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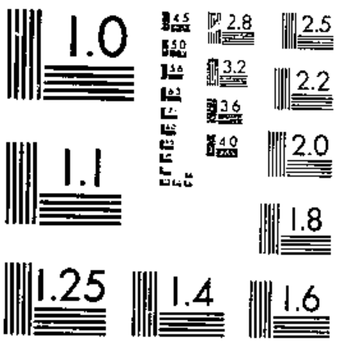

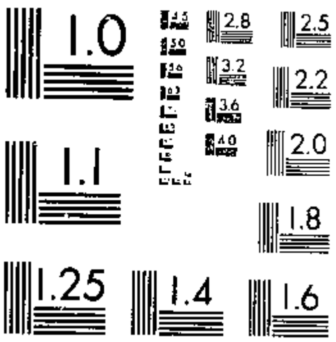

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The Larch Sawfly

Its Biology and Control

Technical Bulletin No. 1212

By A. T. Drooz
Forest Service
U. S. Department of Agriculture

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The Larch Sawfly, Its Biology and Control

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INTRODUCTION

The larch sawfly (*Pristiphora erichsonii* (Htg.)) is the most destructive insect enemy of tamarack (*Larix laricina* (Du Roi) K. Koch) and a potential threat to western larch (*L. occidentalis* Nutt.) and exotic species of *Larix* in North America. The insect feeds on the leaves; this reduces tree growth and may kill the tree. Between 1910 and 1926 an estimated 1 billion board feet of tamarack was killed in Minnesota alone (*43, pp. 7–8*).[3] More recently sawfly populations have increased to serious proportions throughout the heart of the tamarack range. Lejeune and Hildahl (*72*) reported that this outbreak arose in the Spruce Woods-Riding Mountain area of Manitoba about 1938. By 1955 it had encompassed most of the tamarack areas of Alberta, Saskatchewan, Manitoba, Ontario, Minnesota, Wisconsin, and the western part of Michigan's Upper Peninsula.

The problem is especially serious in the Lake States, for they contain about nine-tenths of the tamarack in the United States. Cunningham *et al.* (*22*) estimated the Lake States growing stock in 1953 at 19,900,000 cubic feet, with Minnesota containing 67 percent, Michigan 21 percent, and Wisconsin 12 percent of the total. The wood is fairly strong and usually straight, and its heartwood moderately resistant to rot. At one time it was sought for ship timber and fuelwood. Now it is used locally for ties, poles, posts, mine timbers, rough lumber, and certain types of pulp. Additional information on this species may be obtained from a report by Roe (*99*) in which he reviewed the silvical characteristics of tamarack.

Following the initial work by J. W. Butcher between 1949 and 1951, the author conducted a series of studies from 1952 to 1956 to determine the causes of the present outbreak, the role of parasites and predators of the larch sawfly, seasonal development from oviposition through the final larval instar, the value of several organic insecticides against the larvae, and the effects of

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[1] Now with the Pennsylvania Department of Forests and Waters.

[2] Maintained at St. Paul 1, Minn., in cooperation with the University of Minnesota.

[3] Italic numbers in parentheses refer to Literature cited, p. 45.

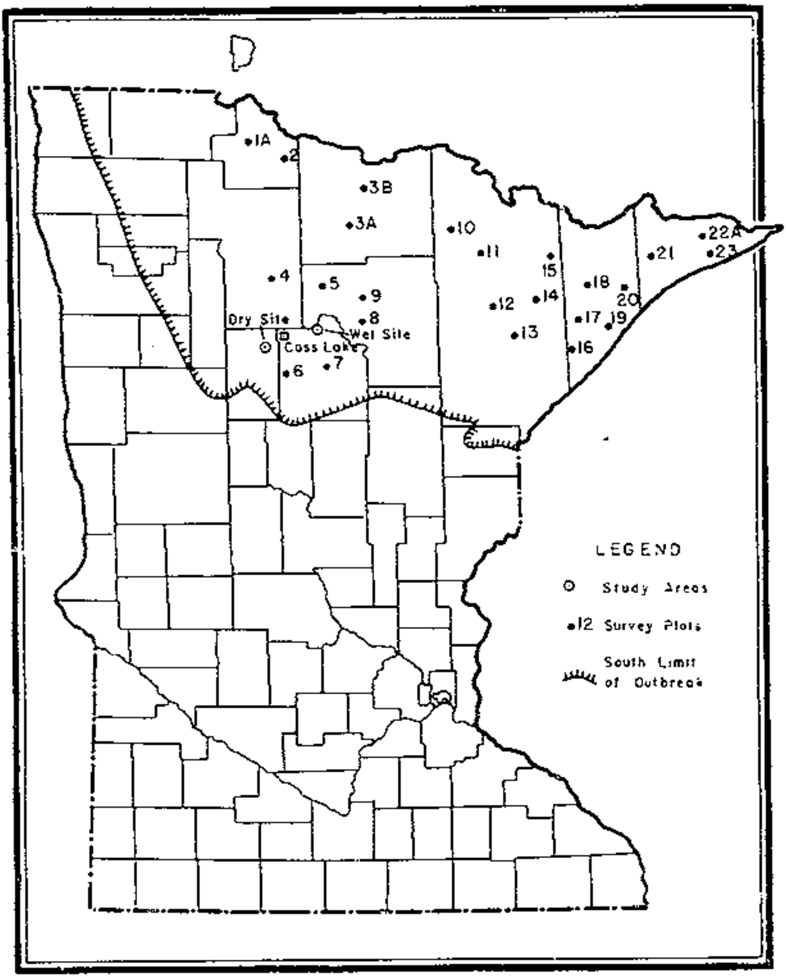

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FIGURE 1.—Area infested by the larch sawfly in Minnesota, in 1956, and locations of study areas and survey plots.

repeated defoliation on tamarack vigor. Ecological studies were also conducted on a limited scale at two permanent plots. In addition, defoliation estimates and cocoon collections were made at 25 survey points in Minnesota (fig. 1).

The results of these investigations are reported herein. To round out the information on the larch sawfly, material is included from world literature.

Some preliminary sections discuss the history of outbreaks; give an account of the distribution, host preference, and synonymy of the insect; and describe the life stages; some observations of the author are included. Research results are then incorporated into sections on the life history and habits, seasonal development, damage, and control of the insect.

SYNONYMY

The scientific name of the larch sawfly, or large larch sawfly as it is called in Europe, has been the subject of many revisions. To facilitate recognition of the names applied to the insect, the following list has been prepared:

Nematus Jurine: *leachei* Dahlbom (Nomen nudum) (*23, p. 10*); *leachii* Dahlbom (*24, pp. 27–28*); *erichsonii* Hartig (*47, pp. 187–188; 25, pp. 220–221*); *erichsoni* Hartig (*2, pp. 102–103; 16, pp. 50–51; 45*); *notabilis* Cresson (*18, p. 7*; and *19, pp. 158–159*).

Tenthredo Linnaeus: (*Nematus*) *erichsonii* Hartig (*95, p. 121*).

Lygaeonematus Konow: *erichsoni* Hartig (*65, pp. 233, 238, 247*; and *66*); *erichsonii* Hartig (*81, pp. 111–112*).

Holcocneme Konow: *erichsoni* Hartig (*66, pp. 61–62*).

Nematus Panzer: *erichsoni* Hartig (*33, pp 368–370*).

Pristiphora Latreille: *erichsonii* (Hartig) (*100, pp. 84, 37*).

Although *Nematus leachii* Dahlbom has priority, it has been used rarely in over 120 years, and it has been all but officially suppressed.

In Canada and the United States the scientific name applied by Ross, *Pristiphora erichsonii* (Htg.), has been accepted, but in other countries some of the earlier synonyms are used.

HISTORY OF OUTBREAKS

Europe.—The earliest records of the larch sawfly were made by Dahlbom (*24, pp. 27–28*) in 1835 in Sweden and, according to Thielmann (*107*), by Saxesen in Germany during the same year. A serious outbreak was underway in Holstein in 1838, and light infestations occurred near Kiel in 1874 and near Sonderburg in 1884. No further mention was made of the insect in Germany until its presence was recorded in Bavaria in 1933 (*107*). In Denmark an outbreak on the island of Bornholm lasted from 1839 to 1848, killing many plantation larch (*8, pp. 423–426*). This was the earliest mentioned larch mortality attributed to the sawfly. In the Västernorrland area of Sweden, damage by the insect occurred between 1913 and 1915 (*109*). Although the sawfly has appeared sporadically on the Continent, it has rarely killed trees. Indeed, McComb (*76*) does not mention it as a serious pest of larch in Europe.

Great Britain.—Accounts of the sawfly in Britain depict a different pattern of infestation from that on the Continent. The insect created serious concern about the growing of *Larix* spp., as a result of heavy tree losses incurred either through the continuing outbreak, premature salvage cutting, or a combination of these. Recorded as an uncommon species prior to 1884 (*16, pp. 50–51*), the larch sawfly made its first known serious population increase at Cumberland in 1904 (*78*). Between 1905 and 1906, it defoliated larch throughout several plantations. Most severely defoliated was a plantation at Dodd Wood near Keswick. As a result of this damage, 3,000 trees on 200 acres had been cut by 1908, and twice that number remained to be felled (*52*). Hickson (*55*) reported that on the slopes of Skiddaw 30,000 larch were removed in 1912. He believed that much of the cutting was unnecessary, and that larch could withstand 2 or more years of severe attack. In 1914 Middleton (*83*) reported details of the outbreak in the Lake District and Wales, including the locations of the infestations and data on parasitism. Among the plantations he examined in 1912 was Dodd Wood; he remarked that the tree crowns were very thin and that part of the Wood had been cut. This seems to corroborate Hickson's belief that much of the timber salvage was premature, since many weakened trees remained alive. Hanson (*46*) stated that the outbreaks subsided after 1913, apparently because of disease and parasites, and that no larch sawflies were reported between 1920 and 1933 in Great Britain. He found cocoons in the Lake District in 1933 and 1934 and light populations of the insect in 1949. The infestations remained light between that year and 1953 when Crooke (*21*) noted that the sawfly had practically disappeared.

The outbreak in Britain between 1904 and 1913 stands as the most costly in tree mortality of any outbreak outside North America.

Siberia.—Polyakov (*91*) described a severe infestation near Omsk in western Siberia. Informants told him the sawfly was present in 1913, and he reported complete defoliation from 1918 through 1921. No mention was made of tree mortality.

North America.—The larch sawfly has been a pest in North America with certainty since 1880. In that year Cresson (*18*) named an adult sawfly, collected in Massachusetts by Henshaw, as *Nematus notabilis*, a synonym for *Pristiphora erichsonii* (Htg.). The next year Hagen (*45*) published a note concerning larvae sent him by Sargent in 1880 from European larch at the Arnold Arboretum near Boston. The larvae were determined as those of the larch sawfly. Criddle (*20*) and Coppel and Leius (*17*) have suggested that Audubon reported an insect, presumably the larch sawfly, as destroying tamarack in Maine early in the 19th century. Actually, Audubon (*4*) recorded statements by a lumberman to the effect that a green caterpillar, three-quarters of an inch in length, not only killed the tamarack but "spruces, pines, and other firs." This record does not positively identify the larch sawfly or permit its recognition in North America prior to the middle or latter part of the 19th century.

In the United States the outbreak of the 1880's was reported by Packard (*89*) and Lintner (*73, 74*). Heavy defoliation in Maine in 1881 had been called to Packard's attention, and in August 1882 he first saw the effects of the feeding. About the same time he noted at Errol, N. H., "numerous trees which had been killed by the worms." In the light of present knowledge concerning the number of successive years of defoliation needed to kill tamarack, either heavy populations of the sawfly probably had been present for several years or radical detrimental changes had occurred in the tamarack environment.

Lintner reported the course of the infestation in New York State between 1883 and 1889 but did not mention tree mortality. He later stated that he believed the annual depredations of the sawfly had killed trees in Essex County in 1891.

The outbreak in Canada followed much the same course as that in the United States. The insect was reported around Quebec City in 1882 (*93*), and an outbreak began in a 640-acre stand near Bury, Quebec, in 1883 and continued to 1891 (*34, p. 17*; and *36*). This stand, which by 1891 had suffered 98 percent mortality, was 200 years old and had 40 merchantable trees per acre averaging 24 inches butt diameter. In 1885 defoliation was reported from Ottawa east to New Brunswick (*35*). The insect was found in southern Ontario in 1888 (*60*), and by 1903 nearly all the larch trees in the Abitibi region had been destroyed by the sawfly (*62*). The gap between eastern infestations and those in the vast tamarack swamps in the Lake States was closed in 1905 (*113*) when defoliation was discovered in the Upper Peninsula of Michigan. The insect was abundant and destructive here in 1908 and was also reported from Wisconsin (*114*). By this time outbreak conditions had been observed between Lake Nipigon and Fort William and Port Arthur, Ont., near the northeast extremity of Minnesota (*7*). The insect had spread almost to Winnipeg, Manitoba, by 1909 and to Battleford, Saskatchewan, by 1910 (*54*).

Minnesota lumbermen were concerned about the insect in 1908, according to Ruggles who noted larch sawfly activity in north central Minnesota in 1909. He concluded, from the dead and dying timber, that the pest had been present 2 or 3 years earlier (*101, 102*).

The westward spread of the sawfly continued. It was reported on a new host, western larch, near Fernie in southeastern British Columbia in 1930 and had reached the western limit of this species, near Vernon and west of the Rocky Mountains, in 1942 (*59*). Defoliation of western larch on the Flathead National Forest, Mont., was reported in 1935 (*27*). According to McLeod (*80*) the British Columbia infestations subsided without seriously injuring the trees.

Aside from recurring outbreaks following the earlier ones in Canada and the United States, the sawfly was found in Vermont (correspondence) in 1913 and in Connecticut in 1915 (*9*).

The return of the larch sawfly problem to central Canada and the Lake States was foreshadowed by infestations arising in the Spruce Woods-Riding Mountain area of Manitoba about 1938 (*72*). By 1944, larch sawfly activity was serious in Manitoba (*72*) and was increasing in Saskatchewan (*97*). Atwood (*3*) noted medium to heavy attack in the Kenora-Dryden area of Ontario, north of Minnesota, and suggested that this might be an extension of the Manitoba outbreak. Stands in eastern Alberta were infested by 1948, and the outbreak had been spreading to the north and west for several years previously (*1*).

The presenc of the sawfly in Minnesota in 1939 and 1940 was reported by Ho..son (*56, 57*), but populations remained low until

1945 when a spot outbreak was found near Pencer in the northwestern part of the State (*58*). In 1946 a widespread increase was noted, and by 1947 outbreak conditions were evident throughout all northern Minnesota. Aerial surveys conducted since 1949 have shown that approximately 300,000 acres of tamarack have annually been moderately to completely defoliated.

The sawfly was detected in Wisconsin in 1949,[4] and in western Upper Michigan by 1951.[5] Evidence of feeding in northern Wisconsin and the western part of Upper Michigan was still spotty in 1952 and 1953, but by 1954 heavy outbreaks were developing in these areas. Populations remained light in Lower Michigan.

Thus the history of outbreaks in North America can be summarized as follows: The passage of 62 years, from 1880 to 1942, saw the larch sawfly cross North America from east to west, causing tremendous losses of merchantable tamarack and becoming a potential threat to western larch. Following the original infestation, outbreaks were scattered until about 1938, when a great wave of defoliation began in western Manitoba. By 1955 it stretched from central Alberta to eastern Ontario and encompassed the stands of northern Minnesota, northern Wisconsin, and western Upper Michigan.

DISTRIBUTION OF THE LARCH SAWFLY

The larch sawfly is "truly a Holarctic species" (*17*), since its presence has been reported across North America and in Japan, Siberia, and Europe, including Great Britain. Lintner (*73*) correctly predicted that the range of the sawfly would eventually match that of larch in the United States and Canada (fig. 2). In Canada it can be found in every Province from the Atlantic Ocean to the western range of western larch in British Columbia. The larch sawfly has been reported in all the northern tier of States from New England to Washington, except Ohio, Indiana, and Idaho, and it could possibly be found in these States if intensive search were undertaken. It has been found in southern Pennsylvania on Japanese and European larch, and in 1956 defoliated the latter species in the Monongahela National Forest at Bartow, W. Va. The sawfly is present in British Columbia to the borders of Montana, Idaho, and Washington (*59*). The north-south range is delimited by about the 38th degree of latitude to just north of the 60th.

The insect has been collected all over northern Europe—Norway, Sweden, Denmark, Holland, France, Germany, Austria, Poland, the Baltic States, Finland, and Russia (*2, 8, 17, 26, 32, 61, 64, 104, 107, 109, 115*).

Very little is known about the distribution in Asia, but an outbreak has been described near Omsk in western Siberia (*91*), and the insect has been reported on Honshu, Japan (*105*).

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[4] Unpublished data on file at Lake States Forest Experiment Station; collected by Charles B. Eaton, U. S. Bureau of Entomology and Plant Quarantine.

[5] Unpublished data on file at Lake States Forest Experiment Station; collected by Charles B. Eaton, James W. Butcher, and R. C. Heller, U. S. Bureau of Entomology and Plant Quarantine.

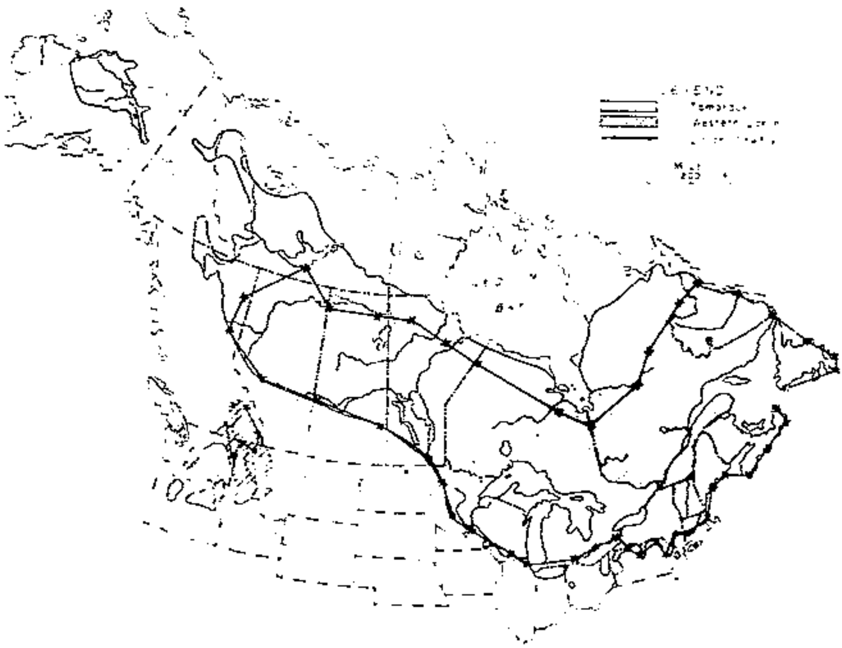

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FIGURE 2.—Geographic distribution of the larch sawfly and its native hosts in North America.

HOST SPECIES AND PREFERENCE

The larch sawfly develops and completes its life cycle on *Larix* species. Riley and Howard (*98*) reported that insects determined as larch sawfly caused great damage to eastern hemlock, *Tsuga canadensis* (L.) Carr., in 1891 in Elk and Potter Counties, Pa., but this is the only report of tree species other than *Larix* being attacked. Possibly this host record resulted from mistaken identity or the use of a local common name. However, in July 1956 the author observed fallen fourth- and fifth-instar larvae feeding upon wilding seedlings of jack pine, *Pinus banksiana* Lamb., near Bena, Minn. He also found that the larvae would feed on seedlings of Chinese golden larch, *Pseudolarix amabilis* (Nels.) Rehd. Adults released on the golden larch attempted oviposition, but possibly because of physical factors relating to the small size of the seedlings the results were negative.

Listed are native and exotic species of *Larix* attacked by the sawfly in the United States and Canada:

Tamarack	*Larix laricina* (Du Roi) K. Koch
Western larch	*L. occidentalis* Nutt.
European larch	*L. decidua* Mill.
Japanese larch	*L. leptolepis* (Sieb. and Zucc.) Gord.
Siberian larch	*L. sibirica* Ledeb.

Subalpine larch, *Larix lyallii* Parl., is the only one of the three native larch species not known to be a sawfly host. The reasons for this are not clear, but the tree is a high-altitude species growing in the extreme environment of timberline isolated from western larch. Possibly the sawfly does not thrive under these conditions; the tree may have some resistance to the insect; or, lacking close study, the susceptibility of subalpine larch has never been observed.

In continental Europe the sawfly has attacked European larch and Siberian larch. Larch is not native to Great Britain; it was introduced into England and Scotland in the 16th and 17th centuries respectively (*76*). The following species are hosts of the sawfly in Great Britain: European larch, Japanese larch, Siberian larch, and the Dunkeld hybrid (*Larix eurolepis* Henry). The last is a natural hybrid originating in Scotland.

Host information from Asia is scant, but defoliation of Siberian larch has been reported from western Siberia and defoliation of Japanese larch from Japan.

There is little reliable information concerning any possible preference of the insect for a particular species of *Larix*. The ability of the insect to rise to outbreak populations on several species of larch and the widespread natural occurrence of host species in North America have probably relegated host preference studies to an inferior position. One test was made in a 5-year-old plantation of mixed blocks of European larch and tamarack on the Argonne Experimental Forest near Hiles, Wis., in 1955. This was the first year of heavy attack on the plantation. The results showed a preference for tamarack over European larch as follows:

Defoliation:	*Tamarack*[1] *(percent)*	*European larch*[2] *(percent)*
None	22.7	42.4
Trace	5.6	11.7
Light	20.8	26.7
Medium	11.6	10.3
Heavy	39.3	8.9
Total	100.0	100.0

[1] Tamarack—216 trees.
[2] European larch—146 trees.

On the other hand, Hewitt (*54*) believed that European larch was favored, but that the insect also fed upon Japanese, Siberian, and eastern (tamarack) larches. At Hiles only about 19 percent of the European larch was moderately to heavily defoliated, whereas over 50 percent of the tamarack was so classed. Only 23 percent of the tamarack was not attacked as compared to 42 percent of the European larch.

DESCRIPTION OF LIFE STAGES

Adult

The adult female is 6 to 9 millimeters long, with black antennae and body. The antennae are filiform and about half the length of the body and have nine segments. The abdomen, which has a broad orange band, tapers sharply toward the rear and is keeled longitudinally along the midventral line. The male, which is 5 to 9 millimeters long, has yellowish antennae and an orange abdominal band. The abdomen, however, is somewhat cylindrical and is rounded at the rear.

Egg

The eggs are subcylindrical with rounded ends. They are translucent when laid, but in a few days dark eye spots become visible.

Larva

At hatching the larva is about 3 millimeters long, with a dusky head, which later becomes brownish. The abdomen is creamy white but becomes bright green lengthwise as soon as feeding occurs and the gut is full. As a larva develops, its head becomes jet black, and the body is whitish beneath and gray green along the back. In the last larval instar the length is about 16 millimeters. Head capsule widths are as follows: First instar, 0.57 millimeters ± 0.018; second instar, 0.80 ± 0.027; third instar, 1.16 ± 0.019; fourth instar, 1.62 ± 0.035; fifth instar, 2.12 ± 0.037 (*29*). There appears to be no overlapping in these widths.

The internal anatomy of this species has been described by Maxwell (*82*).

Cocoon

The brown cocoon consists of a tough papery material of single-wall construction (*118*). It is cylindrical, has rounded ends, and varies in length from 8 to 11 millimeters and in width from 3 to 5 millimeters.

Pupa

The exarate pupa is glossy white except for reddish-purple eyes. As the pupa develops, pigmentation changes to the color of the adult.

LIFE HISTORY AND HABITS

The life history and habits of the sawfly in Minnesota were studied in an area of general and heavy infestation from 1952 to 1955.

The larch sawfly has a prolonged adult emergence—from the middle of May into August. The eggs are laid almost exclusively in the new shoots, and the newly hatched larvae move to the leaves of the older shoots and feed on them. When feeding is completed in the fifth instar, the larvae fall to the ground, enter the organic surface layer to various depths, and spin cocoons where they spend the winter as prepupae. Pupation occurs from late spring to midsummer.

Adult Emergence

Upon transformation from the pupal stage, the adult cuts its way out of the cocoon with its mandibles and crawls through the moss or ground litter to the surface. The time of emergence depends on seasonal temperatures and, according to Lejeune, Fell, and Burbidge (*71*), on moisture conditions during the cocooning period. The peak period of this activity in Minnesota is in June and generally occurs 2 to 3 weeks after the beginning of emergence. When the season is early, as in 1952 and 1955, emergence is nearly complete by July 1. If the season is late, emergence may last another 2 weeks, but only occasional adults issue as late as August.

In the study area in northern Minnesota emergence was noted on May 22, 1952, and on May 17, 1955. At slightly below normal average temperatures in April and May of 1953, the first field emergence was not noted until June 2. Under somewhat colder conditions in 1954 the first adults were noticed on June 7. Normally, there is one generation annually. However, small numbers of second-generation adults are produced some years (*96, 103*). They never exceed 2 percent of the total emergence.

Reproduction

Reproduction is parthenogenetic. However, mating in cages has been observed occasionally. Thielmann (*107*) stated in 1939 that up to that time only Tischbein had observed mating pairs. Coppel and Leius (*17*) and Muldrew[6] also reported the rare occurrence of mating. Smith (*106*) reported that two pairs were induced to mate at the Fredericton, New Brunswick, laboratory. In none of these cases was the transfer of sperm confirmed, but the sex ratio of progeny from the insects tested was not different from that of the parents.

Sex

Various reports of sex ratio are as follows: One male from 58 adults reared from material collected in central New York in 1888 (*73*); 3 percent males from 125 reared adults in Minnesota (*102*); and 0.7 percent males from specimens reared in the Maritime Provinces (*96*). Other estimates conclude that males constitute between 1 and 4 percent of adults in Minnesota (*44*); 0.67 percent in England (*52*); and 4 percent in European Russia (*26*). The proportions of males in May collections from northern Minnesota from 1953 to 1956 were 1.2, 1.7, 1.8, and 1.0 percent respectively.

Smith (*106*) investigated the cytogenetics of the insect and reported that the males were haploid (8 chromosomes in the spermatagonia) and the females diploid (16 chromosomes in the oognia and somatic tissue). He hypothesized that occasional failure of autofertilization produced males, and that high temperatures might increase the proportion.

[6] J. A. Muldrew, entomologist, Forest Biology Laboratory, Winnipeg, in conversation with the author in 1955.

Oviposition

The adult female voids the meconium soon after issuing from the cocoon and may oviposit soon thereafter. After alighting on a branch she searches for a suitable new shoot, vigorously palpating the antennae and, when such a shoot is found, moves to the underside. With the tip of her abdomen facing the tip of the twig, she arches her abdomen and cuts a slit into the tender cortex or bark to receive the eggs (fig. 3). They are laid chainlike along the twig and will be almost covered by the twig tissues (fig. 4). Occasionally they may be inserted in the bark of the previous season's twig near the point where a new shoot has arisen.

Fecundity and Egg Cluster Size

Wide ranges in egg production and in egg cluster size occur among larch sawflies. Food quality and quantity apparently exert a marked influence on fecundity, whereas the length of the new shoot used for oviposition may restrict the egg cluster size. Shoot growth depends upon inherent and environmental influences, such as weather, accumulated moisture in the site, and defoliation history.

Oviposition studies by Reeks (*96*) during the 1933–42 outbreak in the Maritime Provinces showed the following fecundities for 1937, 1941, and 1942: 115.5 ± 20.9, range 60 to 206 eggs; 71.3 ± 6.0, range 24 to 100; and 52.1 ± 4.2, range 20 to 90. Dissections

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FIGURE 3.—Larch sawfly ovipositing.

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FIGURE 4.—New tamarack shoot bearing well-developed larch sawfly eggs.

after oviposition revealed an average of 7 remaining oocytes each year. Heron (*51*) dissected 15 females each from starved and nonstarved field populations. The mean reproductive capacity of the individuals from the starved population was less than 60 percent of that of members of the nonstarved population. Graham (*44*) dissected 23 adults from Minnesota field collections and found that 10 adults contained 41 to 80 eggs, 7 contained 81 to 100, 5 contained 101 to 120, and 1 had more than 120. Butcher[7] dissected larch sawfly adults from Minnesota in 1949 and 1950 and found that the number of eggs varied from 40 to 90, the mode falling between 65 and 70.

Adults from 4 field-collected cocoons were released individually on caged 3-foot tamarack seedlings in northern Minnesota in July 1953. Totals of 117, 103, 78, and 67 eggs were laid. The sawfly that laid 117 eggs lived 7 days; the others were not found.

Egg cluster size varies widely. Wallace (*117*) worked with over 28,000 shoots from trees with different defoliation histories on many areas in Ontario. Under these conditions the mean lengths of the shoots with oviposition scars ranged from 22 to 60 millimeters, and Wallace found that the mean number of eggs varied from 14 to 31. Heron (*51*) calculated the mean number of eggs per shoot from shoots collected in areas where populations had been light and heavy during recent years. The curled shoots from the light populations had a mean length of 44.4 millimeters

[7] Unpublished data on file at Lake States Forest Experiment Station; collected by James W. Butcher, U. S. Bureau of Entomology and Plant Quarantine.

± S.E. 2.6 and contained 15.5 eggs ± S.E. 1.3, while those in the heavy populations had a mean length of 49.8 millimeters ± S.E. 2.4 and contained 18 eggs ± S.E. 1.3 He believed that the sample was too restricted to generalize from it, but that no applicable differences were demonstrated between the mean number of eggs per shoot. Polyakov (*91*) reported 13 to 50 eggs per shoot on Siberian larch.

Occasional shoots about 20 millimeters long from trees in the Minnesota study area were observed to contain from 1 to 10 eggs. Low egg deposition was common early in the period of shoot elongation and during seasons when the weakened trees did not produce vigorous shoots. Counts of oviposition scars on the four tamarack seedlings caged with sawflies, previously mentioned, showed 83, 19, 15, 68, 18, 17, 35, 34, 9, 47, and 20 eggs per shoot. The proper order of the oviposition is not known. The four sawflies used an average of 2.8 shoots each, and their clusters averaged 33.2 eggs per shoot, with a range of 9 to 83, on these vigorous tamarack seedlings.

Hatching

The incubation period for larch sawfly eggs lasts from 7 to 10 days. The expanding eggs cause the oviposition slits to widen, thus exposing a portion of the eggs. The new larvae escape by cutting the eggshells with their mandibles. Then they draw themselves out aided by their tarsi and twisting body movements. All the eggs in a cluster hatch in 2 to 3 hours (*88*).

Feeding

After hatching, some of the first-instar larvae may nibble the single leaves on the new shoots. All of them, however, move back to feed on the leaves comprising the false whorls (fig. 5). The first-instar larvae eat the leaves only along the edges, and the midribs dry and turn brown. Feeding continues in colonies, which may be disbanded by food shortage, weather, or predation. Larvae of the succeeding instars consume the entire leaf. The appearance of infested trees suggests that feeding proceeds from the top down and from the crown periphery inward, probably because of the high proportion of new shoots at the tops and their concentration at the branch edges. The feeding pattern in weakened trees with thin crowns is irregular, depending on the distribution of adventitious shoots, which are principal oviposition sites in these cases.

Frass dropping from larvae of the first three instars is very fine and is difficult to observe in the forest. When fourth- and fifth-instar larvae are prevalent, the frass can be heard falling on the undergrowth. Measurement of frass particle size was not taken, but it is quite simple to distinguish the instars of the larvae responsible for the various sized frass pellets. All that is needed is a reference collection of pellets from larvae carefully reared by instar.

F-486948

FIGURE 5.—Newly hatched larvae move back primarily to feed on leaves of older shoots. Note twig curl caused by oviposition injury.

Hibernation

When the fifth- or final-instar larvae have completed feeding, they drop to the ground, crawl into the moss or duff, and spin their cocoons. Caged larvae formed their cocoons in 5 to 12 hours.

The winter is passed as prepupae in the cocoons. Normally they remain cocooned for about 10 months, but some may remain for 2 or 3 winters. In north central Minnesota during these studies only 1 to 3 percent spent an additional year in diapause. Graham (*44*) reported that about 5 percent remained in diapause over 2 winters and less than 2 percent over 3 winters in northern Minnesota in 1924, 1925, and 1929. Reeks (*96*) found similar extended diapause in the Maritime Provinces. There is a suggestion that prolonged diapause is related to low summer temperatures. Polyakov (*91*) stated that at Omsk in Siberia 50 percent of the prepupae continued in diapause more than 1 winter.

Fresh cocoons were observed in the field in northern Minnesota as early as June 24, 1952, and June 21, 1955. Under somewhat cooler conditions, first cocoons were found on July 4, 1953, and July 5, 1954. The peak of cocooning activity ranged from the first to the third week of July, depending on seasonal temperatures, and by the first week of August nearly all the larvae had cocooned.

Pupation

The pupae (fig. 6) develop within the cocoons from late spring to midsummer. There is very little information concerning the duration of the pupal stage, but Dobrodeiev (*26*) and Polyakov

F-485949

FIGURE 6.—Exarate pupa of the larch sawfly, with cast larval skin and head capsule at caudal end.

F 485950

FIGURE 7.—Fifth- or final-instar larch sawfly larvae feeding on tamarack.

(*91*) in Russia stated that this period lasted 7 to 8 and 8 to 10 days respectively. After pupation the adults emerge and the life cycle begins again.

SEASONAL DEVELOPMENT OF THE LARCH SAWFLY

Because of the complex pattern of seasonal development, laboratory as well as field rearing studies were conducted to acquire a truer understanding of the life history. Individual larval colonies were reared in the laboratory, and oviposition, larval development, and frass-drop data were recorded from field collections.

Laboratory Studies

Larch sawflies were reared in an insectary at Cass Lake, Minn., in 1952 (*5*) and within a building at prevailing summer temperatures in 1953. Individual shoots with eggs were placed in vials of water to keep them fresh. Glass lamp chimneys served as cages for the separate shoots. Nine cages were set up in 1952 and 10 in 1953. Records were kept twice daily, and foliage was added as needed. The larvae were removed at each molt and put into fresh cages. The frass was separated by instar, ovendried, and weighed on an analytical balance.

The results of the rearings are presented in table 1. Larval mortality amounted to 26 percent in the insectary and 95 percent in the building. The primary cause of the latter was judged to be high temperature. Either direct sunlight or prolonged temperatures somewhat above 80° F. proved lethal to the sawfly. Under the conditions which prevailed, the larval stage lasted from about 2½ to 3½ weeks, and over 80 percent (by weight) of the frass was produced by fifth-instar larvae. Similar results were reported by Heron (*50*) in Canada. Because of the large quantity of foliage ingested by the fifth-instar larvae, defoliation becomes evident when they are prevalent (fig. 7).

Field Studies

Weekly branch samples and 48-hour frass samples were collected at 2 field plots during 4 field seasons (1952-55) and provided the basis for the field study of larch sawfly activity. One of the plots is referred to as the "dry site" because it was located in an area of decayed peat, had a cover of herbaceous plants and shrubs, and was characterized by the rapid disappearance of snow water in the spring. The other one is referred to as the "wet site." It was located in a seepage area with a ground cover of sphagnum mosses, pitcher plant, sedges, and Laborador-tea.

TABLE 1.—*Duration of larch sawfly larval stadia and relative frass weight per stadium*

1952

Instar	Number of larvae in test		Duration of stadia in days		Frass yield per larva	
	At start	At end	Mean	Range	Milligrams	Percent
I	81	75	2	2–3		
II	75	73	3	3–4	12.7	5.3
III	73	71	2	2–3		
IV	71	66	4	4–5	29.6	12.3
V	66	60	6	5–6	197.6	82.4
Total			17	16–21	239.9	100.0

1953

Instar	At start	At end	Mean	Range	Milligrams	Percent
I	154	69	3	1–5	.9	.3
II	69	45	3	2–5	1.8	.6
III	45	24	4	3–5	12.7	4.4
IV	24	20	4	3–5	33.0	11.4
V	20	7	10	6–13	241.0	83.3
Total			24	15–33	289.4	100.0

F-485951

FIGURE 8.—Branch sampling of 50-foot tamarack, northern Minnesota, July 1955.

F-485952

FIGURE 9.—Collecting frass from trap in tamarack stand.

Branch samples were taken from each of 5 dominant trees about 2 chains (132 feet) apart in each area. Two branches about 6 feet long were removed from the middle third of each of the 5 crowns (fig. 8). In the laboratory, data were taken on the total number of new shoots one-half inch long or longer that were with or without oviposition injury, on the number of egg clusters hatched or unhatched, and on the number of larvae present according to instar.

Frass traps were established in each plot under 15 dominant or codominant trees about 2 chains apart. Each trap was an inverted cone with a base 2 square feet in area (fig. 9).

Plot establishment was late in 1952, and the reconstruction of events at the dry site was not satisfactory for that reason. Nevertheless the data are presented so that certain aspects of seasonal development may be compared with 1955, the year weather and shoot production were similar to 1952. Very little sawfly activity occurred at the wet site during 1952 because of flooding during the preceding year; records were so scant as to preclude their use.

The weekly field population and 48-hour frass data were calculated on the basis of percent of season's total, and these percentages were constructed cumulatively on arithmetic probability paper. The resulting curves, plotted at 4-day intervals, were transferred to cross-section paper. The mean and standard deviations (S. D.) of seasonal phenomena were computed for each set of data. This information was projected from a common date, April 30 (table 2), as the insect would still be in the cocoon at this date in northern Minnesota. Weather data for the field seasons are given in table 3.

Oviposition activities began about the same time at both plots, from the middle of May until the first week of June, but generally increased at a more rapid rate at the plot on the dry site. The close similarity of patterns of sawfly development at the two plots in 1953 is believed to be related to high precipitation (table 3). Lejeune *et al.* (*71*) have demonstrated that flooding retards development in the cocoon.

Mean monthly temperatures varied slightly below and above normal, and precipitation was well above normal during the spring of 1953. The date of average oviposition occurred only about a day later, June 22, at the wet site. The population means for the various larval instars fell 4 to 6 days later than at the dry site, and the frass-drop mean was 6 days later (table 2).

TABLE 2.—*Larch sawfly development and frass drop in northern Minnesota (days to mean development and frass drop were computed from April 30)*—Continued

Year and Item [1]	Dry site		Wet site	
	Mean	Standard deviation	Mean	Standard deviation
	Days	± *Days*	*Days*	± *Days*
1952:				
Ov	48.6	4.8	....	....
I	50.1	4.8	....	....
II	51.5	5.0	....	....
III	53.2	5.4	....	....
IV	54.7	5.6	....	....
V	57.6	5.8	....	....
Fr	62.7	5.5	....	....
1953:				
Ov	51.4	6.9	52.8	7.0
I	55.4	6.6	59.9	6.2
II	58.4	7.0	64.2	5.9
III	61.4	7.0	67.2	5.3
IV	65.8	6.7	69.7	4.2
V	69.9	7.0	74.0	5.0
Fr	75.4	7.6	81.2	4.6
1954:				
Ov	46.5	7.5	53.8	8.5
I	54.0	7.3	59.4	8.2
II	56.9	7.1	63.4	8.0
III	60.2	7.1	68.0	7.3
IV	65.7	7.8	72.7	6.9
V	71.6	7.5	77.9	6.3
Fr	74.2	7.8	80.2	5.6

See footnote at end of table.

TABLE 2.—*Larch sawfly development and frass drop in northern Minnesota (days to mean development and frass drop were computed from April 30)*—Continued

Year and Item [1]	Dry site		Wet site	
	Mean	Standard deviation	Mean	Standard deviation
	Days	±*Days*	*Days*	±*Days*
1955:				
Ov	37.4	6.3	42.3	7.6
I	38.5	5.7	47.8	6.3
II	44.6	5.3	52.3	5.4
III	46.3	5.4	55.9	5.3
IV	49.6	5.4	60.4	4.7
V	54.1	5.2	64.6	4.8
Fr	58.4	6.6	67.8	4.6

[1] Items refer to sawfly development and frass:
Ov = oviposition
I through V = the 5 larval instars
Fr = frass

TABLE 3.—*Weather data, Leech Lake Dam, Minn. Latitude 47° 15′ N, longitude 94° 13′ W, elevation 1,301 feet*[1]

AVERAGE MONTHLY TEMPERATURES (DEGREES F.) AND DEPARTURES FROM NORMAL

Year	April		May		June		July	
	Temperature	Departure	Temperature	Departure	Temperature	Departure	Temperature	Departure
1952	45.2	5.4	53.8	1.4	65.4	2.9	67.2	−0.3
1953	37.5	−2.3	52.9	.5	64.5	2.0	67.1	−.4
1954	38.3	−1.5	48.2	−4.2	63.7	1.2	67.7	.2
1955	48.0	8.2	57.9	5.5	64.2	1.7	72.1	4.6

AVERAGE MONTHLY PRECIPITATION (INCHES) AND DEPARTURES FROM NORMAL

Year	Precipitation	Departure	Precipitation	Departure	Precipitation	Departure	Precipitation	Departure
1952	0.52	−1.08	0.59	−2.37	5.85	1.94	9.14	5.63
1953	3.16	1.56	6.30	3.34	4.60	.69	5.62	2.11
1954	2.71	1.11	3.08	.12	1.63	−2.28	9.52	6.01
1955	.96	−.64	4.53	1.57	2.24	−1.67	9.03	5.52

[1] This weather station is 7 miles south of the wet-site plot and 23 miles east of the dry-site plot.

In 1954 springtime weather was the coolest of the years under consideration; May–June precipitation was below normal. At the wet site mean oviposition was about 7 days later than at the dry site, larval development 5 to 8 days later, and frass drop 6 days later (table 2).

Temperatures in April and May of 1955 were well above normal, and precipitation was below normal in April and not excessively above normal in May. The sawfly began ovipositing about 2 weeks earlier than in the preceding 2 years. Mean oviposition at the dry and wet sites respectively was attained 14 and 11 days ahead of 1953 and 9 and 12 days ahead of 1954. There were 5 days' difference between the plot means in 1955, with the wet site again lagging. Mean larval development at the wet site followed that at the dry site by 8 to 11 days, and the frass-drop mean occurred about 9 days later.

The length of time between mean first- and fifth-instar populations was similar at both plots within each season but varied somewhat between years. It was 14, 18, and 16 days respectively for 1953, 1954, and 1955.

Larval drop was completed at the dry and wet sites 16 to 21 days after the cessation of oviposition. When oviposition was early and heavy, as in 1952 at the dry site and in 1955 at both plots, few larvae could be found after July 17. Nearly all trees were completely defoliated during these 2 years. Food was not a limiting factor during the 1953 and 1954 seasons as it was in 1952 and 1955. Average monthly temperatures in June and July were close to normal, and the mature larvae had dropped to cocoon by July 27, 1953, and August 2, 1954. Graham (*44*) concluded that high temperatures caused premature larval drop toward the end of July 1929. Evidence at hand indicates that this could be a normal activity for that time of year.

Frass-drop studies primarily reflected the feeding activities of fifth-instar larch sawfly populations and to a lesser extent the fourth-instar populations. Larvae of these instars produced 95 percent of the frass (by weight), and the size of the particles facilitated fall from the trees. Frass samples that were of a practicable quantity for weighing accumulated simultaneously or within a few days of the appearance of fifth-instar larvae. Small but measurable quantities fell a few days after the mature larvae were gone from the trees. Delayed drop of frass resulted from the eventual dislodgment of particles from such places as crevices in the bark.

Frass trapping is of value in determining the presence of the various instar larvae in the field, but differences in the larval and frass trends preclude its use in describing larval populations (figs. 10–12). Characteristically, mean frass drop occurred later than the mean fifth-instar population from which it was derived for the most part (table 2). Possibly the disparity resulted from the greater deflection or longer delayed drop of frass through the heavier foliage at the onset of larval activity. This factor decreases, of course, as defoliation increases. Morris (*84*) showed that frass drop from feeding by the European spruce sawfly

(*Diprion hercyniae* (Htg.)) increased with time within each larval instar. This relationship may also affect larval and frass patterns. Comparison of this data (*84, figs. 1 and 7*) with the larch sawfly data indicates differences between population and frass means similar to those experienced with the larch sawfly in this study.

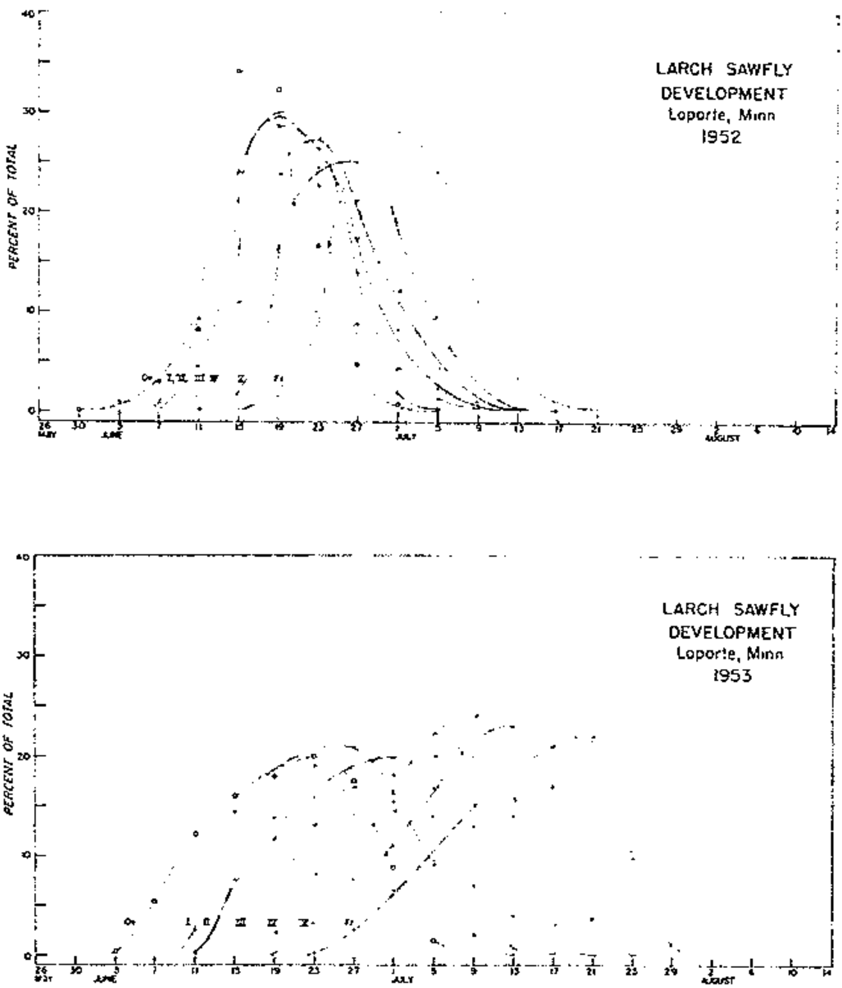

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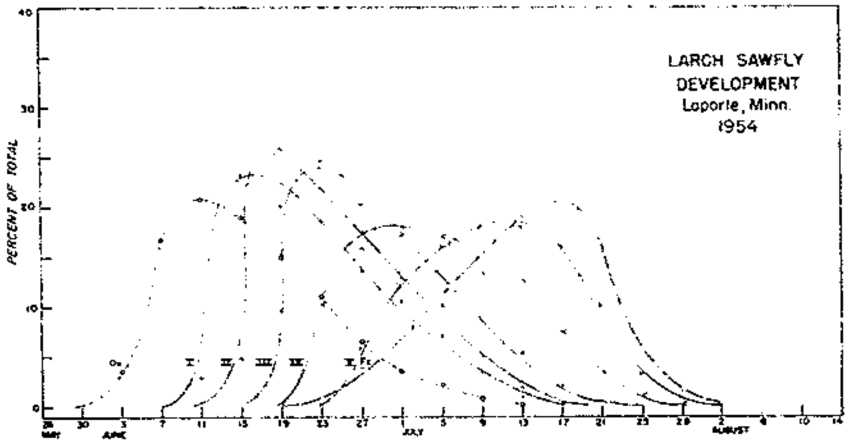
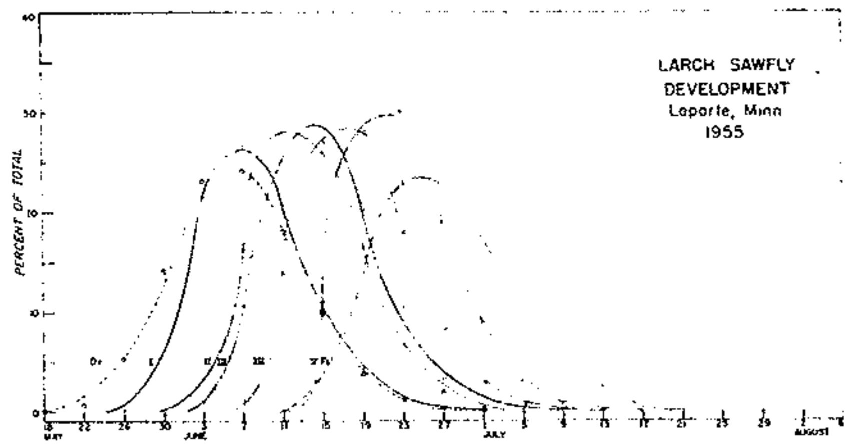
FIGURE 10.—Field development of the larch sawfly at the dry site for 1952 and 1953. Curves are accumulative in 4-day periods to about 100 percent. Ov = oviposition, I = first instar, II = second instar, III = third instar, IV = fourth instar, V = fifth instar, and Fr = frass.





F-488856, 488857

FIGURE 11.—Field development of the larch sawfly at the dry site for 1954 and 1955. Curves are accumulative in 4-day periods to about 100 percent. Ov = oviposition, I = first instar, II = second instar, III = third instar, IV = fourth instar, V = fifth instar, and Fr = frass.

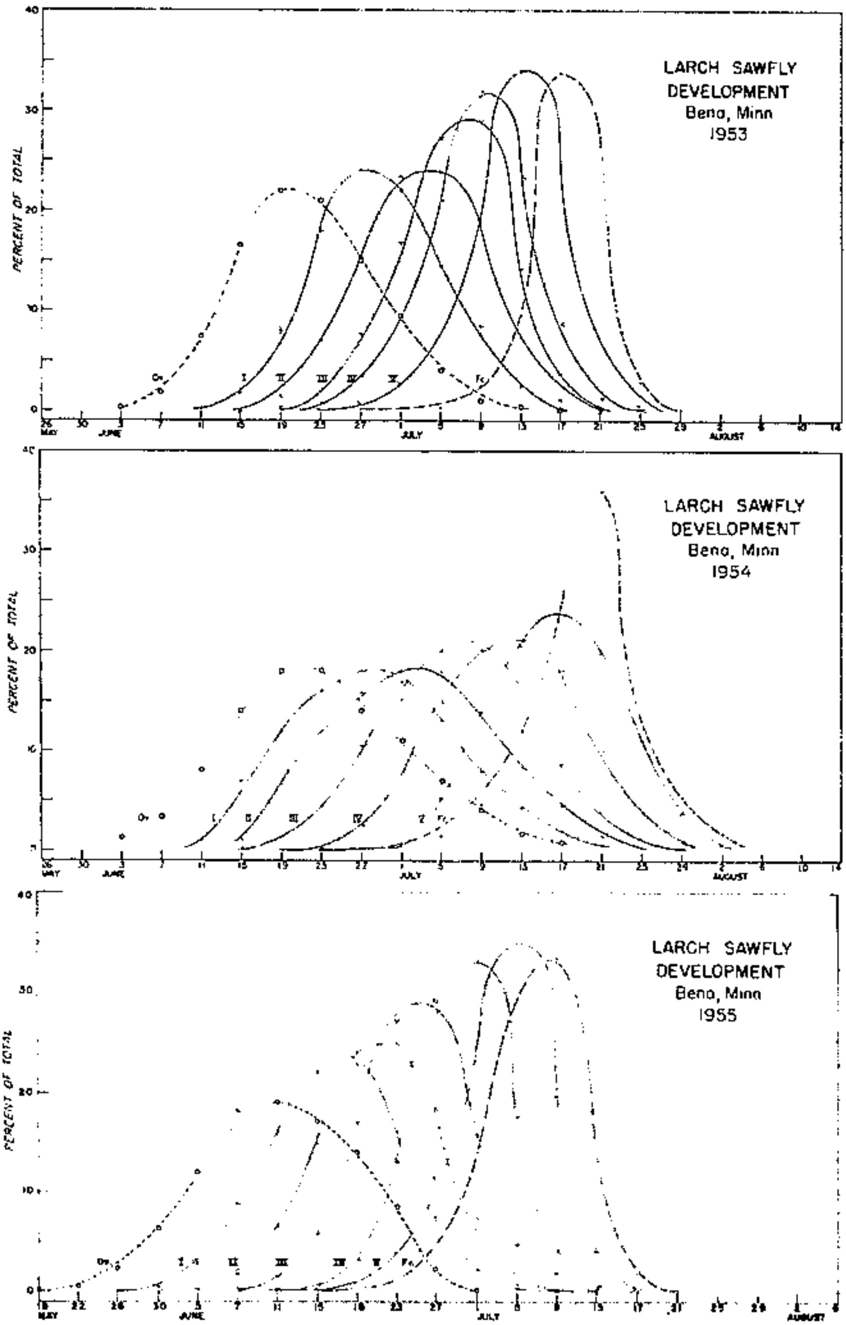


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FIGURE 12.—Field development of the larch sawfly at the wet site for 1953, 1954, and 1955 respectively. Curves are accumulative in 4-day periods to about 100 percent. Ov = oviposition, I = first instar, II = second instar, III = third instar, IV = fourth instar, V = fifth instar, and Fr = frass.

TREE DAMAGE

Tamarack, a deciduous conifer, does not die readily from the effects of defoliation. Under natural outbreak conditions reduced annual increment, thin foliage, low shoot production, and branch mortality are manifestations of declining vigor due to successive defoliations.

Factors Affecting Defoliation

Defoliations encountered in outbreaks vary in intensity among stands and trees within stands with each passing year. Within-stand annual defoliation patterns shown for the dry site (table 4) are representative of conditions in the Minnesota outbreak. The earliest year of a high infestation level at this site is unknown but was probably either 1947 or 1948. Butcher[8] reported complete defoliation in nearby stands in 1949, and also noted heavy defoliation on a parasite release record dated July 16, 1950.

TABLE 4.—*Estimated percentage defoliation of sample trees at the dry site, 1952–56*[1]

Tree sample	1952	1953	1954	1955	1956
1	85	40	10	60	100
2	100	85	30	100	100
3	100	35	30	100	100
4	100	35	35	90	50
5	100	75	50	100	100
6	100	80	50	100	85
7	100	55	65	100	30
8	100	65	100	100	95
9	100	40	65	100	10
10	100	85	70	100	75
11	100	10	25	100	60
12	100	20	30	100	90
13	100	25	95	100	95
14	100	30	30	100	5
15	100	50	95	100	10

[1] Mean diameter was 7 inches and average height 50 feet in 1954.

Decreased population densities with reduced defoliation have followed flooding (*70*), a condition evident at the wet site in 1952. After 4 or 5 successive heavy defoliations, another factor may also reduce populations and defoliation. A sharp decline in number of oviposition sites (new shoots) occurred on the dry site in

[8] See footnote 7, p. 12.

1953 and again at both sites in 1956 (table 5). An earlier shoot loss at the wet site was probably forestalled because of high water levels in 1951 and 1952 that severely reduced the sawfly population. Many of the terminal buds on trees at the dry site failed to produce new shoots (*31*), and most of those that formed in 1953 fell from the trees between July 20 and 27. Defoliation was lighter under these conditions than during seasons of high shoot production.

The relation of population densities to available oviposition sites makes it difficult or impossible to predict defoliation. This was demonstrated when preemergence cocoon samples were taken at the dry and wet sites and at 25 survey plots from 1953 to 1955 to learn if predictions were possible. The results indicate no correlation between live cocoons in May and the degree of defoliation that summer (table 6).

In plot 4, for example, 81 female sawflies emerged from the cocoons that were collected in May 1953, and average defoliation was 80 percent; in 1955 only 10 sawflies emerged from the sample and defoliation still rose to 85 percent, a level close to 1953. Similar relationships at the other plots indicated that reliable defoliation predictions were not practicable during prolonged outbreaks.

TABLE 5.—*Shoot production, infested shoots, and defoliation, 1952–56*

Year and Plot	Live cocoons [1]	Branches	Average new shoots per branch		Infested shoots related to total	Estimated defoliation [2]
			Total	Infested		
	Number	*Number*	*Number*	*Number*	*Percent*	*Percent*
1952:						
Dry	....	30	97	35	36	100
Wet	....	80	14	3	21	30
1953:						
Dry	84	70	31	12	39	50
Wet	16	70	70	11	16	45
1954:						
Dry	33	80	85	10	12	50
Wet	39	80	142	13	9	60
1955:						
Dry	84	70	110	27	25	95
Wet	139	70	129	20	16	90
1956:						
Dry	58	40	22	10	45	65
Wet	116	40	32	13	41	80

[1] Preemergence collections in May of each year. Cocoon samples based on 5-minute collections under each of 15 trees (1¼ hours).

[2] Average of 15 live plot trees.

TABLE 6.—*A comparison of live cocoon populations and defoliation*[1]

Plot	Average diameter at breast height	1953		1954		1955	
		Sawflies	Defoliation	Sawflies	Defoliation	Sawflies	Defoliation
	Inches	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
1a	7.7	(2)	(2)	33	50	11	65
2	5.6	23	90	40	65	7	90
3a	6.1	(2)	(2)	13	40	74	95
3b	8.6	(2)	(2)	23	35	18	80
4	6.3	81	80	12	45	10	85
5	8.3	62	100	48	55	28	70
6	6.1	37	50	34	50	36	75
7	5.5	37	85	24	65	12	100
8	6.2	54	95	18	80	24	95
9	6.0	141	90	19	60	23	80
10	6.0	39	95	22	20	9	25
11	6.1	39	100	35	65	26	70
12	6.4	30	95	44	75	27	100
13	5.7	6	95	18	65	11	80
14	5.4	20	100	11	95	5	95
15	5.4	50	90	25	60	10	60
16	6.9	38	75	31	60	22	80
17	6.2	22	95	28	55	10	65
18	6.2	19	95	8	65	7	75
19	4.2	64	100	13	80	20	80
20	4.4	24	95	25	85	27	95
21	5.4	11	75	25	70	17	80
22	7.0	7	55	11	30	(2)	(2)
22a	6.8	(2)	(2)	(2)	(2)	37	95
23	5.3	35	65	20	70	17	80
Dry site	6.8	84	50	33	50	84	95
Wet site	6.8	16	45	39	60	139	90
Total	....	939	....	652	....	711	....
Average	....	41	83	25	60	27	81

[1] Six-minute collections under 10 trees (1 hour) at each survey plot. At the dry and wet sites, 5-minute collections were made under 15 trees (1¼ hours). Data are based on sawflies emerging from May collections. Defoliation estimates to the nearest 5 percent were taken in July and August.

[2] No collections or estimates made.

Decline in Radial Increment

Radial increment cores, collected from 13 tamarack stands at various locations in northern Minnesota, were examined to determine growth patterns for the species. Cores from black spruce, growing in association with tamarack on several of the sites, were also examined so that growth patterns of the sawfly host tree could be compared with those of the undefoliated black spruce. Only codominant and dominant trees were sampled.

These increment core measurements show that during the years following 1948 the radial increment for tamarack was sharply reduced. In black spruce, however, it remained the same or increased slightly. This would tend to eliminate the possibility of high water levels as causes of the decrease in tamarack growth. The growth variations are shown in table 7, which compares the radial increment on 5 plots for the 2 species during the 2-year periods, 1947–48 and 1953–54. Increment for tamarack was depressed 18 to 83 percent. That for black spruce, on the other hand, increased 1 to 34 percent on 4 plots and decreased only 2 percent on the fifth. The positive change in black spruce increment was a response to below-normal precipitation during the years 1945–48, essentially a release from the above-normal period 1940–44. Minimal growth for the spruce occurred in 1946, but a positive trend developed after this year. No such increases took place with the associated tamarack.

TABLE 7.—*Periodic radial increment variation at five plots for dominant and codominant tamarack and black spruce*

Plot [1]	Species	Trees	Total biennial radial increment		
			1947–48	1953–54	Net change
		Number	*Millimeters*	*Millimeters*	*Percent*
1	Tamarack	20	64.57	10.75	−83
	Black spruce	14	14.16	18.92	+34
2	Tamarack	15	40.80	33.62	−18
	Black spruce	6	8.73	8.82	+1
3	Tamarack	15	36.80	11.95	−68
	Black spruce	6	8.30	8.16	−2
5	Tamarack	15	69.62	15.21	−78
	Black spruce	6	10.32	12.44	+21
6	Tamarack	15	52.09	13.10	−75
	Black spruce	6	17.76	19.52	+10

[1] Plot 4 was omitted from this table because it was on a flooded site and reduction in growth due to sawfly feeding was not positively apparent.

Tamarack Mortality

Although there is much information regarding the dying of tamarack during the early outbreaks in North America, very little has been published concerning the duration of attack preceding tree mortality. In 1891, 8 years after his original observation of an outbreak, Fyles (*36*) reexamined a stand of 200-year-old tamarack in Quebec and noted that 98 percent of the trees were dead and the remainder dying. Walker (*116*) stated that following heavy defoliation between 1898 and 1910 mature tamarack died in 1911 near Lake Simcoe, north of Toronto, Ontario. Ruggles (*101*) observed dead and dying tamarack in Minnesota in the same year he found the insect—1909.

S. A. Graham (*42*) experimentally defoliated young tamarack trees for 4 successive seasons. He found that complete defoliation for 3 seasons killed these young trees, but that partial defoliation up to 75 percent did not. In addition, root examinations showed that complete defoliation affected root health in that all the fine roots and most of the larger roots were dead. Very little injury to the roots of trees defoliated 75 percent was noted. Reeks (*96*) found that in Nova Scotia and New Brunswick tamarack generally endured moderate to severe defoliation through the 1933–42 outbreak. The outbreak rarely persisted in individual areas longer than 6 years, and the highest mortalities, occurring in St. John and Charlotte Counties along the coast in New Brunswick, were estimated at from less than 1 to 5 percent of the trees.

Recent investigations indicate that tamarack mortality in Saskatchewan, Alberta, Manitoba, and Minnesota followed moderate and severe defoliation for 6 to 9 years.

In 1954, 18 to 30 percent mortality was reported in stands near Prince Albert, Saskatchewan, heavily defoliated from 1948 through 1953; an additional 8 to 10 percent mortality occurred by June 1955 (*111*, *112*). Up to 20 percent mortality was noted in stands near Cold Lake, Alberta, after severe defoliation for a number of years (*10*).

Tamarack mortality attributed to the larch sawfly was found on the Whiteshell Forest Reserve, Manitoba, in 1955 (*92*). Defoliation had been severe from 1949 to 1953. The outbreak has continued in this area, but mortality became noticeable following six seasons of defoliation.

Trees began to die in areas having thin duff over mineral soil and rock outcrops in northeastern Minnesota in 1954 following the sixth season of noticeable defoliation (*6*). On the bog tamarack sites in northern Minnesota, dead and dying dominant and codominant tamarack were observed for the first time during the summer of 1956; that is, the season following the seventh or eighth year of noticeable defoliation. Tree mortality became more apparent in these stands in 1957. The outbreak is continuing and spreading eastward through the Lake States. A great loss of tamarack may be expected in the region. It appears that, aside from persistent drought or high temperatures, only a food shortage brought about by extensive timber losses will stop the outbreak.

NATURAL CONTROL

Reduction of field populations of the larch sawfly is caused by insect parasites and predators, spiders, fungal and bacterial diseases, rodents, birds, climatic factors, loss of oviposition sites, declining nutrition resulting from repeated annual defoliations, and eventually by the gross loss of food as host material dies. The relative importance of the various decimating factors had not undergone investigation as a whole until recently (*69*), but accounts have been published of the role played by one or more of the natural control factors in the decline of an outbreak. Figure 13 shows cocoons from which sawflies and parasites

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FIGURE 13.—Larch sawflies are subject to natural control. Upper left, normal emergence; right, rodent predation; center, predation by elaterid larva; lower left and right, parasite emergence holes.

emerged and cocoons in which the pupae were destroyed by predators. These controls will be discussed qualitatively in this section and quantitatively where available information permits.

Insect Parasites

Mesoleius tenthredinis Mor.

This ichneumon was observed as an important parasite during the 1904–13 larch sawfly outbreak in Great Britain where it was identified for a time as *Mesoleius aulicus* Grav. (*52, 55*). Parasitism by this species at Thirlmere rose from 5.8 percent in 1906 to 62 percent in 1910 and contributed materially to the decline of the outbreak. Hewitt (*54*) undertook the importation of this parasite from England, and the early releases were made at points in Algonquin Park and Ottawa, Ontario. Additional releases were made at the above points in 1911. Liberations were also made in Quebec in 1911, and in the Riding Mountain National Park, Manitoba, (*85*), and the Spruce Woods Forest Reserve at Treesbank, Manitoba, in 1913 (*20*). Following the original liberations additional colonies were reared from material obtained in field collections. Rather complete accounts of these activities have been given by Graham (*38, 39*).

The Treesbank liberations gave the first indication of successful colonization. Criddle (*20*) recovered the species from cocoons collected in the spring of 1916 (1915 wintered cocoons) and reported that parasitism by it amounted to 19 percent in the third generation of sawflies produced since its introduction in the spring of 1913. By 1920 parasitism had risen to 66 percent. In 1928 the parasite was well established in Manitoba, killing as high as 88 percent of the sawflies and averaging 75 percent for the whole Spruce Woods Reserve.

Mesoleius tenthredinis was liberated in southeastern British Columbia in July 1934 after dissection of 1,600 cocoons from an estate near Fernie had failed to disclose its presence, according to Hopping, Leach, and Morgan (*59*). They described its status in British Columbia from 1934 through 1942. Because of its own increase, or as a result of colonization, the parasite became an important part of the control complex by 1936. Parasitism was high in 1948, 1949, and 1950—roughly between 55 and 68 percent (*80*) ; and 90 percent parasitism was found in a random collection of prepupae remaining in diapause through the summer of 1950. The species was aslo recovered from cocoons collected in 1935 on the Flathead National Forest, Mont., about 40 miles south of Fernie (*27*).

Reeks (*96*) has reviewed the status of this parasite in New Brunswick and Nova Scotia from the time of release near Fredericton in 1927. When it had failed to establish itself, colonization was repeated in New Brunswick in 1935, 1936, and 1938 and in Nova Scotia from 1937 to 1942. During the larch sawfly outbreak in the Maritime Provinces, the species was recovered in New Brunswick in 1936, with parasitism averaging 5 percent. By 1942 it had risen to 45 percent. In Nova Scotia, establishment was recorded in 1940 when about 17 percent of the collected prepupae were parasitized.

The only release in the United States from the original English stock of *Mesoleius tenthredinis* was made near Munising, Mich., in 1911 (*44*). In 1928 Orr[9] reared the species from 1,927 sawfly cocoons collected at Itasca Park, Minn., which is roughly 200 airline miles from the nearest Manitoba liberations. The status of the parasite from that time until the eruption of the 1947 outbreak was studied intermittently. Graham reported that parasitism amounted to only 9, 10, and 1 percent in 1928, 1929, and 1930 respectively. Orr stated that the species was quite abundant at Itasca Park several years prior to 1935, causing about 30 percent parasitism.

Dowden and Berry[10] reported that the parasite was present in 23 out of 36 living larvae (64 percent) collected at Deer River, Minn., in 1935. They also reported that parasitism in collections from the Chequamegon and Nicolet National Forests in Wisconsin amounted to 10 out of 25 (40 percent) and 9 out of 22 (41 percent) larvae respectively. In a collection from the Upper Michigan Peninsula they found 9 *Mesoleius* specimens in 19 larvae (47 percent), but none was found in 95 live larvae from the Huron National Forest of Lower Michigan. This would indicate that, at least by 1935, this parasite had attained a fair level of importance in the Lake States.

Mesoleius tenthredinis has not reached such high proportions as mentioned above in the current Lake States outbreak. Butcher[11] reported less than 2 percent parasitism for extensive northern Minnesota collections made in 1949. Studies made from 1952 to 1955 indicate that the species can no longer be depended upon as an important biological control factor in Minnesota (*28*). The sawfly has developed a strong immunity to the parasite. The same immunity factor was found earlier in Manitoba and Saskatchewan populations (*68*, *85*). Muldrew, in an excellent analysis of the immunity phenomenon, disclosed that phagocytic capsules formed about the developing *Mesoleius* embryo 3

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[9] Unpublished data on file at Lake States Forest Experiment Station; collected by L. W. Orr, U. S. Bureau of Entomology and Plant Quarantine.

[10] Unpublished data collected by P. B. Dowden and P. A. Berry, New Haven, Conn., Forest Insect Laboratory. Part 1 of Domestic Parasite Report for 1936.

[11] See footnote 7, p. 12.

to 4 days after oviposition in the host. This encapsulation prevented the development of the parasite.

Lejeune and Hildahl (*72*) advanced the hypothesis that the present outbreak in central Canada and Minnesota was caused by the development of a strain of larch sawfly immune to attacks by this parasite. Proof of this is lacking at present; however, it is obvious that the degree of control exhibited in Manitoba, Minnesota, and Wisconsin shortly after the introduction of the species has not been attained in the present outbreak, and that the encapsulation phenomenon is an important feature to be considered in this decline.

The data in table 8 were based on cocoons collected at a series of survey and ecological study plots in northern Minnesota (fig. 1, page 2). Collections were made after the completion of cocooning in late July or early August, and from the same areas the following spring prior to emergence. Sample lots were dissected from the late summer cocoons and the spring collections were reared. The dissection data indicated that host immunity resulted in the failure of an average of about 86 percent of the oviposited *Mesoleius* eggs to hatch during the 1952–55 period. Results from dissections and rearings were in close agreement, showing effective parasitism of only 2 to 4 percent.

Extensive parasite investigations were not carried out in Wisconsin. Dissection of 88 live cocoons collected in Douglas County in 1952 revealed that 17 percent contained *Mesoleius* eggs, but that effective parasitism was only 1 percent. In 1954, 30 live cocoons from Douglas and Bayfield Counties also showed low levels—20 percent oviposition and 3 percent effective parasitism.

It is apparent that *Mesoleius tenthredinis* cannot be depended upon to give material aid in the natural control of the larch sawfly in areas where the immunity factor is operating—central Canada, Minnesota, and Wisconsin. However, host resistance is not important as yet in eastern and western Canada (*85*, *96*), nor has it been observed in New York State. In 1956 C. J. Yops and W. E. Smith of the New York State Conservation Department

TABLE 8.—*Annual parasitism by* MESOLEIUS TENTHREDINIS *in northern Minnesota; results from dissections and rearings*

Cocoon formed	Cocoons collected in July or August of year formed			Cocoons collected in May after year formed	
	Dissected	Attacked by *Mesoleius*	Effective attack	Reared	*Mesoleius* emergence
	Number	*Percent*	*Percent*	*Number*	*Percent*
1952	893	18	3	971	4
1953	389	24	2	737	4
1954	405	23	3	830	3
1955	390	20	4	875	3

provided a sample of 95 live cocoons from Chenango County, N. Y., for examination. There was no indication of egg encapsulation, and *Mesoleius* larvae were present in 56 percent of the sawflies.

Bessa selecta (Meig.)

The taxonomy of the tachinid called *Bessa selecta* in Europe has not been resolved in North America. For example, in the United States systematists refer to it as *selecta*, but in Canada *harveyi* (Towns.), pertaining to North American material, is preferred. It is a common parasite of sawflies in Europe (*48*), and is listed as a parasite of the larch sawfly in Austria and Canada (*108*). Britton (*9*) remarked that *Frontina tenthredinidarum* Towns., which is synonymous with *B. selecta*, was a larch sawfly parasite in New Brunswick. In 1935 it was reported from larch sawfly collections in Montana, Minnesota, Wisconsin, and Michigan (*27*). It was collected in New Brunswick and Nova Scotia in 1934 and 1937 respectively, where it was an important component of the larch sawfly control factors during the 1933–42 outbreak (*96*). Lejeune and Hildahl (*72*) reviewed the status of this parasite in Manitoba between 1944 and 1953 and in Saskatchewan from 1947 to 1953. Graham (*44*) reared it from Minnesota larch sawfly cocoons in 1928 and found 6 percent parasitism.

In field studies conducted in northern Minnesota from 1952 to 1955, cocoons were gathered as soon as possible after formation to prevent the emergence of the maggots before collection, placed in individual gelatin capsules, and held at 40° F. until they were dissected. These data were then compared with rearing records from similar collections, made in the spring prior to sawfly emergence (table 9). Butcher[12] had reported slightly less than 4 percent parasitism (dissected material) in the same general area in 1949. The effectiveness of *Bessa selecta* during the current outbreak in Minnesota did not rise above 10 percent until 1954, or in the seventh or eighth year of outbreak.

TABLE 9.—*Annual parasitism by* BESSA SELECTA *in Minnesota; results from dissections and rearing*

Cocoon formed	Cocoons collected in July or August of year formed		Cocoons collected in May after year formed	
	Dissected	Containing *Bessa*	Reared	Containing *Bessa*
	Number	*Percent*	*Number*	*Percent*
1952	893	4	971	5
1953	389	7	737	5
1954	405	18	830	10
1955	390	23	875	14

[12] See footnote 7, p. 12.

Despite the increasing importance of *Bessa selecta*, it is doubtful that this parasite will play a significant role in the decline of the infestation. Muldrew (*86*) pointed out that in the Prairie Provinces of Canada the species issued by fall from as high as 22 percent of the sawfly larvae attacked in the summer. Parasite losses due to fall issuance in Minnesota amounted to 44 and 39 percent in 1954 and 1955 respectively. The adults that emerge in the fall are not at all synchronized with their larch sawfly host, which is normally not available in numbers after the third week of July. The remaining *Bessa* overwinter within the host and emerge during late spring and summer, attacking the feeding larvae. Other causes of the impaired efficiency of this parasite are sloughing of eggs, embryological mortality, dislodging and sloughing of young maggots, superparasitism, encapsulation of young maggots in the sclerotized funnel, and failure of the maggots to escape the host cocoon before forming the puparium (*48*).

Tritneptis klugii (Ratz.)

The pteromalid *Tritneptis klugii* attacks the sawfly cocoon. It has been reported from Europe and North America. Ratzeburg (*95, p. 198*) noted that it was known as a larch sawfly parasite in Germany in 1841, 3 years before he gave it the name *Pteromalus klugii*. In 1879 it was listed as a larch sawfly parasite in France (*2, p. 103*).

This larch sawfly parasite is believed to be the first described from North America. The name *Pteromalus nematicida* was given provisionally to specimens reared from a sawfly cocoon collection made in Maine in 1882 (*89*). It was found parasitizing sawfly cocoons at Brome and the eastern townships in Quebec during the first infestations in the 1880's (*35, 93*). Ruggles (*102*) mentioned that a parasitic species of *Diglochis* infested 10 to 15 percent of the cocoons he collected in Minnesota in 1910, and Dowden (*27*) reported a *Dibrachys* present among the parasitic fauna of the larch sawfly from the Great Lakes region and western Montana in 1935. It is quite likely that the specimens of *Diglochis* and *Dibrachys* mentioned above were actually *T. klugii*. Parasitism by *Tritneptis* of 1, 21, and 12 percent occurred in Minnesota collections in 1927, 1928, and 1929 respectively; none was found in 1930 (*44*).

Hopping, Leach, and Morgan (*59*) reported that *Tritneptis* parasitized from 17 to 41 percent of British Columbia cocoon samples in 1934. Although not recovered from all their sampling points, it was present on some sites from 1934 to 1942. Under air temperature and humidity conditions in British Columbia, they stated that three generations could be produced in a summer. Averages of 35 first-generation, 66 second-generation, and 45 third-generation adults per cocoon were found; the shortest developmental time for a summer generation was 29 days. Since this parasite attacks the cocoon and may have several generations in a season, larch sawfly cocoons for experimental purposes must be kept in individual containers to prevent repeated parasitism.

During the current larch sawfly outbreak in Manitoba and Minnesota, parasitism by this species has been low or absent. It affected from 0 to about 8 percent of the Manitoba collections between 1939 and 1951, and parasitism varied from 0 to about 6 percent of Saskatchewan cocoon samples between 1949 and 1953 (*72*). The parasite was not found in samples from either of the above Provinces from 1943 to 1948 inclusive.

Butcher[13] recovered this species from sawfly cocoons collected throughout northern Minnesota late in the summer of 1949. He reared the cocoons in lots of 20, and the very high rate of parasitism indicated contamination by *Tritneptis*. These recoveries were the last for Minnesota, as the parasite was not found in samples taken in late summer or spring in Minnesota during 1952 to 1956. It must be considered a minor element of the Minnesota parasite complex.

Miscellaneous

The following list of miscellaneous insect parasites of the larch sawfly has been prepared from the literature and from records of the Division of Forest Insect Research, Lake States Forest Experiment Station, St. Paul, Minn.:

Order and species	*Where collected*	*Reporter*
Diptera:		
Argyrophylax bimaculata Htg.	U.S.S.R.	Dobrodeiev, 1922 (*26*).
Exorista spp.	England	Hewitt, 1910 (*53*).
Fannia sp.	Canada	Lejeune and Hildahl, 1954 (*72*).
Megaselia sp. (doubtful parasite)	do.	Do.
Muscina stabulans (Fall.)	do.	Graham, 1955 (*39*).
Neophoracera hamata (A. & W.)	do.	Do.
Spathimeigenia aurifrons Cn.	do.	Raizenne, 1957 (*94*).
Zenillia pexops B. & B.	England	Long, 1913 (*75*).
Hymenoptera:		
Agrothereutes near *similaris* (Prov.)	Canada	Graham, 1955 (*39*).
Aptesis sp. near *basizonia* (Grav.)	U.S.A.	Drooz[1]
A. indistincta (Prov.)	Canada	Lejeune and Hildahl, 1954 (*72*).
		Graham, 1955 (*39*); Reeks, 1954 (*96*).
	U.S.A.	Dowden, 1937 (*27*).
A. nigrocinctor Foerster	England	Hewitt, 1910 (*53*).
A. sp.	U.S.A.	Beckwith[1]
	Canada	Graham, 1955 (*39*).
Coelichneumon fuscipes Grav.	England	Hewitt, 1910 (*53*).
Cryptus minator Grav.	do.	Do.
Ctenochira sp.	Canada	Lejeune and Hildahl, 1954 (*72*).
Dahlbominus fuscipennis (Zett.)	do.	Reeks, 1954 (*96*).
Dusona sp.	do.	Lejeune and Hildahl, 1954 (*72*).
Eclytus ornatus Holmg.	do.	Graham, 1955 (*39*).
		Lejeune and Hildahl, 1954 (*72*).
		Reeks, 1954 (*96*).
Endasys pubescens (Prov.)	do.	Graham, 1955 (*39*).
E. subclavatus (Say)	do.	Do.
E. sp.	U.S.A.	Dowden, 1937 (*27*).

[1] Reported from the files of the Lake States Forest Experiment Station, St. Paul, Minn.

[13] See footnote 7, p. 12.

Hymenoptera—Continued

Order and species	Where collected	Reporter
Euceros frigidus Cress.	U.S.A.	Drooz[1]
E. thoracicus Cress.	do.	Do.
	Canada	Graham, 1955 (*39*).
		Lejeune and Hildahl, 1954 (*72*).
E. sp.	U.S.A.	Drooz[1]
	Canada	Graham, 1955 (*39*).
		Reeks, 1954 (*96*).
Gratichneumon annulator Fabr.	England	Hewitt, 1910 (*53*).
Ichneutes bicolor Cress.	U.S.A.	Drooz[1].
Macrocentrus uniformis Prov.	Canada	Lejeune and Hildahl, 1954 (*72*).
Mastrus spp.	do.	Graham, 1955 (*39*).
	U.S.A.	Dowden, 1937 (*27*).
Mesoleius sp.	Canada	Graham, 1955 (*39*).
Microcryptus labralis Grav.	England	Hewitt, 1910 (*53*).
Perilampus sp.	Canada	Lejeune and Hildahl, 1954 (*72*).
Phygadeuon sp.	U.S.A.	Dowden, 1937 (*27*).
Smicroplectrus velox Wall.	Canada	Graham, 1955 (*39*).
Spilocryptus incubitor Strom	England	Hewitt, 1910 (*53*).

[1] Reported from the files of the Lake States Forest Experiment Station, St. Paul, Minn.

Insect Predators

The pressure exerted by insect predators against the larch sawfly has never been assessed. The results of observations in North America indicate that species of Pentatomidae, Miridae, Anthocoridae, Elateridae, Formicidae, Vespidae, and Neuroptera attack sawflies. A list of known predators follows:

Order, family, or species	Stage attacked	Where collected	Reporter
Hemiptera:			
Anthocoridae	Egg, larval	Canada	Muldrew, 1955 (*87*).
Apateticus bracteatus Fitch	Larval	do.	Do.
Deraeocoris laricicola Kgt.	Egg, larval	do.	Turnock, 1953 (*110*).
Euschistus sp.	Larval	do.	Muldrew, 1955 (*87*).
Phytocoris neglectus Kgt.	Egg, larval	do.	Turnock, 1953 (*110*).
Plagiognathus repeticus Kgt.	do.	do.	Do.
Podisus modestus Dall.	Larval	U.S.A.	Lintner, 1889 (*73*).
		Canada	Fletcher, 1885 (*35*).
P. near *sericeventris* Uhler	do.	U.S.A.	Drooz[1].
P. sp.	do.	Canada	Muldrew, 1955 (*87*).
Tetraphelps sp.	Egg, larval	do.	Turnock, 1953 (*110*).
Neuroptera:			
Chrysopidae	do.	do.	Muldrew, 1955 (*87*).
	Larval	U.S.A.	Graham, 1956 (*44*).
Coleoptera:			
Coccinellidae	do.	do.	Do.
Ctenicera sp.	Cocoon	do.	Drooz[1].
Ludius lutescens Fall.	do.	Canada	Hopping *et al.*, 1943 (*59*).

[1] Reported from the files of the Lake States Forest Experiment Station, St. Paul, Minn.

Order, family, or species	*Stage attacked*	*Where collected*	*Reporter*
Hymenoptera:			
Formica whymperi adamsi Whlr.	Adult, larval	U.S.A.	Drooz[1].
Vespula sp.	Larval	Canada	Hopping *et al.*, 1943 (*59*).

[1] Reported from the files of the Lake States Forest Experiment Station, St. Paul, Minn.

Arachnida That Attack the Larch Sawfly

Turnock (*110*) observed the orb spider (*Neoscona arabesca* Walckenaer) feeding on larvae trapped in its web; he also reported that mites belonging to the genus *Balaustrum* attacked young larvae in Canada. Several species of spiders and a mite, tentatively determined as *Erythreus* sp., have been observed feeding on adult sawflies in Minnesota.

Experiments in Control With Infective Nematodes

Preliminary laboratory and field tests to determine the possibility of controlling the larch sawfly through the use of infective nematodes were carried out in northern Minnesota in 1956. Infective stage DD-136 nematode larvae (Steinernematidae) were supplied by the Insect Pathology Pioneering Research Laboratory, Entomology Research Division, Agricultural Research Service. The laboratory tests were highly successful in that larvae of all five instars were killed within 48 hours. The dead larvae contained the nematodes and presumably were susceptible to a bacterial disease carried by the nematodes.

Two tests of the effect of this nematode on the sawfly were conducted on the Chippewa National Forest. In one, an attempt was made to control feeding larvae in the trees. Here, each of six 15-foot tamaracks was sprayed with a suspension containing 4 million nematodes in 2 quarts of water. Two 2-square-foot traps were placed under each tree to catch fallen larvae. Two days after treatment the traps were examined, and five larvae were found in them, none of which contained nematodes. In addition, five living larvae were examined from each tree, but none of these contained nematodes.

The second treatment consisted of spraying 44 million nematodes in 3 gallons of water onto the sphagnum surface of the bog. This was applied to $\frac{1}{10}$ acre when fifth-instar sawfly larvae were falling to the ground prior to cocooning. Four days later 51 live and dead larvae that had entered the sphagnum to cocoon were collected and examined. Individual nematodes were found in three of the sawfly cadavers. One week later another collection was made in this plot and the material, consisting of 12 uncocooned and 64 cocooned larvae, was forwarded to nematode specialists at Beltsville, Md., for examination. According to the specialists, two of the cocooned larvae contained nematode-associated bacteria, but the sawfly cadavers were hard, dry, and difficult to dissect and the presence of nematodes in them could not be discerned. If in future years these tests show the successful establishment of nematodes on the larch sawfly host, this control method would be promising for protecting tamarack on moist or wet sites.

Entomophagous Diseases of the Larch Sawfly

Five genera of fungi (*Isaria, Beauveria, Spicaria, Hirsutella,* and *Empusa*) and two species of bacteria (certain strains of *Bacillus cereus* Fr. and Fr. and *Serratia marcescens* Bizio) have been reported parasitic on the larch sawfly in Canada and the United States (*79*).

The fungus *Isaria farinosa* (Dicks.) Fr. has killed the larch sawfly in Russia (*26*), England (*53*), Canada (*59*), and the United States (*44*).

Pathogenic fungi collected in Minnesota and capable of killing the larch sawfly were determined as follows:[14]

Beauveria bassiana (Bals.) Vuill.
B. globulifera (Speg.) Pic.
B. bassiana (yellow strain).
Isaria farinosa (Dicks.) Fr.
Spicaria sp.

Two bacteria in the genus *Bacillus* also were cultured from the Minnesota cocoons. One of these resembled *B. cereus*; the other could not be identified, but it was a gram variable spore former in pure cultures with subterminal spores oval to cylindrical.

Larch Sawfly Predation by Vertebrates

Information concerning the roles of various vertebrates as predators of the larch sawfly is limited, but species of fish, frogs, rodents, and birds have been observed feeding on either the larvae or cocoons of the host.

Fish.—Brook trout (*Salvelinus frontinalis* Mitch.) have been observed feeding on fallen larvae in Minnesota (*101*).

Frogs.—In Manitoba, two species of frogs, *Rana sylvatica* and *R. pipiens,* have been observed consuming respectively 210 and 110 larvae per frog per day (*11*).

Mammals.—Graham (*40*) concluded from studies in Michigan and Minnesota that rodents were more important than parasites and diseases in controlling the larch sawfly. He found that voles (especially *Microtus pennsylvanicus*), deer mice (*Peromyscus maniculatus*), and two species of shrews and skunks were active as controls in Michigan and Minnesota (*44*).

The vole *Microtus agrestis* Flemming fed upon about 25 percent of the cocooned larvae on the Thirlmere, England, watershed during the 1907–08 winter (*52*).

Recent experiments in Manitoba by Buckner (*13*) indicate that although the sawfly is in the cocoon stage for 10 or more months, rodent predation occurs chiefly from late August to a peak in

[14] The organisms were identified at the Canada Department of Agriculture Insect Pathology Research Institute, Sault Ste. Marie, Ont., and the Insect Pathology Pioneering Research Laboratory, Agricultural Research Service, U. S. Department of Agriculture, Beltsville, Md.

mid-September and then ceases when the ground freezes. He also mentioned the relationships between the species of predators and their dominance on certain sites. The voles *Microtus pennsylvanicus* and *Clethrionomys gapperi* preferred a dry to moderately wet site, but the former occupied the habitat with the lighter crown closure. The shrew *Sorex cinereus* was the dominant species on wet sites with heavy crown closure, and apparently was replaced by *S. arcticus* as the site became drier because of draining.

Birds.—Birds, including chaffinches, rooks, jackdaws, starlings, and three species of titmice, have fed upon larch sawfly quite voraciously in England (*52*). In Canada and the United States birds have not materially aided in the reduction of outbreak populations, but the following have been observed feeding upon larvae: The evening grosbeak, black and white warbler, red-eyed vireo, Blackburnian warbler, chestnut-sided warbler, and the Canada warbler in Manitoba (*12*); the western robin in British Columbia (*59*); the white-throated sparrow and olive-backed thrush in northwestern Ontario (*49*); and the chipping sparrow and yellow warbler in Minnesota (*44*). The swamp sparrow, normally a seed feeder, decapitates the larvae and eats the heads (*49*).

Climatic Factors

Extreme drought and high precipitation are both unfavorable to larch sawfly survival. S. A. Graham (*41*) demonstrated that cocoon survival was considerably higher in cool moist situations where mosses were prevalent than on high ground covered with tamarack needles. Higher mortality in the latter site was due to excessive heat. He also found that heavy rains accounted for losses of 50 percent of newly hatched larvae, but the likelihood of their being washed from the branches decreased markedly with larval age. Prolonged drought conditions, in his opinion, caused the disappearance of the larch sawfly from Michigan (*44*). A. R. Graham (*37*) in Canada observed complete mortality of cocooning larvae due to drought and solar radiation.

Lejeune *et al.* (*71*) described in detail the relationships between immersion and sawfly survival. They demonstrated that in diapause the larva is not very susceptible to flooding but that the newly cocooned larva and post-diapause pronymph are readily killed by submergence. Oxygen consumption was highest during the susceptible periods, and this appeared to be directly related to mortality in the cocoon.

In 1949 heavy precipitation in southeastern Manitoba and north central Minnesota during the cocooning period and prolonged immersion of wintered prepupae were responsible for high mortality in the cocoons, which resulted in generally decreased defoliation in 1950 (*15, 70*).

As was mentioned earlier, blocked drainage killed nearly all the cocooned larvae at the northern Minnesota wet study site in 1951 and 1952. The inundated tamarack became heavily infested with the eastern larch beetle (*Dendroctonus simplex* Lec.), and some of the trees died.

The effect of the sun's rays on fifth-instar larvae that attempted to crawl up the tree stems was quite striking at the dry study site in 1952: The larvae were killed and baked hard on the tree trunks.

During the period of investigation, none of these weather factors has been of sufficient importance to alleviate defoliation, except locally for one season.

Oviposition Sites and Nutrition as Reduction Factors

Population reduction due to limited numbers of new shoots and impairment of fecundity has been treated in previous sections.

Heron (*51*) demonstrated experimentally that fifth-instar larvae must feed in excess of 50 percent of their capacity to complete their development successfully. Field samples of fully fed larvae from prolonged outbreak areas were 18 percent lighter than those from recently infested sites.

The implications from these studies are important in the light of the extended oviposition period. After the rapid defoliation in 1952 and 1955 that resulted from early emergence due to warm spring weather, many larvae from eggs laid late in the season starved to death.

Winter Mortality

The loss of 77 to 86 percent of the overwintering cocoons, along with the 13 to 17 percent parasitism, from August 1953 to May 1956 (table 10) apparently did not reduce the Minnesota outbreak. By the spring of 1956 dead and dying tamaracks were found in the north central part of the State on what appeared to be good tamarack sites. It is probable that only host mortality over vast areas will terminate this outbreak. When the density of tamarack stands has been reduced to a low level, natural control factors may become of sufficient importance to keep the remaining sawfly population in check.

TABLE 10.—*Larch sawfly cocoon loss through the winter in northern Minnesota*

Date	Cocoons	Winter mortality	
		All plots	Plot range
	Number	*Percent*	*Percent*
August 1953	5,407		
May 1954	733	86	44–96
August 1954	3,197		
May 1955	740	77	38–95
August 1955	4,417		
May 1956	875	80	38–93

INSECTICIDAL CONTROL

Suggestions concerning the use of insecticides against the larch sawfly are almost as old as the initial commercial attempts to control insects with chemicals. For example, in 1885 Provancher (*93*) recommended that solutions of hellebore or paris green be applied to ornamental larch, and Lintner (*73*) proposed that paris green or london purple be used to kill larvae on small groups of trees. Later, when more potent arsenicals were being employed as agricultural insecticides, Hewitt (*52*) stated that a pound of arsenite of copper mixed with 150 gallons of water, to which 4 to 6 quarts of flour were added as an adhesive, would be effective. Kelsall *et al.* (*63*) tested undiluted derris dust and obtained 100-percent larval mortality. McDaniel (*77*) reported complete kill of larvae with cryolite and calcium arsenate mixed with hydrated lime. She also found that while 0.075-percent rotenone dust killed a number of the larvae the lethal action was slow. For control on large acreages she suggested the use of a power sprayer and a mixture of 3 pounds of lead arsenate and 1 quart of summer oil per 100 gallons of water.

Aerial Spraying

Following World War II the successful control of certain forest defoliators with aerial applications of DDT brought a new dimension into forest insect work. The State of Minnesota applied a DDT solution to infested tamarack in 1948, but the tests were not conclusive.[15] Butcher and Eaton (*15*) tried aerial applications of DDT against the larval and adult stages of the larch sawfly in Minnesota. In 1949 and 1950 they applied DDT to 80- and 90-acre tracts of tamarack at the rate of 1 pound per gallon of fuel oil per acre. Their results indicated that spraying to control the adults could not be recommended. However, larval spraying reduced the population about 70 percent, and they concluded that partial reduction in populations might protect the trees from severe defoliation for more than one season.

Butcher (*14*) tested aerial applications of endrin and dieldrin in 1952 on 400 and 200 acres of Minnesota tamarack respectively. Solutions of the chemicals were sprayed at the rate of 0.1 pound of actual insecticide in 1.5 gallons of fuel oil per acre. Four days after treatment, frass samples from the sprayed and unsprayed check plots indicated that each insecticide caused a population reduction of about 90 percent. Endrin and dieldrin, however, are very toxic to mammals and are not recommended for forest spraying.

In Saskatchewan Peterson (*90*) reported the aerial spraying of Siberian larch plantations with malathion emulsions in 1954 and 1955. In 1954 he added 8.7 gallons of 25-percent emulsifiable concentrate malathion to 15 gallons of water and sprayed this in two applications at the rate of one-half gallon per acre. The

[15] Annual Progress Report—Calendar Year 1948, Forest Insect Laboratory, Milwaukee, Wis., on file at Lake States Forest Experiment Station, St. Paul, Minn.

same techniques were used in 1955, but the spray was made from 6 gallons of 50-percent emulsifiable concentrate malathion in 15 gallons of water. In both applications many larvae were killed and defoliation was reduced considerably, but some live larvae remained on the trees and healthy cocooned larvae were recovered from the ground.

Unfortunately, the larch sawfly remains a difficult insect to control economically. Because of its biology—diapause in the cocoon and prolonged adult emergence—single aerial applications of the postwar organic insecticides gave remedial but not satisfactory long-lasting control.

Insecticidal Smoke

Kukolevskii (*67*) reported that insecticidal smoke bombs gave good control of the larch sawfly in Russia. Hexachlorane bombs designated NBK (G-17) were used by him in several plantations.

Granular Insecticides

No work has been done with granular insecticides on the larch sawfly, but this type of material might prove of value for sawflies that drop to the ground to cocoon. Their residual potency may even be useful against emerging adults. A drawback to their use in forested tracts is their weight, but they might lend themselves to control in plantations.

Laboratory Insecticide Tests

To determine the potency of several organic insecticides against this sawfly, Drooz (*30*) conducted a series of spray chamber tests in the study area in north central Minnesota in 1956. The tests were conducted solely on a contact basis, and the results were calculated according to lethal effects at the end of 3 days. The gamma isomer of benzene hexachloride (BHC), malathion, and DDT were the insecticides formulated in diesel oil for the experiments.

Comparatively high concentrations of DDT were required to give complete kills of first- and second-instar larvae, and only negligible mortality of fourth- and fifth-instar larvae was obtained at concentrations comparable to those of BHC and malathion where over 90-percent mortality resulted. The calculated lethal dosages (LD) at which 50-percent mortality (LD_{50}) of fourth- and fifth-instar larvae would occur were 0.0012 ± 0.00059[16] and 0.0048 ± 0.00004[16] pounds actual weight per gallon per acre for BHC (gamma isomer) and malathion respectively. The LD_{90} for BHC and malathion were 0.0124 ± 0.00071[16] and 0.0170 ± 0.00056[16] pounds per gallon per acre.

Insecticide Recommendations

The decision to apply insecticides should be made by the landholder only after serious consideration of the values to be protected,

[16] The 0.05 level of significance at 2 degrees of freedom.

be they economic or aesthetic, and after consultation with an entomologist who has a good knowledge of the habits of the insect and its effect upon the tree. The treatment of this subject in the text is brief and based upon laboratory tests and a few field trials. Information considered valuable for such a treatment has been arrived at by considering the best available sources of biological data on the insect, and its susceptibility to insecticides.

For ornamentals the decision relative to control is simple for the owner. The problem becomes more difficult in larger acreages of plantations or natural timber. Successful control will be easier to achieve in isolated larch plantations than in contiguous stands. Stand density and size as they affect the movement of ground equipment are other items to be considered. The problem of economic control over the vast outbreak in central Canada and the Lake States might be considered hopeless at present. This is because of the relatively minor importance of tamarack as a tree species, the extent of the outbreak, the parthenogenetic habit of the sawfly, and its prolonged emergence period.

From the seasonal development studies of the larch sawfly, it can be concluded that the better chance for achieving a high degree of control with a single insecticide application would occur following warm weather in late April and early May. This is because there is less overlap between the termination of oviposition and the start of cocooning under this condition. If the weather is cold during these months, emergence and oviposition continue far into the cocooning period.

It has been shown that fifth-instar larvae feed for 5 to 13 days before dropping to the duff to cocoon. Again in reference to development during a warm spring, little oviposition takes place after July 1; most of the larvae are feeding, and only a small proportion of the larvae have cocooned. Therefore, probably the greatest number of larvae would be exposed to insecticides between about June 21 and July 1 in Minnesota. This period follows initial oviposition by about 26 days or the first fifth-instar larvae by 10 days.

Mortality is not likely in tamarack stands as a result of repeated defoliations until between the sixth and tenth year of outbreak. Therefore, it may be assumed that sprays applied in the fifth season of defoliation would protect the stand for that year and possibly the following one. Although no study has been made of this problem, it seems reasonable to schedule successive treatments at 4-year intervals until the outbreak subsides. Without the aid of unusual weather or significant sawfly losses due to parasites and predators, the outbreak could last conceivably until most of the tamarack was killed. This might take 15 to 20 years. Theoretically, therefore, it may require 4 or 5 insecticide applications to protect a tract from loss.

Recommended equipment and insecticide formulations are given below.

Ground equipment.—Ground equipment is best used for control on ornamentals or easily accessible trees in parks or small plantings. The type of equipment to be used will depend upon tree height and the area involved.

If the insect is prevalent on groups of small trees, satisfactory control can be obtained with a knapsack sprayer, using 2½ teaspoonfuls of the following wettable powders per gallon of water: benzene hexachloride (25-percent gamma), 25-percent lindane, malathion, or dieldrin. Lead arsenate may also be used at a concentration of 9 tablespoonfuls plus 1 tablespoon linseed oil in each gallon of water. Control by dusting may be carried out with undiluted derris or 0.075-percent rotenone.

Hydraulic sprayers or mist blowers may be necessary for control of the sawfly on trees 15 or 20 feet tall or for smaller trees over large areas. The dosage for use in a hydraulic sprayer should be 2 pounds of one of the wettable powders mentioned above, or 2 quarts of the emulsifiable concentrate (25-percent active ingredients) of the same insecticides added to 100 gallons of water. Twelve fluid ounces of linseed oil should be added to the wettable powder materials as a sticker. For lead arsenate, add 4 pounds of the poison to 100 gallons of water and 1 quart of summer oil. Good control can be obtained with a mist blower, using a quart of 25-percent emulsifiable concentrate BHC (gamma isomer), lindane, malathion, or dieldrin added to 3 quarts of water.

Aerial spraying.—To control the larch sawfly by aerial spraying, use a formulation consisting of 0.2 pound benzene hexachloride (gamma isomer), 1 quart of a solvent (minimum flash point, 150° F.), and enough No. 2 fuel oil to make a gallon of finished insecticide. Apply at the rate of 1 gallon per acre about 10 days after the first fifth-instar larvae are present. Malathion is not recommended because of its brief residual potency.

It is most probable that treatments will have to be repeated every few years if the sprayed timber is within the outbreak zone.

CAUTION: Benzene hexachloride, lindane, dieldrin, malathion, and lead arsenate are poisonous. Derris and rotenone will kill fish. Store them in plainly labeled containers away from all food products. Care must be used in spraying over or near lakes, streams, and bird nests and baths. In handling these chemicals follow directions and heed precautions printed on the containers.

SUMMARY

Field and laboratory studies of the biology and control of the larch sawfly, *Pristiphora erichsonii* (Htg.), were undertaken in northern Minnesota between 1949 and 1956, and the work has been summarized in this publication.

The larch sawfly is the most destructive defoliator of *Larix* spp. in North America. It has been reported to have killed vast quantities of tamarack since it was first found on this continent in 1880.

Taxonomists have placed this insect in 5 different genera and applied 3 specific names. The name designated by Ross in 1937,

Pristiphora erichsonii (Htg.), has been accepted in the United States and Canada.

The insect spends the late summer, fall, winter, and part of the spring as a prepupa in a cocoon. In Minnesota a small number may remain thus for 2 or 3 winters. Pupation occurs in the cocoon, and later the adult cuts an exit hole with its mandibles. Reproduction is parthenogenetic, and fewer than 2 percent of the adults reared in Minnesota were males. Emergence in Minnesota begins about the third week in May during periods of warm spring weather and is over by the first week in July; in cooler weather the adults begin to appear the first week in June and emergence is completed by late July. A single generation annually is the rule, but occasional second-generation adults have been reported.

Fecundity may be affected by the quality and quantity of food. During the early years of outbreak a female may produce about 100 eggs, but after 5 years of heavy defoliation egg production may average only 50 per female.

The eggs are laid chainlike in the soft cortex of the developing twigs. They hatch in about a week, and the tiny larvae move to feed on the leaves of the spur shoots. Feeding continues until the fifth instar is completed. The larvae then drop to the ground and spin their cocoons in the duff, where they pass the winter. In northern Minnesota, fresh cocoons were found during the third week of June when the spring temperatures were above normal, and during the first week in July under cooler conditions. Pupation generally occurs the following spring or early summer, although some individuals may spend two or more winters as prepupae in the cocoon.

The larvae feed for about 17 to 24 days and 80 to 85 percent of the frass, ovendry weight, is produced in the fifth instar. The average duration of each stadium was computed, and the average frass yield per larva per instar determined.

Seasonal egg, larval, and frass distribution was investigated at study areas in northern Minnesota from 1952 through 1955. The time of mean development for each was calculated. Although oviposition might begin at the same time, emergence and larval development were more rapid in dry site conditions than in wet ones. Therefore, water relationships in the swamps must be considered in timing insecticidal operations.

Defoliation occurs chiefly during June and July, and an early result is impairment of tree growth. Defoliation is dependent upon many variables that control the insect population and tree condition. Frequently it varies between trees in a stand and between nearby stands. Some governing factors are the accumulation of water on the swamp surface at the time of larval drop or adult emergence, the past history of defoliation as it relates to the production of new shoots for oviposition, and eventually the lack of food if tree mortality becomes widespread. The inability to predict new shoot production precludes forecasting defoliation on the basis of preemergence live cocoon populations.

Marked loss of radial increment appeared after 4 to 6 years of outbreak. Increment losses were generally greater than 65 percent by 1955.

After 6 to 9 years of moderate to heavy defoliation, tree mortality will occur. This became apparent in Minnesota's northeastern upland during the fall of 1954, and was observed in scattered pockets in the better swamp sites of the north central part of the State in the summer of 1956.

Only 2 parasite species out of 29 reported have been at all prevalent in North America during the present outbreak. The imported ichneumon, *Mesoleius tenthredinis*, at one time a very important control factor, has been reduced to a minor role in the control of the larch sawfly in the Lake States and central Canada because of a host immunity reaction. The tachinid *Bessa selecta* has increased in importance during the outbreak, but the past history of this parasite does not indicate that it will play a major role in the decline of the outbreak. The pteromalid *Tritneptis klugii* has not been found in Minnesota since 1949. It cannot be depended upon either to control the sawfly in this outbreak.

A number of insect and arachnid predators have been reported, but nothing is known about their effect on the sawfly population.

Infective stage DD–136 nematodes are capable of killing larvae of all instars. Laboratory tests with these nematodes resulted in complete host mortality, but field-test recoveries were small.

Three genera of entomophagous fungi and two species of bacteria in the genus *Bacillus* were cultured from Minnesota larvae.

Fish, frogs, birds, and rodents eliminate parts of the larch sawfly populations. Of these, rodents are most important, probably accounting for about 80 percent of the overwintering cocoons in Minnesota.

Wind, surface water in the swamps, exposure to direct summer sunlight, and high temperatures bring about some mortality.

The problems of ground and aerial insecticide applications are discussed, and spray recommendations based upon field and laboratory tests are given.

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