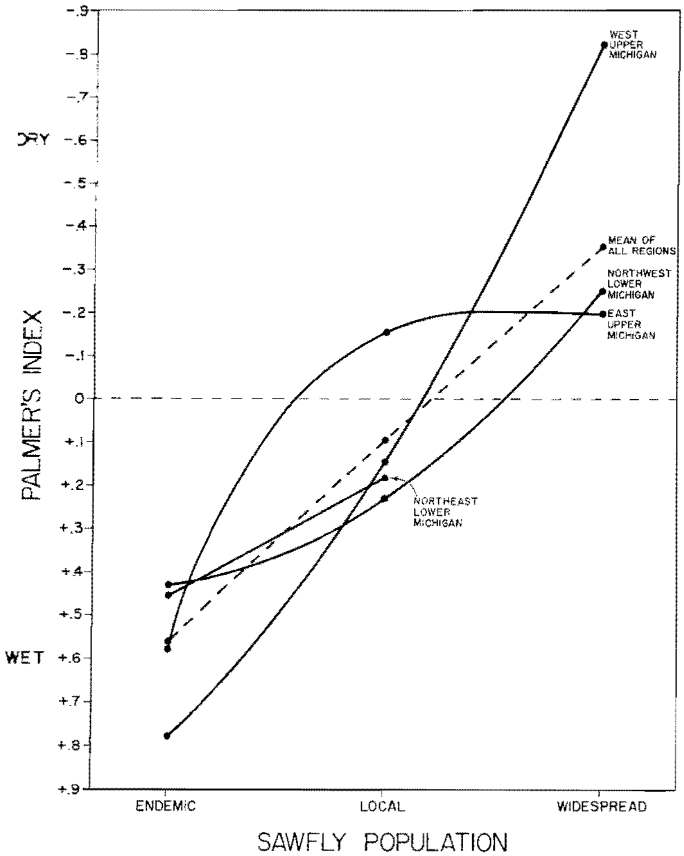

Fig. 11. Relation of mean Palmer's index values to populations of redheaded pine sawfly for Michigan's four northern divisions. (The Northeast Lower Michigan Division did not have widespread population densities.) Negative values are dry, positive are wet.

Not all sawfly release periods appear to be related to drought. This is particularly noticeable in the Northwest Lower Michigan division during the outbreaks in the late 1940's and 1960's when precipitation was generally normal or above normal. Of course, water stress could still have been responsible in such outbreaks, but either very local droughts or other factors such as competing vegetation must have been the principal factors. Should droughty periods be responsible for sawfly population releases, then, with a shift toward less than normal precipitation, trees occupying SC-III areas would become stressed the most and hence most attractive to the sawfly.

DISCUSSION

In this study we examined several aspects of the sawfly's habits, its defoliation injury to red pine, and some environmental relations of pine stands, in order to learn more about injury and impact. The fact that sawfly populations often built up on open-grown trees agreed with the findings of most previous investigators (Beal 1942, Brown and Daviault

1942, Atwood and Peck 1943, MacAloney and Secrest 1944, Griffiths 1958), but our data also indicated that trees on high-stress sites suffer the highest sawfly populations and the greatest injury. Infested trees partially shaded by hardwoods also seemed to be attacked because they were under stress from root competition, rather than from shade preference by the sawfly as suggested by Benjamin (1955). Trees suffering the greatest injury were usually the shortest and weakest in the stand, and growing on sites where soil quality or water availability were inadequate for red pine growth.

Site quality and availability of water to the tree are known to affect populations of sawflies and certain other defoliators. For example, Gremal'skii (1961), summarizing research on the resistance of pine stands to defoliators, concluded that, in many pests, mass breeding occurs only in stands containing physiologically weakened trees. He also presented several cases where survival was higher when the larvae were fed foliage from weakened stands. White (1952) was the first to show this phenomenon for the redheaded pine sawfly. He found that the sawfly died after feeding briefly on jack pine seedlings grown on fertile nursery soil, whereas other larvae completely defoliated seedlings taken from typical pine sites. Schwenke (1962), who studied the sawfly *Diprion pini* (L.) on trees growing on good and poor sites, found that survival and larval size was significantly greater on trees from poor sites. He suggested that the unfavorable water balance on poor sites increased the sugar content of the needles. The exact reason why the redheaded pine sawfly preferred stressed trees in this study is uncertain, but the fact that they did provides the basis for an ecological impact model. This model (below), tempered by sawfly dynamics and socioeconomic constraints, suggests various options for managing the sawfly in red pine plantations.

Ecological Model of the Sawfly

The ecological model for the redheaded pine sawfly, which is a precursor to a mathematical model, is structured on the differences among three site class variations and considers the major interrelations among the insect, the tree, and the environment. Tree vigor appears to be the element upon which the insect-host-site ecosystem pivots (Fig. 12). The three site classes, previously coded SC-I, SC-II, and SC-III, will henceforth be called *site resistance classes* (SRC-I, SRC-II, and SRC-III) to distinguish them from standard site class terminology. These classes reflect different levels of stress on red pine trees, and hence different susceptibilities to sawfly attack.

SRC-I sites are highly resistant to sawfly infestations (Fig. 12). The soils are adequate for good red pine growth, and are relatively undisturbed or have a visible leaching (A2) zone. They also frequently have a B horizon containing texture bands or a well-developed color band. Generally, little competition for available moisture occurs from other vegetation. Bracken fern, if present at all, is sporadic, and hardwood roots are rarely present in the same zone with red pine roots. Soils in this class have sufficient water-holding capacity, are not imperfectly drained, and have adequate nutrients for good red pine growth. The trees are vigorous, as exhibited by their form, color, and annual growth. Although vigor is affected during dry periods, the trees are not weakened enough to be very attractive to the sawfly.

SRC-I sites consistently produce red pine low in sawfly attractiveness; further, larvae that do occur on these trees exhibit symptoms of antibiosis, low larval survival. Perhaps these trees are over-supplied or deficient in a nutrient needed for optimum larval growth. The little feeding that does occur causes only slight damage in terms of foliage removal and seldom causes more than sporadic branch or leader mortality; tree mortality is rare. The stand remains unchanged and injured trees rapidly outgrow the effects of the sawfly feeding.

SRC-II sites are more susceptible to sawfly attack than SRC-I sites (Fig. 12). The upper solum of the soil is disturbed. The A2 horizon is only weakly developed and the B horizon lacks the degree of development found in SRC-I soils. On Kalkaska intergrading to Rubicon soils, the subtle difference between SRC-I and SRC-II is often only exhibited in the degree of development of the A2 horizon. Competition for available soil moisture from other vegetation is slightly greater than in SRC-I. Bracken fern, when present, is scattered or only in small clumps. Hardwoods compete for only a small portion of the available moisture in the red pine root zone. At best, SRC-II sites contain adequate soils for nutrients, but have marginal water-holding capacity and are sensitive to changes in precipitation. Extended

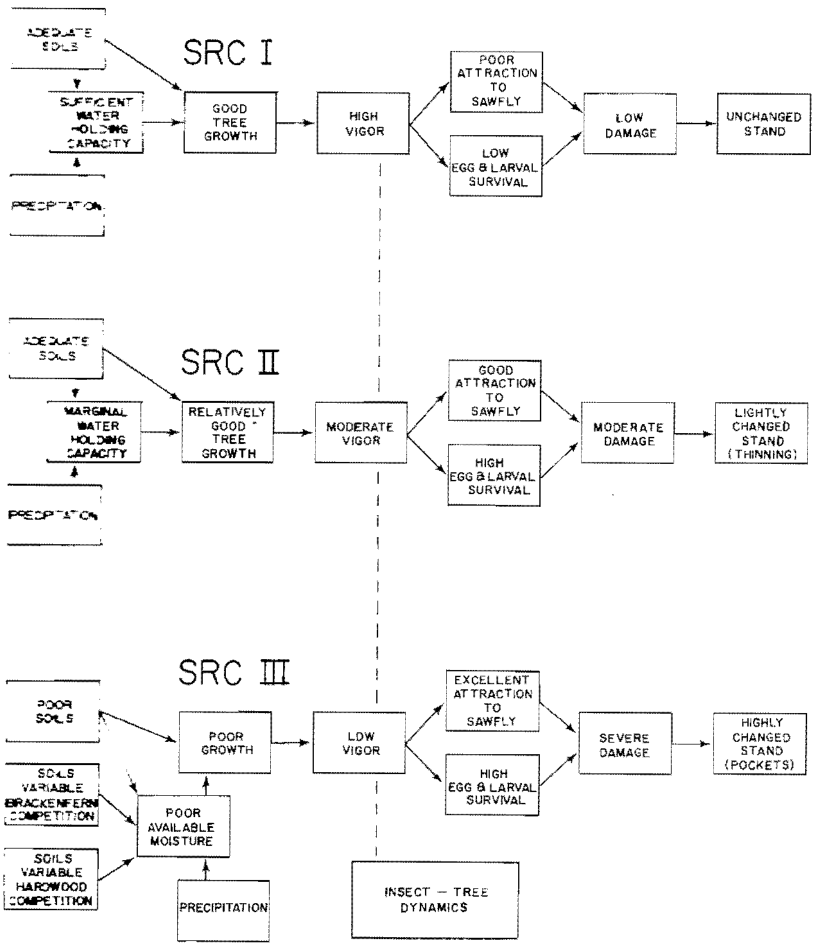

Fig. 12. Ecological impact model of the redheaded pine sawfly.

drought can sufficiently weaken some of the trees, thus making them more attractive to the sawfly. Normal and moist years, however, should provide relatively good growth and moderate vigor.

The sawfly is attracted to SRC-II trees more than to SRC-I trees, especially in dry years. Foliage nutrition appears adequate for good larval survival, maximizing damage from each colony. The sawfly attacks trees almost randomly throughout the SRC-II area. Along interfaces with SRC-III areas, where soil properties tend to be more marginal, there is sometimes a slight edge effect. Resulting damage is usually moderate; scattered trees or those along edges are injured most. Defoliation occurs on apical portions of some trees and all over other trees. Some trees are top-killed and become crooked or forked, and others are killed outright. Tree mortality probably varies by location and amot t of stress imposed during the outbreak. The site is modified slightly by the loss of some trees, resulting in a scattered thinning of the weakest trees.

SRC-III sites are highly susceptible to the sawfly (Fig. 12). The soil conditions in this class vary from poor to good. If poor, the soils may be low in nutrients, unfavorable in pH, or too high or too low in moisture-holding capacity. The soils may be shallow, severely eroded (sand blows), highly compacted, or composed of coarse overburden. On the better soils, trees are water-stressed due to competition from bracken fern, hardwoods, dense sod, or other vegetation. The roots of the competing vegetation form dense mats in the red pine rooting zone, and any trend toward dryness stresses the pine trees further.

Trees in this class are generally stressed in dry, normal, and moist years, and show poor height growth, poor form, off-color foliage, and low vigor. Some degree of sawfly resistance occurs only in the most vigorous trees in this class, and these trees are usually on "islands" with slightly better site conditions.

The female sawfly definitely prefers to oviposit on SRC-III trees. Egg and larval survival are maximal; no antibiotic effect is in evidence. Some attractant, perhaps an abundantly volatilized terpene produced when the tree is highly stressed, may be important in leading the female sawflies to oviposition sites. But whatever the factor, the sawfly population appears to be released when available moisture is reduced.

Sawfly damage is severe in SRC-III areas. The attacked trees are small and often completely defoliated. Tree mortality is rapid and widely spread over the site, and surviving trees become stunted and severely deformed. The stand becomes highly modified by the end of an outbreak; rows of trees are missing along hardwood edges, and small to large pockets open up where poor soils or competing vegetation, such as bracken fern, occur. Stands with large or numerous SRC-III areas that coalesce may be almost completely depleted of trees or left with only a few islands of trees following an outbreak.

The ecological impact model described above will be influenced by still other factors that act on the sawfly and affect the tree. A look at these factors, which are best expressed by a population dynamics submodel (Fig. 13) of the ecological impact model, is necessary for a better understanding of sawfly outbreaks and subsequent pest management programs.

Using host vigor as the pivotal point of the system once again, the dynamics submodel can be linked to the ecological model (Figs. 12 and 13). As we have shown, vigor determines the tree's attractiveness to the female sawfly and affects egg and larval survival (Fig. 13). (In our study, we found significantly higher egg parasitism on SRC-I trees.) But many other factors also limit the egg and larval stages; for instance, Benjamin (1955) listed 58 parasites and predators that feed on several of the sawfly's life stages, and more natural enemies have been found since. Part of the cyclic nature and rapid collapse of the sawfly's outbreaks may be due in part to natural enemies. The larval stage has the most natural enemies, and an effective larval parasite or predator can decimate a population. Even so, the colonial habits of this sawfly and the individuals' ability to act in unison to ward off enemies, tends to discourage parasites and predators. Small colonies, however, are more vulnerable to attack; so when large colonies split up while on the tree or migrate to other trees they have less chance for survival.

The larvae are readily infected by disease agents, particularly viruses, which have been known to nearly eliminate a sawfly population before the outbreak reached levels that could permanently damage the trees. The colonial habit of the sawfly is a disadvantage in a viral epizootic, because once a larva is infected, the disease spreads rapidly throughout the colony.

Inclement weather also adversely affects the larvae. Heavy rains knock young larvae off the trees. A heavy, unseasonal snowfall in 1938 nearly destroyed a population in northern Michigan (Benjamin 1955). Migrating larvae in search of food may encounter high soil temperatures on sandy sites and die before reaching new hosts.

Natural enemies and weather also affect the prepupa and pupa. Insects and rodents prey on these resting stages in the cocoon. Very low temperatures in winter can kill prepupae not protected by snow cover.

The tree, too, has enemies other than the redheaded pine sawfly, and these agents can weaken a healthy SRC-I type tree and make it susceptible to the sawfly. For example, insects such as the pine root collar weevil, *Hylobius radicis* Buchanan, weaken red pines and stunt their growth. The sawfly may find such weakened trees as attractive as normal trees on SRC-III sites.

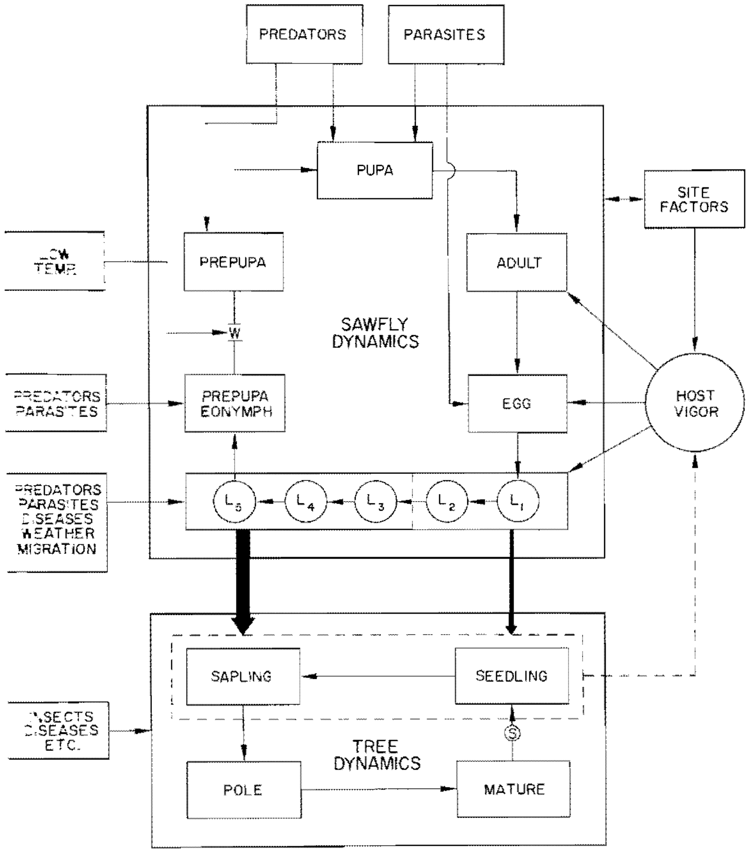

Fig. 13. First-order population dynamics submodel of the redheaded pine sawfly pine ecosystem. Host vigor (in circle) links this submodel to the ecological impact model. (W = winter, S = seed, L_1 to L_5 = larval instars.)

From the above we can see that factors other than host vigor can change the fate of the stand under the right circumstances. Some of these factors can be manipulated, but a thorough population dynamics study is still needed to isolate key factors and mechanisms most useful for sawfly population control.

Socioeconomic Considerations

Land management is concerned with satisfying human needs relative to available natural resources; its goals are to supply wood, water, forage, wildlife, and recreational opportunities.

The redheaded pine sawfly, like most other forest pests, is usually thought of as a deterrent to the achievement of one or more of these management goals because it appears to cause a negative effect on the forest and associated lands. Consequently, sawfly activities have historically been evaluated in terms of adverse impact instead of land-use goal attainment. In planning with one or more management goals, however the sawfly need not always be perceived as destructive. Under certain circumstances, it can achieve specific land-use goals and thus have a *positive* effect on the forest ecosystem. Redheaded pine sawfly management, therefore, can be used as a tool in land management, similar to the use of fire in a prescribed burn. This does not necessarily mean that an outbreak should purposely be initiated, but rather, an existing outbreak might be allowed to run its course when deemed advantageous to forest management. What we are suggesting is a change in thinking from the "all insects are bad and must be suppressed vigorously" syndrome to a "let's evaluate the situation and capitalize on it if possible" attitude.

In practice, because sawfly management involves social and economic considerations, it is basically a concern of the economist; it is his job to synthesize the effects of the insect into socioeconomic parameters useful as decision-making criteria for land managers. We do not propose an economic analysis here, but only a brief discussion to point out how some of the effects of the sawfly might relate positively or negatively to land management goals under a multiple-use concept.

Timber. In the Lake States, red pine is valued for wood products and is the major species planted. The sawfly kills and deforms young red pines on high-stress (SRC-III) areas which generally have site indices for red pine near or below 50. The better SRC-I areas have site indices of 60 or higher. Manthy et al. (1964) showed that well-stocked red pine stands of site index 60 will return financial yields for pulpwood rotations from 2.5 to 4.6% and for sawlog rotations from 2.9 to 6.9%. In contrast, the site index 50 trees can expect a financial yield of less than 3.0% for pulpwood rotations and 2.7 to 5.3% for sawlog rotations, and then only if appropriate stocking is maintained. In this study the poorest SRC-III areas had an average of 31% of the trees left after the sawfly outbreak. Surviving trees were deformed, stunted, and unevenly dispersed over the area. Merchantable volume then would yield less than 1% on these sites and would certainly not be worthy of additional forest management input. Not all of the loss on these sites was from sawfly; about 32% occurred from poor survival or early competition, so even without the sawfly some SRC-III areas are not economically productive. Without the sawfly they would yield very little pulpwood, and few trees would reach sawlog quality. Averill (1977) has provided a brief impact analysis based on future product potential on sawfly-damaged sites.

Tree mortality and deformity on SRC-I and SRC-II areas appear insufficient to affect future sawlog harvest, and at most would result in a slight reduction of pulp yield. Future yield on these sites would probably be much more affected by silvicultural treatment applied to the stand than by the sawfly.

From the current viewpoint of the manager, the sawfly has a negative effect on the financial yield of red pine, but because the sawfly affects the least productive trees, this effect is really quite small. Although trees on high-stress areas can be saved from sawfly injury by one or two chemical applications, it is doubtful whether the benefits would justify the cost of control. Large SRC-III sites might be better left unplanted in the first place and thus be available for other more productive uses. Small SRC-III sites within SRC-I and II sites can be planted, but losses should be anticipated and be judged acceptable in the overall management objective.

Wildlife. Red pine plantations provide little variety, and hence are generally unfavorable as long-term habitat for edge wildlife species such as deer, bear, hare, and grouse. The early stages of a plantation provide some habitat for some edge wildlife, but only briefly. Mature red pine stands are generally favorable for interior wildlife species such as squirrels, owls, and warblers (Ohman et al. 1978).

Openings in large pine stands, if properly managed and kept open for several years, can provide forbs, grasses, and shrubs that supply food, nesting sites, and shelter for edge wildlife. Tubbs and Verme (1972) and Ohmann et al. (1978) recommended wildlife openings be established in large stands, and McCaffery (1970) suggested that red pine not occupy more than 30% of an area to be beneficial to wildlife. The best places to create openings in a stand or leave openings during planting, according to Tubbs and Verme (1972), are excessively or poorly drained soils, on shallow soils, and in frost pockets. These areas have little advance reproduction and are the easiest areas to maintain as openings. Tubbs and Verme (1972) also recommended that the openings border trails and other timber types to provide a variety of vegetation and allow escape cover. Openings 0.4 to 4.0 ha (1 to 10 acres) in size are best, and several smaller areas are preferred over a few large ones. Irregular shapes provide longer perimeters and thus more edge vegetation, and are aesthetically more pleasing.

The SRC-III areas fit exactly the criteria suggested above for wildlife openings. As tree mortality occurs on these sites, irregular openings about 0.4 to 2.0 ha (1 to 5 acres) in size appear after the outbreak, favoring edge wildlife species. Small clumps of remaining pines provide ideal escape cover. Such sites can be managed to remain in the forb-grass-brush stage for many years. And, if such areas are identified prior to planting, they can be left unplanted to trees and be managed exclusively for wildlife.

The sawfly, then, can have a strong positive effect on development of edge wildlife habitat. Many of the edge species are also game species, so that proper management also enhances recreational opportunities.

Water yield and quality. Red pine trees have relatively high evapotranspiration and respiration losses, and thinning dense pine stands usually increases water yield (Urie 1971). Thus, SRC-III areas partly or completely denuded of trees by sawflies should have greater water yield, but since these areas usually occupy only a few acres, the increase would be small. Also, any changes would be for only a short duration because shrubs, grasses, and other vegetation will eventually compensate for the pines and trap as much or more water. Except for sand blows, which revegetate slowly, most areas commonly revegetate rapidly following such stand disturbances. Water yield changes on SRC-I and SRC-II areas would be insignificant because of the few trees killed and injured.

Sawfly-injured trees should not normally affect stream sedimentation and nutrient enrichment from waste products, unless the injury is extensive and adjacent to a stream, because of the relatively flat terrain and highly permeable soils characteristic of most red pine plantations. Water quality could be affected if a pesticide were used against the sawfly, especially if treated areas were adjacent to streams or lakes. The effect and duration of water quality change would largely depend on the pesticide and amounts applied. In general, for northern areas at least, the sawfly appears to have little or no long-term effect on water yield and quality, and only a slight short-term positive or negative effect under conditions of extensive stand change.

Recreation and visual quality. Red pine trees become more aesthetically pleasing as they age. The redheaded pine sawfly seldom attacks pole-sized or larger trees, and when it does, only a branch or two are defoliated. Young dying, dead, and defoliated trees are not aesthetically pleasing. Also, distorted trees left on the site after an attack may or may not be visually appealing. Visitors may avoid infested sites during the few weeks the larvae are active because of the negative visual impact or because of a nuisance factor. The large colonies of larvae are impressive but the larvae would only be a nuisance if they wandered in search of food. When someone encounters a sawfly colony devouring the foliage, reaction varies from non-interest to excitement or concern. Concern is often about the welfare of the tree, and the level of excitement depends on the number of insects present and tree's ownership. To some, an infestation may encourage nature study. Hunting opportunities may improve from the change in edge wildlife habitat following a sawfly outbreak. Fishing will probably change little unless there is a water quality change from silting or pesticide contamination.

All in all, the socioeconomic impact of the sawfly, from the standpoint of recreation or visual impact, can range from very negative to very positive depending on desires and attitudes of the people involved. Pesticide use would likely be justified in areas such as campgrounds, where people are generally repelled by pests, and avoided where the sawfly is a benefit or of little concern.

Management Guidelines

The redheaded pine sawfly can be controlled in pine plantations by preventive, cultural, and chemical means that are consistent with forest management practices and goals. We have seen that on certain sites, risk from the sawfly is low; on these sites a specific prescription or treatment will seldom be necessary. In high- or moderate-risk areas, however, a prescription and treatment may be needed if the sawfly is perceived as a problem and the benefits of treatment justify the costs. One must consider recreational, aesthetic, watershed, and wildlife values as well as forest products as integral parts of the benefit-cost analysis before impact is truly perceived and treatment decisions finalized.

The redheaded pine sawfly must be considered early in the planning stages and not dealt with only on an emergency basis when an outbreak occurs. The place to start is by rating potential planting sites as to sawfly susceptibility. Prevention and control practices should be provided for in the planting plan or prescription. And, the costs of prevention now versus emergency control later should be weighed.

Prevention of outbreaks may be the most cost-effective way of dealing with the sawfly. By limiting planting of pine to low-risk (SRC-I) and some moderate-risk (SRC-II) sites, sawfly damage can be minimized. This also means avoiding high-risk (SRC-III) areas, such as sites that support dense growths of bracken fern or sod, zones adjacent to hardwoods, fields with a high water table, frost pockets, and areas where soils are excessively poor in nutrients or have a very high or very low moisture-holding capacity.

Cultural practices can be used both for prevention and suppression of outbreaks, and any activity that improves the site or the tree's ability to use the site hampers the sawfly population. Destroying bracken fern by deep plowing or chemical means before or after planting will improve the site if the soil has adequate nutrients and water-holding capacity. Site treatments such as fertilization, irrigation, and drainage, although not normally feasible, may be a part of future forest management as the disposal of waste water becomes critical and intensive silvicultural programs become the norm. Breeding for sawfly resistance or more efficient site utilization might be feasible for jack pine or other hosts of the sawfly, but probably not feasible for red pine, which has low genetic variability. Release of parasites, predators, or pathogens might be used as well. We know that parasitization of adult sawflies increases following cultural improvement in a pine stand (Syme 1966). More information is needed on adequate releases of most natural enemies, but there is a virus that is effective against this sawfly. Viruses are generally easy to handle, store, and apply. Also, they usually affect only the target organism and, once established in an area, they persist for many years.

Suppression by chemical or mechanical means may be used effectively as a last resort when other measures are impractical and when adverse environmental impacts of the chemical are not significant. Chemicals should be directed against the young larvae before much defoliation occurs, and they can be spot-applied or broadcast depending upon the size of the infested area and number of trees involved. Mechanically destroying colonies of sawflies is possible when only a few trees are affected. Each colony can be knocked to the ground with a stick and the larvae stepped on.

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