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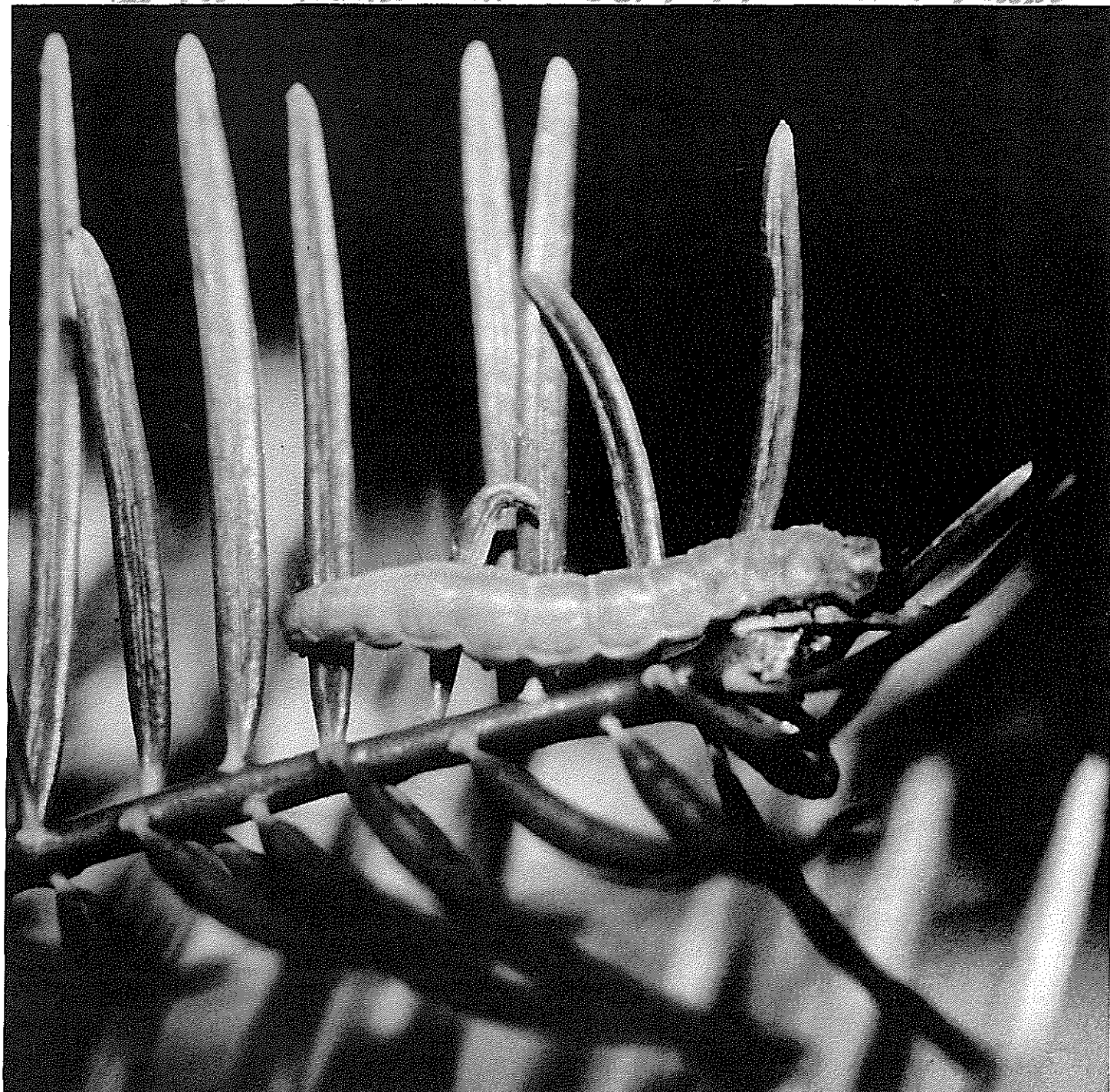
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Growth of White Firs Defoliated by Modoc Budworm in Northeastern California

George T. Ferrell

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IN BRIEF . . .

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Retrieval Terms: Modoc budworm, *Choristoneura viridis*, white fir, *Abies concolor*, defoliation effects, growth, injury

Outbreaks of Modoc budworm (*Choristoneura viridis*) defoliating white firs (*Abies concolor*) occurred during the years 1959-62 and 1973-75 in the Warner and nearby ranges of northeastern California.

Effects of the outbreaks on fir growth were analyzed by two methods. In 1974, combined totals of 24 firs and 9 nonhost ponderosa pines were sampled from three stands which were defoliated during both outbreaks. Growth of the two species was compared during both outbreak and nonoutbreak periods over the years 1950-74. This method was used because, during the earlier outbreak, defoliation records from individual firs were lacking.

In 1976, a combined total of 36 firs was sampled in four other stands defoliated by the 1973-75 outbreak. Based on defoliation and budworm larval density ratings made in 1974, growth in these firs during the years 1973-76 was compared.

The same growth sampling methods were used in 1974 and 1976. To improve growth comparability, only open-grown, pole-sized trees 40 to 80 years old were sampled. After the trees were felled, height and radial increments (the latter at upper, mid and lower bole levels) for 1950 through the year of sampling were measured. These measurements were converted to growth indexes expressing annual growth as a percentage of increment predicted by fitting a linear regression to each increment series. Growth index analysis, developed by dendrochronologists, eliminated growth patterns due to tree, site, and stand factors in order to isolate growth fluctuations caused by weather and defoliating insects.

Results of fir-pine comparisons for the stands sampled in 1974 indicated that height, but not radial, growth of the two species differed more during outbreak than nonoutbreak periods. Both species had height and radial growth depressions in response to droughts associated with the outbreaks. Compared to pines, however, firs averaged a 14.5 percent or 34.0 cm (1.1 ft) cumulative deficit in height growth over the years during and immediately following the outbreaks. Annually during these periods, the sizes of such deficits were related to the incidence of topkilling in the firs sampled. During the years of the earlier outbreak, both the height growth

deficits (0 to 15 percent), and the incidence of topkilling (0 to 3 percent), were low. During the more recent and extensive outbreak, however, both the height growth deficits and the incidence of topkilling increased, rising to 77 and 50 percent, respectively, in 1974—the peak year of the outbreak. Much of the latter height growth deficit, however, was expected to be only temporary because only the current year's growth was killed and, judging from previous topkills, would have been replaced by new tops.

Results of analyzing fir growth in the stands sampled in 1976—1 year after the more recent outbreak had subsided—allowed additional interpretation of the effects of budworm defoliation. Fir growth deficits related to percent crown defoliation during this outbreak were largely limited to 1974. In this year, compared to firs with light (less than 50 percent) defoliation, deficits in firs with medium (50-70 percent) defoliation averaged 33 and 14 percent in height and upper bole radial growth, respectively. These deficits were again related to the incidence of topkilling in these defoliation ratings (10 percent light, 48 percent medium). In 1974, however, results of growth comparisons among firs rated for larval density were largely nonsignificant or contrary to the results expected. Some firs evidencing reduced growth had low larval densities but were heavily defoliated and consequently abandoned by the budworms, resulting in low larval density estimates for these trees.

Host tree effects of the relatively short (3- to 4-year-long) Modoc budworm outbreaks appeared minor compared to the effects on the growth and mortality of conifer hosts by other, more protracted *Choristoneura* budworm outbreaks. Fir mortality associated with Modoc budworm outbreaks was not reported; because topkilling was usually limited to the current year's growth, only a slight crook or fork, and no decay, occurred in the stem in later years. Fir cone crops and Christmas tree values were probably temporarily reduced, but unless future Modoc budworm outbreaks are more protracted or otherwise intensified, this insect can be considered only a marginal pest of firs in California.

Defoliation of white firs (*Abies concolor* [Gord. and Glend.] Lindl.) by feeding green larvae of a tortricid moth has been detected in northeastern California over the last three decades. The defoliation, primarily in the current year's growth and heaviest in the tops of the firs, was formerly attributed to a green form of the spruce budworm (*Choristoneura fumiferana* Clements). Recently, Freeman (1967) recognized this form as a separate species (*C. viridis*) from either the spruce budworm or the western spruce budworm (*C. occidentalis* Free). Although *C. viridis* also infests white fir and grand fir (*A. grandis* [Doug.] Lindl.) in south-central Oregon (Stehr 1967), outbreaks in California have been confined to the Warner Mountains and neighboring ranges in Modoc County; thus, this insect is commonly referred to as the Modoc budworm.

Defoliation in the Warner Mountains has fluctuated from levels characterized in pest detection reports¹ as very light to heavy during the period 1949-76, with considerable local variation within years. From 1949 to 1958, defoliation ranged from very light to light, but in 1959 the infestation enlarged and some topkilling was noted in 1960. By 1961, light to heavy defoliation as well as some topkilling occurred on about 32,000 acres. The infestation subsided the next year and remained at low levels until 1973 when populations again increased. By 1974, the acreage infested was larger than that recorded in any previous outbreak; defoliation ranging from slight to severe was detected on 143,000 acres in the Warner and nearby Manzanita and Knox Mountains. But populations again subsided in 1975, and only 13,000 acres were defoliated. By 1976, Modoc budworm populations were again at an endemic level and no detectable defoliation was expected in 1977.

Serious growth reduction and mortality have been reported in conifer stands defoliated by outbreaks of other *Choristoneura* budworms in both western and northeastern North America (Johnson and Denton 1975, Kulman 1971). The

effects of defoliation by Modoc budworm on white fir growth have not, however, been previously studied.

This paper investigates growth patterns and topkilling in white fir stands which were defoliated during the 1959-62 and 1973-75 Modoc budworm outbreaks in northeastern California to determine if this insect is an economic pest justifying control measures.

METHODS

The use of growth increment patterns to estimate growth reduction in conifers defoliated by species of *Choristoneura* budworms in the western United States has been hampered by the occurrence of other defoliating insects and weather phenomena affecting the growth of both host and nonhost trees (Johnson and Denton 1975). Growth fluctuations due to these other agents frequently mask growth reductions caused by budworm defoliation. Similar difficulties were expected in estimating the effects of defoliation by Modoc budworm, since conifer stands in the Warner Mountains and vicinity have also been subjected to periods of subnormal precipitation and defoliation by other insects during the last three decades. During this period, annual summaries of California weather published by the U.S. Weather Bureau indicate that annual precipitation was below normal at nearby Alturas Ranger Station in the years 1949, 1954-61, 1966-68, and 1972-76. The Modoc budworm outbreaks in 1959-62 and 1973-75 were each associated with periods of 3 years or more when precipitation averaged at least 25 percent below normal (fig. 1), although extensive defoliation was not detected following lesser precipitation deficits in other years.

In addition to Modoc budworm, infestations of other insects defoliating white firs have been reported in the Warner Mountains and vicinity over the last three decades. During the 1959-62 Modoc budworm outbreak, larvae of a tortricid moth (*Argrotaenia* sp.) contributed to the defoliation as did the coneworm *Dioryctria reniculella* (Grote). During the 1973-75 outbreak, the fir needleminer *Epinotia meritana* Heinrich ap-

¹ California Forest Pest Control Action Council. 1949-1976. Annual reports. (Unpublished reports on file, Pacific Southwest Forest and Range Exp. Stn., Forest Serv., U.S. Dep. Agric., Berkeley, Calif.)

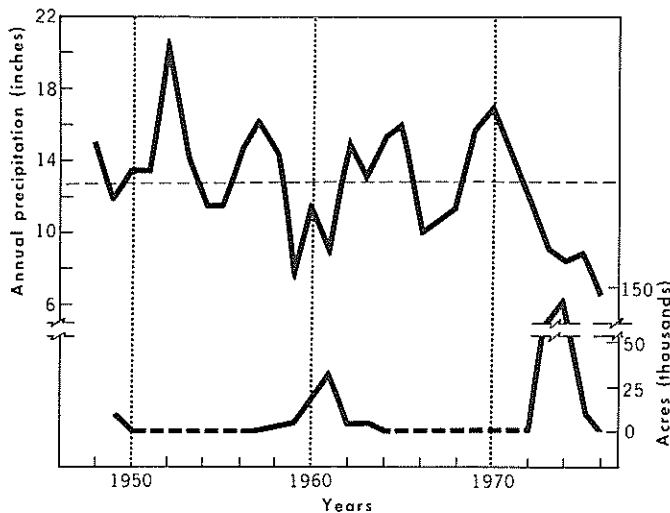


Figure 1—Modoc budworm outbreaks in 1959-62 and 1973-75, depicted as peaks in the acreage defoliated, were each associated with periods of 3 or more years when precipitation was at least 25 percent below normal (horizontal line) at nearby Alturas Ranger Station, in northern California. Dashed lines indicate periods when the infestation was endemic and no acreage estimates were made.

peared in localized areas. An outbreak of the Douglas-fir tussock moth *Orgyia pseudotsugata* McDunnough seriously defoliated limited acreage in the Warner Mountains and vicinity in the period 1964-65. Persistent, localized defoliation of white firs by white fir sawflies (*Neodiprion* sp.) was also reported in these areas during the period studied.

Due to these possibly complicating influences and to the fact that estimates of Modoc budworm population and defoliation on individual sample firs were available only for the year 1974, two different methods were used to try to isolate possible growth reductions in white fir resulting from defoliation by Modoc budworm.

Growth Comparisons Between Host and Nonhost Trees

In the stands sampled in 1974, growth patterns in white firs were compared with those in nonhost ponderosa pines (*Pinus ponderosa* Dougl. ex Laws.). The stands were selected because the fir component was defoliated during the Modoc budworm outbreaks, but no insects or diseases influencing growth of the pines were reported. This approach assumes that growth patterns of host and nonhost trees growing in the same stand should be similar, except during outbreak periods when host trees were defoliated but nonhost trees were not. Any deficits in host, versus nonhost, growth associated with these outbreak periods were then assumed attributable to the effects of the defoliation. Although these assumptions may be subject to error (Kozlowski and Keller 1966, Nairn and others 1962), this method was nevertheless resorted to in the present study because of the absence of individual tree defoliation records from the earlier 1959-62 outbreak. To check the validity of these assumptions, the analysis first compared pine-fir growth differences between outbreak and non-outbreak periods. Commonly, outbreaks of other conifer-feeding budworms

have resulted in host tree growth depressions persisting for at least several years after the outbreaks have subsided (Johnson and Denton 1975, Kulman 1971). Therefore, for the 1959-62 Modoc budworm outbreak, fir growth deficits during the period 1959-64 were attributed to the effects of the outbreak. The similar period for the 1973-75 outbreak, however, was only 1973-74, as the trees were felled for sampling in 1974. Further sampling was undertaken in 1976, after the outbreak subsided, to assess more complete growth effects of this outbreak.

For purposes of comparison with the outbreak growth periods, nonoutbreak periods were defined as growth periods during the years 1950-58 and 1965-72, assuming that the very light to light fir defoliation reported during these periods caused little or no growth reduction in the firs.

In 1974, three plots were sampled in mixed white fir-ponderosa pine stands, in which the firs were defoliated by Modoc budworm during the years 1959-62² and 1973-75 (no outbreaks of other defoliating insects were reported during the period 1950-74). The plots were located at elevations of 1800 to 2400 m (6000 to 8000 ft) along 64 km (40 mi) of the north-south backbone of the Warner Mountains. The plots were sampled during the period July 22 to August 15 when current height and radial growth were expected to be essentially completed, judging from long-term records for comparable elevations in the Sierra Nevada (Fowells 1941). On each plot eight white firs and three ponderosa pines were sampled. Only young, rapidly growing trees 40 to 80 years old, 15 to 35 cm in dbh, and 8 to 20 m tall, with dominant or open-grown crowns were sampled to avoid the effects of suppression and improve growth comparisons. Study results of other conifer-feeding *Choristoneura* sp. indicated that such firs were also expected to support higher budworm populations (Williams and others 1971) and to suffer larger percentage growth reductions (McLintock 1955) than slower growing firs with less exposed crowns.

At the time of sampling, defoliation of the firs appeared as a reddening of the new growth on the branch tips, concentrated mainly in the tops, giving the fir a scorched appearance. Many of the current year's buds or shoots were killed, as were most of the new needles once they had been partially consumed and loosely webbed together. The budworms also fed on the older needles but to a lesser extent. Foliage of a few top whorls of many firs was sparse and faded (fig. 2), contrasting strongly with foliage beneath the top which was often abnormally bushy and clumped, probably due to the growth of adventitious buds and shoots in response to the death of buds during earlier defoliations, as described for other conifer-feeding *Choristoneura* sp. (Schmidt and Fellin 1973, Williams 1967).

The trees were severed 45 cm above ground and the following measurements were taken: *stump*—age by ring count with 6 years arbitrarily added for the tree to reach stump height, diameter outside bark (cm); and *bole*—total tree height (m)

² Pacific Northwest Region, Forest Service. 1961-1964. Spruce budworm egg mass biological evaluation. (Unpublished report on file, Pacific Southwest Region, Forest Serv., U.S. Dep. Agric., San Francisco, Calif.)

and the lengths (cm) of internodes for the years 1950-74. Uncertainty over delimitation of internodes was resolved by sectioning the bole and comparing ring counts made above and below the specific internode. Topkill in previous years was visible as a dead terminal issuing from a fork or crook in the bole (*fig. 3*). Both the length of the killed tip (cm) and the year it was killed (by counting the internodes on a regrown leader) were recorded. Because growth reduction in grand firs defoliated by western spruce budworm was found to vary with height in the bole (Williams 1967), a 2-cm-thick cross-sectional disk was sawn from three levels in the bole, defined as midbole (1950 internode); upper bole (midway between the 1950 internode and the top), and lower bole (stump height). Three 2-cm-wide radial sections were then sawn from each disk. On lower bole and midbole sections, the width of each annual ring formed in the years 1950-74 was measured (± 0.01 mm). All rings formed in the years 1960-74 were measured on upper bole sections from a region of the stem that was too young to have increments from the 1950's. After cross-checking the sections for false (traumatic) and missing

or discontinuous rings, averages of each ring width on the three radial sections from each disk were used in the growth analysis.

Growth index analysis developed by dendrochronologists (Fritts 1966) was used to isolate growth effects attributable to the outbreaks. The indexes were designed to increase comparability of tree growth by isolating growth fluctuation caused by weather and defoliation and eliminating growth patterns attributable to differences in species, age, site, and surrounding stand characteristics. Other methods to separate the effects of these factors on radial growth of trees have been developed but require more complete stem dissections (Duff and Nolan 1953, Mott and others 1957, Stark and Cook 1957) or more elaborate statistical analysis (Williams 1967).

The growth indexes were calculated by fitting a least squares regression line with positive, negative, or zero slope to both height and radial increments formed in each tree in the years 1950-74, or in the upper bole radial increments from the early 1960's through 1974 (*fig. 4*). Linear regression was considered adequate after plotting increment series from a



Figure 2—Recent defoliation by Modoc budworm left fir tops with thin, faded foliage. Bushy, clumped foliage in lower crowns resulted from adventitious growth response of trees to past defoliation.



Figure 3—Topkilling attributed to previous outbreaks of Modoc budworm was limited to the former terminal shoot (central dead twig), which was later replaced by upturned branches forming a forked stem.

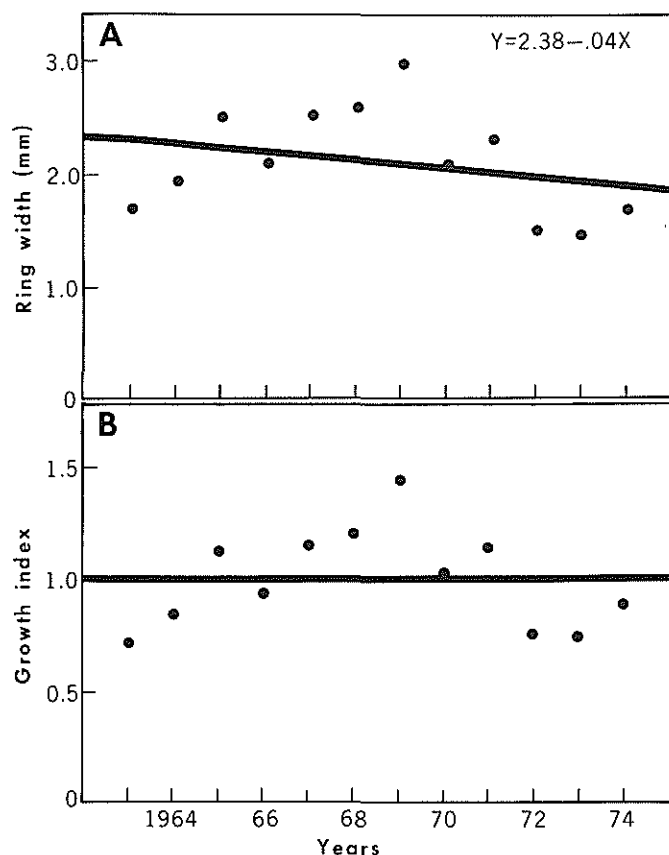


Figure 4—Annual growth indexes calculated for radial increments in the upper bole of white fir for the years 1963-74. The measurements are divided by values predicted by regression line (A) to obtain indexes varying about 1.0, representing predicted or expected growth (B).

subsample of trees, which indicated that curvilinearity could be ignored due to the short length of the series studied. Each year's index was then obtained by dividing the measured increment by that predicted by the regression line. Indexes with a value of 1 represented growth equal to expected growth patterns in the absence of unusual factors such as drought or defoliation. Indexes with a value less than 1 indicated growth below that expected from long-term patterns in the tree, while indexes greater than 1 indicated growth above predicted levels. When multiplied by 100, the indexes expressed annual growth as a percentage of predicted growth based on increments over the entire 1950-74 study period.

Pine-fir growth differences during outbreak periods were compared with those during nonoutbreak periods, as follows. For each year studied, the signed difference between the mean growth index of pines and that of firs (pine-firs) was obtained on each plot. To provide a firm basis for comparison, periods associated with the outbreaks (1959-64, 1973-74) were combined, as were nonoutbreak periods (1950-58 and 1965-72), and data from all three plots were analyzed. Since neither the indexes nor their differences were expected to be normally distributed, the nonparametric Fisher's randomization test (Bradley 1960, Green 1977) was used, although it was realized that the growth differences were not completely independent observations. The probability of randomly obtaining a mean growth difference between periods larger than that observed

was calculated and declared significant at the 5 percent level. For increments in which signed differences between pines and firs during outbreak periods significantly exceeded differences during nonoutbreak periods, the average growth deficit in firs during outbreak periods was obtained as the difference between the mean growth index of the two species—expressed as a percentage of predicted increments.

Growth Comparisons Among Host Trees Grouped by Defoliation and Larval Density Ratings

Methods used in 1976 to sample stands and calculate growth index to search for growth reductions and topkilling attributable to the 1973-75 outbreak were similar to those methods for stands sampled in 1974. In 1976, a total of 16 firs was sampled from three stands in the Warner Range, and an additional 20 firs were sampled from a single stand at nearby Manzanita Mountain. All four stands were currently being defoliated and had been sprayed with insecticide in late June 1974 when Modoc budworms were fifth to sixth instar larvae. Both before and after treatment, budworm population density and crown defoliation were estimated in these trees in order to gauge the efficacy of the insecticide spray. Results of this evaluation indicated that, although over 90 percent of the larvae were killed, little or no defoliation was prevented,³ enabling these trees to be used for growth impact studies.

Defoliation of each fir was rated as light, medium, or heavy by the following method. The crown was visually divided into six horizontal strata. Separate ocular estimates were made of the percentage defoliation of both the new (current year's) and the old (previous years') foliage in each stratum. These estimates were recorded as defoliation scores. The scores and the percentage defoliation they represented were 0 (none), 1 (less than 50 percent), 2 (50 to 90 percent), and 3 (greater than 90 percent). New and old foliage scores were averaged over all strata. Due to retention of foliage produced in previous years, the ratio of old to new foliage in the crown was estimated at about 4:1. Thus, the same score for both old and new foliage was interpreted to indicate that the biomass of old foliage lost was about four times that of new foliage. Therefore, average scores for old and new foliage were weighted by factors of 4 and 1, respectively, when averaged to obtain an overall defoliation score for the entire crown. A light defoliation rating was arbitrarily represented by an overall score less than 1.0, indicating less than 50 percent crown defoliation. Scores of 1.0 to 1.5 represented medium, or about 50-70 percent defoliation. A score over 1.5 was rated as heavy, or in excess of 70 percent crown defoliation. It appeared that not all of this defoliation occurred in 1974; some of the defoliation of old growth probably occurred in 1973. Thus, the tree's score was interpreted to represent the cumulative amount of defoliation during the period 1973-74.

³ Pierce, J.R. 1974. Pilot control project of Dyllox on the Modoc budworm. (Unpublished report on file, Pacific Southwest Region, Forest Serv., U.S. Dep. Agric., San Francisco, Calif.)

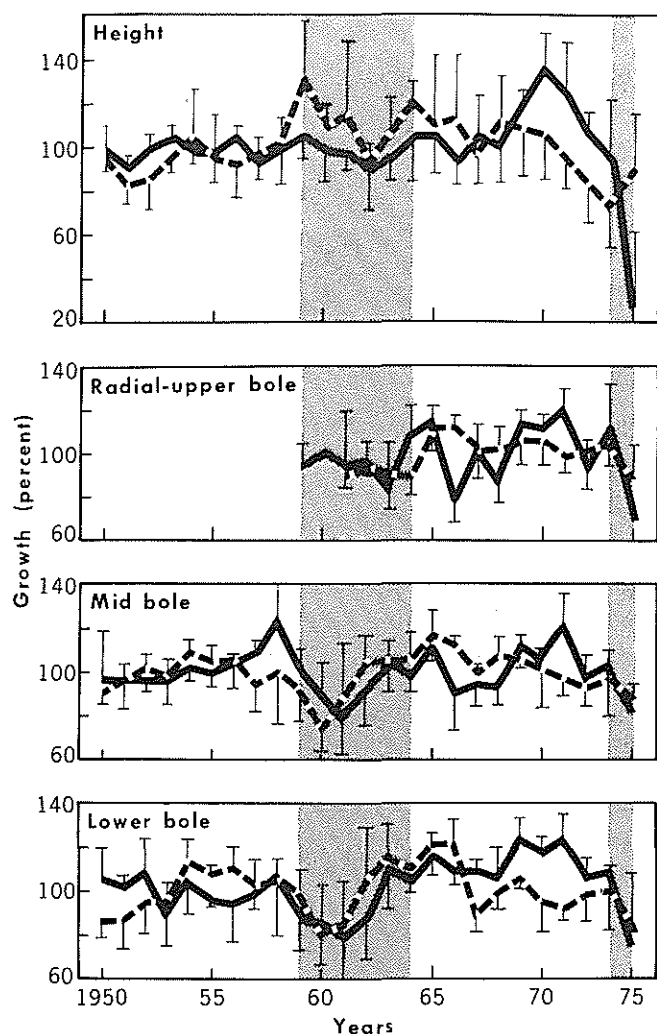


Figure 5—Mean annual height and radial growth as percentages of predicted increments in white firs (solid lines) and ponderosa pines (dashed lines) in three fir stands defoliated by both the 1959-62 and 1973-75 Modoc budworm outbreaks. For growth comparisons, outbreaks (shaded) were compared with nonoutbreak (unshaded) periods. Vertical lines extend one standard deviation from means.

Similarly, the budworm population density on each tree was rated as light, medium, or heavy. Budworm counts were made on four mid-crown branches of each tree. The foliage surface area on each branch was calculated by measuring the maximum dimensions of the foliage, both along and normal to the branch axis. These dimensions were considered to represent the altitude and base, respectively, of a triangular surface area of foliage on each branch.

From the budworm counts and the foliage surface areas on the four branches from each tree, the mean density of budworms per 1000 square inches of foliage surface was calculated for the tree. Budworm densities averaging less than 100 per 1000 square inches foliage were arbitrarily rated as light, 100 to 200 as medium, and over 200 as heavy.

Annual growth indexes for each tree were calculated by measuring annual height and radial increments for the years 1965-76. Increments from earlier years were ignored, since some of the firs in the Manzanita Mountain area were de-

Table 1—Mean annual height and radial growth differences between nonhost ponderosa pines and white firs during Modoc budworm outbreak compared with nonoutbreak years during the period 1950-74 on three plots, Warner Mountains, California

Increments and bole level sampled	Growth as a percentage of predicted increment		
	Outbreak (O)	Nonoutbreak (N)	Differences (O-N)
Height growth:			
Pines	104.4	97.8	6.6
Firs	89.9	104.7	-14.9
Diff. ¹	14.5	-6.9	21.5*
Radial growth:			
Upper bole:			
Pines	92.4	104.0	-11.6
Firs	96.9	101.5	-4.6
Diff.	-4.5	2.5	-7.0†
Midbole:			
Pines	94.4	102.2	-7.8
Firs	93.3	102.8	-9.5
Diff.	1.1	-0.6	1.7†
Lower bole:			
Pines	96.4	101.4	-5.0
Firs	91.3	104.1	-12.8
Diff.	5.1	-2.7	7.8†

¹Signed difference (pines-firs). Only differences followed by symbols were tested statistically.

*Statistically significant at 5 percent level (Fisher's test).

†Not significant.

foliated by tussock moth in 1964-65. Mean and standard deviation were calculated for annual growth indexes of firs in each of the defoliation ratings. For each of the years between 1973-76, variation in the mean annual growth index for firs in the defoliation and larval density ratings was analyzed for significance (5 percent level) by the nonparametric Kruskal-Wallis test (Kruskal and Wallis 1952) and, where significant, used as a basis for paired comparisons between ratings also at the 5 percent level of significance (Miller 1966, p. 166-167).

RESULTS

Growth Comparisons Between Host and Nonhost Trees

Growth comparisons between firs and pines during outbreak and nonoutbreak periods indicated that the height growth of firs might have been affected by the outbreaks. Trends in mean annual growth as percentages of predicted increments indicated that both height and radial growth of both species was depressed during the outbreaks in response to the associated periods of subnormal annual precipitation (fig. 5).

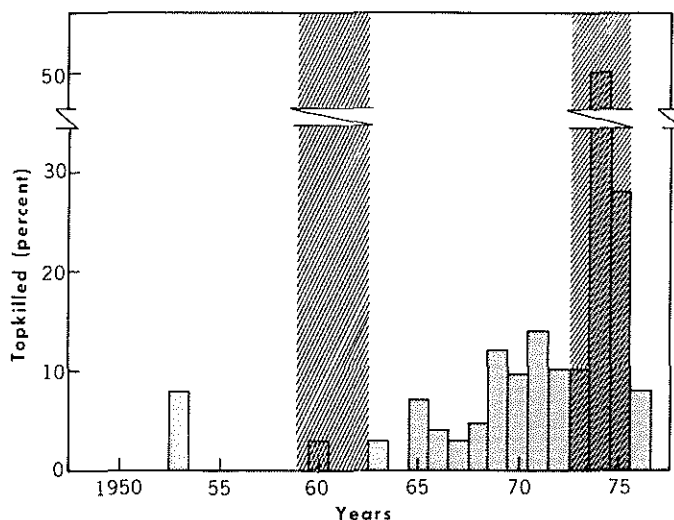


Figure 6—During the outbreaks (hatched periods), the annual percentage of fir trees topkilled (1974 and 1976 samples combined) had not exceeded 3 percent during the years 1959-62, but increased to 50 percent during the more extensive outbreak in 1973-75.

During outbreak periods, however, differences in height growth between species were significantly greater than during nonoutbreak periods, although such differences in radial growth were not significant at any bole level sampled (*table 1*). During outbreak periods, height growth of firs averaged 89.9 percent of predicted increments, compared with a 104.4 percent growth rate for pines, indicating that the firs had an average annual height growth deficit of 14.5 percent during these periods. The reverse occurred during nonoutbreak periods, however, when the height growth of firs exceeded that of pines by an average of 6.9 percent per year.

Based on these growth percentages and the average height growth of firs during the outbreak periods as predicted by the regressions, the cumulative deficit in height growth of firs compared with pines over these periods can be calculated in centimeters or feet. Predicted height growth of firs over these years should have averaged 236.1 cm (7.8 ft). If, however, the firs had grown at the rate averaged by the pines during these periods, their cumulative height growth should have averaged 104.4 percent of predicted growth, or 246.0 cm (8.1 ft). Instead, fir height growth averaged only 89.9 percent of predicted growth, or 212.0 cm (7.0 ft). Compared to pines, therefore, the firs had an average height growth deficit of 34.0 cm (1.1 ft) attributable to the two outbreaks.

During the years of the outbreaks, height growth deficits in the firs were related to the incidence of topkilling (*fig. 6*). During the 1959-62 outbreak, such deficits ranged from 0 to 15 percent and percentages of topkilled firs varied from 0 to 3 percent. During the more extensive outbreak of 1973-75, both the deficits and percentage of firs topkilled increased to 77 and 50 percent, respectively. During nonoutbreak periods, however, considerable topkilling also occurred, which was only partially related to subnormal precipitation or outbreaks of other defoliating insects.

Host Tree Growth Related to Defoliation and Larval Density Ratings

In firs sampled in 1976, growth reductions related to percentage of crown defoliation during the 1973-75 outbreak were largely limited to 1974—the peak year of the outbreak and the year when the defoliation estimates were made. During the years 1973-76, the height growth of firs in all ratings remained near predicted levels. Radial growth, however, declined at all three bole levels, probably in response to declining annual precipitation during this period. In 1974, however, firs with medium ratings (50-70 percent defoliation) averaged growth deficits of 33 percent in height and 14 percent in upper bole radius, compared to predicted increments in firs with light (less than 50 percent defoliation) ratings (*table 2*). These deficits were related to the percentage of firs in those ratings which were topkilled in 1974, 48 and 10 percent in medium and light ratings, respectively (*table 3*). In two comparisons, only firs rated as having heavy (greater than 70 percent) defoliation had significant growth deficits compared to firs in the other ratings. In 1974, heavily defoliated firs averaged a 16-percent deficit in lower bole radial growth compared to firs with light ratings. Comparable deficits were not found in height and upper bole radial increments for 1974, however, probably because none of the heavily defoliated firs was topkilled in that year. At the upper bole level in 1976, however, these firs averaged a radial growth deficit of 20 percent and had a higher incidence of topkilling (67 percent), compared to firs

Table 2—Mean annual height and radial growth as percentages of predicted increments for white fir with light, medium and heavy defoliation ratings during the 1973-75 Modoc budworm outbreak, Warner and Manzanita Mountains, California

Defoliation rating	Mean percentage of predicted growth (standard deviation) ¹			
	1973	1974	1975	1976
Height				
Light	100.3(33.5)	108.2(42.4)a	113.5(29.9)	105.1(26.8)
Medium	95.8(36.5)	77.5(48.7)b	102.9(29.5)	101.6(49.6)
Heavy	115.9(28.5)	92.0(58.0)ab	132.1(49.9)	117.6(57.1)
Radial-upper bole				
Light	118.6(23.5)	105.7(17.1)a	82.8(13.7)	85.0(11.3)a
Medium	124.2(19.5)	91.5(19.6)b	80.8(20.4)	95.0(33.3)a
Heavy	130.8(16.1)	104.9(12.7)ab	73.4(15.6)	64.8(14.4)b
Radial-midbole				
Light	121.5(15.6)	113.0(11.4)	81.9 (8.7)	91.2(13.2)
Medium	120.6(14.3)	109.6(10.7)	84.3(13.5)	79.9(20.1)
Heavy	113.4 (9.9)	105.1 (8.6)	88.2(12.7)	79.9 (5.3)
Radial-lower bole				
Light	126.0(21.6)	116.4(12.9)a	82.2(15.0)	84.8(17.6)
Medium	114.1 (8.2)	111.9 (9.2)ab	87.6(15.7)	84.4(16.8)
Heavy	112.4 (5.5)	99.7 (8.8)b	91.4(25.5)	87.9(11.2)

¹Means followed by different letters differ significantly; those means followed by the same letter do not. Variation among unlettered means was not significant at the 5 percent level (Kruskal-Wallis test).

Table 3—Annual percentages of white firs topkilled in the years 1973-76 compared by defoliation, and larval density, ratings during the 1973-75 Modoc budworm outbreak in northeastern California

Rating	Percentage topkilled				
	Trees	1973	1974	1975	1976
Defoliation ¹					
Light	10	10.0	10.0	20.0	0.0
Medium	23	17.4	47.8	30.4	4.3
Heavy	3	0.0	0.0	33.3	66.6
Larval density: ²					
Light	17	23.5	47.1	35.3	11.8
Medium	13	7.7	30.8	23.1	7.7
Heavy	6	0.0	16.6	16.6	0.0

¹Percent crown defoliation rated as light (less than 50), medium (50-70), or heavy (greater than 70).

²Mean number of larvae per 1000 square inches of foliage on four midcrown branches, rated as light (less than 100), medium (100-200), or heavy (greater than 200).

with light ratings. No comparable deficit was found in that year's height growth, although judging from older topkills, some permanent height growth loss probably resulted from this topkilling. Results from firs with heavy defoliation ratings, however, are somewhat uncertain due to only three trees in this rating.

Agreeing with results from defoliation ratings, only a few fir growth deficits related to budworm larval density in 1974 occurred in years associated with the 1973-75 outbreak. A growth deficit in firs with heavy, versus medium or light, larval density ratings occurred only in 1976 radial increments at the lower bole level (table 4). This growth deficit was not related to incidence of topkilling in these ratings (table 3). In the only other significant differences found between these ratings, radial growth deficits in firs with light larval densities occurred in 1973 (lower bole level) and 1974 (upper bole level). These results were opposite to those expected as was the incidence of topkilling in the ratings for these years. Underlying these results was an inverse correlation ($r = -0.49$) between defoliation and larval density in these trees, evidently caused by budworms abandoning heavily defoliated firs in favor of less defoliated trees.

CONCLUSIONS

The relatively short, 3- to 4-year-long outbreaks of Modoc budworm during the last 25 years have evidently had less effect on the growth and survival of white firs in northeastern California than the more protracted outbreaks of other budworms (*Choristoneura* sp.) on their coniferous host trees in eastern and western North America. For example, beginning the second year of defoliation of Douglas-fir, spruce, and true fir by western spruce budworm (*C. occidentalis*) in British

Table 4—Mean annual height, and radial growth, as a percentage of predicted increments, for white firs with light, medium, and heavy larval density ratings during the 1973-75 Modoc budworm outbreak, Warner and Manzanita Mountains, California

Defoliation rating	Mean percentage of predicted growth (standard deviation) ¹			
	1973	1974	1975	1976
	Height			
Light	100.9(39.4)	74.9(51.5)	106.2(39.1)	92.3(53.4)
Medium	96.0(33.0)	88.9(44.6)	115.2(17.8)	117.2(34.2)
Heavy	98.6(28.6)	112.0(44.7)	99.3(32.7)	108.3(26.0)
	Radial-upper bole			
Light	130.1(20.7)a	86.2(19.9)a	72.4(20.4)	91.8(35.8)
Medium	120.2(19.6)a	106.2(12.1)b	87.8(13.1)	85.3(24.0)
Heavy	110.5(11.9)a	108.2(16.3)ab	92.0 (9.5)	94.1(11.7)
	Radial midbole			
Light	115.0(13.2)	105.5 (9.4)	82.6(11.7)a	76.7(17.7)
Medium	122.9 (9.8)	112.9(10.8)	84.1(12.6)a	90.8(18.9)
Heavy	129.4(20.2)	117.4 (9.1)	87.6(13.4)a	84.1(11.3)
	Radial-lower bole			
Light	110.3(10.1)a	107.9(11.0)	87.0(16.5)	81.0(15.3)ab
Medium	121.9(14.9)ab	116.3 (9.1)	85.8(17.7)	93.8(17.2)a
Heavy	127.2(12.8)b	115.3(11.3)	86.3(13.7)	76.4 (6.9)b

¹Variation among means followed by letters was significant. Means followed by different letters differed significantly in pair-wise tests, while means followed by the same letter were not statistically different. Variation among unlettered means was not significant (Kruskal-Wallis test, 5 percent level).

Columbia, annual increments were reduced 30 to 60 percent over a 4-year period (Silver 1960). In Oregon, depending on the severity of damage from past defoliation and species of host tree, growth during a 10-year outbreak of this budworm was reduced by as much as 40 percent of the growth in the previous decade when no outbreak occurred (Williams 1967). Also, tops of the more severely damaged trees were killed by as much as 6 m (19.8 ft) down the bole, and death of some trees appeared imminent.

In reviewing the effects of severe defoliations of spruce and fir by *C. fumiferana* in northeastern North America, Kulman (1971) found that 30 to 100 percent of the trees died in severely defoliated stands which were subsequently attacked by bark beetles, with most of the surviving trees suffering topkill.

In contrast, the ponderosa pine-white fir growth comparisons estimated that white fir had an average deficit of 14.5 percent or 34.0 cm (1.1 ft) in height increment attributed to outbreaks during both the periods 1959-64 and 1973-74. Included in this average, however, was a 77 percent deficit in 1974, associated with the relatively high incidence of topkilling in that year. But judging from the older topkills examined, much of the 1974 deficit was expected to be only temporary due to subsequent replacement of the dead tops by up-turned branches of the uppermost whorl. A more accurate estimate of permanent height growth loss in firs topkilled in 1974 is perhaps obtained from firs sampled in 1976 which had two years to recover from topkilling in 1974. Of these firs,

those which had medium defoliation ratings and a 48 percent incidence of topkilling in 1974 had height growth deficits averaging 33 percent, compared with firs with light defoliation ratings and a lower incidence (10 percent) of topkilling.

Radial growth losses associated with the Modoc budworm outbreaks were even more limited than the height growth effects. In stands sampled in 1974, the fir-pine comparisons failed to detect any radial growth deficits attributable to the outbreaks at any of the three bole levels sampled in the firs. In stands sampled in 1976, however, firs with medium-to-heavy defoliation ratings in 1974 had average deficits of 14 percent in that same year and 25 percent in 1976 for radial increments at the upper bole level. Again, these deficits were associated with the high incidence of topkilling in those years. Similar deficits were not detected at the lower and mid-bole levels, except in 1974 when a 13 percent deficit was found at lower bole levels in trees with heavy defoliation. Finding radial growth reductions greater in the upper regions of the bole agreed, however, with the vertical distribution of radial growth effects found in trees defoliated by other *Choristoneura* budworms feeding preferentially on new growth of conifers (McLintock 1955, Williams 1967).

Topkilling was confirmed to be a direct result of defoliation. During the 1973-75 outbreak, the incidence of topkilling increased as the outbreak expanded and declined as the outbreak subsided. In 1974, the peak year of the outbreak, firs with medium to heavy defoliation had a higher incidence of topkilling than firs with light defoliation. The droughts associated with the outbreaks also may have contributed to the topkilling. Considerable topkilling, however, occurred inexplicably in years not associated with either outbreaks or droughts. Growth losses in both height and upper bole radius were strongly associated with topkilling; many of the sample trees were topkilled more than once during the two outbreaks. Because of the small size of killed tops, however, the resulting stem defects were limited to a slight crook or a fork, and no decay was observed.

Host tree mortality resulting from Modoc budworm infestations has not been detected. Increased killing of white firs by the fir engraver bark beetle (*Scolytus ventralis* Lec.) was reported in the Warner Mountains in the years 1960-64, 1967-68, and 1972, and localized mortality of firs infested by needle miner (*Epinotia meritana*) occurred on Manzanita Mountain in 1977. However, in none of these instances was defoliation by Modoc budworm implicated as an important factor contributing to the death of these trees.⁴

Defoliation by Modoc budworm left much of the tree crowns intact. Defoliation estimates made at the peak of the recent outbreak indicated that from 50 to 100 percent of the new or current year's foliage, but less than 50 percent of the old foliage from previous years, was destroyed on most trees. The new foliage, although more heavily fed upon, was esti-

mated to comprise only about 25 percent of the foliage mass of the entire crown due to retention of the old foliage. Consequently, expressed as a percentage of the entire crown, 10 of the 36 white firs rated in 1974 had less than 50 percent of their crowns defoliated. Observations in 1976, after the outbreak subsided, indicated that the trees responded to the defoliation by producing adventitious buds and shoots to compensate for the destroyed foliage. Failure to find growth reductions in trees defoliated to this extent is not uncommon; a recent review of the literature on growth effects in trees defoliated by insects (Mattson and Addy 1975) indicated that trees with less than 40 to 50 percent of their crowns defoliated frequently suffer no detectable growth reductions.

Although not studied, impairment of aesthetic, forage, and watershed values appeared negligible due to the small proportion of the fir canopy which was damaged. Undoubtedly, the value of defoliated firs for Christmas trees was temporarily reduced. Also, cone production, which occurs exclusively in tops of white fir, may have been reduced in fir with heavy upper-crown defoliation and topkilling. Only open-grown pole-sized firs were sampled; but if these results are indicative, unless future outbreaks are of longer duration or otherwise intensify, the Modoc budworm may be considered a marginal economic pest of white fir in California.

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Open-grown, pole-sized white firs defoliated by Modoc budworm (*Choristoneura viridis*) in northeastern California in the years 1959-62 and 1973-75 suffered only minor growth reductions and topkilling compared with the effects that more protracted budworm outbreaks have had elsewhere on their conifer hosts. Growth index analysis indicated that the firs averaged a cumulative height growth deficit of 14.5 percent, or 34 cm (1.1 ft), over both outbreaks. Firs heavily defoliated during the 1973-75 outbreak were more frequently topkilled and consequently suffered larger height growth deficits. Topkilling during both outbreaks, however, was limited to the terminal shoot, resulting in slight crooks or forks, but no decay, in the stems. Radial growth deficits attributable to the outbreaks were not found and, unless future outbreaks are more protracted or otherwise intensify, the Modoc budworm can be considered only a marginal economic pest of firs in California.

Retrieval Terms: Modoc budworm, *Choristoneura viridis*, white fir, *Abies concolor*, defoliation effects, growth, injury.