EFFECTS OF DEFOLIATION BY THE WESTERN FALSE HEMLOCK LOOPER ON DOUGLAS-FIR TREE-RING CHRONOLOGIES

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ABSTRACT

Annual rings of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, which sustained 1 year of defoliation by the western false hemlock looper, *Nepytia freemanii* Munroe (Lepidoptera: Geometridae), showed a period of decrease in breast height ring width starting in the year that followed the damage. The magnitude of the decrease was related to the degree of defoliation: there was no ring width decrease on trees that were 0-10% defoliated; the decrease became progressively more noticeable in trees which sustained increasingly higher defoliation; and it was maximum in trees which sustained 91-100% defoliation. This period of reduction lasted 1 to 5 years and was followed by a period of above-normal growth which was related to defoliation in a similar manner: it was absent in trees 0-10% defoliated and maximum in the 91-100% tree defoliation class. Increase in defoliation caused a significant increase in index standard deviation, autocorrelation and mean sensitivity.

INTRODUCTION

Sound forest pest management requires the preparation of hazard maps that describe areas of past insect activity. Such maps can be used to determine areas with a high probability of infestations and to prepare protection plans accordingly. It has long been recognized that the occurrence of past defoliator infestations can be established by studying the pattern of ring widths (Blais 1958, 1962; Alfaro et al 1982). However, relatively few studies have described in detail the pattern of ring reduction and recovery caused by different insect species (Koerber and Wickman 1970, Kulman 1971, Wickman et al. 1980, Alfaro et al. 1982). Blais (1958, 1962, 1983) studied the tree ring pattern in balsam fir, *Abies balsamea* (L.) Mill., and white spruce, *Picea glauca* (Moench) Voss, under defoliation by the spruce budworm, *Choristoneura fumiferana* (Clements). Brubaker (1978) and Brubaker and Greene (1979) described and compared the effects of western spruce budworm, *Choristoneura occidentalis* (Freeman), and Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunnough), on growth of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, and grand fir, *Abies grandis* (Dougl.) Lindl., in the western United States. Swetnam et al. (1985) described a procedure to date and quantify the effects of western spruce budworm on the growth of New Mexico Douglas-fir trees. Alfaro et al. (1982) and Alfaro (1985) demonstrated that the reduction in ring width of Douglas-fir trees was related to the severity and duration of defoliation by the western spruce budworm. Morrow and LaMarche (1978) quantified the impacts of insect feeding on growth rates of two species of *Eucalyptus* in Australia.

In this paper we describe the effects of defoliation by the western false hemlock looper, *Nepytia freemanii* Munroe (Lepidoptera: Geometridae), on Douglas-fir tree rings in a locality of British Columbia. Populations of the western false hemlock looper periodically increase to outbreak levels for periods of 1 to 4 years (Harris et al. 1985), causing localized defoliation and tree mortality. In British Columbia, the western false hemlock looper feeds primarily on Douglas-fir and has one generation per year. Eggs are laid in late summer and early fall and hatch in the next spring. The larvae consume the new foliage preferentially and then the old foliage if necessary (Furniss and Carolin 1977).

MATERIALS AND METHODS

An infestation of western false hemlock looper was detected near Chase, British Columbia in the summer of 1973 (Cottrell and Adams 1974). In the fall of 1974, one research plot, consisting of 100 randomly selected trees, was established in each of two stands within an area of new defoliation. Both stands were of pure Douglas-fir, multi-aged, and were located less than 1 km apart, on medium, well-drained sites. Average tree age was 60 years (range 22-109) and average diameter at breast height was 26 cm (range 7-75). Defoliation of every plot tree was ocularly estimated to the nearest 10% by dividing the living crown into one-third height sections and assessing the amount of foliage missing (all foliage age classes) from each section. A defoliation estimate for the tree was developed by averaging the estimates for the three crown sections. In the fall of every year until 1980, the plot was revisited and defoliation of each tree recorded.

A survey in the fall of 1985 (12 years after the defoliation) indicated that 188 of the original 200 trees were still alive and that the death of only two trees could be attributed to feeding by western false hemlock looper; the rest died of other causes (wind damage, etc). All surviving plot trees were sampled for annual ring growth as follows: one core was collected at breast height with an increment corer from each of 154 trees; in addition, 34 trees were felled and discs obtained at several points along the stem, including one at breast height (1.37 m). The analysis that follows is concerned only with the pattern of ring width at breast height, and for this reason, the breast height disc and the core samples were pooled. Several samples were discarded because of difficulties in crossdating or because of damage. Thus, the combined number of samples available for analysis was 172. Ring width variation along the stem due to defoliation will be reported separately.

Annual ring widths in discs and cores were measured to the nearest 0.01 mm, using a DIGIMIC measuring instrument, and the software described by Alfaro et al. (1984). Discs were measured along two average radii (Chapman and Meyer 1949) which were averaged into a single series per disc. Both sample types were crossdated (Stokes and Smiley 1968) with missing rings accounted for when detected.

In order to separate any reduction caused by defoliation from the confounding effects of the natural reduction in growth which occurs as the tree ages, the techniques developed by dendroclimatologists were used (Fritts 1976). A mathematical model is fitted to each tree ring series in order to describe its long-term trend. Annual ring widths are then divided by the corresponding model values. The resulting series of ratios is called an index series and is said to be standardized because it has a mean that approximates the value of one and a homogeneous variance. Standardized series from several trees in a locality can then be averaged into a site chronology.

In this study, the ring series of every tree was standardized by fitting a linear function to the annual rings from the center of the tree to the year of peak growth (determined visually) and a negative exponential for the remainder of the series (Figure 1). Both curves were fitted using the least squares method. For each tree index series, mean ring index and index standard deviation, as well as the series first order autocorrelation and mean sensitivity (a measurement of the average annual change in index value (Fritts 1976)), were calculated. Regression analysis was used to study the effects of defoliation on each of these measurements. Trees were sorted into six defoliation classes: 0-10, 11-30, 31-50, 51-70, 71-90 and 91-100%, and an average chronology was produced for each class. Also, a site chronology (average index series of all trees in both plots) was produced.

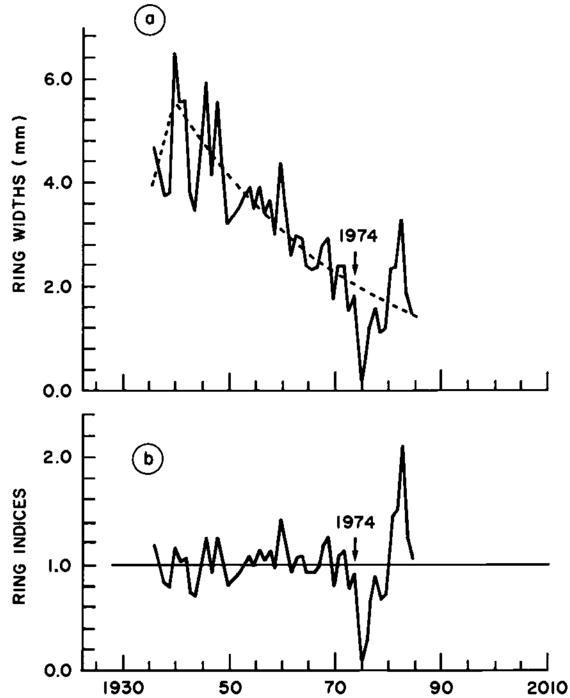

Figure 1. Example of the standardization procedure used to remove the growth trend from ring width series of Douglas-fir trees defoliated by the western false hemlock looper. a) annual ring widths (————) and fitted linear and negative exponential curves (———). b) Annual ring indices. Defoliation occurred in 1974.

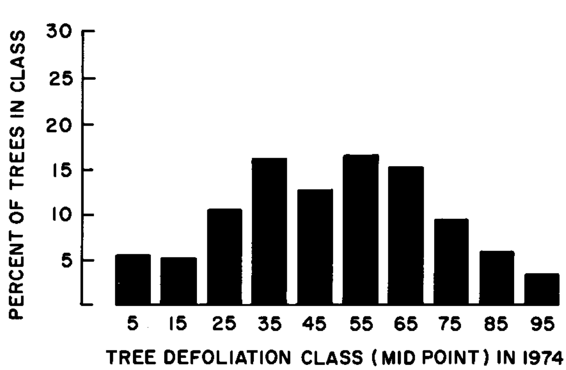

Figure 2. Frequency distribution of the percentage of trees sorted by defoliation class in 1974. Class width was 10% defoliation. N=172, Mean=50.6%.

RESULTS

The infestation remained active in the Kamloops Region of British Columbia from 1973 to 1975. Although no population estimates are available, field observations indicated that the population reached maximum numbers in 1974 and collapsed in 1975 (Cottrell and Koot 1976).

No estimates of defoliation for the plot trees were available for 1973; however, since the Forest Insect and Disease Survey of the Canadian Forestry Service did not detect any defoliation in this particular area, defoliation was probably nil or light on the study plot trees in 1973.

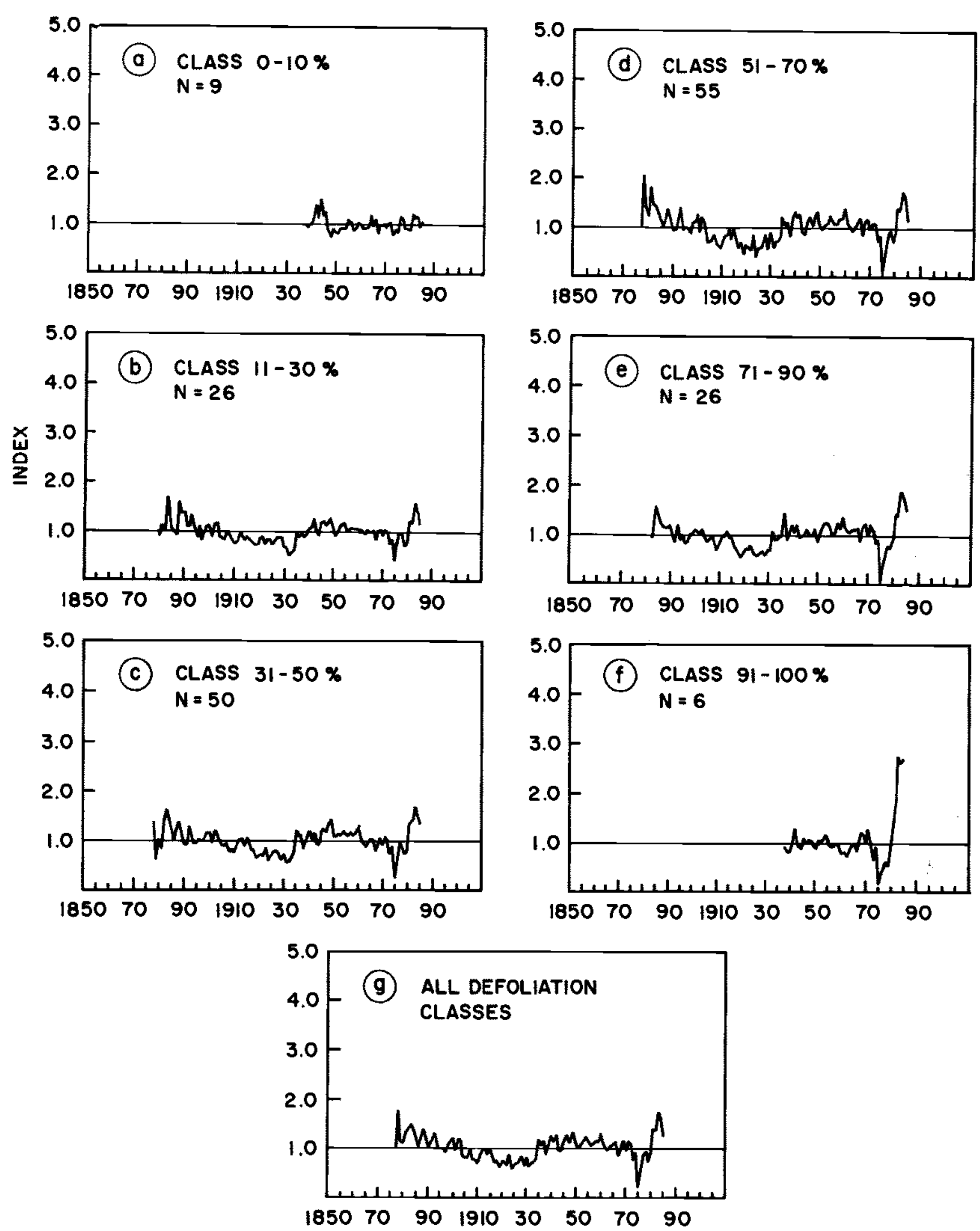

Figure 3. Ring index chronologies of Douglas-fir trees defoliated by the western false hemlock looper near Chase, British Columbia. a) to f) average chronologies in trees sorted by defoliation class; g) site chronology, i.e. average ring chronology for all trees in the locality, in all defoliation classes.

Therefore, it is assumed that any growth reduction incurred by the trees is the result of only one feeding season (1974). Tree defoliation averaged 50.6% in 1974 but varied widely from tree to tree in a distribution that approximated the normal (Figure 2). Only two trees remained undefoliated and only one tree sustained 100% defoliation and survived. Tree crowns began to grow new foliage in 1975 and had normal appearance by 1979, five years after defoliation.

The combination of linear and exponential curve fitting produced ring indices that eliminated the growth trend of the tree but displayed the variation induced by the 1974 defoliation. Examination of the chronology for the trees in the 0-10% defoliation class (Figures 3a, 4) showed no marked evidence of defoliation effects, either on the 1974 index or thereafter. Departures of indices in this chronology from the expected index value of one (the long-term trend represented by the fitted curve) were assumed to be caused by random or environmental variation.

The site chronology and the chronologies by defoliation class (Figures 3, 4) clearly showed the effects of increasing levels of defoliation in 1974. Growth declined sharply in 1975; the effect had a lag of one year. The index for year 1975 was progressively reduced with increasing defoliation, from 0.85 among the trees in the 0-10% defoliation class to 0.00 (no growth) among the trees in the 91-100% defoliation class (Figures 3, 4).

After 1975, ring indices began to increase rapidly. The number of years the trees took to reach annual growth rates that were within 10% of the trend was proportionally longer in the higher defoliation classes: trees in the 0-10% class already had an index value above one in 1976; trees in the 11-30% and 31-50% classes took 1 year to reach the annual trend (back to a value of approximately one by 1977); trees in the higher defoliation classes took 5 years to return to that level. After recovery from defoliation, many trees displayed above-normal growth rates. The magnitude of the increase was related to the degree of defoliation; the increase was absent in the trees that sustained 0-10% defoliation and maximum in the trees in the 91-100% defoliation class (Figure 4).

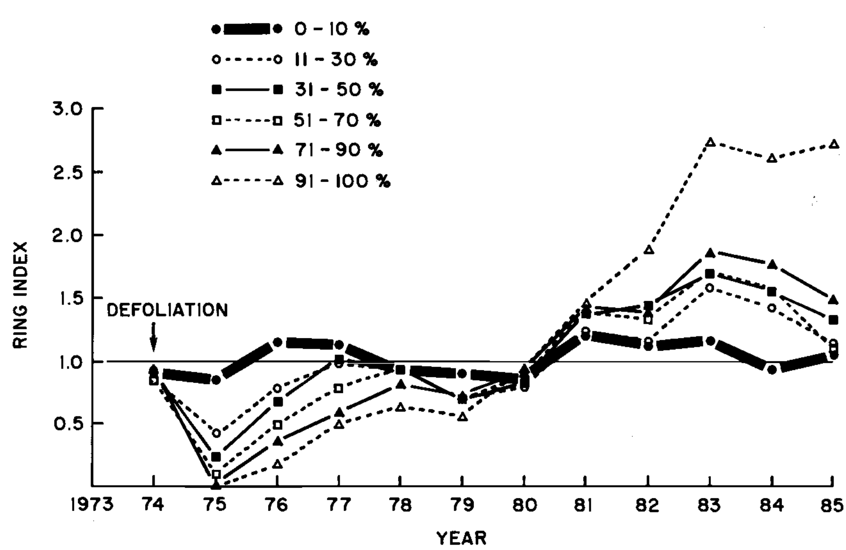

Figure 4. Last 12 years of the average annual ring index chronologies of Douglas-fir trees sorted by defoliation class. Defoliation is by the western false hemlock looper. Indices represented by the thicker line are those of the 0-10% defoliation class.

Regression analysis indicated a significant positive correlation of mean tree ring index, index standard deviation, first order autocorrelation and mean sensitivity with degree of tree defoliation (Figure 5, Table 1). All regressions had statistically significant intercept and slope. However, the regression of mean tree index on defoliation was barely significant ($F=5.7$, $P<0.05$), and was probably a consequence of the standardization method used.

Variability in mean tree index was strongly correlated with defoliation as evident from the scattergram of mean index versus defoliation (Figure 5a) and by the highly significant regression between index standard deviation and defoliation ($F=38.4$, $P<0.001$) (Figure). This increase in variability was caused by the severe reduction of the 1975 index and the period of vigorous growth increase that followed severe defoliation. The significant regression between mean tree sensitivity and defoliation ($F=41.1$, $P<0.001$) (Figure) is another indication of the increased index variability with defoliation as this parameter measures the average change in ring index from year to year (Fritts 1976). The significant increase of index autocorrelation with defoliation ($F=27.9$, $P<0.001$) was caused by the period of increasing growth that followed defoliation, which created a consistent and lasting upwards trend in the indices after 1975. This trend lasted for about 8 years (1976-1983).

DISCUSSION

The pattern of growth decline in Douglas-fir caused by western false hemlock looper was similar to that described by Brubaker (1978) for the impact of the Douglas-fir tussock moth on Douglas-fir ring widths. The impact consisted of a sharp decline followed by a recovery over a number of years (according to Brubaker (1978), a "check mark" pattern). This similarity is to be expected since both insects are very similar in their feeding habits — they feed voraciously and wastefully — and both are able to totally defoliate a tree of its foliage in a single season. This feeding habit causes the sharp decline in growth rates.

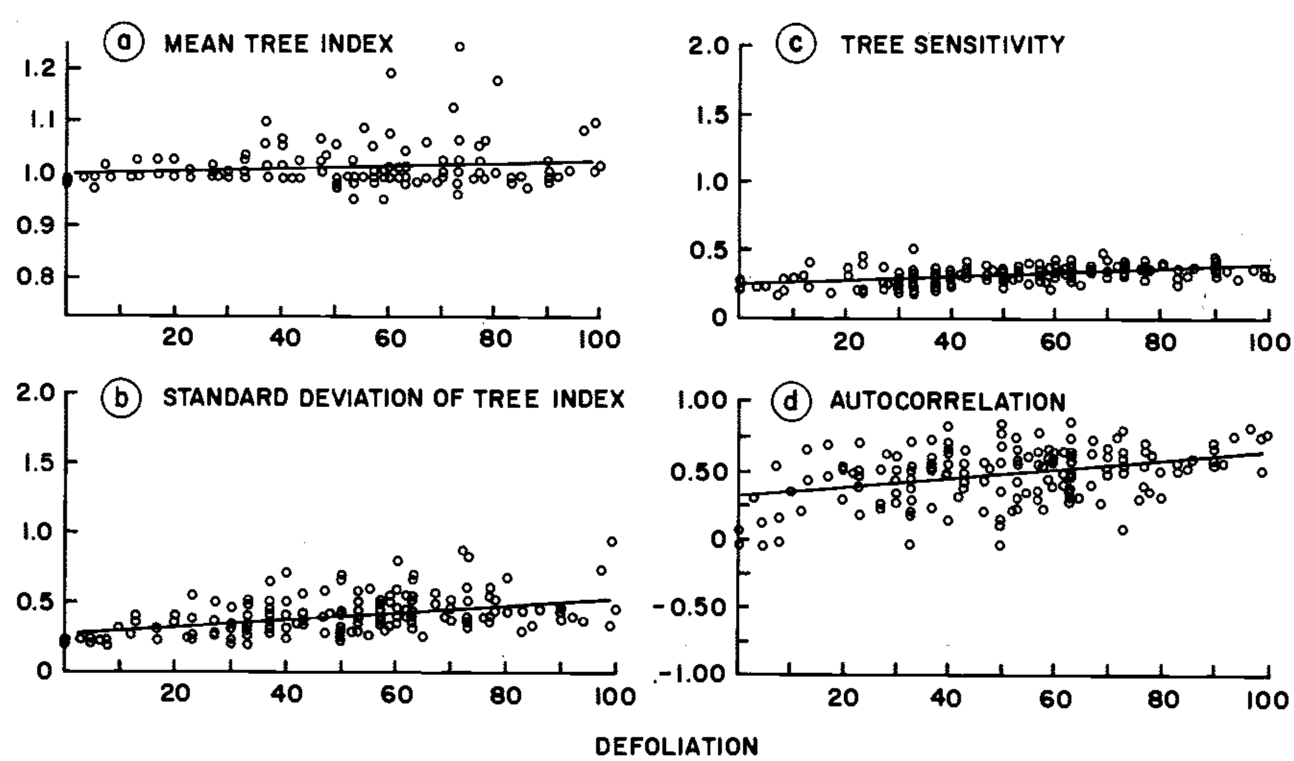

Figure 5. Relationship between a) mean tree ring index, b) Ring index standard deviation, c) mean sensitivity, and d) first order autocorrelation versus individual tree defoliation. Data are from 172 Douglas-fir trees defoliated by the western false hemlock looper, near Chase, British Columbia.

Table 1. Summary statistics for ring index chronologies for Douglas-fir trees tabulated by degree of defoliation caused by the western false hemlock looper, *Nepytia freemanii.*

Defoliation class(%)	Trees #	Mean defoliation	Mean index	Index SD	Index autocorr.	Mean sens.
0-19	9	5.1	1.00	0.24	0.16	0.24
11-30	26	23.6	1.01	0.33	0.44	0.28
31-50	50	41.2	1.01	0.39	0.47	0.31
51-70	55	60.3	1.01	0.42	0.50	0.35
71-90	26	80.0	1.03	0.47	0.54	0.36
91-100	6	96.8	1.04	0.54	0.70	0.38
All classes	172	50.6	1.01	0.40	0.48	0.32

The decline lags 1 year behind the defoliation presumably because the tree has food reserves to complete growth in the year of defoliation. In addition, in this year, the tree is capable of producing some photosynthate in the early part of the season, before total foliage destruction. A normal Douglas-fir tree usually carries foliage grown over the last five or six years. It therefore takes several years for ring width to recover because the tree needs several years to accumulate its full complement of foliage.

Increase in growth rate after defoliation has been reported by Wickman (1980) who found that, after defoliation by the Douglas-fir tussock moth, the growth of white fir, *Abies concolor* Lindl. ex Hildebr., was significantly higher than nondefoliated host trees nearby. This researcher hypothesized that the increased growth was due to a thinning effect caused by within-stand mortality due to defoliation and to increased nutrients in the form of insect frass. In our study, a thinning effect due to tree mortality was not a factor because the two stands had little mortality, and because the increase was absent from the less defoliated trees (0-10% class). A study of the overall productivity of the tree stem (which is now in progress) will indicate whether the observed growth increase at breast height also occurred at other levels. Such a study will also indicate what was the net effect of 1 year of defoliation, after any growth increase is balanced against earlier losses.

Construction of chronologies of past insect infestations (entomochronologies) requires a different sampling approach from that used for climatic chronologies. Trees selected for studies of past climate are collected preferably on "sensitive" sites, i.e., sites where precipitation or some other climatic variable is a limiting factor. Sampling to detect past insect infestations should be conducted based on the known feeding patterns of the insect. Some insects such as the western spruce budworm develop into infestations which extend over extensive areas. Therefore, sampling the known distribution of the insect will likely yield chronologies of past infestations. Other insects, however, are very patchy in their defoliation habits; therefore, sampling in areas where the insect is known to occur will not necessarily reflect the outbreak history for that general locality. This is the case of the western false hemlock looper. Infestations of this insect are highly variable both within and between stands. Therefore, whether increment core sampling will detect past infestations in a stand will depend on the extent of the past infestation in the stand and on its severity.

ACKNOWLEDGEMENTS

Our thanks are extended to Dr. G. A. Van Sickle and retired technician D. Collis who established these plots.

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