Mortality and Growth Reduction of White Fir Following Defoliation by the Douglas-fir Tussock Moth

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– The Author –

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ne of the problems confronting the forest manager when an insect pest breaks out in a forest stand is to determine if the damage potential of the infestation is great enough to make it economically justifiable to suppress the outbreak. An important consideration is the effect of the pest on the tree. The attacks of some insects promptly kill the tree; others reduce its growth rate, sometimes bringing about a lingering death. Generally the damage potential is better known for pests in the first category, which includes tree-killing bark beetles, than for those in the second. But knowledge of the destructiveness of even the most common forest insects is quite variable and considerably less than what is needed to provide an adequate basis for judicious control decisions.

Several years ago an opportunity arose to develop information on this subject after an outbreak of the Douglas-fir tussock moth, Hemerocampa pseudotsugata McD., a common defoliator of white fir (Abies concolor [Gord. & Glend.] Lindl.) in California. This outbreak occurred in mixed-conifer stands in Calaveras and Tuolumne Counties, mostly on lands of the Stanislaus National Forest. It was first discovered in 1954. By 1955, 10,000 acres of white fir in several centers of infestation were affected. Previous experience had shown that tree mortality and growth reduction could be appreciable if an infestation were not checked. Consequently, in July 1956, the moth was controlled by spraying the entire area with DDT insecticide at the rate of 1 pound of DDT in 1 gallon of diesel oil per acre (Stevens 1957).

After the control job was completed, foresters wanted to know which defoliated trees should be logged. They knew that some trees were too badly



Figure 1. — Full-grown Douglas-fir tussock moth larvae feeding on white fir needles.

damaged to survive. They also were concerned about the long-term effects of defoliation on growth of the surviving trees because both mortality and growth losses affect the management and economy of timber. These questions could not be answered satisfactorily, for the only information available was from a limited study of a 1934 tussock moth outbreak in Mono County on the Inyo National Forest, conducted by Patterson.¹ The data from this study were not complete enough to make reliable predictions about the amount of damage that could be expected, but they did provide some clues. To learn more about the effects of such outbreaks, a study was started in 1956 in some of the stands that had been infested. This report describes the results of this work.

¹Patterson, J. E. Tussock moth, *Hemerocampa oslari:* Preliminary examination of infested areas on the Inyo and Mono National Forests, California. June 23-25, 1937. U. S. Bur. Ent. and Plant Quar. Forest Insect Lab., Berkeley, Calif., 4 pp., illus. (Unpublished report on file at the Pacific Southwest Forest and Range Experiment Station.) July 20, 1937.

The Insect

The Douglas-fir tussock moth is a native insect and a major defoliator of Douglas-fir and true fir forests in western North America. Outbreaks of this insect periodically destroy large quantities of timber. At least 300 million board feet of timber were killed as a result of an outbreak in eastern Washington in 1929 and 1930 (Keen 1952). Losses of even greater magnitude were prevented by spraying another serious infestation which developed over a 500,000-acre area in Idaho, Oregon, and Washington in 1946 and 1947. Tussock moth outbreaks have been noted in California ever since forest insect studies began nearly 60 years ago. Only recently, however, was it recognized that the species involved here is Hemerocampa pseudotsugata McD., not H. oslari (Barnes) as previously thought (Eaton and Struble 1957).

The Douglas-fir tussock moth has a 1-year life

cycle. The adults appear late in August or early September. They are brown pubescent moths, each about one-half inch long. The male is winged. The female is wingless and does not move far from the cocoon from which she emerges. The eggs are laid in masses on top of the old cocoon and there they overwinter. The next spring the eggs hatch into hairy, tufted caterpillars (fig. 1) which feed on the new foliage. The caterpillars become fullgrown early in August, and pupate in grayish brown cocoons attached to the twigs, trunks, or other parts of trees or adjacent shrubs.

Damage to the tree results from the feeding activities of the larvae (fig. 2). If feeding is intensive enough to destroy all of the new foliage, the tree loses some of its capacity to grow. Injury of this type inflicted for several successive years results in death.



Figure 2. — White fir severely defoliated by the Douglas-fir tussock moth, Mammoth Lakes, 1937.

Study Objectives

The objectives of this study were to determine the effects of defoliation on the growth and mortality of white fir, as follow:

- a. Mortality, over a five-year post-defoliation period, caused by both tussock moth feeding and attacks of other insects.
- b. Top damage due to defoliation.
- c. Growth reduction associated with different degrees of defoliation.
- d. How long reduced growth persists.

Investigations were made in both the recently infested stands on the Stanislaus National Forest and in those that had been infested some 20 years earlier on the Inyo. It was anticipated that data from separate outbreaks would provide a stronger basis for estimating the tussock moth's damage potential. The Stanislaus area, however, was studied more intensively than the Inyo because we had firsthand knowledge of the infestation, and because it was larger and hence afforded a wider variety of conditions.

Stanislaus Infestation

Study Area

The Stanislaus infestation of 1954-1956 occurred in a mixed conifer forest on good sites at elevations ranging from 5,000 to 6,500 feet. The timber type consisted primarily of white fir, with intermingled California red fir (Abies magnifica A. Murr.), sugar pine (Pinus lambertiana Dougl.), Jeffrey pine (P. jeffreyi Grey. & Balf.), ponderosa pine (P. ponderosa Laws.), and incense-cedar (Libocedrus decurrens Torr.). Most of the oldgrowth timber had been logged at various periods in the past, some quite recently. The stands in the southern part of the infestation area were predominantly mature, with a fir volume averaging 54,527 board feet per acre; those in the northern part consisted mostly of poles and young sawtimber with an average volume of 16,346 board feet per acre.

There were seven separate infestation centers or blocks within an outbreak area, with a total area of 10,000 acres. The largest and most heavily defoliated block, on Hell's Mountain at the southern end of the area, consisted of about 5,000 acres. The other six blocks were strung out to the north for a distance of 20 miles, and were much smaller in size. Within the blocks, the defoliation generally was heaviest on ridge tops and lighter down slope, with very little damage in valley bottoms.

Methods

Information on the effects of the tussock moth on white fir survival and growth was collected over a 5-year period and 23 sample plots established in different infestation blocks. The sampling unit for data on trees 6 inches in diameter and larger was a $\frac{1}{2}$ -acre circular plot. Within most plots a $\frac{1}{40}$ -acre subplot was established to provide data on the smaller trees. The plots were distributed so as to sample stands representing light (5-25 percent), moderate (26-50 percent), and heavy 51-99 percent) defoliation intensity.

When the plots were established in 1956, all trees 6 inches or more in diameter were numbered, their diameter breast high (d.b.h.) measured, and an estimate made of the degree of defoliation. Smaller trees on the subplots, about 24 inches in height, also were measured. From the time the plots were established through 1960, they were re-examined annually in August to collect data on the amount and cause of mortality. Trees that died were classed ,as killed by defoliation only if no cambium-mining insects were found beneath the bark in basal examination. Where such insects were found, they were considered to be the cause of death.

At the time of the final examination in 1960, selected study trees were felled in mid-August, the time when most of the radial growth ceases (Fowells 1941). Three discs were cut from each tree to determine the effect of defoliation on growth rate. One disc was taken at breast height representing the base, one at the 17th internode from the top representing the midcrown, and one at the 10th internode representing the top. A total of 40 trees, ranging from 6 to 18 inches d.b.h., were sampled in this way. These samples were augmented by increment cores taken at breast height from three trees 36 to 44 inches d.b.h. on heavily defoliated plots. In addition, discs were cut from

two nondefoliated white fir trees from each end of the outbreak area, and five nonhost ponderosa pine, sugar pine, and incense-cedar trees scattered throughout the area, so that comparisons could be made of the growth pattern in attacked and nonattacked trees.

The width of the annual rings in each disc was measured along four radii with an increment measuring device attached to a binocular microscope (fig. 3). Average ring width per year was calculated from these measurements. The rings were dated from the outer ring. Attempts to use the two-level vertical sequence method developed by Mott, Nairn, and Cook (1957) for analyzing radial growth were unsuccessful. This failure was due largely to the difficulty of tracing internodes during periods of heavy defoliation when severely damaged trees did not put on any terminal growth.

Height growth was determined from measurements of some of the dominant trees felled for discs, and of dominant standing trees of sapling size or smaller.

Results

Mortality

There were two main causes of death in white fir from the effects of tussock moth feeding (fig. 4). The first, mortality due to defoliation alone, showed up in 1957 (Wickman 1958). This mortality occurred mostly in the heavily defoliated



Figure 3. — Radial increment was measured on white fir discs with this binocular microscope mounted on a sliding micrometer stage.

stands during the year of heaviest defoliation, 1956, and was most severe among the smaller trees (fig. 5). Beetle attacks on trees weakened by defoliation were the second cause of death. Two beetle species were chiefly responsible: the fir engraver, *Scolytus ventralis* Lec., and the roundheaded fir borer, *Tetropium abietis* Fall. Some of the trees that died from this cause might have died from the effects of defoliation alone if they had not been attacked by beetles. This type of mortality continued until 1959.

Total losses in stands that had been heavily defoliated were considerable during the 5-year

Figure 4. — Dead white fir at Hell's Mountain: A, saplings killed in 1956 by tussock moth feeding; B, sawtimber-size trees killed between 1956 and 1959 by the combined effects of tussock moth and beetle attacks.





Figure 5. — Distribution of white fir mortality due to tussock moth defoliation alone. by diameter classes. Hell's Mountain, 1956.

post-defoliation period (table 1). Over 20 percent of the sawtimber size trees and 50 percent of the smaller trees were killed. The ones most heavily defoliated sustained the greatest mortality (fig. 6); those that were completely defoliated at the start of the study died. In the most severely damaged

Figure 6. — Distribution of white fir mortality from all insects for different degrees of defoliation. Hell's Mountain, 1956-1960.

stands, yearly losses of merchantable white fir amounted to as much as 11 percent of the green stand (table 2).

The only losses in moderately defoliated stands were in poletimber trees. No losses occurred in the lightly defoliated stands.

Table 1. Mortality of white fir per acre, by defoliation intensity class and cause, Stanislaus National Forest, 1956-1960

| SAWTIMBER ¹ | | | | | | | | | |
|---------------------------------------|--------------------|---------------------|----------------------------|------------------------|---------------------------|---------------------------------|---------------------------|----------------------------|----------|
| Defoliation intensity class | No. of plots | Orio St Trees | ginal and Volume | Trees k defol al | illed by iation one | Defoliate killed by insec | d trees 7 other cts | Total mo | ortality |
| | | Number | Board feet ² | Board feet² | Percent | Board feet ² | Percent | Board feet ² | Percent |
| Heavy | 9 | 92 | 54,527 | 271 | 0.5 | 10,800 | 19.8 | 11,071 | 20.3 |
| Moderate | 7 | 85 | 13,747 | 0 | 0 | 0 | 0 | 0 | 0 |
| Light | 7 | 73 | 18,946 | 0 | 0 | 0 | 0 | 0 | 0 |
| Average | | 84 | 31,286 | 106 | 0.3 | 4,226 | 13.5 | 4,332 | 13.8 |
| SAPLINGS AND SMALL POLES ³ | | | | | | | | | |
| | | Number | | Number | Percent | Number | Percent | Number | Percent |
| Heavy | 9 | 204 | | 58 | 28.3 | 44 | 21.7 | 102 | 50.0 |
| Moderate | 7 | 291 | | 17 | 5.9 | 29 | 10.0 | 46 | 15.8 |
| Light | 7 | 91 | | 0 | 0 | 0 | 0 | 0 | 0 |
| Average | | 197 | | 28 | 14.2 | 26 | 13.2 | 54 | 27.4 |

 1 Trees 11 inches d.b.h. and larger. 2 Scribner rule. 3 Trees less than 6 inches d.b.h.



Figure 7. — Sapling and pole-sized white fir nearly stripped of foliage by the Douglas-fir tussock moth, Hell's Mountain, 1956.

Top Damage

Where defoliation was not severe enough to kill the trees completely, the upper part of the crown often died. Top damage was most serious in mature trees that had been heavily defoliated. This type of damage showed up in 12 percent of the merchantable timber on the plots in the heavy defoliation area during the 5-year study period. Some tops started dying at the peak of defoliation in 1956 and each year died back a little further, probably because of the attacks of beetles. Top kill was the most prolonged effect of heavy defoliation found in the study. Many large, old trees succumbed after 3 or 4 years of progressive injury. Undoubtedly, heart rot fungi entering through the dead tops will add further to the attrition.

Death of the terminal shoot often occurred in the smaller trees in heavily defoliated areas (fig. 7). Damage of this type was evident by the second year of the infestation. Many of the damaged trees subsequently developed new leaders, but the tops were deformed as a result. The dead terminals also may have provided access for fungi.

Radial Growth

Many factors affect the radial growth of trees, among them a tree's age. Maul (1958) reported that white fir growth is exceptionally slow up to about 30 years of age. The trees sampled in this study all were older. Ring counts of representative samples showed that trees 6 inches d.b.h. averaged 50 years in age; 9-inch, 60 years; 12-inch, 80 years; and 18-inch, 110 years. Discs were not taken from larger trees, but calculations based on increment borings indicated white fir 50 inches d.b.h. to be more than 300 years old.

Annual ring patterns in the discs (fig. 8) showed

| Year | Green stand volume | Volume killed | Green stand killed |
|-------|-------------------------|-------------------------|-----------------------|
| | Board feet ¹ | Board feet ¹ | Percent |
| 1956 | 54,526 | 4,509 | 8.3 |
| 1957 | 50,017 | 5,644 | 11.3 |
| 1958 | 44,373 | 162 | 0.4 |
| 1959 | 44,211 | 756 | 1.7 |
| 1960 | 43,455 | 0 | 0 |
| | | | |
| Total | | 11,071 | 20.3 |

Table 2. Volume of white fir per acre killed yearly on heavily defoliated plots, Hell's Mountain

¹ Scribner rule.

that defoliation had both immediate and pronounced effects on radial growth. Normally, the annual ring for a given year is wider in the upper part of the stem than at the base, and ring measurements for the years preceding the outbreak showed this to be true (fig. 9).

After the outbreak, the growth pattern changed. Defoliation caused a significant decrease in ring width at all levels examined, but the magnitude of the decrease was proportionately greater in the, upper part of the tree where feeding damage was heaviest. Samples from the most heavily defoliated stands showed the greatest radial growth decreases, but even light defoliation caused a significant decline. The reduction during the years of greatest growth depression (1955-1957), calculated as a percentage of the growth during the 4 years immediately preceding, was as follows: heavy, 74 percent; moderate, 67 percent; light 31 percent. Growth recovery did not become complete until about 4 years after the tussock moth infestation was controlled.

Nondefoliated trees showed no such drastic growth changes (fig. 10). The annual increment



Figure 8. — Discs from nondefoliated (left) and defoliated (right) white fir trees. Arrows point to corresponding growth rings. Narrow area in disc at right is growth for 1956 and 1957, the first and second years after the infestation ended.

fluctuated somewhat from year to year and even declined slightly during the infestation period, due probably to extrinsic factors, such as weather, which sometimes affect growth (Keen 1937; Thomas 1957). But extreme reductions in radial growth did not take place in these trees as they did in the defoliated ones.

Pre- and post-defoliation growth rates of trees that had been attacked were studied in relation to defoliation intensity. Sample trees were arranged into classes according to percent defoliation in 1956. Then the annual growth of the trees in each class was plotted for the years 1951, 1956, and 1960. The results (fig. 11) show only slight differences in predefoliation growth. However, for 1956, the year the outbreak was controlled, a definite relationship between growth and percent defoliation is evident, the more heavily defoliated



Figure 9. — Radial increment trends at top, middle, and base of light, medium and heavily defoliated white fir trees in the Stanislaus tussock moth infestation areas.



Figure 10. — Radial increment trends in nondefoliated trees in the Stanislaus tussock moth infestation area.



Figure 11. — Radial growth of white fir before, during, and after tussock moth attack, by degree of defoliation in 1956. Stanislaus infestation.

trees showing the greatest growth reduction. By 1960, growth had almost returned to the 1951 level.

Reductions in radial growth due to the outbreak resulted in significant losses in the volume of timber that would have occurred on the trees had they not been attacked. This is best illustrated by data for the heavily defoliated plots which have been translated into terms of board feet. This translation was done by finding the average growth of white fir in the different diameter classes during the 4 years preceding the outbreak, calculating the expected increment for the 3 years of greatest growth reduction, and taking the difference between the actual and expected growth as the loss in volume (table 3). Growth losses totaled 1,113 board feet per acre during the 3-year period, or 371 board feet per acre per year. Actual growth was only 36.5 percent of expected growth during this period.

| Diameter class | Number of trees | Expected ¹ growth | Actual ² growth | Growth deficiency |
|-------------------|-----------------------|---------------------------------|-------------------------------|----------------------|
| Inches | | – – – Board | feet ³ | |
| 12 | 5.6 | 55.7 | 20.3 | 35.4 |
| 14 | 4.0 | 40.1 | 14.6 | 25.5 |
| 16 | 3.6 | 53.4 | 19.5 | 33.9 |
| 18 | 4.4 | 89.1 | 32.5 | 56.6 |
| 20 | 4.0 | 100.2 | 36.6 | 63.6 |
| 22 | 2.2 | 77.9 | 28.5 | 49.4 |
| 24 | 2.6 | 106.9 | 39.0 | 67.9 |
| 26 | 1.3 | 60.1 | 22.0 | 38.1 |
| 28 | 2.9 | 159.2 | 58.2 | 101.0 |
| 30 | 1.8 | 106.9 | 39.0 | 67.9 |
| 32 | 1.6 | 101.3 | 37.0 | 64.3 |
| 34 | 1.3 | 100.2 | 36.6 | 63.6 |
| 36 | . 4 | 35.6 | 13.0 | 22.6 |
| 38 | 1.8 | 160.3 | 58.6 | 101.7 |
| 40 | 1.1 | 105.8 | 38.6 | 67.2 |
| 42 | .7 | 63.5 | 23.2 | 40.3 |
| 44 | 1.1 | 128.0 | 46.8 | 81.2 |
| 46 | . 7 | 80.2 | 29.3 | 50.9 |
| 48 | | | | |
| 50 | . 4 | 60.1 | 22.0 | 38.1 |
| 52 | | | | |
| 54 | | | | |
| 56 | | | | |
| 58 | . 2 | 32.3 | 11.8 | 20.5 |
| 60 | | | | |
| 62 | | | | |
| 64 | . 2 | 36.7 | 13.4 | 23.3 |
| Totals | 42.0 | 1,753.5 | 640.5 | 1,113.0 |

Table 3. Volume per acre of growth loss due to defoliation in white fir sawtimber, 1955–1957, Hell's Mountain

 $^{\rm 1}$ Based on an average annual increment of .167 inch from 1951 to 1954.

 2 Based on an average annual increment of .161 inch from 1955 to 1957.

³ Scribner rule.

Height Growth

Height growth, particularly in understory trees 6-inch d.b.h. and smaller, was severely affected by defoliation. As mentioned earlier, some of the heavily attacked trees did not grow at all in 1956 because the terminal shoot died. Measurements of sample trees representing all degrees of defoliation showed that in 1954, the year the outbreak started, terminal growth averaged 4.5 inches. In 1955

and 1956, the growth averaged only 0.5 inch per year. The trees started to recover in 1957, putting on 1.2 inches of terminal growth. In 1958, the growth averaged 5.8 inches. This remarkable recovery probably was influenced by precipitation, which was especially heavy in 1958. Terminal growth in 1959 and 1960, when precipitation deficiencies occurred, averaged only 4.5 and 3.5 inches, respectively.

Inyo Infestation

Study Area

The Inyo infestation, according to unpublished data collected by Patterson,² lasted from 1934 to 1938. The outbreak occurred in mature coniferous stands growing at an elevation of about 8,000 feet near Mammoth Lakes, Mono County, California. White fir was the principal tree species in these stands then, the average volume per acre being 36,394 board feet. Other important species present in small amounts included California red fir, Jeffrey pine and lodgepole pine (Pinus contorta Dougl.). Much of the merchantable white fir that survived the outbreak, together with the pine in these stands, has since been logged. The area that Patterson studied most intensively was cut in 1945, and at the time of our observations was only sparsely stocked with white fir reproduction.

When the tussock moth was discovered in 1936, the infestation was centered in four widely separated areas ranging from 1,000 to 2,500 acres in size (Patterson 1938). The larvae were very abundant in 1937, and many trees were stripped of their foliage. Late in the season, however, a wilt disease appeared which apparently caused the outbreak to collapse. Patterson's observations showed that by 1938 the population had declined greatly.

Methods

Data on the damage to the white firs were collected by Patterson from a single 5-acre plot established in 1938, and reexamined annually for 5 years. At the time the plot was set up, all trees over 4 inches d.b.h. were measured and numbered, and the amount of defoliation estimated. Records were kept of the trees that died between 1938 and 1942, and the cause of death. The year before these records were started, Patterson had taken increment cores from five trees in each of three defoliation categories: none, light, and heavy. He took one core from each tree and averaged the measurements for the five trees to get the growth for the different classes.

To obtain additional information, particularly on growth recovery in the white fir in later years, we felled seven of the study trees in 1960, and took discs from them for radial increment analyses, as was done on the Stanislaus plots.

Results

Mortality

When the first stand inventory was made in 1938, Patterson found that many of the 163 white fir trees on the plot had been severely defoliated. The distribution of the trees by defoliation classes was:

| Defoliation | Number of | Percent of | |
|-------------|-----------|------------|--|
| percent | trees | total | |
| 0 | 18 | 11 | |
| 25 | 42 | 26 | |
| 50 | 48 | 29 | |
| 75 | 22 | 14 | |
| 100 | 33 | 20 | |

All of the completely defoliated trees, comprising over 12 percent of the green stand, were dead at the start of his study. And although they contained sparse broods of the bark beetle *Scolytus subscaber* Lec., and the roundheaded fir borer, Patterson concluded that they had died from the effects of defoliation. Subsequent mortality from beetle attacks on the weakened trees raised the total volume killed to 29.1 percent by 1942 (table 4).

Patterson kept no record of top damage result-

²See footnote 1.



Figure 12. — Radial increment trends in white fir trees defoliated to varying degrees by tussock moth in the Inyo infestation area.

Table 4. Volume of white fir per acre killed yearly, Mammoth Lakes

| Year | Green stand | Volume | Green stand | |
|-------|-------------------|--------|-------------|--|
| | volume | killed | killed | |
| | Board feet Percer | | | |
| 1938 | 36,394 | 4,436 | 12.2 | |
| 1939 | 31,958 | 4,287 | 13.4 | |
| 1940 | 27,680 | 722 | 2.6 | |
| 1941 | 26,958 | 1,450 | 4.3 | |
| 1942 | 25,798 | 0 | 0 | |
| Total | | 10,596 | 29.1 | |

ing from defoliation, but in 1960 snag-top trees were abundant in the study area. These trees were in various stages of decay, and some had fresh bark beetle attacks, indicating that the effects of defoliation can be prolonged.

Radial Growth

Radial growth in the increment cores studied by Patterson showed a pronounced downward trend from about 1934, when the outbreak started, to 1937, the year the cores were taken (fig. 12). Trees that were completely defoliated did not grow in 1937. Those 75-percent defoliated declined sharply in growth; and even trees only 50percent defoliated had a subnormal growth ring.

The growth pattern for the outbreak years was virtually the same in the disc samples cut in 1960 as in the cores taken in 1937. The growth rates were not identical, partly because by 1960 the trees sampled in 1937 could not be identified; thus, the samples came from different groups of trees. The discs showed that between 1938 and 1943 the trees gradually recovered from the effects of defoliation. Five years after the infestations ended, annual increment surpassed the predefoliation rate.

Stanislaus and Inyo Infestations Compared

Some interesting similarities are evident in the findings from the Stanislaus and Inyo studies. These similarities strengthen our basis for estimating the damage potential of tussock moth infestations. The Hell's Mountain outbreak of 1954-1956 on the Stanislaus was comparable to the Mammoth Lakes outbreak of 1934-1938 on the Inyo in defoliation intensity, stand density, and age. About the same size of sample (total area) was used in the two areas for the data on white fir mortality.

The volume of merchantable timber killed in the 5 years after each outbreak was about the same. At Hell's Mountain the loss amounted to 20 percent; at Mammoth Lakes, 29 percent of the green stand volume. The loss in board feet (11,071 and 10,596 for the two areas, respective-ly) was slightly higher at Hell's Mountain because of the greater stand density there. Most of the mortality took place during the first 2 years after the infestation ended, and all of it occurred within 4 years (fig. 13).

The main difference between the two areas was in amount of mortality assigned to different causes. At Mammoth Lakes, 12.2 percent of the green stand volume killed was attributed to defoliation



Figure 13. — Volume of white fir per acre killed by all insects following the decline of tussock moth infestation areas.

alone; whereas at Hell's Mountain only 0.5 percent was attributed to this cause. This discrepancy probably is not as great as it seems, for in the Inyo study, trees were classed as dead from defoliation even though many of them were infested by the roundheaded fir borer; whereas in the Stanislaus study, only dead trees which were not infested with other insects were placed in this category.

It is more difficult to compare the findings from the Stanislaus and Inyo studies regarding the effects of defoliation on radial growth. Different defoliation classes were used, and the growth data for the Mammoth Lakes plot, in particular, are based on very small samples. It is hard to believe that any of the white fir on this plot escaped attack, as the observations made at the time suggest. None escaped in the heavily defoliated plots at Hell's Mountain. Actually, radial growth reduction in trees classed as nondefoliated at Mammoth Lakes matched the reduction in trees classed as lightly defoliated at Hell's Mountain. And growth for the "light" class in the former matched the growth in the "medium" class for the latter. The magnitude of the radial growth losses for the Mammoth Lakes samples was considerably less than for Hell's Mountain, but the growth trends in relation to the time of outbreak were very similar. In both situations, there was a rapid decline of fir growth the same year feeding became heavy. After defoliation stopped, growth began to recover almost immediately, and the data available indicate that annual increment was almost back to preinfestation levels within two years.

Recent studies of the effects of spruce budworm feeding on tree growth have shown a time lag of two or more years between defoliation and growth response in balsam fir (Blais 1961). Our data indicate that response to tussock moth feeding in white fir is more immediate than this.

A promising lead that should be investigated further is the apparent relationship between periods of drought and tussock moth population increases that showed up in this study. The U. S. Weather Bureau's monthly summaries for California indicate that extended periods of subnormal precipitation occurred just before both the Stanislaus and the Inyo outbreaks. At the Hetch-Hetchy Station near the southern end of the Stanislaus infestation, and at the Calaveras Big Trees Station near the northern end, precipitation was below normal for the years 1953 to 1955, when tussock moth populations increased (fig. 14A). At the Gem Lake Station on the Inyo, subnormal precipitation occurred from 1929 to 1934, the year the Inyo outbreak started (fig. 14B).

Studies by Pilon and Blais (1961) and Silver (1960) have shown that periods of subnormal precipitation often precede increases in spruce budworm and black-headed budworm populations. For the black-headed budworm, Silver also found a correlation between above-normal precipitation and the decline of populations. Our observations suggest that similar relationships may prevail for the Douglas-fir tussock moth.



Figure 14. — Annual precipitation at weather stations near: A, the Stanislaus and B, Inyo infestation areas before, during, and after an outbreak.

Significance of the Damage

Knowledge of the amount of damage caused by outbreaks of such insects as the tussock moth is of highest importance because it is essential in making sound judgments of the need for control and in weighing the values to be saved against the control costs. Such information also helps the resource manager decide the amount of loss to tolerate before taking control action.

The value of damage done by a defoliating insect is difficult to assess, but the Stanislaus outbreak shows that economic loss can be large.

The principal types of white fir damage resulting directly from this outbreak were tree mortality, radial growth reduction, and top damage. Mortality and growth losses in sawtimber are the easiest to assign monetary values to, assuming that all the losses would have been merchantable. The volume of merchantable white fir killed at Hell's Mountain totaled 11,071 board feet per acre from 1956 to 1960. Growth losses totaled 1,113 board feet per acre. At \$5 per thousand board feet (the stumpage price for white fir in 1956) this represents a loss of \$55 and \$5.50 per acre, respectively, or a total of more than \$60 per acre in heavily defoliated stands. The total loss undoubtedly would have been higher had not the outbreak been halted by spraying in 1956; white fir mortality (percent of stand) from the Invo outbreak, which ran its course 20 years earlier, was half again as high as from the Stanislaus. Thus the \$1.60 per acre cost of controlling the Stanislaus outbreak seems to have been well spent.

The loss of smaller trees is much harder to evaluate, but in the heavily defoliated area 50 percent of the trees 6 inches d.b.h. and under died between 1956 and 1960. Some of these trees were worth \$1 or more each as Christmas trees. Their future stumpage value is anyone's guess, but it is probably not below today's values, which range from \$1.30 to \$2.75 per thousand board feet. The mortality of small fir trees due to defoliation has taken several thousand acres out of full production for many years to come.

Top damage resulting from the defoliation cannot be properly evaluated from the data available, but it should be remembered when considering the total impact of losses caused by the tussock moth. Twelve percent of the heavily defoliated trees suffered permanent top injury, and this can be expected to lead to future losses from heart rots, and lower quality lumber.

Direct losses from the outbreak on the Stanislaus were partly offset by logging dead and dying merchantable trees before they deteriorated. But emergency salvage operations of this type mean the disruption of long-range management and cutting plans aimed at realizing maximum returns consistent with sustained productivity. In this case, heavier volumes per acre were salvaged than would normally be logged, leaving an understocked stand that will take years of careful management to return to optimum production.

These studies show clearly that the Douglas-fir tussock moth can cause staggering losses in white fir stands. Consequently, when there are sound biological indications that moth populations are increasing, the entomologist should not hesitate to recommend control. And the forester should not delay in applying control in valuable stands threatened by this insect.

Summary

1. Damage caused by the Douglas-fir tussock moth was studied in white fir stands in California. The data were collected from the Stanislaus infestation of 1954-1956, and the Inyo infestation of 1934-1938.

2. Mortality of white fir was caused by defoliation alone and by a combination of defoliation and attacks by cambium-mining beetles. More small trees were killed than large ones. In the most heavily defoliated stands, 20 percent of the sawtimber volume (11,071 board feet per acre) died in the 5 years immediately after the end of the Stanislaus outbreak. Twenty-nine percent of the volume (10,596 board feet per acre) was killed in the 5 years after the Inyo outbreak.

3. Top damage in the Stanislaus infestation was most severe in the heavily defoliated trees, 12 percent of them being top-killed as a result of tussock moth feeding. Many small trees suffered temporary top dieback, but later grew new leaders. 4. Loss of radial growth was pronounced and similar for both infestations. The loss was most noticeable in trees more than 30 percent defoliated. Defoliation had an immediate effect upon white fir growth, and when feeding stopped, growth increased immediately.

5. Differences in growth between top, midcrown, and base were noticeable before and after the defoliation. In almost every case the base was growing more slowly, and the magnitude of loss was proportionally greater in the upper crown.

6. Records from stations near both the infested areas showed periods of deficient precipitation before the outbreaks, indicating that precipitation may be important in regulating tussock moth populations.

7. Growth losses of merchantable white fir amounted to 1,113 board feet per acre in stands heavily defoliated during the Stanislaus outbreak. These losses combined with mortality totaled 12,-184 board feet per acre, or more than one-fifth the original stand volume. Their stumpage value was \$60 per acre in 1956.

8. The study shows that the Douglas-fir tussock moth has a capacity for destruction far above that of some other well-known forest insect pests. Further studies are needed in order to predict these occasional but extremely destructive outbreaks.

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