EFFECTS OF DEFOLIATION BY DOUGLAS-FIR TUSSOCK MOTH ON RING SEQUENCES OF DOUGLAS-FIR AND GRAND FIR

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ABSTRACT

Increment cores were collected from 10 stands in mixed-conifer forest stands which had suffered varying levels of Douglas-fir tussock moth defoliation during 1946, 1964, and 1973 infestations in north central Idaho. Ring-width measurements, standardized to remove inherent growth trends, were compared between host (Douglas-fir and grand fir) and nonhost (western larch, ponderosa pine, western white pine) species for evidence of growth losses due to defoliation. Heavy defoliation caused growth of host species to decrease 75%-90% in one year. Normal growth rates returned within 3-4 years after maximum defoliation, however. The effect of moderate defoliation could not be reliably indentified in the data.

Des échantillons ont été recueillis dans dix stations de la forêt mixte à conifères ayant souffert à des degrés divers de la défeuillaison due à "Douglas-fir tussock moth" durant les invasions de 1946, 1964 et 1973 dans le centre nord de l'Idaho. Des mesures d'épaisseur standardisées pour éviter les tendances de croissance individuelles ont été comparées entre des espèces hôtes (Douglas et Abies grandis) et des espèces non attaquées (Larix occidentalis, Pinus ponderosa, et Pinus monticola) afin de mettre en évidence les pertes d'accroissement dues à la défeuillaison. Les fortes défeuillaisons ont entraîné des pertes annuelles de 75 à 90%. Ces valeurs sont redevenues normales trois ou quatre ans après la défeuillaison maximale. Les défeuillaisons modérées n'ont pas pu être identifiées de façon significative.

Es wurden Zuwachsbohrungen in 10 gemischten Nadelholzbeständen im nördlichen Zentral-Idaho durchgeführt, die durch unterschiedlich intensive Entlaubung durch Douglasien-Trägspinner in den Jahren 1946, 1964 und 1973 geschädigt worden waren. Die Jahrringfolgen wurden standardisiert, um endogene Wachstumstrends auszuschalten. Zum Nachweis der durch die Entlaubung verursachten Zuwachsverluste wurden die Jahrringbreiten der Wirtsbäume (Douglasie und Große Küstentanne) und Nicht-Wirtsbäume (Westamerikanische Lärche, Gelbkiefer und Westliche Weymouthskiefer) miteinander verglichen. Eine starke Entlaubung verminderte den Zuwachs um 75-90% pro Jahr. Jedoch normalisierten sich die Zuwachsraten wieder 3-4 Jahre nach der maximalen Entlaubung. Der Einfluß einer leichteren Entlaubung konnte anhand der Daten nicht zuverlässig nachgewiesen werden.

INTRODUCTION

Douglas-fir tussock moth (*Orgyia pseudotsugata* [McDunnough]) is an important defoliator of Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco.), grand fir (*Abies grandis* [Dougl.] Lindl.) and white fir (*Abies concolor* [Glend.] Lindl.) in western North American forests. Infestations of tussock moth are typically short-term events, with populations building explosively and collapsing over a period of three years (Wickman et al. 1973a). The larvae, which hatch soon after bud burst, can severely defoliate host trees within 10-12 weeks (Wickman et al. 1973b). Such defoliation may cause tree mortality, but more often results in temporary growth losses or increased susceptibility to secondary insects and diseases (Wickman 1963).

Although native to North America, tussock moth was not reported defoliating forest stands until 1908 (Tunnock 1973). Records since that time suggest that infestations occur synchronously every 8-10 years over wide geographic areas (Wickman et al. 1973a; Clendenen 1974; Tunnock 1973). Regional weather conditions may interact with local site factors to trigger and synchronize insect populations that are separated by hundreds of kilometers.

The objective of this research is to determine whether defoliation by tussock moth produces a recognizable ring-width pattern at breast height in host trees. It is part of a larger study to analyze ring-width sequences of old-growth trees for evidence of past epidemics.

A variety of methods have been used to study the effects of defoliation on the radial growth of trees (O'Neil 1963; Stark and Cook 1957; Mott et al. 1957; Kulman 1971). Because defoliation influences diameter growth differently at different heights within a stem, most investigators caution that ring-width sequences from breast height increment cores may not accurately reflect changes which occur in the living crown (Mott et al. 1957; Kulman 1971). Duff and Nolan (1953) developed an effective sampling procedure for assessing differential growth responses within the stem. They suggest analyzing ring widths along vertical or oblique sequences through successive internodes. While their approach is probably the most sensitive one available for detecting the effect of defoliation of diameter growth, it has not been used extensively (Kulman 1971) because it is too time consuming to be practical for most studies (Stark and Cook 1957; Leaphart and Stage 1971).

Standard dendrochronological procedures of crossdating and ring-width standardization (Fritts 1976) were used in this study. Results indicate that the effect of severe tussock moth infestations can be readily identified in breast height increment core samples. It is likely, therefore, that breast height samples provide useful information about the history of the activity of this insect species in North American forests.

LOCATION OF STUDY SITES

All sites were located within the Coeur d'Alene and Clearwater mountains which form the northern boundary of the Palouse Prairie in Latah and Benewah counties, Idaho (Figure 1). The topography of the area is governed by quartzite bedrock hills and east-west trending ridges covered by 4 ft to 8 ft of loess. Forests belong to the *Abies grandis-Pachystima* association (Daubenmire 1966) but their composition varies greatly depending on age and past logging history. Tussock moth infestations occurred in this area in 1946, 1964, and 1973 (Tunnock 1973). Ten stands were selected to determine the effect of a range of defoliation levels during the 1946 and 1964 outbreaks. Defoliation levels and insecticide treatments, as described below, were obtained from Forest Service records (Tunnock 1973; Pierce, personal communication).

Stands 1-6, along Skyline Drive, were heavily defoliated (50 percent to complete elimination of foliage) during an infestation which started in 1945, reached maximum severity in 1946, and subsided in June-July 1947 after the application of one pound of DDT per acre. This outbreak would probably have declined in 1947 even without DDT treatment, however, because infestations nearly always crash naturally during their third year due to disease, predation and/or starvation (Wickman et al. 1973a). Stand 7 at Skyline was moderately defoliated (10 to 50 percent foliage removed) during this infestation. Stands 8-10, near East Dennis, were at the edge of a moderately defoliated area, but the records available are not detailed enough to determine whether they suffered any defoliation. If damage occurred at all, it was probably very light.

The next infestation reached peak levels in 1964 and declined in 1965. All of the sites along Skyline Drive were moderately defoliated in this infestation, but none of the East Dennis sites suffered visible defoliation. Much of the study area was sprayed with one pound of DDT per acre in 1965.

The 1973 infestation is not discussed here because its long-term (five to ten years) effects could not be determined at the time of this study (1975).

METHODS

At each study site two increment cores were collected at breast height from each of 15 dominant and codominant Douglas-fir or grand fir. This sample size was chosen because it is adequate for most types of dendrochronological analyses (Fritts 1976). Stand compositions were too variable to sample the same number of Douglas-fir or grand fir trees at every site. Approximately 10 nonhost species trees were cored at each site for comparison with host species. The nonhost species sampled were ponderosa

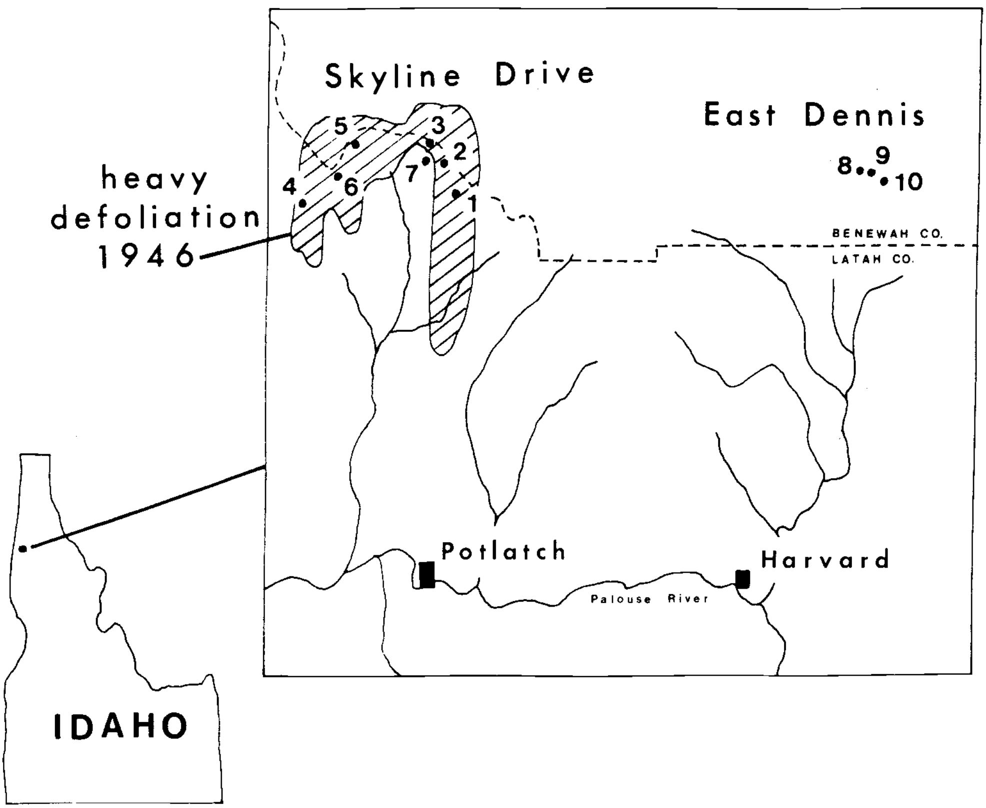

Figure 1. Study area, showing locations of stands 1-10 and limits of heavy defoliation during the 1946 infestation.

pine (*Pinus ponderosa* Laws.), western white pine (*Pinus monticola* Dougl.), and western larch (*Larix occidentalis* Nutt.). Increment cores were stored in paper straws and transported to the laboratory where they were mounted in permanent holders and hand sanded until highly polished.

All rings were dated by crossdating methods (Stokes and Smiley 1968) and measured to the nearest 0.01 mm using a Bannister incremental measuring machine. Measurements were recorded by a modified Hewlett-Packard data-logging system. The ring-width measurements for each core were standardized to form ring-width indices using exponential or linear equations (Fritts 1976).

Tree chronologies were formed by averaging the indices from the two cores of each individual tree. The Douglas-fir and grand fir tree chronologies were pooled and averaged to form a general host species chronology (host chronology) for each site. These data were combined because it was impossible to sample the same number of each species at every site and because these species responded quite similary to defoliation (see Results).

A nonhost species chronology (nonhost chronology) was also formed at each site by averaging the tree chronologies of ponderosa pine, western white pine and/or western larch. Since tussock moth does not normally attack these species, their chronologies can be combined as a control for comparison with host species chronologies. The host and nonhost species chronologies were plotted and examined for evidence of damage from the 1946 and 1964 tussock moth attacks. Decreased growth in host species with normal growth in nonhost species was used as the evidence for past tussock moth attack.

RESULTS AND DISCUSSION

Missing Rings

Eighteen percent of the host species cores from heavily defoliated stands (stands 1-6 in 1946) appeared to have one missing ring, eight percent two missing rings, and less than one percent (only one core) three missing rings. A single missing ring in a core was assumed to be 1947; two missing rings in a core were assumed to be 1947 and 1948; and three missing rings assumed to be 1947, 1948, 1949. This decision was made because the 1947, 1948, and 1949 rings were the first, second, and third narrowest rings, respectively, in complete cores (see next section). None of the moderately defoliated stands (stands 1-6 in 1964, stand 7 in 1946 and 1964) showed evidence of missing rings, nor were missing rings detected at the control sites (stands 8-10), which suffered no or light defoliation during the 1946 infestation and no damage during the 1964 outbreak (Pierce, personal communication). It appears from these results, therefore, that defoliation by tussock moth must be quite severe (i.e., reported to be at least 50 percent) to cause missing or discontinuous rings at breast height.

Evidence for 1946 Infestation

Host species' indices at heavily defoliated stands fell abruptly in 1947 to 10-25 percent of their 1946 values, but returned steadily to preinfestation levels during the next three to four years. Figure 2, an average of all host chronologies from these stands, shows that this attack reduced growth more than any other event in the history of these stands. The host species' indices at each site follow a characteristic pattern which resembles a check mark (✓) (Figure 3). To verify that this pattern is typical for both Douglas-fir and grand fir, the tree chronologies from all heavily defoliated stands were pooled and averaged according to species (Douglas-fir = 35 trees, grand fir = 42 trees). As expected, plots of the Douglas-fir and grand fir chronologies showed the check mark pattern (Figure 4). Other investigators have found similar patterns of growth loss in host species. For example, this pattern was reported (1) by Lessard (1973) for Douglas-fir defoliated in 1945-1946 in northeastern Washington, (2) by Wickman (1963) for white fir defoliated in 1954-1956 in northern California, and (3) by Wickman (personal communication 1977) for Douglas-fir and grand fir defoliated in 1972-1973 in northeastern Oregon. It seems reasonable to assume, therefore, that the check mark pattern is a characteristic result of heavy defoliation by tussock moth. The consistency of this response by host species no doubt results from the extraordinarily strong tendency of tussock moth populations to follow well-defined three-year outbreak cycles.

Nonhost species' indices at six of the seven Skyline Drive sites showed only minor changes between 1946 and 1947 (Figure 3). This evidence supports the idea that growth losses in host trees were due to damage by tussock moth and not from other environmental factors (e.g., fire, drought) which affect a stand as a whole. It is very important to use nonhost chronologies in this way to verify that growth decreases in host species are caused by tussock moth defoliation and not weather anomalies. Stand 6 was the exception because rings of nonhost species were very narrow in 1947 and 1948 (Figure 3). According to Mason and Baxter (1970), tussock moth larvae will feed on nonhost trees after host species' foliage has been consumed. Such a shift in larval feeding may account for the anomalous growth losses in nonhost species at this stand.

Growth losses at the moderately defoliated stand (site 7) were less extreme than those at heavily defoliated stands (Figure 5). At this stand the 1947 index values of host species averaged 75 percent of their 1946 values (in contrast to 25 percent of 1946 growth at heavily defoliated stands). The basic pattern of narrow rings here is similar to that found at heavily defoliated sites but is difficult to distinguish from that caused by other factors (e.g., variations in weather) because the growth reduction is so slight.

Host chronologies at the East Dennis sites (sites 8-10) show no evidence of the 1946 defoliation, since 1947 indices averaged 95 percent of 1946 values and differences between host and nonhost chronologies during the late 1940's are no greater than during noninfestation periods. These results are consistent with records (Pierce, personal communication) that these stands, located at the border of defoliated areas, were not affected or only minimally damaged during this attack.

Figure 2. Average ring-width indices for stands heavily defoliated in 1946. Growth losses following this infestation are the most severe during the 134-year record.

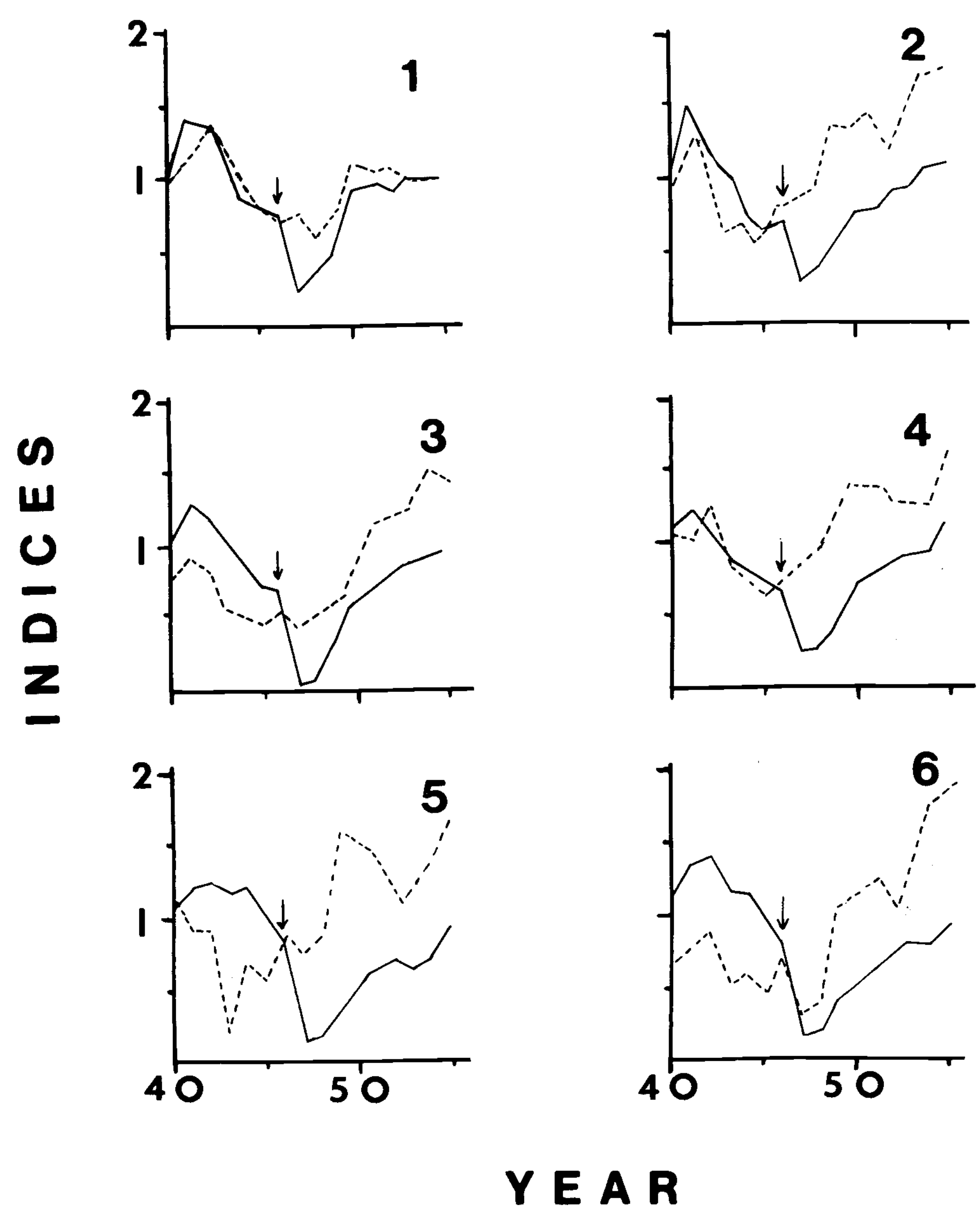

Figure 3. Host (—) and nonhost (---) species' indices (1940-1955) from stands heavily defoliated in 1946.

Estimating Growth Losses from 1946 Infestation

Ring-width indices can be used to estimate percentage growth losses due to defoliation by (1) comparing host species' indices at defoliated stands to those of host species at nearby undefoliated stands and by (2) comparing host indices at defoliated stands to those of nonhost species growing in the same stands. Following the first approach, the host species at East Dennis were used as undefoliated controls and their chronologies compared to host chronologies at heavily defoliated Skyline Drive stands during five and ten year periods following attack. According to this comparison (Figure 6a) the host species' indices at defoliated stands averaged 52 percent (five years) and 81 percent (10 years) of those at the control stands.

The second type of comparison suggests greater growth losses in host species. For example, indices of host species averaged only 44 percent (five years) and 56 percent (10 years) of their nonhost species competitors (Figure 6b). However, this type of comparison probably exaggerates the growth losses of host species because nonhost trees may have actually grown especially well following the attack, due to reduced competition from host trees. The data shown in Figure 6b support this idea because nonhost species' indices remained greater than those of host species for 15 years following the attack. This is the only extended period in which the growth of nonhost trees was consistently higher than the growth of hosts at these sites. In contrast, nonhost trees growing among undefoliated host trees at East Dennis did not show accelerated growth rates during the same period.

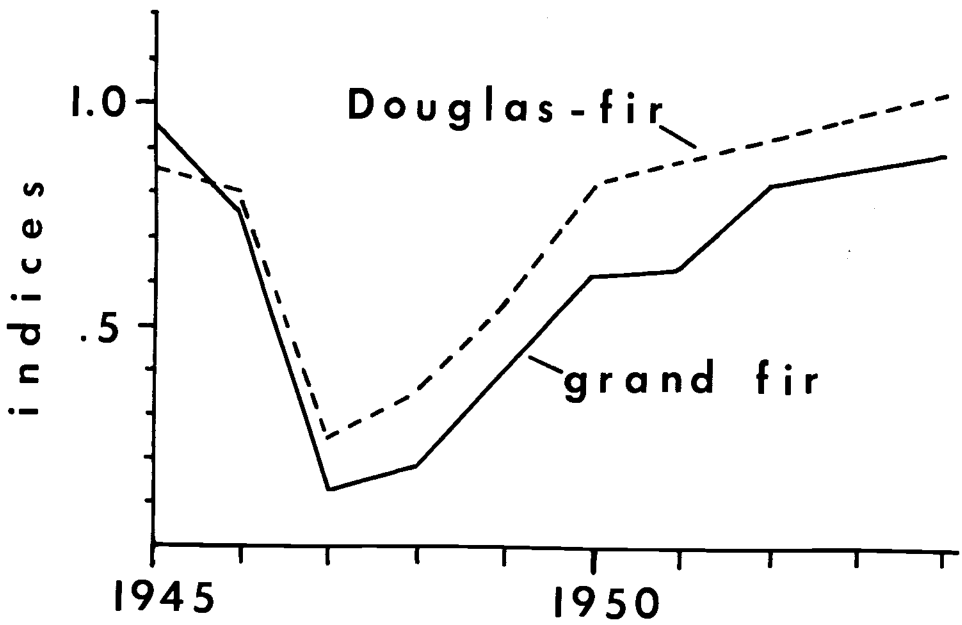

Figure 4. Average Douglas-fir and grand fir indices from all stands heavily defoliated in 1946. Douglas-fir values are an average for 35 trees and grand fir for 42 trees.

Lagged Response to 1946 Defoliation

Narrow rings did not form in host species at any stand until 1947—one year after major defoliation. Other studies on natural and artificial defoliation of upper crown foliage have shown similar results (Rook and Whyte 1976; Kozlowski and Kramer 1960; Kulman 1971; O'Neil 1963). Many authors speculate that growth losses are delayed at the base of stems because xylem production there depends to a large degree on photosynthates manufactured prior to cambial growth. This idea can explain the observed one-year lag in response of host species to tussock moth defoliation. For example, normal growth could occur in 1946, the year of maximum defoliation, because cambial tissues were supplied by carbohydrates produced in late 1945 or early 1946, when the foliage was undamaged. Accordingly, severe growth reductions would occur first in 1947 because the extensive foliage losses in 1946 prevented sufficient food production for normal growth. Finally, ring widths would return gradually to normal levels as foliage was gradually restored in yearly increments.

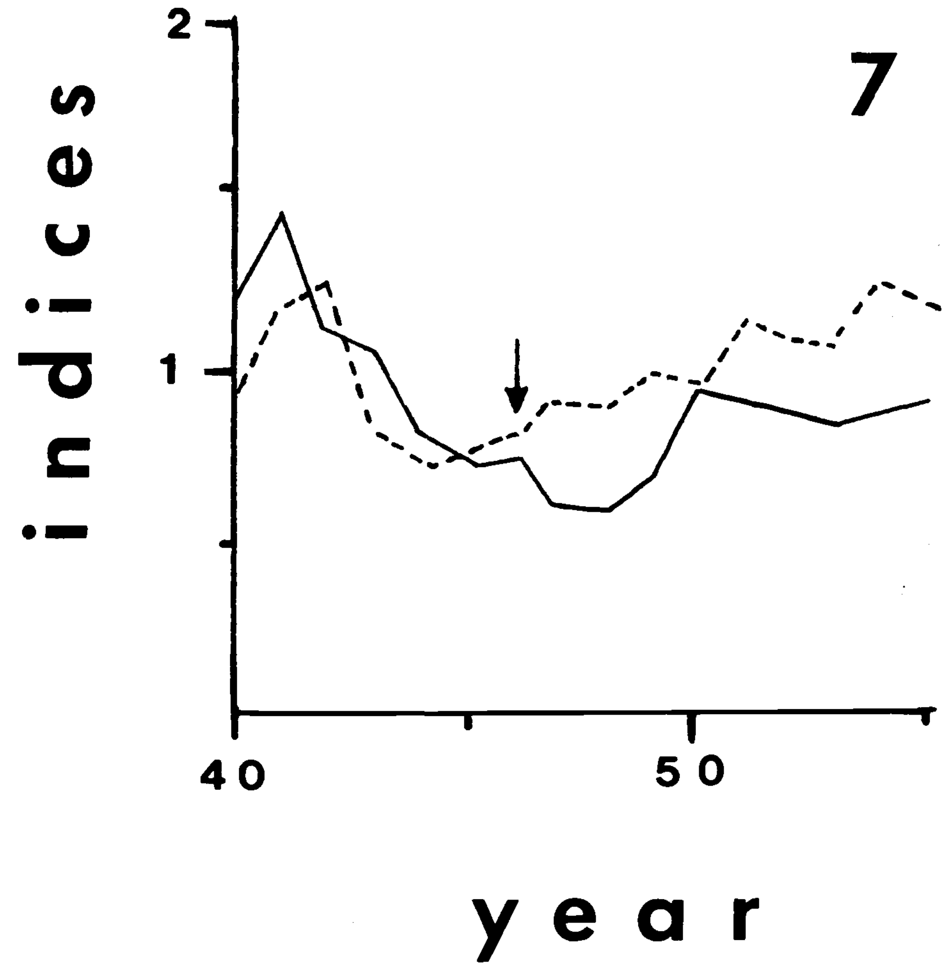

Figure 5. Host and nonhost species indices for stand 7, moderately defoliated in 1946.

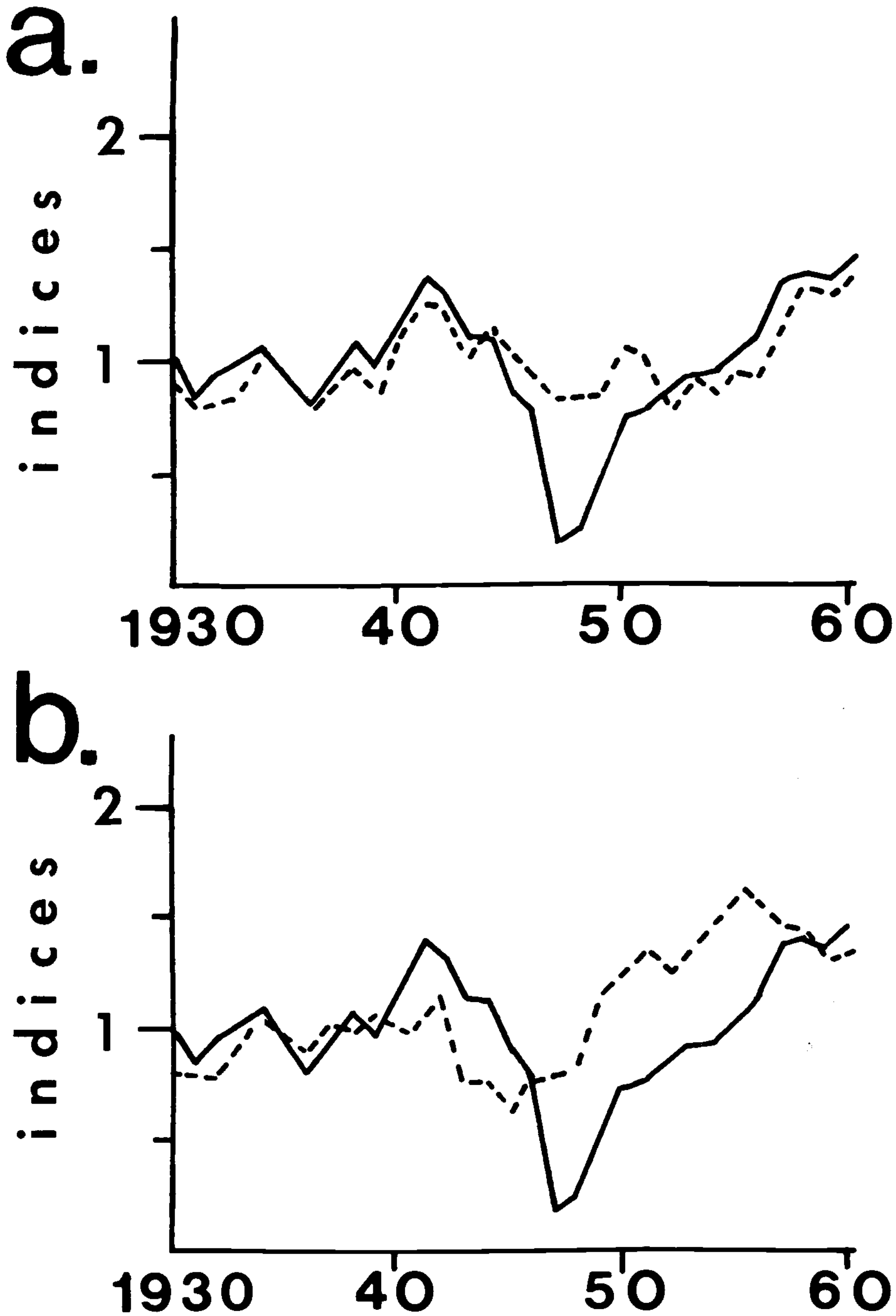

Figure 6. *a*, Host species' indices at heavily defoliated (—) and control (---) stands during the 1946 infestation; *b*, Host (—) and nonhost (---) species' indices at heavily defoliated stands during the 1946 infestation. Differences between solid and dashed lines can be used to assess the magnitude of growth losses due to defoliation.

1964 Infestation

Moderate levels of defoliation during this infestation had minor effects, if any, on basal radial growth. The average growth of host species at Skyline Drive sites fell less than one percent between 1964 and 1965. Furthermore, during 1965-1967, host trees at Skyline averaged only five percent less than their nonhost competitors and two percent less than undefoliated host trees at the East Dennis sites. These growth losses are much less than those found at the 1946 moderately-defoliated stand and are certainly indistinguishable from growth variations which occur during noninfestation periods.

Other Insects

Host chronologies at each of the East Dennis sites showed an extended period of below average growth from about 1900 to 1910 (Figure 7). These chronologies contrast sharply with nonhost chronologies which are at normal levels during this period. The growth losses in host species were not caused by tussock moth since the 1900-1910 patterns are not like ones observed for the 1946 tussock moth infestations. Instead, this pattern of low growth is similar to that caused by western spruce budworm (*Choristoneura occidentalis*) (Williams 1971; Brubaker and Green, in press), whose populations build and subside more gradually than tussock moth's. It is very likely, in fact, that spruce budworm caused the 1900-1910 growth losses because the only species damaged (Douglas-fir and grand fir) are the preferred hosts of spruce budworm. Unfortunately, no historical records are available to provide descriptions of these stands at the turn of the century. Fire and/or adverse weather could not have caused the low growth because these agents would have affected all species in these stands.

CONCLUSIONS

1. Heavy defoliation (50 percent to total foliage loss) by tussock moth can be identified from ring-width patterns in breast height increment cores. Moderate (10 percent to 50 percent foliage loss) and lesser levels of defoliation probably cannot be identified reliably from radial ring patterns.

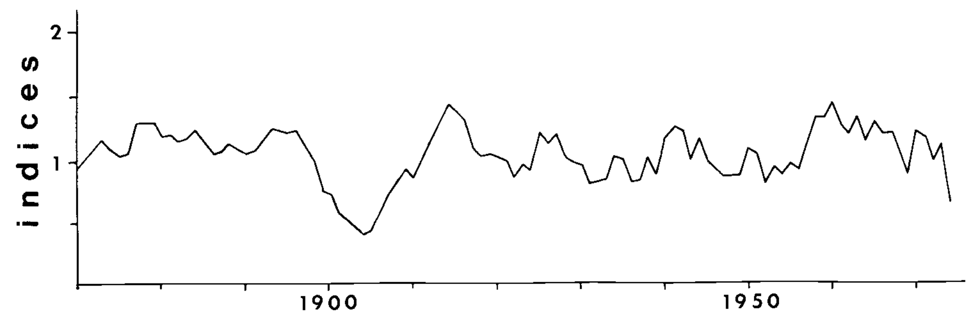

Figure 7. Average host species' indices from East Dennis stands. The pattern of low growth during 1900-1910 resembles reported effects of western spruce budworm, rather than those of tussock moth.

2. The responses of dominant and codominant Douglas-fir and grand fir to defoliation are sufficiently alike to pool their data when analyzing diameter growth records for evidence of past tussock moth attacks.

3. Nonhost species should be sampled in tree-ring studies to verify that narrow rings in host trees were not caused by factors (e.g., drought) that affect a stand as a whole.

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REFERENCES

Brubaker, L.B. and S.K. Greene
In press Differential effects of Douglas-fir tussock moth and western spruce budworm on radial growth of Grand fir and Douglas-fir. *Can. J. For. Res.*

Clendenen, G.
1974 Tussock moth *Orgyia pseudotsugata* McD: Outbreaks and climatic factors: A correlation analysis. Preliminary report, USDA Forest Service, University of Washington Cooperative Study.

Daubenmire, R.
1952 Forest vegetation of northern Idaho and adjacent Washington, and its baring on concepts of vegetation classification. *Ecological Monographs* 22:301-330.

Duff, G.H. and N.J. Nolan.
1953 Growth and morphogenesis in the Canadian forest species. 1. The controls of cambial and apical activity in *Pinus resinosa* Ait. *Can. J. Bot.* 31:471-513.

Farrar, J.L.
1961 Longitudinal variations in the thickness of the annual ring. *For. Chron.* 37:323-330.

Fritts, H.C.
1976 *Tree rings and climate.* Academic Press, London.

Kramer, P.L., and T.T. Kozlowski.
1960 *Physiology of trees.* McGraw-Hill, New York.

Kulman, H.M.
1971 Effects of insect defoliation on growth and mortality of trees. *Ann. Rev. Ent.* 16:289-324.

Leaphart, C.D. and A.K. Stage.
1971 Climate: A factor in the origin of the pole blight disease of *Pinus monticola* Dougl. *Ecology* 52:229-239.

Lessard, D.E.
1974 Climatic, host tree, and site factors affecting the population dynamics of the Douglas-fir tussock moth, *Orgyia pseudotsugata* McDunnough. Master's thesis, University of Washington, Seattle.

Mason, R.R. and J.W. Baxter.
1970 Food preferences in a natural population of the Douglas-fir tussock moth. *J. Econ. Ent.* 63(4)1257-1259.

Mott, D.G., L.D. Nairn, and J.A. Cook.
1957 Radial growth in forest trees and effects of insect defoliation. *For. Sci.* 3(3)286-304.

O'Neil, L.C.
1963 The suppression of growth rings in jack pine in relation to defoliation by the Swaine Jack-pine sawfly. *Can. J. Bot.* 41:227-235.

Rook, D.A. and A.G.D. Whyte.
1976 Partial defoliation and growth of 5-year-old radiata pine. *N. Zea. J. For. Res.* 6:40-56.

Stark, R.W. and J.A. Cook.
1957 The effects of defoliation by the lodgepole needle miner. *For. Sci.* 3:376-396.

Stokes, M.A. and T.L. Smiley.
1968 *An introduction to tree-ring dating.* University of Chicago Press, Chicago.

Tunnock, S.
1973 The Douglas-fir tussock moth in the northern region — A cartographic history of outbreaks from 1928 to 1973. *USDA Forest Service Division of State and Private Forestry, Northern Region, Report No.* 73-27:1-16.

Wickman, B.E.
1963 Mortality and growth reduction of white fir following defoliation by Douglas-fir tussock moth. *USDA Forest Service Research Paper* PSW-7:1-14.

Wickman, B.E., R.R. Mason, and C.G. Thompson.
1973a Major outbreaks of the Douglas-fir tussock moth in Oregon and California. *USDA Forest Service General Technical Report* PNW-5:1-18.

Wickman, B.E., G.C. Trostle, and P.E. Buffam.
1973b Douglas-fir tussock moth. *Forest Pest Leaflet* 86:1-6.

Williams, C.B.
1966 Differential effects of the 1944-56 spruce budworm outbreak at eastern Oregon. *USDA Forest Service, PNW Report* 33:1-16.