STUDIES ON EUROPEAN PINE SHOOT MOTH BIOLOGY AND INTERMACTIONS BETWEEN THE INSECT ITS ENVIRONMENT AND MICHIGAN HOST SPECIES

> Thesis for the Degree of Ph. D. MICHIGAN STATE UNIVERSITY Dean L. Haynes 1960

This is to certify that the

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STUDIES ON EUROPEAN PINE SHOOT MOTH BIOLOGY AND INTERREACTIONS BETWEEN THE INSECT, ITS ENVIRONMENT AND MICHIGAN HOST SPECIES

presented by

Dean L. Haynes

has been accepted towards fulfillment of the requirements for

____Ph.D.__degree in __Entomology

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ABSTRACT

STUDIES ON EUROPEAN PINE SHOOT MOTH BIOLOGY AND INTERACTIONS BETWEEN THE INSECT, ITS ENVIRONMENT AND MICHIGAN HOST SPECIES

by Dean L. Haynes

This study investigates some of the basic relationships between the European pine shoot moth (<u>Rhyacionia buoliana</u> (Schiff.)) and its environment. Host influence is evaluated in terms of insect oviposition, larval mortality, insect size, rate of development and sex ratio. The course of a shoot moth infestation was followed and the effects of injury to red pine growing under different conditions of soil moisture and fertility were evaluated.

Various body measurements of the larvae were compared in order to determine which best expressed changes in dry weight or larval growth.

Winter mortality was studied in several southern and northern plantations of Lower Michigan. No differences were observed in winter mortality under these conditions.

A pattern of spring larval activity related to spring temperatures was shown to exist. Spring activity was initiated first on the lower south side of the tree and progressed around to the north side and up the tree, while summer activity was begun first in the top of the tree and continued longer in the lower branches.

High larval mortality during the early part of the egg hatch rapidly declined to a lower level and remained uniformly low during the summer. Summer larvae rapidly increased in dry weight after egg hatch and reached a peak about August 1st. Their dry weight then declined until the following spring when it was about half of the maximum summer weight.

After July 15th, the proportion of individual larvae with undigested food residue in their guts declined. By August 15th only relatively small traces of food were found in a few larvae. Larvae brought indoors after September 15 took 6 to 24 days to resume feeding.

More eggs were deposited on red pine per unit of shoot length than on Scotch pine, and this coupled with higher egg parasitization on Scotch pine, resulted in a higher summer larval population on red pine. Scotch pine had a greater volume of bud tissue and more lateral buds than red pine. This minimized the economic impact of feeding on Scotch. There was no significant difference between the numbers of adults emerging from the two pine species.

Pupation proceeded at a significantly faster rate on red pine than on either jack or white pine; while adult emergence occurred earlier on Scotch than on red pine. In 1959, both male and female pupae collected from red pine were significantly smaller in dry weight than were those collected from Scotch, Austrian and Ponderosa pine. The largest pupae came from Scotch pine. No difference in sex ratios could be attributed to host or place of collection.

Maximum spring growth rate of the larvae corresponded closely with the maximum elongation rate of red pine shoots. Spring growth is resumed about a week to ten days sooner in red pine than in the insect.

The influence of different soil moisture and fertility conditions on resulting insect injury was studied. The study trees were growing on a the more ence nifi was the bran ment bott

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on a slope adjacent to a swamp. A site evaluation demonstrated that the trees positioned at the bottom of the slope were growing under more favorable conditions than those at the top. A significant difference in injury from year to year was observed in all trees, and a significant interaction between year of attack and position on the slope was also detected.

The tendency to produce "forks" appeared greater at the bottom of the slope, while "bushing" was more frequent at the top. Irregular branching was the most common type of injury while "post horn" development was the least common. Terminal tree growth was greater at the bottom of the slope every year. • ST B

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By

Dean L. Haynes

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INTRODUCTION

The European pine shoot moth, <u>Rhyacionia buoliana</u> (Schiff.) was first described by Schiffermüller in 1776 as <u>Tortrix buoliana</u>, (Busck 1915). The species is also synonymous with <u>Rhyacionia buoliana</u> Hübner, <u>Retinia buoliana</u> Guenée and <u>Evetria buoliana</u> Meyrich, (Heinrich 1923). <u>Evetria buoliana</u> is still commonly used in the European and English literature.

The European pine shoot moth was first detected in the United States in 1914 on Long Island, New York. It had apparently been introduced repeatedly on infested nursery stock (Busck 1914). The first infestation in Michigan was reported by McDaniel (1930) from the southeastern part of the state. It has subsequently been found in all Michigan counties.

Many entomologists have studied the European pine shoot moth since its introduction into North America. A detailed account of its life cycle and biology was published by Friend and West in 1933. One of the more recent publications by Miller and Neiswander (1955) reports on investigations carried out in Ohio. Recently, an interest in more effective and practical methods of controlling the insect has led to a series of papers dealing with this problem (Haynes et al. 1958, Butcher and Haynes 1958, Butcher and Haynes 1959, Miller and Haynes 1958, Miller and Haynes 1958, Donley 1960, and Butcher and Haynes 1960). Most of these papers have demonstrated a need for closely correlating the time and method of spray application with insect development. B t b 0 i i v ŝ t P 1 S e S Butcher and Haynes (1960) discussed the influence of insect biology on the effectiveness of insecticidal control of European pine shoot moth.

Miller and Heikkenen (1959) reported on the relative susceptibility of eight pine species to attack by European pine shoot moth. Other than this paper little has been published on the relation of the insect to its environment.

Figure 1 illustrates the life history of European pine shoot moth in Michigan, based on observations made during the course of these investigations. It shows the initiation, progress, and termination of some observable life history and behavioral phenomena. For any particular date, it is possible to ascertain the magnitude of any phenomenon with respect to any other. Reading from top to bottom, the life history phenomena recorded are (a) live larvae in 100 infested shoots; $\frac{1}{-}$ (b) number of pupae in 100 infested shoots; (c) number of empty pupal cases in 100 infested shoots (reliable measure of progressive adult emergence); and (d) number of unhatched eggs on 100 shoots.

Records on larvae, pupae, and pupal cases were obtained from shoot dissections while unhatched egg counts were derived from microscopic inspection of new shoots dissected and examined in the laboratory. Dissections under magnification in the laboratory were used to detect the presence of larvae in the needles and buds. All observations were made at 3- or 4-day intervals, and the pictograph

^{1/}Shoots with pitch blisters were considered infested. Early counts necessarily were made of old blisters ("tents") containing overwintered dormant larvae, 90 percent of which were dead. When spring feeding resumed, the fresh blisters were easier to find and contained more live larvae than those made the previous year. The apparent increase in population shown by sampling from April 17 through May 3 is caused by the manner in which infested shoots were selected.



configurations represent a line drawn through points (counts) made 3 or 4 days apart, with one-half of the total above and one-half below a horizontal base line. As can be seen in Figure 1, the adult moths begin to emerge in the early part of June and oviposition begins within a few days. The eggs are laid on the bark and needles, singly or in small groups. Each mass seldom contains more than 5 eggs. Eggs may be laid on any part of the tree but the smooth part of new growth appears to be preferred. Hatching usually occurs about 2 weeks after oviposition. Newly hatched larvae feed at the base of the current year's needles, and later, their summer feeding activity is confined to the terminal and lateral buds. The larvae burrow into buds and remain there until the following spring. The appearance of brown needles and a hardened resin exudate on the buds is the only external evidence of the insect's presence. Overwintering larvae resume activity again about April 20 in Michigan. They feed heavily and grow rapidly. It is at this time that injury is most severe and bud and shoots are killed and deformed. Many shoots are weakened and break off later in the season. Pupation takes place within the buds sometime in late May to early June. In approximately 16 days the adults start to emerge and the cycle is completed.

The purpose of this paper is threefold: (1) to investigate some of the more basic relationships between the insect and its environment and to evaluate some of the behavioral responses of the insect which might be attributed to measurable changes in the environment; (2) to evaluate the influence of different hosts in terms of oviposition preference, larval mortality, insect size, rate of development and sex ratio; and (3) to follow the course of a shoot moth outbreak and

measure the effects of feeding on red pine growing under different conditions of moisture and fertility.

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BIONOMICS OF EUROPEAN PINE SHOOT MOTH IN MICHIGAN

Measuring Insect Growth

When considering the growth of individuals within an insect population, the problem arises as to what measurements will best express growth rate through time or permit comparisons from place to place. Conventional measurements used in this study included head capsule width, body length, and dry weight. As animals grow, they must assimilate nutrients from their environment and transform or fix it in their own body. This could be expected to bring about a change in the dry weight of the organism. Some of the material contributing to the overall dry weight will be temporary or transitional, such as undigested food material; but this, in many cases, should be a fairly constant value for any particular dry weight.

In this study, dry weight was used to portray growth rate. However, to demonstrate the relationship between the various body measurements and to determine which alternative measurement might most closely predict dry weight, the correlation betweeen dry weight and other body measurements was studied. Larvae were collected on 28 different dates throughout the season, and pupae on 9 different dates. All collections were made from red pine, (Pinus resinosa Ait). The insects were killed in Peterson's KAAD solution and preserved in 95 percent alcohol (Peterson 1948). Each collection contained from 6 to over 150 insects. From each of these collectins, 10 insects were selected at random, except in three cases where less than 10 insects were available. The

three body measurements made on each individual were (1) head capsule width, (2) body length, and (3) dry weight. The limits of accuracy of each measurement were: (a) head capsule to the nearest .03 millimeter; (b) body length to the nearest .2 millimeter; and (c) dry weight to the nearest .02 milligram. At the time these measurements were made, it was felt that since both head capsule width and body length are linear measurements, a volumetric measurement might more closely correlate with an increase in dry weight. A simple volumetric estimate was arrived at by combining the two linear measurements. The estimate consisted of taking the square of one-half the head capsule width and multiplying this by the body length. Then, if the body index were multiplied by the constant 3.1416, an estimate of the insect's total volume would be obtained, expressed as cubic millimeters. The procedure, in effect, entails computing the volume of a cylinder, with the diameter equal to the head capsule width and the length equal to the body length. Since 3.1416 is a constant for all observations, it was not necessary to complete the multiplication for statistical analysis.

Figure 2 shows mean values of four parameters throughout the year; dry weight, head capsule width, body length, and the computed body index. It is apparent from figure 2 that head capsule width closely approximates similar increases in dry weight during time of maximum growth but is completely insensitive to negative growth or losses in dry weight. It also appears that the body index is most sensitive in expressing changes in dry weight. To put the interpretation of figure 2 on a statistical basis, a multiple correlation was made of the two linear body measurements and dry weight. A separate correlation analysis was made on the body index and dry weight. It was thought advisable



not to include the body index in the multiple correlation analysis. since it was a function of the two measured variables and might confuse interpretation of the analysis. The multiple correlation coefficient, $Ry.x_1x_2$ equaled .870, where y = dry weight, $x_1 = head$ capsule width, and $x_2 = body length$. It can be stated that (.870)² or .7573 percent of the variation in dry weight could be eliminated if x_1 and x_2 were held constant. However, by taking both x_1 and x_2 and computing a body index x_3 , and obtaining a zero order correlation between body index and dry weight, a correlation of .923 is obtained. This correlation, r_{yx_3} can account for 85 percent of the variation in dry weight by holding the body index constant. Obviously, there is considerable advantage in converting head capsule and body length measurements to this index. It can account for 10 percent more variation in dry weight than does the multiple correlation coefficient. In considering the multiple correlation coefficient, $Ry.x_1x_2$ it is of considerable interest to compare it to the zero order correlation coefficients; r_{yx_1} , which equals .775 and r_{yx_2} , which equals .870. As stated before, $Ry.x_1x_2$ accounts for .7573 percent of the variation in dry weight but the zero order correlation of r_{yx_2} accounts for .7569. By making all of the measurements on head capsule width and computing the multiple correlation coefficient, only an additional .0004 percent of the variance in dry weight is accounted for. It can be considered from this that practically all of the variance in dry weight which can be accounted for in head capsule width is also accounted for in body length. Practically nothing has been gained in making head capsule measurements unless the body index is computed.

By establishing the 95 percent confidence limits for the prediction of mean dry weight from either head capsule width, body length, or body index, it was possible to estimate the sample size needed to predict the mean dry weight within 0.1 milligrams. This estimated sample size indicates in a different way the relative predictive value of the various measurements. It would take an estimated sample size of 119 head capsule widths to estimate within .1 milligram, with 95 percent confidence, the mean dry weight of insects of average head capsule width. To make this same estimate of dry weight would require 72 body lengths or 44 body index values of insects of average body length or of average body index. This approach does show the relative value of the various predictions, however in another respect is quite unrealistic. To predict a mean dry weight to within 0.1 milligrams is undoubtedly more accurate than would be expected from dry weight measurements themselves.

Nine pupal collections were made between May 27 and June 24. Since European pine shoot moth pupae have a sharply tapered abdomen which cannot be estimated readily with a volumetric body index, it was thought that some other measurement would be more satisfactory for them. However, the body index computed for the 82 unsexed pupae had a correlation coefficient of .803 with dry weight, while head capsule widths had a correlation of .749 with dry weight and body length .714 with dry weight. Nothing was gained by using the body index over the multiple correlation of head capsule width, body length, and dry weight. The multiple correlation coefficient accounted for .650 percent of the variance in dry weight while the body index accounted for .645 percent.

Winter Mortality

The northern distribution limits of the European pine shoot moth has been a subject of much speculation since its introduction in 1914. Rudolf (1949) published a paper in which he divided Michigan into five temperature zones of shoot moth tolerance. He examined weather records for the preceding 20 years, and using the number of times in a 10-year period that -18 degrees F. was reached, he established the zone boundaries. Zone 1 was thought to be most favorable for the insect. It included two narrow strips of land along both lakes, south of a Muskegon-Bay City line. The degree of injury expected was then graduated through Zones 2, 3, 4, and 5. Zone 5 was considered to be an area where a population of European pine shoot moth could not develop. Since this paper appeared, extremely heavy outbreaks have occurred in all of the zones.

When an outbreak of European pine shoot moth was first reported from Cadillac, it was thought by Batzer and Benjamin (1954) that a cold-hardy strain might exist there. They collected larvae from both Cadillac and Lansing, and exposed them to identical low temperatures in the laboratory. No mortality was recorded when the temperature was O degrees to -4 degrees F. for seven days. Exposure of -22 degrees F. for eight hours killed all the larvae, and -13 degrees F. for eight hours killed approximately half of them from both places. There was no indication that a cold-hardy strain existed at Cadillac.

West (1936) published the results of a three-year study on winter mortality of the European pine shoot moth in Connecticut. He reported that in the winter of 1933-34, extremely low temperatures were recorded, with a minimum of -15 degrees F. In over half the plantations he

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examined, there had been 100 percent mortality and in the rest, mortality was very high; in most cases above 95 percent. West made a survey of the Connecticut weather records 20 years prior to the winter of 1933-34. He observed that the winter of 1933-34 had a deficiency of 300 day-degrees below the average, and three other winters since the introduction of the moth had similar deficiencies. They were the winters of 1917-18, 1919-20, and 1922-23. He suggested that these years of extremely low temperatures were probably the reason for the long latent period in which little damage was done after the moth was introduced in 1914. It was not until 1926 that it began to be a serious forest pest in Connecticut.

It might easily be concluded from West's work that since a minimum low of -15 degrees F. caused 100 percent mortality in half the plantations of Connecticut, that the moth might not spread into colder regions. But it has become a major plantation pest in areas where, almost yearly, these assumed lethal temperatures are reached.

In the fall of 1936, two plantations were selected for investigation of winter mortality. One plantation was located in Ottawa County at the corner of Lakeshore Drive and Croswell Street, near West Olive, Michigan. This site was approximately 500 yards from the shore of Lake Michigan. It consisted mainly of red pine which was heavily infested, eight years old, and five to eight feet tall. The second study plantation was located near Cadillac in a five-year-old plantation about two miles northwest of Boon, in Wexford County. These trees were also red pine, heavily infested, and three to six feet tall. Thus, one plantation was located in Rudolf's Zone 1 and the other in Zone 5. Monthly samples were collected from each area from September through May. Records of the maximum and minimum temperatures in the plantations were recorded starting in December in Wexford County and in January in Ottawa County. Each sample consisted of 60 infested shoots collected three per tree from the top four whorls. These shoots were brought back to the laboratory and held at 40 degrees F. until they could be dissected. Counts of the number of buds examined, number of live larvae, number of dead larvae, and number of missing larvae were recorded.

The shoots were cut off two to three inches from the bud cluster. In the laboratory, the buds were removed from the shoot and the infested and damaged ones counted. The infested buds were cut open to determine the condition of the larvae. Live and dead larvae were recorded from direct observations. If a bud was obviously infested and no live or dead larvae could be found in or near it, a larva was considered missing. If two or more infested buds were connected with a common pitch mass and only one larva could be found, it was assumed that the larva was infesting more than one bud.

Figure 3 graphically shows the results of these samples. The percent of living larvae present in infested shoots declines from north (Boon) to south (West Olive). There is no significant difference in the shape of curves for the two areas but one is higher than the other.

To avoid the influence of missing larval values which are included in the complement of the graphed observations, the proportions of dead larvae were analyzed to determine if a difference existed between the two plantations. Missing larvae may result from factors other than mortality and disintegration. However, it undoubtedly does represent a



Proportion of European pine shoot moth larvae observed as living insects on different dates during the winter of 1956-57 at West Olive and Boon, Michigan. Minimum temperatures in degrees Fahrenheit occurring between sample dates are indicated on the graph. Figure 3.

valid category when the insects are not feeding. This question is completely avoided, however, by an analysis which deals solely with the proportion of those larvae observed which were dead. By using paired samples taken during the same month, it was demonstrated that there was more mortality in the southern plantation than in the high risk northern plantation. The mean monthly percent dead insects was 34.1 for West Olive and 21.5 for Boon. The difference was demonstrably significant at the 1 percent level. No temperatures in the range considered lethal by West (1936) were recorded in either plantation. The coldest temperature $(-10^{\circ}F)$ was recorded at West Olive in January. The winter of 1956-57 may have been unusually warm, but the high population level continued at Boon and was present for at least three years prior to this study. It had maintained itself until a commercial spray was applied in 1959. Obviously, climatic records alone are not sufficient to predict future European pine shoot moth populations. Of the larvae collected for the preceding study, samples were preserved from four different collections for further study as indicated in Table 1. The relative size of living and dead larvae was evaluated by measuring head capsule width. As indicated earlier, either dry weight or body length would express the relative size of the insects more accurately than would head capsule width. The dead insects were in varying degrees of decomposition, and neither dry weight nor body length could properly express larval size at time of death. The head capsule, on the other hand, held its shape long after the body had decomposed. The differences encountered between living and dead larval head capsule widths show an orderly relationship within each plantation, but an extremely puzzling one between plantations. In West Olive, the measurements made

Mean head capsule width of living and dead larvae collected on different dates during the winter of 1956-57 from two climatic regions in Michigan. Table 1.

		Sample) Size	Mean Head Cap	sule	Width (mm)
Date of Co	llection	Live Larvae	Dead Larvae	Live Larvae		Dead Larvae
West Olive, O	ttawa County					
Dec. 5		50	38	. 580	<u>1</u>	.574
Jan. 1	6	51	35	. 624		. 586
Apr. 1		38	45	. 628	5	. 576
May 3		64	23	1.109	15	.730
Boon, Wexford	l County					
Dec. 1	4	50	20	. 563	Ŀ	. 568
Jan. 1	3	50	16	. 579		.610
Apr. 1	5	50	38	. 572	21	. 624
May 9		50	14	1.178	5	. 752

 $^{^{1/}}$ Differences between mean head capsule width of living and dead larvae are not statistically significant.

 $[\]frac{2}{2}$ Difference between means is significant at the 1 percent level.

during December and January show that the mean head capsule width of living larvae is larger than that of dead larvae, but the difference is not statistically significant. This identical situation in an opposite direction is true at Boon. In the May collection, after larval growth was well under way, live larval head capsule width is considerably larger than for dead larvae. The May collection is as expected since spring growth had resumed and the difference displayed by the December and January collections could be completely discarded on sound statistical grounds if it were not for the April sample. The April collection was taken shortly before larvae resumed activity in the spring and, therefore, represents the total effect of winter mortality as it may influence mean head capsule width. The mean head capsule width for living larvae in Ottawa County was 9 percent larger than for the dead larvae. The exact opposite was true at Wexford County. Both of these differences were significant at the 1 percent level and in light of the observed trends of all samples in each plantation probably represents a real difference. It cannot be rejected on statistical grounds, but at present, it cannot be explained by biological observations. The answer can be found only in further study which will necessarily include accurate environmental measurements and population data.

It might be speculated that this anomaly is the result of a genetic phenomenon which is regulating overwintering larval size. One can conceive of a mechanism with a positive selection value under certain environmental conditions and a negative value under others. For example, larvae feeding in large buds at the top of the tree will have larger body measurements (including head capsule width) than will larvae feeding on the smaller buds at the base of the tree. In a severe

winter air temperatures can and do greatly reduce the larval population in the upper part of the tree while the smaller larvae which may have been insulated by snow, are less affected. In mild winters, when insects' metabolic activity may drain stored food reserves, larger larvae may have a greater survival potential. Thus, the mean head capsule width would oscillate from year to year or place to place instead of remaining constant at a specific value. At any one location or year, the influence of such a selection pressure could be observed in the relationship between mean head capsule width of living and dead larvae.

Spring Activity and Mortality

<u>Spring Activity</u>. The winter of 1958-59 appears to have markedly reduced subsequent spring shoot moth populations. Mortality in the vicinity of East Lansing was of the magnitude reported by West in Connecticut (1936). At Dansville, Michigan, 93 percent of the insects observed were dead; at Rose Lake, 97 percent. The Rose Lake larval collection was divided into subsamples from the upper and lower portion of the tree. In the upper half, 100 percent mortality was observed, and in the lower half 92 percent. The collection was not stratified at Dansville but the distribution maps of spring activity shown in Figure 5 established the occurrence of a similar situation there.

Resumption of larval feeding in the spring is indicated by the appearance of fine silken webbing that becomes impregnated with a resinous material, frass, and perhaps masticated plant tissue. Initial webbing or "tent" construction takes place in the same shoot in which the larva overwinters. This is apparently true even if all the green tissue has been destroyed the previous summer. From April 17 until April 27 all



Dansville, Michigan and effective temperature values (0) or degree-hours of tempera-The appearance of new "tents" (X) on 30 red pine trees during the spring of 1959 at ture above 46° F. Figure 4.

"tent" formation was in shoots with summer injury present (Figure 4). On April 27 evidence of the first migration was observed. This was established by the presence of a larva in a previously uninfested shoot and in the vicinity of a nearby shoot tagged as active on an earlier date. By closely observing the tagged population, and new "tents," it was possible to keep migrating larval "tents" separate from initial "tents" until May 4. After this date the presence of migrants was too great to account for all movement. Figure 4 is a frequency graph which shows the number of new "tents" appearing on 30 red pine trees at Dansville, Michigan, during the spring of 1959. A rapid increase in new "tents" commencing on April 17 and culminating on April 27, is the most striking feature of the graph. The rapid drop after April 27 is due primarily to the decrease in the number of dormant larvae. However, this decline would be much deeper if migrant "tents" are excluded from initial tents." Of the 41 "tents" appearing on May 1, 28 resulted from initial activity on the part of dormant larvae. One migrating larval "tent" was found on the 69 observed "tents" on April 27, while 13 were found among the 41 observed on May 1. The second peak on May 6 and the subsequent maintenance of the decreasing slope is due to larval migration. It is of interest to note that new "tent" formation is a continuing process, observable in a population throughout the spring feeding period and ultimately terminated by pupation.

Initial "tent" formation covered an interval of about 13 days during the spring of 1959 at Dansville, Michigan (Figure 4). Approximately 57 percent of the total initial "tent" formation took place during the five-day interval between April 22 and 27. This corresponds to a peak of effective temperature for the first three days of the period. The

temperature evaluation was made from the charts of a hygrothermograph maintained in a standard weather bureau type shelter among the sample trees. Effective temperature for each day was calculated by computing the area under the thermograph trace and above a minimum temperature of 46 degrees Fahrenheit. The values expressed on the right side of Figure 4 are actually degree hours or the number of degrees maintained for 1 hour duration above a specified minimum value. This is expressed as "effective temperature per day." The selection of the minimal value of 46 degrees Fahrenheit was not completely arbitrary. Under field conditions, activity has been observed at 50 degrees Fahrenheit and all of the collections in this study were refrigerated at 40 degrees Fahrenheit where development is not known to occur. At the lower temperatures the larvae can be forced to produce webbing but they apparently will not initiate the process unless they are removed from the bud. Therefore, the ecological minimum for observable larval activity in the field is somewhere between 40 and 50 degrees Fahrenheit. Between these limits it was arbitrarily fixed at 46 degrees for convenience.

The comparison of "effective daily temperature" and "tent" formation brings to light several interesting points. High temperatures alone are not sufficient to cause immediate activity on the part of overwintering larvae. The high temperatures must be of sufficient duration to initiate the process if it is indeed the sole initiating mechanism. The first peak of effective temperature between April 3 and 10 did not correspond to any new "tents." In the second peak a single "tent" appeared. The cold period which followed the incipient "tent" appears to account for the extended period over which new "tents" were

formed. Though no quantitative data are available, the duration of new "tent" formation during the spring of the proceeding two years appeared to have been much shorter. Once the larval population has been conditioned, or is ready to break dormancy, it can progress very rapidly even when a short period of adequate temperature prevails. Subsequent migration peaks after initial activity appear to be closely correlated with days of peak effective temperatures. The most extensive migration took place shortly after May 1. The magnitude of this movement is not particularly evident from Figure 4 unless it is pointed out that of the 41 new "tents" occurring on May 1, 28 resulted from initial activity. If only migrants are considered, the second peak in the graph would be much more sharply defined. The May 1 observation would be 13 migrants, increasing to 48 on May 8.

As each new "tent" was observed, it was tagged and dated. All of the observable larval activity on the 30 sample trees at Dansville, Michigan, were treated in this manner. On June 18, all of the tagged shoots were dissected and the state of the insect noted. The position of each shoot with regard to compass direction, height above ground, condition of the insect, the presence of remaining green tissue, and the date the "tent" was observed were placed on a map. Such a distribution map is shown in Figures 5 and 6 with most of the vertical and horizontal lines removed. The compass directions were obtained by placing a four inch compass mounted on top of a four foot pointed staff next to the main trunk. A circle corresponding to the crown periphery was then laid out on the ground and divided into 12 equal arcs. The arcs were given compass designations based upon their compass orientation from tree center to periphery. These same arc designations were



23

(1 foot vertical increments).

used for all trees. The position above ground for each "tent" was measured to the nearest four inches and individual maps were made up for each tree. The results are summarized as totals for 30 trees in Figures 5 and 6. It is apparent from Figure 5 that early spring "tent" formation is not initiated at the same rate on all parts of the tree. It can be observed in Figure 5 that practically all of the "tent" formation up until April 22 took place on the lower south side. The activity between April 17 and April 20 took place during a period of very low effective temperature. On April 19 and 20 the temperature rose above 46 degrees for only a few minutes (all temperature measurements were made four feet above the ground in a shaded weather shelter).

The shoots positioned on the south side of the tree and unprotected from direct radiation undoubtedly had considerably higher temperatures than are indicated by the graph. The early activity recorded from the lower south side closely follows a lack of activity in the same position on April 27 and May 1. This is as expected. On April 27 and May 1 tent formation took place predominantly on the north side of the tree and above the two foot level. The first terminal activity was observed May 1 above the four foot level. This pattern of activity closely correlates with temperature relations in various levels of the tree.

Figure 7 graphically demonstrates the differences encountered in maximum and minimum temperatures between ground level and the top of the tree. A minimum-maximum thermometer was placed under the pine and another tied to the main stem seven feet above the ground. Both thermometers were protected from direct solar radiation. Readings were taken approximately every three days and the maximum and minimum temperature occurring between these observation dates were recorded. The







degrees fahrenheit

comparison of maximum temperatures at same levels (X-X). On dates when points occur above middle line, the reading was higher at ground level. When points Comparison of minimum temperatures recorded at 2 levels in stand (0-0); and occur below the middle line, the reading was higher at the 7 foot level. Figure 7.

difference between the maximum and minimum temperature occurring between the bottom and top of the tree is graphed in Figure 7. Since this procedure results in paired observations of extremes in a vertical temperature gradient, the maximum temperature is a good index of the corresponding effective temperature to which the larvae will be exposed. It would be expected that in a vertical gradient of this type, the duration of temperature above a particular minimal threshold would not be very different, but the magnitude of the difference would be a good index to the amount of effective temperature governing larval activity.

Temperatures are considerably higher near the ground early in the spring at the time larvae resume activity. Ground temperature strongly influences the layer of air immediately above it. The plantation itself exerts a retarding influence on air movement which keeps the lower layers of air in contact with the heated active surface for longer periods. The turbulence of the air several feet above the ground would cause it to be constantly mixed with cooler air. It is probable that warming through a combination of direct insolation of the twigs plus the higher temperatures of lower layers of air combine to initiate the activity pattern shown in figure 5.

Figure 6 shows the position of emerging adults on 30 red pine trees and the total "tent" formation activity for the entire spring. From the 201 "tents" constructed, only 19 adults emerged. On the average, therefore, 10.6"tents" were constructed during the spring for each adult moth that emerged. This value, of course, reflects both larval mortality and larval migration.

Spring Mortality. Once spring larval activity was resumed, mortality was almost as high as it was among over-wintering larvae. Dead larvae in the spring sample consisted only of those which had resumed activity, so that it was not possible to confuse winter with spring mortality. The seven larval collections made during the spring showed a progressive increase in the proportion of dead larvae from May 13 to June 5, when it reached 100 percent. Of both larvae and pupae collected on June 5, 89 percent were dead. The greatest increase was observed between May 5 and May 13 (figure 8). This coincides with the peak larval migration period in figure 4. At this time the dead larvae had a characteristic wilted or flaccid appearance. With such a large proportion of the larvae displaying this condition, it was thought that an epidemic of some pathogen was occurring in the population. Two such larval collections on May 18 were sent to Dr. Clarence G. Thompson at the U. S. Department of Agriculture, Insect Pathology Laboratory at Beltsville, Maryland. Dr. Thompson was not able to isolate any virus, protozoa or fungus but did find a mixed bacterial flora. None of the bacteria which were isolated showed marked pathogenecity to laboratory test insects. Unfortunately several of the isolated cultures were lost through contamination, resulting from mite infestation. The bacteria were not tested against healthy European pine shoot moth larvae so it was not possible to show if any of the bacteria were primary parasites. Dr. Thompson did state, however, that the bacterial flora found were of the type usually associated with mortality occurring in insect cultures maintained under unfavorable conditions.

In comparing figure 8 to the effective temperature hours shown in figure 4, a tentative explanation may be made about unfavorable





conditions. Although it may be only a fortuitous development as a result of limited samples, nevertheless a relationship between increase in mortality and low effective temperatures can be seen. In each case, where the increase in the proportion of dead insects over the preceding collection is 9 percent or more, a relatively large drop in effective temperature occurs between the sample dates. The way in which this contributes to larval mortality is not understood.

Summer Activity and Mortality

Figure 9 shows the distribution of summer tent formation during the summer of 1959 at Mason, Michigan. The sampling procedure used was the same as that followed in the spring. The extremely large number of active larvae at this time of the year necessitated reducing the sample size from 30 to 5 trees. Even with a five-tree sample, the total number of "tents" observed in the summer exceeded the size of the spring sample by 25 percent. Approximately 55 percent of all "tents" observed were formed between July 3 and July 16. Two conclusions can be drawn from figure 9. It appears that summer "tent" formation is not abruptly terminated, but gradually declines and is still observed as late as August 18. Secondly, the formation of "tents" in the upper one third of the tree is more intense early in July and is terminated in this area long before it is in the lower two thirds of the tree. Only 6 percent of the new "tents" formed after July 21 occurred in the upper one third of the trees. Whether this resulted from a difference in environmental factors or was simply the dropping or movement of larvae from the higher to lower positions was not determined.

Summer "tents" are formed in the buds after the larvae have fed in the pine needles for an indefinite period. Figure 10 shows the

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Distribution graphs showing the position of summer "tent" formation on 5 red pines at Mason, Michigan (1959) in relation to distance above ground and compass direction (see figure 5) Figure 9.



Figure 10. Proportion of larval collection observed as dead at Mason and Dansville, Michigan compared to the percent live larvae in needles and formation of summer "tents" in buds at Mason.



Figure 11. Percent dead larvae resulting from the emergence of the parasite Hyssopus spp. (primarily H. thymus (Girault)) at Dansville and Mason, Michigan in 1959.

proportion of live larvae in the needles, along with "tent" formation and percentage of dead larvae found. Mortality of larvae feeding in the needles is very high. In the June 26 sample, over 80 percent of the observed larvae were dead from unknown causes. This collection date corresponds with the period when no larvae were present in the buds. After the majority of the population had entered the buds and "tent" formation was 50 percent completed, the mortality rate rapidly declined and continued relatively low throughout the summer. The increase in larval mortality in mid-August was due to the emergence of a hymenopterous parasite (Hyssopus spp. primarily H. thymus (Girault)). Figure 11 shows the proportion of dead larvae which can be attributed to these parasites.

In comparing the percent live larvae in the needles to the proportion of the larval population observed as dead, a conclusion that high mortality is due primarily to the relatively exposed position of the larvae in the needles is not entirely compatible with the results. The decline in percent larval mortality is far steeper than the line representing larval movement from the needles to the buds. Figure 12 shows the rate of egg hatch and the proportion of the larval population observed as dead. It can readily be seen that larval mortality is very high early in the period of egg hatch, and declines at a rate approximately equal to the reciprocal of the egg hatching rate. Apparently as egg hatch progresses, larval mortality decreases. This does not, however, establish a causal relationship between these two phenomena, since many other events occurring simultaneously with these are not graphed. It does appear that once the larvae start entering the buds, mortality takes place at a lower, more uniform rate. This could not



Figure 12. Proportion of eggs observed as unhatched, the percent dead larvae in samples and the percent larvae active in the buds of red pine at Mason, Michigan, 1959.



explain the high mortality observed between June 26 and July 6, however. The percentage of dead larvae drops from 83 percent to 21 percent, when at the end of this time interval only 13 percent of the live larvae were observed in the buds (figure 12). An attempt to interpret this high mortality rate in terms of host phenology was not fruitful. Shoot elongation, needle growth, or environmental measurements showed no marked deviations which would account for it. The changes in observed mortality may simply be a result of insect growth. More than 50 percent of the population had hatched prior to July 1. As these early hatching larvae grow, mortality may be as high as in the later newly hatched larvae. However, as time progresses the survivors may reach a stage where they are subjected to less risk and this could affect observed mortality during the latter part of the hatching period. An alternative hypothesis might be that the mortality rate is in fact higher during the early hatch period but the larvae condition the shoot in such a way that subsequent larvae have more favorable conditions in which to develop.

Figure 2 demonstrates that dry weight increase is not a continuous process throughout the potential feeding period. It reaches its peak during the first two weeks in August and then declines until feeding is resumed the following spring. It could be inferred from this that the larvae ostensibly cease feeding and live on stored body fats or at least cease to assimilate food. In order to ascertain if the insects do, in fact, stop feeding long before the onset of cold weather, the alimentary tract of 378 larvae were examined. The larvae were collected from two red pine plantations in central Michigan on the dates indicated in figure 13. Samples for each date were obtained



by taking the top four inches of ten or more new shoots and quickfreezing them in the field. Dry ice and a portable ice chest were used to accomplish the rapid freezing. The shoots were transferred from the ice chest to a cold storage room where they were held at -15degrees Fahrenheit until the insects could be removed. At a later date the insects were placed in 50 percent alcohol and their alimentary tracts dissected out. Larvae killed in KAAD were not satisfactory for determining gut content, apparently due to the clearing action of the fixative used. The percent larvae with undigested food present is shown in figure 13. The number of observations on which each percentage is based is indicated in the table. Each larval dissection resulted in scoring the particular individual as either a "plus," food present, or a "minus," food absent. This method proved very satisfactory for collections made before August 1. After August 1, however, these two categories were not as satisfactory. In many cases, only very small particles, or a single fecal pellet in the rectum would cause the individual to be scored as "plus." On September 8, for example, a single individual from the Mason plantation had a portion of undigested bud scale in its digestive tract. This was scored as "plus" but it would appear that bud scales contribute little to the nutritional needs of the larvae. Prior to August 1, however, the intestines of many insects were well packed with green tissue and the distinction between feeding and nonfeeding larvae could readily be made.

It is apparent from figure 13 that the proportion of individuals in the population with undigested material in their gut drops off rapidly after July 15. By the first of August approximately 50 percent

of the population had purged the gut of food that has not been replenished. By August 15 only relatively small traces of food can be found in the digestive tracts of larvae. This condition is maintained throughout the last of August and September despite apparently favorable weather which allows the larvae to remain active. The larva goes through the winter without any food in its digestive tract.

These observations strongly suggest that larvae are more likely to survive the winter if there is no food in their alimentary tract or if some related (or even unrelated) but unrecognized physiological change takes place. Comparing fall conditions to the spring feeding period would indicate that there is enough time in the fall to allow the insect to complete growth and even oviposit. However, the life cycle of most insects is frequently closely synchronized with that of the host. Whether cessation of feeding is caused by cyclic phenomena which regulate both host and insect physiology or if it is the cyclical event bringing about physical or chemical changes in the host is difficult to discern. Fall feeding would greatly shorten the life cycle. Results of this study demonstrate that larval feeding takes place over a relatively short period in the summer and an equally short period in the spring. A total of less than eight weeks is probably spent in actual feeding. The delay mechanism which causes cessation of summer feeding is conceivably an adaptation which allows the insect to synchronize its development with that of its host.

The occurrence of a mechanism which halts an organism's development at a specific growth stage is not uncommon in many Lepidoptera. The breaking of diapause so that larvae can continue developing usually requires a lapse of time or a specific temperature, or an

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interaction of the two. Making the assumption that diapause was a factor, an experiment to demonstrate its existence was carried out. Results are shown in table 2. Ten infested shoots were collected and brought into the laboratory on the seven different dates indicated in the first column of table 2. The number of new "tents" was recorded on various dates after this initial collection. The date of collection appears to have little influence on the rate of tent formation once activity is resumed. Only a significant drop in the total number of insects in each collection is discernable. Larvae either became active or died. Pupation was observed from shoots collected on all dates and these produced apparently normal adults. Adults were obtained during the last week in October from shoots collected on September 15. If a diapause is present it is not of the type which is broken by cold weather. Since the constant room temperature is not greatly different from day temperatures from August and early September there seems to be no apparent reason why the larvae do not resume feeding. It takes from 6 to 24 days for larvae to resume activity in cut shoots once they are removed and placed at room temperature. It could be that only a partial diapause takes place, which can be broken by a slight shift in daily temperatures, or the increased daylight caused by artificial light indoors.

Although the exact relationship of factors causing resumption of activity can only be speculated upon from the results of this study, they do suggest that the insect's distribution may be strongly controlled by this phenomenon. The insect is abundant in northern Michigan; but intensive outbreaks do not occur in the extreme northern limits of potential hosts. Low winter temperatures appear to be a

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Rate of new tent formation on ten shoots collected on different dates and held at a constant 70°F. temperature and 50 nercent relative humidity Table 2.

 $rac{1}{-}$ Dissected for living and dead pupae.

significant factor in minimizing the insects occurrence in the maximum northern range of its host. This is certainly not true of its southern distribution. The insect is seldom encountered in the southern counties of Ohio, Indiana, and Illinois. Extension literature from these states establishes it as an economic problem only in the northern counties. Miller and Neiswander (1955) reported a similar distribution in Ohio. The southern distribution seems to be sharply delimited. It may be that fall temperature conditions are sufficient to induce resumption of activity of the larvae. It could be hypothesized also that the extension of the warm period between cessation of feeding and onset of cold weather may be sufficient to cause the larvae to utilize an excessive amount of stored nutrients and starvation results before spring.

It was possible to test the first hypothesis as to its influence on cold induced mortality after feeding is resumed. It was theorized that if feeding was resumed in the fall, even for a short period, the engorged gut with a high water content might freeze at low temperature and rupture the intestinal walls. In order to determine if resumption of feeding in the fall would increase mortality at low temperatures, an experiment producing the results shown in table 3 was conducted. During the first week of October 120 infested shoots were collected and divided into two subgroups. One group was kept at room temperature and the other was held at 40 degrees Fahrenheit until feeding activity was resumed, as indicated by new tent formation and frass production. Samples were paired so that at each temperature there were 10 shoots in which insects had resumed feeding and 10 shoots in which the insects were in a natural condition. The shoots were subjected to a 24-hour treatment at temperatures indicated in the first column of table 3.

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Treatment	Shoots with Active Total Insects	Insects % Live	Shoots with Inactive Total Insects	Insects % Live
70° F	16	100	13	92
40° F	11	16	ø	86
30° F	œ	100	14	93
20° F	7	87	14	93
10° F	14	93	ø	86
-10° F	18	0	13	80

Mortality counts were taken at the time of pupation to insure that no fatally injured larva could be scored as a living insect. There was no significant difference in the proportion of living insects listed as "active" or "inactive" which could be attributed to insect activity. There was very little mortality in either group at temperatures ranging as low as 10 degrees Fahrenheit. Practically all insects were killed at the -10 degree Fahrenheit temperature in both groups. The presence of food in the gut of winter larvæ seemed to have little influence on their longevity when exposed to subfreezing temperature for 24 hours. The perplexing problem as to what causes the larva to cease feeding and what prevents it from resuming feeding during the warm days of August and September still remains. It obviously entails a synchronizing of insect and host life cycle but there is no information available on the causal factors regulating this synchronization.

In 1958 a study area was established at the Rose Lake Wildlife Experiment Station in Clinton County, Michigan, for the purpose of studying differential mortality and larval migration resulting from different degrees of competition. Forty red pine trees of uniform height were selected in a small, isolated plantation. Four population levels of 1, 3, 6, and 10 insects per terminal shoot were established on August 1 and 2 by transferring larvae from lower branches to the terminals and destroying all excess larvae. This resulted in having a known number of larvae in the terminal shoot and the rest of the tree entirely free of insects. Any subsequent injury to lateral shoots could occur only after larval migration. Two hundred larvae were transferred and recorded. Observations made on August 27 showed that larvae were established in all terminal shoots. Winter mortality was

extremely high and only eight insects showed activity the following spring. Of these only one emerged and no migration was observed. With mortality of this magnitude it is quite clear that intraspecific competition was of little importance in the late fall and during spring feeding. This type of competition is probably much more important shortly after egg-hatch while the larvae are just moving to and becoming established in the buds.
STUDIES ON HOST PREFERENCE AND ITS INFLUENCE ON EUROPEAN PINE SHOOT MOTH SUCCESS AND DEVELOPMENT

It has been known for many years that all species of pine in a mixed plantation are not equally injured by European pine shoot moth attack. Even plantations of a single species show differential injury, with single trees and sometimes small groups of trees escaping conspicuous attack. Four possible explanations for this phenomenon include:

1. The adults could have an oviposition preference for a particular host species and even for individual trees within this species.

2. Oviposition could be random, but differential larval mortality could ultimately produce different population levels.

3. Variable host response to the attack could occur even if there were no differences in insect density between trees.

4. A combination of any of these factors could be responsible.

Oviposition Preference and Larval Mortality

In order to determine the relative importance of the several phenomena listed above, a number of study areas were selected in Lower Michigan. Plantations of at least two species of seven to nine year old pines were chosen. One complete generation of European pine shoot moth was studied at Rose Lake, Michigan, on $\operatorname{Scotch}^{1/}$ and red pine, and supplementary data were collected throughout Michigan in other stands. In order to determine if the adult female moth had a preference for

 $\frac{1}{Pinus} \frac{sylvestris}{sylvestris} L.$

oviposition on a particular host, paired egg samples were collected from red-Scotch, red-jack, $\frac{1}{2}$ and red-white $\frac{2}{2}$ pine from Rose Lake, Dansville, and West Olive, Michigan, respectively. Samples were obtained by counting all of the eggs on 30 shoots of the current year's growth on each pine species. The shoots were examined under a four power magnifying lamp in the laboratory. Although eggs are also found on the needles, preliminary observation on egg distribution indicated that by counting only eggs adhering to the new bark the highest number of eggs would be obtained with the least amount of effort. Eggs were observed on all parts of the tree and even on the walls and floors of cages holding adult insects. They appeared to be more concentrated in the new growth than in any other location. Many eggs, however, were observed on bark scales of branches and on the main stem. Since it was obvious that these could accidentally have been dislodged in the process of sampling, and since a preliminary sample showed that the eggs occurring on needles of red and Scotch pine were consistently less than six percent of those found, practical considerations made it desirable that they be discounted for purposes of the investigations described here. Shoots were refrigerated at 40 degrees Fahrenheit until the eggs could be counted. This temperature was found to be very effective in halting both egg development and insect activity.

The results of these studies (table 4) indicate an oviposition preference for red pine in all plantations. By considering only the mean number of eggs per shoot, this preference was not pronounced or

 $\frac{1}{Pinus} \frac{Pinus}{Pinus} Lamb.$

		Total Eggs	Mean Eggs	Mean Shoot	Adjus	ted Mean
Plantation 8	Species	Observed	Per Shoot	Length	Shoot	Eggs Per
					Length	Shoot
Rose Lake	Red	129	4,37	9.46	21.06	9.13*
	Scotch	146	4.87	21.06	21,06	4.87
Dansville	Red	43	1.43	13.97	22.57	3.41**
	Jack	23	.73	22,57	22.57	.73
West Olive	Red	25	. 83	9.96	Not	. 83
	White	4	.13	10,71	Adj.	.13

Table 4. European pine shoot moth oviposition preference for three pine species growing with red pine in three different plantations.

*Significantly different at 5 percent level.

****Significantly different** at 1 percent level.

Table 5. Incidence of egg parasitization by Trichogramma minutum Riley. $\frac{1}{}$

Plantation	Species	Total Eggs Observed	Mean Percent of Eggs Parasitized/Sample	Percent Eggs Parasitized
Rose Lake	Red	129	15**2/	46
/	Scotch	146	85	84
Dansville	Red	42	29 ^{3/}	38
	Jack	23	· 56	61
West Olive	Red White	25 4	6 ^{4/} 0	4 0

****Significantly different** at 1 percent level.

 $\frac{1}{2}$ Identified by U. S. Nat. Museum

 $\frac{2}{3}$ Significantly different at the 1 percent level.

 $\frac{3}{5}$ Significantly different at greater than 10 percent but less than 5 percent.

 $\frac{4}{-}$ Not analyzed statistically.

statistically significant in any of the plantations. However, considerable error is introduced when the Rose Lake and Dansville samples are compared due to the large difference in mean shoot length. Any analysis which seeks to discern if there is an actual difference in numbers of eggs present on the shoots of different species must account for this discrepancy in shoot size. An analysis of covariance as described by Snedecor (Chapter 13) appears to be particularly well-suited to this problem. Accordingly, data were analyzed and the adjusted means tested for significance with the "F" distribution. The adjusted means were computed from their regression line at the point of highest mean shoot length, instead of at the average of the two means. Results are shown in the last two columns of table 4. The adjusted means estimate what the mean difference between mean number of eggs would be if the shoot length were as shown, and if the insect population density was sufficient to produce this number of eggs. As a result, the difference between the adjusted means is an estimate of how many more eggs, on the average, one would expect to find on red pine, than on the other species at this insect density.

The mean difference of 4.25 more eggs on red pine than on Scotch pine at the Rose Lake location was significant at the two percent level. The mean difference of 2.68 at the Dansville location was significant at the one percent level. The number of eggs obtained from white pine at West Olive was too small to allow a valid statistical comparison with red pine. However, the mean eggs per shoot was over six times more for red pine than for white pine; which even without the use of parametric statistics, strongly suggests a preference. There is apparently some mechanism operating which results in more eggs

being deposited per unit of red pine shoots than on comparable units of jack, Scotch, or white pine shoots. This mechanism would not have to be a preferential response on the part of the ovipositing female, but could be simply a mechanical effect of the shoot's morphology at the time of oviposition. The red pine shoots, with dense and long needles, may simply present a larger area upon which ovipositing females can come to rest. If this is the case, one would expect that individual shoots of red pine would have more eggs per unit of shoot length but equal numbers of eggs on trees presenting the same total surface area. There are no data available for egg numbers deposited on the entire tree and inferences can only be obtained from larval samples. The larval populations are subjected to different mortality factors on the two hosts and it is hazardous to draw heavily on such counts for specific conclusions. Nonetheless, at Rose Lake, a total insect per tree estimate was made on June 12 at the end of the 1958 generation. The mean Scotch pine tree height was 8.8 feet, and for red pine six feet, on the ten trees selected for sampling. There was a mean of 7.9 insects per tree on Scotch pine and 6.8 on red pine. The variance in these samples was too great to show significant regression of insects per tree on tree height so an analysis of covariance could not be used to correct for tree height differences. After collecting the samples, it became evident that tree height of infested pine is not the best estimate of total surface area presenting itself as a resting site for ovipositing females. A better method may be to actually make an area estimate of the crown surface area. However, there was no difference in the population on a per tree basis.

The greater number of eggs per red pine shoot results in an increase in the number of summer larvae feeding in infested shoots even though the larval population per tree may not be significantly higher than on other host species. This undoubtedly results in intensified summer injury on red pine. Also, the egg parasite, Trichogramma minutum Riley, is apparently more efficient at finding eggs on Scotch pine than it is on red pine. Table 5 shows that at Rose Lake the mean percent of eggs parasitized per sample was 15 on red pine and 85 on Scotch pine. This difference was shown to be significant at the one percent level. The 56 percent parasitization per sample on jack pine was not demonstrably greater than the 29 percent on red pine, at the five percent level of significance. However, it was significantly different at the 10 percent level of probability. (The West Olive collection was not analyzed due to the small sample sizes.) The last column in table 5 shows the proportion of the total eggs which were parasitized at the 3 locations. This column was not analyzed due to the extreme deviation from normality encountered in the proportion of parasitized eggs per shoot. This was apparently caused by the behavior of the parasite. On 19 of the 29 red pine shoots, egg parasitism was either zero or 100 percent; and on Scotch pine, of the 27 shoots with eggs present, 17 were either zero or 100 percent parasitized. The T. minutum parasite appeared to be very efficient in ovipositing in all of the eggs after it once reached a shoot where eggs were present. The original egg sample was stratified so that three dominant shoots were collected from a limited area on ten different trees in the plantation. By reverting back to this group of three shoots and using the sample size of ten instead of 30, the within species variance was greatly reduced and a

bimodal frequency of proportion of eggs parasitized was avoided. It was on this basis that the analysis was made.

The data collected at Rose Lake relegated both the differential oviposition per shoot and the differential egg mortality to a relatively minor influence on the insect density of over wintered larvae and spring pupae. However, a sample of summer larvae taken on September 4 shows that there were still significantly more larvae per bud on red pine than on Scotch; (the difference was significant at the one percent level). This population density differential was totally lost after winter mortality had occurred. Mortality during the spring continued the trend of high larval mortality on red pine and resulted in a slight increase in both insects per infested bud and insects per tree on Scotch pine by the time pupation was completed. Figure 14 shows the results of this progressive mortality on the two host species. In considering the over-all mortality from healthy eggs to fall larvae it appears that a larger proportion died on red pine than on Scotch. This could be due to the superior nutrient quality of the insects native host or to intra-specific competition in infested buds. Observations made on summer tent formation indicate that location for these tents became extremely scarce. Laboratory tests conducted by Haynes (1959) indicated that in close confinement cannibalism is frequently encountered. This suggests that competition may be the most plausible explanation for the difference in larvae mortality between Scotch and red pine.

It was thought that the buds of Scotch pine would be much smaller and the competition for food in tent sites would be greater on this species than on red pine. In order to evaluate this phenomenon, infested bud samples were collected on September 4 from both pine species and



the remaining tissue was determined volumetrically by displacement of water. The buds were scored as to the presence or absence of green tissue. The results are summarized in table 6 for both pine species and from high and low positions on the trees. Injured Scotch pine shoots had over twice as many buds as red pine but did not have a proportionately larger volume of remaining tissue. At the end of summer feeding Scotch pine buds had a significantly larger volume of tissue remaining in both the upper and lower portions of the tree. Since the increase in volume for Scotch over red pine in number of buds per shoot does not approximate the increase in volume of tissue remaining after summer feeding, some explanation must be sought. Either the individual buds were of a smaller size or the differential larval population resulted in a much greater destruction of bud tissue in red pine than in Scotch. By observing table 7 it appears that the first explanation is the more logical. The upper area of red pine contained almost twice as many larvae per shoot as Scotch pine, while there was no observed difference between the lower areas of the two species. In the upper area Scotch pine had only 22 percent more tissue remaining, whereas the lower region, with equal insect density, had 40 percent more. The amount of remaining tissue and the larval population density is not a very reliable indicator of the relative competitive pressure being exerted on the two populations. Actually, it is a view of the problem after all of the intraspecific competition is completed. The insects have completed feeding at this time and it is impossible to discern how much of the destroyed tissue should be attributed to larvae which succumbed during the summer. Nevertheless, it is of interest to note that Scotch pine had significantly more buds per shoot, with more tissue remaining at the end of the

Position on Tree	Species	Mean Buds Per Shoot	Mean Volume of Remaining Tissue	Percent Buds Without Remaining Green Tissue
Upper half	Red	3.32	. 80	10.6
	Scotch	6.97**	1.02	3.1
Lower half	Red	2.63**	.17*	0
	Scotch	5.93	.28	. 8

Table 6 .	Estimate of availab	le usable food for	r larvae at termination
	of summer feeding.	Collections made	on September 4.

*Significantly different at 5 percent level.

****Significantly different** at 1 percent level.

Scotch

Position on			Date of C	ollection	
Tree	Species	Septe	mber 4	Apri	1 17
		Live	Dead	Live	Dead
Upper half	Red	2.17	.10	0	1.13
	Scotch	1.15	.13	0	.80
Lower half	Red	. 72	. 07	.07	. 83

.75

.02

.05

.43

Table 7. Mean number of living and dead insects per shoot on two different dates.

summer feeding. The high density level in the upper tree areas apparently resulted in red pine having a larger percentage of completely destroyed buds than Scotch. As one might expect, the presence or absence of fall larvae did not appear to be associated with the amount of the remaining tissue. Even in cases where the buds were completely destroyed, the live larvae were present after summer feeding had ceased. These data seem to indicate that of the many factors which may cause a differential larval mortality on Scotch and red pine, competition for green bud tissue is not of pronounced importance. It can be seen in figure 14 that mortality occurring between egg hatch and development of larvae up to September, was much greater on red pine than on Scotch pine. The only observable factors which may contribute to the higher mortality rate on red pine was that this species initially had a larval population 2.5 times larger than was present on Scotch pine. Summer mortality from egg hatch to fall larvae was 44 percent on red pine and eight percent on Scotch pine. The fall population was 1.4 larvae per bud on red pine and .95 per bud on Scotch pine. This difference may have been too small toward the end of the feeding season to cause much difference in remaining bud tissue.

These data indicate two reasons why red pine is more severely damaged than Scotch pine. First, more eggs are deposited on red pine per unit of shoot length; and this, coupled with more egg parasitization on Scotch pine, gave a higher larval population on its buds. Secondly, Scotch pine has more bud tissue and lateral buds, which minimized the insect attack in terms of economic damage. Red pine did not appear to be a superior host from the standpoint of shoot moth population growth. For the generation studied, the final figures showed no significant difference between adult emergence from the two pine species on either a per shoot or a total tree basis. The presence of completely destroyed buds with no remaining green tissue is much more common after spring feeding than after summer feeding. However, there was no significant difference between the 76 percent on red and 79 percent of infested buds completely destroyed on Scotch pine after spring feeding.

Influence of Host Species on Population Density

In the fall of 1958, in Ottawa County, Michigan, a paired sample was taken from adjacent heavily infested red and white pine trees, and all of the infested shoots on each tree were counted. Sample pairs were taken only where the two pine species were of similar shape and height. The mean height for red pine was 52.4 inches and for white pine 52.9 inches. The mean number of infested shoots per tree was 102.6 for red and 61.6 for white pine. The difference between paired samples was shown to be significant at the 5 percent level of probability, using the "t" distribution. In this situation, where trees of equal size and shape could be compared directly, it can be demonstrated that a higher summer larval population is present on red than on white pine. Of the 26 insects observed on June 5, 1958, 8 percent had pupated on white pine and 70 percent on red pine. At the time of 100 percent pupation on red pine, there was less than 50 percent pupation on white, and migrating larvae or fresh "tents" were observed on the white It appears that the small buds of white pine are sufficient to pine. support a high population of summer larvae, but they are too small to supply enough food for the much larger spring larvae without their resorting to numerous migrations. Many of the larvae which successfully pupated on white pine were observed in situations where two or more

closely associated shoots were incorporated into one large pitch mass or tent. The white pine in the stand had undergone considerable deformation due to shoot moth attack. Shoots were stunted as a result of summer feeding. Summer populations on white pine appeared to be relatively high, compared to the extremely small population at the time of pupation. This indicates that a differential larval mortality is taking place on these two species.

Additional collections were made on June 4, 12, and 18 in six different plantations in Ottawa County during the spring of 1958. Each plantation had two or more species present, one of which was always red pine. The main purpose of these collections was to determine if the host influenced the rate of development, insect size, and/or sex ratio. However, since counts were taken from the entire tree, supplementary data on population density on each of the six pine species were also obtained. Table 8 shows the total number of insects observed on each pine species and the total number of trees on which these insects were counted. A definite population gradient can be observed for "mean insects per tree", with red pine supporting the highest insect density. These means are the average from several plantations and, since the insect density was not the same from plantation to plantation and all species were not present in all plantations, the between-species difference could not be subjected to statistical analysis. However, there was a single plantation in which all of the species were present. These data and their analysis are shown in table 9. The insect densities on these species show essentially the same order as the summed values obtained from all plantations. Only the relationship between Scotch and ponderosa $\frac{1}{pine}$ was reversed. The statistical analysis demonstrated 1/Pinus ponderosa Laws.

that this difference would be expected more than 5 percent of the time, through chance or sample variance. It is also of some interest to note that in both tables 8 and 9 the percentage of trees attacked follows closely the order of "largest to smallest" which is evident in the mean insects per tree picture.

Rate of Development on Different Host Species

Samples were collected on three different dates in the various plantations in order to obtain information on the relative proportion of the insect population which was present as larvae, pupae, or adults on the different host species. In table 10 only the June 4 and June 12 collections were analyzed statistically. This consisted of an analysis of variance of the proportion of the population which appeared as larvae. This is the complementary proportion of the population appearing as both pupae and adults. Percent larvae were transformed, using the arcsin technique described by Snedecor (1957) page 248. Since equal replications per species were not present, the mean proportions of larvae per host species were compared, using the technique described by Duncan in 1957, for the multiple range comparison of heteroscedastic means. However, the Studentized range tables presented in Snedecor (1957), which possesses the highest protection levels were used to obtain the least significant differences. The June 4 collection was analyzed using blocks of ten trees in paired samples from the various plantations. In all cases the collection was made from a group of ten red pines adjacent to a similar group of another species. The labor involved in this type of sample was too extensive to obtain results for all pine species on any particular date. The June 12 and June 18 collections consisted of single tree replicates selected in the same manner.

			Percent		No. of Plan-	Mean
Pine Species	Mean Tree Ht.	Total No. In- sects Observed	of Trees Infested	Total of Trees Observed	tations Re- corded From	Insects Per Tree
						(T)
Red	45.7	2399	98.5	130	9	18.45
Scotch	50.4	435	72.5	80	4	5.44
Ponderosa	73.4	184	100.0	20	1	9.20
Austrian	38.7	174	65.0	40	2	4.35
Jack	64.0	70	34.0	100	4	.70
White	53.2	38	20.0	120	4	.35

Total number of insects, trees and plantations from which population data were obtained and the mean number of insects per tree. Table 8.

- (1) These means were not subjected to a statistical analysis due to the lack of uniformity between samples and the distinct difference in population density from one plantation to another in which all pine species were not represented.
- Data Population difference in a single plantation when all pine species were present. collected on June 13 and 18. A 20-tree sample was taken from each pine species. Table 9.

Trees Mean Inst	sted Per Tr	28.9	95 13.9 1	00 9.2 1	80 7.5 (75 2.4	10
Percent	Infe	1		1			
Mean Tree	Height	65.3	71.5	73.3	51.3	66.5	66.5
	Species	Red	Scotch	Ponderosa	Austrian	Jack	White

Any two means with a common letter are not significantly different at the 5 percent level, using the multiple range comparison of mean described by Snedecor. 3

Tabli Spec Red Scott Austi Pondt Jack (1) (1)	e 10. The Jund cles ch ch crian erosa e rian erosa a level. The mean	mean proportion 12, and June 16 June 4 Mean Prop. of Larvae 38.0 73.0 98.4 insects present number of insect	of insects pres 8, 1958. (1) No. of In- sects Obs. 1387* 1387* 1387* as larvae are s as larvae are s ts present as la	ent as larvae or <u>Date of Co</u> <u>June 1</u> <u>Mean Prop.</u> of Larvae 10.1 10.9 5.7 14.7 27.9 10.00** ignificantly di	n six different <u>llection</u> <u>2 (2)</u> <u>150</u> 578 150 150 150 150 22 22 22 22 22 22 23 26 66 22 22 22 22 22 22 22 23 22 23 22 23 22 23 22 23 26 26 26 27 26 26 26 26 26 26 27 26 27 26 27 26 27 26 27 26 27 26 27 26 27 26 27 26 27 26 27 26 27 26 27 27 27 27 27 27 27 27 27 27	pine species on y <u>Mean Prop.</u> of Larvae .31 2.70 0 2.55 9.33 100.00 h other at the 5 ntly different fi	June 4, 18 (3) 18 (3) 18 (3) 18 (3) 10 - of In- 5 ects Obs. 434 285 24 118 34 4 4 4 10 ects 118 34 4 4 10 ots 110 ots
Ì	pine spe large num proportic	cies at a probability at a probability of larva pres	dity level of J pines had only sent per tree.	l percent. Jack a single insect	pine was not si per tree. This	gnificantly differences greatly influence	erent, but a ces the mean
(3)	No analy: tion. Hc species.	sis of mean propo wever, from the	ortion of insect analysis, it is	s and larvae was apparent that v	s made due to th white pine is ag	e very large perc ain different fro	cent pupa- om the other

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*Significant at 5 percent level.

****Significant** at 1 percent level.

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	Table 11.	

Pine	Mean Percent Adu	ult Total Number of	No. of Plantations
Species	Emergence per Ti	ree Insects Observed	Studied
Red	17.1 (1)	434	r
Scotch	41.8 (1)	285	n
Austrian	17.1	24	1
Jack	5.5	34	0
White	0	4	1

The mean percent adult emergence was significantly higher on Scotch than on red. The difference was shown to be significant at the 1 percent level. Other means were not analyzed due to the frequent occurrence of only one insect per tree which greatly increased the sample variance. .

The June 4 collections showed that differences as great or greater than those noted between the rate of pupation on red, jack, and white pine would be expected less than 5 percent of the time, if in fact the means were equal. Jack pine is intermediate between red and white pine. An analysis of the June 12 collection demonstrated that the only significant difference remaining is between white pine and all other species. The difference between jack pine and red pine is no longer significant. This is undoubtedly due to the very large proportion of pupation on red pine and the corresponding slowing down of this phenomenon as pupation reaches 100 percent. The June 18 date could not be analyzed due to the very large percent pupation on all pine species other than white pine. Since pupation had progressed so far that the presence of larvae was very rare, it was thought that this collection would yield more positive results if it were analyzed for the proportion of its population which had emerged. To do this, the analysis was made on the complementary proportions of percent emergence or the proportion of the population which appeared as larvae and pupae. This eliminated numerous zeros where emergence had not taken place. In the plantation where ponderosa pine was present a record of emergence was not made, so this pine species could not be included in table 11.

Noticeable differences were observed with respect to proportion of adult emergence. To overcome the large variance observed from one part of the plantation to another which would obscure any statistically significant difference, a paired sample analysis was used. Austrian, white, and jack pine were not included in this analysis due to the small number of insects available for comparison in the samples. However, the observed difference between adult emergence on red pine and Scotch

would be expected in such a sample less than one percent of the time, due to chance. It can be concluded, therefore, that adult emergence is more rapid on Scotch pine than on red pine.

This acceleration in developmental rate on Scotch pine was not observed on June 12 when the analysis was made on percent pupation, suggesting that the acceleration occurred primarily after pupation had taken place. Since feeding has essentially ceased for the population after June 12, the relative food value of the host would be of little importance here. A more plausible source of explanation is the respective insulating values of the bud tissue and/or more efficient shading of lower buds on med pine than on Scotch. No data are available on internal bud temperatures of the two species; although the longer, more abundant needles on red pine would appear to provide a greater shading effect.

It has been emphasized in recent years that the timing of summer insecticide sprays is extremely important if adequate control is to be obtained with a single spray. The most important factor limiting the time available for successful spray application, is the protracted period over which eggs hatch. In a red pine plantation in 1959, this hatch extended from about June 26 to July 16. The spray must be applied before larvae have entered the buds, but the insecticidal residue must still be present as the last egg hatches. The particular calendar date on which an individual egg will hatch will depend on its genetic constitution, the environment, and the date of oviposition. If adult emergence commenced early on Scotch pine, it appears reasonable to assume that in a plantation where both species are present, adult emergence will take place over a longer period of time than it would if only one species were present. Pursuing this line of thinking, egg hatch will take place over a longer period of time in plantations where both host species are present, than it will in plantations where only one host species is present. The extension of egg hatch undoubtedly would adversely affect efforts at chemical control with a single spray. Of course, the validity of this hypothesis can be definitely established only by closely controlled spray experiments, but the assumption appears tenable in the light of existing knowledge.

Influence of Host on Insect Size

In addition to mortality and rate of development, the host may also influence the size of individuals within the population. It was thought that measurements of pupae would best show such differences. At this stage, growth or dry weight increase has ceased and all factors which have contributed to the size of an individual have had their effect. At this time it is also possible to remove considerable variance from the insect collections by sexing (Friend and West 1933). This is easily seen when it is pointed out that the estimate of means square from analysis of variance for dry weight of males equals 3.85, for females 15.98, and for the combined male and female population 17.19. The corresponding means of 6.68, 12.10, and 9.39 had a coefficient of variation of 34.17, 37.70 and 48.00 percent, respectively.

Tables 12 and 13 show the mean dry weight of pupae collected from different host species and under different environmental conditions on red pine. In Plantation No. 1, where all of the study pine species except white are present, both the males and females show the same order of mean dry weight with one exception. The male pupae collected on

Host and :	Date of :	No. of Insects	: Mean Dry	: Significant1/
Collection Source : (Collection :	Observed	: Weight in Mg.	: Differences
	1958			
Plantation #1				
Red	6/13	54	4.88	Α
Scotch	6/13	58	6.75	CDE
Austrian	6/13	61	5.88	В
Ponderosa	6/13	65	6,21	BD
Jack Dientetion #2	0/13	13	5,20	AB
Plantation #2	6/14	7	7 96	שת
Neu Maite	6/14	а - с А	2.45	Dr A
white	0/14	4	5.45	A
Plantation #3				
Red	6/18	22	9.77	G
Collections from 25	foot tall red	l pine stand		
edge of stand	6/19	26	7.67	EF
Top of tree within stand	6/19	39	6.95	DE
Lower branches within stand	6/19	4	4.68	ABC
Collections from top	1/4 of tree	in red pine sta	nds	
25 feet high	6/19	26	7.67	EF
6 feet high	6/19	48	8.03	F
2 feet high	6/25	12	4.90	AB
Collection from adjac sulting from summer s	cent l-acre p spraying	plots with diffe	rent population	density re-
High pop. density	6/14	41	7.46	EF
Low pop. density	6/14	41	7.31	EF

Table 12. The comparison of mean dry weights in milligrams of male pupae collected from different pine species, and under different conditions on red pine.

 $\frac{1}{Any}$ means having common letter are not significantly different. Comparisons between all means can be made at the 5 percent level.

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Host and :	Date of	: No. of Insects	: Mean Dry	: Significant
Collection Source :	Collection	: Observed	: Weight in Mg.	: Differences
	1958			
Plantation #1				
Red	6/13	52	7.68	D
Scotch	6/13	55	13.41	Α
Austrian	6/13	6 0	11.75	В
Ponderosa	6/13	42	10. 6 0	BC
Jack	6/13	8	7.85	CD
Plantation #2				
Red	6/14	7	8,94	BCD
White	6 /14	2	4.70	CD
Plantation #3				
Red	6/18	22	9.82	BCD
edge of stand	6/19	38	14.48	Α
edge of stand	6/19	38	14.48	Α
Top of tree	a (n a			_
within stand	6/19	30	11,73	В
Lower branches				
within stand	6/19	2	7.60	B
llections from top	0 1/4 of tre	e in red pine sta	ands	
25 feet high	6/19	38	14.48	Α
6 feet high	6/19	66	13.27	A
2 feet high and stunted	6/25	9	9.18	В
 lection from diff	erent popul	ation densities 1	resulting from s	ummer spray-
ligh pop. density	 7 6/14	54	14.69	A
	G / 1 A	40	14 14	
ow pop. density	0 /14	49	14.14	A

Table 13. The comparison of mean dry weight in milligrams of female pupae collected from different pine species and under different conditions on red pine

Any means having a common letter are not significantly different at the 5 percent level. Cannot compare letter across dotted lines (see table 11).

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ponderosa pine were larger than those from Austrian $pine^{1}/$, while the reverse was true for the females. The difference was not significant. Both male and female pupae collected from red pine were significantly smaller than all those from other tree species except jack pine in Plantation No. 1. The largest insects in all cases were collected from Scotch pine. Even with the small number of observed pupae on white pine, it is apparent that the insects exist under extremely unfavorable conditions on this host (Plantation No. 2, table 12,13; plantation 2,4, table 14).

The statistical analysis of the data presented in tables 12, 13, and 14 consisted of analyses of variance for heteroscedastic means as described by Duncan, 1957. In table 12, all possible comparisons were made at the 5 percent protection level using Duncan's table (Duncan 1955). In tables 13 and 14, only the obviously meaningful comparisons were made. This saved considerable computation in the analysis and only those means within the same subsection can be compared for significance by using the letters in the last column. However, at the bottom of each table the square root of the mean square, with its corresponding degrees of freedom is presented so that additional comparisons can be made if the reader deems it necessary.

The statistical analyses of these data demonstrate that the statement "pupae collected from red pine, male or female, are smaller than those collected from Scotch, Austrian, and ponderosa pine," is probably correct, since the differences were significant at the 5 per cent level. It can be confidently accepted then, that a real difference in insect dry weight does exist between pupae collected from the different pine species. The statistical analyses cannot test the

^{1/}Pinus nigra Arnold

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Host and :	Date of a	NO. OI Insects	: Mean Dry	: Significant
collection source :	LOIIection	Ubserved	: weight in Mg.	Differences
	1958			
Plantation #1				
Scotch	6/13	16	14.46	Α
Austrian	6/13	7	7.86	BC
Ponderosa	6/13	23	12.40	AB-
Jack	6/13	1	7,20	ABC
Plantation #2				
Red	6/13	. 10	13.91	Α
White	6/13	23	4,53	С
Plantation #4				
Red	6/5	26	14.20	Α
White	6/5	26	2.92	С
To all	6/5	8	6,86	С
Jack Collections from 25 Top of tree at	feet tall r	ed pine stand		
Collections from 25 Top of tree at edge of stand	6/19	ed pine stand 14	9,62	 A
Collections from 25 Top of tree at edge of stand	6/19	ed pine stand 14	9,62	A
Collections from 25 Top of tree at edge of stand Top of tree within stand	6/19 6/19	ed pine stand 14 9	9.62 13.36	A A
Collections from 25 Top of tree at edge of stand Top of tree within stand Lower branches	6/19 6/19	ed pine stand 14 9	9.62 13.36	A
Collections from 25 Top of tree at edge of stand Top of tree within stand Lower branches within stand	6/19 6/19 6/19 6/19	ed pine stand 14 9 2	9.62 13.36 6.9	A A A
Collections from 25 Top of tree at edge of stand Top of tree within stand Lower branches within stand Collections from to	6/19 6/19 6/19 6/19 9 1/4 of tree	ed pine stand 14 9 2 e in red pine sta	9.62 13.36 6.9 and with an aver	A A A rage height of
Collections from 25 Top of tree at edge of stand Top of tree within stand Lower branches within stand Collections from to 25 feet	6/19 6/19 6/19 6/19 9 1/4 of tree 6/19	ed pine stand 14 9 2 e in red pine sta 14	9.62 13.36 6.9 and with an aven 9.62	A A A rage height of A
Collections from 25 Top of tree at edge of stand Top of tree within stand Lower branches within stand Collections from to 25 feet 6 feet	6/19 6/19 6/19 6/19 9 1/4 of tree 6/19 6/19	ed pine stand 14 9 2 e in red pine sta 14 8	9.62 13.36 6.9 and with an aven 9.62 8.51	A A A rage height of A A
Collections from 25 Top of tree at edge of stand Top of tree within stand Lower branches within stand Collections from to 25 feet 6 feet Collections from ad resulting from summ	6/19 6/19 6/19 6/19 6/19 9 1/4 of tree 6/19 6/19 6/19 1jacent 1-acre	ed pine stand 14 9 2 e in red pine sta 14 8 e plots with diff	9.62 13.36 6.9 and with an aven 9.62 8.51 ferent populatio	A A A rage height of A A on densities
Collections from 25 Top of tree at edge of stand Top of tree within stand Lower branches within stand Collections from to 25 feet 6 feet Collections from ad resulting from summ High pop. densit	6/19 6/19 6/19 6/19 6/19 9 1/4 of tree 6/19 6/19 6/19 6/19 1jacent 1-acre ber spraying sy 6/14	ed pine stand 14 9 2 e in red pine sta 14 8 e plots with diff 19	9.62 13.36 6.9 and with an aven 9.62 8.51 ferent population 13.05	A A A cage height of A A on densities A

Table 14. The comparison of mean dry weight of larvae collected from different pine species and under different conditions on red pine.

 $\frac{1}{-}$ Any two means having a common letter within a sample section are not significantly different at the 5 percent level. Cannot compare means across dotted lines without additional computation. The mean square needed for additional computation = 5.037 with 194 degrees of freedom.



validity of presumed causes, however. The obvious criterion for separating the pupal collection is pine species, but other possible causes for this phenomenon were not measured. Such things as insect density, host vigor on a particular site, and possibly even genetic differences within the shoot moth and host populations could greatly confuse the picture. It is well known that the five pine species under study do not do equally well on all sites. Table 9 shows the differences encountered in shoot moth density in this same plantation. Red pine is supporting twice the population as Scotch pine. As indicated by Miller and Heikkenen (1959), the Scotch has more than twice as many shoots as red pine and the difference in insects per infested shoot must be even greater than the insect density difference indicated in table 9. Before the differences in dry weight can be specifically attributed to basic differences in the respective hosts, all of the other factors will have to be held constant. This could be done either with artificially regulated populations under controlled conditions or the variables could be measured along with insect size. The data could then be subjected to a multiple analysis of covariance. In this case the data were not collected in such a way that they could be subjected to this type of analysis. Nevertheless, the differences shown in tables 12, 13, and 14 are demonstrably real even though their causes are not immediately discernable. These differences do demonstrate that future population studies involving different host species or possibly even of different populations will have to account for extreme and significant differences in insect size if the growth rate of the population is to be estimated. It is possible that measurement of living and dead insects is not sufficient to portray what an insect population is doing from year to year.



s it reasonable to believe that a female pupa reared from Scotch pine, ith a mean dry weight of 13.41 milligrams, is 43 percent more effiient at increasing the population than the female pupa reared from adjacent red pine with a mean dry weight of 7.68 milligrams? The difference in dry weight is highly significant, but is the population increase potential also significantly different in a linear manner? These questions have not been subjected to experimentation in this study, but the data in tables 12, 13, and 14 strongly suggest the usefulness of such an approach.

The data in the lower three subsections of tables 12, 13, and 14 are equally deficient as a result of the artificially selected categories. These are unrelated to measurements of causal phenomena and their interpretation is subject to some hazards.

The second subsection of the three tables shows the result of insect collections from different positions in a 30-year-old red pine plantation, having a mean tree height of 25 feet. Collections were made at the top of the tree near the edge of the stand, at the top of trees within the stand, and from lower branches within the stand. There was no significant difference in size of pupae and larvae collected from the top of the pine at the edge of and from the inside of the stand. In collections from the lower branches, the males were significantly different from those at the top of the trees, whereas the females could be shown to differ only from those at the top of the trees at the edge of the stand. The collection produced only eight females from the lower branches, and even though the magnitude of the differences is equal to or greater than that observed for the males, it could not be shown statistically that significant differences exist. The relationship of the

Antonian re- 1 at 15

mean in these three tables strongly suggests, however, that a true difference probably does exist.

The third section consists of collections from the top one-fourth of red pine crowns from three different plantations of different sizes. There was no difference between pupal or larval size on red pine 25 feet or 6 feet high. The male and female pupae collected from the 2feet high stunted red pine were significantly different from the other two plantations. No larvae were found on the small trees and a comparison was not made.

The last section of tables 12, 13, and 14 shows the mean dry weight of insects collected from adjacent one-acre plots which had extreme differences in number of insects per tree. These differences resulted from a summer spray experiment in 1957. In the high insect density plot, 75 percent of the shoots were infested, while only 5 percent of the shoots were infested in the low insect density plots in September of 1957. The spray had been applied at the time of egg hatch, so competition had been markedly reduced from the start of the generation. A comparison of these two means is the most conclusive comparison in tables 12 and 13. The difference in pupal dry weight for the two density levels was not demonstrably different for either male or female If categories of high and low insect populations truly reprepupae. sent the competitive situation as it exists in the plantation, the population density is not as important as might at first be expected. However, it must be noted that the adjacent one-acre plots were exposed to equal population densities up until the time of spraying. The summer population did not have the advantage of increased shoot growth due to the summer spray. Even though the population densities were
truly different, the condition of the red pine would be the same as if equal population densities existed, since growth for 1957 had essentially ceased by July 5, when the spray was applied.

Influence of Host on Insect Sex Ratio

A fourth influence which the different host and other environmental factors may impose on the European pine shoot moth population may express itself in the form of different sex ratios. The pupae collected for the data presented in tables 12 and 13 came from 15 different subcategories of the European pine shoot moth population in Ottawa County, Michigan. Each one of these sub-categories was subjected to a chi square frequency test to discern if the observed frequency of the two sexes deviated significantly from a 50-50 ratio.

Only the pupal collections from ponderosa pine showed a signific ant deviation from the expected ratio. Even though this frequency of 65 males and 42 females showed significance at the 5 percent level alone, it can also be evaluated in light of the 14 other available chi squares. In doing this, all 15 chi squares were tested for heterogeneity at the 5 percent level. This series of chi squares could not be shown to deviate significantly from a homogeneous series. Therefore, the significant difference encountered in the case on ponderosa pine must be rejected on the basis that it does not deviate significantly from the other chi squares within this series. It is apparently one of the exceptions which is expected 5 percent of the time. Therefore, no difference in sex ratios could be attributed to the place of pupal collection.

The relationship between dry weight of males and females collected from different ecological situations has a bearing on some of the sample

techniques which might be developed through the sexing of male and female pupae. In order to determine what relationship exists, the mean dry weight of males and mean dry weight of females from the three different collections were correlated. The correlation coefficient equalled .65. It can be stated, then, that .42 percent of the variance observed in the male pupae can be accounted for in the variance of the female and vice versa. It is of interest to note that 58 percent of the variance of one sex cannot be accounted for by measuring the other sex. It is apparent that those factors which regulate dry weight of a pupal population do not equally and concurrently influence both sexes. If they did, the correlation coefficient would undoubtedly be much larger.

The regression equations for estimating dry weight of one sex from individuals of the other equals:

 $\hat{\mathbf{x}}$ (males) = 6.47 + .354 (y - 10.65) $\hat{\mathbf{y}}$ (females) = 10.65 + 1.188 (x - 6.47)

MEASUREMENTS ON TREE PHENOLOGY IN RELATION TO SOME PHYSICAL ENVIRONMENT PHENOMENA AND INSECT BIOLOGY

A small, two-acre red pine plantation at Dansville, Michigan, was selected for this study. The trees were growing on a ten degree slope, bordered on one side by a cultivated field and on the other by a swamp. The pine trees were of two age classes. The pine on the slope were all planted in 1949, while those at the top of the hill were planted about 1952.

Phenological observations were made on those trees growing on the upper part of the slope and on the younger trees growing at the edge of the flat field. None of the trees growing under highly favorable conditions adjacent to the swamp were included in these measurements. The **physical** environment within the plantation was measured as intensively as time and equipment would allow. A hygrothermograph was maintained in a standard weather shelter four feet above the ground, and about half way down the slope. A continuous record of temperature and humidity was obtained from March 31 to October 6, except for a four-day period in May when the recording needle left the chart. Maximum and minimum temperatures were recorded under trees at various positions on the slope, and at different elevations on the trees. A recording rain gauge maintained a continuous record of the amount and intensity of precipitation. Soil moisture was measured in two different ways. First, Bouyoucos blocks were placed in replications of three blocks each under trees at a depth of six inches in the soil. These were located at the top and bottom of the slope. Unreplicated blocks were

also buried in the open, 6, 12, and 24 inches deep at the top, middle, and bottom of the slope. Resistance across these blocks was measured at approximately three-day intervals during the growing period of the pine and at one week intervals in late summer and early fall. Second, gravimetric moisture determinations were made on eight different dates throughout the same period. Samples replicated three times were collected from the bottom and top of the slope with a Viehmeyer tube from depths of 0-6, 9-15, and 18-24 inches. Bulk density samples, replicated three times, were collected at the end of the season from these same depths, so that percent moisture could be converted into inches of water in the soil. Three soil pits were dug from the top, middle, and bottom positions on the slope: A mechanical soil analysis was made from each of the distinguishable horizons in the profile. The pits at each level were dug to a depth of approximately five feet and then a Viehmeyer tube was driven down four more feet to see if the last observed layer changed in texture. A nutrient analysis was made from three composite samples collected from the top, middle, and bottom positions on the slope. Each composite sample was made by collecting approximately 50 cores from the top six inches of soil from one of the three transects laid out along the slope. The soil was analyzed by James A. Porter, Michigan State University Extension Specialist in Soils. The nitrates were extracted with a .016 normal acetic acid solution.

Phenological measurements were made on the red pine from April 8 to October 8. Two methods of sampling were used. Shoot elongation was evaluated by measuring a terminal, primary lateral, secondary lateral, and tertiary lateral at approximately three-day intervals from ten

different trees. The measurements on any particular date were replicated ten times for each of the four types of shoots. Measurements were made from a marked needle on last year's growth to the top of the terminal bud. Shoot elongation rates were taken from the same 40 shoots throughout the year. This is in contrast to the second sampling procedure in which ten shoots were collected at random at approximately one-week intervals. These shoots were brought into the laboratory and measured for length, width, needle length, needle dry weight, terminal bud length, lateral bud length, number of lateral buds, dry weight of the buds, cone length and weight, and the development of water shoots. These collections were made from May 13 to September 14.

Figure 15 shows the daily fluctuation in degree hours above 46 degrees Fahrenheit, precipitation, and soil moisture. A degree-hour is here defined as one degree Fahrenheit sustained for a period of one hour. Early spring and late summer values appeared to be much more variable than those recorded in late spring and summer. The majority of the lows in degree hours correspond to days or periods of precipitation. This relationship was very strong between May 15 and September 10. Precipitation at Dansville was above the average for Central Michigan. The total precipitation for the six-month period at Dansville equalled 21.12 inches while the average for the area was 17.84 inches for the same period. During the month of July, 5.22 inches of rain fell, while the reported average for the area was 2.67 inches.

Figure 15 also shows the amount of water present in the top 24 inches of soil on different dates. "Inches of water" was computed from gravimetric determination of soil moisture and soil density samples taken from the same area. The soil water value shown in Figure 15



represents only the area at the top of the hill. It does not include soil moisture measured at the bottom of the gradient next to the swamp. Seasonal depletion and subsequent recharging of the soil water is readily observed in the graph. Soil water was at its spring peak at the time of maximum red pine shoot elongation, and the seasonal low corresponds to the minimal elongation rate. All of the soil water shown in Figure 15 was not available for plant utilization. Daubenmire (1959), presented some permanent wilting percentages reported by Viehmeyer in 1938. For sandy loam, the permanent wilting percentage was 2.9 and for sand 1.0 percent. Since the percent moisture at Dansville for June was 2.1 percent and 2.4 percent for July, it is doubtful whether much of the soil water was available for plant use at this time. The soil and the red pine should have been calibrated to determine the wilting point; and the soil water could have been expressed as available soil water.

Figure 16 shows the relationship between the mean growth elongation rate per day of terminal red pine shoots and the daily temperature and soil moisture. The mean elongation rate was computed by taking the total increase in shoot length between two successive sample dates and dividing by the number of days elapsed between the samples. This was necessary since the interval between measurements was not constant. This method of presenting shoot elongation shows a high correlation with degree hours. Apparently, when the red pine is in a physiological state capable of elongation, temperature has a profound and controlling influence on the rate of this elongation. Only terminal elongation of red pine is shown in Figure 16, but primary, secondary, and tertiary laterals follow this same relationship closely with only the magnitude of the response being reduced. Figure 17 shows the uniformity of the







response between the shoots throughout the period of measurement. The small but uniform growth of the shoots after rapid elongation had ceased in early June appears to be primarily due to the growth of the terminal bud (table 15). Growth appears to be initiated in all shoots at the same time, but proceeds at a different rate, and continues for different periods of time. The descending order of magnitude for the rate and period of elongation is terminal, primary lateral, secondary lateral, tertiary lateral.

In figure 18 the average elongation rate per day of all four shoot types is shown, along with the average growth rate per day of spring larvae. Maximum growth rate of the larave corresponds closely with the maximum elongation rate of pine shoots. It is apparent that the resumption of growth is initiated a week to ten days sooner in red pine than it is in the insect. Also shown in figure 18 is the dry weight increase of summer larvae. It was not possible to graph summer larvae in terms of mean growth rate per day due to the loss of weight in the larval population after the first of August. It is believed that this loss of weight is not due to the rapid utilization of stored food, but simply to the fact that the population is purging its gut content and undigested food is no longer contributing to the individual dry weights of larvae. Since cessation of feeding occurs about this time, some loss in dry weight may be due to the utilization of stored food or even to ecdysis. However, this could not account for the rapid loss in weight which occurred from August 14 to August 28, since the utilization of stored food should be a uniform process throughout the late summer and fall. The mean growth rate per day of the needles, dry weight increase of the needles, mean shoot width, and mean dry weight

-	Mean				
Date	Shoot Length	Terminal Bud Length (ins)	Lateral Bud Length (ins)	No. of Lateral Buds	Cone Dry Weight (mg)
May 13	2.04	0	0	0	QO
May 18	7.97	.22	.13	1.89	17
June 1	12.72	.28	. 19	2.78	33
June 8	16.82	. 38	. 23	4.14	57
June 16	22.72	. 50	. 33	4.67	61
June 19	22.06	. 56	. 28	4.50	75
June 24	18.93	.61	. 42	4.20	85
June 30	21.78	. 68	.45	4.38	83
July 6	20.57	.73	. 48	4.80	80
July 10	21.46	.82	. 54	4.90	
July 13	20.25	.73	. 50	4.60	89
July 2 0	18.26	. 78	. 55		73
Aug. 3	18.24	.84	. 59		86
Aug. 17	18.25	.88	. 70	· · ·	90
Aug. 25	17.83	.93	. 75		67
Aug. 31	1 6.7 0	.90	. 63		112
Sept. 8	15.70	.87	.70		110
Sept. 14	18.51	1.05	. 79		103

Table 15. Some phenological observations made on 10 shoot samples collected at Dansville, Michigan, during 1959.

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of the buds is also shown in figure 18. There seems to be no striking relationship between these parameters and the dry weight increase of the summer larval population. It was thought that since the early instars of the larvae feed on the needles, needle elongation rate might warrant more detailed consideration. Figure 19 shows the mean needle length from the bottom, middle, and top position on the shoot at different dates. The needles are not all the same age or size throughout the length of the shoot on any particular date. At the time of peak hatch (July 6) the length of needle growth at the top lags about a week behind the needle growth at the bottom. The difference in age of the needles is undoubtedly even greater than this, since the top needles elongate for a longer period than do those at the middle or bottom. Newly hatched larvae have a variety of needle sizes and ages to feed on within the limits of a single shoot. The importance of this has not been evaluated in this study.



Figure 19. Mean needle length from bottom (first bar), middle (second bar) and top (third bar) positions on red pine shoots at Dansville, Michigan, 1959.

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AN ATTEMPT TO INTERPRET INSECT INJURY TO RED PINE IN LIGHT OF AN OBSERVED SOIL MOISTURE-NUTRIENT GRADIENT

This study was conducted in the Dansville plantation where the phenological observations discussed earlier were made. The red pine, which was growing on a ten degree slope adjacent to a swamp, exhibited differential growth from the bottom to the top of the slope. This growth response was observable from the time of planting up to 1960. Figure 20, which presents the growth rate of the pine at the top of the slope as the percentage of the growth rate at the bottom, clearly demonstrates this. Growth rates were obtained by measuring the internodal distance on each of 20 trees from the (a) bottom and (b) the top of the slope. From 1951 until the time of the study in 1960, all of the trees were subjected to attack by the European pine shoot moth. To determine what factors may have contributed to the differential growth response, a detailed evaluation was made of the environment along the slope.

Figure 21 presents the results of a nutrient analysis and a description of the soil profile, from the top, middle, and bottom positions on the slope. Only two major differences existed in the soil fertility from the bottom to the top of the slope. No nitrogen could be found at the top of the slope, while 25 pounds per acre of NO_3 were present at the bottom. Potassium tests showed that there was 36, 84, and 86 pounds present from top to bottom respectively. This situation probably resulted from the movement of these elements down the slope along with the accumulation of organic material at lower levels.



Mean growth rate, by year, of red pine growing at the top of the slope (low moisture-(Dansville, nutrient condition) expressed as a percentage of the mean growth rate of red pine growing at the bottom of the slope (high moisture-nutrient conditions). Michigan).







The soil profile for the three positions on the slope demonstrates a much stronger gradient than does the nutrient analysis. Figure 21 shows the mechanical analysis of soil samples collected from the various layers of the profile. The Bouyoucos or hydrometer method was used to determine the sand, silt, and clay percentages. At the top of the slope a seven inch layer of sandy loam overlaid a deep layer of coarse sand and gravel. Just beneath this deep coarse sand and gravel there was a six inch layer of sandy clay loam. This narrow layer undoubtedly had a pronounced and beneficial influence on the soil water available for plant use in the top 30 inches of soil. In contrast to this, the soil profile at the bottom of the slope had a very deep layer of sandy loam. There was very little if any textural stratification in the top 68 inches of soil. However, below the 22 inch level the sand was discolored by a high organic content. There was considerable unincorporated organic material present. It appeared as if this dark sand, with a high organic content, was once the bottom of the adjacent swamp which had been subsequently filled in through erosion down the slope. At the 30 inch level, free soil water began moving into and filling up the soil pit. Considerable root growth was observed just above this level. The 1941 Ingham County Soil Survey classified the entire plantation area as Oshtemo loamy sand (Veatch et al. 1941).

Figures 22 and 23 show the magnitude of the difference in soil moisture between the bottom and top of the slope. Figure 22 presents the results from a series of resistance readings across Bouyoucos blocks from April to September. Each point on the graph is an average of two successive readings taken approximately three days apart on a Bouyoucos moisture meter. The meter reads directly in percent available moisture.



WOISTURE (%)

Available soil moisture at various depths from the bottom and top of the slope as recorded from a Bouyoucos moisture meter at Dansville, Michigan, 1959. Figure 22.



Figure 23. Comparison of soil water in the top 2 feet of soil from the bottom and top of the moisture-nutrient gradient at Dansville, Michigan, 1959.

Since the blocks and the meter were not calibrated in this specific soil type, not much significance should be given to the available moisture units presented, at least for comparative purposes with other soil types. However, the comparison of the units from the bottom to the top of the slope can be made and itcan be assumed with confidence that the observed difference does approximate the real difference which existed between the extremes in this particular moisture gradient. The less uniform moisture conditions observed at the six inch level under the tree crown is due to rapid utilization of water by the pine and its replenishment by light rainfall. It would appear that the pine growing at the bottom of the slope are not limited by low quantities of soil moisture.

A gravimetric method was also used to evaluate the moisture gradient from the bottom to the top of the slope. The percent soil moisture, based on oven dry weight was converted into inches of water by taking soil density samples from various depths. Figure 23 shows the seasonal change in soil water in the top 24 inches of soil from the bottom to the top of the slope. During July when the soil water level was lowest from both positions on the slope, there was more water in the soil at the bottom of the gradient than was present during the periods of maximum soil water condition at the top of the slope.

Despite the presence of shoot moth from 1951 to 1960 (figure 24) the pine at the bottom of the slope was able to produce far better terminal growth than were those at the top. Figure 25 shows the accumulative mean terminal growth of 20 trees at the bottom and 20 from the top of the gradient. The pine at the bottom of the slope were able to take advantage of the better environmental conditions every year



(Points with a common letter do not differ significantly at the 5 per-The percent uninjured shoots on red pine in the Dansville study from 1948 to 1960. (Points with a common letter do not differ significantly at the 5 nercent level of significance.) Figure 24.



level) and top (low moisture-nutrient level) of slope at Dansville, Michigan, The mean height of red pine growing at the bottom (high moisture-nutrient from 1949 to 1960. Figure 25.

throughout the European pine shoot moth outbreak (figure 20 and 25). Figure 24 shows the course of the European pine shoot moth outbreak in terms of percent uninjured shoots. At the peak in 1956, only 15 percent of all the shoots in the stand escaped injury. Four years later, less than one percent of the shoots were injured. Every year after 1957, there was a significant drop in the injury caused by the European pine shoot moth population. Figure 26 shows the relationship between shoot moth caused injury at the bottom and top of the gradient. No significant difference could be shown in the frequency of injury at the extremes of the gradient when injury during years of shoot moth presence were analyzed together. However, the difference between injury from year to year was highly significant (figure 24) and a significant interaction between years and position on the gradient was also observed. A separate analysis of each year, independent of other years, showed that in 1958, significantly greater injury was sustained at the top of the gradient than at the bottom (top, 76 percent injured; bottom, 49 percent injured). This difference was shown to be significant at the one percent level of probability. No explanation can be offered as to the causes which may have produced the situation in 1958. Figure 27 (uninjured shoots) shows that the proportion of shoots injured was less at the bottom of the slope in 1955, 1956, 1957, 1958, and 1959. However, only in 1958 was the difference statistically significant. It may be that a sample size larger than 20 trees would have produced more consistent results.

The various types of injury observed were bushing, irregular branching, forks, and posthorn. The bushing injuries resulted when larval feeding destroyed all of the terminal and lateral buds and numerous .



The comparison of uninjured shoots on red pine growing at the top of the slope (low moisture-nutrient conditions) to those on red pine growing at the bottom of the slope (high moisture-nutrient conditions), from 1948 to 1960 at Dansville, Michigan. Figure 26.

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ope at Dansville, Michigan.

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adventitious buds develop on the side of the shoot. When a "bush" develops, it represents a total loss of at least one year's growth on that particular shoot. The many shoots produced from the adventitious buds are usually very small and short. It is usually not until the second year after bushing that a dominant shoot takes over. Bushing on a single stem appears to occur most commonly at intervals of two or more years. It likely is due to the high probability of at least one shoot in the bush escaping injury until it takes a dominant position on the tree. However, at the top of the hill during the years of peak injury, it was not uncommon for bushy shoots to show no discernible growth for as many as three years. This probably resulted from the destruction of the terminal and lateral buds by spring larvae and the destruction of all subsequently produced adventitious buds by the summer larvae. In any case, shoots attacked in this manner were often killed, and lower branches took over the terminal position.

Irregular branching was the most common type of injury produced. It varied somewhat in appearance, but the frequent presence of old pupal cases embedded in the bark was sufficient to establish the relationship between abnormal branching and the presence of European pine shoot moth larvae. The main stem of a healthy shoot usually produces five lateral branches. A variation of four to six branches would not necessarily indicate the presence of insect larvae for that year, since many trees in uninfested stands appear to display this type of branching. Lateral branches arising from the main stem at haphazard angles or the reduction in number of branches to one or two laterals was recorded as shoot moth injured.


Forking injury takes place when larval feeding destroys the terminal bud, and two or more uninjured laterals take a dominant position. If one of the branches comprising the fork is subsequently injured by shoot moth, the other branch may obtain sufficient growth to produce a single stemmed tree. Only a very few forks maintain themselves and produce multiple stems of equal size. "Forks" frequently result from previously "bushed" stems.

"Posthorns" occur relatively infrequently, compared to other types of injury. Only three percent of all injury to the main stem showed a condition of posthorning and less than one percent of the injury sustained by lateral branches showed this condition. A "posthorn" results when the spring larvae fails to prevent the shoot from elongating, and the shoot grows up past the point of attack. The attack weakens the base of the new shoot and it frequently falls over, with the growing tip in a downward direction. If the tip is not killed, it responds with a negative geotropic growth movement. If the point of attachment is sufficient to maintain the shoot until the wound heals, a "posthorn" will become established in the tree.

Counts of past injury were made on 15 trees at the bottom of the gradient and 15 trees at the top. The presence and type of injury was recorded from the node of each main stem and two laterals arising from the 1952 or 1953 node. This gave approximately 430 points where injury could occur at each end of the gradient. No significant difference could be shown in the relative proportion of the types of injury sustained by pine growing at the top and bottom of the slope during years when shoot moth was present. However, as figure 24 demonstrates, insect injuries significantly differed from year to year in the .

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plantation, and this difference significantly interacted with the location of the tree on the slope. This type of interaction would induce considerable variance in any type of analysis which would involve more than one year. An analysis was not made for each year independently of other years. Figure 27 presents the relative proportions of nodes affected with different categories of injury on pine growing at the bottom and top of the slope. Only in "bush" and "fork" development is a difference suggested. Bushing was more common at the top of the slope, while forking was more common at the bottom. This difference was not uniformly evident in all years. The difference was greatest during years of peak shoot moth injury except for the forks produced in 1955. The difference suggested by these curves is consistent with growth characteristics of the pine in light of the observed soil-nutrient gradient between the top and bottom of the slope. Forking is a process in which the host is vigorously growing past the insect attack, while bushing results because the insect is successful in completely stopping the growth of the host for at least one year. Those trees at the bottom of the slope would be expected to be more capable of producing growth under severe shoot moth attack than would those from the top of the gradient.



SUMMARY

This study investigates some of the basic relationships between the European pine shoot moth (<u>Rhyacionia buoliana</u> (Schiff.)) and its environment. The course of a shoot moth infestation was followed and the effect of injury to red pine growing under different conditions of soil moisture and fertility was evaluated.

Frequent insect collections supplied information on insect development, mortality and behavior through the course of a life cycle. Various measurements of larval size were evaluated in order to determine which best expressed changes in dry weight. A body index, computed from head capsule width and body length, was arrived at which accurately reflected changes in dry weight.

Winter mortality was studied in several southern and a northern plantation in Lower Michigan. There was no greater mortality in northern plantations than in southern.

By tagging new "tents" (pitch masses formed as a result of larval feeding) a pattern of spring activity correlated to spring temperatures was shown to exist. Mortality during the spring after larval activity was resumed was almost as high as overwinter mortality. Spring mortality appeared to result from disease but no primary pathogens could be isolated. Periods of increased mortality corresponded to periods of low spring temperatures.

Patterns of summer "tent" formation were studied in the same manner as spring activity. While spring activity was initiated first on the



lower south side of the tree and progressed around to the north side and up, summer activity was begun first in the top of the tree and continued longer in the lower branches.

Larval mortality in the needles was very high. This mortality rapidly declined to a uniform rate during the summer after the majority of the population reached the buds. The summer larvae increased in dry weight very rapidly after they hatched. The mean dry weight of individuals in the population reached a peak about the first of August and then declined until the following spring when they were about half of their maximum summer weight.

The alimentary tract of 378 larvae collected throughout the summer were examined in an effort to ascertain why the insects ceased to increase in dry weight during the summer. After July 15 the proportion of individuals in the population with undigested material in their gut dropped off rapidly. By August 1, approximately 50 percent of the larval population had purged the gut of food that had not been replenished, and by August 15th only relatively small trages of food could be found in the digestive tract. This condition was maintained throughout the last of August and September despite apparently favorable weather conditions. The larvae go through the winter without any food in their digestive tract. Larvae brought indoors during the fall in infested shoots took 6 to 24 days to resume activity. What caused the larvae to cease feeding and what prevented their resuming feeding activity could not be ascertained.

More eggs were deposited on red pine per unit of shoot length than on Scotch pine. This, coupled with more egg parasitization on Scotch pine, gave a higher summer larval population on red pine. Scotch pine

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had more bud tissue and lateral buds, which minimized the insect's attack in terms of economic damage. Red pine did not appear to be a superior host for population growth. For the 1958-59 generation, studied at Rose Lake, Michigan, the results showed no significant difference between adult emergence from the two pine species on either a shoot or tree basis. Larval mortality was consistently higher on red pine than on Scotch pine. However, pupal collections made from the 1957-58 generation in Ottawa County showed that red pine was supporting the highest insect population, with successively lower populations on Scotch, ponderosa, Austrian, jack and white pine.

Pupation rate was significantly faster on red pine than either jack or white pine. Adult emergence was shown to have occurred earlier on Scotch pine than red pine. The differnce in proportion of adult emergence on June 19 between red and Scotch pine was significant at the 1 percent level.

At the end of the 1958-59 generation both male and female pupae collected from red pine were significantly smaller in dry weight than those collected from Scotch, Austrian, and ponderosa pine. The largest pupae came from Scotch pine. No difference could be shown to exist between the dry weight of pupae collected from summer sprayed and unsprayed red pine plots which had different insect density. No difference in sex ratios could be attributed to the host or place of pupal collection.

A small, two-acre red pine plantation at Dansville, Michigan, was selected for studying the relationship between red pine phenology and some physical environment influences on the biology of European pine shoot moth. Detailed measurements on tree growth and the physical

environment within the plantation were made as intensively as time and equipment would allow. Soil water was at its spring peak at the time of maximum red pine shoot elongation, and the seasonal low corresponds to the minimal elongation rate. It appears that when red pine is in a physiological state capable of elongation, temperature has a profound and controlling influence on the rate of shoot elongation. The terminal as well as primary, secondary and tertiary laterals all closely followed this relationship with only the magnitude of the response being affected by shoot type.

Maximum spring growth rate of the larvae corresponded closely with maximum elongation rate of red pine shoots. Growth was resumed about a week to ten days sooner in red pine than was feeding activity in the insects. There was no striking relationship between dry weight increase of the summer larvae population and the following: (1) mean growth rate per day of the needles, (2) dry weight increase of the needles, (3) mean shoot width, and (4) mean dry weight of the buds. However, it was demonstrated that newly hatched larvae have a variety of needle sizes and ages to feed on within the limits of a single shoot.

A small plantation containing about 600 red pine growing on a 10 percent slope adjacent to a marsh was selected to study the effects of European pine shoot moth attack on red pine growing under the influence of different soil moisture and fertility conditions. The pine at the bottom of the slope had a mean height of 15 feet, while those at the top, within 30 yards of the others, averaged only 10 feet. The entire stand had been attacked by European pine shoot moth from 1951 to 1960. The intensity of the attack varied from less than 1 percent damaged shoots in 1960 to over 80 percent in 1956.

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A soil study demonstrated that the trees at the bottom of the slope were growing under more favorable conditions than those at the top. A significant difference in injury from year to year was observed in all trees and a significant interaction between year and position on the slope was also observed. Only in 1958 was there significantly greater injury sustained at the top of the slope than at the bottom. The types of injury observed were "bushing," "irregular branching," "forks," and "posthorns." The tendency for "forking" was greater at the bottom while "bushing" was more frequent at the top of the slope. "Irregular branching" was the most common type of injury while "posthorn" development constituted only a very small percentage of the total injury. Terminal tree growth was greater at the bottom of the slope each year in which shoot moth injury was present. The difference between growth of those trees at the top and bottom was smallest during years when the shoot moth population was at its peak, and largest when shoot moth was least abundant.



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