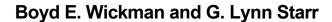
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**Abstract** 

For five decades after an outbreak of Douglas-fir tussock moth (*Orgyia pseudotsugata* (McDunnough)), radial growth of defoliated white fir trees (*Abies concolor* (Gord. & Glend.) Lindl.), was significantly greater than that of nondefoliated host trees nearby. The increased growth probably was due to the thinning effect of tree mortality and increased nutrient availability.

Keywords: Douglas-fir tussock moth, white fir, tree growth.

Introduction

One of the earliest recorded Douglas-fir tussock moth (DFTM; *Orgyia pseudotsugata* (McDunnough)) outbreaks on white fir (*Abies concolor* (Gord. & Glend.) Lindl.) occurred at Mammoth Lakes, California, from 1936 to 1938 (Wickman and others 1973). A 5-acre plot was established there in 1938 to study the effects of defoliation. This infestation caused mortality (30 percent of the stand), growth loss, and top-kill (Wickman 1963). The plot was reestablished in 1970 to investigate pathological-entomological relations on top-killed trees (Wickman and Scharpf 1972). In 1977 the plot was relocated, boundaries were marked, and selected trees were cored for measurement of radial growth of survivors. We found that radial growth of defoliated white fir was significantly greater than that of nondefoliated host trees nearby for 36 years after the outbreak, but in 1977 growth of all trees declined sharply as a result of a severe drought (Wickman 1980).

Information on long-term effects of DFTM outbreaks on growth of host trees is rare but has been recorded for a few sites in California and Oregon. A study 10 years after a DFTM infestation in northeastern California showed that growth of both host and nonhost trees in the defoliated area surpassed preoutbreak rates, but the reverse was true for nearby nondefoliated trees (Wickman 1978). The same area was remeasured 20 years after the outbreak with similar findings, but nonhost pine basal area has increased 32 percent (Wickman 1988). Radial growth measurements 10 years after a DFTM outbreak of grand fir (Abies grandis (Dougl. ex D. Don) Lindl.) and Douglas-fir (Pseudotsuga menziesii var. glauca (Beissn.) Franco) in northeastern Oregon showed a similar relation: postoutbreak growth of defoliated trees was significantly greater than preoutbreak growth (Wickman 1986b). But in another old outbreak area in the central Sierra Nevada, there was little difference between preoutbreak white fir growth and growth 30 years later (Wickman 1986a). The actual defoliation history of the sample trees was unknown in this study because the old research plots were destroyed by fire. The sample could have been taken in an area of light or moderate defoliation, in which case little or no thinning effect may have resulted from outbreak-caused tree mortality, and the defoliated stands were also on better sites than those in other study areas (Wickman 1986a). .

The increased growth found at the Mammoth Lakes study area nearly 40 years after a DFTM outbreak subsided and the fact that the stand was still being protected from harvest by the Inyo National Forest encouraged us to make a 50-year postoutbreak measurement of tree growth in 1987. In addition, we wanted to know how the different classes of trees would respond after the severe 1976-77 drought. Would defoliated white fir growth regain the predrought dominance exhibited in the 1977 measurement?

## Methods

The study area is in the Inyo National Forest on the east side of the Sierra Nevada several miles north of Mammoth Lakes Ranger Station. Elevation is about 8,000 feet. The mixed conifer stand is composed mainly of white fir and Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) but also contains scattered California red fir (*Abies magnifica* A. Murr.) and lodgepole pine (*Pinus contorta* Doug.). Before the outbreak, the livetree volume of white fir was 36,400 board feet per acre. Volume of pine was not recorded. Many old-growth white fir were killed by secondary insects shortly after the infestation. A total of 10,900 board feet per acre or 29.9 percent of the stand was dead by 1942. In 1945 the area was selectively logged for some old-growth pine and any remaining overmature fir. The first relogging took place in spring 1970, when about 2,000 board feet per acre was removed in a sanitation cut (removal of top-killed, diseased, or damaged trees).

Sample size was limited by lack of long-term records and the area of the plot available for measurements. Twenty dominants or codominants were selected from each of three tree classes: defoliated white fir, nonhost Jeffrey pine on the defoliated plot, and nondefoliated white fir nearby. Eight Jeffrey pine also were sampled on the non-defoliated site. The defoliated white fir were on the 1938 plot; on average, defoliation in 1938 was 53 percent but ranged from 10 to 100 percent. In 1987, white fir average age was 125 years, and diameter at breast height (d.b.h.) was 30 inches. The Jeffrey pine on the plot averaged 186 years in age and 35 inches in d.b.h. Because of the small size of the plot (5 acres), every dominant or codominant fir and pine was included in the sample in addition to three white fir and two pines that were boundary trees and may or may not have been on the original plot. Because the plot was in the middle of the 600- to 1,000-acre 1938 infestation, exact location of the trees was not considered critical.

Twenty nondefoliated white fir were located in a similar stand 1 to 2 miles northwest of the plot. Average age was 151 years, and average d.b.h. was 30 inches. Four clusters of five dominant or codominant fir were selected, each in a 2- or 3-acre area every 0.25 mile along an old logging road. These trees were not always the same white fir that were measured in 1977 because one of the clusters had been logged just before the 1987 visit. Increment cores taken in 1977 showed that growth of all check trees had increased rather than declined during 1937 and 1938, an indication that the area was outside the main infestation (fig. 1). The check spots were similar to the defoliated plot in elevation, soil, plant cover, tree species, and stocking and had been logged at the same time, except for, new Jogging in 1987. In addition, two dominant or codominant Jeffrey pine. were cored at each of the four nondefoliated, clusters. Average age of the pine was. 171 years, and average d.b.h. was 36 inches.

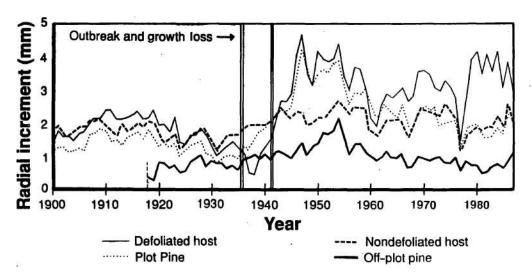


Figure 1—Average annual radial growth of white fir and Jeffrey pine at Mammoth Lakes, DFTM outbreak area.

From each tree at breast height, two increment cores were taken 90 degrees from each other (usually from the north and west quadrants). Cores were glued to blocks of wood and measured on an incremental measuring machine integrated with a desktop computer. Cores were averaged for each tree and each class. Analysis of variance was used to determine if radial growth differed among the four classes of trees or between time periods. A least significant difference (LSD) test was used to compare the individual means.

## Results and Discussion

In the 1977 study, analysis of variance of growth rates for the 36-year preoutbreak period (1900-35) showed no significant difference (P > 0.05) between defoliated and nondefoliated fir trees. The pine grew slower than both defoliated fir and nondefoliated fir throughout this period. Fluctuations in growth during this period were similar for all tree classes, an indication that all classes probably were affected similarly by environmental factors, mainly precipitation (Wickman 1980).

During the 36 years after the outbreak (1942-77), defoliated fir grew considerably faster than nondefoliated fir (fig. 1). Thus, the defoliated fir grew faster during the entire postoutbreak period, even though rates for nondefoliated and defoliated trees were similar before the outbreak (Wickman 1980).

From 1978 to 1987, more than 40 years after the outbreak, analysis of variance of growth rates and the LSD test showed significant differences (P < 0.01) between defoliated fir and the other three classes and between both nondefoliated fir and Jeffrey pine and off-plot Jeffrey pine (table 1). This relation is evident in figure 1, which shows defoliated white fir with the highest growth rate, nondefoliated white fir and on-plot Jeffrey pine with lower and almost identical growth rates, and off-plot Jeffrey pine with the slowest growth.

Table 1—Average annual radial growth for 4 classes of trees during preoutbreak (1900-36) and postoutbreak (1978-87) periods

	1900	1978
	to	to
Number	1936	1987
	Millimeters	
20	1.80b*	3.58a
20	1.75b	1.98b
20	1.36bc	1.88b
•	.81c	.77c
	20 20	10 Number 1936

<sup>\*</sup> Means with different letter are significantly different at the 0.01 level.

Comparing the preoutbreak period (1900-36) with the last 10-year postoutbreak period (1978-87) (table 1) shows that defoliated white fir are still growing significantly (P < 0.01) faster than before the outbreak, but nondefoliated fir and both groups of pine returned to their preoutbreak growth rates (fig. 1). The severe 1976-77 drought depressed growth of all classes to a low and similar level, but only the defoliated white fir rebounded to their predrought high levels. The long-term growth of defoliated white fir was still almost double what it was before the outbreak. Unfortunately, because of logging on the study sites, this cannot be related to a comparison of net stand growth for defoliated versus nondefoliated white fir. It therefore is not appropriate to infer that long-term growth response to the outbreak surpassed the short-term tree mortality and growth losses. The outbreak-area white fir stand is similar in appearance, however, to the nonoutbreak white fir stand in terms of age, species composition, and stocking. Fifty years after the outbreak, both fir and pine are growing faster on this site than on nonoutbreak sites.

The effects of thinning caused by tree mortality and the probable increased nutrient availability during and after the outbreak may have resulted in some long-term positive growth effects that are still accruing 50 years later. The results to date indicate, for this stand at least, that DFTM played an important role in primary forest productivity (Mattson and Addy 1975) through increased nutrient availability in these nitrogendeficient deep pumice soils. Similar nutrient availability enhancement has been suggested by Klock and Wickman (1978) and Stoszek (1988.)

In a study reported by Alfaro and MacDonald (1988), defoliation and radial growth reduction of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) by the western false hemlock looper (*Nepytia freernanii* Munroe) was similar to that caused by DFTM. After recovery from defoliation, many Douglas-fir had greater than average growth rates for 5 years; however, because there was little or no tree mortality, a thinning effect was not a factor. They also found that the postoutbreak growth increase was absent in the less defoliated (0 *to 40*- percent) tree class. At the Mammoth Lakes plot, records of the defoliation history of individual trees have not been maintained, but 39 of the 163 trees originally had 10 to 25 percent defoliation. Presently only. 20 dominant or codominants on the plot are large enough to have been recorded *in* 1938, and all these trees exhibit enhanced growth.

In other studies after DFTM outbreaks, the lightly defoliated classes (10 and 20 percent) have shown enhanced growth after the outbreak (Wickman 1978,1986b). There are often 2 years of severe defoliation in DFTM outbreaks versus 1 year in western false hemlock looper outbreaks, and this additional year of frass and litterfall may help to explain the difference.

Outbreaks by DFTM in these situations provide a stabilizing feedback system (Odum 1969) that promotes the vigor and survival of host trees and may dampen or delay for many decades future DFTM population eruptions. Because data on nutrient cycling in forest stands before and after insect outbreaks are scarce, only continued long-term studies will uncover these intriguing insect-plant relations. In the meantime, pest managers should not ignore the long-term beneficial aspects of some DFTM outbreaks.

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