

A Tree-Ring Reconstruction of Western Spruce Budworm History in the Southern Rocky Mountains

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ABSTRACT. Tree-ring width chronologies from ten mixed-conifer stands in the Colorado Front Range and New Mexico Sangre de Cristo Mountains were used to reconstruct the timing, duration, and radial growth impacts of past outbreaks of western spruce budworm (*Choristoneura occidentalis* Freeman). At least nine outbreaks were identified in the stands from 1700 to 1983. Severity and timing of outbreaks was highly variable. The average duration of reduced growth periods caused by budworms was 12.9 years and ranged from 5 to 26 years. The average interval between initial years of successive outbreaks was 34.9 years and ranged from 14 to 58 years. The average maximum and periodic radial growth reductions were 50% and 21.7%, respectively. There was a relatively long period of reduced budworm activity in the first few decades of the twentieth century, and since that time outbreaks have been markedly more synchronous among the sampled stands. It is hypothesized that the increased synchronicity of outbreaks in the latter half of the twentieth century is due to changes in age structure and species composition following harvesting and fire suppression in the late nineteenth and early twentieth centuries. FOR. SCI. 35(4):962-986.

ADDITIONAL KEY WORDS. Dendrochronology, insect outbreaks, *Pseudotsuga menziesii*, disturbance ecology.

APERIODIC OUTBREAKS OF WESTERN SPRUCE BUDWORM have occurred throughout forested regions of western North America. Defoliation of conifers by this insect causes radial and height growth reduction, top-killing and associated product degrade, reduced regeneration, and mortality (Carlson et al. 1983, MacLean 1985). Appropriate response to this problem by forest managers depends on accurate assessments of resource impacts and alternative management actions, as well as consideration of the insect's historic and ecologic role in forest dynamics.

A long-term perspective of the frequency, extent, duration, and severity of budworm outbreaks is needed to evaluate the importance of this insect in the regulation of productivity, age class structure, and species composition of natural and managed stands. Long histories of budworm outbreaks derived from tree-ring studies may be particularly useful in the study of budworm population dynamics and interactions with factors such as fire, climate, harvesting practices, and air pollution (Volney 1985).

Both defoliation and climatically induced stress may cause reduction in

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the growth rate of trees (Fritts 1976, Brubaker and Greene 1979, Hughes et al. 1982). The effects of defoliation by insects on radial growth can be isolated from the effects of climate and other disturbances by a comparison of tree-ring measurements between host and nonhost trees, or between defoliated and nondefoliated trees (Blais 1962, 1965, Morrow and LaMarche 1978, Brubaker and Greene 1979, Carlson and McCaughey 1982, Swetnam et al. 1985). Methods of projecting pre-outbreak growth in host trees to estimate expected growth during periods of defoliation have also been widely used (Williams 1967, Ferrell 1980, Thomson and Van Sickle 1980, Alfaro et al. 1982, 1985, Ferrell and Scharpf 1982).

Blais (1983) examined tree-ring width series from balsam fir (*Abies balsamea* [L.] Mill.) and spruce (*Picea* sp.) forests of eastern Canada, and found an apparent increased incidence of spruce budworm, *C. fumiferana* Clemens, outbreaks in the twentieth century. He proposed that this was due to past harvesting practices, fire control, and insecticide spraying that led to more susceptible and vulnerable stands. Carlson et al. (1983) and Fellin et al. (1983) also report that Northern Rocky Mountain forests have become increasingly susceptible and vulnerable to western spruce budworm because forest management practices have led to dense, multiple-storied stands with shade-tolerant species that are favored by budworms. McCune (1983) and Anderson (1985) reconstructed western spruce budworm and fire histories from tree-rings in western Montana and found that reduced fire frequency corresponded temporally with increased budworm activity.

This paper reports the results of a dendrochronological study of western spruce budworm defoliated trees in ten mixed-conifer stands of the Southern Rocky Mountains in Colorado and New Mexico. The objectives were to (1) identify the dates of occurrence and duration of past budworm outbreaks, (2) estimate the radial growth reduction during current and past outbreaks, and (3) compare estimates of budworm history and effects between stands and time periods. Recent human-caused changes (since the mid-1800s) in mixed-conifer stands are described in the context of a historical explanation of observed changes in budworm occurrence.

METHODS

STUDY AREA

The sampled stands were located on three National Forests in Colorado and one in New Mexico (Figure 1). Stands in Colorado were distributed along the Front Ranges. They were located in the lower ranges east of Rocky Mountain National Park (Devil's Gulch and Big Elk Meadows), along the Rampart Range west and north of Colorado Springs (Ormes Peak and Indian Creek) and in the Wet Mountains southwest of Pueblo (Oak Creek and Ophir Creek). The New Mexico stands were within the Rio Fernando de Taos watershed west of Taos (Garcia Park and Capulin Canyon), on the eastern slope of the Sangre de Cristos above the Moreno Valley (Osha Mountain), and on the western side of the Rio Grande in an extension of the San Juan Mountains west of Tres Piedras (Burned Mountain). Topographic position of the stands varied from steep and moderate slopes to relatively level ridge tops. Aspects of four stands were generally to the north. Two stands had east aspects, two stands had west aspects, and two stands were on relatively level ground with variable aspects. Elevations ranged from approximately 2,400 to 3,050 meters.

Stands were mixed-conifer and composed of varying proportions of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco.), ponderosa pine (*Pinus*

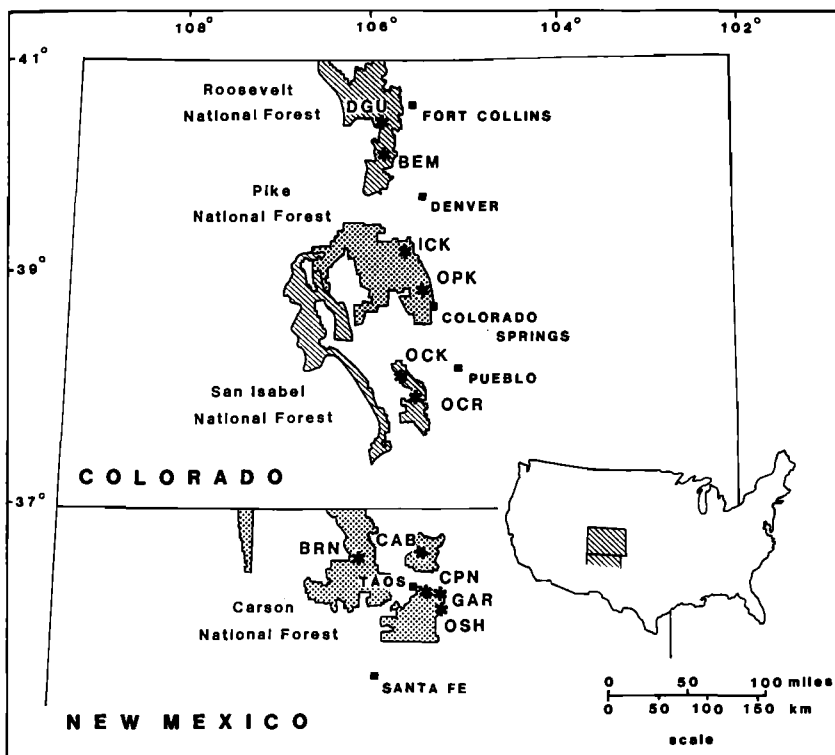


FIGURE 1. Locations of sampled stands in Colorado and New Mexico. Stands are shown by asterisks and three-letter codes. DGU = Devil's Gulch, BEM = Big Elk Meadows, ICK = Indian Creek, OPK = Ormes Peak, OCK = Oak Creek, OCR = Ophir Creek, BRN = Burned Mountain, CPN = Capulin Canyon, GAR = Garcia Park, OSH = Osha Mountain.

ponderosa Laws.), white fir (*Abies concolor* [Gord. and Glend.] Lindl.), aspen (*Populus tremuloides* Michx.), lodgepole pine (*Pinus contorta* Dougl.), and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) (Table 1).

Stand and Tree Selection

The 10 sampled stands were originally selected by USDA Forest Service entomologists for monitoring impacts and budworm populations (Raimo 1983, Rogers 1984). The stands were selected to be representative of mixed-conifer areas that were defoliated during the 1960s and the most recent outbreak, which began in the 1970s. Fixed plots were established by the Forest Service within these stands, and more-or-less yearly measurements of budworm populations and defoliation were recorded. The four New Mexico stands, comprising 11 0.4 ha plots, were sampled in 1983. The six Colorado stands, comprising 64 0.04 ha plots, were sampled in 1984 and 1985.

For purposes of this study, at least ten dominant and codominant Douglas-fir (budworm hosts) exceeding approximately 20 cm diameter at breast height (dbh, 1.37 m above ground level) were sampled within each stand (Table 2). The trees were selected by traversing back and forth in a haphazard fashion through the stands and sampling each dominant or codominant tree as it was encountered. Two increment cores were extracted parallel to the topographic contour at approximately dbh from each sampled tree. An additional 10 to 20 of the oldest appearing Douglas-fir within or nearby the study plots were also selected and cored in order to obtain the maximum

TABLE 1. Basal area and density in the sample stands. Trees greater than 12.4 cm (4.9 in.) dbh are included.

Stand name & species ^a	Importance ^b value	Basal area		Density	
		m ² /ha	Rel. (%)	Stems/ha	Rel. (%)
Devil's Gulch					
PSME	95.5	18.9	95.9	578	95.1
PIPO	4.5	0.8	4.1	30	4.9
		<u>19.7</u>		<u>608</u>	
Big Elk Meadows					
PSME	73.0	14.7	70.0	477	76.2
PIPO	24.4	5.8	27.6	133	21.2
PICO	1.8	0.3	1.4	14	2.2
JUSC	0.4	0.1	0.5	1	0.2
POTR	0.4	0.1	0.5	1	0.2
		<u>21.0</u>		<u>626</u>	
Indian Creek					
PSME	58.3	16.8	57.7	390	58.9
PIPO	38.4	11.8	40.6	239	36.1
POTR	3.3	0.5	1.7	33	5.0
		<u>29.1</u>		<u>662</u>	
Ormes Peak					
PSME	58.4	14.7	61.8	356	55.0
PICO	14.2	3.5	14.7	89	13.8
PCEN	12.6	2.7	11.3	89	13.8
PIPO	8.8	2.4	10.1	49	7.6
POTR	6.0	0.5	2.1	64	9.9
		<u>23.8</u>		<u>647</u>	
Oak Creek					
PSME	47.9	12.1	51.3	193	44.4
PIPO	39.5	9.0	38.1	178	40.9
ABCO	11.9	2.4	10.2	59	13.6
JUSC	0.7	0.1	0.4	5	1.1
		<u>23.6</u>		<u>435</u>	
Ophir Creek					
PSME	62.9	19.0	67.4	259	58.3
PIPO	14.0	4.8	17.0	49	11.0
PICO	12.1	2.9	10.3	62	14.0
ABCO	8.3	1.3	4.6	62	14.0
POTR	1.7	0.2	0.7	12	2.7
		<u>28.2</u>		<u>444</u>	
Burned Mountain					
PSME	83.6	20.6	85.4	410	81.8
PCEN	8.7	1.6	6.7	54	10.8
ABCO	7.7	1.9	7.9	37	7.4
		<u>24.1</u>		<u>501</u>	
Capulin Canyon					
PIPO	49.9	9.2	58.8	72	41.0
PSME	31.9	4.5	28.6	62	35.2
ABCO	16.5	1.9	12.0	37	21.0
PIFL	1.7	0.1	0.6	5	2.8
		<u>15.7</u>		<u>176</u>	
Garcia Park					
PSME	78.9	20.9	72.8	509	85.0
PIPO	17.1	6.8	23.7	62	10.4

TABLE 1. Continued.

Stand name & species ^a	Importance ^b value	Basal area		Density	
		m ² /ha	Rel. (%)	Stems/ha	Rel. (%)
ABCO	3.7	0.9	3.1	26	4.3
PCEN	0.3	0.1	0.4	2	0.3
		<u>28.6</u>		<u>599</u>	
Osha Mountain					
PSME	49.5	11.9	56.1	231	42.9
PCEN	28.5	4.9	23.1	182	33.8
ABCO	10.6	2.2	10.5	57	10.6
PIPO	5.7	1.3	6.1	30	5.6
ABLA	5.6	0.9	4.2	38	7.1
		<u>21.2</u>		<u>538</u>	

^a PSME = *Pseudotsugae menziesii*, PIPO = *Pinus ponderosa*, PICO = *P. contorta*, JUSC = *Juniperus scopulorum*, POTR = *Populus tremuloides*, ABCO = *Abies concolor*, PCEN = *Picea engelmannii*, ABLA = *Abies lasiocarpa*, PIFL = *P. flexilis*, PIED = *P. edulis*.

^b Importance value is the average of the relative percent (Rel. %) basal area and density measurements.

possible record length of budworm history in each stand. At least 10 ponderosa pine (nonhosts) were sampled within the stands, or where possible, in pure or nearly pure nearby stands (within 1 km) in order to minimize any growth release effects in the pine due to defoliation of competing host trees.

Increment Core and Ring-Width Data Processing

Dendrochronology procedures and techniques for analyzing radial growth in budworm-defoliated trees were described and illustrated by Swetnam et al. (1985). These procedures included the following steps:

(1) Increment core samples were crossdated by the skeleton plot technique to identify false rings (two growth layers formed in one year) and absent rings (years in which no growth layers were formed) (Stokes and Smiley 1968). Absent rings typically result from stressful environmental conditions, such as drought or insect defoliation, when cambial growth takes place only along portions of the stem, or not at all (Keen 1937, Evenden 1940, O'Neill 1963, Fritts 1976).

(2) The ring widths were measured on a sliding-stage micrometer (Robinson and Evans 1980) and then were transformed to growth indices by fitting curves to the series and dividing the ring widths by the values of the fitted curves (Fritts 1976). Depending on the shape of the age-related growth trend, a negative exponential, straight line of negative slope, or cubic spline was fit to each core series (Graybill 1979, Cook and Peters 1981). Tree and stand chronologies were derived by simple averages of the core indices.

(3) The host (Douglas-fir) and nonhost (ponderosa pine) tree-ring series were graphically and statistically compared to determine if the different species responded similarly to climate but differently during periods of known budworm defoliation. These comparisons involved overlaying plots of host and nonhost index series and computation of correlation coefficients. Correlation coefficients were also computed for low-pass and high-pass filtered series and for prewhitened series. The filtered series were produced using 13-weight digital filters (LaMarche 1974, Fritts 1976), and the prewhitened series were computed as the residuals of autoregressive models (Cook 1985, Monserud 1986, Biondi and Swetnam 1987). Additional statistical com-

TABLE 2. Number of samples by stand and species.

Colorado			New Mexico		
Stand & species	Cores	Trees	Stand & species	Cores	Trees
Devil's Gulch			Burned Mountain		
PSME	53	25	PSME	90	45
PIPO	31	16	PIPO	22	14
Big Elk Meadows			Capulin Canyon		
PSME	113	57	PSME	113	60
PIPO	60	30	PIPO	26	13
Indian Creek			Garcia Park		
PSME	91	46	PSME	91	48
PIPO	50	25	PIPO	24	12
Ormes Peak			Osha Mountain		
PSME	42	21	PSME	221	106
PIPO	25	12	PIPO	31	16
Oak Creek					
PSME	20	10			
PIPO	12	6			
Ophir Creek					
PSME	40	20			
PIPO	31	17			
Totals Colorado			Totals New Mexico		
PSME	359	179	PSME	515	259
PIPO	184	106	PIPO	103	55
Totals Colorado + New Mexico					
PSME	874 cores	438 trees			
PIPO	287 cores	161 trees			

parisons of host and nonhost chronologies, including climatic response function and spectral analyses (Fritts 1976) are reported elsewhere (Swetnam 1987).

(4) The nonhost tree-ring series were used to subtract the climatic or other nonbudworm environmental signals from the host series, resulting in a corrected chronology for each stand. Individual tree effects were studied by applying the correction procedure to tree chronologies using the nonhost stand chronologies. The corrected tree-ring indices were derived using the following equations:

$$R = \frac{SD_h}{SD_{nh}} (INDEX_{nh} - MEAN_{nh}) \quad (1)$$

$$C = INDEX_h - R \quad (2)$$

Where R was the rescaled index value for each year of the nonhost series; SD_h and SD_{nh} were the standard deviations of the host and nonhost series; $INDEX_h$ and $INDEX_{nh}$ were each index value of the host and nonhost series respectively; $MEAN_{nh}$ was the mean of the nonhost series (about 1.0); and C was the corrected index value for each year of the host series. This

procedure was developed by Nash et al. (1975) in a study of air pollution effects on tree growth; however, the equations were reported in error.

Swetnam et al. (1985) describe the correction procedure and its assumptions and limitations for analyzing the effect of insect outbreaks on radial growth. In the first step, the nonhost index departures are rescaled to approximately the same variance of the host indices to be corrected, Equation (1). Next, the rescaled nonhost chronology is simply subtracted from the host chronology, Equation (2). If the relative growth response of the host and nonhost trees to climate is approximately the same (which should be tested graphically and statistically) and their response to budworm-caused defoliation is different, then the differences of the two chronologies should retain primarily the effect of budworm defoliation. In practice, there are inevitably some species-related differences in response to climate or other environmental variation in addition to budworms, and the corrected indices retain varying amounts of "noise" superimposed on a "budworm signal."

(5) Forest Service documentation of budworm outbreaks, insect population measurements, and defoliation estimates were compared with host chronologies to determine the precision of the corrected growth indices in identifying the timing of outbreaks and relative growth reduction. Forest Service documents were researched, and forest entomologists were consulted to determine if other insects or pest impacts have occurred within the sampled stands.

USDA Forest Service documents referred to here and elsewhere in the text are records of budworm occurrence derived from several different sources. These records generally covered the past 60 to 70 years (post-1920). Sources included annual Insect Survey and Insect Condition reports, Biological Evaluations, and maps of aerial detection of budworm defoliation. Summaries of budworm history in New Mexico and Arizona by Lessard (1975) and an unpublished report by M. E. McKnight (n.d.) titled "Outbreaks of Western Spruce Budworm in the Central and Southern Rocky Mountains" were very useful in identifying regionwide trends and occurrences of budworm outbreaks in specific areas and National Forests.

Interpretation of Timing, Duration and Growth Loss

General characteristics of twentieth century budworm-induced low-growth periods observed in the corrected tree-ring series and verified by Forest Service documentation were used as criteria for identifying budworm-induced low-growth periods that occurred prior to the documented period (pre-1920). Other criteria were used to screen out short duration or only moderately reduced growth periods that could have been due to sources other than budworm. These sources include differential response of host and nonhost tree species to climate, other insects or pathogens, or unknown disturbance and environmental factors. Low-growth periods corresponding to documented outbreaks were referred to as "known outbreaks," while the low-growth periods identified in the pre-1920 period were referred to as "inferred outbreaks." The screening criteria for identifying inferred outbreaks based on characteristics of twentieth-century known outbreaks were as follows:

1. Values of the corrected indices were less than expected growth (1.0) for 3 or more consecutive years, and,
2. The lowest growth value during this period was greater than 1.28 standard deviations below the mean of the series.

Duration of outbreaks was the number of years between the beginning and

ending years of an identified outbreak. The beginning year was the first year of low-growth (index values below 1.0) during the period. The ending year was the last year of low-growth that preceded 2 or more years of growth exceeding an index of 1.0. Thus, computed duration included the years of recovery, and was probably proportional but not necessarily equivalent to the time that budworms were actually present and feeding on the foliage.

Radial growth reduction during known and inferred outbreaks was computed as the difference between the observed corrected index values and the expected index value for each year, which is 1.0 for a tree-ring index series. Multiplied by 100, these values are the percent growth reduction. Maximum growth reduction values were computed, and years of maximum growth reduction were recorded. Periodic growth reduction was computed as the sum of yearly growth reductions during an outbreak divided by the number of years in the period.

The timing and duration of known and inferred budworm outbreaks were compared graphically between stands and time periods. Two-sample t-tests were employed to test for differences between time periods and between Colorado and New Mexico stands in estimates of mean growth reduction, duration, or intervals between outbreaks.

RESULTS

ABSENT RINGS

Crossdating revealed that relatively few annual rings were locally absent along the studied radii. The ponderosa pine had a higher proportion of absent rings (0.45%) than Douglas-fir (0.27%). However, the majority of Douglas-fir absent rings occurred during low-growth periods that were subsequently identified as budworm outbreaks, while the absent rings in ponderosa pine series did not consistently occur during identified outbreaks. This was most clearly evident during the recent outbreak; more than 26% of all Douglas-fir ring absences occurred since 1977. Only 2.6% of all ponderosa pine ring absences occurred during this same period (Table 3). This evidence suggests that the most recent outbreak may have been the most severe defoliation episode recorded by the sampled trees.

The higher overall rate of ring absence in ponderosa pine than in Douglas-fir was probably due to more stressful microsites occupied by many of the pines. Most of the pines sampled in New Mexico were from pure or nearly pure nearby stands, and the sites were generally more xeric and better drained than the Douglas-fir sites. Even where the nonhost pines were sampled from the same mixed-conifer stands as the Douglas-fir host trees, the pines were often situated in more exposed or rocky settings than the Douglas-fir.

An important consideration is that the Douglas-fir were necessarily survivors of past outbreaks. Therefore, growth reductions caused by severe outbreaks in the past may not be fully represented because trees that died during a severe outbreak or during subsequent outbreaks were not represented. However, even in stands that were very heavily damaged, such as Devil's Gulch, which sustained more than 60% mortality of overstory trees during the recent outbreak, many of the surviving trees had missing rings after 1980. Growth of most of the sampled trees was already increasing in 1985 in an apparent recovery phase. Thus, evidence of this very severe outbreak, as reflected in the unusually high number of absent rings, was preserved in the record despite a relatively high mortality rate.

TABLE 3. Number and percent absent rings by species and state.

State & species	No. of rings measured	No. of absent rings	Percent absent rings
Colorado			
PSME	39,741	152	0.38
PIPO	27,002	138	0.51
New Mexico			
PSME	53,368	97	0.18
PIPO	23,233	94	0.37
Colorado + New Mexico			
PSME	93,109	249	0.27
PIPO	50,235	232	0.45

	Absent rings since 1977	
	Number	Percent of total
Colorado		
PSME	45	29.6
PIPO	4	2.9
New Mexico		
PSME	21	24.4
PIPO	2	2.1

HOST AND NON-HOST TREE RING COMPARISONS

Tree-ring indices of host and nonhost trees show good visual crossdating, or matching of high and low growth during most years (Figure 2A). Figure 2B compares the same chronologies after smoothing the index values with a low-pass filter. The low-pass filter removed most of the variations occurring over time periods from 2 to 8 years and preserved most of the low frequency variance related to longer time periods (LaMarche 1974, Fritts 1976). The low-pass comparisons de-emphasized the short-term fluctuations that were in common between the host and nonhost species, while emphasizing the longer term growth differences that were most likely due to the effects of budworm defoliation (Swetnam et al. 1985).

The graphical low-pass comparisons revealed that growth trends in the two species were generally similar during some periods while they were different during other periods. Known budworm outbreaks consistently appeared as periods with declining trends in the Douglas-fir and increasing or relatively unchanging growth trends in the ponderosa pine series.

Statistical comparisons of the two species' tree-ring chronologies showed highest correlation in the high frequencies, indicating that short-term year-to-year growth changes were generally similar in the two species across the length of the chronologies (Table 4). High-pass correlations were consistently higher than index comparisons, and low-pass comparisons were consistently lower than either ordinary index or high-pass comparisons.

Correlations of the prewhitened series were also higher than the ordinary index or low-pass series. The autoregressive modeling had the effect of removing some low-frequency differences between the two species that may have been due to differences in autocorrelation and response to the budworm. Defoliation of host trees probably increased autocorrelation, especially during the outbreak periods. The prewhitened host series generally retained the initial sharply reduced growth values at the beginning of out-

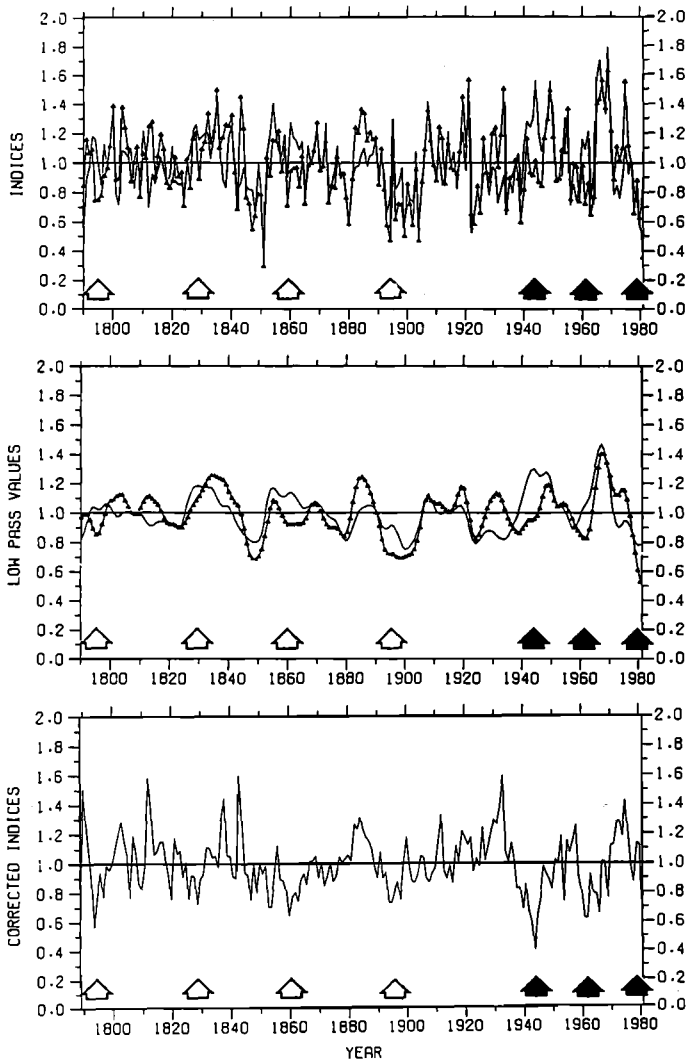


FIGURE 2. A. Comparison of Douglas-fir (line with triangles) and ponderosa pine (line) tree-ring width indices from the Capulin Canyon stand in New Mexico. B. The same chronologies after smoothing with a digital filter. C. The corrected Douglas-fir growth Douglas-fir indices. Blackened arrows indicate timing of known outbreak periods verified by Forest Service records. Open arrows indicate timing of inferred outbreaks.

breaks, but growth during latter portions of outbreaks was sometimes increased relative to the ordinary index series (Swetnam 1987).

Both the graphical and statistical comparisons indicated that the ponderosa pine was generally a good estimator of Douglas-fir growth, especially between outbreaks. Therefore, ponderosa pine was considered a reasonable estimate of expected Douglas-fir growth during known and inferred outbreaks. These findings provided a logical basis for applying the correction procedure (Figure 2C).

VERIFICATION TESTS OF THE CORRECTED HOST GROWTH INDICES

The corrected indices from 1920 to the 1980s for two stands are shown in Figure 3. This and similar comparisons for all stands revealed that growth

TABLE 4. Correlation coefficients for Douglas-fir and ponderosa pine paired chronologies from Colorado and New Mexico stands. All coefficients are significant at $P < 0.05$ with degrees of freedom adjusted for autocorrelation (Quenouille 1952).

	Period of comparison	No. of years	Correlation coefficients			
			Indices	Low pass	High pass	AR residuals
Devil's Gulch	1740-1980	241	0.649	0.361	0.843	0.759
Big Elk Meadows	1820-1983	264	0.646	0.535	0.795	0.743
Indian Creek	1860-1983	124	0.474	0.314	0.672	0.626
Ormes Peak	1720-1984	265	0.630	0.434	0.793	0.733
Oak Creek	1900-1983	84	0.761	0.665	0.813	0.811
Ophir Creek	1780-1984	205	0.640	0.548	0.724	0.678
Burned Mountain	1790-1983	194	0.640	0.652	0.672	n.c.
Capulin Canyon	1790-1981	192	0.665	0.602	0.719	n.c.
Garcia Park	1710-1981	272	0.745	0.699	0.803	0.780
Osha Mountain	1700-1981	282	0.537	0.492	0.632	n.c.
		Mean:	0.638	0.530	0.747	0.733

n.c. = not computed.

usually responded to changes in budworm population and defoliation levels in the same year, or sometimes with a single-year lag. For example, budworm populations in most of Colorado collapsed in 1946, possibly because of a severe late spring frost in June 1945 that may have resulted in killing of the new Douglas-fir buds, leading to budworm mortality (USDA Forest Service documents). Budworm populations were reported as persisting in the late 1940s in some stands, and then populations resurged in the early 1950s, especially on the Pike National Forest. All of the Colorado corrected growth series show reduced growth in 1946. Growth rates were reduced in the early 1940s at Ormes Peak and Indian Creek on the Pike National Forest, and then growth increased in 1946 following the collapse of budworm populations in this area as described in the Forest Service records (Figure 3).

The twentieth century portion of New Mexico chronologies also corresponded well with the Forest Service documentation (Figure 4). Records indicated that budworms were first reported in this region in 1922 on the western division of the Carson National Forest, but not on the eastern division (Lessard 1975, USDA Forest Service documents). The Burned Mountain stand, which is located on the western division of the Carson (see map, Figure 1, and uppermost plot in Figure 4), recorded an outbreak in the 1910s to 1920s while the stands in the eastern division do not. The Forest Service records also listed 1944 as the peak outbreak year on the eastern division of the Carson near Taos, while defoliation was not reported on the western division. The minimum growth years recorded by the three stands on the eastern division of the Carson were 1943, 1944, and 1945, corresponding well to the Forest Service documentation.

Swetnam (1986, 1987) presented statistical evidence that the tree-ring growth indices were good indicators of budworm activity. This analysis used budworm population and defoliation data that was recorded for individual sampled trees in the New Mexico plots by Forest Service personnel (Rogers 1984). The following exponential models were estimated using linear least squares regression of logarithmic transformed growth indices:

$$\text{Growth Index} = 1.310 * e^{(-0.004 * \text{cumulative plot defoliation})}$$

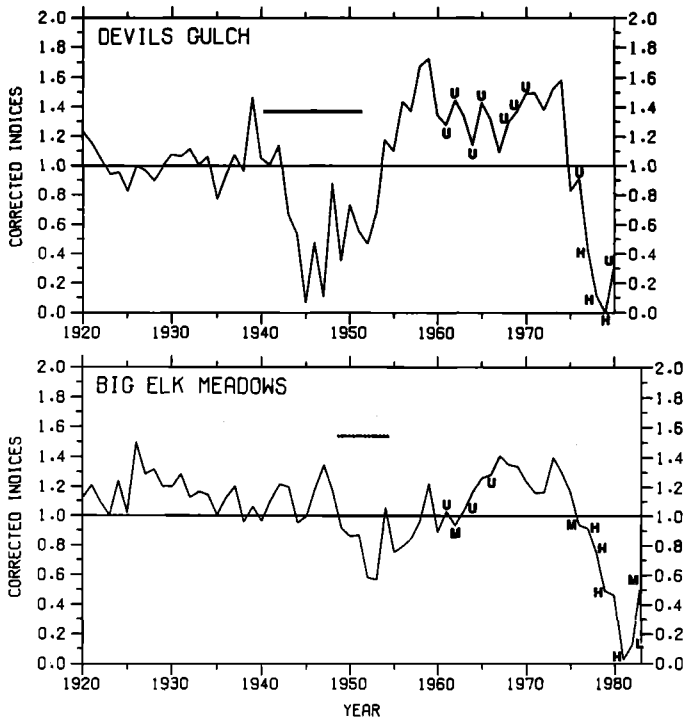


FIGURE 3. Corrected growth index series and defoliation estimates from two stands in Colorado. Letters refer to available aerial and ground estimates of defoliation (loss of current year's needles) from Forest Service records. U = undetectable, 0 to 10% defoliation; L = light, 10% to 35%; M = 35% to 65%; H = 65% to 100%. The reduced growth period during the 1940s and 1950s (short horizontal lines) is an outbreak recorded in the general area of these stands, but without quantitative measurements of insect populations or defoliation. Both stands were sampled in 1984 and 1985, but due to numerous absent rings in the Devil's Gulch cores it was not possible to date the rings in many of the samples after 1980, so corrected indices were computed only up to 1980 in this stand.

$$R^2 = 0.584 (n = 28, P < 0.01)$$

$$\text{Growth index} = 1.180 * e^{(-0.014 * \text{previous year egg mass density})}$$

$$R^2 = 0.670 (n = 21, P < 0.01)$$

Cumulative plot defoliation was the sum of defoliation estimates in each successive year, where defoliation was percent reduction of current year needle growth. Egg mass densities were the number of egg masses per m^2 of foliage. The intercepts in these models were greater than 1.0 (expected index value if cumulative defoliation or egg masses were zero), which suggests that the models are inadequate at low defoliation levels. One possible explanation for this is that, at low average plot defoliation and egg mass levels, there were a few individual trees that apparently were not defoliated at all, and may actually have been increasing their growth rates because of reduced competition from competing host trees that were impacted. Alfaro et al. (1982) noted a similar phenomenon in a study of budworm defoliation of Douglas-fir in British Columbia. They were able to derive an improved exponential model, explaining 85% of proportional increment in individual trees, by including cumulative plot defoliation and individual tree defoliation

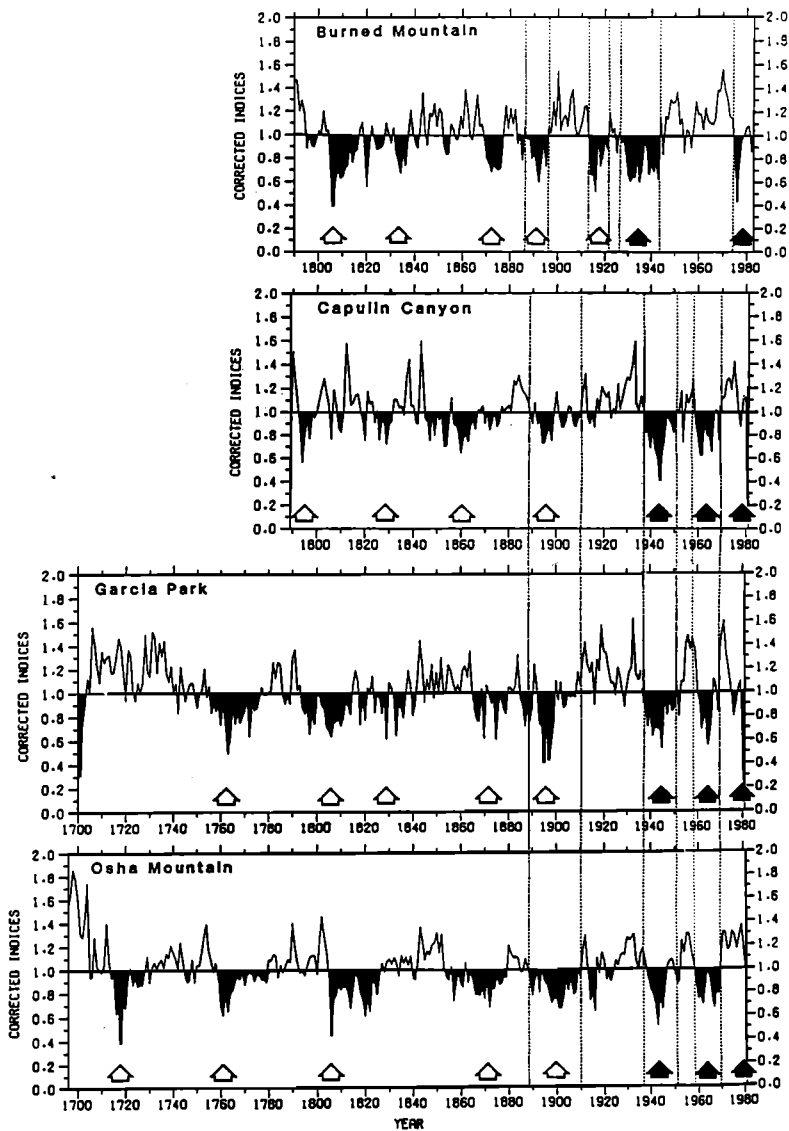


FIGURE 4. Corrected growth index series from the New Mexico stands. Vertical dotted lines show timing and synchrony of outbreaks that have occurred since the late 1800s. Blackened arrows indicate timing of known outbreak periods verified by Forest Service records. Open arrows indicate timing of inferred outbreaks.

measurements as predictor variables. This approach was not feasible in the current study because consecutive year measurements of defoliation and egg mass numbers for individual trees were not available.

Evidence indicating that other pests were responsible for the observed growth reductions was lacking. Review of historic records suggest that Douglas-fir tussock moth, *Orgia pseudotsugata* McDonnough, could possibly cause the aperiodic growth reductions observed in the tree-ring samples. However, this seems unlikely because tussock moth impacts in the Southern Rocky Mountains have typically been limited to short-term local infestations with white fir as the principal host (Wickman 1980, Wickman et al. 1971).

Reduced growth in living trees is unlikely to be due to attack by bark beetles (e.g., *Dendroctonus* spp. and *Scolytus* spp.) because such attacks are usually fatal.

GROWTH RELEASES

Large positive corrected Douglas-fir indices were observed in most of the stands between the known and inferred outbreaks (Figure 4). In most cases this effect was due to growth releases in Douglas-fir that were not matched in ponderosa pine. Other researchers have noted similar growth releases in nonhost trees and surviving host trees following insect outbreaks (Wickman 1980, Alfaro et al. 1982, Carlson and McCaughey 1982, Beveridge and Cahill 1984). Examination of the ring series and age structure in several stands indicated that some of these growth releases were responses to mortality of neighboring trees during the preceding outbreak. For example, strong growth releases were observed in the older tree chronologies from Garcia Park and Osha Mountain during and following the 1890s-1910 outbreak. A large cohort of trees germinated and became established within these stands after 1900, suggesting a general opening of the stand.

Many of the growth release effects observed in older individual trees were slightly nonsynchronous between trees (see 1890 to 1910 period in Figure 5). Nonsynchronous growth release would be expected from budworm-induced mortality, where the timing of mortality within stands varies over the period of the outbreak. Growth releases following partial harvesting or a fire that caused mortality would probably be more synchronous among trees within the stand.

TIMING AND DURATION OF BUDWORM-INDUCED GROWTH LOSSES

The history of budworm outbreaks as derived from the corrected growth index chronologies from all ten stands is illustrated in Figure 6. The most obvious feature was apparent synchronization of severe outbreaks during the latter half of the twentieth century relative to previous periods. There was evidently more variability in timing of outbreaks between stands during earlier periods.

The illustration of initial and maximum growth reduction years shown at the bottom of Figure 6 reveals that some periods had a greater incidence of outbreaks. Periods of increased budworm activity were recorded as groupings of initial and maximum growth reduction years, while periods of decreased budworm activity were visible as an absence of these events. A relatively long period without budworm activity in most stands occurred during the first two or three decades of the twentieth century (Figure 6).

The line graphs running through the bar graphs at the bottom of the chart (corresponding to the scale on the right Y-axis), represent the total number of Douglas-fir trees included in the tree-ring chronologies. The number of trees in the sample declines rapidly before 1930. It is obvious that the earliest time periods represented include fewer data because fewer trees of sufficient age were sampled. Thus, the overall lower values shown by the bar graphs in this period were dependent on the number of stands with tree-ring data extending back that far in time.

The earliest outbreak periods were necessarily recorded only by trees that were younger in these periods, but which are now the oldest sampled trees. If these trees were less consistent in recording outbreaks during earlier periods than they were in more recent decades, the pattern observed in the

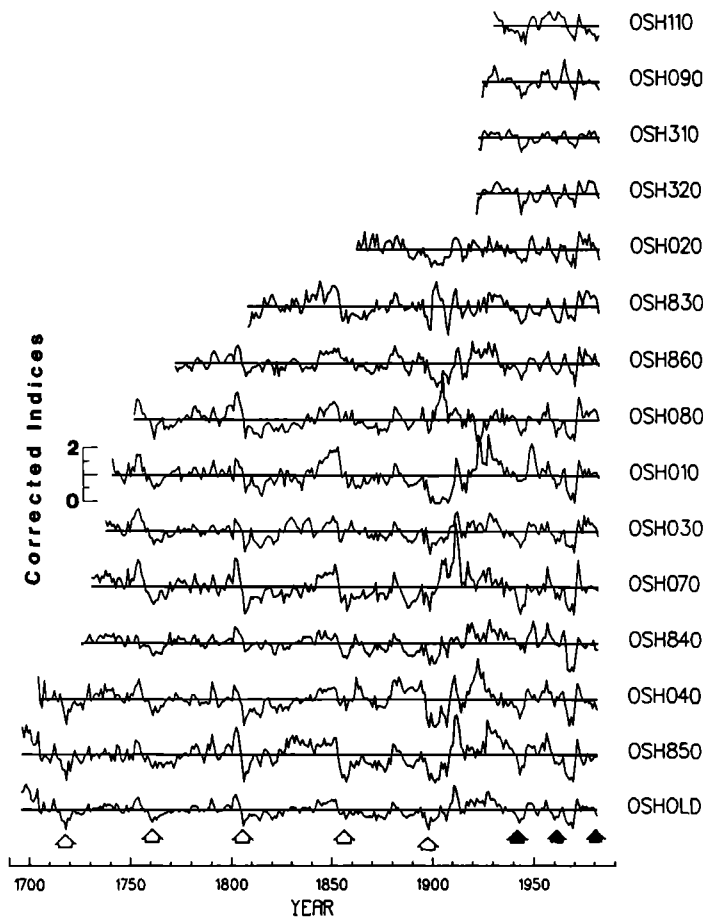


FIGURE 5. Corrected index chronologies from different aged Douglas-fir in the Osha Mountain stand. Two core series were averaged per tree. Outbreaks are visible in both young and old trees. The lowermost plot is the mean chronology from all trees that established before 1850. A nonsynchronous growth release is visible around 1900.

chronologies (upper portion Figure 6) should show an absence of record in individual chronologies for the earliest periods, rather than the observed difference in outbreak timing. Examination of individual tree chronologies at each site shows that most sampled trees recorded most of the outbreaks, regardless of age (Figure 5). Severe outbreaks were usually detectable even in the earliest periods represented by only a few older trees. Therefore, despite temporal changes in sample depth and tree ages included in the sample, these changes would not necessarily result in the observed pattern of low synchrony between stands in the pre-1900 period.

Some of the few apparent gaps in the record in individual stand chronologies (unusually long periods without arrows in Figure 6) appear to be due to the problem of detecting the shorter, less severe defoliation periods in the average stand chronologies. For example, a consistent low growth period among most trees in the Ophir Creek stand occurred during the late 1850s. A budworm outbreak during this period would correspond to increased budworm activity in most other stands (see Figure 6). However, this period did not pass the screening criteria described in the methods section for identifying past budworm outbreaks.

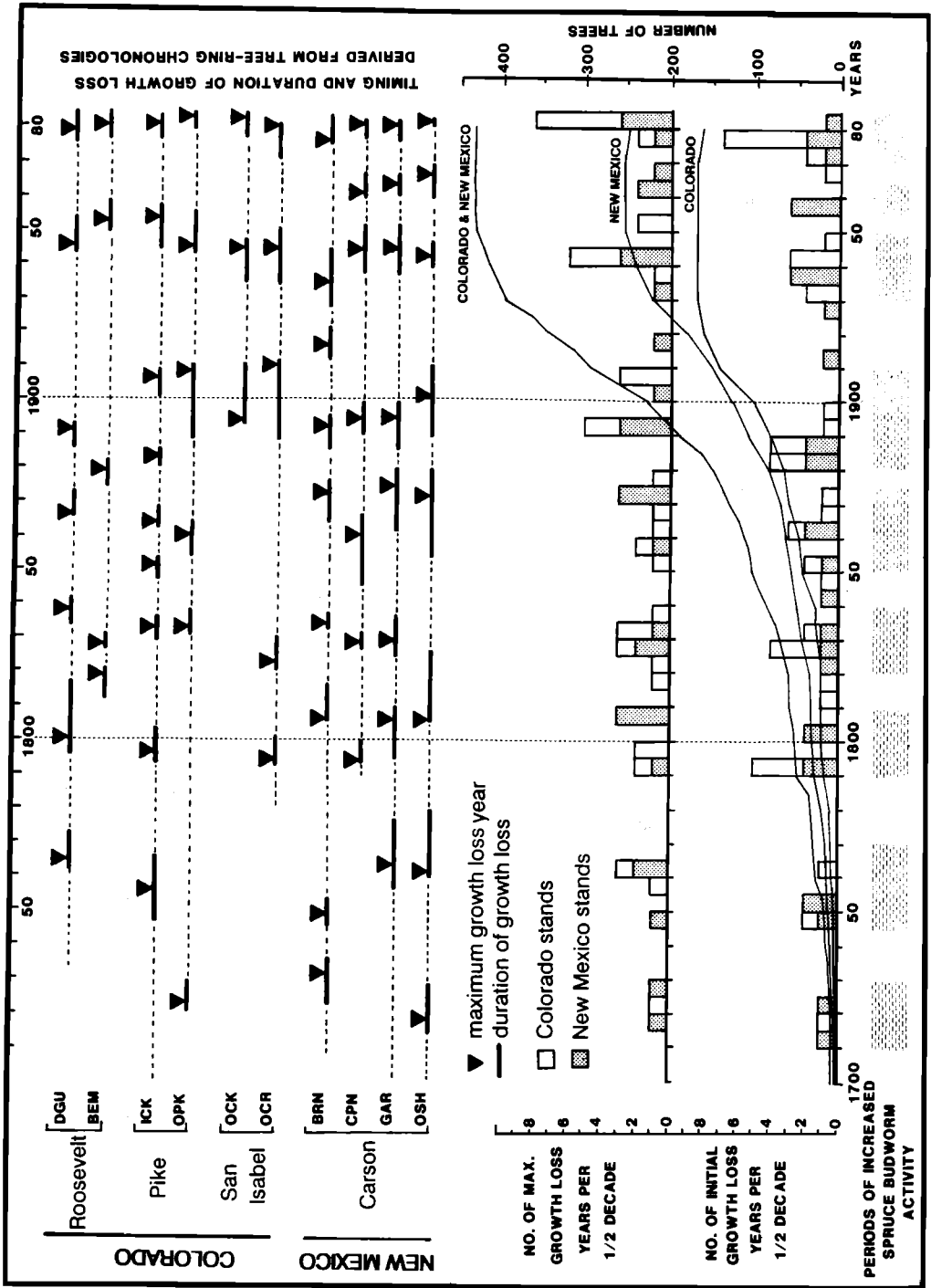


Figure 6 Timing and duration of budworm outbreaks derived from corrected tree-ring chronologies from 10 stands in Colorado and New Mexico

Figures 4 and 6 also show that three New Mexico stands on the eastern division of the Carson recorded the early 1960s outbreak while the Colorado stands did not. Forest Service records indicate that the 1960s outbreak in New Mexico was relatively severe, while only moderate or low defoliation was recorded in four of the Colorado stands during a single year (1961, 1962, or 1963). The Colorado stands had slight growth declines in the early 1960s, and the Indian Creek stand had a larger growth decline in the late 1960s. None of the 1960s growth reduction periods in the Colorado tree-ring series passed the screening criteria for documenting an outbreak. Thus, brief or minor defoliation episodes may not be resolvable from the other variations that remain in the corrected ring series, and so the budworm outbreaks shown in Figure 6 are probably best representative of moderate to severe defoliation episodes.

The problem of low resolution in budworm detection methods, including tree-ring reconstructions and aerial surveys, were discussed by Régnière (1985). He pointed out that low to moderate defoliation may not always be detectable, so historical sequences of outbreaks often depict sudden changes in budworm activity, when in fact budworm densities may change in a gradual and aperiodic manner along a continuum of densities. Even if some outbreaks of low severity were not detected and were omitted from the data shown in Figure 6, it seems most likely that all of the severe outbreaks that occurred in these stands were detected.

DURATION AND GROWTH REDUCTION ESTIMATES

Estimates of growth reduction were generally higher in the Colorado stands than in New Mexico stands (Figure 7 and Table 5). Maximum 1-year growth reductions were approximately 15% higher, and periodic growth reductions were approximately 5% higher in Colorado stands than in New Mexico stands. These measurements are consistent with our observations that Colorado stands generally sustained greater mortality than New Mexico stands during the recent outbreak.

Estimates of duration of reduced growth periods caused by budworm were usually 2 or more years shorter in Colorado stands than in New Mexico stands. Intervals between outbreaks, computed as years between the final year of the previous outbreak and the initial year of the subsequent outbreak (Interval A, Table 5), and years between initial years of successive outbreaks (Interval B, Table 5), were more similar between Colorado and New Mexico stands. At this time we have no satisfactory explanation for the observed differences between Colorado and New Mexico stands.

Average growth reduction by periods appear to have become more severe since the late 1800s, although earlier outbreaks (1710s–1810s and 1850s–1870s) were also relatively severe (Figure 7). The average maximum 1-year growth reductions for the 1970s–1980s period were the highest recorded for any period in both the Colorado and New Mexico stand groupings. This result was a reflection of the greater rate of absent rings during the most recent outbreak.

Estimates of duration, intervals between outbreaks, and growth reductions were grouped into pre- and post-1910 periods, and means were tested for differences (Table 5). This division seemed reasonable given the observed absence of outbreaks in most stands during the 1920s and early 1930s, and the apparent shift to more synchronous outbreaks in later decades. When the 1970s to 1980s growth reduction estimates were omitted (Table 5), differences in duration, maximum, and periodic growth reduction between

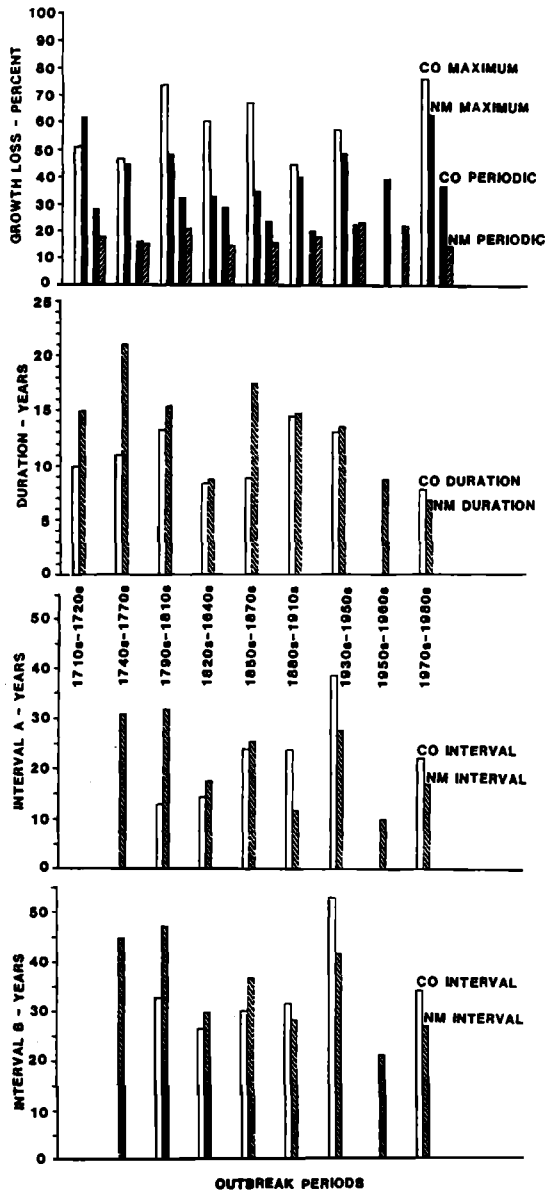


FIGURE 7. Estimates of average growth reduction, duration, and intervals between outbreaks for Colorado and New Mexico stands by time period. Interval A is the period in years between the final year of the previous outbreak and the initial year of the following outbreak. Interval B is the period between initial years of successive outbreaks.

the pre- and post-1910 periods could not be established with reasonable certainty. When the 1970s-1980s outbreak was included, however, post-1910 growth reductions were somewhat greater than the pre-1910 estimates (maximum growth reduction, pre- and post-1910 periods respectively: 49.9% and 58.8%, $t = 1.750$, $P = 0.085$; periodic growth reduction: 21.3% and 25.4%, $t = 1.403$, 0.166). Intervals between outbreaks were generally longer in the post-1910 period than in the pre-1910 period (Table 5), but when the 1970s-1980s outbreak was included, this difference was less pronounced (Interval

TABLE 5. Comparison of budworm occurrence in Colorado and New Mexico stands. Differences in means were tested by state (A) and period (B). Outbreak data from 1700 to 1960s were included, while current outbreak data (1970s–1980s) were excluded. The *t* statistic is from a two-sample *t*-test, and probability levels are two sided. See text for explanation of parameters.

A.								
Parameter	Colorado		New Mexico		<i>t</i>	Prob. level	CO + NM	
	Mean	Std. Dev.	Mean	Std. Dev.			Mean	Std. Dev.
Duration (yr)	11.6	5.1	13.8	6.0	1.476	0.146	11.9	5.5
Interval A (yr)	26.5	16.1	21.4	12.3	1.212	0.232	23.2	13.3
Interval B (yr)	36.8	17.2	34.9	13.1	0.430	0.670	34.9	14.3
Maximum growth loss (%)	57.8	16.9	42.9	10.5	3.757	<0.001	50.4	15.7
Periodic growth loss (%)	24.4	9.8	18.9	5.1	2.496	0.016	21.7	8.1
B.								
	Pre-1910		Post-1910					
Duration (yr)	12.8	6.1	12.0	3.5	0.468	0.642		
Interval A (yr)	21.7	12.5	29.4	17.5	1.665	0.103		
Interval B (yr)	33.0	13.4	42.8	17.1	2.066	0.045		
Maximum growth loss (%)	49.9	16.6	51.7	14.2	0.348	0.730		
Periodic growth loss (%)	21.2	7.7	22.8	9.7	0.578	0.566		

A, pre- and post-1910 periods respectively: 21.7 and 25.3 years, $t = 0.989$, $P = 0.327$; Interval B: 33 and 37.7 years, $t = 1.194$, $P = 0.238$).

EFFECTS OF AGE ON GROWTH LOSS ESTIMATES

Published research on growth impacts caused by western spruce budworms in relation to age of host trees is lacking, but literature on spruce budworms in eastern North America supports the contention that older trees and stands are more susceptible and vulnerable to infestation than younger stands (Carlson et al. 1983, MacLean 1985). If greater growth reductions occur in older trees than younger trees, then any observed increase in growth reduction during recent periods could be due to the older trees included in the sample for these periods.

As a test of differences in growth reduction between age classes, individual tree data from all of the New Mexico stands were stratified into "old" and "young" age groups. This stratification was relatively objective because the sampled stands were typically composed of only two or three age classes. The average age of the young-age classes in four stands was 61, 71, 107, and 107 years for a total of 139 trees. The average age of the old-age classes in the four stands was 125, 134, 220, and 237 years for a total of 112 trees. Radial growth reductions (maximum and periodic) were computed for the three most recent outbreaks which occurred during the lifetime of all sampled trees.

The older trees appeared to have sustained slightly greater growth reductions than the younger trees during these outbreaks, but average growth

reductions were not greatly different. The average maximum growth reduction for all three outbreaks in the old-age classes was 64.2%, while it was 57.3% in the young-age classes ($t = 1.02$, $P = 0.32$). The average periodic growth reduction was 26.8% in the old-age classes, while it was 22.7% in the young-age classes ($t = 1.00$, $P = 0.32$).

Also, considering that the proportion of old trees (exceeding 150 years in age) in the sample during the twentieth century period was less than 20% of the total sample, slightly greater growth reductions due to their inclusion would have been at least partly compensated by the larger number of young trees in this period. Thus, a bias due to age effects was not a problem in the interpretation of the changes in estimated growth reductions through time (Figure 7).

DISCUSSION

The results indicate that a change in budworm incidence has taken place in the twentieth century within the sampled stands. The nature of this change is somewhat different from that reported by Blais (1983, 1985a, 1985b) for the spruce budworm in eastern Canada, or by McCune (1983) and Anderson (1985) for the western spruce budworm in the Bitterroot Mountains in western Montana. These workers found an increase in the frequency (number of outbreaks per time period) and/or severity of outbreaks in the twentieth century relative to outbreaks occurring in previous centuries. We found that moderate to severe outbreaks during the last 70 years were not clearly less or more frequent than during the previous two centuries, but the temporal and spatial pattern of occurrence has changed. There was some evidence that severity has increased since 1900, and that the most recent outbreak may be more severe than any other recorded outbreak.

The most distinct change observed in this history was a greater synchrony of outbreaks among sampled stands during the latter half of the twentieth century than during earlier centuries (Figure 6). This evidence suggests that recent outbreaks were more extensive than previous outbreaks.

A change from the nineteenth to the twentieth century budworm outbreak regime is also marked by a relatively long period in the first few decades of the 1900s with an absence of budworm activity. This period lasted 30 or more years within individual stands. The early 1920s outbreak, which was the first documented western spruce budworm infestation in several areas of the western United States (Johnson and Denton 1975), was not recorded in most of the stands sampled for this study. This outbreak appears to have been limited to areas on the western side of the Rio Grande (Burned Mountain stand in New Mexico, Figure 4).

Evidence of a high proportion of absent rings in Douglas-fir and high estimates of growth reduction during the recent outbreak suggests that it may have been more severe than previous outbreaks. This outbreak was ongoing in the stands when they were sampled, so the growth reduction and duration estimates for this period are incomplete. The number of trees killed during past outbreaks is unknown, so comparison of severity estimates between periods relies only on comparison of radial growth reductions in survivor trees. Changes in the age structure of the sample may also introduce some bias; however, older trees were found to sustain only slightly greater growth reductions than younger trees, so this may not affect the observed changes in growth reduction through time. The resolution of the tree-ring reconstructions (Figure 6) may be limited to detection of the moderate to severe outbreaks, but the observation of greater synchrony in the twentieth century among sampled stands is not affected by this limitation.

A major question remaining is: To what extent are the sampled stands representative of budworm outbreak history in the Southern Rocky Mountains? The sampled stands were originally selected by USDA Forest Service entomologists within areas that were currently being defoliated by budworm or had a known history of past defoliation. Thus, the observed synchronicity of the most recent outbreaks may be a result of this selection. Although this problem clearly limits the generalization of these results, it is clear from observations of the extent of the 1970s–1980s outbreak that this event was “regional,” occurring throughout very large areas of the mixed-conifer type. In 1983 more than 1.09 million ha of a total estimated 1.25 million ha (or 87%) of Douglas-fir “cover-type” forests in Colorado and Wyoming were defoliated by budworm (Lessard et al. 1987). Indeed, it would be fairly difficult to find a mixed-conifer stand in the Colorado Front Ranges that was not defoliated to some extent during the 1970s–1980s outbreak. Based on observations of the current outbreak and Forest Service records, twentieth century outbreaks in the study area of northern New Mexico have occurred within, and generally throughout, specific large watersheds within the region (e.g., Rio Fernando de Taos, Rio Pueblo, Cabresto, and Red River). Over 150,000 ha was defoliated in New Mexico in 1983 (Linnane 1984). Thus, it is likely that sampling almost any mixed-conifer stand within the Colorado Front Ranges or these large New Mexico watersheds would have revealed similar outbreak histories, including the apparent increased synchrony in the twentieth century. A thorough test of any hypothesized change in the budworm outbreak regime on a larger regional scale will require additional sampling in mixed-conifer stands in areas where budworm has occurred, and has not occurred, within the documentary period (post 1920).

HISTORICAL HYPOTHESIS

Several well-established facts of Colorado and New Mexico forest history, in addition to observations of stand age structure, suggest that possible changes in outbreak synchrony may be associated with harvesting, fire suppression, and the widespread establishment of an understory of shade-tolerant, budworm host trees in the 2 or 3 decades before and after the turn of the century. Large tracts of old-growth timber were harvested from the Colorado Front Ranges and Sangre de Cristo Mountains in the late 1800s and early 1900s for railroad ties, mining operations, and for the building of new towns (Marr 1961, Schubert 1974, Peet 1981, DeBuys 1985, Veblen and Lorenz 1986). Specific historical documentation of harvesting within the sampled stands was not found, but stumps and old logging roads were observed within or nearby many of the stands.

The largest proportion of trees in sampled stands appear to be between 60 and 100 years in age. This age structure is reflected in the sample depth shown in Figure 6, although this is a somewhat biased estimate due to the sampling of additional older trees within and nearby the plots to increase the record length. Age structure of mixed-conifer stands inferred from a larger sample of diameter measurements (Swetnam 1987) are also similar to age-class distributions in Colorado measured by Peet (1981), Veblen and Lorenz (1986), and Lessard et al. (1987), i.e., most stands are composed of two or three components. The oldest components are a few scattered Douglas-fir and ponderosa pine occupying the highest canopy level. These trees have survived numerous outbreaks and harvesting since their establishment in the 1700s or earlier. The sampled stands also include a component of scattered trees that became established during different periods of the 1800s. The

largest component, exceeding 70% of all trees in some stands, are the relatively young pole-size host trees that became established between about 1880 and 1920. These trees occupy a canopy level below the oldest and intermediate-age trees.

The historical origin and development of the stands as multistoried second growth with a few older scattered remnants of the presettlement forest suggests that they have followed a typical pattern in western forests that may have led to greater susceptibility and vulnerability to budworm outbreaks (Carlson et al. 1983). One historical scenario that may explain observed changes in budworm incidence includes the following stages: (1) Intensive and selective harvesting of more desirable old-growth trees from many stands in the Southern Rockies before and just after the turn of the century would have resulted in a general opening of stands. Where present, ponderosa pine would likely have been favored over white fir and Douglas-fir. Intense fires burned through some stands in the late 1800s, possibly due to accumulated logging slash being set on fire by people (Skinner and Laven 1983, Veblen and Lorenz 1986). (2) The period from about 1910 to the early 1920s was a very wet period with high precipitation and winter snowfall (Schulman 1956, Rose et al. 1981), and many trees successfully germinated and established in the open stands. (3) The beginning of organized fire control during this same period effectively eliminated the low intensity periodic fires that had burned through Rocky Mountain mixed-conifer stands before 1900 at intervals of about 20 years or less (Dieterich 1983, Skinner and Laven 1983). Without periodic fire, many more of the young seedlings were able to survive than might have been otherwise possible. The previously open stands then developed for two or more decades in a juvenile or seral state, which may have conferred some increased resistance to budworm outbreaks. (4) By the mid-1930s many of the stands that were harvested and opened before the century were now dominated by the more shade-tolerant host species in relatively closed stands with multiple-level canopies. The stands were now more heavily stocked, with a more homogeneous age structure, and with a larger proportion of shade-tolerant host trees than before 1900 and the harvesting era. The stand conditions since this time have been more susceptible and vulnerable to budworm attack, leading to the extensive and severe outbreaks of the last 40 years.

This historical explanation also suggests a process that can be viewed from the perspective of patch dynamics theory (Pickett and White 1985). For example, it is clear that presettlement Rocky Mountain forests were generally more open, with clearings maintained by frequent low intensity surface fires. Budworm may also have been partly responsible for open stands with mixtures of hosts and nonhosts through selective mortality of host trees. These forests were probably more patchy and, interactively, budworm outbreaks were also more patchy. In the several decades following the settlement period, establishment of large numbers of trees in the former forest mosaic led to a much less patchy forest structure and species composition, and consequently a less patchy budworm outbreak regime. This hypothesis is in accord with one of the central tenets of patch dynamics theory, i.e., disturbance regimes and ecosystem structures and intimately linked. Thus, the budworm regime has at different times been both a source and a consequence of the spatial heterogeneity of its forest habitat.

The generalized history and process proposed in preceding paragraphs certainly does not apply to all areas of the Southern Rocky Mountains or southwestern mixed-conifer type. A test of the general hypothesis that budworm incidence has increased in the twentieth century in western mixed-

conifer stands will require additional long-term reconstructions of budworm history in other Southern Rocky Mountain stands and in other areas of the west where the western spruce budworm is a recurring disturbance. The potential for reconstructing long-term budworm histories for other areas of the western United States and Canada is good because many long-lived host species are present. Evidence of changes in age structure, species composition, fire history, harvesting practices, and climate must be considered in combination with tree-ring records of past budworm outbreaks. This type of holistic analysis offers the potential of clarifying the ecological role of budworms from a time perspective that is scaled to the centuries-long cycle of forest dynamics.

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