# HARVARD FOREST

## BULLETIN No. 22

# FOREST SITE CONDITIONS AND THE GYPSY MOTH

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# PREFACE

The gypsy moth is a serious pest in the forests of the northeastern United States. Since its introduction in 1869, it has become indigenous to a large portion of New England, has caused serious defoliation, and has markedly affected the timber, aesthetic, and recreational values of many acres of woodland.

Foresters and entomologists alike have long been interested in the possibilities of controlling the gypsy moth by silvicultural practices,—practices designed to create natural conditions unfavorable to the moth. The Harvard Forest, in cooperation with the U. S. Bureau of Entomology and Plant Quarantine, has conducted research in this field since 1935.

The three integrated papers in the present bulletin are designed to present information concerning factors which affect gypsy moth abundance, and to show how these factors can be regulated through forest practice. Part I summarizes ecological studies by the Bureau of Entomology and Plant Quarantine which form the basis of the later parts. Part II is an attempt to show how stands can be identified as being resistant or susceptible to gypsy moth defoliation. In Part III forest practices are suggested which should build up stand resistance to defoliation.

The study was made possible by the cooperation of a number of organizations, including the U. S. Bureau of Entomology and Plant Quarantine, the New York State Conservation Department, the Connecticut Agricultural Experiment Station, and the Harvard Forest. The interest and cooperation of R. C. Brown, A. C. Cline and R. A. Sheals were invaluable.

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HUGH M. RAUP, *Director*,
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*Petersham, Massachusetts.*
*March 1, 1947.*

## PART I

# RELATION OF FOREST AND SITE TO
# GYPSY MOTH ABUNDANCE

### By HENRY A. BESS

The gypsy moth (*Porthetria dispar* (L.)) has been in New England for three-quarters of a century. Although for many years it has caused widespread defoliation in eastern and central New England, it has seldom caused defoliation elsewhere in the Northeast. In 1937 studies were initiated by the Division of Forest Insect Investigations, Bureau of Entomology and Plant Quarantine, U. S. Department of Agriculture, to determine as far as possible the controlling effect of various natural factors operating in different parts of the infested region. The information obtained from these studies indicates that the abundance of the gypsy moth is strongly influenced by forest and site conditions.

Many of these studies were conducted in and near the Harvard Forest, which lies within the town of Petersham, Massachusetts. The facilities of the Forest were placed at the disposal of the Bureau, and the resident staff has aided in many ways in the prosecution of the work. R. B. Friend, State Entomologist of Connecticut, and W. M. Foss, Superintendent of Forest Pest Control, New York State Conservation Department, have given their full support to the studies made in their respective states, and have made personnel available to carry out some of the field work. Members of the Division of Gypsy and Brown-tail Moths Control of the Bureau of Entomology and Plant Quarantine have been in constant contact with the study and have supplied personnel to aid in carrying out certain work.

### FLUCTUATIONS IN THE ABUNDANCE OF THE MOTH

The history of the spread of the gypsy moth in the Northeast is discussed by Craighead and Collins (1934) and summarized in a series of maps published in 1944 by Brown and Sheals. These maps show that the moth was well distributed over the greater part of New England in 1925. It was well established in northeasten Connecticut and central Massachusetts ten years prior to that date.

The length of time an introduced species has been present in an

area must be considered in the prediction of future populations. Friend (1945) concluded that the moth has become indigenous in Connecticut. It seems feasible to assume that the history of the moth over the area where it has been well distributed for twenty or thirty years should be a useful index to its future abundance within the same area. However, major changes in ecological conditions, whether provoked by man or nature, may have a tremendous influence on the populations of introduced or indigenous species during different periods. If ecological conditions within the infested region become more favorable for the survival of the insect, it will inevitably increase in abundance; if they become less favorable, it will decrease in abundance. This premise is fundamental to the recommendations in Part III of forest practices designed to reduce the gypsy moth hazard.

*Defoliation Records*

For many years the Bureau of Entomology and Plant Quarantine and cooperating state agencies have procured records on gypsy moth defoliation throughout the infested region. These records form the basis for the map of gypsy moth defoliation (Fig. 1).

Occurrence and frequency of outbreaks in different parts of the infested region indicate, to some extent at least, the relative susceptibility of the forests. In the pine-oak region and in parts of the white pine-transition hardwoods region, defoliation occurs practically every year; but near the western extension of the white pine-transition hardwoods region there have been few outbreaks, and then the defoliation has been localized or "spotty." For example, in the Petersham area, where the moth became established prior to 1910, there have been two outbreaks (Appendix A). The first one reached its peak in 1935, when nearly 1,000 acres were heavily defoliated (Baker and Cline 1935). The second occurred when, following a great increase in the population in 1943, nearly 2,000 acres were stripped in 1944, and approximately 3,500 acres in 1945.

In the oak woodlands of Connecticut, western Massachusetts, and western Rhode Island, there is frequently less than one gypsy moth egg mass per acre, despite the long history of infestation. However, in favorable years, the moth has increased in abundance over hundreds of square miles within this region. During such periods a few isolated trees and small susceptible "pockets" have been noticeably defoliated. In unfavorable years the number of moths has decreased in both light and heavy infestations. For example, between 1935 and 1939 the moth could be readily found throughout the northern half of Connecticut. Noticeable feeding occurred on a few trees in the vicinity of Woodstock, and 3,000 to 4,000 acres were defoliated near Granby in 1938 and 1939. This build-
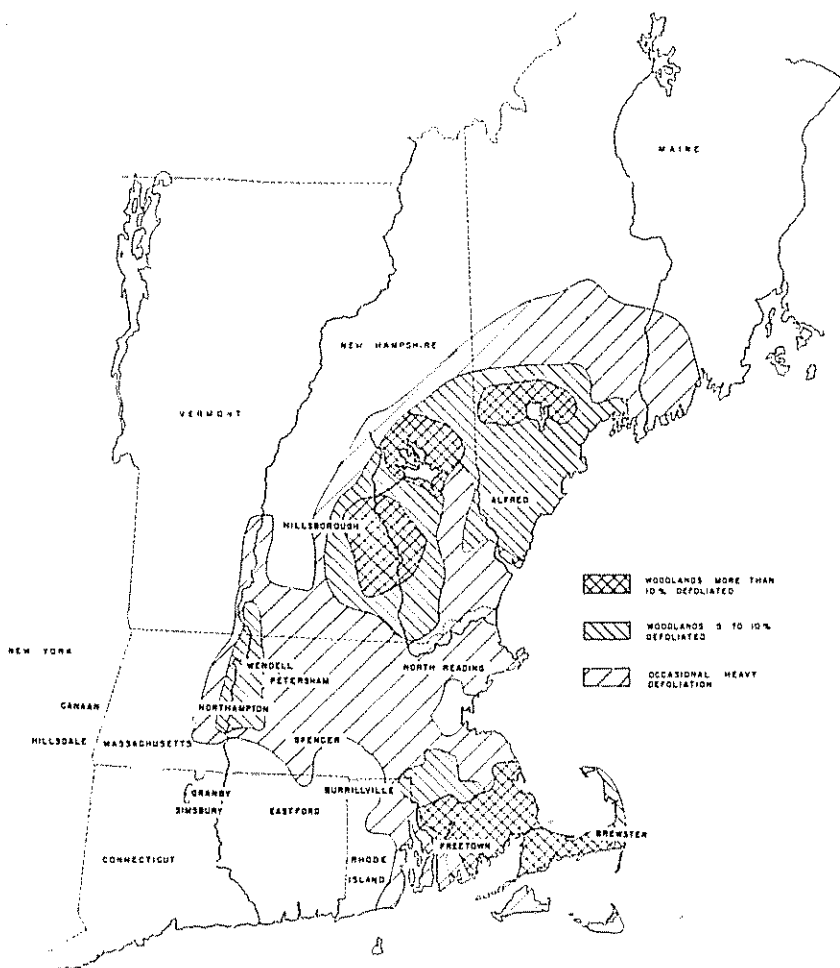
GYPSY MOTH DEFOLIATION 1931-1940

Fig 1 GYPSY MOTH DEFOLIATION IN NEW ENGLAND

up in Connecticut occurred more or less simultaneously with the build-up in the Petersham area, but the peak was reached a little later. In 1940 there was a great reduction in the population throughout northern Connecticut. Then in 1943 the number of moths began to increase over most of New England, and by the following season the insect had become relatively abundant again in northern Connecticut. One or more large white oaks growing along the roadsides were defoliated at about twenty points in that area in 1944, but there were no woodlands defoliated.

*Egg Mass Population in Experimental Areas*

More concrete information on the fluctuations in abundance of the moth has been obtained during the past few years in experimental study areas located in different parts of the infested region. Observations in these areas show that the moth persisted at a higher population level in southeastern Massachusetts than it did in other sections (Table 1).

TABLE 1

## FLUCTUATIONS IN GYPSY MOTH ABUNDANCE AT KEY POINTS

| | Number of Egg Masses Deposited per Acre | | | | |
| Year | Freetown, Mass. | Alfred, Maine | Petersham, Mass. | Granby, Conn | Eastford, Conn. |
|------|------|------|------|------|------|
| 1937 | 2,005 | ---- | ---- | — | 0 [1] |
| 1938 | 88 | ---- | 360 | — | 0 |
| 1939 | 52 | 3,100 | 2 | 640 | 0 |
| 1940 | 1,027 | 250 | 5 | 6 | 0 |
| 1941 | 2,417 | 30 | 10 | 2 | 0 |
| 1942 | 2,153 | 25 | 12 | 2 | 0 |
| 1943 | 1,092 | 85 | 273 | 1 | 0 |
| 1944 | 898 | 1,080 | 7,195 | 7 | 0 |

[1] A few egg masses were observed within the area in 1937, 1938, 1939, and 1940, but none fell within the sample.

Within the Freetown plots in southeastern Massachusetts, 1,000 egg masses or more per acre were found in five out of eight years, with minimum populations of between 50 and 100 egg masses per acre for two years. Contrasted to this, far less than one egg mass per acre was found in Eastford, Connecticut, about sixty miles to the west. The significance of this variation is great. About 1,000 egg masses are required per acre to cause noticeable defoliation. A population of 100 egg masses per acre can expand to this figure in just one favorable season. Conse-

quently, in Freetown, the residual population was sufficient at all times to cause noticeable defoliation within one or two seasons relatively favorable to an increase in the population. In Eastford, on the other hand, at least four successive favorable seasons would probably be necessary before the moth population could reach epidemic proportions. This has never occurred.

The fluctuations of the population in these plots and in the other areas were largely representative of the fluctuations that occurred during the same period in the surrounding territory. For the most part they were also representative of the fluctuations within these regions for many years.

LARVAL BEHAVIOR UNDER DIFFERENT FOREST AND SITE CONDITIONS

It has been observed that the larger gypsy moth larvae feed mostly at night and tend to congregate in sheltered places during the daylight hours. Forbush and Fernald (1896) stated that, "before the caterpillars had attained half their growth, they daily left the leaves on which they fed during the night and clustered in sheltered places, such as cavities in the trunks of trees or the under sides of branches or other natural objects. . . . As they grew larger the tendency to seek shelter during the day became more and more noticeable. They often wandered in search of shelter, leaving trees which did not offer secure hiding places and retiring to rubbish heaps, stone walls, and other places of refuge, to pass the day. It was seen that whenever old garments, cloth, or paper were thrown in the forks or wound around the trunks or branches of infested trees, the shelter of such materials was sought by the larvae during the heat of the day."

In the same publication, Forbush and Fernald (1896) also noted that "the large caterpillars leave the burlap or other places of concealment for their places of feeding between 7 and 8 o'clock in the evening, or sometimes a little later. . . . They cease feeding at day light (between 3 and 4 o'clock in the morning), but when it is cloudy they feed later. It would seem that the first indication of daylight is the signal for them to return to their places of concealment."

Observations made in Petersham in 1941, when the gypsy moth population was far too low to cause noticeable defoliation, revealed that generally many of the large larvae congregated in the loose litter during the day and molted there, while in a few small spots or stands the large larvae remained well above the ground or forest floor. Subsequently, the behavior of the large larvae under diverse ecological conditions in various

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parts of the infested region has been intensively studied in an effort to relate forest and site conditions to larval behavior.[2]

Several thousand larvae were collected during May, June, and July of 1942 at widely separated points in New England to study larval mortality and to determine where they rested during the day. Most of these locations were in stands composed largely of oak, and with the exception of those at Petersham were considered more or less typical of oak stands in the different regions. The points in Petersham were selected because they had been defoliated during the 1935 outbreak, and therefore were considered the most susceptible oak stands in the town.

Records at each point were made of the number of each instar found in the following four strata: foliage, branches and twigs, tree trunks and litter, and debris on the ground. At each point an attempt was made to collect in a spiral around a temporary marker, all parts of the environment being examined until 35 to 50 larvae were collected, or until two hours had been spent in the search. Since larvae are found more easily in certain places than in others, the data obtained do not show the exact proportion of the larvae in the different parts of the environment. Nevertheless, they are sufficient to demonstrate that the larval behavior at certain points was entirely different from that at others.

Everywhere practically all of the first- and second-instar larvae were found to molt and to remain during the day on the underside of the foliage, on small twigs, or in crevices in the bark. As they grew larger, however, fewer were found on the foliage. They tended rather to spend the day and to molt in more secluded places, such as in tree cavities, under loose bark, loose stones, and debris, and in loose litter on the ground (Fig. 2).

A far greater percentage of the larvae were found in the litter at certain points than at others (Table 2). Furthermore, the survival was lower where the large larvae were found in the litter. In areas characterized by large gypsy moth populations and by frequent heavy defoliation, few larvae were found in the litter. For example, in Freetown none of the larvae collected were in the litter, about 11 percent were on the trunks of the trees, and over 60 percent were on the foliage. On the other hand, a large percentage of the larvae were found in the litter in areas similar to Spencer, where the gypsy moth population was very low. This striking correlation suggests that the habits of the larvae in

FIG. 2 — UNDERSIDE OF LEAF ON GROUND NEAR BASE OF TREE
SHOWING RESTING LARVAE

TABLE 2

PROPORTION OF LARGE LARVAE FOUND IN LITTER AND
NUMBER OF EGG MASSES IN STUDY AREAS NEARBY, 1942

| Locality | Larvae | | Egg Masses No per acre |
|---|---|---|---|
| | No Observed | Percent in Litter | |
| Spencer, Mass | 166 | 90 | 0 |
| Petersham, Mass. | 973 | 35 | 40 |
| Northampton, Mass. | 186 | 30 | 95 |
| Granby, Conn. | 154 | 22 | 2 [1] |
| North Reading, Mass. | 203 | 17 | 90 |
| Hillsborough, N. H. | 320 | 8 | 110 |
| Brewster, Mass. | 430 | 2 | 550 |
| Wendell, Mass. | 513 | 0.6 | 1,360 |
| Alfred, Maine | 107 | 0 | 40 [2] |
| Freetown, Mass. | 921 | 0 | 3,150 |

[1] Area defoliated severely in 1939, but had never been before and has not been since.
[2] Area frequently severely defoliated, but population at low ebb in 1942.

spending the day in trees or in seeking shelter on the ground during the day are closely related to their survival.

This relationship is corroborated by data collected in Petersham. Here the behavior of the moth has been studied for a number of years in three stands, one of which was characterized by a low population of the moth; another, by a relatively high population; and the third, by the largest population year after year of any stand in town (Table 3). In the most resistant stand, in which red oak and paper birch were the predominant species (Fig. 3), a large percentage of the larvae were found in the litter. In the more xerophytic oak stand (Fig. 4), 35 percent of the larvae were found in the litter, about 60 percent were on the trunks of the trees, most of these being less than five feet above the ground, and less than one percent was found on the foliage. In the gray birch pasture (Fig. 5), none of the 256 fifth- and sixth-instar larvae collected were found on the forest floor.

The foregoing observations in Petersham were made in 1942, a year when there was little change in the gypsy moth population. Observations made in 1943 and 1944 revealed that relatively few large larvae were in the litter during the day, even though large numbers had been in the litter of the same woodlands during 1941 and 1942. The increase in the population was also great in both 1943 and 1944. This change in larval behavior and abundance apparently was associated with climactic conditions. Rainfall was about normal during the early spring of 1942.
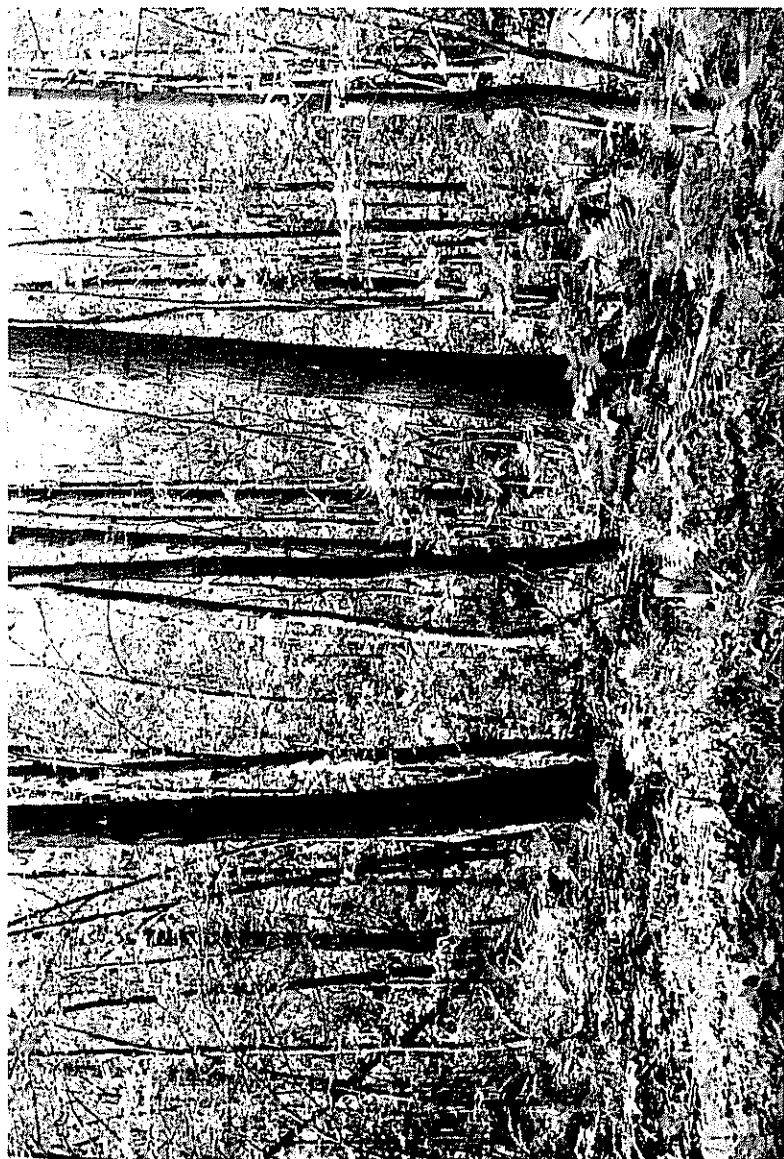
FIG. 3. RED OAK STAND RESISTANT TO DEFOLIATION
Table 3, Stand A

## TABLE 3

### YEARLY FLUCTUATIONS IN THE POPULATION OF THE GYPSY MOTH IN ONE-FIFTH ACRE PLOTS IN PETERSHAM, MASSACHUSETTS

| Description | 1940 [1] | 1941 | 1942 | 1943 | 1944 | 1945 |
|---|---|---|---|---|---|---|
| A. Red Oak and Paper Birch Fully stocked, moist site | 3 | 1 | 0 [2] | 5 | 783 | 346 |
| B. Black Oak, White Oak, and Red Oak Medium stocked, dry site | — | 16 | 7 | 147 | 5,031 [3] | 45 |
| C. Gray Birch Medium stocked, dry site, pastured | 400 [4] | 86 | 363 | 1,498 | 16 [5] | 288 |

[1] Year in which egg masses were deposited
[2] No egg masses were found in the plot, but a few were seen in the stand.
[3] Plots about 50 percent defoliated
[4] Estimated on the basis of defoliation in 1941.
[5] Plots completely defoliated in June with subsequent starvation of larvae

Later about 3.4 inches fell between May 1 and June 10, and 7.0 inches from June 10 to July 22. During this latter period in 1943, when fifth- and sixth-instar larvae are normally present, the precipitation was only 1.1 inches, of which 0.8 inch fell in one day. Unusually dry conditions persisted throughout 1943 and until the summer of 1944. From December 1, 1943 to June 10, 1944, precipitation was only about 40 percent of normal. From May 1, about the time that gypsy moth eggs hatch, to June 10, 1944, less than one inch of rain fell. Although the drought was broken in mid-June, practically no larvae could be found in the litter during June, and even in early July.

An analysis by Stephen H. Spurr of the precipitation records of the Harvard Forest for the past twenty years shows that the combination of a late spring drought in one season followed by an early spring drought the following season has occurred only twice, in the years 1935-1936 and 1943-1944. During both periods, and only during those periods, has the population of the gypsy moth increased greatly, causing heavy defoliation.

During 1943 and 1944 additional data on larval behavior were obtained from points in the infested zone, not only in New England but also in Pennsylvania. Observations were made throughout the day and night, and many larvae were crushed at all hours to determine the condition of the food in the alimentary tract. The information obtained showed that most of the feeding by large larvae was done at night.

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There was a definite tendency for the larger larvae to molt and spend the day in cool, moist, secluded places, provided such places were available. The movement of the large larvae to the foliage at dusk and to the litter at dawn was very marked. For example, in one woodland where practically no larvae could be seen at sunset, as many as 50 came out of the litter around a single tree within a few minutes of dusk, hastily ascended the tree, and began feeding immediately. In many instances, immediately prior to pupation, more than 90 percent of the larvae remained in the ground litter throughout the day.

## SURVIVAL OF LARGE LARVAE AND PUPAE IN DIFFERENT TYPES OF WOODLAND

In 1941 in Petersham few large larvae survived in woodlands where they congregated and molted in the litter, whereas large numbers survived where they avoided the forest floor. Since then additional data have been obtained on the survival of large larvae and pupae under different forest conditions. These show that survival and abundance are influenced by ecological conditions in the forests, although further studies are needed to ascertain and evaluate specific controlling factors.

### Larval Liberations

To determine their survival under various forest conditions, groups of 1,000 fifth- and sixth-instar larvae were liberated at different points in New England in 1942. A total of 10,000, collected in a gray birch stand in Petersham, were placed in typical oak stands in different parts of the infested region. These stands had few or no larvae present at the time of liberation.

Survival varied greatly in the different localities and showed trends similar to those of the natural population in study areas nearby in the same towns (Table 4). For instance, 113 egg masses resulted from 2,000 larvae in Freetown, while no egg masses were found following a similar liberation in Eastford. Yet both areas contained highly favored food species.

That these differences in survival could not be attributed to differences in local weather conditions was shown by the exposure of 200 similar larvae in large wire cages at three of the liberation points. About one egg mass was deposited for every four larvae confined, regardless of the locality.

Apparently, then, the differences in survival were due to some factor other than food supply, parasites, or weather. That this factor operated upon larvae resting in the ground litter was indicated by the fact that survival was poorest where they left the trees in large numbers during

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TABLE 4

NUMBER OF EGG MASSES DEPOSITED PER 1,000 LARGE LARVAE
LIBERATED IN OAK STANDS AS COMPARED WITH THE NUMBER
FOUND PER ACRE IN STUDY AREAS NEARBY, 1942

| Locality | Egg Masses Deposited per 1000 Liberated Larvae | Egg Masses Found in Nearby Study Areas |
|---|---|---|
| Freetown, Mass. | 73 | 3,150 |
| | 40 | |
| Alfred, Maine | 37 | 115 |
| Petersham, Mass. | 17 | 40 |
| | 9 | |
| Simsbury, Conn. | 0 | 2 [1] |
| | 2 | |
| Eastford, Conn. | 0 | 0 |
| | 0 | |

[1] Study area in Granby, Conn., about six miles from liberation point, but within an essentially similar stand.

the day. A clue to the possible nature of this controlling factor was furnished in Eastford in 1942. Here a deer mouse gnawed a hole in the bottom of the cage confining the larvae, built a nest inside, and ate a large number of pupae.

Larval liberations were repeated in 1943 on a scale somewhat larger than in 1942. Unfortunately the larvae were diseased, and few survived at any of the liberation points. About five egg masses were produced per 1,000 liberated larvae at the Freetown points, and an average of less than two per 1,000 at the Connecticut points.

Inasmuch as the studies indicated higher survival where larvae failed to seek shelter on the ground during the day, attempts were made in 1944 to induce them to remain above the forest floor. Loose burlap bands were applied to trees as a means of providing shelter during the day. In some instances three bands were placed about two feet apart on the trunk of each tree, and the number of larvae found under each band was recorded. It was found, as had been observed before, that the smaller larvae were not attracted to the bands to the same extent as the larger larvae. Furthermore, the majority of the larvae attracted to the bands in June and the first week in July were found under the upper band. During the remainder of July, only about half were under the upper band

Also in 1944, more than 45,000 large larvae were liberated to check

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on their survival under different conditions. The season was exception-
ally droughty over much of the infested area, and there was a general
increase in population in New England. Survival at the liberation points
in Connecticut, where it had been low in 1942, was even higher in 1944
than it had been at the Freetown points in 1942. In central New England,
where extreme droughty conditions prevailed during the early larval
season of 1944, the large larvae did not descend into the litter in the better
woodlands to the extent that they had in previous years. However, where
the rainfall was nearly normal, as in Albany County, New York, and
in Pennsylvania, the larvae descended the trees and entered the litter to
rest and molt.

The liberations in 1944 confirmed previous findings: that more larvae
survived when induced to remain in trees by means of burlap bands
than when free to descend to the ground (Table 5; also Appendix B).

TABLE 5

EFFECT OF BURLAP BANDS ON DEPOSIT OF EGG MASSES, 1944

| Locality | Number of Series Studied | Trees Banded | | Trees Not Banded | |
|---|---|---|---|---|---|
| | | Larvae Liberated | Egg Masses Deposited | Larvae Liberated | Egg Masses Deposited |
| Petersham, Mass. | 2 | 2,000 | 861 | 2,000 | 397 |
| Simsbury, Conn. | 2 | 2,000 | 352 | 2,000 | 268 |
| Pittston, Pa. | 6 | 1,200 | 466 | 1,200 | 71 |
| Jenkins, Pa. | 6 | 1,200 | 234 | 1,200 | 33 |
| Canaan, N. Y. | 1 | 300 | 71 | 300 | 16 |
| Saratoga and Fulton Counties, N. Y. | 4 | 0 [1] | 168 | 0 [1] | 86 |
| Albany County, N. Y. | 2 | 0 [2] | 565 | 0 [2] | 223 |

[1] No larvae were liberated, but a few larvae were observed in all plots at the start of the experiment
[2] No larvae were liberated, but 2,260 larvae were found in the banded plots and 1,591 in the unbanded plots at the start of the experiment

In the twelve plots in Pittston, where 200 large larvae were liberated in
each plot, the survival where burlap bands were applied was from five
to twenty times greater than in the check plots 200 feet away. Similar
results were obtained at the other liberation points and in the areas in
New York state where natural rather than liberated populations were
tested.

To determine whether predators could cope successfully with large
numbers of larvae simultaneously, different numbers were released in
the same woodland at various study points. No significant trends in

survival were noted (Appendix D). However, at Simsbury and East-ford there was some evidence that a larger percentage of larvae survived from the larger liberations.

Since the studies of native populations and of larval liberations had indicated that there was considerable mortality of fifth- and sixth-instar larvae on the ground, and since small mammals were suspected of being responsible for much of this mortality, tests were run in which large larvae were liberated within small plots 100 feet in circumference from which all mammals had been removed and were thereafter excluded by a hardware cloth fence. One such plot at Eastford was set up in 1943, and the results were phenomenal. From the 1,000 large larvae liberated within the enclosure, 67 egg masses were deposited. However, from four lots of 1,000 larvae each, liberated in the open near the enclosure, a total of only 12 egg masses was deposited.

The enclosure tests were repeated in 1944 in Petersham and Simsbury. Although conditions were such that there was a high survival of larvae in the open, survival followed the same trend as in the previous year. Nearly twice as many egg masses were produced in the enclosures as in the open, and even more were deposited where the larvae were dis-couraged from leaving the tree by the burlap bands around the trunk (Table 6). These studies showed conclusively that much of the mortality

TABLE 6

NUMBER OF EGG MASSES DEPOSITED PER 1,000 LARGE LARVAE
LIBERATED UNDER DIFFERENT CONDITIONS, 1944

| Conditions of Larval Liberation | Petersham, Mass. (Two Series) | Simsbury, Conn. (One Series) |
|---|---|---|
| No confinement | 214 183 | 96 |
| Hardware cloth enclosure | 289 345 | 130 |
| Burlap bands on trees | 432 429 | 180 |

of the gypsy moth in the later larval stages occurred on the ground, and indicated strongly that small mammals were responsible for much of it.

*Pupal Exposures*

Experiments involving the exposure of pupae in the litter in different woodlands have corroborated the conclusions drawn from the various liberations of larvae.

On July 23, 1942, several lots of twenty female pupae each were placed in the litter in a good oak woodland in Petersham and in a dry oak woodland in Freetown. Subsequent observations revealed that far more pupae were destroyed in Petersham than in Freetown (Table 7). More

TABLE 7

SURVIVAL OF PUPAE EXPOSED IN TWO LOCALITIES AND
NUMBER OF EGG MASSES FOUND IN STUDY
AREA NEARBY, 1942

|  | Petersham, Mass. | Freetown, Mass. |
|---|---|---|
| Pupae exposed | 379 | 374 |
| Adults emerged | 150 | 315 |
| Pupae eaten or removed | 210 | 32 |
| Pupae parasitized or dead from other causes | 19 | 27 |
| Egg masses per acre in nearby study area | 40 | 3,150 |

galleries made by small mammals were observed in the woodland in Petersham than in the one in Freetown. The logical conclusion is that pupal predators were more abundant and active in the Petersham area. Inasmuch as the Petersham woodland was more densely stocked and had a moister, deeper litter, it may be inferred that such ecological conditions are conducive to a higher population of predators. This conclusion is in accord with the published information on the relation of forest conditions to forest biota.

The following year several lots of pupae were exposed in the litter in a good oak woodland in Eastford, while others were confined in small wire cages placed in the litter. The cages, containing ten female pupae each, were located on the north side of an oak tree about one foot from its base. A like number of pupae were placed in the litter just outside each cage. A few leaves were placed over the cages. Survival was much higher within the cages than outside in the litter (Table 8). No natural

TABLE 8

SURVIVAL OF PUPAE EXPOSED IN EASTFORD, CONN., 1943

|  | Not Confined | Caged |
|---|---|---|
| Pupae exposed | 140 | 140 |
| Adults emerged | 46 | 128 |
| Pupae eaten or removed | 88 | 0 |
| Pupae parasitized or dead from other causes | 6 | 12 |

egg masses were found in study areas nearby. As in the other pupal exposures, the differences in survival were apparently due largely to the action of predators. In the course of the examination of the pupal skins, excrement, presumably from a skunk, was found which contained many unfertilized gypsy moth eggs.

*Natural Populations*

The data collected in the present study on the fluctuation of gypsy moth abundance in natural populations (Table 1 and Appendix A) confirm the results of larval and pupal exposures, and indicate strongly that the moth can maintain itself at a higher population level in open dry stands than in dense moist woodlands. Of particular interest are the records of population fluctuations which have been kept for the town of Petersham since the first serious outbreak in 1935 (Table 1 and unpublished material). Here, when the general population was relatively low, the highest populations were in stands of the poorer, drier types. Furthermore, these stands or isolated trees which supported the highest populations during the lean years of the moth were, almost without exception, the first ones to be defoliated in both the 1935 and the 1944 outbreaks. From 1938 through 1942, the population was extremely low in the more mesophytic oak stands in the town; but a few egg masses and larvae could always be found by diligent search. The fluctuations in representative stands in this town have already been given in Table 3. Tables 9 and 10 in Part II show the relation of stand composition to defoliation in Petersham.

That natural populations encouraged to remain in the trees survive better than natural populations allowed to migrate freely to the ground is demonstrated by results obtained from sample plots in Albany County, New York (Appendix B). Where the trees were not banded, larvae and pupae were found chiefly in the litter. Their numbers decreased from 322 on June 5 and 6 to only 9 on July 18. Where the trees were banded with burlap, however, most of the larvae and pupae were found under the bands. Their numbers increased from 312 on June 5 and 6 to 459 on June 13, and decreased only to 196 on July 18. Final survival for the unbanded trees was less than 3 percent; and for the banded trees, nearly 63 percent.

Throughout the infested zone, isolated roadside trees have been defoliated more frequently than any other type. This is illustrated by the record of the distribution of the egg masses within an acre of woodland in Glastonbury, Connecticut, in 1944. Here, a large roadside white oak stood along the edge of a young stand composed chiefly of white and black oak. There were 654 egg masses within the acre, and 500 of them

were on this one white oak shade tree. Elsewhere along a roadside strip, 16 feet wide and 208 feet long, there were 65 additional egg masses; whereas in the twelve strips immediately back of the road, only 89 egg masses were found, or less than 8 per strip.

Also illustrating the high susceptibility of large, open-grown white oaks is the record obtained within the study area in Pittston. A careful cruise of the ninety-acre tract in 1944 revealed only 51 egg masses outside of those on a single large white oak, which had approximately 300 on it.

### ECOLOGICAL FACTORS INFLUENCING ABUNDANCE

The work of previous investigators, and the evidence obtained in the present study, make it clear that a number of ecological factors are closely related to gypsy moth abundance. A discussion of some of the factors which produce mortality,. without attempting to evaluate each factor quantitatively, will emphasize the probable relation of forest and site conditions to the abundance of this insect.

*Food Supply*

The gypsy moth, like other defoliators, prefers certain plants for food. Some species are highly favored by all larval stages; other are not fed upon by larvae of early instars, but are highly favored by larger larvae. Other species are not favored by larvae of any age. The original classification of food plants was based on extensive laboratory tests (Mosher, 1915) and, with modifications, have served as a basis for all subsequent silvicultural control suggestions. Baker and Cline (1935) found that in the town of Petersham the percentage of favored food plants in a stand was closely proportional to the amount of defoliation by the gypsy moth.

While suitable food must be present for larvae to survive, the history of this insect in the oak forests of Connecticut and western Massachusetts shows that food supply does not normally limit the abundance of the moth in these areas. Only in infestations where practically all the suitable food is consumed, does the quantity of favored food foliage become the factor actually limiting the size of the moth population.

*Parasites, Predators, and Diseases*

Parasites, predators, and the wilt disease kill vast numbers of the gypsy moth. A particular parasite is frequently far more abundant in one part of the infested region than in another. Various predators, also, are commonly most abundant in certain types of woodlands.

Brown and Sheals (1944) analyzed data obtained between 1929 and 1934 in different forest regions in New England and concluded that

"the percentage of parasitization by the principal egg parasite, *Anastatus disparis* Ruschke, was highest in the heavier infestations of the pine-oak and white pine regions. The most important larval parasite, *Compsilura concinnata* Meig., attained its highest percentage in the lightly infested central hardwoods region and in portions of the white pine region where the infestation was relatively light. The principal pupal parasite, *Sturmia scutellata* R.-D., maintained a fairly high percentage of parasitization regardless of host density or forest region, except in the pine-oak region, where parasitization was relatively low." The information obtained in recent years corroborates these conclusions for the most part.

Considerable evidence indicates that insectivorous small mammals, and predaceous insects and other arthropods destroy many fifth- and sixth-instar larvae in habitats where they spend the day in the ground litter. The results of the larval and pupal liberations detailed above constitute strong circumstantial evidence to this effect. In woodlands where the larvae characteristically descend to the ground about dawn, many freshly destroyed larvae have been found. In Granby, Connecticut, the remains of 13 larvae, characteristic of those killed by *Calosoma* beetles were seen while 50 living larvae were collected on June 12, 1942. Of the latter, 38 were in the litter, and the others were on the lower parts of the tree trunks. Two weeks later the population had so decreased that by diligent search for more than one hour only one larva could be found in the same area. It was safely lodged under a piece of loose bark on a tree trunk. A similar decrease in population was noted in Petersham the same year. In many instances, 30 to 40 large larvae were collected in oak woodlands there within fifteen minutes in the middle of June. Two weeks later a diligent search was made at one of these points for two hours, and only five larvae and pupae were found. Less time was spent at the other points, but all egg-mass counts made in the fall revealed that similar reductions had occurred.

The importance of small mammals in destroying insects has been emphasized by Hamilton and Cook (1940). They state that many insect populations are apparently held in check principally by small mammals. They consider that the number a given area will support is dependent upon "the forest stand, the ground cover, the presence or absence of litter, the character and moisture content of the soil, and numerous other factors, some of which are as yet obscure." All work to date, however, has indicated that the population of small mammals is highest in dense forest stands with a moist and deep forest floor—stands where little gypsy moth defoliation occurs—and lowest in open stands with a dry compact floor devoid of litter—stands which ordinarily are heavily defoliated if composed of favored food species.

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In the present study, some census trapping was done through the co-operation of the U. S. Fish and Wildlife Service at a few widely separated points. Although there was considerable variation in the number of animals caught in the different quadrats, the catches in a good hardwood stand in Petersham were consistently high for the three-year period. Most abundant were the short-tailed shrew (*Blarina brevicauda brevicauda* (Say)), and the deer mouse (*Peromyscus leucopus noveboracensis* (Fischer)), both voracious insect eaters. No defoliation by the gypsy moth occurred in this stand during the same period, but some larvae were observed each year.

## Climate and Weather

The climate in the coastal region is less hazardous to the moth than that in the interior of New England. Winter temperatures are seldom low enough along the coast to kill gypsy moth eggs, whereas they frequently destroy many or all of the exposed eggs in the more northern parts of the interior. The relatively cool temperatures on Cape Cod during the larval and pupal periods are probably unfavorable to the development of the wilt disease in this area. In the interior, large numbers of small larvae have died of starvation as a result of late spring frosts. Cold driving rains during May and early June have also killed large numbers. In contrast, prolonged hot and dry weather during the larval and pupal periods appears to be favorable to the survival of the insect.

## Land Abuse

The same unfavorable ground conditions that are temporarily brought about by droughty climatic conditions are more or less permanently achieved by land abuse. Forest fires, repeated clearcutting, and woodlot grazing all cause the deterioration of the forest floor and create conditions favorable to the increase of the moth. These factors have a tremendous influence on gypsy moth abundance in eastern New England, and also bring about an increase in the percentage of favored food species in the forest stand. Natural disasters also affect the forest floor in such a way as to favor the gypsy moth. The elimination of chestnut by the chestnut blight and the widespread destruction of the 1938 and 1944 hurricanes have undoubtedly made conditions more favorable to the moth.

## Population Density

In partially defoliated stands, repeated observations indicate that survival is high. In such stands the large larvae are likely to stay up in the trees, while the predators in the litter are likely to be driven out or

reduced in numbers by the hot dry condition of the forest floor. Thus, within certain limits, the moth in its epidemic state creates conditions favorable to its own survival.

Although moderate defoliation may produce ecological conditions favorable to the moth, heavy defoliation will cause high mortality from starvation. For example, the gypsy moth population in a gray birch stand in Petersham was practically eliminated by starvation in a year when less susceptible stands supported heavy populations (Table 3).

## PART II

# ECOLOGY OF SUSCEPTIBLE AND RESISTANT FOREST TYPES AND STANDS

*By* Stephen H. Spurr, E. W. Littlefield, and Henry A. Bess

The investigations described in Part I demonstrate that the entire forest environment plays a part in the size of the gypsy moth population maintained in a given area over a period of years. Bess has shown that dry, open woods provide a more favorable habitat than the fully stocked forest on medium to moist sites. Since these relationships are of interest not only to the entomologist, but to the forester and plant ecologist as well, a more detailed analysis is presented here of the various elements that comprise susceptible and resistant forest types and stands. During 1944 and 1945, observations on which the following discussion is based were made at some fifty points in New England, New York, and Pennsylvania. These stations were located principally as follows: Maine: York and Cumberland Counties; New Hampshire: all of the state south of the White Mountains; Massachusetts: all of the state east of the Berkshires; Connecticut: Windham, Tolland, and Hartford Counties; New York: Saratoga, Fulton, Albany, Greene, Ulster, and Sullivan Counties, and Long Island; Pennsylvania: the infested area surrounding Wilkes-Barre, and the Poconos.

### CHARACTERISTICS OF SUSCEPTIBLE STANDS

Even the most casual inspection of the heavily infested area of south-eastern New England will impress the observer with the extremely dry, open conditions under which repeated severe defoliation by the gypsy moth takes place. Such susceptible areas are characterized by light sandy or gravelly soils; a history of repeated fires; stand canopies covering less than half the ground; short, scrubby timber; and a ground cover in which certain plants are abundant, notably, blueberry, sweetfern, and bracken. Leaf litter is sparse or absent; and in the more open types, especially where grazed, mats of grass of *Carex* may be frequent. Dominant in the forest are gray birch, aspen, or oaks characteristic of fairly dry sites,

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particularly scarlet oak, white oak,[3] and black oak. An abundance of white pine and oak reproduction in the understory is frequently characteristic. Both in New York and Pennsylvania, such pockets of gypsy moth infestation as have developed are nearly always found in forest communities similar in kind to those of eastern Massachusetts, though xerophytic perhaps to a lesser degree

The tree species commonly found in susceptible stands are favored food plants of the gypsy moth. The mere presence of these species, however, does not necessarily indicate susceptibility. Oaks, in particular, may occur in both highly resistant and highly susceptible stands. The occurrence of gray birch on the other hand, does indicate stand susceptibility, *not primarily because it is a favored food species*, but because its presence is associated with fire, grazing, overcutting, or other forms of abuse that create conditions favorable to survival of the gypsy moth larvae.

Because forest cover types often are closely related to a given site and land-use history, it is possible to classify them according to their susceptibility to defoliation by the gypsy moth. In Table 9 the types listed as susceptible contain a large percentage of favored food plants. These types are known to develop following land abuse, and are quite generally distributed throughout the heavily infested zone (Fig. 1), as well as throughout the general region wherever forest fires are frequent.

Borderline types generally contain a large proportion of favored food, but are liable to be defoliated only when the environment is also favorable. Of these, the mixed oak (white oak-black oak-red oak) type is by far the most extensive and important, being the predominant type of the central hardwood forest region. It is the principal type of Rhode Island, Connecticut, southeastern New York, New Jersey, and much of Pennsylvania. Red pine and pitch pine types characteristically occur on dry sites, but are liable to be defoliated only when containing a sizable proportion of favored food plants.

Perhaps the best classification of areas as to susceptibility to defoliation by the gypsy moth, however, is that based upon soils and physiography. Within the forest regions where the gypsy moth has reached epidemic proportions, heavy defoliation has been largely confined to specific physiographic sites.

The most important of these sites are the extensive areas of sandy soils in eastern New England. These soils are frequently burned over and generally support a forest growth of the most susceptible type. The

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[3] The relegation of white oak to this category may be somewhat confusing to those familiar with the species in regions such as the Hudson Valley or the Ohio Basin, where its occurrence is associated with coves and moist bottom lands. The wide habitat range of the species, however, is well known; and in New England, near its northern limit of distribution, it occurs mainly on sand plains, ridges, and other dry sites.
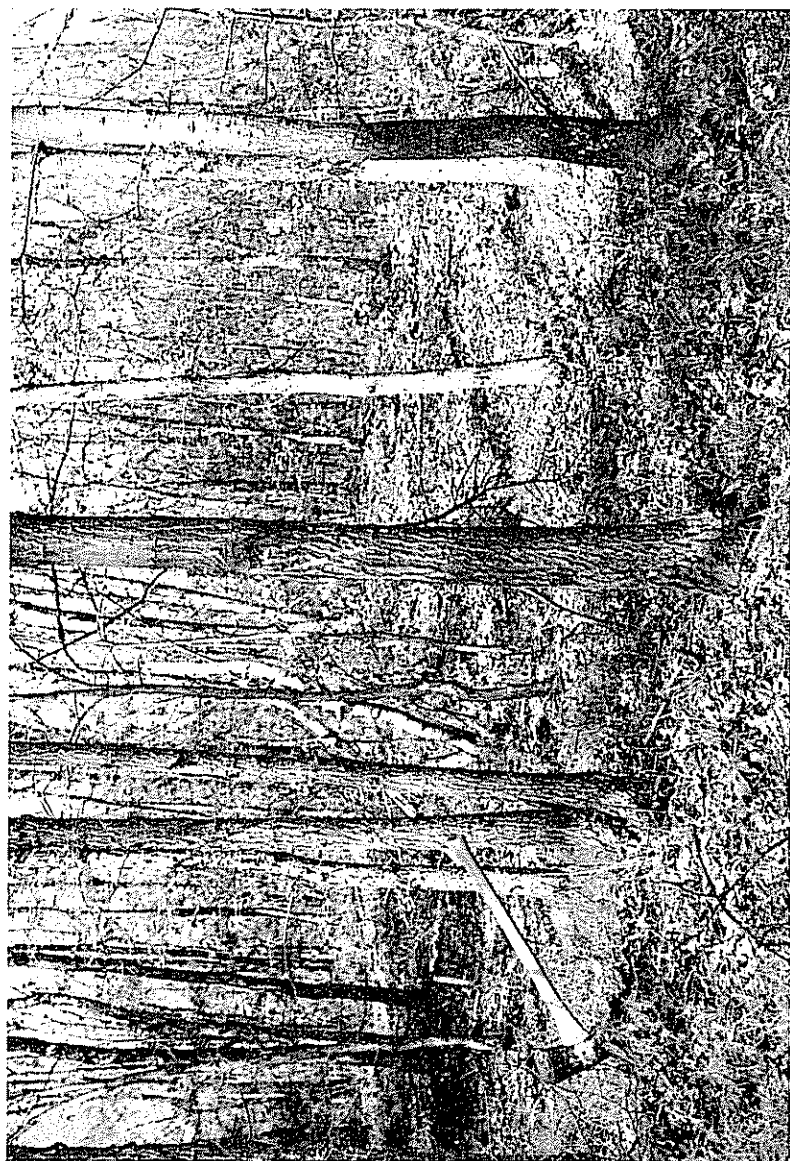
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FIG. 4. MIXED OAK STAND SUSCEPTIBLE TO DEFOLIATION

Note its open character and the absence of understory and ground cover. Table 2, Stand B

TABLE 9

## CLASSIFICATION OF FOREST COVER TYPES ACCORDING TO SUSCEPTIBILITY TO DEFOLIATION BY GYPSY MOTH

| Type S.A.F. No [1] | Type Designation |
|---|---|
| SUSCEPTIBLE: | *Likely to be defoliated under a wide variety of conditions.* |
| 4 | Aspen |
| 5 | Pin cherry (with aspen and birch) |
| 7 | Gray birch |
| 35 | Scrub oak |
| BORDERLINE: | *Susceptibility depends upon site, actual composition and condition of stand.* |
| 3 | Red pine |
| 6 | Paper birch |
| 36 | Chestnut oak |
| 37 | Pitch pine |
| 49 | White oak-black oak-red oak |
| 50 | White oak |
| RESISTANT: | *Not likely to be defoliated unless badly abused or surrounded by susceptible types.* |
| 7 | Red maple |
| 8 | White pine-red oak-white ash |
| 9-11 | White pine types |
| 12-15 | Northern hardwood types |
| 17-22 | Spruce-fir types |
| 26 | Black oak-American elm-red maple |
| 51 | Red oak-basswood-white ash |
| — | Red oak |
| 59 | River birch-sycamore |
| 60 | Silver maple-American elm |

[1] Committee on forest types, Society of American Foresters. 1940 Forest cover types of eastern United States Third edition, revised. Society of American Foresters, Washington, D.C 39 pp

majority of the perennial outbreaks of the gypsy moth have occurred here (Fig. 1).

Extensive outbreaks of the gypsy moth, however, are not confined to these sandy soils. They also occur on high, rocky ridges, sites ecologically similar to the lower sand plains. Fortunately, the extent of such ridges with a forest cover of favored foods is not large in New England, though occurring frequently in New York. Rocky ridges that are covered with favored food species include the hills of the Lake Sebago region

Fig. 5    GRAY BIRCH IN OLD PASTURE
Such areas are highly susceptible to gypsy moth defoliation (Table 3, Stand C)

in Maine, of the Lake Winnepesaukee region in New Hampshire, the Blue Hills south of Boston, Wachusett Mountain in central Massachusetts, the upland of Wendell, Shutesbury, and Pelham east of Greenfield, and the traprock ridges in the lower Connecticut Valley. The 1940 outbreak in Granby, Connecticut, was on the latter type of ridge. In eastern New York such ridges are found in the Helderbergs, south of Albany, in the southeastern Adirondacks, and along both sides of the Hudson Valley below Albany, especially on the Shawangunk Mountains in Ulster and Sullivan Counties.

Although stands such as those described above are most susceptible to defoliation, and will generally be the first ones attacked in any locality, they may not be the only stands defoliated. Even normally resistant stands may be stripped occasionally if the local moth population reaches an epidemic stage. Consequently, small forest stands in an area predominantly covered by susceptible stands cannot be considered safe from the gypsy moth regardless of their composition, the site upon which they grow, or other characteristics. It is also true that less favored or non-favored food species may be severely defoliated when growing in open stands lacking in leaf litter, or as individual trees along roads or fence rows, or in pastures. During the 1944 outbreak, examples were seen in Pennsylvania of black cherry heavily fed upon, sugar maple defoliated in Petersham, and other cases where defoliation was not associated with food preferences, but rather with the lack of forest conditions and the occurrence of habitats suitable for harboring the larvae, such as decay cavities, rough bark, and nearby stone walls. If such habitats are available, the larvae are apparently less likely to take refuge in the forest floor, and are therefore more likely to survive.

## CHARACTERISTICS OF RESISTANT STANDS

Stands which have remained relatively free from severe defoliation within the heavily infested zone, and stands of a similar nature elsewhere in the region, exhibit an easily recognizable structure quite different from that of susceptible stands. Resistant stands are characterized by loamy soils, a moderately dense crown canopy, vigorous timber growth, and the deep litter of a well-developed forest floor. Certain herbaceous and shrub indicators will almost certainly be present in some abundance (Fig. 6). Among the most reliable of these are (1) wild sarsaparilla, (2) maple-leafed viburnum or arrowwood, and (3) certain woodland ferns (Table 10). The forest composition of these stands may be predominantly oak, as in Connecticut, central Massachusetts, northeastern Massachusetts, southwestern Maine, and in certain areas in New York and Pennsylvania.

FIG. 6. GROUND COVER CHARACTERISTIC OF RESISTANT STANDS

Note *Aralia*, New York fern, white ash, and *Lycopodium*. Table 2, Stand A

In these resistant oak stands there will usually be a high proportion of red oak, few black or white oaks, and seldom any scarlet oak. Still more characteristic of these resistant stands are hardwood species such as sugar maple, white ash, sweet birch, basswood, and yellow poplar, together with occasional hemlock. These latter species, which are typically confined to the better sites, are good indicators of resistance, whether occurring in the main stand or the understory.

Such forest conditions are ordinarily found on the better soil types, but they may also occur on sandy and gravelly soils provided the crown canopy is dense and the site generally has not suffered from fire or other recent disturbance. In periods of drought, normally resistant stands may become heavily defoliated, but will recover with a return to normal precipitation levels.

An outstanding example of a forest type composed predominantly of favored species which, nevertheless, has escaped repeated or widespread defoliation, is furnished by the mixed oak stands of eastern Connecticut. Though chronically infested for more than twenty-five years, attack by the gypsy moth has continued to be local and sporadic. It must be admitted, in this case, that not all the factors involved are clearly in evidence. While these stands, on the average, are more fully stocked, more vigorous, and apparently better protected from fire and grazing than oak stands elsewhere in New England, the absence of defoliation in the more open woods and on the drier sites is not readily explained.

Another example, wholly different in character, is the scrub-oak forest of the Pocono region, in Pennsylvania. Here, the dense shade and heavy leaf litter produced in this type is evidently sufficient to offset the presence of favored species throughout the stand, and little, if any, defoliation takes place.

Many forest types and, in fact, whole forest regions are resistant to heavy defoliation by the gypsy moth, either because they contain little favored food, or because they are largely confined to the better sites. The northern hardwood and the spruce-fir regions, in particular, contain almost no favored food. As the climates of these regions, also, are unfavorable to the gypsy moth, they form natural barriers on the north and west of the present infested area. Such barriers include the uplands of New Hampshire, the Berkshire Hills-Green Mountain chain of Massachusetts and Vermont, the Adirondack Mountains of New York, and the Allegheny hardwoods plateau of northern Pennsylvania and southern New York.

*Indicator Plants*

The use of ground vegetation to indicate site quality and to designate

forest type conditions has been the subject of much research. The plants listed in Table 10 as indicators of resistant and susceptible stands have

TABLE 10

## PLANT INDICATORS USEFUL IN EVALUATING STAND SUSCEPTIBILITY TO GYPSY MOTH ATTACK

INDICATORS OF SUSCEPTIBLE STANDS:

Overstory
  Black oak, scarlet oak, white oak *(Quercus velutina, Q. coccinea, Q. alba)*
  Gray birch *(Betula populifolia)*
  Aspen *(Populus tremuloides, P. grandidentata)*

Understory
  White pine *(Pinus strobus)* when abundant
  Scrub oak *(Quercus ilicifolia)*
  White oak *(Quercus alba)* when abundant

Ground Cover
  Lowbush blueberry *(Vaccinium angustifolium* and *V. pallidum)* when
    abundant
  Sweet fern *(Comptonia peregrina)*
  Huckleberry *(Gaylussacia* spp.)
  Bracken *(Pteridium latiusculum)* when abundant
  Sedges *(Carex pennsylvanica* and *C. umbellata)*
  Bayberry *(Myrica pensylvanica)* along coast
  Bush honeysuckle *(Diervilla lonicera)* ledges, especially southern Adiron-
    dacks

INDICATORS OF RESISTANT STANDS:

Overstory and Understory
  Sugar maple *(Acer saccharum)*
  White ash *(Fraxinus americana)*
  Black birch *(Betula lenta)*
  Basswood *(Tilia americana)*
  Yellowpoplar *(Liriodendron tulipifera)*
  Hemlock *(Tsuga canadensis)*
  Beech *(Fagus grandifolia)*

Ground Cover
  Wild sarsaparilla *(Aralia nudicaulis)* when abundant
  Mapleleaf viburnum *(Viburnum acerifolium)* when abundant
  New York fern *(Dryopteris noveboracensis)*
  Wood fern *(Dryopteris spinulosa)*
  Christmas fern *(Polystichum acrostichoides)*

been checked in all parts of the infested zone. The same plants have been extensively used by other investigators to classify site.

Working with second-growth pine types in Wisconsin, Gevorkiantz and Zon (1930) cited all the plants of our susceptible stands as characteristic of poor sites, and those of our resistant stands as characteristic of medium sites. The species listed by these authors as characteristic of good sites appear to be mostly those which in the Northeast commonly occur in very rich woods, often on calcareous soils, highly resistant to defoliation by the gypsy moth.

The floral types of Hazard (1937) are not entirely comparable to those of the present work, because they relate only to pure white pine stands. Nevertheless, they are quite informative, as the general relationships are the same in both studies. These types, arranged in xerophytic-mesophytic sequence, include (A) *Cladonia*, (B) *Vaccinium*, (C) *Maianthemum-Vaccinium*, (D) *Maianthemum*, and (E) rich herbaceous. In this sequence, *Aralia* does not appear until Type D, and becomes dominant only in subtype 4 (*Aralia* subtype) of Type E. This last is the richest type recognized, a white pine type on good soil that contains a more or less dense understory of hardwoods. Only in this type were the New York fern and mapleleafed viburnum noted as being present. In discussing the successional relationships of these various types, Hazard states that the *Cladonia* type develops on severe burns, the *Vaccinium* type on heavily grazed pastures, and the *Maianthemum* type on slightly grazed pastures. Plant succession gradually brings about a change of ground vegetation up the scale toward the more mesophytic types until the climax type for the site in question is reached. This varies from the Vaccinium type on poor dry sites to the rich herbaceous types on heavy moist sites.

The ground-cover types established by Heimburger for the eastern Adirondacks (1934) are generally comparable to those of the region infested by the gypsy moth, although representing a more northern flora. The *Vaccinium-Myrica*, and the *Aster-Gaultheria* types of the Adirondacks represent the drier woodlands favorable to the gypsy moth; while stands containing the *Aster-Corylus*, *Maianthemum-Viburnum*, and *Aralia-Oryzopsis* types would tend to be resistant. The last named type is particularly interesting, since its counterpart may be found without difficulty in the more resistant stands of New England. The ground cover includes *Aralia*, *Aspidium*, and *Polygonatum*, which, according to the author, are indicative of a "dry but rich site," characterized by good red oak mixed with basswood, white ash, sugar maple, and hornbeam. In this type, shrubs occurring in the understory include dogwood and mapleleafed viburnum.

Raup (1938) classified the forest types of the Black Rock Forest in southeastern New York, giving due consideration to the understory and ground cover. His type classifications are of special interest, as they represent the more common types of the lower Hudson Valley, a locality where the gypsy moth problem is of vital interest at the present time. Here, the principal upland types are (1) chestnut oak, characteristic of extremely dry sites, and (2) red oak, a type intermediate between the chestnut oak association and the various cove forest types. In the chestnut oak association, mapleleafed viburnum, an indicator of gypsy moth resistant stands, is found only on the northern slopes; while blueberry and huckleberry, indicative of susceptible stands, occur on the south exposures. Chestnut oak comprises 62 percent of these stands; red oak, an additional 27 percent; and white oak, sugar maple, and red maple, the remainder. In the red oak association, the proportion of red oak and chestnut oak are approximately reversed, and mesophytic species, such as white ash, yellow poplar, basswood, and hemlock, make up a portion of the stand. The herbaceous ground cover includes several of the mesophytic ferns. The cove forests are divided into (1) the mixed hardwood association, (2) the hemlock-hardwood association, and (3) the beech-maple association, all of which are definitely mesophytic and highly resistant to the gypsy moth.

The role of ground cover as a diagnostic feature of susceptible and resistant stands has been purposely emphasized in the present paper in an attempt to create a broader picture of conditions throughout the Northeast than is afforded solely by the analysis of stand composition. Ground vegetation has been used, not to indicate inherent site value, but rather to indicate an existing condition brought about by site factors and land-use history together. Although the use of indicator plants has definite limitations in site diagnosis (Coile, 1938), they may yet be used to advantage as a tool for rapid evaluation of forest conditions, provided that their limitations and usefulness are clearly understood. Throughout the region infested with and threatened by the gypsy moth, knowledge of a few easily recognizable plants in the ground cover is a valuable aid in classifying forest stands as to their resistance or susceptibilty to defoliation.

## RELATION OF FOREST SUCCESSION TO DEFOLIATION

Forest succession, by altering both the composition of the overstory and conditions on the ground, affects the resistance of the forest type to defoliation by the gypsy moth. Behre, Cline, and Baker (1936) point out that the forest conditions most favorable to gypsy moth outbreaks

are the direct results of "a transient agriculture and the destructive lumbering practices of the past." That subsequent forest succession tends to alleviate this condition in the absence of any interference from man is an important consideration in the silvicultural control of the insect. The climatic climax forest of much of the Northeast is a hemlock-hardwood association (Nichols, 1935), highly resistant to defoliation. Subclimax associations throughout the region also are highly resistant. Among these are red oak-red maple-white ash forests of central Massachusetts, the mixed oak forests of Connecticut, the cove hardwoods of Pennsylvania and southern New York, and the Allegheny-northern hardwood stands of Pennsylvania, New York, and northern New England.

Only among the pioneer forest associations of the Northeast are highly susceptible stands to be found. Chief among these, as stated previously, are stands containing a high percentage of gray birch or aspen, and pioneer oak types on sandy and other dry sites. Even these may in time develop a considerable degree of resistance if left relatively undisturbed. Disturbance, however, may set back the succession and result in the creation of vast areas highly susceptible to gypsy moth outbreaks. Thus, several centuries of fire and overcutting on sandy soils in southeastern Massachusetts have resulted in the development of scrubby forests of this type.

The moth itself markedly influences forest succession, thus affecting stand susceptibility over a period of years. Moderately heavy infestations help to reduce the proportion of gray birch, aspen, and other short-lived weed trees, thus creating resistant types in areas where nonfavored food plants are relatively abundant. This tendency is illustrated by the records of a large number of sample plots maintained for many years after 1912 by the U. S. Bureau of Entomology and Plant Quarantine in eastern Massachusetts, New Hampshire, and the southern tip of Maine (Baker, 1941). Here mortality of the favored food trees (gray birch, aspen, and the like), whether due to gypsy moth defoliation or to other causes, such as the short life of most of these species, greatly changed the composition of the stands. During this time, also, parasites were extensively introduced into this region. At the same time, the gypsy moth population sank to a low level (Burgess and Baker, 1938).

That such a trend may well be regional is shown by the maps of gypsy moth defoliation published by Brown and Sheals (1944). Although the gypsy moth first became established and defoliated thousands of acres along that portion of New England seaboard between Plymouth, Massachusetts, and Maine, no extensive defoliation has occurred in that region in the last fifteen years or more. This phenomenon can be explained at least partially on the basis of the natural mortality of the

highly favored weed trees coupled with the increasing protection of the forests, a result of the rapid growth of towns and cities in the area.

Although moderately heavy infestations may create more resistant forest types by reducing the proportion of favored food in the stand, frequent severe defoliation will generally create conditions highly favorable to future epidemics. The stand will be opened up, the litter will dry out, and forest succession will be set back. This is particularly true in regions where the forest cover consists predominantly of favored food plants growing on poor soils. For instance, frequent heavy defoliation has undoubtedly been a contributing factor, along with fire and over-cutting, in the continuance of the epidemic status of the moth in south-eastern Massachusetts.

Significantly, the gypsy moth did relatively little damage as long as it was confined to the better sites of the metropolitan area of Boston and the region to the north. Not until 1905, after the insect had been in this country for thirty-six years, did the moth migrate into southeastern New England and northward into southern New Hampshire and Maine, all regions where damage has since become excessive. That the moth happened to escape from captivity in the vicinity of a forest region that contained an abundance of favored food species and had been rendered highly susceptible by generations of abuse was a peculiar and unfortunate accident. Although the moth has subsequently spread westward beyond the Hudson River, the area of repeated severe defoliation is thus far confined to the sandy or ledgy sites of southeastern Massachusetts, south-eastern New Hampshire, and southwestern Maine, where the combination of favorable factors operates. Many factors, both known and unknown, will determine the spread of the insect and its future abundance in other areas. It is probably safe to assume, however, that heavy repeated defoliation everywhere will be confined largely to stands ecologically similar to those that have proved susceptible in New England.

# PART III

# THE ROLE OF SILVICULTURE IN MAINTAINING CONDITIONS UNFAVORABLE TO THE GYPSY MOTH

*By* E. W. Littlefield and Stephen H. Spurr

Conditions biologically conducive to the building up of a large gypsy moth population, with resultant heavy defoliation year after year, are brought about through disturbances long regarded by foresters as undesirable. It is well known, for instance, that clearcutting and fire, especially on light soils, tend to produce open scrubby woods, of which Cape Cod has many examples. Heavy grazing of woodlands inhibits reproduction, reduces stocking, favors sprouts over seedlings, and compacts the soil. Under the environment thus produced, all the biological activity common to the undisturbed forest is reduced to a minimum, and progressive deterioration of the site takes place. Recurrent defoliation by the gypsy moth aggravates conditions by allowing further drying out of the forest floor and reducing the vigor of the trees. Fire hazard is increased also, and thus a retrogressive cycle is inaugurated.

On the other hand, woodlands with full canopy, vigorous understory, and an undisturbed forest floor, while not immune from occasional or periodic defoliation, are remarkably resistant to the type of defoliation which recurs on abused sites, because the gypsy moth population can exist under such conditions only at a low level. This we have seen (Parts I and II) is true even of stands containing a high proportion of certain favored food species.

When the ecology of the gypsy moth in relation to forest site conditions is understood, it will be possible to recommend practices which may assist either (1) in reducing the severity of gypsy moth attack within the heavily infested area, or (2) in retarding the build-up of heavy gypsy moth concentrations on the western fringe of the territory known to be infested. The present paper is concerned solely with the silvicultural aspects of gypsy moth control, and not with the use of insecticides, introduction of parasites, or administrative policies. Only those points will be discussed which have a direct bearing on control through forest practices.

## REDUCTION OF FAVORED FOOD SPECIES

### Outline of the Theory

The application of silviculture in the control of the gypsy moth has, for many years, been recognized as a possibility by entomologists and foresters. Particularly since 1935, when the first outbreak of epidemic proportions occurred in Petersham and neighboring towns in central Massachusetts, there has been a growing interest in measures designed to increase the resistance of forest stands to gypsy moth attack.

Until recently, emphasis has been laid almost wholly on the reduction of favored food species, such as oak, poplar, and gray birch. This doctrine is based on the theory that severe defoliation is unlikely to take place where the volume of favored food tree foliage in a stand comprises less than half the total foliage. Reduction or elimination of such species was believed, accordingly, to furnish the most practicable means of control.

This concept of favored food species is substantiated by considerable evidence, but has nevertheless failed to explain certain phenomena associated with gypsy moth abundance. In particular, it gives no adequate reason for the presence, in the same region, of stands similar in composition but differing widely in susceptibility over a period of several decades. The study of environmental factors other than food preference, described in the two previous sections of this bulletin, has done much to provide an answer to such apparent contradictions. In the light of these investigations, it seems desirable to review the background of silvicultural control and to point out some of the limitations involved in its application.

### Historical Development

The work of Mosher (1915), referred to in Part I, laid the foundation for classifying plants by the extent to which they are preferred as food by the gypsy moth. Prior to this time, however, on the basis of field observation, Fiske (1913) had suggested the removal of oak and some other species from infested woodlands as a means of slowing down the attack of the insect. A similar idea was elaborated by Clements and Munro (1917), who noted, significantly, that oaks growing on thin soils, very sandy soils, and rocky ridges were defoliated far more heavily than oaks on the better sites. More interesting still is their report that white oak was a more favored food in the field, though not in the laboratory, than the black oak group. In drawing conclusions from these observations, however, the authors apparently did not examine the ecological relation-

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ships critically, but merely pointed out, in a general way, the desirability of eliminating favored species from the stand.

The Petersham outbreak in 1935 provided an exceptional opportunity for studying the relation of gypsy moth defoliation to forest cover types and tree species. This town lies outside the heavily infested zone of eastern New England, so that extensive defoliation occurs only at intervals, and then locally. The Harvard Forest, lying within the town, furnished a wealth of case-history material in which stocking, composition, and other pertinent data were known in considerable detail. Studies here by Baker and Cline (1935), and Behre, Cline and Baker (1936) emphasized the possibilities of silvicultural control. In the latter paper, the existing information on food preferences was summarized, and recommendations were made for the treatment of various forest types in New England to decrease the hazard of gypsy moth defoliation. In outlining these recommendations, the authors made plain the close relationship between such forest practices and those which would be required for ordinary forest stand improvement.

More recently Behre (1939) restated this position with particular reference to Massachusetts woodlands, pointing out at the same time that exploitation and fire have generally created conditions extremely favorable to the moth; and that silvicultural control by the reduction of favored food plants is largely consistent with natural ecological trends. Behre and Reineke (1943) gave specific recommendations for treating the forest stands of southwestern Maine, assigning priorities to the various cover types. Priority A (value at stake largest in relation to cost of treatment) was assigned to types containing relatively small amounts of favored food species, while conversion by planting was recommended for stands of little economic value, composed predominantly of favored foods.

*Limits of Application*

It will be seen from the above review that a majority of the silvicultural investigations dealing with gypsy moth behavior have been concerned primarily with the host selectivity which is exhibited so prominently by this insect. Obviously gypsy moths prefer oak; the most serious outbreaks occur in oak types; cut out the oaks, then, or replace them with pine or maple, and the gypsy moths will disappear. This, in essence, is the reasoning on which the theory of silvicultural control is based. In the relative abundance of favored food species, it states, "lies the key to the silvicultural control" of the insect. While this is undoubtedly true to a degree, its importance can easily be overemphasized. The analysis presented in Part II has revealed that (1) a high proportion

of favored food species in a stand or forest type does not necessarily indicate susceptibility; (2) all favored food species are not defoliated equally under all conditions; and (3) nonfavored species may be defoliated where environmental conditions are particularly well suited for maintaining a high larval population.

Data collected during the 1944 outbreak at Petersham are summarized in Table 11. No red oak was found seriously defoliated when growing

TABLE 11

## AVERAGE COMPOSITION OF THE OVERSTORY IN RESISTANT AND SUSCEPTIBLE OAK STANDS IN PETERSHAM, 1944

|  | Resistant | Susceptible |
|---|---|---|
| Number of stands examined | 16 | 10 |
| Average percent defoliation | 5 | 90 |
| *Species* | *Percent* | *Percent* |
| Red oak | 71 | 42 |
| White oak | 4 | 26 |
| Black oak | 3 | 20 |
| Red maple | 8 | 4 |
| Paper birch | 6 | 2 |
| Hemlock | 2 | 1 |
| White ash | 2 | 0 |
| Gray birch | 0 | 2 |
| Others | 4[1] | 3 [2] |

[1] Other overstory trees in resistant stands included black birch, white pine, yellow birch, sugar maple, and beech
[2] Other overstory trees in susceptible stands included hickory and scarlet oak.

in a closed forest stand in which the more xerophytic oak species were absent. Of the stands examined, sixteen were resistant with an average defoliation of 5 percent, and ten were susceptible with an average defoliation of 90 percent. Additional records were obtained in the 1935-1937 outbreak (Table 12). These records, which have been continued by the U. S. Bureau of Entomology and Plant Quarantine in cooperation with the Harvard Forest show also that many stands of favored food species in Petersham have never been severely defoliated at any time, even though complete stripping has taken place on an aggregate of 2,000 acres in various parts of the town.

Throughout the heavily infested zone, badly abused sites, lacking in leaf litter and characterized by stands of gray birch or aspen, are invariably the most severely attacked. Outside the oak region, a large majority

TABLE 12

## NUMBER OF CASES OF DEFOLIATION BY FOREST COVER TYPE IN PETERSHAM, 1935–1937

|  | 1935 | 1936 | 1937 | Total |
|---|---|---|---|---|
| Gray birch–aspen | 64 | 9 | 12 | 85 |
| White oak–black oak–red oak | 9 | 1 | 5 | 15 |
| Red oak–red maple–white ash | 1 | 0 | 0 | 1 |
| Others | 2 | 2 | 0 | 4 |
| Total | 76 | 12 | 17 | 105 |

of the stands regularly defoliated are composed principally of these two species, which, in the scale of food preference, rate no higher than many other species abundant in the same neighborhood. In the New York barrier zone region also, initial outbreaks in a given locality are almost always found in stands of this character.

Regarding the whole theory of favored food species and proposals for the application of silvicultural practices in accordance with it, one fact seems to stand out: many of the tree species which are favored by the gypsy moth *happen* to occur on the poorer, run-down sites in New England; and it is this purely accidental association, we believe, that has long obscured the more fundamental relationship between gypsy moth population and environmental factors.

### RECOMMENDED PRACTICES

*Heavily Infested Area*

Increasing stand resistance to gypsy moth attack can be accomplished by (1) preventing further land abuse; (2) developing and maintaining healthy biological conditions in the forest floor; and (3) reducing the proportion of favored-food species where their presence is a major factor in promoting gypsy moth abundance.

Forest land abuse is responsible, more than anything else, for holding the gypsy moth at an epidemic level. If this can be prevented or materially curtailed, natural successional trends will eventually develop conditions less favorable to the insect. On the other hand, if uncontrolled fires, woodland grazing, and repeated clearcutting are not checked, no gypsy moth control practices will be undertaken with any permanent success. Thus, in the heavily infested zone of eastern New England, intensified fire protection and restriction of grazing could well be justified on the grounds of gypsy moth control alone.

Any forest practices which lead to the development of open stands of favored food species with a dry and compact forest floor must be avoided if the gypsy moth population is to be permanently reduced. Clearcutting is the most obvious practice of this type, but other practices less flagrantly undesirable are nevertheless favorable to the moth. For instance, very heavy thinnings and other heavy cuttings open up the stand excessively, and create conditions in the forest floor differing only in degree from clearcutting. In fact, some types of treatment aimed at reducing the proportion of favored food species might actually be harmful, if they result in opening up the stand while leaving an appreciable amount of gypsy moth food. Excessive cleaning-up operations should be avoided, whether in connection with gypsy moth control or forest stand improvement, if they tend to eliminate the understory, ground cover, and dead material on the ground. If left undisturbed, this material provides habitats attractive to the larvae, and accessible to predators. If it is removed, however, the larvae generally stay up in the trees where they are relatively safe.

The above recommended procedures, though essential to a successful control program, are purely negative in character, and do not require positive action by the silviculturist. There are, however, some clearly defined and recognizable conditions where cutting practices may be applied specifically for the purpose of gypsy moth control.

In general, the proportion of favored food foliage in stands within the heavily infested zone should be reduced whenever consistent with good silviculture. White pine and other resistant species should be favored by practices which can be carried out at a moderate cost without opening up the stand unduly or decreasing markedly the value of the forest. Specific examples of such practices follow:

(1) **Even-aged white pine-gray birch mixture:** The presence of gray birch is a potential hazard anywhere within the infested area. Where there is an adequate stocking of white pine in the mixture, the removal of the gray birch is the best insurance against gypsy moth defoliation.

(2) **Young, even-aged white pine-oak mixtures on dry sites:** Weeding or cleaning operations to favor the growth of the white pine will do much toward increasing the proportion of pine; and resistant hardwoods in the stand can be similarly favored. This operation can generally be undertaken at a moderate cost only on relatively dry sites, such as sandy plains or rocky ridges. On better sites, an excessive amount of weeding is usually needed to enable the pine to compete successfully with the hardwood sprouts.

(3) **White pine under mature oak:** Stands of this type are confined largely to dry sites, as white pine is seldom found in the understory under

mesophytic conditions. Consequently, this type is ordinarily susceptible to heavy defoliation by the gypsy moth. The removal of the oak is desirable because (a) the oak is merchantable; (b) sprouting from the old oak stumps will be relatively weak; (c) the young pine will tend to suppress the oak sprouts and produce a cover within a relatively short time. Here, as in the case of the white pine-gray birch mixture, the oak overstory is a major hazard, and by its removal the pine has a good chance of developing without being subject to serious defoliation.

(4) **Artificial conversion:** Conversion of susceptible stands to resistant stands by clearcutting and planting is rarely, if ever, justified from the standpoint of the value of forest products produced. The high cost involved, the risk of such an undertaking, and the great amount of work necessary to produce the desired results, have brought such strong-arm methods into disrepute (Spurr and Cline, 1942; Hawley and Lutz, 1944). Conversion by artificial reforestation and repeated weedings can be recommended only for public parks, picnic grounds, roadside strips, and other restricted forest areas where intensive public use justifies the high cost involved. Such operations might well materially reduce the cost of direct control of the gypsy moth over a period of years.

*Western Fringe*

The heavily infested zone of eastern New England is bordered on the north by a lightly infested area covered largely by resistant forest types, the spruce-northern hardwood types of northern New England. On the west of the heavy infestation lies an area made up of both resistant and potentially susceptible stands. This area includes that portion of New England west of the Connecticut River, eastern New York state, and the anthracite region of northeastern Pennsylvania.

The same silvicultural principles are valid in this western fringe as in the heavily infested zone. Their application, however, would naturally be more restricted, and confined to those localities in which danger of an increase in the population of the gypsy moth is most acute.

In the Hudson-Champlain Valley, first of all, an intensified program of fire control and woodland management would materially reduce the likelihood and extent of future defoliation by the gypsy moth. In this same region, and in adjoining counties to the west where the gypsy moth has become established, numerous and extensive stands of gray birch and aspen constitute a real hazard. Though the wholesale elimination of these species is obviously an impossibility, a reduction of the area covered by them would certainly add to the effectiveness of any direct control measures. Gray birch stands, in particular, are extremely hazardous areas where new infestations are liable to start and build up a high

population. Encouragement of white pine reproduction in both gray birch and lowland aspen types, either by planting or release cuttings, would help to convert such stands to more resistant types.

With the oak stands in this region, the situation is quite different. The acreage covered by the oak forest cannot be materially reduced, as oak is one of the relatively permanent forest types, is of considerable commercial importance, and ordinarily cannot be converted into types composed of unfavored food species by controlling cutting practices. Fortunately, however, there is little need of considering such stringent measures. In the light of unpublished work by Bess, it seems evident that the susceptibility of these vast oak forests to the gypsy moth can be appreciably reduced if forest fires, woodlot grazing, and overcutting are controlled, and if the forests are kept adequately stocked, in good vigor, and with a well-developed forest floor.

# SUMMARY AND CONCLUSIONS

For two decades or more the gypsy moth has caused widespread defoliation every year in eastern New England, especially in southeastern Massachusetts. On the other hand, it has seldom caused defoliation, even on a small scale, over most of the remainder of the infested area in New England, eastern New York, and northeastern Pennsylvania. Studies were initiated in 1937 to determine the reasons for these facts and to aid in the development of feasible methods for combatting this pest in America. The fluctuations in the abundance of the moth were studied within specific woodland areas in different seasons. These investigations revealed that gypsy moth abundance was closely associated with forest and site conditions.

In seasons favorable to the moth, it has increased in abundance over practically the whole of the infested region, both in the lightly and heavily infested woodlands, as it did in 1944. Since the population recedes to a very low level in the oak woodlands in central and southern New England, three or more favorable seasons in succession are required to build up defoliation populations over extensive areas. However, in eastern New England, especially on Cape Cod, the minimum populations are usually relatively high, and certain woodlands are probably defoliated five years or more out of every ten.

The large larvae feed mostly at night. During the day most of them retire to cool, moist, secluded places to rest, provided suitable places are available. In well stocked, mesophytic woodlands with a well developed forest floor and an abundance of loose litter, many of the larvae normally spend the daytime in the litter. Under more xeric conditions, however, the large larvae spend the day in trees well above the forest floor.

Investigations in different types of woodland revealed that large larvae survived in much greater numbers where they molted and rested above the forest floor, rather than in the litter on the ground. To check on these differences in larval behavior and survival observed in natural populations, thousands of large larvae were collected, liberated, and their survival observed. These liberations demonstrated that the mortality rate was much higher among larvae that were allowed to reach the ground than where larvae were confined to cages, protected from small mammals by a hardware cloth fence, or induced to remain in the trees by means of burlap bands applied to the trunks. When the larvae descended into the litter, they were subjected to depredations by their natural enemies, and

the number destroyed was much greater than when the larvae remained above the forest floor. Apparently small mammals and predaceous arthropods play an important role in the destruction of larvae in the litter.

Pupae exposed in the litter of relatively dense mesophytic forests were destroyed in large numbers, while few of those exposed in comparatively open dry stands were destroyed. Both small mammals and predaceous arthropods destroyed pupae; but the relative importance of the different predators was not determined.

Forest areas may be recognized as susceptible or resistant to gypsy moth attack by specific features of site and vegetative cover. The driest sites, sand plains and rocky ridges, are the most likely to support open forest stands and pioneer vegetative associations, especially where the site in question has been subjected to repeated forest fires and other forms of land abuse. Such areas are potential centers of gypsy moth distribution.

Certain of the forest types of the eastern United States are inherently susceptible, others inherently resistant, while a third group varies according to the particular combination of local factors. Some resistant types normally contain a high proportion of favored food species under site conditions which reduce the possibility of defoliation.

Resistant stands occur more commonly on soils having an adequate supply of moisture and organic matter, and are characterized by full stocking and relatively vigorous growth. They are also found, however, on the poorer sites where there has been a minimum of disturbance. On both rich and poor sites, the predominant characteristic of the resistant stand is a deep accumulation of litter, in which rodent tunnels are easily found.

Certain plant indicators are useful in recognizing susceptible and resistant stands. In particular, the predominance of lowbush blueberry on a given site is a positive index of susceptibility.

Climax and subclimax associations ordinarily furnish resistant types. Where occurring over large areas together with climatic or physiographic features which are unfavorable to the gypsy moth, they act as natural barriers to its further distribution.

Forest succession may be affected favorably by light gypsy moth infestations, but recurrent heavy defoliations tend to perpetuate the pioneer associations, thus further increasing susceptibility.

Those who have studied the problem of silvicultural control have concluded that forests under good management tend to become increasingly resistant to gypsy moth attack. Opinions differ, however, as to what specific silvicultural methods should be employed. It is apparent from the studies and observations recorded here that attempts to alter

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| Locality | 1925 | 1926 | 1927 | 1928 | 1929 [2] | 1930 [2] | 1931 [2] | 1932 | 1 |
|---|---|---|---|---|---|---|---|---|---|
| Brewster (Cape Cod) | 2,770 | 10,520 | 2,315 | 765 | 116 | 350 | 1,500 | 5,000 | 5, |
| Freetown (southeastern Mass.) | 0 | 50 | 2,000 | 0 | 0 | 0 | 2,000 | 7,100 | |
| Alfred (southwestern Maine) | 0 | 0 | 0 | 0 | 250 | 135 | 0 | 52 | |
| North Reading (eastern Mass.) | 0 | 0 | 110 | 300 | 8 | 0 | 0 | 0 | |
| Hillsborough (southern N. H.) | 0 | 0 | 0 | 40 | 1,000 | 15 | 2 | 0 | |
| Wendell (central Mass.) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| Northampton (central Mass.) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| Petersham (central Mass.) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| Spencer (central Mass.) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| Granby (northern Conn.) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| Eastford (eastern Conn.) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| Burrillville (northwestern R. I.) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |

[1] This information was supplied by the Bureau of Entomology and Plant Quarantine.
[2] Fifty to 100 percent defoliated.

| 1934 | 1935 | 1936 | 1937 | 1938 | 1939 | 1940 | 1941 | 1942 | 1943 | 1944 | 1945 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 4,000 | 4,500 | 500 | 375 | 1,150 | 3,000 | 900 | 700 | 150 | 500 | 2,000 | 0 |
| 135 | 116 | 6,877 | 8,325 | 20 | 265 | 1,900 | 2,600 | 800 | 1,100 | 3,100 | 3,400 |
| 83 | 303 | 0 | 0 | 2 | 344 | 670 | 0 | 0 | 0 | 30 | 415 |
| 0 | 0 | 0 | 160 | 30 | 25 | 195 | 103 | 0 | 0 | 0 | 293 |
| 125 | 500 | 0 | 0 | 0 | 300 | 100 | 0 | 0 | 0 | 0 | 148 |
| 30 | 883 | 10 | 1,625 | 340 | 735 | 25 | 200 | 0 | 0 | 1,250 | 3,000 |
| 0 | 0 | 0 | 625 | 1,050 | 260 | 0 | 75 | 0 | 0 | 0 | 4,400 |
| 55 | 810 | 15 | 45 | 0 | 0 | 0 | 0 | 0 | 0 | 1,930 | 3,480 |
| 35 | 115 | 0 | 85 | 40 | 0 | 0 | 0 | 0 | 0 | 1,070 | 4,335 |
| 0 | 0 | 0 | 0 | 1,043 | 2,462 | 0 | 0 | 0 | 0 | 0.5 | 2.3 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

# APPENDICES

# APPENDIX B

## NUMBER OF LIVING LARVAE AND PUPAE FOUND AT DIFFERENT LOCATIONS ON TEN BANDED AND TEN UNBANDED TREES AND IN THE LITTER, ALBANY COUNTY, NEW YORK, 1944

| *BANDED TREES*<br>Location | June 5-6 | June 13 | June 20 | June 27 | July 3-5 | July 18 |
|---|---|---|---|---|---|---|
| Above 7 ft. (trunk and foliage) | 30 | 3 | 9 | 5 | 0 | 0 |
| Under burlap bands, 5 ft. | 1 [1] | 393 | 262 | 359 | 271 | 190 |
| One to 7 ft. (not under bands) | 232 | 25 | 30 | 5 | 1 | 0 |
| Ground to 1 ft. | 19 | 0 | 0 | 1 | 0 | 0 |
| Litter | 31 | 38 | 27 | 21 | 16 | 9 |
| Totals | 312 | 459 | 328 | 391 | 288 [2] | 199 [3] |
| *UNBANDED TREES* | | | | | | |
| Above 7 ft. (trunk and foliage) | 12 | 9 | 6 | 1 | 1 | 0 |
| One to 7 ft. | 94 | 44 | 30 | 23 | 4 | 2 |
| Ground to 1 ft. | 35 | 9 | 7 | 9 | 3 | 2 |
| Litter | 181 | 93 | 117 | 96 | 71 | 5 |
| Totals | 322 | 155 | 160 | 129· | 79 | 9 [4] |

[1] Bands applied on June 5 and 6.
[2] Two hundred eighty-five larvae, 3 pupae
[3] Thirty-four larvae, 165 pupae
[4] Seven larvae, 2 pupae

| Locality | Site Conditions[1] | Trees Banded with Burlap | | | Trees Not Banded | | |
|---|---|---|---|---|---|---|---|
| | | Plot No. | Larvae Liberated | Egg Masses Deposited | Plot No. | Larvae Liberated | Egg Masses Deposited |
| **Massachusetts** | | | | | | | |
| Petersham | Well-stocked oak stand | 5 | 1,000 | 432 | 6 | 1,000 | 183 |
| | | 7 | 1,000 | 429 | 2 | 1,000 | 214 |
| **Connecticut** | | | | | | | |
| Simsbury | Well-stocked oak stand | 5 | 1,000 | 180 | 7 | 1,000 | 96 |
| | | 9 | 1,000[2] | 172 | 8 | 1,000 | 172 |
| **Northern New York** | | | | | | | |
| Perth | Well-stocked oak stands | 1 | | 10 | 2 | — | 13 |
| Corinth | | 1 | | 35 | 2 | — | 50 |
| Greenfield | | 1 | | 92 | 2 | — | 14 |
| Mayfield | | 1 | | 31 | 2 | — | 9 |
| **Eastern New York** | | | | | | | |
| Canaan | Well-stocked oak stand | 1 | 300 | 71 | 2 | 300 | 16 |
| Coeymans | Chestnut oak stand | 1 | 1,219[3] | 273 | 2 | 900[3] | 119 |
| New Scotland | " " | 1 | 1,041[3] | 292 | 2 | 691[3] | 104 |
| **Pennsylvania** | | | | | | | |
| Pittston | Well-stocked oak stand | 1 | 200 | 103 | 2 | 200 | 7 |
| | | 3 | 200 | 66 | 4 | 200 | 17 |
| | | 13 | 200 | 90 | 14 | 200 | 16 |
| | | 15 | 200 | 79 | 16 | 200 | 4 |
| | Poplar stand | 9 | 200 | 76 | 10 | 200 | 21 |
| | | 12 | 200 | 61 | 11 | 200 | 6 |
| Jenkins | Well-stocked oak stand | 9 | 200 | 17 | 10 | 200 | 6 |
| | | 11 | 200 | 16 | 12 | 200 | 4 |
| | Under-stocked oak stand | 6 | 200 | 65 | 5 | 200 | 8 |
| | (Litter destroyed by spring fire) | 8 | 200 | 73 | 7 | 200 | 15 |
| | Isolated oak tree | 1 | 200 | 56 | 2 | 200 | 0 |
| | (Litter destroyed by spring fire) | 3 | 200 | 7 | 4 | 200 | 0 |

[1] Very dry season in New England and northern New York points; near normal rainfall in Pennsylvania and eastern New York points.

[2] Larvae were present in all plots but the population was light.

[3] Number of larvae (natural infestation) found on June 5-6 in the $\frac{1}{10}$ acre plots. A crew of men spent a half day in each plot, but there were without doubt a few larvae present that they failed to find.

# APPENDIX D

## NUMBER OF EGG MASSES DEPOSITED IN PLOTS IN WHICH DIFFERENT NUMBERS OF LARGE LARVAE WERE LIBERATED, 1944

| Locality | General Site Conditions | Plot No | Larvae Liberated | Egg Masses Deposited | Egg Masses per 100 Larvae |
|---|---|---|---|---|---|
| Pittston, Pa. | Good oak woodland but on drier site than the ones at the points below in New England; rainfall near normal | 2 | 200 | 7 | 3.5 |
| | | 4 | 200 | 17 | 8.5 |
| | | 5 | 400 | 24 | 6.0 |
| | | 6 | 400 | 40 | 10.0 |
| | | 7 | 800 | 39 | 4.9 |
| | | 8 | 800 | 56 | 7.0 |
| Gill, Mass. | Gray birch-white pine stand in Conn. River Valley; sandy soil; unusually dry season | 1 | 250 | 100 | 40.0 |
| | | 2 | 500 | 176 | 25.2 |
| | | 3 | 1,000 | 399 | 39.9 |
| Petersham, Mass. | Good oak woodland; unusually dry season | 1 | 500 | 129 | 25.8 |
| | | 2 | 1,000 | 214 | 21.4 |
| | | 3 | 2,000 | 381 | 19.0 |
| | | 4 | 4,000 | 1,071 | 26.8 |
| Simsbury, Conn. | Good oak woodland; unusually dry season | 1 | 500 | 7 | 1.4 |
| | | 2 | 1,000 | 80 | 8.0 |
| | | 3 | 2,000 | 153 | 7.6 |
| | | 4 | 4,000 | 674 | 16.8 |
| Eastford, Conn. | Good oak [2] woodland; unusually dry season | 1 | 500 | 13 | 2.6 |
| | | 5 | 500 | 2 | 0.4 |
| | | 2 | 1,000 | 163 | 16.3 |
| | | 3 | 2,000 | 142 | 7.1 |
| | | 4 | 4,000 | 208 | 5.2 |

[1] The larvae liberated in Petershaw, Simsbury, Eastford, and Gill were collected in Petersham. Four lots of 250 each were held in wire cages and 382 egg masses were deposited, or 38.2 egg masses per 100 caged larvae.

[2] Unfortunately there was noticeable variation in the site conditions within the individual plots in Eastford, even though they were within the same woodland. Plots 1 and 2 were considerably drier than the others and were composed largely of white oaks. Plots 4 and 5 were on relatively moist sites, plot 5 having considerable surface water in it when the egg mass counts were made in the fall. There was a preponderance of red oak in plots 3, 4, and 5.