THE SARATOGA SPITTLEBUG: A DESTRUCTIVE PEST IN RED PINE PLANTATIONS

Ewan, H. G.
START
The Saratoga
Spittlebug

A Destructive Pest in
Red Pine Plantations

by
Herbert G. Ewan, Lake States Forest Experiment Station

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Foreword

This technical bulletin summarizes some 15 years of research on the life history of the Saratoga spittlebug and measures for its control. In the course of the more recent research, the author was granted the degree of Doctor of Philosophy, and much of the bulletin is a condensation of thesis material.

The writer wishes to express appreciation to R. F. Anderson, H. C. Secrest, and H. E. Milliron, whose earlier work on the project was freely drawn upon from unpublished reports; and to L. C. Beckwith who gave material assistance in some of the fieldwork. Special acknowledgment is also due to Professor A. C. Hodson, Department of Entomology and Economic Zoology, University of Minnesota, for his helpful counsel.
## Contents

<table>
<thead>
<tr>
<th>Section</th>
<th>Pages</th>
</tr>
</thead>
<tbody>
<tr>
<td>Introduction</td>
<td>1</td>
</tr>
<tr>
<td>Distribution and synonymy</td>
<td>2</td>
</tr>
<tr>
<td>Description of life stages</td>
<td></td>
</tr>
<tr>
<td>Adults</td>
<td>3</td>
</tr>
<tr>
<td>Nymphs</td>
<td>3</td>
</tr>
<tr>
<td>Eggs</td>
<td>4</td>
</tr>
<tr>
<td>Life history and biology</td>
<td>5</td>
</tr>
<tr>
<td>Nymphs</td>
<td>6</td>
</tr>
<tr>
<td>Nymphal development rate</td>
<td></td>
</tr>
<tr>
<td>Humidity effects</td>
<td>8</td>
</tr>
<tr>
<td>Hosts</td>
<td>9</td>
</tr>
<tr>
<td>Distribution of the nymphs within a plantation</td>
<td>10</td>
</tr>
<tr>
<td>Adults</td>
<td>11</td>
</tr>
<tr>
<td>Rate of appearance</td>
<td>11</td>
</tr>
<tr>
<td>Sex ratio</td>
<td>12</td>
</tr>
<tr>
<td>Peculiarity</td>
<td>13</td>
</tr>
<tr>
<td>Feeding habits</td>
<td>14</td>
</tr>
<tr>
<td>Hosts</td>
<td>14</td>
</tr>
<tr>
<td>Eggs</td>
<td>15</td>
</tr>
<tr>
<td>Damage caused</td>
<td>16</td>
</tr>
<tr>
<td>Adult feeding-frequency studies</td>
<td>17</td>
</tr>
<tr>
<td>Gross symptoms of tree damage</td>
<td>18</td>
</tr>
<tr>
<td>Relation of damage to host density and size</td>
<td>19</td>
</tr>
<tr>
<td>The feeding-scar</td>
<td>20</td>
</tr>
<tr>
<td>Effect of feeding on twig- and needle-moisture content</td>
<td>21</td>
</tr>
<tr>
<td>Sucrose and reducing sugars in injured twigs</td>
<td>22</td>
</tr>
<tr>
<td>Distribution of feeding injury</td>
<td>23</td>
</tr>
<tr>
<td>Burn blight</td>
<td>24</td>
</tr>
<tr>
<td>Changes in tree form</td>
<td>25</td>
</tr>
<tr>
<td>Survey methods</td>
<td>26</td>
</tr>
<tr>
<td>Population levels and subsequent tree damage</td>
<td>27</td>
</tr>
<tr>
<td>Damage prediction</td>
<td>28</td>
</tr>
<tr>
<td>Control</td>
<td>29</td>
</tr>
<tr>
<td>Weather effects</td>
<td>30</td>
</tr>
<tr>
<td>Biological agents</td>
<td>31</td>
</tr>
<tr>
<td>Silvicultural control</td>
<td>32</td>
</tr>
<tr>
<td>Insecticidal control</td>
<td>33</td>
</tr>
<tr>
<td>Summary</td>
<td>34</td>
</tr>
<tr>
<td>Literature cited</td>
<td>35</td>
</tr>
</tbody>
</table>

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III
The Saratoga Spittlebug
A Destructive Pest in Red Pine Plantations

By

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Introduction

The Saratoga spittlebug, *Aphrophora saratogensis* (Fitch), is a major pest of red pine plantations in the Lake States. Outside this region, this insect has not been of great importance over any large area. Nevertheless, it is native throughout the commercial range of red pine in North America, and recently isolated infestations have appeared in increasing numbers in the Northeastern States and in southern Canada.

During the early 1940's, when the spittlebug was first recognized as a plantation pest, jack pine was severely damaged. However, the current impact on this species is relatively insignificant because the planting of jack pine has decreased markedly since the 1940's, and most of the previously established plantations have grown out of the spittlebug-susceptible height range.

In contrast, the economic impact of the spittlebug on red pine is steadily increasing because of the popularity of this species in reforestation programs. In the Lake States alone, it has been estimated that, in addition to the roughly three quarters of a million acres of red pine plantations established through 1950, about 4 million acres were still in need of planting to red pine (2).

The spittlebug is one of the few forest insects in the Lake States for which a major insecticidal control program has been established. Over the past 11 years, an average of about 10,000 acres of red pine and jack pine plantations has been sprayed annually in Wisconsin and Michigan. Routine spittlebug appraisal surveys are made annually in nearly all young red pine plantations less than 15 feet in height on national-forest land in northern Wisconsin and Upper Michigan. Susceptible areas on State and private lands are also being watched closely and, where necessary, chemical control is applied to prevent serious tree damage by the spittlebug.

The Saratoga spittlebug was taxonomically described in 1856, but did not attract the attention of forest entomologists until 1941. At that time, tree degeneration and mortality were noted in young red

1 Maintained at St. Paul 1, Minn., in cooperation with the University of Minnesota.
2 Italic numbers in parentheses refer to Literature Cited, p. 51.
pine and jack pine plantations in northern Wisconsin and parts of Minnesota and Michigan; this damage was caused by the feeding of the adult Saratoga spittlebug.

Epidemics of the Saratoga spittlebug are a major consideration in modern forest management programs in the heavy infestation area of northern Wisconsin and Upper Michigan. The desirable ultimate goal in controlling this pest is prevention of outbreaks by proper silvicultural techniques. Complete achievement of this goal may be impossible because preventive measures effective against the pest may not be compatible with other silvicultural practices. However, the problem at hand is much more direct; namely, how to differentiate dangerous from innocuous infestations so that modern control procedures can be employed on sound economic and biological bases. To develop accurate appraisal criteria, resolution of the following points is necessary: (1) Development of accurate techniques for population measurements, (2) determination of the amount of host injury associated with the various population levels, and (3) appraisal of the significance of host injury.

With the above three points serving as general objectives, a study of the Saratoga spittlebug was conducted in young red pine plantations in the Lakes States from 1954 through 1957. Because of the paucity of published information on this pest, the results of previous workers' studies on biology and control (1941-52)—largely contained in unpublished office reports on file at the Lake States Forest Experiment Station—are also summarized in this report.

The first half of the report gives the essentials of available knowledge on the biology and ecology of the pest—its distribution, life history, and life stages. The last half treats the nature of tree damage, reliable methods of predicting damage, and population controls.

Distribution and Synonymy

The Saratoga spittlebug, as a major pest in red pine and jack pine plantations, is largely limited to northern Wisconsin and Upper Michigan. Infestations causing severe damage have occurred less frequently in Minnesota, Lower Michigan, and Ontario. The pest has also been reported in relatively large numbers in localized areas in Pennsylvania and New York.

The widest species distribution of the Saratoga spittlebug was given by Ball (5) as coast to coast in Canada and the northern United States, as well as in California, Florida, and some of the East Central and Southern States. However, taxonomists disagree as to whether a single species or several closely related species are included. Walley (25) contends that the western specimens represent two different species, Aphrophora canadensis and A. punctipes Walley. Doering (8) suggests that records of A. saratogensis in Florida, Georgia, Maryland, Mississippi, North Carolina, South Carolina, and Washington, D.C., probably actually refer to A. distritus. Moore (26) in a recent revision of the genus Aphrophora pro-
posed that A. detritus is a synonym of A. saratogensis—inferring that the Saratoga spittlebug has a complete north to south distribution in the United States.

*Aphrophora saratogensis* was originally described as *Lepthyonia saratogensis* by Fitch in 1851. Doering (8) places *Ptyelus goldiana* Walker, 1851, as a synonym of *A. saratogensis*. Moore (90) gives *P. detritus* Walker, 1851, as an additional synonym.

**Description of Life Stages**

The life stages of the Saratoga spittlebug are typical of the family Cercopidae, order Hemiptera. In the following paragraphs, this species will be differentiated from other members of the genus that may be found on pine. Also, the nymphs are described in enough detail to enable entomologists to differentiate between the five instars.

**Adults**

The adult Saratoga spittlebug is a smoothly contoured, somewhat boat-shaped insect. In its natural habitat it is quite inconspicuous. Figure 1 shows how well the adults are camouflaged. The base color is brown, and the markings are tan to silvery white, a color pattern very similar to that of a young red pine twig. The markings form two irregularly-mottled transverse bands on the hemelytra; a median dorsal light stripe is usually present on the head and pronotum.

Females are distinguished from males by the sword-shaped ovipositor, which constitutes approximately one-fourth of the length of the abdomen.

The average length of adult Saratoga spittlebugs, derived from 50 specimens of each sex, was 9.0 mm. for the male (range—8.2 to 9.8) and 9.8 mm. for the female (range—9.0 to 10.5). Anderson (4) lists the average length of 30 males as 8.7 mm. (range—8.0 to 9.1) and of 30 females as 9.6 mm. (range—9.0 to 10.0).

Although several species in the genus *Aphrophora* may be found on pine (24), only two, the Saratoga spittlebug and the pine spittlebug, *A. parallela* (Say), are abundant enough to be of economic importance. Another species, *A. signoreti* Fitch, resembles the Saratoga spittlebug quite closely and is also reported to choose pine as an adult host and low-growing shrubs as an alternate host. From a practical standpoint, there is little danger of confusing *A. saratogensis* and *A. signoreti* because of the extreme scarcity of the latter. Speers (24) lists some of the morphological differences.

The pine spittlebug very rarely attacks red pine (24). The Saratoga spittlebug, on the other hand, exhibits at least a 3 to 1 preference for red pine over other pines. The most easily discernible morphological difference between the two species is the relative degree of inflation of the anteclypeus. In *Aphrophora parallela* the anteclypeus is strongly inflated and extends beyond the postclypeus; in *A. saratogensis* the anteclypeus is weakly inflated and does not exceed the postclypeus. This difference can be seen with the unaided eye.

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4 Unpublished data on file at Lake States Forest Experiment Station, collected by H. C. Secrest, U.S. Bureau of Entomology and Plant Quarantine, 1943.
Figure 1.—Two Saratoga spittlebug adults on a red pine twig. Note how inconspicuously spittlebugs blend with surroundings.

Nymphs

Body lengths of the nymphs range from about 2 mm. (first instar) to about 8 mm. (fifth instar). Considerable variation occurs in size of the abdomen among individuals of each instar. Head capsule size, however, is quite constant. Measurements of head widths just in front of the antennae (10 individuals per instar) gave the following averages: First instar, 0.4 mm.; second instar, 0.6 mm.; third instar, 0.8 mm.; fourth instar, 1.0 mm.; fifth instar, 1.3 mm. (4).

The general shape and markings of the nymphs are illustrated in figure 2. The abdomens of the first four instars are scarlet except for black markings at the pleural angle. The head, thoracic tergites, and portions of the leg segments are jet black. The compound eyes are red. Initially, fifth-instar nymphs have pale red abdomens and tan thoraces, legs, and head (except for a white to light-gray clypeus). Later during the fifth instar, the nymphs become uniformly brown to mahogany colored; the clypeus remains light.

To differentiate the first three nymphal instars, the black markings on the pleural region of the caudal abdominal segments are most useful: First instar—abdomen entirely crimson, black pigmentation
lacking except for the caudal tergite where the color ranges from gray to black; second instar—a dorsal projection of pigment is present on segment VIII; third instar—a dorsal projection of the pigment is present on segments VII and VIII. The fourth instar is characterized by the presence of developing wing pads and an increase in black pigmentation in the pleural abdominal region. The fifth instar is readily identified by its lack of the striking black and crimson color combination: it is uniformly tan to dark brown.

Figure 2.—Outline sketches of the Saratoga spittlebug: A, First instar; B, second instar; C, third instar; D, fourth instar; E, fifth instar; F, adult female—left wings partially removed (lateral views—10X).
Egg

The eggs are shaped like an elongated teardrop—rounded at one end, and tapered to a curved point at the other (fig. 3). They are about 1.8 mm. long and 0.6 mm. wide at the widest point. Initially, the eggs are depressed along the long axis; prior to hatching in the spring they become turgid. Their color varies from a glistening, light buff just after deposition to shiny red or purple in early spring. Eggs that are partially exposed in the outer bud scales weather to a darker color than those more centrally located in the bud.

Shortly after being laid, the eggs develop a characteristic red spot (actually a spherical inclusion in the tapered end of the egg).

Life History and Biology

There is one generation of the Saratoga spittlebug per year, and overwintering occurs in the egg stage. On red pine, eggs are laid under the outer scales of buds in the upper part of the trees. In the Lake States, hatching is usually complete by the middle of May. The young nymphs crawl to the ground, begin feeding at the base of the alternate host stems, and soon generate the characteristic spittle masses around themselves. The period of nymphal development varies from 40 to 70 days, depending on the weather. Upon completion of feeding, nymphs vacate the spittle masses and climb to the upper parts of the alternate host stems where they transform to adults. The adults then fly to the pine hosts and begin feeding on the needle-bearing twigs.

In the Lake States, there is a moderate amount of overlapping of life stages. That is, a small percentage of adults can be found as early as the latter part of June, and an occasional nymph can still be found in late August. Adult transformation, however, is usually 80 percent complete about the middle of July.

Population occurs within a few days after transformation, and the peak of egg-laying is reached about 2 or 3 weeks later. Some adults remain active until killing frosts occur in the fall, but the population is about one-third of the mid-July peak level by the end of August and drops to an insignificant level by the end of September. About 90 percent of the season’s feeding damage is inflicted in the month following the peak of adult transformation (mid-July to mid-August). Most of the feeding apparently occurs during the period of maturation of the oocytes.

Nymphs

The nymphal stages last from about the middle of May to early July. Examination of terminal red pine buds in infested plantations reveals the presence of numerous hatched spittlebug eggs about the time of the beginning of shoot elongation for Lake States red pine. Newly hatched nymphs crawl to the ground and actively seek suitable alternate host plants. In the laboratory, the vigor of the young nymphs is attested by their appearance on the floor or walls at a distance of 20 feet from the hatching site 10 minutes after release.
The nymphs generally feed singly or in small groups. First- and second-instar nymphs are frequently found at the axils of the lowest whorl of leaves of herbs. They may also be found beneath the leaves near the root-collar region of the stem or, less frequently, an inch or two above the ground on the main stem. The spittle masses formed by the first-instar nymphs are about one-eighth inch in diameter. As a nymph matures, it increases its spittle mass until the mass attains a diameter about one-half inch for a single fifth-instar nymph. Usually, the spittle masses can be observed only by pressing the ground litter away from the stem.

The average number of nymphs per spittle mass seldom exceeds 2 or 3 even in heavy infestations. Occasionally, conspicuous spittle masses 2 or 3 inches in diameter project above the ground litter. These large masses usually encompass several alternate host stems and may contain from 10 to 50 or more nymphs (fig. 4).

A general description of the spittle of Cercopid nymphs and a discussion of the various theories that have been put forth concerning the generation and function of the spittle are given in Weaver and King's (20) bulletin on the meadow spittlebug. The composition
and microbiology of insect spittle have recently been studied by Wilson and Dorsey (27).

**Nymphal Development Rate**

Table 1 shows the duration of each stadium in the years 1944, 1954, and 1957 on the Nicolet National Forest in northeastern Wisconsin. The length of both the first and the fifth stadia are only approximate since no precise techniques were used to determine the rate of hatch and the rate of adult transformation. These two factors were simply estimated by periodic observations of relative abundance. The data for the 1944 nymphal development rate were obtained by Anderson.

Local variation adds a complicating factor in determining nymphal development rate. In 1956, for instance, adult transformation was judged to be about 80 percent complete on two permanent study plots on July 11. Checks in other plantations—some in adjacent town-

*Unpublished data on file at the Lake States Forest Experiment Station, collected by R. F. Anderson, U.S. Bureau of Entomology and Plant Quarantine, 1944.*
ships—showed that nymphal development was slower and transfor-

mation did not reach the 80-percent level until July 23.

### Table 1.—Nymphal development rates of the Saratoga spittlebug,
### Nicolet National Forest

<table>
<thead>
<tr>
<th>Year</th>
<th>Approximate date of complete hatch</th>
<th>First</th>
<th>Second</th>
<th>Third</th>
<th>Fourth</th>
<th>Fifth</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Days</td>
<td>Days</td>
<td>Days</td>
<td>Days</td>
<td>Days</td>
<td>Days</td>
<td>Days</td>
</tr>
<tr>
<td>1944</td>
<td>May 21</td>
<td>11</td>
<td>6</td>
<td>10</td>
<td>9</td>
<td>11</td>
<td>July 5</td>
</tr>
<tr>
<td>1954</td>
<td>May 27</td>
<td>15</td>
<td>6</td>
<td>4</td>
<td>11</td>
<td>17</td>
<td>July 19</td>
</tr>
<tr>
<td>1955</td>
<td>May 10</td>
<td>21</td>
<td>9</td>
<td>10</td>
<td>11</td>
<td>13</td>
<td>July 18</td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td>15</td>
<td>7</td>
<td>9</td>
<td>10</td>
<td>15</td>
<td>—</td>
</tr>
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</table>

1 Approximate only. Rate of hatch and of adult transformation were based on periodic observations of relative abundance.

### Humidity Effects

Moisture is a very important limiting factor in the environment of the young nymphs. In the laboratory, newly hatched unfed nymphs lived for a maximum of 2 or 3 days when kept at 100-percent relative humidity in desiccator jars. They succumbed in less than 12 hours when held at approximately 30-percent relative humidity (table 2).

Nymphs reared in the laboratory on potted tomato and barberry plants died unless plastic bags were placed tightly over the plants to maintain a high relative humidity. Even after the nymphs had begun feeding and forming spittle, they would succumb within 24 hours.

### Table 2.—Survival of newly hatched unfed nymphs of the Saratoga spittlebug at 100- and 30-percent relative humidity in the laboratory, March 1950

<table>
<thead>
<tr>
<th>Hours of exposure</th>
<th>100-percent relative humidity</th>
<th>30-percent relative humidity</th>
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<tbody>
<tr>
<td>Percent</td>
<td>Percent</td>
<td>Percent</td>
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<td>0</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>3</td>
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<td>93</td>
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<td>6</td>
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<tr>
<td>60</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td>72</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

1 100-percent relative humidity maintained in desiccator jars with distilled water; 229 nymphs initially.
2 30-percent relative humidity was the room humidity as determined with a sling psychrometer at the beginning of the test. The nymphs were kept in cheesecloth-covered desiccator jars; 250 nymphs initially.
hours when the plastic bags were removed. Once the nymphs succeed in covering themselves with spittle under field conditions, they have a unique and effective control over their environment. However, first- and second-instar nymphs are still subject to desiccation during periods of very hot dry weather if they are in open plantations with sparse ground cover. This vulnerability has certain practical implications discussed under the section on control.

Death from desiccation has not been observed in nymphs reaching the fourth instar. When fourth-instar or older individuals were taken from their spittle masses and placed on the ground in direct sunlight, they quickly sought other plants and reestablished themselves.

**Hosts**

If a list were made of every plant species upon which Saratoga spittlebug nymphs have been found, it would include nearly every shrub, herb, tree seedling, and fern growing in Lake States pine plantations. A list of about 30 of the more common alternate hosts has been published by Anderson (4). Entomologists have reported that sweetfern is the most common host of the mature nymphs even though, on occasion, other woody plants such as *Salix* sp. have been observed to support more nymphs per stem than did sweetfern. Absence of sweetfern in a particular plantation does not forestall the possibility of a spittlebug infestation, since the nymphs are capable of surviving on many low-growing plants—not, however, on grasses.

How many alternate host plants are needed to support a damaging spittlebug population? Available data indicate that epidemic populations in the Lake States occur in areas containing a total of 60 or more alternate hosts per acre. This observation has little practical value since only closed plantations or those established on sod land would contain lower densities of alternate hosts.

The admixture of woody and herbaceous alternate hosts in a particular plantation does affect the likelihood of an infestation. In spite of the wide variety of plants that may serve as alternate hosts for the nymphs, woody plants are generally prerequisite for the buildup of heavy spittlebug populations. Nymphal surveys in northern Wisconsin show clearly that the majority of fifth-instar nymphs are found on sweetfern and *Rubus* spp. Of 3,459 nymphs observed during routine sampling on approximately 6,000 acres of red pine in 1957, 2,062 nymphs were on sweetfern and *Rubus* spp. The remaining 1,397 individuals were found largely on herbs, but an undetermined number were on other woody plants such as aspen sprouts, prairie willow, and blueberry. Sweetfern and *Rubus* spp. were absent in only 2 of the 50 plantations sampled. In 36 of the plantations, 50 percent or more of the nymphs were found on sweetfern and *Rubus* spp. This evidence strongly indicates that plantations that do not contain woody alternate hosts—especially sweetfern and *Rubus* spp.—will seldom harbor more than a light population.

A further indication of the importance of woody alternate hosts in the buildup of damaging spittlebug populations is the number of
infestations on the five ranger districts of the Nicolet National Forest.

The percentage of plantations infested on the Lakewood District is about twice that found on the other four districts (table 3). Of the 1,701 nymphs in a sample on the Lakewood District in 1957, 86 percent were on sweetfern and Rubus spp. In a sample of 1,755 nymphs on the four less heavily infested districts (Laona, Florence, Eagle River, and Argonne), only 34 percent were on sweetfern and Rubus spp.

Although fifth-instar nymphs prefer woody hosts, the majority of early instar nymphs are found on succulent, herbaceous plants. Table 4 shows the results of a study of the change in host preference as the nymphs mature. Two major host categories were considered as follows: (1) Sweetfern and Rubus spp., which constituted most of the woody alternate hosts found in the plantations, and (2) others, which included the few remaining woody plants plus a variety of herbs. Four study areas were sampled at weekly intervals beginning when most of the nymphs were in the first and second instars.

The first count revealed that between 75 and 95 percent of the nymphs were on the herbaceous plants. Two weeks later only 10 to 40 percent remained. The movement of nymphs from reseeded low-growing herbs to woody plants occurred largely during the third stadium in 1956 (about June 10).

That this represents a migration and not a differential mortality on the two kinds of host plants can be seen by the total population counts—they did not change appreciably on plots A and B throughout the nymphal sampling period. The directed nature of this movement becomes more apparent when it is noted that sweetfern and Rubus spp. constitute only a small percentage of the total possible hosts. Mature nymphs are also capable of such migration. When fifth-instar nymphs were placed in a cage covering a variety of plants, they crawled through or over the duff as necessary and established themselves almost exclusively on the woody plants (4).

The reason why nymphs occur on herbs in the early instars and on woody plants in the later instars is not definitely known. The moisture requirements of the young nymphs may cause them to choose the more protective herbs; or a newly hatched nymph may

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Table 3.—Incidence of spittlebug infestations requiring control on the five ranger districts, Nicolet National Forest

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<td>Lakewood</td>
<td>12,782</td>
<td>1,305</td>
<td>2,434</td>
<td>1,180</td>
<td>2,542</td>
<td>7,011</td>
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<td>Eagle River</td>
<td>5,994</td>
<td>765</td>
<td>1,128</td>
<td>0</td>
<td>230</td>
<td>1,942</td>
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<td>Florence</td>
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<td>414</td>
<td>754</td>
<td>777</td>
<td>1,966</td>
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<td>Laona</td>
<td>10,347</td>
<td>768</td>
<td>1,027</td>
<td>60</td>
<td>1,040</td>
<td>2,064</td>
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<td>Argonne</td>
<td>7,630</td>
<td>50</td>
<td>148</td>
<td>0</td>
<td>94</td>
<td>292</td>
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</tbody>
</table>

From the results of a survey by National Forest Administration personnel completed in 1955. Approximately 93 percent of the acreage shown is pure red pine; the remainder is mixed with white pine or spruce or both.
simply establish itself on the first plant encountered. This would result in about 70 to 90 percent of the nymphs starting out on herbs since the woody plants are outnumbered to that extent. The differential survival or growth rate of the nymphs if confined on certain hosts has not been thoroughly investigated. However, Anderson reported that fourth-instar nymphs can be reared to adults on a wide variety of alternate hosts. Fourth- and fifth-instar nymphs generally survived better on the woody hosts, but at least a certain percentage also survived on the herbs.

### Distribution of the Nymphs Within a Plantation

In beginning infestations, spittlebug damage in red pine plantations is generally uneven. This is because the nymphs are concentrated in the areas that contain an abundance of suitable alternate hosts, and the adults tend to remain near the patches that foster nymphal development. Consequently, the tree damage is also concentrated in these areas. However, in long-standing infestations such as occurred in the past, widespread tree mortality occurs in large areas where the infestation loci progressively encroach on surrounding healthy trees until the pockets of damage coalesce.

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2 See footnote 5, page 8.
At least four factors are responsible for the openings or pockets in a plantation that favor abundant alternate host development: (1) Absence of trees in rocky or stumpy spots, or other places that were considered undesirable for planting, (2) uneven planting so that areas even as small as one-tenth acre may be considered as fully stocked but still will contain openings of 40 or more square feet, (3) failure of the trees in localized areas due to various biotic and climatic factors in the early life of the plantation, and (4) the spittlebug itself, which stunts or kills the young trees thereby creating its own openings.

In addition to the uneven distribution of nymphs over the plantation as a whole, there is also a population gradient spreading outward from each pine host. This, of course, is the result of the eggs being located on the pine hosts. As a rule, the nymphal population in a moderately to heavily infested plantation is concentrated largely on the alternate hosts within a radius of about 10 feet of the trees. However, on the edges of heavily infested plantations or in internal openings, a few nymphs can be found as far as 100 feet from the nearest pine.

To determine the population gradient in the immediate vicinity of the pine hosts, the nymphal density in a very heavily infested plantation was sampled to determine the average number of nymphs per sweetfern plant in concentric 1-foot rings around the pine stem. This undoubtedly represents a wider distribution of nymphs than would be found in more lightly infested areas. The nymphs (mostly fifth instar) were counted on 516 sweetfarns around 20 trees. The

![Diagram](Figure 5.—Relation of nymphal density to distance from pine host, June 1955.)
average tree height was 8 feet, and the average crown radius at the base was 2.5 feet.

Figure 5 shows the inverse linear relationship between the average number of nymphs per sweetfern and the distance from the pine host. This indicates that the nymphs would be evenly distributed between the trees in any plantation averaging 680 or more trees per acre since theoretically there would be no point at a distance of more than 4 feet from a tree. However, it should be emphasized again that most plantations moderately to well stocked contain frequent openings with 12 or more feet separating the trees. An uneven distribution of nymphs is the rule, and systematized sampling techniques are necessary in estimating populations.

Adults

Rate of Appearance

Adult transformation takes place on the upper part of the stems and on the leaves of the alternate host plants as attested by the presence of exuviae on these parts during early July. The transformation has not been observed directly, and possibly it takes place at night. In the Lake States, periodic sweeping of the trees reveals the first adults during the latter part of June.

![Graph showing adult transformation](image)

**Figure 6.**—Transformation of caged nymphs of the Saratoga spittlebug during July 4–13, 1955.
In 1955, 10 cages were set up over sweetfern plants infested with fifth-instar nymphs to determine the time of adult transformation. Each wire-screen cage encompassed an area of about 2.5 square feet and contained from 2 to 10 infested sweetfern stems. The first adult was found on July 4, and the last on July 13. Outside the cages, adults transformed before and after the caged individuals. The peak transformation occurred on July 11 when 28 adults (56 percent of the total) were removed (fig. 6). In 1944, the first adult was

Table 5.—Adult population counts of the Saratoga spittlebug throughout the season in three heavily infested plantations, Nicolet National Forest

<table>
<thead>
<tr>
<th>Date</th>
<th>Adults observed</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Per 5 minute period</td>
</tr>
<tr>
<td></td>
<td>Number</td>
</tr>
<tr>
<td>1944: 1</td>
<td></td>
</tr>
<tr>
<td>June 15-30</td>
<td>0</td>
</tr>
<tr>
<td>July 1-15</td>
<td>50</td>
</tr>
<tr>
<td>15-31</td>
<td>32</td>
</tr>
<tr>
<td>Aug. 1-15</td>
<td>29</td>
</tr>
<tr>
<td>16-31</td>
<td>24</td>
</tr>
<tr>
<td>Sept. 1-15</td>
<td>15</td>
</tr>
<tr>
<td>15-30</td>
<td>1</td>
</tr>
</tbody>
</table>

Average per sweep in relation to peak number

<table>
<thead>
<tr>
<th>Date</th>
<th>Number</th>
<th>Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td>1946: 2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>July 22</td>
<td>7.8</td>
<td>100</td>
</tr>
<tr>
<td>28</td>
<td>4.3</td>
<td>56</td>
</tr>
<tr>
<td>Aug. 7</td>
<td>3.7</td>
<td>47</td>
</tr>
<tr>
<td>17</td>
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<td>41</td>
</tr>
<tr>
<td>27</td>
<td>2.0</td>
<td>26</td>
</tr>
<tr>
<td>Sept. 6</td>
<td>1.7</td>
<td>22</td>
</tr>
<tr>
<td>16</td>
<td>.6</td>
<td>8</td>
</tr>
<tr>
<td>26</td>
<td>.06</td>
<td>1</td>
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</table>

1955:

<table>
<thead>
<tr>
<th>Date</th>
<th>Number</th>
<th>Percent</th>
</tr>
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<tbody>
<tr>
<td>June 29</td>
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<td>3</td>
</tr>
<tr>
<td>July 1</td>
<td>.02</td>
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<td>7</td>
<td>3.60</td>
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<td>17</td>
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<td>64</td>
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<tr>
<td>15</td>
<td>1.30</td>
<td>35</td>
</tr>
<tr>
<td>Sept. 1</td>
<td>.22</td>
<td>9</td>
</tr>
<tr>
<td>11</td>
<td>.10</td>
<td>3</td>
</tr>
</tbody>
</table>

1 Data taken from Anderson (3).
2 Data taken from H. B. Milliron, 1946; unpublished, on file at the Lake States Forest Experiment Station.
observed on July 2, and 88 percent of the nymphs had transformed by the end of the following week.  
Egg laying begins about the middle of July and reaches a peak about 2 weeks later. Immediately thereafter, the population declines on an average of about 15 percent per week (table 5). A few adults can be found late into October.

**Sex Ratio**

The sex ratio of the adults is approximately 1 to 1 as determined by collections of at least 100 adults per week over a 10-week period beginning July 1, 1955. Of the 1,088 adults collected, 47.2 percent were females. At the beginning of transformation, males outnumbered females. After a few days, the approximately 1 to 1 ratio was achieved and maintained for most of the season. In September, when the population had dropped considerably, females outnumbered males by about 2 to 1.

**Fecundity**

The fecundity of the Saratoga spittlebug is not precisely known, and determining the number of eggs produced by a single female in one season is complicated by several factors: (1) The oocytes develop over a period of about 2 or 3 weeks following adult transformation, (2) oviposition is a prolonged process and the eggs are not all laid in one batch, (3) the eggs are thrust between the scales of red pine buds with uneven distribution within a tree and between trees. Direct attempts at solving these problems by caging adults and counting the resulting eggs have been largely unsuccessful. General activity of the adults was found to be quite abnormal when confined in sleeve cages for periods longer than 1 week (fig. 7). Poor survival of both sexes in the cages made it difficult to determine whether or not females died after depositing a few eggs.

These cage studies were abandoned in favor of periodic collections and dissections of adult females to determine the potential egg production. This is a relatively simple procedure since the eggs are large, and there are seldom more than 15 in one individual.

In the dissected females, no full-grown oocytes were found until about the end of July. As the oocytes developed, there was no gradation in size between those situated anteriorly and posteriorly in the ovarioles. Each ovariole contained only one developing oocyte plus 1 to 3 tiny cells about 0.1 mm. in length, situated anteriorly. These small cells lacked the yellow yolk granules visible in the oocytes and may have been the nurse cells characteristic of a polytrophic ovary described by Snodgrass (29).

On the other hand, no detailed anatomical studies were made, and the small cells may be immature oocytes with the potential to grow and replace oviposited eggs in the posterior parts of the tubes. However, if the latter had been true, one might have expected to find partially developed, intermediate-sized oocytes in the ovarioles during the latter part of August. Since these were never found, it

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5 See footnote 5, page 8.
is apparent that only one batch of oocytes matured during the life of the adult female under study. Studies by Anderson in 1944 also revealed only fully developed oocytes in females after the middle of July.

In 1955, about 20 unparasitized females were dissected every week from July 22 to September 16. The egg complement averaged 14.6 ±0.57 (standard error). Dissections made in other years, and by other workers, have indicated a similar number of eggs per female. Since only one batch of eggs is matured, and the sex ratio is 1 to 1, the maximum potential increase in a population from one year to the next is only by a factor of 7 or 8. This is an extraordinarily low

*See footnote 5, page 8.
reproductive potential for an insect. However, the “environmental resistance,” or the sum of the factors tending to reduce Saratoga spittlebug populations, is relatively ineffectual. The actual net increase in spittlebug populations from year to year appears to be just as great as that found in most other forest insects.

Feeding Habits

The adult Saratoga spittlebugs actively move around and feed on the needle-bearing parts of the pine twigs. They distribute themselves throughout a plantation more uniformly than nymphs do, and they do not seem to be gregarious. Occasional specimens have been observed feeding without movement for periods of 5 or 10 minutes, but close or prolonged observation on the duration of feeding is difficult. Upon the least disturbance, the adult characteristically springs away at such high velocity that even the direction of flight often cannot be observed. Feeding-frequency studies indicate that each adult makes from 2 to 5 feeding punctures per day; the average feeding in one place may last several hours.

Feeding and activity in general are entirely inhibited during certain weather conditions. For instance, during inclement weather and also in the early morning when the temperature drops to about 60°F, the adults become very lethargic and can be handled without disturbing them. This suggests that feeding does not occur during cool nights or cool rainy days. Conversely, the adults become very active and feed frequently during the heat of the day.

Hosts

In the older taxonomic literature, it was not determined whether the hosts recorded were actually sustaining the spittlebug or whether some of the “host” trees were merely convenient resting places. The hosts listed in the past are tamarack, Larix laricina (Du Roi) K. Koch.; jack pine, Pinus banksiana Lamb.; pitch pine, P. rigida Mill.; and eastern white pine, P. strobus L. (9).

Since the insect achieved economic importance in the Lake States, the preferred host of the adults is red pine, Pinus resinosa Ait. Jack pine is also attacked and occasionally this species is stunted and dies but only to about one-third the extent of red pine (3). White pine is also fed upon, but damage has seldom been noted. However, Drooz² reported severe damage to white pines growing within a heavily infested red pine plantation in Pennsylvania. Adults can be collected from the young seedlings of a number of other coniferous species when the latter are growing in association with infested red or jack pine, but it is doubtful that much, if any, feeding occurs on conifers other than those in the genus Pinus.

In 1934, adult host preference was observed in an irregularly shaped 7- to 13-year-old red pine plantation totaling about 200 acres on the Argonne Ranger District of the Nicolet National Forest. Other volunteer conifers scattered in and around the plantation were balsam fir, northern white-cedar, white pine, and tamarack. Within

²See footnote 3, page 2.
the boundaries of the plantation were also two small areas planted to jack pine and white spruce. Adult Saratoga spittlebugs could be collected in abundance from all these conifers except the planted white spruce, which was separated from the nearest red pine by a 200-yard strip of hardwoods. In spite of the abundance of adult spittlebugs, only the red pine saplings showed mortality or severe stunting. The jack pine showed some twig mortality but did not appear to be in immediate danger of whole-tree mortality or top killing. The white pine did not show any gross symptoms of feeding damage, but a few tiny feeding punctures could be detected in the cortex of the needle-bearing twigs. No evidence of feeding could be discerned on the remaining conifers.

Reports in the literature since the Saratoga spittlebug became an economic pest in 1941 (22) and observations during the present study offer almost certain proof that red pine and jack pine are the only native hosts in danger of severe damage in the Lake States region.

There was no opportunity to test the susceptibility of exotic pines during this study.

Eggs

Eggs of the Saratoga spittlebug are present in the field from late July through fall and winter and until hatching occurs in early May. The primary oviposition site is between the dead outer scales of buds in the upper whorls of young red pines. In infested jack pine, eggs are found in the needle sheaths; the buds are presumably too hard and resinous to allow oviposition. Eggs have also been found in the buds and under loose bark scales of various hardwoods (22).

Oviposition sites most frequently selected are the large loose terminal and branch tip buds near the tops of red pine trees 3 to 12 feet in height. The buds harboring eggs have a characteristic lumpy surface, which can be felt with the thumb and forefinger. When buds are heavily infested, a few eggs can generally be seen protruding from crevices in the surface (fig. 3). The eggs can be removed by peeling back the layers of dead bud scales; usually they are in single-layered rows of 2 to 10 between the scales. The total number per bud depends on the infestation level and the position of the bud; in the large terminal buds of heavily infested trees, 100 eggs are not uncommon.

A newly laid egg contains an embryo of sufficient differentiation to be easily recognized. Giese and Wilson (19) reported that eggs dissected from gravid females contained embryos that had reached the normal diapausing length of 0.649±0.025 mm. (standard deviation). This means that fertilization takes place before the eggs pass down the oviduct.

The embryo overwinters in an obligatory quiescent state, which is normally terminated by exposure to low temperature. Eggs collected in the fall and held at room temperature have never hatched. Those collected in early January, or later, have always hatched in 1 to 3 weeks. The exact temperature, or sequence of temperatures, necessary to stimulate diapause release is not known. Limited rearing experiments, however, have revealed some facts. Several hun-
dried eggs collected in October and exposed to 0° F. for 1 week failed to hatch in 3 months at room temperature and 100-percent relative humidity. Death of these eggs due to cold shock is unlikely because eggs are normally exposed to below zero (°F.) field temperatures in the Lake States.

Another group of eggs collected in September and held at 20° F. for 60 days hatched in about 3 weeks after being returned to room temperature (15). From this it appears that a prolonged exposure to moderately subfreezing temperature is more effective in stimulating diapause release than a brief exposure to a very low temperature.

It is unlikely that physical factors other than temperature are normally involved in diapause release. Giese and Wilson (15) reported that fall-collected eggs exposed to a water extract of red pine needles did contain embryos significantly longer than diapausaing embryos. However, they did not report hatching. Since fall-collected eggs do not hatch in the laboratory even when left inside the red pine buds, there is probably not a chemical release of diapause in nature.

The diapausaing egg contains a red inclusion near the sharply tapering end (fig. 8). It is a granular sphere occupying about 10 percent of the volume of the egg. A similar inclusion is reported in the egg of the meadow spittlebug (26). Examination of fixed and stained sections as well as living material revealed that the inclusion is noncellular and is separated from the embryo by undifferentiated yolk. The red spot remains unchanged in the egg until diapause release in the spring. After the embryo resumes development, the inclusion diminishes in size and disappears on about the twelfth day (15). Figure 9 A illustrates diagrammatically the position of the diapausing embryo and the red inclusion. Figure 9 B shows the egg prior to hatching without the red spot and the embryo in the normal reversed anterior-posterior position.

As the red spot shrinks after diapause release, there is a simultaneous accumulation of red pigment in the lateral-ventral region.

![Figure 8](image-url)

*Figure 8.—Four eggs showing red inclusions (25X).*
of the abdomen of the embryo. The red pigmentation remains visible in the abdomens of the first four nymphal instars but is covered over by brown cuticular pigmentation in the fifth instar and adult. Dissection of fifth-instar nymphs and adults revealed that the red pigmentation is still present as a lining applied to the somatopleure. It has been suggested that the inclusion in the egg is a mycetome (15). This hypothesis is given further credence by the facts that (1) the characteristic red pigmentation is found in the abdomens of all the life stages, and (2) eggs that do not contain the inclusion (1 percent or less) invariably fail to develop.

Between 3 to 5 days before hatching, a bulge appears and gradually increases on the convex surface of the narrowed end of the egg. This marks the expansion of the egg-burster on the head of the embryo. Soon a slit appears in the chorion covering the bulge, and the slow wriggling process begins, which eventually frees the young nymph
from the egg shell. The hatching process requires from about half an hour to several hours in the laboratory. The appendages of the newly emerged nymphs remain closely pressed to the body for one to several hours before normal activity commences.

**Damage Caused**

Red pine plantations heavily infested with the Saratoga spittlebug are generally economically ruined if the infestation is not controlled. The time lapse from the first scattered flagging (twig mortality) to severe stunting or complete tree mortality is usually no more than 2 or 3 seasons. And the effects of one season's feeding do not become evident on the trees until the following year. Therefore, if control is delayed until the trees are already flagged, much of the plantation may have already sustained lethal feeding.

For these reasons, it became evident early in the studies of the spittlebug that the usual type of damage appraisal survey, based on gross symptoms of tree damage, would not be applicable to Saratoga spittlebug infestations. The only alternative was to develop a reliable method of damage prediction based on insect population levels. This method requires an accurate understanding of the specific reactions of the tree to spittlebug feeding and a knowledge of the insect population that will cause critical damage to the trees in a particular plantation.

**Adult Feeding-Frequency Studies**

Various studies of the feeding habits of pine-feeding spittlebugs have been conducted by Speers (24) and Anderson (3). More recent studies by the writer have centered on determining the average number of feeding scars resulting from a given adult population per unit of time.

![Graph: Bug-hours exposure versus feeding scars per pest branch number]

**Figure 10:** Adult feeding frequency in sleeve cages, 1954.
Wire-screen sleeve cages containing from 10 to 95 adults each were placed on 3- and 4-year-old red pine branches at approximately weekly intervals from mid-July until mid-September of 1954. The adults were allowed to feed for periods of 24 to 80 hours. At the end of each test period the branch was removed and the feeding scars counted. Since no plantation entirely free of spittlebugs could be found, the study was carried out in a very lightly infested plantation, and adjustments were made for the small number of native feeding scars already present. A further adjustment for the adult mortality within the test cages was necessary. Thus, if 20 adults were placed in a cage and 18 were found living at the end of the test, the feeding scars were assumed to have been produced by 19 adults. Mortality did not constitute a great problem with the relatively short caging times used in this study: of the 526 adults in 25 cages, 16 adults died.

In summarizing the data from this study, the number of "insect-hours" to which each of the test branches was exposed was also calculated. The test branches received 2,680 feeding scars during a total exposure of 22,163 insect-hours—an average of 0.11, or 2.63 feeding scars per insect per 24-hour period. Figure 10 illustrates the variation in the number of feeding scars per insect-hour on the 25 branches used.

During these studies, several factors affecting variation in the adult feeding frequency were noted. Although no quantitative studies were made, the feeding activity obviously decreased as the air temperature dropped. Below about 60°F, no feeding occurred.

The length of the test twig also appeared to influence feeding activity, but the results of the above tests were inconclusive on this question. Later, more extended tests indicated a significant correla-

![Graph](image-url)  
**Figure 11.**—Feeding frequency of caged adults versus branch length; caging time was 7 days.
tion between feeding frequency and branch length (fig. 11). Since this phenomenon occurred only at very high levels of crowding, it has no practical significance in the relationship between the insect population and tree damage. The flagging threshold is far exceeded before crowding begins to influence feeding frequency.

The age of the adults also had a definite influence on feeding frequency. During the last week in July and the first week in August, feeding activity was at a peak level—each adult made about 3.5 feeding scars per day. Feeding activity decreased thereafter, and by the middle of September each adult made only about 1.5 feeding scars per day. Information concerning other possible influences on adult feeding habits, such as sex ratio, host species, and host vigor, is not available.

**Gross Symptoms of Tree Damage**

At no time during the course of a Saratoga spittlebug infestation can subeconomic damage to the trees be easily appraised. There is no more-or-less extended period during which certain gross symptoms (defoliation, chlorosis, shoot deformation, die-back, etc.) can be used as indices of the trend of the infestation. When obvious external injury symptoms appear in red pines, the threshold of economic importance has already been far exceeded. When flagging becomes apparent, the infested trees have most likely already sustained enough feeding damage to result in mortality or serious deformation even

<table>
<thead>
<tr>
<th>Damage symptom</th>
<th>Ease of detection</th>
<th>Time of appearance</th>
<th>Duration and intensity of adult feeding preceding symptoms</th>
</tr>
</thead>
<tbody>
<tr>
<td>Slight, uneven reduction in lateral shoot elongation.</td>
<td>Can be detected only by careful lateral-terminal growth measurements.</td>
<td>Summer.</td>
<td>2 or more years of light to moderate feeding.</td>
</tr>
<tr>
<td>Almost imperceptible yellowing of foliage on twigs attached to 2-year-old growth of lateral branches.</td>
<td>Difficult to perceive even with normal foliage available for comparison.</td>
<td>Full-winter.</td>
<td>1 or 2 years of heavy feeding.</td>
</tr>
<tr>
<td>Twig mortality—foliage turns yellow to red (flagging).</td>
<td>Easily detected but may be confused with flagging due to other agencies, such as drought and mechanical damage.</td>
<td>Spring-summer.</td>
<td>2 or 3 years of heavy feeding.</td>
</tr>
<tr>
<td>Branch mortality, top killing, tree mortality.</td>
<td>Easily detected; generally occurs in characteristic patches; surviving trees are crooked, misshapen.</td>
<td>Spring-summer.</td>
<td>3 or more years of heavy feeding.</td>
</tr>
</tbody>
</table>
FIGURE 12.—Severe flagging of young red pines after 2 years of heavy Saratoga spittlebug infestation. These trees were dead the year after photograph was taken.
if the current population is controlled (fig. 12). Therefore, though gross symptoms of damage to red pine are readily identifiable, they are of no use in the development of an appraisal system designed to determine need for control.

The typical progression of the gross symptoms is shown in table 6. The right column in this table lists the average duration and intensity of an infestation necessary to cause the particular damage symptom. However, rapid buildup of an extremely heavy infestation may result in tree mortality in 1 or 2 seasons. On the other hand, light to moderate infestations—especially in larger, more vigorous trees—may persist for years without causing serious tree damage.

Relation of Damage to Host Density and Size

Often ignored in appraising the damage potential of a plantation pest are the great differences in size of trees among the various plantations studied (2/1). Spittlebug-susceptible red pines may differ in height by a factor of 5 or more. This is important because a doubling in tree height will result in at least a tripling in the length of the needle-bearing branches. Naturally then, the smaller the trees, the more rapid and severe will be the damage from a given spittlebug population. It was noted early in studies of this insect that trees are practically out of danger after they reach a height of about 15 feet. Since spittlebug-feeding damage is in many ways similar to that caused by drought, and since drought-damaged red pine trees have been observed to be largely among those under 15 feet tall, it is not surprising that spittlebug damage is limited to these smaller trees.

Equally important to the host-size problem is the variation in the number of trees per acre in the various plantations. Here again the damage potential of a given pest population will depend on tree density.

Thus, to predict the tree damage that will result from a particular Saranac spittlebug population, a quantitative expression of tree size and density must be incorporated into the prediction system. Ideally, the total length of the needle-bearing internodes on the trees in a plantation should be used: this is the total feeding universe of the insects. However, such measurements are too time consuming to be used in a practical survey.

The alternative is to use an index of the total amount of “food.” Since red pine is a symmetrical, unimodal tree, it lends itself quite readily to an index of crown-size measurement. Also, since the trees are planted in comparatively even rows, the average number of stems per acre can be easily estimated. A combination of these factors that correlates closely with the actual length of the needle-bearing internodes is the product of tree height (in feet) and the average number of living branch whorls (fig. 13). Therefore, the expression used as a measure of host size and density in a particular plantation is a product of the average tree height (in feet), the average number of branch whorls, and the average number of stems per acre. For con-
Regression of the total length of needle-bearing branches of young red pines on the product of tree height and number of whorls.

The Feeding Scar

During the feeding process, the stylets of the spittlebug's mouth parts follow a direct path through the cells in the cortex of the twig. The stylets generally terminate at about the level of the cambium. It is difficult to find any evidence of feeding on the bark of injured red pine twigs. However, heavy feeding over a period of several seasons leaves the surface of the xylem uneven and lumpy (fig. 14). Also, severe residual scars are detectable exteriorly as disorganized, pitch-filled pockets in the bark. They become more prevalent as the trees decline in vigor. In infested trees nearing the mortality threshold, residual scars make up about 10 to 20 percent of the injury observable on the current wood.

Examination of fixed and stained microtome sections of spittlebug-injured red pine twigs reveals that each feeding scar consists of a necrotic, resin-filled pocket in the phloem and a varying amount of injured cambium. As the season progresses, a disrupted, pitchy area in the xylem becomes visible adjacent to the injured cambium. Still later, the injured spot on the cambium is gradually repaired by
proliferation from healthy cells bordering the scar, but the pitchy defect in the xylem remains permanently as a small block to conduction. Occasionally, the injured cambium does not heal over for two or more seasons. This results in a pitch-filled, necrotic streak extending through two or more growth rings and terminating in a cuplike scar in the phloem—a residual scar (figs. 14 and 15). The occurrence of residual scars has been observed only on trees having several seasons of heavy injury.
Anderson (4) studied the feeding scars on jack pine immediately after the stylets of the mouth parts had been withdrawn. He concluded that the first evidence of necrosis occurs within 24 to 48 hours. Current studies of feeding scars on red pine twigs indicated that a slight discoloration at the cambial-xylem interface could be detected about 17 hours after feeding.

Anderson (4) also observed the effects of excised spittlebug salivary glands on the cambial-xylem interface of jack pine twigs. His studies clearly demonstrated that necrosis of the cortical tissues following spittlebug feeding is due to a heat labile substance—probably an enzyme—contained in the spittlebug’s salivary glands. He discounted the possibility of micro-organisms being responsible for the necrosis because he was unable to produce the effect by inoculating healthy tissue with tiny chips obtained from or near feeding scars.

The histological appearance of a feeding scar in cross section is shown in the four views in figure 16, beginning with an uninjured area (A) and proceeding to the center of the feeding scar (D).

The twigs used in these pictures were injured in early summer and collected for examination in winter. Healing of the injured cambium was almost completed over the necrotic areas, and no residual scars would have appeared the following season. However, even though the cambium had nearly healed over, there remained a characteristic malformation of the tracheids in the vicinity of the scar. Specifically, the xylem cells that lie immediately beneath the affected cambium are arranged with their long axes in a circumferential plane instead of in the normal plane parallel to the twig’s longitudinal axis. These abnormally arranged tracheids undoubtedly contribute to faulty conduction in the xylem.

Examinations of several hundred transverse sections of feeding
scars in 2- and 3-year-old red pine twigs indicated that each scar, exclusive of the surrounding abnormal tracheids, blocked about 1 to 5 percent of the cross-sectional area. The twig pictured in figure 13 had a cross-sectional area of 7.07 square cm. The feeding punctures—in the single plane shown—occupied about 0.38 square cm, 5.2 percent of the total conductive area. If serial sections of this twig had been made, they would undoubtedly have shown that every square millimeter of the cross-sectional area was blocked by feeding scars somewhere along the length of the twig.

**Effect of Feeding on Twig- and Needle-Moisture Content**

The twig- and needle-moisture content of spittlebug-damaged trees is affected in two ways: (1) Primarily—the feeding adult withdraws plant juice, and (2) secondarily—the necrotic, resin-filled feeding scars act as blocks to water conduction.

Concerning the direct or primary effect, studies have shown that during a single adult feeding an average of 0.42 cc. of plant juice was withdrawn. Considering that the inner bark of the needle-bearing twigs is 1 to 2 mm. thick and contains moisture equivalent to about 213 percent of the dry weight, the 0.42 cc. of water and
elaborated food removed is equal to the total moisture content of 3 to 6 square cm. of inner bark (4). Thus the direct withdrawal of liquid by feeding adults constitutes a tremendous strain on moisture-content regulation in the tree. If this liquid were not replaced by rapid conduction, the phloem in an average twig 15 cm. long and 0.6 cm. in diameter would become completely "dried out" from the effects of only 4 to 9 adult feeding periods. This, of course, never happens in reality, but it brings to light the importance of the associated conduction blockage caused by an accumulation of feeding scars in the xylem.

Anderson (4) made a field test of the water-conduction capacity of injured twigs by attaching 5-cm. segments of 1-year-old branches to a water head of 4.5 feet. This maintained a constant pressure of 1.95 pounds per square inch in the twig. The results showed an inverse relation between the number of feeding scars and the conductivity. The feeding injury was not assessed in the previous year's xylem, nor was the conductivity of completely uninjured twigs tested. Therefore, an exact quantitative relationship between conductivity and feeding injury was not established, but the disruptive effect of feeding injury on water conduction in the twig was amply demonstrated.

Evidence of the significance of moisture imbalance in spittlebug-damaged trees was gained from total water-content determinations in injured and normal twigs. Very heavily damaged twigs beginning to turn yellow had a moisture content below the permanent wilting point (about 79 percent of normal) for red pine (4).

To determine whether moisture imbalances occurred immediately after feeding, green- and dry-weight determinations were made on healthy branches and on adjacent caged branches with a known amount of feeding. These branches were from the same whorl of vigorous trees (average height 5.0 feet) with no previous spittlebug injury. Each caged branch was fed upon by 10 adults for 1 week. Green weighings were made immediately after removal of the insects. Table 7 shows that there are only slight differences in the moisture content of the injured and healthy shoots immediately after the adult feeding.

Parallel caged branches that received the same amount of adult feeding injury as the branches removed for moisture-content determinations were left in the field to determine the gross effects of the injury over an extended period. The foliage of these branches yellowed in the fall and died the following spring. Therefore, since the shoot moisture content was not drastically reduced immediately after the adult feeding, the feeding scar disruption of water conduction—during the following growing season—was the prime cause of moisture imbalance and twig mortality. No systemic effects were noted during this study. Only the twigs that had been fed upon showed any evidence of injury.

In summary, the shoot moisture content of severely injured red pine drops below the permanent wilting point prior to the appearance of flagging, partly because of direct withdrawal of plant juices by the feeding adults but mostly because of disruption of the water conduction in the branches due to the necrotic, resin-filled feeding
TABLE 7.—Moisture content of the new shoots of normal and spittlebug-injured red pines

<table>
<thead>
<tr>
<th>Date of test and kind of shoots tested</th>
<th>Moisture content as a percent of dry weight and standard error</th>
<th>Needles</th>
<th>Bark and xylem</th>
<th>Xylem</th>
</tr>
</thead>
<tbody>
<tr>
<td>August 1:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Injured shoots</td>
<td></td>
<td>264±2.8</td>
<td>214± 6.4</td>
<td>253± 9.1</td>
</tr>
<tr>
<td>Uninjured control</td>
<td></td>
<td>266±6.0</td>
<td>234±10.8</td>
<td>288±11.4</td>
</tr>
<tr>
<td>August 8:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Injured shoots</td>
<td></td>
<td>366±6.1</td>
<td>221± 1.9</td>
<td>274±10.1</td>
</tr>
<tr>
<td>Uninjured control</td>
<td></td>
<td>266±2.8</td>
<td>235± 4.2</td>
<td>291± 6.0</td>
</tr>
<tr>
<td>August 15:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Injured shoots</td>
<td></td>
<td>215±6.4</td>
<td>201± 2.8</td>
<td>287± 2.9</td>
</tr>
<tr>
<td>Uninjured control</td>
<td></td>
<td>236±1.0</td>
<td>208± 4.0</td>
<td>244± 6.0</td>
</tr>
</tbody>
</table>

1 Measurements were made immediately following 1 week’s feeding.

sears. The latter point is by far the most important because the moisture content of shoots immediately after heavy feeding does not vary significantly from that of normal, uninjured twigs. Even though an adult withdraws a relatively large quantity of the plant juice during a single feeding, the tree compensates for this loss very rapidly. Perhaps, in view of the normally large transpiration losses, the additional loss of moisture due to spittlebug feeding does not seriously tax the water-conduction system until the necrotic areas in the xylem become fully developed.

No information is available on the possible influences of certain potentially complicating factors, such as high temperature and low soil moisture. It seems safe to assume that anything tending to aggravate a moisture deficiency condition in the tree (summer drought, etc.) would certainly hasten the appearance of spittlebug damage symptoms.

Sucrose and Reducing Sugars in Injured Twigs

A test for the carbohydrates and the relative amounts present in the new shoots was made to further elucidate the effects of spittlebug feeding on red pine. It is well known that ringing or girdling a twig or stem (removal of a continuous strip of phloem around the circumference) increases the carbohydrates and causes an overgrowth of tissue distal to the ring. Below the ring, the phloem and root system finally dies for lack of elaborated food. Thus, if the accumulation of spittlebug feeding scars in the phloem of the 1-year-old internodes acted as a girdle, the new growth would contain a surplus of carbohydrates prior to flagging.

The injured twigs used in this study were new shoots with normally colored foliage from heavily infested red pines 8 to 15 feet...
in height. The new growth on the trees had been reduced to 50 to 70 percent of normal because of several previous seasons of moderate to heavy spittlebug feeding. Although light flagging of secondary and tertiary twigs was evident, no branch mortality or extensive deterioration in form had occurred. Uninjured twigs were collected from similar-sized trees (about 8 feet in height) in a plantation about a mile away from the infested area. Both the injured and uninjured shoots were collected during the second week in August after about 90 percent of the season's feeding damage had been inflicted. The ceric-sulfate reduction method was employed for estimating the reducing-sugar content (17).

These data showed that Saratoga spittlebug feeding does not produce twig injury similar to girdling. The phloem of the injured twigs contained a consistently lesser amount of sucrose than did the normal twigs (table 8). The difference in reducing-sugar content was not significant in view of the small number of samples. Brief tests of the carbohydrates in the roots of the injured and uninjured trees gave a similar picture. A sample of root about one-fourth of an inch in diameter weighing 126 grams (fresh weight) from an injured tree was found to contain 2.92 mg. of free reducing sugars but no sucrose per gram of root. A similar sample of roots from a healthy tree yielded 4.50 mg. of sucrose per gram of root.

Thus, these data show that the carbohydrate content of girdled twigs is very unlike that of spittlebug-injured twigs. Since the carbohydrate content and especially the sucrose content of the phloem of new shoots and the roots of spittlebug-injured trees were found to be lower than in normal trees, the feeding injury is similar to a plugging of the xylem, with a subsequent shortage of water and reduced food production in the foliage.

**Table 8.-Reducing sugars and sucrose content of the phloem of the new shoots of red pine branches**

<table>
<thead>
<tr>
<th>Sample</th>
<th>Feeding puncture density per square centimeter in 2-year-old growth</th>
<th>Percent water and extractable material</th>
<th>Percent reducing sugars</th>
<th>Percent sucrose</th>
<th>Total carbohydrates</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0</td>
<td>81.7</td>
<td>10.6</td>
<td>4.4</td>
<td>15.0</td>
</tr>
<tr>
<td>2</td>
<td>0</td>
<td>82.4</td>
<td>14.0</td>
<td>4.3</td>
<td>18.9</td>
</tr>
<tr>
<td>3</td>
<td>0</td>
<td>83.3</td>
<td>14.9</td>
<td>4.0</td>
<td>18.4</td>
</tr>
<tr>
<td>4</td>
<td>0</td>
<td>82.6</td>
<td>13.2</td>
<td>4.6</td>
<td>17.0</td>
</tr>
<tr>
<td>5</td>
<td>1.5</td>
<td>84.4</td>
<td>13.3</td>
<td>0.0</td>
<td>13.3</td>
</tr>
<tr>
<td>6</td>
<td>2.5</td>
<td>85.5</td>
<td>12.8</td>
<td>1.9</td>
<td>13.7</td>
</tr>
<tr>
<td>7</td>
<td>4.8</td>
<td>76.5</td>
<td>10.5</td>
<td>1.4</td>
<td>11.9</td>
</tr>
<tr>
<td>8</td>
<td>4.8</td>
<td>74.0</td>
<td>11.5</td>
<td>1.2</td>
<td>12.5</td>
</tr>
<tr>
<td>9</td>
<td>2.5</td>
<td>74.0</td>
<td>14.2</td>
<td>1.0</td>
<td>15.2</td>
</tr>
</tbody>
</table>

1 A sample consisted of about 2 grams of phloem from the current growth of branches in the upper one-third crown area.

2 Expressed as a percent of the extracted dry weight.
Distribution of Feeding Injury

In the past, one of the methods used to classify the seriousness of a spittlebug infestation was based on the density of feeding scars on the injured twigs. The amount of feeding injury is, of course, proportional to the adult population, and it is easily assessable by scraping away the bark and counting the scars on the xylem. Although nymphal-population surveys are now considered the most useful and accurate, occasions arise that require an estimate of the spittlebug infestation levels during fall or winter. On these occasions, the feeding-injury survey is still a useful tool. However, before it can be employed, the distribution of the adult feeding scars on the various parts of the tree must be known.

Studies have shown that the adult feeding scars occur in characteristic gradients on the tree. The differences in feeding scar counts on four sampling universes were considered as follows: (1) Circumferential—between the upper and lower surfaces of the twig, (2) radial—between the phloem and xylem, (3) horizontal—along the lengths of the branches; and (4) vertical—between the branch whorls in the upper and lower portions of the tree. The trees used in the studies were 6 to 15 feet in height and heavily infested, but not top-killed or seriously deformed. Briefly, the results revealed a concentration of feeding scars on the 1-year-old internodes (fig. 17). The current growth and the older needle-bearing internodes showed lower feeding scar densities. The same preference for 1-year-old growth was found in infested jack pine.

No difference in feeding scar densities was found between the top and bottom surfaces of the branches, nor between branches from the upper and lower whorls on the tree. Between the xylem and the phloem of the 1-year-old internodes, there was a consistently significant difference: about 30 percent more feeding scars were found in the phloem than on the xylem. However, feeding scars were not conventionally counted in the phloem because of the difficulty of removing the outer bark without exposing the cambial-xylem interface at irregular intervals.

The most consistent feeding-injury sample can be obtained from the 1-year-old internodes. The lower the infestation level, the greater the variation in number of feeding scars. The coefficients of variation for scar counts taken from the 1-year-old internodes of heavily infested trees ranged from 11 to 22 percent. In a heavily infested plantation showing about 50 feeding scars per 10 linear centimeters of the 1-year-old internodes, 13 samples yielded a standard error equal to about 5 percent of the mean. In a lightly infested plantation (about 13 feeding scars per 10 linear centimeters), 109 samples had to be taken to achieve a standard error equal to 5 percent of the mean.

Burn Blight

During the early years of investigation of Saratoga spittlebug injury to pine (1943-45), a study was conducted by Gruenhagen et al. (16) to determine the role of a fungus, *Chilonecrotia cucurbitula* (Curt.) Sacc., which often fruited on dead jack pine twigs in spittlebug-injured plantations. They reported that the fungus, previously not known to be pathogenic, was capable of causing twig, branch, and whole-tree mortality when inoculated under the proper conditions. The disease (called the "burn blight disease") was reported to be carried by the adult Saratoga spittlebug. Gruenhagen et al. stated: "The evidence suggests that these adults not only acted as vectors but also as agents to weaken the twigs more or less and to provide the *Chilonecrotia* with a favorable entry." On spittlebug-injured red pine, the fungus was found to be only weakly pathogenic. Burn blight has not developed in plantations where insecticidal control has been carried on.
Changes in Tree Form

One early indication of spittlebug damage to red pine is a reduction in terminal and lateral twig elongation. A reduction in growth can also be caused by one or more adverse edaphic or climatological factors. However, the growth damage caused by these factors is markedly different from that caused by the spittlebug (7). Growth reduction due to poor site, drought, etc., tends to occur evenly throughout all the twigs on the tree; i.e., the elongation pattern remains the same as that of trees in more vigorous condition. Growth reduction due to spittlebug damage occurs erratically, with some twigs—particularly near the bottom of the tree—achieving normal growth and other twigs achieving only a fraction of normal growth.

Especially in prolonged light-to-moderate spittlebug infestations, the analysis of the lateral-terminal growth pattern of the infested trees will reveal the early stage of tree damage prior to twig or branch mortality. When a rapid population buildup occurs, however, growth pattern analysis fails to reveal the impending mortality because there is a 1-year lag between the adult feeding damage and subsequent effects on growth. By the time the adult spittlebugs begin feeding (July), shoot elongation is complete, and the feeding injury will not affect the growth until the following season. Twig and branch mortality would then occur simultaneously with a deterioration in the lateral-terminal elongation ratios.

In 1954, advanced flagging and some branch mortality due to heavy spittlebug feeding in a roadside plantation in northern Wisconsin were noted for the first time. The forest manager said that the plantation appeared healthy the previous season. Growth measurements of the injured trees confirmed the observation that the damage had occurred suddenly. Figure 18 shows the regression of the lateral-terminal elongation ratios on the branch whorl age. The “L:T” ratios are computed by dividing the lengths of the various internodes for one growth year by the length of the terminal growth for the same year. The correlation and regression coefficients for the 1953 and previous growth years fall within the zones of normalcy as established by Benjamin et al. (7). Therefore, even though the deterioration in form occurred in 1954, the twig and branch mortality could not have been predicted from the previous years' growth measurements.

A population that builds up slowly over several seasons does, on the other hand, have a perceptible effect upon the growth pattern before serious tree damage occurs. From a practical standpoint, the lateral-terminal growth pattern analysis may be employed in plantations having a moderate-to-heavy spittlebug population over several seasons—but not heavy enough to require control. Calculation of the L:T growth ratios would, in this analysis, be a useful tool in deciding whether the trees are being damaged by, or are successfully tolerating, the population.

The Duff and Nolan (10) method of radial increment analysis did not reveal any significant differences between injured and uninjured trees. Presumably, the trees were too young (7 to 15 years old) to have developed characteristic increment patterns.
When appraising Saratoga spittlebug infestations for control needs, it is necessary to differentiate between plantations that are in danger of serious damage and those that are not. Since it was recognized in early studies that an efficient appraisal system could not be based upon tree damage symptoms alone, various methods were attempted to correlate nymphal or adult populations with subsequent tree damage. Although generally workable, these early appraisal surveys were frequently inaccurate because they did not include two additional variables that affect the impact of a given insect population: namely, the number of pine hosts per unit area and the size of the pine hosts (72). The way in which these factors are measured and combined in the appraisal survey is described below.

Population Levels and Subsequent Tree Damage

Although spittlebug population can be measured during any of the three life stages, certain practical considerations favor measurement of the nymphal population for appraisal purposes: (1) Control spraying must be done before the adults deposit eggs; this timing requirement can be met only by carrying out the population
surveys before adult transformation. (2) Measurement of the egg population presents great sampling difficulties and is inaccurate because of the decimating factors that may affect the early nymphal instars.

Because of wide variations in alternate host densities in infested plantations, nymphs must be sampled on a unit-area basis. The relatively large acreage encompassed by the average spittlebug infestation and the uneven distribution of insects and hosts make impractical estimating either the total population or the total amount of tree damage. An alternative method of relating population levels and subsequent tree damage is through intensive sampling of small plots. This technique was employed on several spittlebug-infested red pine plantations in northern Wisconsin.

The infested plantations were systematically chosen to contain trees from 4 to 12 feet tall and infestations ranging from light to heavy. A square 1/10-acre study plot was established in each of the plantations. Each study plot was further divided into milacre plots by stakes driven into the ground at 6.6-foot intervals along the borders. Plastic ropes, marked with rings of paint at 6.6-foot intervals, were stretched between the border stakes to delimit any chosen milacre subplot within the 1/10-acre study area. Each of the milacre subplots was designated with a column number and row letter after the manner of theater seating (fig. 19). The nymphal population was measured by counting all the nymphs on systematically located milacre plots per study area, at each sampling date.

**Table 9.—A summary of data on populations, tree size, and damage from the permanent sampling plots**

<table>
<thead>
<tr>
<th>Nymphs</th>
<th>Average tree height (feet)</th>
<th>Average number whorls</th>
<th>Average nymphs per milacre</th>
<th>Average adults captured per tree-unit²</th>
<th>Adults feeding score per 10 cm., 2-year-old internodes ³</th>
</tr>
</thead>
<tbody>
<tr>
<td>6.4±3.2</td>
<td>6.0±</td>
<td>19.7</td>
<td>0.325</td>
<td></td>
<td>12±1.0</td>
</tr>
<tr>
<td>25±9.7</td>
<td>7.0±</td>
<td>69.9</td>
<td>0.357</td>
<td></td>
<td>14.5±1.4</td>
</tr>
<tr>
<td>43±9.4</td>
<td>7.6±</td>
<td>107.2</td>
<td>0.401</td>
<td></td>
<td>16.7±1.8</td>
</tr>
<tr>
<td>29±8.2</td>
<td>5.7±</td>
<td>31.8</td>
<td>0.913</td>
<td></td>
<td>22±1.7</td>
</tr>
<tr>
<td>52±16.4</td>
<td>8.5±</td>
<td>71.3</td>
<td>.729</td>
<td>0.650±0.19</td>
<td>24±2.8</td>
</tr>
<tr>
<td>21±0.6</td>
<td>4.7±</td>
<td>22.4</td>
<td>0.365</td>
<td></td>
<td>25±1.8</td>
</tr>
<tr>
<td>73±13.9</td>
<td>13.0±</td>
<td>73.3</td>
<td>0.996</td>
<td></td>
<td>26.5±1.3</td>
</tr>
<tr>
<td>63±10.8</td>
<td>6.3±</td>
<td>58.9</td>
<td>1.070</td>
<td>.972±0.061</td>
<td>28.9±3.2</td>
</tr>
<tr>
<td>25±6.9</td>
<td>5.0±</td>
<td>35.2</td>
<td>.709</td>
<td>.690±0.096</td>
<td>27.9±1.6</td>
</tr>
<tr>
<td>29±5.5</td>
<td>7.0±</td>
<td>39.4</td>
<td>.736</td>
<td></td>
<td>28±2.7</td>
</tr>
<tr>
<td>39±9.8</td>
<td>8.2±</td>
<td>54.2</td>
<td>.719</td>
<td></td>
<td>32.1±1.3</td>
</tr>
<tr>
<td>32±10.9</td>
<td>4.5±</td>
<td>22.1</td>
<td>1.450</td>
<td></td>
<td>37.3±2.8</td>
</tr>
<tr>
<td>100±22.1</td>
<td>13.0±</td>
<td>73.3</td>
<td>1.365</td>
<td></td>
<td>48±2.6</td>
</tr>
<tr>
<td>31±6.8</td>
<td>4.3±</td>
<td>22.9</td>
<td>1.395</td>
<td></td>
<td>56.1±1.8</td>
</tr>
<tr>
<td>61±12.6</td>
<td>10.0±</td>
<td>37.2</td>
<td>1.640</td>
<td></td>
<td>60.0±2.4</td>
</tr>
</tbody>
</table>

1 Mean and standard error.
² A tree-unit is 1 foot-whorl per unit area. This figure was obtained by multiplying the average tree height (in feet) by the average number of branch whorls and the average number of stems per milacre.
³ Whole-tree sampling method.
Additional data taken in each of the study plots were as follows: Location, height, and number of branch whorls of each tree (plotted as in figure 19), and, in three of the 1/10-acre plots, a whole-tree sampling of the adult population. After the insects had finished feeding in the fall, the feeding punctures were counted on the 2-year-old internodes. A summary of the data obtained on the 15 study areas is given in table 9.

To determine whether there was any decline in population between the fourth- and fifth-instar nymphe and the adults, the adult population was measured immediately after transformation. A relatively accurate measurement of the adult spittlebug population was ob-
tained by capturing all the adults on representative trees throughout the infested plantation (fig. 20) (19). A product of the average number of adults captured per tree and the tree density yielded an estimate of the total adult population per unit area. Table 9 shows that there was very little population decline from nymphs to adults.

The technique of determining relative adult population levels by sweeping the infested trees was employed on each of the study areas. Since the adults are easily disturbed and shy, it is not surprising that sweep-net sampling proved to be a rather inaccurate technique for population measurements. Figure 21 shows the relation between adults per sweep and nymphs per tree-unit obtained on nine permanent plots in 1956. Broad infestation levels can probably be established with this technique, provided that adjustments are made for...
normal population decline where sampling is not carried out immediately after the peak of adult transformation.

**Damage Prediction**

When the nymphal populations in the study plots were plotted directly against the adult feeding scar counts, the correlation approached significance at the 5-percent level. However, when the nymphal populations per unit of host size and density were used (nymphs per tree-unit), an excellent correlation resulted (fig. 22). The regression of feeding scar density on the number of nymphs per tree-unit can be used to predict tree damage and establish priority for control. That is, if the spring nymphal population and the number of tree-units in an infested plantation are known, it is possible to predict the subsequent amount of tree damage.

Empirical observations of natural infestations and caged branches show that if infested trees exhibit 35 or more feeding scars per 10 centimeters of the 2-year-old internodes, twig mortality and growth deterioration will generally occur within 1 or 2 seasons. This has been incorporated into the following formula in order to estimate the feeding damage that will result from a given nymphal population in an infested plantation:

\[
R = 0.466 \\
R^* \text{ at } 1 \text{ percent} = 0.785 \\
y = 0.181 + 1.434x
\]
Figure 22.—The regression of feeding scar density on nymphs per tree-unit. Feeding scars are expressed as the number per 10 centimeters of the 2-year-old internodes.

\[
X = A \frac{X}{B}
\]

where:
- \(X\) = number of feeding scars per 10 linear centimeters of the 2-year-old internodes.
- \(A\) = number of nymphs per 1/10 milacre.
- \(B\) = number of tree-units per 1/10 milacre.
- \(\kappa = 31.3\) (constant).

An average of about 1 nymph per tree-unit will result in 35 adult feeding scars per 10 centimeters and serious tree damage.

Control

In dealing with natural control of economic insects, emphasis is generally placed on relatively short-range, catastrophic factors that are capable of bringing about a rapid reduction of heavy populations—population "crashes" as described by Allee et al. (7). For the Saratoga spittlebug, adverse weather appears to be the most important catastrophic factor as long as host conditions remain suitable. Interspecific competition or crowding to the point of host destruction will also cause a population collapse, but this has little, if any, practical significance. The effectiveness of various biological agents in exerting continuous but less spectacular control cannot be discounted. However, rapid reduction of heavy infestations due to these agents has not been observed. Insecticidal control, judiciously applied to those plantations in danger of serious tree damage, re-
mains as a necessary and efficient tool in combating the Saratoga spittlebug.

**Weather Effects**

As discussed previously, the early instar nymphs are susceptible to desiccation during periods of hot dry weather—especially in open plantations where they are not afforded sufficient protection by the trees and ground cover. The practical implications of this were observed during the spring of 1956. Study plots established in red pine plantations in northern Wisconsin were sampled for first- and second-instar nymphs during the week of June 5. During the 5 days between June 10 and June 13, very hot dry weather prevailed over most of Wisconsin, with the daily maximum temperatures averaging 80°F and above. This is about 20 degrees above normal for the northern part of the State. During the following week, population counts were made again when most of the nymphs were in the second and third instars. A striking drop in the nymphal populations was observed in two of the plots (table 10, C and D) with relatively small trees and light stocking. Apparently, this condition allowed the temperature to rise and the humidity to fall to critical levels, resulting in desiccation of large numbers of the young nymphs.

The populations in the other two plots (A and B) were protected by heavy shade, and little mortality occurred. The possibility that plots C and D did not have suitable alternate host conditions was discounted because favorable alternate hosts in sufficient numbers occurred in all four areas (table 4). Nymphal predation, parasitism, and disease were not observed in this study.

<table>
<thead>
<tr>
<th>Study plot</th>
<th>Average daily temperature June 10-13</th>
<th>Average nymphs¹ per 1/10 acre on June 5</th>
<th>Nymphs on June 20 as percent of initial population</th>
</tr>
</thead>
<tbody>
<tr>
<td>A (shaded)</td>
<td>91</td>
<td>6.2±1.2</td>
<td>4.2±0.9</td>
</tr>
<tr>
<td>B (shaded)</td>
<td>93</td>
<td>4.9±1.5</td>
<td>4.1±0.9</td>
</tr>
<tr>
<td>C (open)</td>
<td>90</td>
<td>3.2±2.2</td>
<td>5.3±2.2</td>
</tr>
<tr>
<td>D (open)</td>
<td>90</td>
<td>8.2±2.3</td>
<td>2.5±0.5</td>
</tr>
</tbody>
</table>

¹ Measure of tree size and stocking: a product of average tree height in feet, average number of branch whorls, and number of stems per acre.

² From Climatological Data, Wisconsin, U.S. Dept. Commerce, Weather Bureau, LXXI(6), June 1956. Actual plot temperatures may have varied from those of the nearest weather station listings.

³ Mean and standard error.

Hot dry weather of this description does not often occur during the early instars. Also, most plantations in the Lake States contain undergrowth dense enough to afford young nymphs protection against desiccation.
The effect of late spring frosts on the nymphs has also been an important factor in the natural control of the spittlebug. Laboratory studies indicated that short exposures of third-instar nymphs to air temperatures in the low 20's (degrees Fahrenheit) will cause nearly complete mortality (22, 4). Although air temperatures as low as this are not unusual during May in northern Wisconsin and Upper Michigan, there is good indication that temperatures in the ground litter at the nymphal habitat level remain considerably higher. Anderson (4) found that duff temperatures during seven June nights averaged 8.6 degrees higher than air temperatures at a level 3 inches above the ground when the air temperatures were in the 20's or 30's. He also reported that third-instar nymphs caged on alternate hosts above the litter suffered 80-percent mortality when the air temperature remained between 27.5° and 32° F. for 7 hours. No mortality occurred in a group of nymphs similarly caged but covered with a normal layer of litter.

On May 16, 1957, air temperatures in the low 20's and lower were recorded in northern Wisconsin and Upper Michigan; population reductions of about 80 percent were noted (13). Populations in the more southerly areas, in which temperatures dropped only into the low 30's, were not materially affected.

**Biological Agents**

Information on parasites, predators, and diseases of the Sarutoga spittlebug is scanty. Anderson (3) stated: “Biological agencies did not appear to be very active in reducing the spittle insect population. A few dead mummified nymphs were collected, which suggested fungus activity, parasite larvae were removed from the abdomens of 3 out of a total of 220 adults dissected, and one spider was observed feeding on an adult.” Milliron (18, 19) reared and described two new species of hymenopterous parasites from the eggs of the Sarutoga spittlebug. One of these was an aphelinid, *Tumidiscapus cercopiphagus* Milliron; the other was a mymarid, *Ooctonus aphrophora* Milliron. No studies have been made of the biology or importance of these parasites.

Collections of 200 to 300 eggs during March of 1955 and 1956 revealed parasitism by *Tumidiscapus cercopiphagus* to the extent of 3 percent for the first collection and 5 percent for the second. *Ooctonus aphrophora* was not found. Eggs containing these parasites have a characteristic shiny, black color. They are slightly more turgid than normal eggs but not noticeably distorted or enlarged. The parasite adults emerged 3 to 4 weeks after the hatching of the spittlebug nymphs.

A dipterous parasite of the adult spittlebug was prevalent in 1955 in several heavily infested plantations in northern Wisconsin. Weekly collections of adult spittlebugs from two plantations on the Nicolet National Forest revealed that the parasite larva can be obtained by dissection only for a short time during the summer. Figure 23 shows that during early August about 50 percent of the spittlebug adults dissected contained parasites of this species. During early July and late August, however, the numbers of parasites
obtained were significantly less. It could not be determined when the parasitism occurred. Mature nymphs and newly transformed adults contained no parasite larvae. Careful dissection did not reveal any obvious parasite eggs, either. Brief attempts to rear parasite cocoons obtained from caged spittlebug adults were not successful. Adult parasites were not obtained and an exact identification from the larval specimens was, unfortunately, not possible. Hardy \textsuperscript{12} identified the larvae and puparia as belonging to the family Pipunculidae. Figure 24 illustrates the mature parasite larva.

None of the parasitized female spittlebugs contained any eggs, and a pronounced population decline occurred the following year. However, tree damage in these two heavily parasitized areas had already exceeded the critical level; the parasite thus became effective too late

![Graph A](image1)

![Graph B](image2)

Figure 23.—Percent parasitism of the adult spittlebugs by an unknown dipterous species, identified as belonging to the family Pipunculidae, 1955.

\textsuperscript{12} Correspondence with D. Elmo Hardy, University of Hawaii, on file at Lake States Forest Experiment Station, 1956.
Figure 24.—Sketch of fully developed dipterous parasitic larva.
during the course of the spittlebug infestations. In all the infested plantations that did not contain obvious symptoms of tree damage, 5 percent or less of the spittlebugs were parasitized by this dipterous insect.

Predation of spittlebug nymphs by ants and spiders was observed occasionally. Although no studies were made, these predators were considered of little importance in controlling spittlebug populations. Likewise a large red mite, commonly found on spittlebug adults during late August and early September, is probably not important because spittlebug feeding damage and egg deposition are largely completed by the time the mite appears. No other parasites, predators, or diseases have been identified or observed in Saratoga spittlebug infestations.

Silvicultural Control

The presence of an alternate host in the life cycle of the Saratoga spittlebug presents the interesting possibility of controlling the insect by ridding the plantations of alternate hosts. However, herbicidal treatments to accomplish this have proved ineffective so far. Dosages sufficient to kill hardy perennials such as sweetfern may injure the trees. Also rapid reestablishment of the ground cover from seeds and underground plant parts frequently occurs. Since herbicides are more expensive than insecticides and their effectiveness, if any, is only temporary, they have not been used as a routine tool to control the spittlebug.

The proper time to consider alternate host conditions is during the establishment of a plantation. If possible, plantations should be established only on sites considered good for red pine. In the past, the suppressed, scarcely trees in off-site areas allowed the development of ideal alternate host conditions and tremendous spittlebug populations. Where such poor plantations exist, the spittlebugs not only ruin the trees within the plantation, but they encroach on surrounding healthy trees as explained under the section on the distribution of nymphs (page 12).

Insecticidal Control

Entomologists generally agree that insecticides should be used only as a last resort to prevent serious economic loss—and then only when it is known that harmful side effects will be minimal. In pine plantations, application of approved insecticides at approved dosages is relatively harmless to wildlife. Also, no serious imbalances between harmful and beneficial insects have resulted from past insecticidal control of the Saratoga spittlebug. Therefore, when a spittlebug population survey indicates that serious tree damage is imminent, the use of insecticides is fully warranted.

The application of insecticides for controlling damaging Saratoga spittlebug infestations began soon after the commercial advent of DDT. Preliminary tests in 1944 indicated that DDT was more effective as a ground spray than were the older inorganic or botanical insecticides tested (3). In 1945, a field test was conducted in which
400 acres of Federal land in northern Wisconsin were aerially sprayed with DDT-in-oil solutions. The results showed that excellent control of adults could be obtained with aerial applications of 1 gallon of formulation containing 1 pound of DDT per acre. This technique has given consistently good control to the present time. Table 11 shows the plantation acreage sprayed on Federal land in Wisconsin and Michigan during the 1945-57 period.

**Table 11.** Acreages of pine plantations on Federal land in Wisconsin and Michigan sprayed for control of Saratoga spittlebug infestations, 1945-57

<table>
<thead>
<tr>
<th>Year</th>
<th>Acres sprayed</th>
<th>Year</th>
<th>Acres sprayed</th>
</tr>
</thead>
<tbody>
<tr>
<td>1945</td>
<td>400</td>
<td>1953</td>
<td>11,280</td>
</tr>
<tr>
<td>1946</td>
<td>2,500</td>
<td>1954</td>
<td>7,000</td>
</tr>
<tr>
<td>1947</td>
<td>3,700</td>
<td>1955</td>
<td>9,323</td>
</tr>
<tr>
<td>1948</td>
<td>1,200</td>
<td>1956</td>
<td>2,825</td>
</tr>
<tr>
<td>1949</td>
<td>8,771</td>
<td>1957</td>
<td>5,662</td>
</tr>
<tr>
<td>1950</td>
<td>10,235</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1951</td>
<td>5,064</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1952</td>
<td>3,876</td>
<td>Total</td>
<td>67,923</td>
</tr>
</tbody>
</table>

The Saratoga spittlebug nymphs cannot be controlled by aerially applied insecticides because of their cryptic habitat; therefore, control spraying must be directed against the adults. Although the adults can be killed any time during the summer, timing of the control operation is critical for the following reasons: (1) Spraying before the peak of adult transformation will result in survival of many of the later transforming adults (DDT is residually effective for only about 1 week in the field), and (2) spraying more than about 10 days after the peak of adult transformation will result in a certain amount of feeding damage on the trees, as well as a proportionate amount of egg deposition (the eggs are not susceptible to DDT). The initial spray date can tentatively be set for 15 days after the peak of the fifth-instar nymphal stage. However, a constant vigilance must be maintained to ascertain continued normal development. Occasionally, adult transformation is retarded because of cool, rainy weather in late June and early July.

Red pine plantations requiring insecticidal treatment are determined by surveying the nymphal population. A standardized survey has been developed and is routinely employed on State, private, and Federal lands in the Lake States. Using this procedure, the nymphal population can be sampled any time during the third, fourth, and fifth stadia (beginning about mid-June). A square sampling frame, used to delimit 1/10 milacre of the ground cover, is placed at systematically chosen points under the tree crowns throughout the plantation, and the number of nymphs found on the alternate hosts within the frame are recorded. The 1/10-milacre samples are taken at the rate of 20 per 100 acres of plantation. However, plantations of 50 acres or less should contain a minimum of 10 plots. Other data
taken in the plantation include average tree height, average number of living branch whorls per tree, and average number of stems per acre. The product of these three factors is a measure of the host size and density (tree-units). The number of nymphs per tree-unit at each sampling station then determines the need for control.

For example, a plantation with trees 7 feet in height with 6 branch whorls and 800 stems per acre would have 33,600 tree-units per acre. If a 1.10-mile sample contains 3 nymphs there would be 1.49 nymphs per tree-unit. This exceeds the critical damage level of 1 nymph per tree-unit for that sampling station (fig. 22). If one-third or more of the sampling stations average one or more nymphs per tree-unit, the plantation as a whole is considered in danger of serious damage.

The cost of an aerial control operation varies from about $1.50 to $4 per acre. The larger the total area, the lower the cost per unit area.

Infestations in small roadside and ornamental plantings can be controlled by applying ground sprays. The use of an emulsion concentrate or wettable powder presents less of a phytotoxicity hazard in ground applications than do DDT-in-oil solutions. Generally, in small ornamental red pine plantings, clean cultivation to destroy the alternate hosts may be less costly and more effective in controlling the Saratoga spittlebug.

**Summary**

The Saratoga spittlebug was first noted as a destructive pest in red and jack pine plantations in 1941 in northern Wisconsin and Lower Michigan. Since then, severe outbreaks of the species have been recorded almost every year on thousands of acres of plantations. Damaging populations have also occasionally developed elsewhere in the northern part of the United States from Minnesota to New York and in adjacent parts of Canada. The distribution of the Saratoga spittlebug has been reported to include all the aforementioned area plus much of the south central and southeastern United States.

The adult spittlebug is about 1 cm. in length, smoothly contoured, and generally streamlined in appearance. Coloration varies from tan to brown with a silvery, irregular motling over the wing covers. Adults first appear in late June and can be found throughout the summer until late September.

The egg, about 2 mm. in length with an elongated, teardrop shape, is glistening yellow to purple. Beginning in late July, eggs are deposited under the scales of red pine buds, generally in the upper part of the tree crown, where they remain over winter and hatch the following May.

Spittlebug nymphs undergo five instars before transforming into adults during late June. During the first four instars they have scarlet abdomens and shining black heads. Fifth-instar nymphs are tan to brownish, similar to the adult.

Saratoga spittlebug nymphs and adults do not feed upon the same host plant. Nymphal hosts are always low-growing herbs or shrubs (sweetfern, blackberry, hawkweed, etc.), whereas the adult host is
a coniferous tree. Red pine and jack pine are the favored adult
hosts in the Lake States.

The nymphs feed by inserting their mouth parts into the stem of
the alternate host near the root collar. They are generally concealed
beneath a thin layer of ground litter. When feeding, they withdraw
plant juice and eject a white frothy liquid—thus forming the charac-
teristic spittle mass around themselves. From one to many indi-
viduals may be found within a single spittle mass. Suitable alternate
hosts must be present in sufficient numbers before a damaging spittle
bug population can develop. Most plantations in southern Wisconsin
and southern Michigan are comparatively free of spittlebug damage
because they have been established in grassy fields where there are
insufficient numbers of shrubs and herbs to serve as alternate hosts.

The minimum alternate host density necessary to support an
infestation is not known. It depends upon the kinds of hosts present
and the ability of each to support more than one nymph.

Adults feed by inserting their mouth parts into the cortical part
of young pine twigs, mostly on the 2-year-old internodes.

The Saratoga spittlebug may occur epidemically throughout the
northern tier of States in the United States and in adjacent parts
of Canada, where host conditions are suitable. Suitable conditions
mainly include the presence of red pine or jack pine trees between
2 and 15 feet in height and sufficient quantities of alternate hosts.

Severe late spring frosts can cause mortality of the young nymphs,
and periods of hot dry weather during the early instars can cause
desiccation of nymphs in the more open plantations.

Information on parasitism of the Saratoga spittlebug is very
scanty. Positive identification of only two parasites has been made;
these are the chalcid egg parasites Gactanus aphrophorae Mill. and
Tamidiscus eceropiphojus Mill. A dipterous parasite that emerges
from the adult is found quite commonly, but its identity and life
cycle are not known.

Predation of migrating spittlebug nymphs by ants and spiders
has been observed occasionally. Heavy mite predation of adults is
very common but, since the mites do not appear until late in the
season, they probably do not have a great effect on the spittlebug
populations.

Silvicultural control of the spittlebug is largely a matter of pre-
venting the development of ideal alternate host conditions. This
can best be achieved during the establishment of a plantation by
avoiding areas that are completely unsuitable for red pine. The more
rapid and vigorous the tree growth, the more unlikely that suitable
alternate host conditions will persist for an extended period. The
use of herbicides to control the alternate hosts has not proved to be
biologically and economically effective.

Insecticidal control of the adults, using aerial applications of 1
gallon of formulation containing 1 pound of DDT per acre, has
given consistently good results on over 100,000 acres of plantations
in the Lake States. Generally, one application will control the spittle
bug for at least 3 years. Seldom are more than one or two appli-
cations needed to protect the trees until they grow out of the
spittlebug susceptible height range. Timing of the control operation
is critical because: (1) The adults must be killed before eggs are deposited, and (2) the spraying must be delayed until adult transformation is at least 80-percent completed. This optimal time includes only about 15 days, usually in early July.

Control of the spittlebug on ornamental or roadside plantings can be achieved by removal of the alternate hosts or by ground application of insecticides.

From an economic standpoint, red pine and jack pine are the only tree species that suffer spittlebug damage. Currently, there are very few jack pine plantations within the spittlebug-susceptible height range. Therefore, red pine can be considered the only important primary host.

Primary host size and density do not affect the abundance of the spittlebug directly, at least within wide limits; but these factors do affect the damage potential of a given spittlebug population. The practical significance here is great: The decision as to whether a given infestation is in need of control measures rests not only on the size of the insect population, but also on the size and density of the trees.

The gross effects of heavy feeding--mortality progressing from smaller twigs to whole branches, eventually resulting in the death of the whole tree--are caused by a combination of at least three factors: (1) Mechanical injury to stylet-pierced cells, (2) dehydration caused by withdrawal of sap, and (3) blockage of conducting tissue caused by an accumulation of old, resin-filled feeding scars.

Because gross tree-damage symptoms do not become apparent before irreparable harm has been done, infestation appraisal techniques have had to be based on population surveys.

A survey of the late-instar nymphal population is the most satisfactory appraisal technique. Indications are that there is no appreciable difference between the last nymphal instar and adult populations. Good correlations exist between nymphal populations and resulting tree damage in the fall. Infestation levels are determined primarily by nymphal surveys.

Feeding damage ultimately results in obvious symptoms of tree decadence, such as flagging or changes in growth pattern. Less obvious symptoms of injury, including changes in the water and carbohydrate content of the needles and twigs, and changes in histology of the twigs, were studied. Feeding damage levels were correlated with spittlebug populations during the preceding spring. A very good correlation was found to exist between spring nymphal population and subsequent adult feeding damage where tree size and density were taken into consideration. A method of recognizing dangerous infestations by measuring the nymphal population and the tree size and density is described.
Literature Cited


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