EFFECTS OF DEFOLIATION BY THE PINE BUTTERFLY (NEOPHASIA MENAPIA FELDER) UPON PONDEROSA PINE

by

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INTRODUCTION

Insects which feed upon the foliage of forest trees occupy a definite position in thoughts of forest culture and protection. Such insects become of economic importance only when occurring in an epidemic status, as forest trees readily withstand the slight destruction of foliage associated with normal feeding. Effects of severe defoliation are recorded in the direct mortality of trees, their susceptibility while in a weakened condition to the attacks of bark beetles, and a temporary reduction in the annual growth of those which survive.

Many records are available portraying the destruction of forest trees by defoliating insects. Depredations of the larch sawfly (Lygaeonematus erichsonii Konow) within the larch forests of the eastern United States and Canada are of knowledge to all foresters. Tremendous sums of money have been spent in the New England States in combating the gypsy moth (Porthetria dispar L.) and brown-tail moth (Euproctis chrysorrhoea L.). The spruce budworm (Cacoecia fumiferana Clem.) has taken a tremendous toll of commercial timber throughout the forests of the northeastern United States and Canada, and is now an important enemy of Douglas fir in the northern Rocky Mountains. Tremendous volumes of commercial Douglas fir and hemlock in western Oregon and Washington have been destroyed during outbreaks of the hemlock looper (Ellopia fiscellaria var lugubrosa Hulst).

There are other insects of perhaps less importance that could be included with this list of forest defoliators to depict the importance of the position which they occupy in the management of our forests. The pine butterfly (Neophasia menapia Felder), though not as serious an enemy of forest trees as some of the insects mentioned, is an important enemy of ponderosa pine throughout the forests of Oregon, Washington, and Idaho. The last serious outbreak of this insect occurred in 1921 and was located on the headwaters of the Little Salmon and Payette Rivers, Idaho. Though this outbreak was not reported until 1922, when the defoliation became so severe as to attract public attention, there was undoubtedly considerable destruction of foliage in 1921. This outbreak continued through 1923, but decreased so rapidly that in 1924 very few caterpillars could be found.

HISTORY OF PINE BUTTERFLY EPIDEMICS

The first available record of a pine butterfly epidemic dates back to the year 1882. At that time R. H. Stretch (15), while on the North Transcontinental Survey, reported a severe epidemic of this insect as occurring in the ponderosa pine stands near Spokane, Washington. Mr. Stretch's report was a splendid description of this epidemic and contained a number of observations relative to the seasonal history and habits of the insect, many of which were substantiated during later investigations. Additional information on subsequent outbreaks was given by C. V. Piper (12), Professor of Entomology at Pullman, Washington, who reported that in 1883 the bay at Seattle, Washington, was nearly covered by the floating bodies of the butterflies.

Professor Piper also reported that in 1890 and 1895 the insects were so abundant in the Olympic Mountains of Washington that thousands of the dead adults were strewn about the ground. A severe outbreak of this butterfly in ponderosa pine stands near the Payette Lakes, Idaho, was recorded by Mr. H. C. Shellworth (14), Boise-Payette Lumber Company, as occurring in 1893. In 1894 a large number of butterflies were recorded (12) on Mount Hood, Oregon, and the following year areas of nut pine (listed as Pinus monticola) were reported as dying. In 1895 some 600,000,000 board feet of ponderosa pine were destroyed by this insect on the Yakima Indian Reservation near Goldendale, Washington. The outbreaks which occurred during this period were apparently associated with the disturbance of some natural factor of control throughout the Northwest.

Severe epidemics (12) occurred in the ponderosa pine stands of the Boise Basin and Moscow Mountain areas in 1897 and 1898, in the vicinity of Mount Adams in 1903, and near Spokane, Washington, for the second record in 1907. The next epidemic of which records are available is the one which occurred in 1921 in the vicinity of Payette Lakes, Idaho, some 30 years following the previous outbreak recorded in 1893 (14).

DISTRIBUTION AND HOSTS

Epidemics of the pine butterfly have been recorded from various sections of the Northwest (15, 7, 14). Essig (5) records its presence in California, Nevada, Utah, Colorado, Oregon, Washington, Idaho, and British Columbia. Holland (11) gives its occurrence as the Northern Pacific States, while Edwards (4) records the range as being the pine forests of the Pacific slope, extending as far east as the eastern or front range of the Rocky Mountains.

Though throughout the range of this insect practically all species of pine are attacked, ponderosa pine (Pinus ponderosa Laws.) is apparently the preferred host. Fletcher (7) records the pine butterfly as severely injuring Douglas fir (Pseudotsuga taxifolia (Poir) Britt.) in the coast regions of British Columbia, and Stretch (15) lists white fir (Abies balsamii (undoubtedly Abies grandis)) as a host. The writer has no record of this insect attacking any other tree species than pine. During the late Idaho epidemic, Douglas fir trees in association with and adjacent to infested areas of ponderosa pine were severely defoliated, and many observers believed the pine butterfly to have been responsible for the injury. However, the variation in the time of attack with marked difference in the character of defoliation, as well as the presence of empty pupal cases, readily established the spruce budworm (Cacoecia fumiferana Clem.) as being responsible for the injury to Douglas fir.

DESCRIPTION*

Adult

Stretch (15) has very accurately described both the male and female. Nevertheless a brief description intended for field determinations may not be out of place in this paper. The pine butterfly very closely resembles the common cabbage Pieris. It has a wing expanse of about 43 mm.; antennae black; head and body black above and white beneath; covered with hairs (pl. 1, A).

MALE.--The scales of the fore wings of the male are pure white, except for the black markings on the tips and a streak along the costal vein. On the under side the same general markings occur.

The hind wings are white, except along the tips, which are lightly touched with black. On the under side the markings are heavier, and the black veins show through on the upper side.

FEMALE.--The scales of the fore wings of the female are of a light yellowish color. The black markings are like those of the male, with a black apical margin in addition. On the under side the markings are the same.

The hind wings have the same yellowish tint as the fore wings, but they differ from those of the male in having heavier black lines along the tips. More black appears on the under side, all of the veins being marked with broad lines. On many specimens, but not all, there are

* The descriptions given in this paper have been previously published by the writer (6) in the Journal of Agricultural Research, Vol. 33, No. 4, Aug. 15, 1926.

bright orange-red spots along the apical margin.

Egg

The eggs (pl. 1, A), 1-1/2 mm. in length, are laid along the pine needle, in rows of 5 to 20, at an angle of 45° pointing toward the end of the needle, and are firmly cemented together. Fletcher (7) has described them as the "most beautiful objects, resembling minute emerald-green Florence flasks, vertically lined with delicate lines and with a beaded rim of porcelain-white knobs."

Larva

Although the larval stages have been described fully by Edwards (4), a brief description of the young and mature larvae is included here for the convenience of the reader in determining the insect in the field. The larva is 2 mm. in length as it hatches from the egg; body a pale green, and head shiny black. The mature larva (pl. 1, A) is approximately 25 mm. in length; body a dark green, with two white lateral stripes down each side; head pale green, dotted with raised white tubercles, each giving rise to a short hair; anal shield similarly covered with white tubercles, produced behind into two blunt, well-separated projections; body skin covered with a fine pubescence; prolegs on abdominal segments 3, 4, 5, and 6 and the normal anal prolegs; crochets of prolegs biordinal, arranged in longitudinal band.

BIOLOGY AND HABITS *

There is but one generation of the pine butterfly yearly in Idaho. This fact, however, is rather confusing to the casual observer or collector, since there is a marked overlapping of the seasonal history events by individuals of this one brood. Elevation and exposure have a marked influence on the development of the insect. Imagoes, especially males, are often seen at high elevations as late as October.

The overwintering eggs hatch about the time that the new needles begin to appear on the western yellow pine. This occurs during the first half of June, depending upon the season. The development of the young larvae is very slow during the first two weeks. They feed in clusters, encircling the needle, with their heads pointing toward the tip of the needle, making a tiny ring of black beads.

Only the fleshy part of the needle is eaten by the young larvae, but after the first molt the entire leaf is destroyed. During the first molt the shiny black head covering is shed, the subsequent color being a yellowish green. When the larvae are about half grown the habit of feeding in clusters is no longer continued, but often two or more may be found upon the same needle, especially if there is a shortage of food material. After the second molt growth is very rapid, and the larvae are approximately full-grown by the last of July, or about 50 days after hatching.

* The biology and habits given in this paper have been previously published by the writer (6) in the Journal of Agricultural Research, Vol. 33, No. 4, Aug. 15, 1926.

When mature, the larvae lower themselves by a silken thread, which sometimes is 75 feet or more in length, from the trees to the ground, where they pupate as chrysalids on shrubs, grasses, limbs, fences, tree trunks, or other objects. The pupal stage lasts from 15 to 20 days. Mating occurs almost immediately after the emergence of the adult, and oviposition takes place a few hours later. These eggs overwinter and hatch the following June.

The normal habit of the female is to deposit her eggs on the needles at the top of mature trees. However, in areas which have been severely defoliated she apparently is forced to seek suitable foliage on younger trees or else migrate to other areas, which she does in numerous instances.

NATURAL ENEMIES

As all recorded outbreaks of the pine butterfly were evidently of short duration, it is evident that this insect must be subjected to powerful biotic influences. Records of outbreaks that dropped into obscurity between seasons apparently support this position. Between outbreaks this insect is held under rather definite economic biological control.

The existence of this influence was forcefully portrayed during the recent Idaho outbreak. Though in 1923 this outbreak was still in a severe epidemic status, in 1924 it was very difficult to find any caterpillars, and but few adults were observed. This sharp reduction was due primarily to an increased activity of natural enemies, as an examination of several lots of larvae in 1923 revealed the fact that over 90 percent were parasitized. The most important enemy of this destructive forest insect is a parasitic ichneumonid, Theronia fulvescens Cress. (pl. 7). This insect apparently oviposits on the butterfly caterpillars, which, though severely weakened, are usually able to reach the pupal stage. The adult parasite emerged from the pine butterfly pupae in September, and in 1923 the defoliated areas were reported to have been alive with these so-called wasps. The parasitized pupae are easily distinguished by their dark brown color, the normal pupae ranging from pale to dark green.

Aldrich (1) records a similar reduction in an outbreak of the pine butterfly at the time of the 1896 outbreak in the Moscow Mountains, Idaho. He writes of this remarkable occurrence as follows:

"- - - - - -At this point Theronia fulvescens attracted my attention as a parasite of the butterfly, material reared by me from pupae of the latter being determined by the Bureau of Entomology. The parasite reached its maximum in 1898, at which time it swarmed in the woods in late summer in incredible numbers. In places the air was full of them and they made a very perceptible humming sound like a swarm of bees. At the University of Idaho, about seven miles from the forests, it was abundant, and on one occasion I collected 40 specimens by picking them off the walls of the administration building while going once round it--and this seven miles from where any of them matured.

"The next spring the extermination of menapia seemed complete all over the Northwest. In ten years afterwards I think I saw only one specimen alive. Only in the - - - - -

"The parasite died out at once, and was not seen again for several years. It may have other hosts here, but no other caterpillar is abnormally abundant in our forests, so the numbers of the parasite of necessity fell at once almost to zero, on the disappearance of the principal host. I have never seen another case so striking of the effects of parasitism on both host and parasite. I have made no observations on fulvescens as a secondary parasite."

The seasonal history of this parasite is not known, but as the adults appear in the fall and the butterfly caterpillars the following summer, it is apparent that it must have an alternate host or else the adults overwinter.

During the recent Idaho outbreak a predacious hemiptera (Podisus placidus Uhler) was present in fairly large numbers and was apparently attacking living pine butterfly larvae. Stretch (15) recorded the occurrence of a Pentatomid at the time of the outbreak near Spokane, Washington, in 1882. Though this insect is undoubtedly primary in its attack, the importance of the role which it plays in reducing epidemics is not known.

ECONOMIC IMPORTANCE OF PINE BUTTERFLY DEFOLIATION

Reports of former pine butterfly outbreaks did not include any record of the destruction of timber as a result of the defoliation. This lack of information left an impression that the injury associated with this defoliation was not sufficiently severe to cause tree mortality. However, it was believed that many of the trees defoliated in 1922-23 had been so severely injured as to make their recovery rather doubtful. To substantiate or disprove this contention a study of the actual effects of pine butterfly defoliation was instituted in 1924, the results being presented in this paper. This study plot was located in an infested area near New Meadows, Idaho, in Sec. 9, R. 2 E., T. 19 N. Annual examinations were made from 1924 to 1930, and in 1933 and 1935, when all effects of the injury were believed to be over.

Description of Study Plot (pls. 1 & 2)

The plot selected for this study was located on the east side of Meadow Valley, Idaho, in an area of mature ponderosa pine lying between the valley and a belt of fir at a higher elevation. Though there were some scattered Douglas fir trees, the area supported a very heavy stand of ponderosa pine. The defoliation of this area was considered as being representative of the injury throughout the infested area. One hundred trees varying in diameter from 12 inches to 58 inches d.b.h., with an average of 34.6 inches, and of a height to indicate a site 4 classification were marked for this study.

Though in 1923 the caterpillars were still present in epidemic numbers, the defoliation within the study area was not as severe as that which occurred the previous season. Furthermore, the 1923 defoliation was largely confined to small trees and reproduction. This condition is perhaps due to the fact that following the 1922 defoliation there was not sufficient foliage remaining in the tops of old trees for egg-laying purposes and the females were obliged to depart from this normal habit and oviposit upon the foliage of smaller trees. As a result of this condition the 1923 growth of needles in the tops of the larger trees was not very severely injured.

At the time this study was instituted data were taken from all trees relative to the d.b.h. and height, the degree or severity of defoliation, character of 1923 and 1924 foliage growth, crown classification as an indication of growth, and increment cores.

Three broad measurements of defoliation were recorded. Unfortunately, a closer refinement in the measurement of defoliation was not feasible. This condition is regretted, as such data would undoubtedly have been of material benefit in establishing a clearer relation between the injury and subsequent mortality.

A - Very light defoliation. 75-90 percent of old foliage remaining.

B - Medium defoliation. Approximately 50 percent of old foliage destroyed, which permitted an unobstructed view through the crown.

C - Severe defoliation. Practically all of the old foliage destroyed except small tufts of 1922 growth at end of branches.

The 1923 and 1924 foliage was recorded in three broad classifications. It is also regretted that more specific measurements of foliage growth could not be made; however, with mature trees the securing of such data is a difficult task.

V - Vigorous - normal, full-length needles

M - Medium - short, sparse, off-color foliage

F - Feeble - stubby growth, yellowish needles

The crown classifications were recorded as follows:

∧ Thrifty - pointed crown indicating rapid growth.

∩ Medium - round tops.

⌒ Very poor - flat top with thick, large branches, which is an indication of slow growth.

Increment cores were taken during all examinations, which served to provide a continuous history of basal growth.

Mortality of Defoliated Trees

During the period of this study, 14 of the trees within the study plot were attacked and killed by the western pine beetle (Dendroctonus brevicomis Lec.), 12 died from the effects of defoliation, and there was 1 windfall. This windfall has been disregarded in the analysis of data, and all compilations are based on 99 trees instead of 100. Though no question exists as to the responsibility of bark beetles for the death of some trees, one may be reasonably sure that some of those attacked by beetles would have died from the effects of defoliation alone. Though the agency responsible for the death of a few trees was difficult to determine, with such border-line cases a decision was made after a careful analysis of all data.

Trees killed by defoliation were usually easily recognized from a sour or fermented sap condition, the odor of which was often detected for a distance of several feet. It is possible that the increased temperature to which the boles of the trees were subjected due to the opening of the stand by defoliation may have been a factor in creating this fermented sap condition. The inner bark and sapwood of some trees were saturated with an excess of moisture which flowed quite freely from any opening made through the bark. So excessive was this moisture that on some trees the bark on the lower 12-15 feet of the bole was actually saturated, a condition which was noticeable for a considerable distance. The elimination of the processes of transpiration through the destruction of all or a large percentage of the foliage is directly responsible for this condition. Maximov (10) states:

> "Only an inappreciable part of the water required by the plant for its growth and development is actually assimilated in the process of photosynthesis. By far the greater part absorbed from the soil is eliminated unchanged, being either dispersed as vapor in the process of transpiration, or, more rarely, exuded as drops of liquid in the process of guttation. A land plant, indeed, represents as it were a kind of wick along which a continual stream of water ascends from the soil and escapes into the atmosphere. The total water content of a plant at any given moment is small in comparison with the quantity that may pass through the plant in twenty-four hours, for we have seen above that, even under shade conditions, the leaves of some plants are able to replace the whole of their water in the short space of an hour."

Therefore, as defoliation has no immediate physical effect upon the bole or roots, an unimpaired root system which continues to supply moisture to a tree that is unable, owing to the lack of foliage, to expell the surplus will result in the accumulation of an abnormal quantity of water in the lower bole.

The effects of the injury apparently last for several years, with trees dying 8 or 10 years after the cessation of defoliation. Studies of the effects of spruce budworm defoliation on balsam fir made by Craighead (3) show that tree mortality continued for 9 or 10 years following the cessation of the outbreak. In these studies Craighead shows that in severely defoliated areas from 50 to 70 percent of the trees which fail to recover from the injury died within the first four years, and that during the subsequent 5 or 6 years the additional 30 to 40 percent succumbed. Graham (8) records the recovery of tamarack, which to all appearances had been dead for ten years following defoliation by the larch sawfly.

Table 1. - Dates of tree deaths

Year	Number of trees: Killed by defoliation	Number of trees: Attacked by western pine beetle
1924	0	4
1925	3	3
1926	1	3
1927	1	3
1928	2	0
1929	1	0
1930	0	0
1931	2	1
1932	0	0
1933	1	0
1934	1	0
1935	0	0

From the preceding table it will be noted that trees succumbed to the effects of defoliation as long as 11 years after the cessation of the outbreak. One may properly assume that the factors responsible for this mortality, as well as for the weakened condition of the trees attacked by beetles, were the loss of foliage and the physical condition of the trees at the time of defoliation.

Table 2. - Severity of defoliation and tree mortality

Degreesof defoliation	Number of trees: In plot	Number of trees: Living 1935	Number of dead trees: Killed by defoliation	Number of dead trees: Killed by D. brevicomis	Percent of trees killed
A (Light)	1	1	0	0	0
B (Medium)	15	15	0	0	0
C (Heavy)	84	58	12	14	30.9

Though 30.9 percent of the heavily defoliated trees were killed, it is believed that a closer refinement in the measurement of defoliation would have shown them to be the most severely injured individuals. In the analysis of the data secured it has been necessary to consider

that the defoliation of all the dead trees was equal in severity. The only conclusion to be drawn from the preceding tabulation is that all trees which died from defoliation or the attacks of bark beetles were severely defoliated. Though these data can be properly construed as closely associating the mortality of trees with the severity of the defoliation, the available data will not permit the drawing of a closer relationship.

Table 3. - Crown forms and tree mortality

Crown class	Number of trees in plot	Killed by defoliation		Killed by D. brevicomis		Number of trees living 1935
		Number	Percent of total	Number	Percent of total	
∧	20	2	10.0	1	5.0	17
⌒	46	5	10.8	10	21.7	31
‿	33	5	15.1	3	9.1	25

Graham (9) states that dominant trees are more resistant than suppressed individuals in that such trees have a larger reserve of stored food. Data available from this study were not sufficient to establish this correlation.

Aside from the preference shown by the western pine beetle for trees with round crowns, no apparent relationship existed between the different crown classifications and mortality following defoliation. To check the relationship of crown forms to the vitality or growth of trees, the average basal growth for the five years preceding defoliation was determined for the three classifications.

Table 4. - Crown forms and radial basal growth

Crown classification	Pointed tops	Round tops	Flat tops
Average radial increment of all trees 1917-1921	5.29 mm.	4.31 mm.	4.24 mm.

The above data show an expected correlation in the relation of crown forms to tree vitality as indicated by radial growth. There is not a great difference in the basal increment of the round crowns and flat tops, which would be a normal condition in such a mature timber stand. As the data used absorbed some rather marked individual departures from the averages, the above correlation would not hold for individual trees.

Table 5. - Diameters, heights, and tree mortality

	Living 1935	Killed by D. brevicomis	Killed by defoliation
Average d.b.h.	34.27"	36.85"	35.83"
Average height	95.95'	99.28'	97.50'

Though a difference is shown in both diameters and heights for the different groupings, it is so slight that no significance has been given to it.

Table 6. - Foliage growth in 1923 and tree mortality

Trees	Number of trees	Condition of foliage		
		U-Normal	M-Short	F-Stubby
Living 1935	73	9	58	6
Killed by defoliation	12	-	11	1
Killed by D. brevicomis	14	-	11	3

The only conclusion to be drawn from these data is that the occurrence of normal foliage the first year after defoliation is an indication of trees with high resistance to the injury and of rather assured recovery. However, it would appear that a close association exists between the severity of defoliation and subsequent foliage condition, as the 9 trees with normal foliage were listed as having a medium defoliation in 1922. The remaining 6 trees with medium defoliation all produced "M", or short, foliage in 1923. Some interesting facts were drawn from a comparison of the 1923 and 1924 foliage. All trees with normal foliage in 1923 produced comparable growth in 1924, and all of these trees recovered from the injury. Only 6 of the trees with "M" (short) foliage in 1923 showed a reduced, or "F" (stubby), foliage in 1924. Three of these six trees died, one failed to add any growth from 1923 to 1933 inclusive, another added no growth from 1923 to 1930 inclusive, while the other after adding no growth from 1923 to 1925 apparently effected a recovery from the injury. All trees with "F" (stubby) foliage in 1923 either showed an increased growth in 1924 or else died some few years later. It would seem that a comparison of foliage growth for the two years following defoliation offers a fair indication of the tree's ability to recover from the injury. Here again the necessary brood classification in the measurements of foliage growth is unfortunate, as it does not permit a closer correlation of these data.

Summary of Preceding Tabulations

The preceding tabulations offer no explanation of the marked variations in the final effects of defoliation; however, as previously stated, it is believed that a finer measurement of the amount or percent of leaf surface destroyed would have shown a closer relationship between the injury and subsequent tree mortality. Craighead (3) shows a direct correlation in the death of spruce and balsam to the severity of the defoliation by the spruce budworm. Though defoliation is obviously the principal factor contributing to the death of the trees, it would seem that the chemistry of the tree at the time of attack is a factor in determining its power of recovery. As such vital functions in tree growth as transpiration, assimilation, and respiration are directly affected by defoliation, a variation in the chemistry, or food reserve, of different trees would perhaps be met with a corresponding variation in resistance. Graham (8) records variations in the reaction of tamarack to defoliation.

The water content of defoliated trees is undoubtedly an important factor in their reaction. Though it is apparent that with a marked excess of moisture trees die very quickly after defoliation, the importance of lower concentrations is not known. As excess water is expelled through the foliage, it would seem that a low moisture content would be advantageous to the recovery of defoliated trees. Under such a premise a dry season or a period of drought might prove to be beneficial during epidemics of defoliating insects.

RELATION OF BASAL INCREMENT TO DEFOLIATION

The following tabulations are offered as depicting the peculiar and variable conditions of growth at the base of defoliated trees as indicating their reaction to the injury. These data were compiled from a series of increment cores taken from the same general location on each tree so as to secure comparable records. This continuous record permitted the establishment of a definite history of the basal growth for each tree (pl. 5). It is unfortunate that this plot was not established until 1924, as no data are available for the years during which defoliation occurred.

From a careful analysis of all increment cores, which included those from uninjured trees on a check area some few miles distant, a very distinct ring-growth pattern was established for the area. In this pattern the 1921 growth ring was very distinct, with a wide spring wood and an unusually wide summer wood which followed the narrow spring and very narrow summer growth of 1920. Though all illustrations included with this paper show this peculiar pattern, it is clearly depicted in core No. 12, Plate 4. Though from this pattern the 1922 growth could be identified, difficulty was experienced with cores where only one growth ring was made during the years of 1923 and 1924. Though it was impossible to definitely determine the year this growth was made, it is assumed that it occurred in 1923. This decision was influenced by the data from trees which missed no annual increment and showed the 1924 growth to be less than that of 1923. This position is supported by Craighead in his studies of the spruce budworm (3), who states:

"Following the defoliation, the first indication of lowered vitality is the reduction in the current year's wood on the terminal portion of the trees. The second or third season following severe defoliation, the tree may fail to add an annual ring at the base and in some trees as much as three years' wood is lacking on the lower trunk before the tree dies."

The measurements of all cores were made with a precision comparator graduated to 1/100 part of a millimeter, with a binocular microscope as an aid to greater accuracy.* To eliminate the mechanical variations which occur in different cores from the same tree, the material secured in 1935 was used for the final measurements.

* The writer wishes to acknowledge the assistance given by T.T.Terrell, Scientific Aide, Bureau of Entomology and Plant Quarantine, in the measurement of the increment cores secured in connection with this project.

Table 7. - Years of no basal increment

Years of no increment subsequent to 1922	Number of trees: Living 1935	Killed by defoliation	Killed by D. brevicomis
No years of increment missed (pl. 3)	7	0	1
No increment added	0	8	11
Years 1923-4 missed (pls. 4 and 6)	18	0	0
Years 1923-4-5 missed (pls. 5 and 6)	23	1	1
Years 1923-4-5-6 missed	2	0	0
Years 1923-4-5-6-7-8-9-30 missed	1	0	0
Years 1923-4 and 32 missed	1	0	0
Years 1923-4 and 33-34 missed	0	1	0
Years 1923-4-5 and 29-30 missed	0	1	0
Years 1923-4-5 and 31-32 missed	2	0	0
Years 1923-4-5-6 and 30 missed	1	0	0
Years 1923-4-5-6 and 29-30 missed	0	1	0
Years 1923-4-5-6 and 34-35	1	0	0
Years 1923-4-5-6-7 & 30-31-32 missed	1	0	0
Years 1923-4-5-6-7-8-9-30 & 35 missed	1	0	0
Years 1923-1933 inclusive (pl. 7) *	1	0	0
Years 1923 and 1925 missed	0	0	1
Years 1923 and 1926-7-8-9 missed	1	0	0
Year 1924 missed (pl. 4)	12	0	0
Year 1925 missed	1	0	0
	73	12	14

A reduced or in many instances the entire loss of basal increment is a normal condition associated with the defoliation of coniferous trees. However, no explanations are offered for the outstanding and peculiar variations which occurred in the basal growth of the defoliated trees as shown in the preceding tabulation. Many trees apparently recovered only to lapse into another period of no basal growth, demonstrating the continuing effects of defoliation. The tabulation shows that all 19 trees which added no basal increment after the first year of severe defoliation either died from the direct effects or were attacked by bark beetles. In contrast to the fate of these trees only one of the 8 trees which added increment each year was lost during the period of this study. This tree, attacked by <u>D. brevicomis</u> in 1931, was one of the most severely weakened individuals of this group, with the radial basal growth being reduced from 1.34 mm. in 1921 to .08, .19, and .13 mm. for the years of 1923, 24, and 25.

With the necessity of accepting the broad classifications of defoliation, the many variations in the preceding data are difficult to explain except through the possible differences in the chemical reaction of different trees to comparable injuries.

Table 8. - Years of no basal increment and basal growth prior to defoliation

Basal increment subsequent to defoliation	Number of trees	Average annual radial growth 1917-1921 inc.	Percent dead in 1935
No years of increment missed	8	1.52 mm.	0%
No increment in 1924	12	1.31 mm.	0%
No increment in 1923-24	18	1.02 mm.	0%
No increment in 1923-24-25	25	.83 mm.	8%
No increment subsequent 1922	19	.56 mm.	100%
AVERAGE ANNUAL RADIAL GROWTH FOR ALL 99 TREES - .91 mm.			

The preceding data show a distinct relationship between the rate of growth prior to defoliation and the number of subsequent years during which no basal increment was made. It is regretted that this tabulation could not be extended to include all variations in growth as shown in the table on page 22; however, sufficient cases were not available to permit the establishment of an average figure. Though there were individual departures from the averages used in establishing the preceding tabulation, it would seem that the rate of growth prior to defoliation is a fair index of the rapidity and perhaps the permanency of the recovery from such injuries.

Table 9. - Growth prior to defoliation and tree mortality

Trees	Number	Average annual radial growth 1917-1921 inc.	Departure from the average annual radial growth (.91 mm.) for all trees
Living 1935	73	.98 mm.	+ .07 mm.
Killed by _D. brevicomis_	14	.71 mm.	- .20 mm.
Killed by defoliation	12	.67 mm.	- .24 mm.

Though these data show that prior to defoliation the rate of growth was more rapid for the trees which survived the injury than for those which died, there were of course marked individual departures from the average figures used. Though the trees killed by bark beetles showed a slightly greater growth than those which died from the effects of defoliation, it was not considered as being of any significance.

Table 10. - Growth prior and subsequent to defoliation and tree mortality

Classifications of radial growth	Number of trees	Average annual radial growth 1917-1921	Average radial growth of group after defoliation*	Died during study: By defo-liation	Died during study: By *D. brevicomis*
1.00-2.00 mm.	12	.33 mm.	.17 mm.	2	3
2.00-3.00 mm.	25	.48 mm.	.22 mm.	6	6
3.00-4.00 mm.	14	.74 mm.	.31 mm.	0	0
4.00-5.00 mm.	12	.93 mm.	.44 mm.	2	1
5.00-6.00 mm.	16	1.08 mm.	.51 mm.	1	3
6.00-7.00 mm.	4	1.32 mm.	.52 mm.	0	0
7.00-8.00 mm.	4	1.54 mm.	.62 mm.	1	1
8.00-9.00 mm.	5	1.66 mm.	.59 mm.	0	0
9.00-10.00 mm.	4	1.87 mm.	.94 mm.	0	0
10.00-11.00 mm.	1	2.01 mm.	.55 mm.	0	0
11.00-12.00 mm.	2	2.34 mm.	1.17 mm.	0	0

The preceding table again shows slower growing trees to be more susceptible to the effects of defoliation and attacks of bark beetles than thrifty growing individuals. Here again the variation in the data suggests the existence of other factors which are undoubtedly of primary importance.

* The average radial growth subsequent to defoliation refers to living trees only and is the average from 1922 to 1935 inclusive.

Table 11. - Radial growth record of trees killed by defoliation

Measurements in millimeters

Tree number	1917	1918	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935
2	.99	1.13	1.16	.48	1.13	.55	0	0	0	0	0	0	Dead						
5	1.09	.96	1.11	1.32	.95	1.58	0	0	Dead										
19	.66	.65	.37	.31	.47	.38	0	0	0	0	0	0	0	0	0	0	0	Dead	
37	.50	.48	.36	.39	.49	.29	0	0	0	0	0	Dead							
43	.36	.66	.67	.44	.67	.28	0	0	0	0	.18	.10	0	0	Died 1931 or 1932				
52	.27	.33	.22	.29	.41	.15	0	0	0	Dead									
54	1.19	2.16	1.42	.94	2.22	1.33	0	0	0	.08	.15	.06	0	0	Dead				
55	.46	.36	.45	.30	.69	.38	0	0	0	0	0	Dead							
57	.50	.60	.34	.32	.48	.30	0	0	.13	.18	.05	.05	.09	.08	.07	.06	0	0	Dead
65	.56	.43	.48	.48	.55	.35	0	0	Dead										
67	.39	.36	.38	.32	.42	.35	0	0	0	.07	Dead								
69	.42	.39	.36	.28	.44	.36	0	0	Dead										

The preceding table graphically presents the losing fight which the trees made for recovery. Trees number 43, 54, 57, and 67 at one time seemed to have effected a recovery only to lapse into a second period of no basal increment and ultimate death. Tree number 5 shows a rapid growth prior to defoliation far in excess of the average for the plot, though it died in 1925. Prior to defoliation the growth of tree number 19 was far less than the average for the plot, yet it lived for 11 years, with no basal increment before dying. Though these variations must be partially explained by the difference in the severity of defoliation, there were undoubtedly other contributing factors. Tree number 57 was an interesting example of a losing struggle for survival when it would seem that the battle had been won. The tree lost only two years of growth immediately following defoliation, recovering in 1925 and 1926 with a radial growth of .13 and .18 mm. However, in 1927 this growth dropped to .05 mm., remaining practically the same for the subsequent five years, with no growth whatever in 1933 and 1934. In 1935 the tree was listed as dead with a typical "sour sap", though there was no great excess of water.

Table 12. - Radial growth record of trees killed by *Dendroctonus brevicornis*

Measurements in millimeters

Tree number	1917	1918	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935
23	1.03	1.58	1.64	1.38	2.27	1.51	0	0	0	.56					Attacked 1927				
32	.21	.30	.25	.24	.30	.24	0	0	0						Attacked 1926				
33	.94	1.20	.96	.92	1.14	.97	0	.14	0						Attacked 1926				
53	1.06	1.25	1.26	.98	1.34	.87	.08	.14	.13	.40	.51	.61	.32	.76	Attacked 1930				
68	.17	.23	.44	.38	.43	.18	0	0							Attacked 1925				
70	.36	.52	.58	.40	.44	.47	0	0							Attacked 1925				
72	.43	.46	.47	.46	.50	.46	0	0	0	0					Attacked 1927				
73	.55	.66	.58	.38	.76	.47	0	0							Attacked 1925				
74	.35	.50	.46	.32	.51	.29	0								Attacked 1924				
75	.73	.32	.13	.75	.81	.16	0								Attacked 1924				
76	.60	.56	.55	.39	.54	.47	0								Attacked 1924				
77	.16	.38	.48	.30	.49	.36	0								Attacked 1924				
78	1.39	1.41	.94	.83	1.16	.94	0	0	0	0					Attacked 1927				
92	.27	.28	.28	.54	.68	.24	0	0	0						Attacked 1926				

The preceding tabulation also graphically presents the effects of defoliation upon the growth of trees prior to an attack by bark beetles. It will be noted that the average life of the trees killed by beetles was much shorter (3 years) than for those which died from the effects of defoliation (5-1/2 years). Though theories could be advanced in explanation of this difference, there is no solution which could be considered as being at all positive. However, it is possible that some of the beetle-attacked trees were more severely injured than most of those which died from the effects of defoliation alone, and were therefore promptly selected by the insects as favorable host material. The one tree (number 53) attacked subsequent to 1927 had apparently made a fairly complete recovery, and it would seem that this loss should be considered as a normal beetle attack. It is rather difficult to determine what the future of these trees would have been had they not been attacked by beetles. However, from the evidence available it is believed that a large percent of them would have died from the direct effects of defoliation if the beetle had not hastened their deaths.

Table 13. - Radial growth record of a selected number of trees still living in 1935

Measurements in millimeters

Tree number	1917	1918	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935
11	1.33	1.26	1.21	1.05	1.95	1.39	0	.28	.20	0	0	0	0	.15	.05	.09	.19	.24	.26
16	.68	.67	.90	.65	.82	.43	.21	.34	0	.88	1.28	.93	.46	.67	.63	.53	.67	1.02	.42
26	.30	.25	.28	.14	.23	.21	0	0	0	0	0	0	0	0	.21	.14	.07	.04	0
36	.66	.98	.90	.45	.91	.88	0	0	0	0	0	0	0	0	.09	.06	.16	.34	.15
59	.35	.41	.47	.31	.56	.56	0	0	0	.21	.30	.33	.22	.10	0	0	.03	.51	.53
64	.32	.38	.47	.41	.41	.45	0	0	0	0	0	0	0	0	0	0	0	.23	.15
82	.59	.30	.33	.36	.54	.38	0	0	0	0	.14	.22	.15	.09	.08	.08	.08	0	0
83	.33	.41	.52	.58	.80	.62	0	0	.27	.46	.52	.30	.25	.34	.27	0	.32	.22	.45
96	.17	.22	.35	.23	.37	.21	0	0	0	0	0	.13	.09	0	0	0	.07	.11	.05
100	.27	.64	.57	.28	.57	.41	0	0	0	.21	.22	.14	.07	.12	0	0	.12	.19	.09
9	1.45	1.45	1.44	1.48	2.55	2.17	.47	.30	.39	.20	.41	.45	.50	.60	.79	.92	.76	1.11	.77
49	2.04	2.55	2.51	1.94	2.90	1.72	.35	.31	.63	1.10	1.96	1.56	1.53	2.00	1.78	1.68	1.65	1.59	1.10

The preceding tabulation is offered as depicting the peculiar growth behavior of a few trees that were still living at the time of the 1935 examination. From these data it is evident that the effects of defoliation are still portrayed in the basal growth. Furthermore, the future of such trees as numbers 26, 36, 64, 82, 96, and 100 is questionable, and it is entirely possible that some of them will finally succumb to the effects of the injury. Tree number 26 was the slowest growing of all trees prior to defoliation, and though still alive its recovery is doubtful, as no growth was added in 1935.

Furthermore, as the 1935 radial increment of the living trees only averaged .60 mm., as compared with a growth of .98 mm. prior to defoliation, it is evident that at the end of 14 years the trees have not as yet recovered from the injury.

ECONOMIC IMPORTANCE OF PINE BUTTERFLY DEFOLIATION

During the period of this study the actual destruction of timber on the study plot amounted to 45,740 board feet, or 29.51 percent of the total volume of 155,000. Of this loss 25,340 board feet, or 55.40 percent, is questionably credited to the attacks of D. brevicomis, while 20,400 board feet, or 44.60 percent, died from the effects of defoliation.

In addition to the actual destruction of trees, a less important though very definite loss existed in the reduction of annual growth. During the 14 years prior to defoliation the annual increase in the basal diameter of all trees within the study plot averaged 1.82 mm., or .072 of an inch. With trees of this diameter such an increment would amount to 7.2 board feet annually or 720 for the entire plot of 100 trees. If we assume that under normal conditions the subsequent 14 years growth would have been equal to that which occurred prior to defoliation, the total volume of timber on the plot would have been increased by 10,080 board feet. However, during this subsequent period the diameter growth of the trees now living was reduced to .86 mm., or .034 of an inch, which only increased the volume of these trees by 3,474 board feet, or a decrease from the growth normally expected of 4,191 board feet. So as a result of the defoliation, instead of having a total of 165,080 board feet on the plot in 1935 there were only 112,734, a total loss of 52,766 board feet, or 31.8% of the expected volume.

Summers and Burgess (16) advance a method of determining monetary losses to definite forest acreage as a result of defoliation. No attempt has been made to use this formula to show the monetary loss as per acre of defoliation, as the stumpage value of the timber in question varies materially and the exact area of the plot was not determined.

Though defoliation is considered as being responsible for the marked reduction in the increment as shown in the previous statement, the natural variations in growth must be considered in arriving at such conclusions. To check the possibility of there having been a natural reduction in tree growth during this period, 21 increment cores were taken from trees growing under comparable conditions some few miles from the study area that had not been defoliated. Unfortunately, these trees were considerably younger than those within the study area;

however, an uninjured timber stand of the same age could not be located. Though the basal increment of the younger trees was considerably in excess of those within the study area, it was assumed that the same growth variation would prevail in all ponderosa pine trees throughout the New Meadows Valley.

Table 14. - Growth rate of injured and uninjured trees

	Average annual radial basal growth prior to defoliation	Average annual radial basal growth subsequent to defoliation	Percent of change
	1916-1921	1922-1933	
Uninjured check trees	1.40	1.76	+ 25
Defoliated trees living 1935	.98	.39	- 60

The preceding data show an increased growth for uninjured trees, with a marked decrease for the defoliated ones. This natural increase in the growth rate would indicate that defoliation was responsible for even more than the reduced growth rate of injured trees as shown in the preceding table. A more complete comparison of the growth rate of uninjured and injured trees is shown on plate 8.

CONCLUSIONS

In summarizing the contents of this paper there is not a great deal that can be added to statements already made. From data submitted it is evident that as a result of the defoliation 12 percent of the trees died from the direct effects of the injury and 14 percent were so weakened as to make them attractive hosts for western pine beetle attacks. As there is wvery reason to assume that some of the trees attacked by beetles would have died from the effects of defoliation alone, the actual loss as a direct result of this injury rests somewhere between 12 and 26 percent. Furthermore, the future of a few trees which were still living in 1935 is questionable, as the effects of defoliationare still evident. The severity of the loss resulting from this injury is supported by a salvage cutting of a defoliated area of ponderosa pine near McCall, Idaho, owned by the Boise-Payette Lumber Company. During this operation, which occurred in 1925, all dying trees were removed, and it was estimated that nearly 40 percent of the stand was cut.

In addition to the actual loss of timber, the reduction in the annual growth of trees surviving defoliation is an important consideration. It has been shown that during the period of this study the average annual growth of the living trees was but 44 percent of the increment during a comparable period prior to defoliation. Furthermore, these trees have not yet recovered from this injury, for the 1935 growth was only 61 percent of the prior defoliation increment.

It was also apparent that as a class the thrifty-growing trees were more resistant to the effects of defoliation than slower-growing individuals. This fact was evidenced not only by a comparison of the average growth between dead and living trees within the study plot but from a practical demonstration on a timber sale at Cascade, Idaho, in 1924. During the marking of trees on this sale of publicly owned timber, which had been severely defoliated by the pine butterfly in 1922 and 1923, the writer's advice was requested as to the advisability of departing from standard silvicultural practices and cutting all trees, regardless of their size, that had any commercial value as a means of salvaging the injured trees. As this stand was of an uneven age, which when marked under normal conditions would leave a residual stocking of young, thrifty, growing trees, it was recommended that the defoliation be disregarded and that standard marking regulations be employed. The soundness of this recommendation was substantiated during an examination of the area some few years later, as apparently none of the residual stand had failed to recover.

It is also evident that, though the severity of the injury is governed by the percent of foliage destroyed, there is a marked variation in the reaction of different trees. This variation can perhaps be explained partially at least by the effect of disturbed physical functions upon the reserve food supply, or chemistry of the tree, the moisture content, or the increased temperature of the bole due to excess solar heat resulting from the destruction of the forest canopy. These are intangible factors, it is true, yet they will need be considered in any future fundamental studies of the effects of defoliation.

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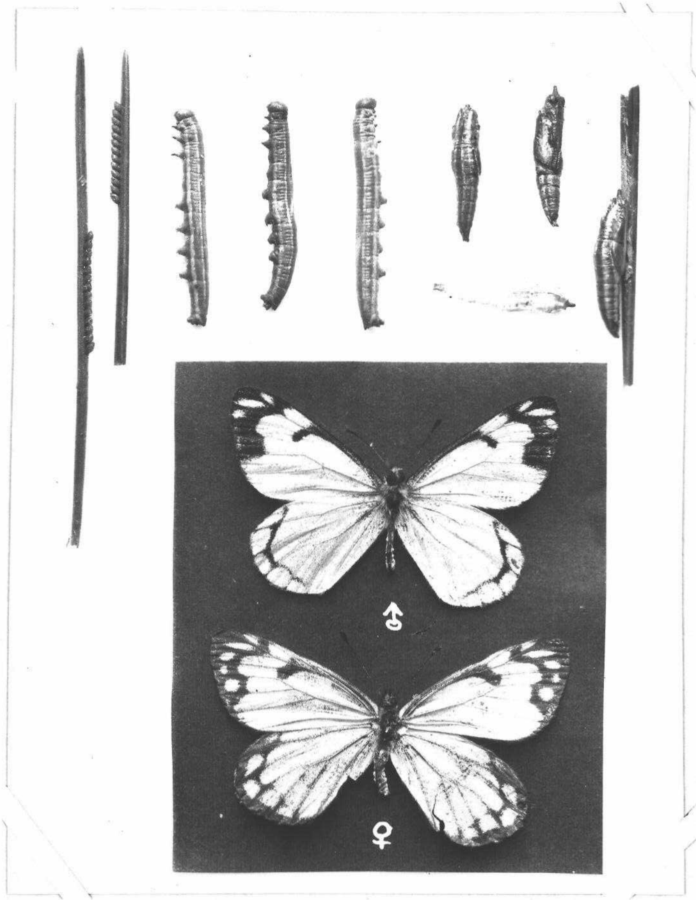
(16) Summers, J. N. and Burgess, A. F. A method of determining losses to forests caused by defoliation. Journal of Economic Entomology 26: 51-54, 1933.

PLATE 1

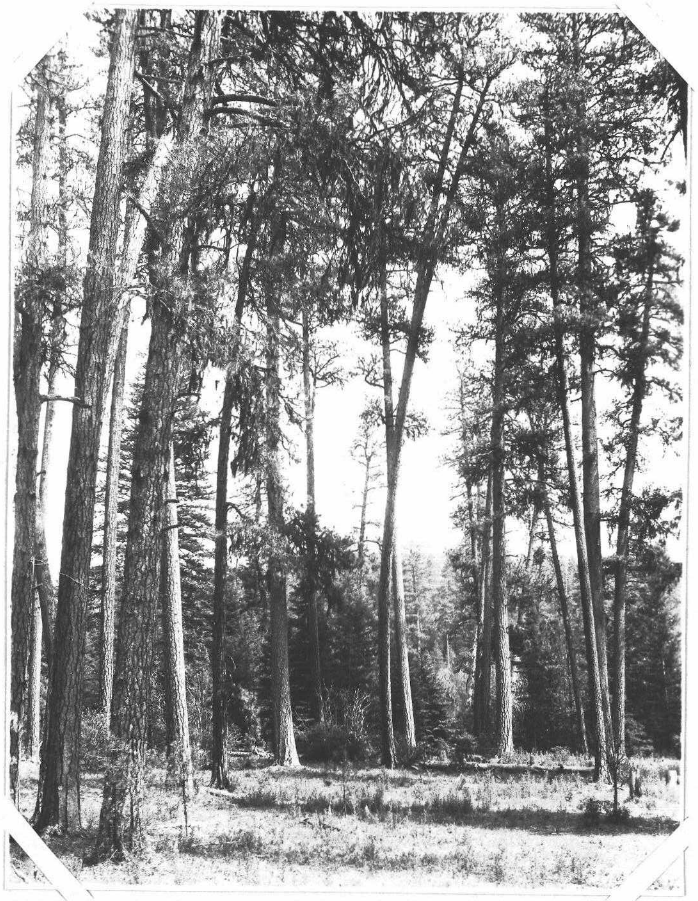
A - Eggs, larvae, pupae, and adults of the pine butterfly (Neophasia menapia Felder).

B - Portion of study plot showing character of ponderosa pine stand included.

PLATE 1



A



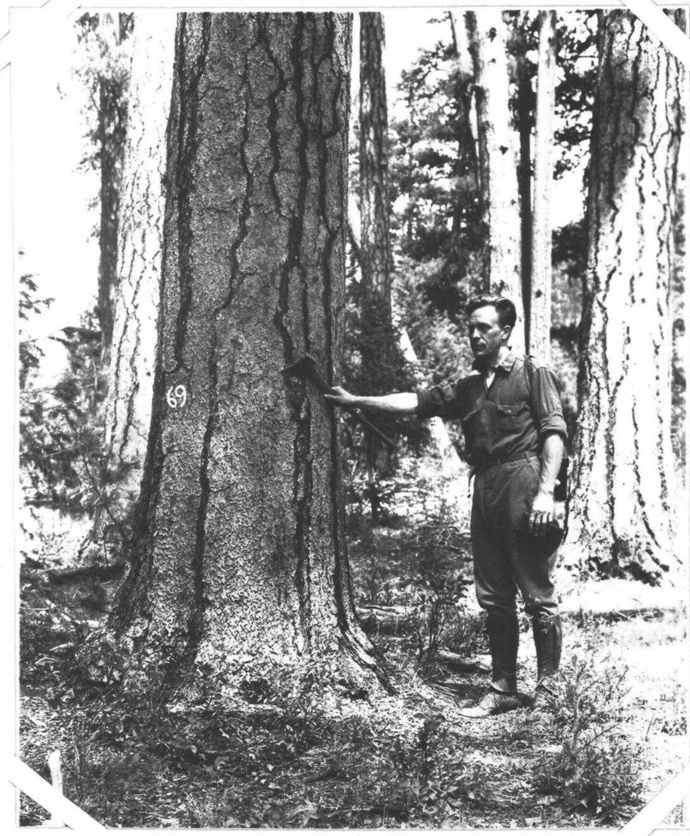
B

PLATE 2

A - Tree 69 killed by defoliation. Died in 1925. Added no basal growth in 1923 or 1924. Doctor F. C. Craighead, Chief, Forest Insect Investigations, Bureau of Entomology and Plant Quarantine, in foreground.

B - Photograph showing condition of foliage following 1923 defoliation.

PLATE 2



A

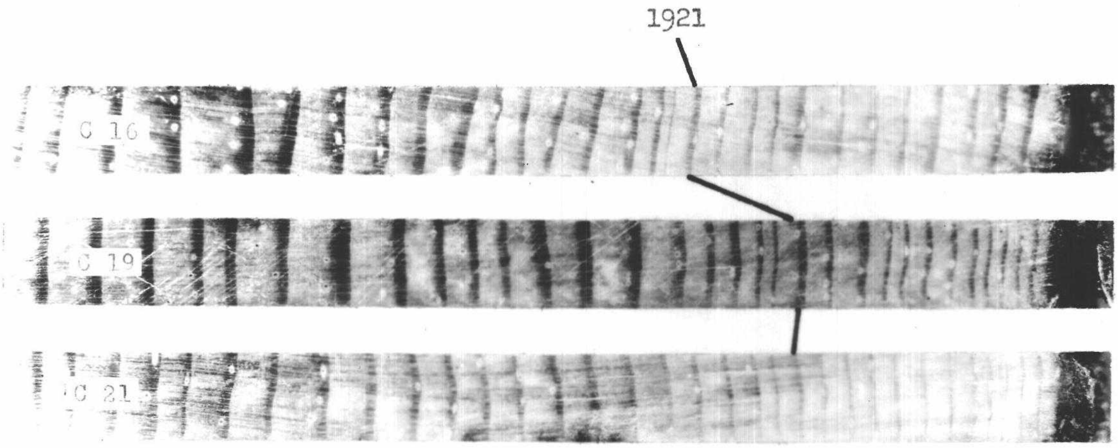
B

PLATE 3

A - Cores C 16, C 19, and C 21 are 1933 increment cores taken from check trees uninjured by pine butterfly defoliation. These cores show the distinctive 1920 and 1921 growth rings with an uninterrupted growth subsequent to that time.

B - Cores 10, 28, 49, and 61 are 1935 increment cores taken from numbered trees within the study area. Though these trees show a marked reduction in their annual increment due to defoliation, they did not fail to add some growth during each year of the study. On core 61 the 1923 ring is rather difficult to distinguish from the photograph. The 1922, 1923, and 1924 growth lies between the 1921 growth and the next distinct line of summer wood, which is 1925. On core 28 the 1924 ring can only be seen at the lower side of the core.

PLATE 3



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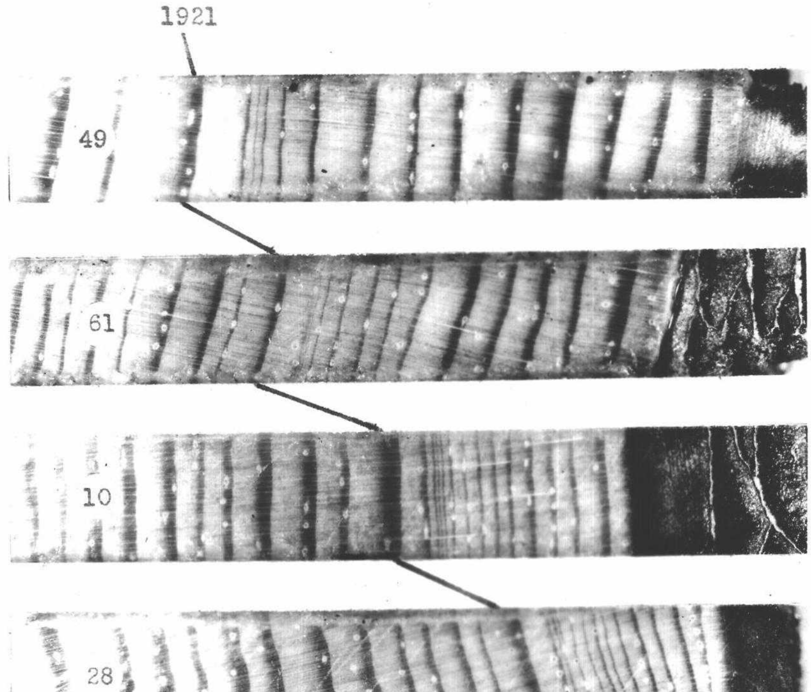


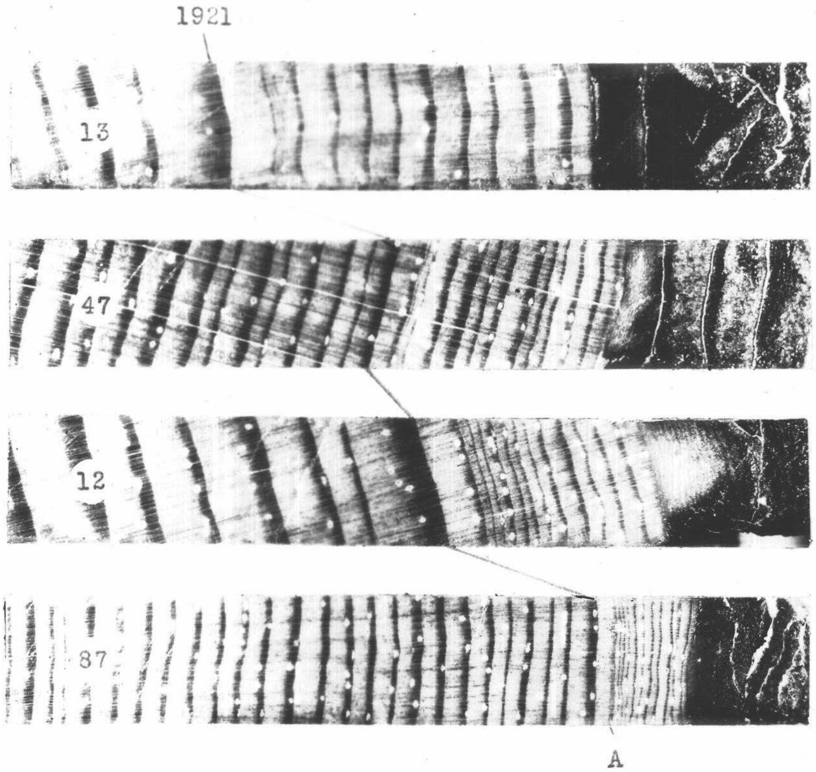
B

PLATE 4

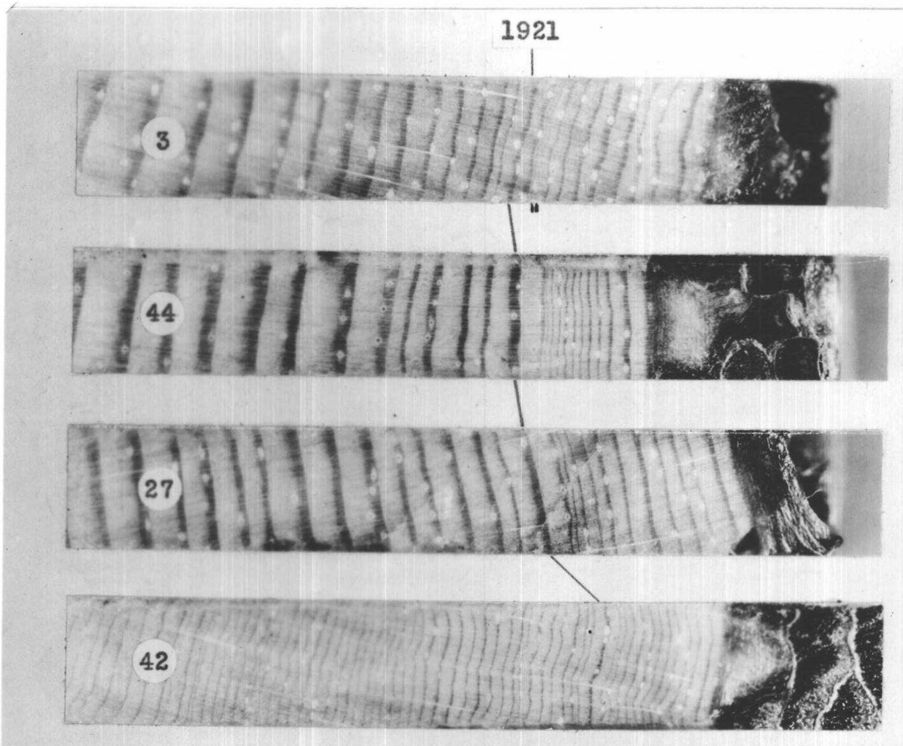
A - Cores 13, 47, 12, and 87 are 1935 increment cores taken from numbered trees within the study area. No 1924 growth was added to any of these trees. Though growth was added each subsequent year, it was materially reduced, especially in core 87. In core 87 the 1924 growth is only separated from the 1923 growth in spots, the increment being measured as .09 mm., which is hardly discernible.

B - Cores 3, 44, 27, and 42 are 1935 increment cores taken from trees of corresponding number within the study plot. No growth was added to these trees during the 1923 and 1924 seasons. As on core 3 the 1925 and 1926 growth does not show very plainly, slight marks have been made as an aid in identifying these rings. Core 42 shows nearly a resumption of normal growth, except for the two years missed.

PLATE 4



A



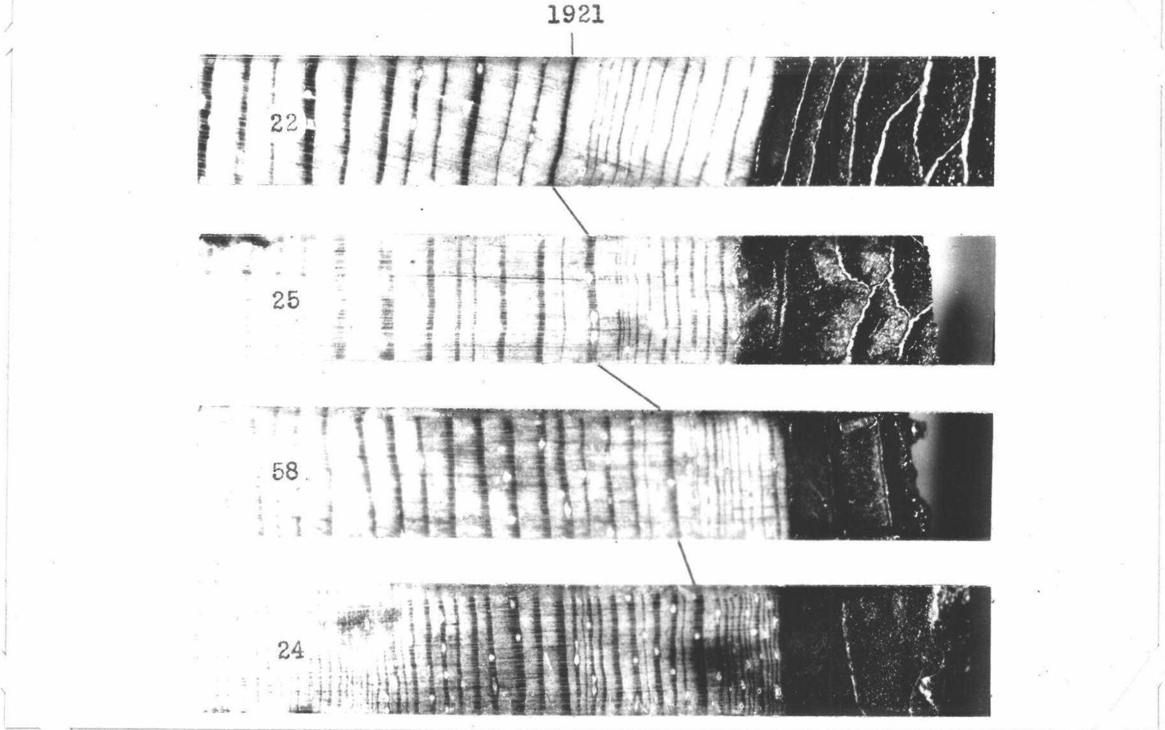
B

PLATE 5

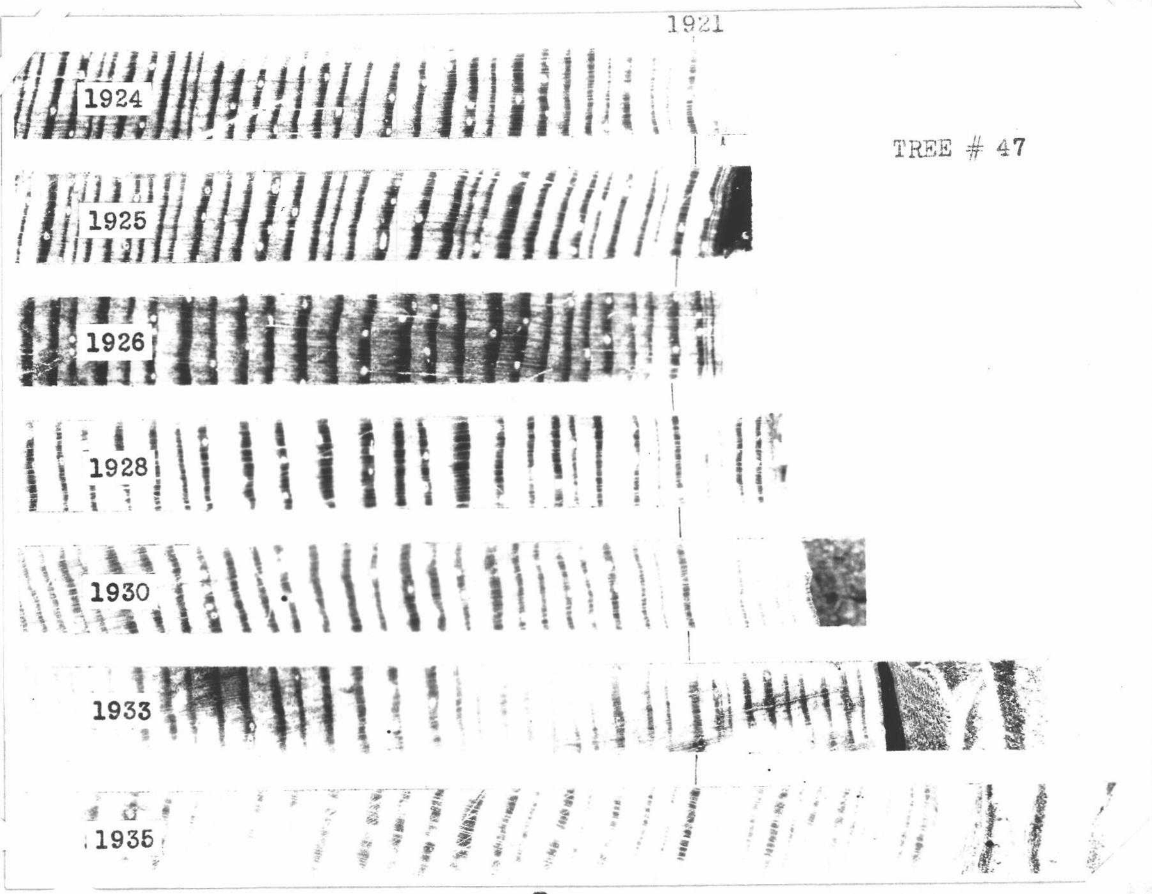
A - Cores 22, 25, 58, and 24 are 1935 increment cores taken from numbered trees within the study area. None of these trees added any growth during the 1923, 1924, and 1925 seasons. Core 22 shows a return to nearly a normal growth rate, while the others still show the effects of defoliation.

B - A series of increment cores taken at different years from tree number 47 of the study area. These figures depict the method used in determining the years when no growth is added. This tree did not add any growth in 1923. The shaded portion of the 1924 core is the end of the core with the bark removed and not an annual ring. In the 1935 core there appears to be an extra ring, which is but the shaded portion of the 1935 summer wood.

PLATE 5


1921
22
25
58
24

A


1921
1924
1925
1926
1928
1930
1933
1935
TREE # 47

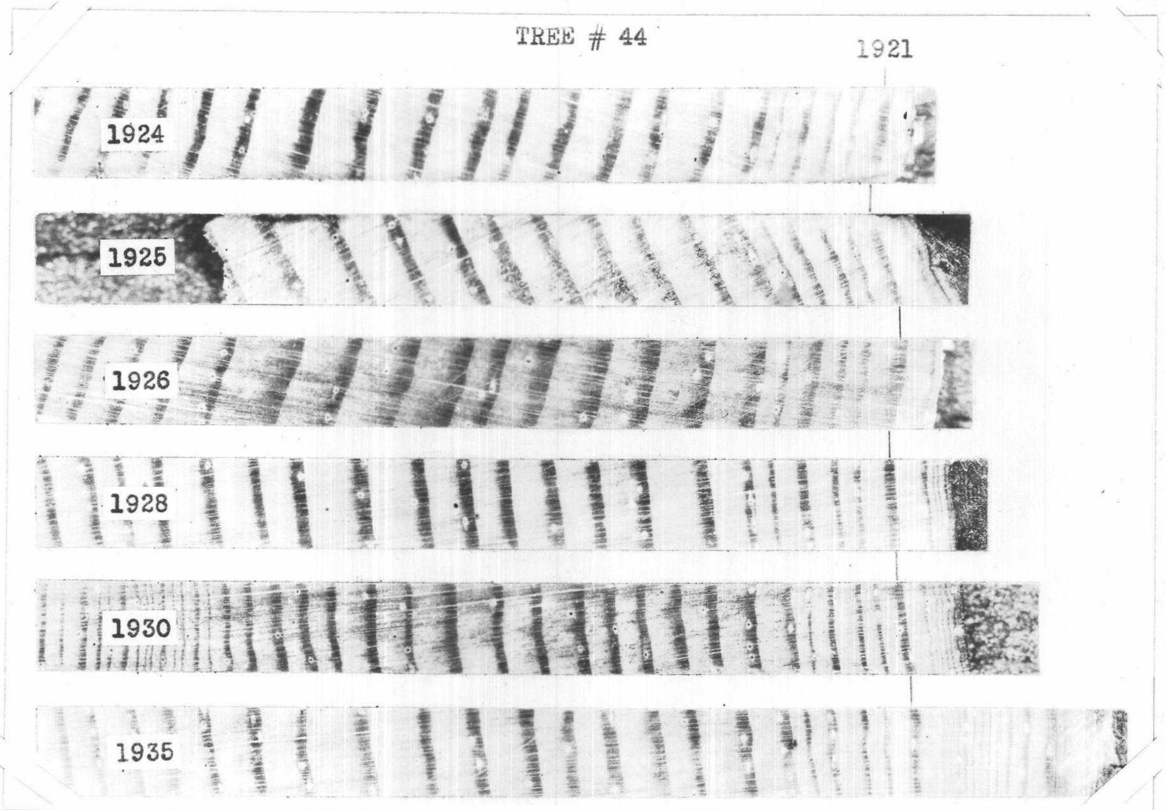
B

PLATE 6

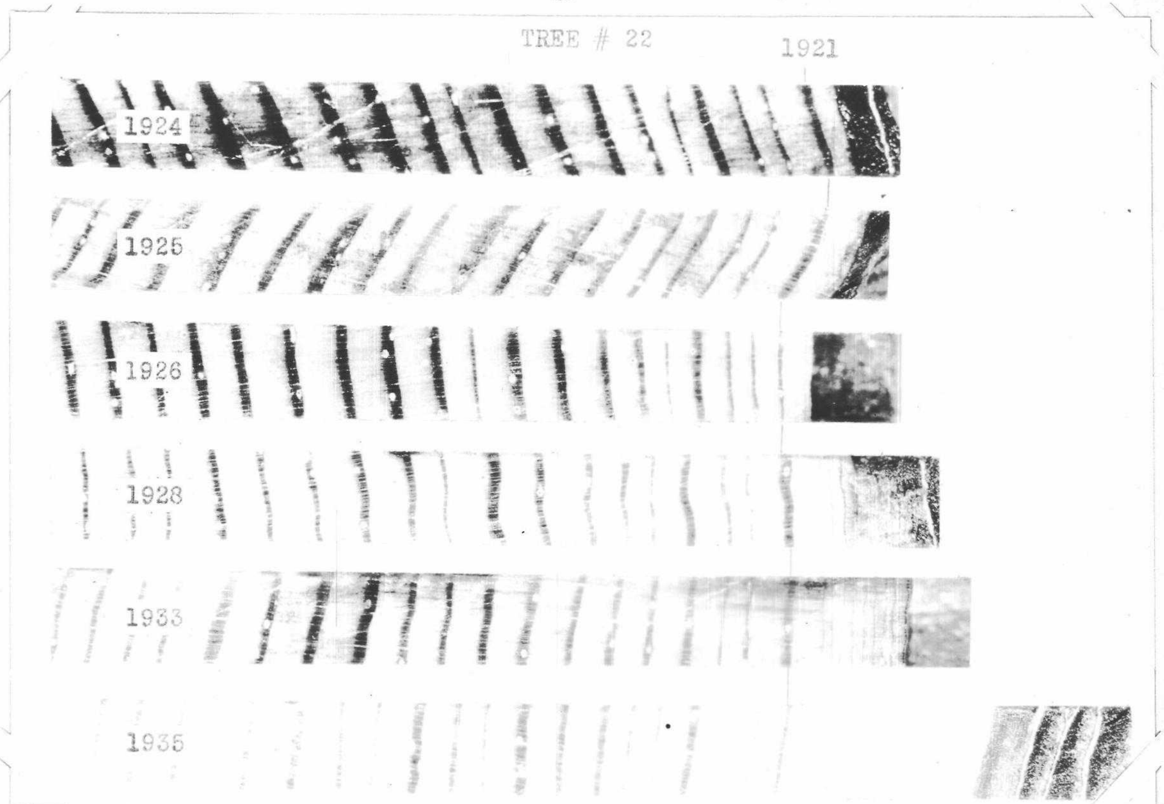
A - A series of increment cores taken at different years from tree number 44 of the study area. This tree added no growth during 1923 and 1924, with a subsequent reduction in annual increment.

B - Same as A, being from tree number 22, with no growth during the years 1923, 1924, or 1925.

PLATE 6


TREE # 44
1921
1924
1925
1926
1928
1930
1935

A


TREE # 22
1921
1924
1925
1926
1928
1933
1935

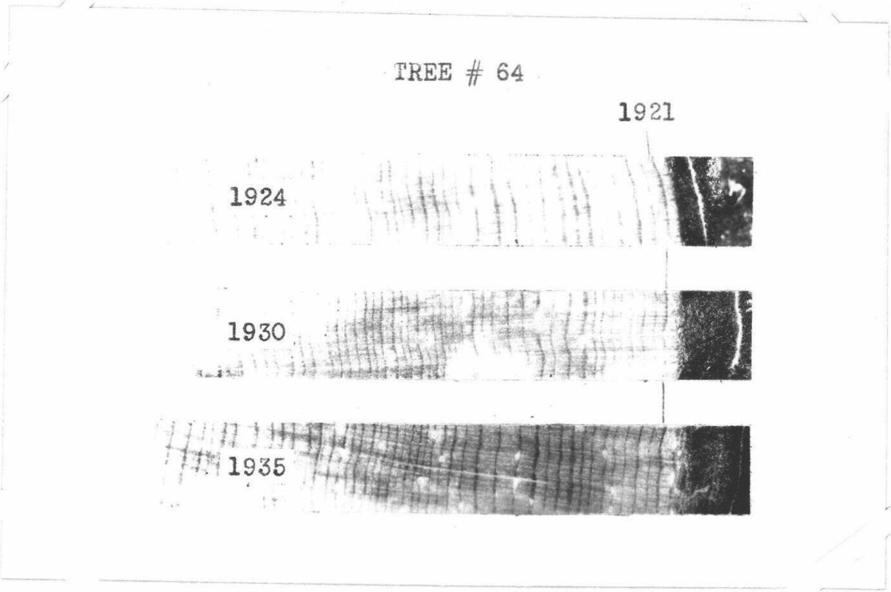
B

PLATE 7

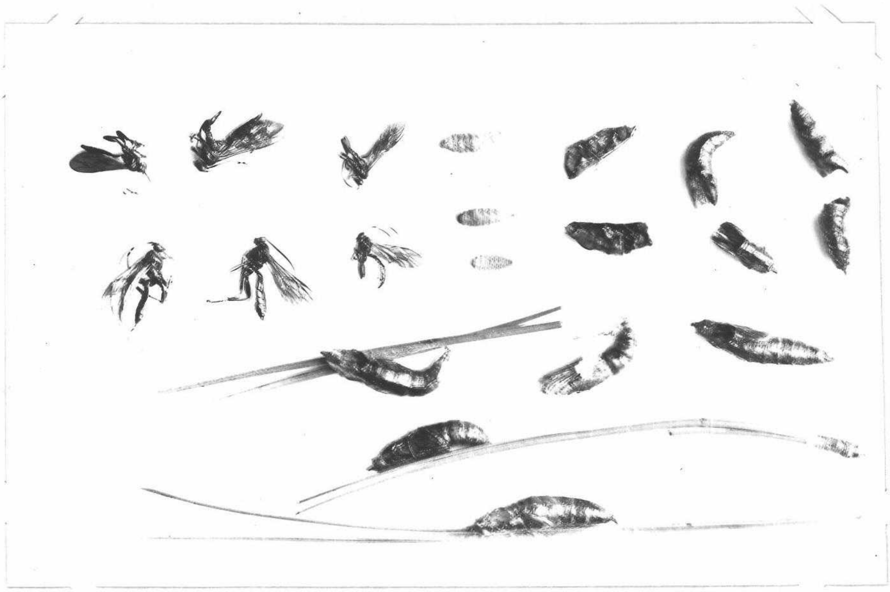
A - Three increment cores taken in 1924, 1930, and 1935 from tree number 64 of this study plot. This tree, though still living in 1935, failed to add any growth during the years 1923 to 1933 inclusive.

B - Illustrating the larval and adult forms of _Theronia fulvescens_, with parasitized pupal cases of the pine butterfly.

PLATE 7

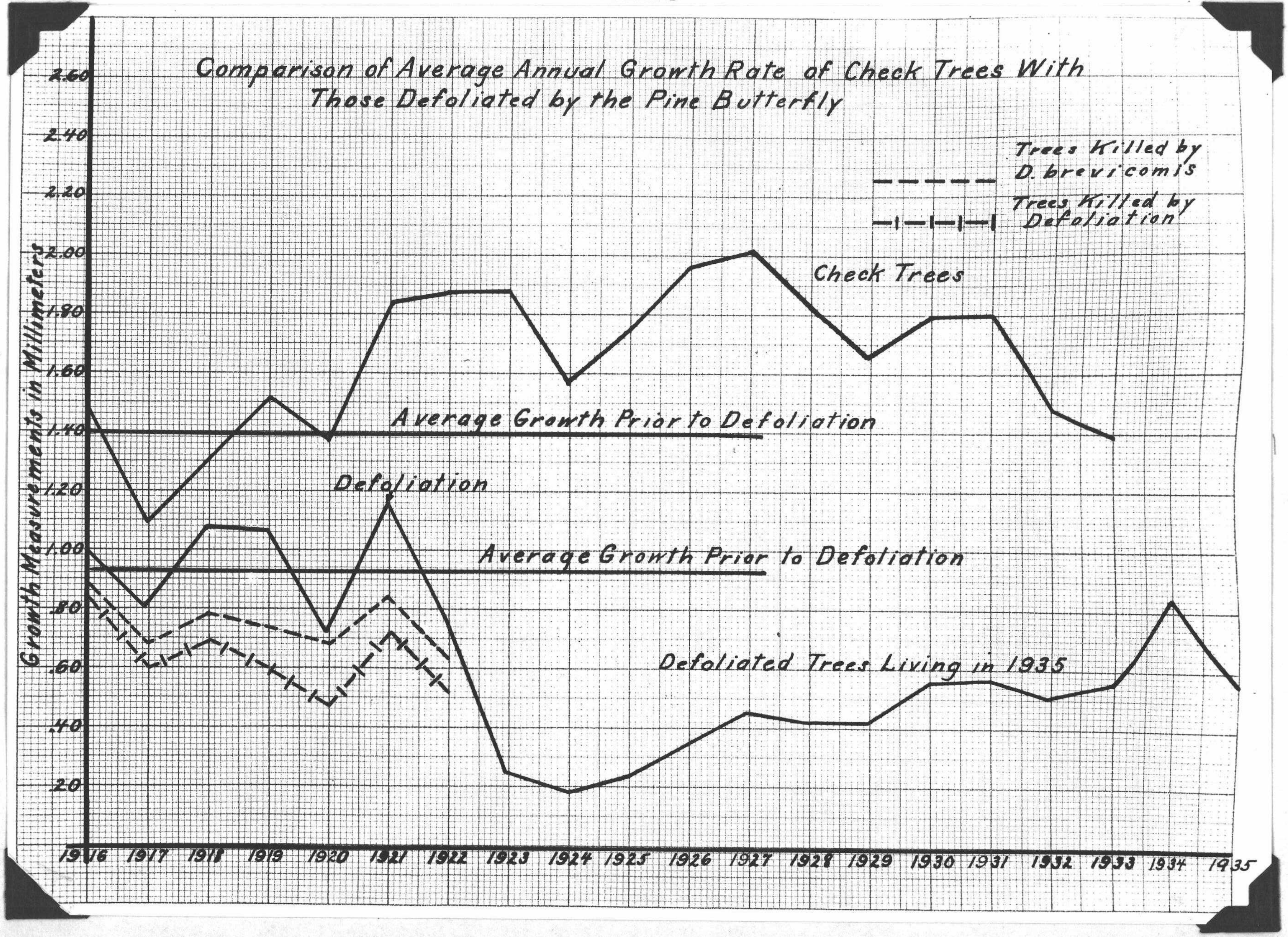


A



B

PLATE 8


Comparison of Average Annual Growth Rate of Check Trees With Those Defoliated by the Pine Butterfly
Trees Killed by D. brevicomis
Trees Killed by Defoliation
Check Trees
Average Growth Prior to Defoliation
Defoliation
Average Growth Prior to Defoliation
Defoliated Trees Living in 1935
Growth Measurements in Millimeters
2.60
2.40
2.20
2.00
1.80
1.60
1.40
1.20
1.00
.80
.60
.40
.20
1916
1917
1918
1919
1920
1921
1922
1923
1924
1925
1926
1927
1928
1929
1930
1931
1932
1933
1934
1935