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MULTICENTURY, REGIONAL-SCALE PATTERNS OF WESTERN SPRUCE BUDWORM OUTBREAKS[1]

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Abstract. Tree ring chronologies from 24 mixed-conifer stands were used to reconstruct the long-term history of western spruce budworm *(Choristoneura occidentalis)* in northern New Mexico. Temporal and spatial patterns of budworm infestations (within-stand occurrences) and outbreaks (more-or-less synchronous infestations across many stands) were investigated to identify local-scale to regional-scale forest disturbance patterns. Nine regional-scale outbreaks were identified from 1690 to 1989. One ancient stand of Douglas-fir trees *(Pseudotsuga menziesii)* exceeding 700 yr in age revealed that budworms and overstory trees can coexist for extraordinary lengths of time. Using spectral analysis we found that the regional outbreak record contained important cyclical components with periods varying from ≈20 to 33 yr. The statistically significant $(P < .05)$ but variable periodicity of regional outbreaks suggests the forest-budworm dynamic is pseudoperiodic (i.e., a stable limit cycle or damped oscillator perturbed by noise).

Duration of infestations within stands was ≈ 11 yr and has not obviously changed in the 20th century; however, infestations tended to be more synchronous among stands in this century than during earlier centuries. Regional budworm activity was low from the mid- 1920s to late 1930s and mid-1960s to late 1970s, and the most recent outbreak, beginning in the late 1970s, was unusually severe. These results, and contrasting infestation patterns in mountain ranges with different land use histories, generally support a hypothesis that human-induced changes in Southwestern forests have led to more widespread and intense budworm outbreaks in the late 20th century.

Despite human-induced changes in the 20th century, climate variation also appears to have been important to budworm regimes in this century as well as in earlier times. Regional outbreaks in the 20th century tended to occur during years of increased spring precipitation, and decreased budworm activity coincided with decreased spring precipitation. No clear association with temperature was identified. Comparisons of regional outbreak history since AD 1600 with a reconstruction of spring precipitation from limber pine (*Pinus flexilis*) ring width chronologies also shows that periods of increased and decreased budworm activity coincided with wetter and drier periods, respectively. This finding contrasts with results from shorter time-scale studies conducted in northwestern U.S. and Canada (western spruce budworm) and eastern Canada (spruce budworm C. *fumiferana*), where low precipitation and/or warmer temperatures were generally associated with outbreaks. Different patterns of budworm population response to changing moisture regimes might be due to differences in regional forest-budworm systems, or to differences in the spatial and temporal scales of observation.

We conclude that changes in forest structure in the southwestern U.S. may have shifted the spatial and temporal pattern of budworm outbreaks. The dynamic behavior and statistically significant association between multicentury, regional budworm and climate time series also suggest that complex budworm dynamics are driven by a combination of internal and external factors.

Key *words:* Abies concolor; Choristoneura occidentalis; *climate change; dendroecology; forest disturbance; forest dynamics; old growth; plant-herbivore interactions; population dynamics;* Pseudotsuga menziesii; *tree rings; western spruce budworm.*

INTRODUCTION

The western spruce budworm *(Choristoneura occidentalis* Freeman, Lepidoptera: Tortricidae) is one of the most widespread North American forest pests displaying spatial and temporal outbreak patterns (Brookes et al. 1987). Large population fluctuations and extensive impacts of this defoliator on continental forest resources have stimulated numerous population dynamics studies and large organized research efforts (e.g.,

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Morris 1963, Ludwig et al. 1978, Royama 1984, Sanders et al. 1985). In the western part of the continent Douglas-fir (*Pseudotsuga menziesii*) and true firs (*Abies* spp.) are usually the main hosts, while pines (*Pinus* spp.) are not defoliated. Budworm populations erupt episodically in many stands over large regions, defoliation continues for a few years to more than a decade, and then budworms become relatively rare in affected stands for years to decades. Unlike the eastern spruce budworm (*Choristoneura fumiferana* Clemens) in the northeastern U.S. and Canada, the western species has generally not resulted in high levels of overstory tree mortality during the historic period (≈1920 to present, Perry 1925, Johnson and Denton 1975, Lessard 1975, U.S. Department of Agriculture Forest Service records). A recent outbreak (late 1970s–1980s) in the Southern Rockies, however, resulted in massive tree mortality in large areas of the Colorado Front Ranges and in a few watersheds in northern New Mexico.

Although the recent overstory mortality may be unusual, the long-term historical impacts of western spruce budworm on forest ecosystems are profound. Forest composition and structure are significantly affected because the insect often kills numerous understory trees, growth rates and cone crops are reduced in overstory trees, and true firs are more severely damaged than other species (Brookes et al. 1987). Over the long term, in the presettlement era these impacts may have led to spatially heterogeneous forest stands with mixtures of host and nonhost trees, and perhaps lower overall forest densities. Infestations also have cascading effects across trophic levels because budworm populations interact directly with predator populations such as birds and ants (Torgerson 1985). Furthermore, nutrient cycling is increased in infested stands by the rain of insect bodies and frass onto the soil surface, and the changing nutrient and light conditions benefit understory plants and surviving trees (Mattson and Addy 1975, Schowalter 1981). Thus, as an episodic disturbance in mixed-conifer forests, western spruce budworm infestations may be of equal or greater ecological importance than fires. Little is known, however, about the long-term dynamics of the forest–budworm system, especially with regard to possible influence of climate variations or human activities such as fire suppression and timber harvesting.

We used centuries-long tree ring records in defoliated trees to reconstruct the history of western spruce budworm outbreaks in northern New Mexico. This history provided an opportunity to examine current theories of plant–herbivore interactions and insect outbreak dynamics with a multicentury and regional perspective. Of special interest were historical factors affecting the forest–budworm system, particularly the influence of seasonal to decadal-scale climate fluctuations, and human-caused changes in forest community structure. We show that a regional network of tree ring reconstructions from many stands was useful for distinguishing local and regional-scale patterns and their association with environmental changes. (We use the term "infestation" for defoliation events within specific stands, and "outbreak" for more-or-less synchronous infestations in multiple stands.)

Tree ring perspectives of the forest–budworm system

Retrospective studies using tree rings as indicators of past infestations identified possible 20th-century changes in western spruce budworm regimes in the Northern Rockies (McCune 1983, Anderson et al. 1987). Blais' tree ring studies (1962, 1965, 1983, 1985) also documented temporal changes in spruce budworm (*C. fumiferana*) outbreaks in eastern Canada. Increased frequency, duration, or intensity of outbreaks were attributed to human-caused changes in forest stand structure and composition. These authors proposed that a combination of fire suppression, logging practices, and insecticide spraying led to budworm susceptible and vulnerable stands by enhancing forest conditions favorable to budworm. For example, multilevel forest canopies dominated by host trees may have resulted from past management practices, and are generally thought to favor the western spruce budworm (Carlson et al. 1983, Fellin et al. 1983, Anderson et al. 1987, Schmidt 1987, Mutch et al. 1992, Wickman 1992).

In a tree ring study of 10 mixed-conifer stands in Colorado and New Mexico we reported that budworm outbreaks were not measurably more frequent in the 20th century relative to the 19th and 18th centuries (Swetnam and Lynch 1989). However, temporal patterns showed increased synchrony of infestations in widely dispersed forests of the Southern Rockies. The intensity of the most recent outbreak (1970s and 1980s) was also greater than previous outbreaks. We hypothesized that the greater extent and intensity of budworm outbreaks in this century were related to human-caused forest changes. In particular, selective harvesting of ponderosa pine during the Anglo-American settlement era (≈1850–1910), large fires in the late 1800s, and fire suppression after 1900 led to 20th-century forests with higher proportions and densities of budworm host trees than existed in presettlement forests. Modern forests provide a spatially continuous and suitable food base for the budworm, which promotes extensive and severe outbreaks.

A competing hypothesis is that budworm populations were directly or indirectly regulated by weather and, therefore, observed temporal changes in this century might be largely explained by climatic fluctuations. Previous studies of weather and climate effects on eastern spruce budworm in eastern Canada (e.g., Wellington et al. 1950, Greenbank 1956, 1957) and on the western spruce budworm in northwestern U.S. and Canada (e.g., Thomson et al. 1984, Kemp et al. 1985) reported that drier and warmer conditions generally favored budworm populations. These observations

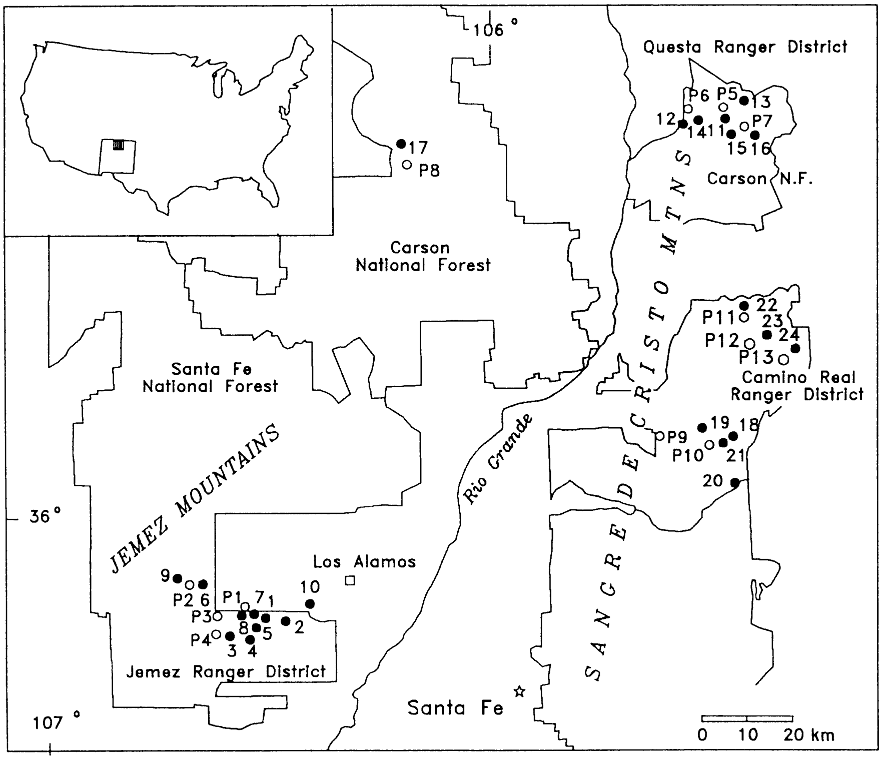

FIG. 1. Stands sampled in the Jemez and Sangre de Cristo Mountains in the north–central region of New Mexico. ●, mixed-conifer stands; ○, pine sites. The stand numbers refer to descriptions in Table 1.

seem to support the plant stress hypothesis, which states that stressed plants have a higher food quality for insects than nonstressed plants, probably because of greater amounts of soluble nitrogen and carbohydrates or reduced amounts of defensive secondary compounds in plant tissues (White 1976, Rhoades 1979). Hence, drought-stressed trees may trigger the "release" of insect populations (Mattson and Haack 1987*a, b*).

Contradictory results of experimental studies on stressed plants, however, have also led to a broad recognition of the importance of insect feeding and reproductive ecology, and the heterogeneity of environments in plant–herbivore interactions (Mattson and Haack 1987*b*, Meyers 1988, Larsson 1989, Price 1990, 1991, Wagner 1990, 1991, Mattson et al. 1991, Hunter and Price 1992, Mopper and Whitham 1992). For instance, it is apparent that different insect feeding guilds may respond very differently to stressed trees, with cambium feeders (e.g., bark beetles) having the most consistent positive response to drought and leaf feeders having a weaker or even negative response (Mattson and Haack 1987*b*, Larsson 1989). Furthermore, there appears to be a continuum of types of herbivores that most commonly attack stressed plants to herbivores that most frequently attack vigorous plants (Price 1991).

Spatial diversity and temporal variability of host plant environments also play an important role in plant–herbivore interactions. The response of insects to short-term climatic fluctuations (e.g., droughts or wet periods) may depend upon the long-term average conditions of the host plant environment (e.g., xeric or mesic sites) (Mopper and Whitham 1992). Such temporal variability could alter relative stress levels and productivity in different sites, and hence the amounts and allocations of plant defenses and biomass within different plant modules (Price 1991, Wagner 1991).

The search for long- or short-term climate–insect outbreak associations has been impeded by lack of adequate data and methodological problems (Martinat 1987). In particular, relevant weather data for affected forest stands were usually unavailable, spatial patterns were hard to interpret, time series and statistical treatment of data were inappropriate, and insect population records were too short or imprecise (Martinat 1987). Long-term reconstructions from tree rings have been the main source of century-length outbreak histories, but they are noisy proxies of budworm population fluctuations because they can only reflect the effects of defoliation filtered through the complicated growth physiology of trees (Swetnam et al. 1985).

Although tree ring reconstructions are an indirect and inferred estimate of past budworm population changes, they currently provide the longest record of the forest–budworm system. Tree rings in nonhost species growing in carefully selected sites can also provide an independent record of past climate variations (Fritts

TABLE 1. Stand descriptions. Stand numbers correspond to locations shown in Fig. 1.

Stand no. and name		Aspect (degrees)	Slope (%)	Elev. (m)	Habitat type*	Stocking† (m²/ha)	Density (stems/ha)
Jemez River watershed							
1	Peralta West	325–030	20–50	2720	ABCO/ACGL	65	629
2	Peralta High	10	30–60	2790	ABCO/VAMY	55.5	649
3	West Vallecitos	30	40–60	2510	ABCO/QUGA	26.5	612
4	Los Griegos High	345	50–60	2930	ABCO/ACGL	44.8	783
5	Los Griegos Low	345	10–50	2870	ABCO/ACGL	43.4	597
6	Fenton Lake	340–360	40–50	2500	ABCO/ACGL	41.1	834
7	East Fork	340–360	40–50	2580	PIPU/LIBO	50.3	765
8	Lower East Fork	350–010	45–50	2410	PIPU/EREX	51.7	715
9	Barley Ridge	flat	flat	2610	ABCO/QUGA	15.5	216
P1	Baca	150–180	50–60	2450	ND	...	...
P2	Fenton Lake	140–160	20–50	2750	ND	...	...
P3	Abouselman Sprin	180	60–80	2600	ND	...	...
P4	Cat Mesa	130	5–50	2530	ND	...	...
Rio Grande watershed							
10	Frijoles Canyon	230	10–20	2730	ABCO/QUGA	73.3	1052
Cabresto Creek watershed							
11	Bonita Canyon	300–360	10–43	2780	ABLA/VAMY	29.6	685
12	Singing River	300–040	50–70	2710	ABCO/SYOR	35.8	947
13	Rito Claro	110–190	10–30	2870	ABCO/ARUV	44.3	1074
14	Cabresto Canyon	360	20	2500	ND	17.6	379
P5	Italian Canyon	180–220	50–80	2870	ND	...	...
P6	Cabresto pinyon	200–220	40–70	2550	ND	...	...
Red River watershed							
15	Fawn Lakes	010–020	20–80	2850	ABCO/ARUV	22.5	449
16	Red River	350–050	40–65	2770	ABCO/ARUV	34.4	932
P7	Elephant Rock	180–200	10–50	2600	ND	...	...
Rio Vallecitos watershed							
17	Burned Mountain	270	10	2710	ND	24.1	501
P8	Burned Mountain	30	flat	2710	ND	...	...
18	Policarpio Canyon	140–190	50–85	2760	PIPU/EREX	36.9	396
19	Flechado Canyon	100–150	10–30	2740	ABCO/VAMY	34.8	665
20	Alamitos	320–040	1–15	3050	ABCO/VAMY	60.5	467
21	La Junta	120–190	30–60	2730	ABCO/QUGA	22.2	143
P9	Rio Pueblo	220–280	30–80	2480	ND	...	...
P10	Boca de la Junta	160–190	50–70	2700	ND	...	...
Rio de Taos watershed							
22	Capulin Canyon	90	5	2900	ND	15.7	176
23	Garcia Park	225	20	2880	ND	28.6	599
P11	Capulin Canyon	...	...	...	...	...	...
P12	Gracia Park Pine	225	20	2880	ND	...	...
Coyote Creek watershed							
24	Osha Mountain	90	5	3050	ND	21.2	538
P13	Osha Mtn. Pine	90	5	3050	ND	...	...

* Habitat types are described by Moir and Ludwig (1979) and Develice et al. (1986). "ND" indicates that habitat type was not determined. Species abbreviations are: PSME = *Pseudotsuga menziesii,* ABCO = *Abies concolor,* ABLA = *Abies lasiocarpa,* PIEN = *Picea engelmannii,* PIPU = *Picea pungens,* PIPO = *Pinus ponderosa,* PIFL = *Pinus flexilis,* POTR = *Populus tremuloides,* PIAR = *Pinus aristada,* ACGL = *Acer glabrum,* LIBO = *Linnaea borealis,* VAMY = *Vaccinium myrtillus,* QUGA = *Quercus gambelii,* EREX = *Erigeron eximius,* SYOR = *Symphoricarpos oreophilus,* ARUV = *Arctostaphylos uva-ursi.*

† Stocking is total basal area of tree stems in the stand.

1976, 1991). These multicentury records are especially useful for studying long-term climate–budworm patterns because they provide replicated observations of many past outbreaks and climatic fluctuations. A limitation of our earlier tree ring study was that relatively few stands were sampled in a very large region. Here we describe a larger data set concentrated in the mountains of northern New Mexico.

STUDY AREAS

Study sites are clustered in three areas in northern New Mexico, USA (Fig. 1 and Table 1) within the boundaries of the Carson and Santa Fe National Forests. The three areas correspond to ranger district names. *Jemez:* These stands are in the Jemez Mountains and are located along the upper Jemez River, Rio Vallecitos, and Rito de los Frijoles watersheds. Stand 17 is

TABLE 1. Continued.

Relative importance (% of total stand basal area)							
PSME	ABCO	ABLA	PIEN	PIPO	PIFL	POTR	<1%
41	24	1	10	1	4	19	ACGL
23	18	38	4	<1	2	14	ACGL
30	20	...	...	49	...	...	...
82	1	...	1	...	...	15	...
78	6	...	...	...	...	16	...
86	4	...	...	6	1	1	...
67	6	1	16	3	1	7	...
42	38	...	8	12	...	...	QUGA
25	50	...	...	17	6	3	...
...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...
46	28	...	...	19	6	1	...
62	1	7	20	4	...	6	...
16	71	...	...	4	8	...	...
82	9	...	3	...	4	3	...
75	7	1	...	16	1	...	...
...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...
65	13	...	...	2	16	3	...
45	46	...	1	1	1	5	...
...	...	...	...	...	...	...	...
85	8	...	7	...	...	...	...
...	...	...	...	...	...	...	...
73	10	11	1	5	...	...	PIAR
59	26	...	...	2	...	12	...
86	6	2	...	...	1	6	...
35	8	...	1	49	6	...	PIAR
...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...
29	12	...	...	59	1	...	...
73	3	...	...	24	...	...	...
...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...
56	11	4	23	6	...	...	...
...	...	...	...	...	...	...	...

on the Tres Ritos ranger district to the north of the Jemez Mountains. We grouped this stand with the Jemez data because of similarities in infestation history. *Questa:* These stands are in the Sangre de Cristo Mountains north of Taos and are located along the west-flowing Cabresto Creek and Red River watersheds. *Camino Real:* These stands are in the Sangre de Cristo Mountains south and east of Taos and are located along the west-flowing Rio Pueblo and Rio de Taos watersheds.

Elevations of sampled stands are between 2410 and 3050 m (Table 1). The seasonal distribution of precipitation in the region is distinctly unimodal, with a dominant rainfall period in July and August, when at least 30% of the rainfall is usually received via convective thunderstorms. Los Alamos, New Mexico (2210 m elevation) is located in a forest area just below the typical elevation of our stands, but its climate regime is generally representative. The average annual precipitation at Los Alamos for the period 1911–1988 was 43 cm, of which 18 cm (40%) fell during 3–6 wk periods in July and August. The remaining precipitation was more-or-less evenly distributed throughout the year (Bowen 1989). The coldest months, December, January, and February, were also the driest. Winters were temperate, with mean January temperatures of −1.7°C. Summers were generally arid and hot until late July when afternoon thundershowers were typical.

Topographic position of sampled stands varied from steep slopes to flat ridge tops. Aspects in most stands were generally north and northeast, but were south for stands 13, 18, 21, and 23 (Table 1). Stand 19 had an east aspect. Parent material was volcanic (rhyolite, tuff, pumice) in the Jemez mountains, and primarily sandstones, shales, and limestones in the Questa and Camino Real districts.

Sampled stands were mixed-conifer composed of varying proportions of budworm host species (see Table 1) Douglas-fir (*Pseudotsuga menziesii* var. glauca [Mirb.] Franco.), white fir (*Abies concolor* [Gord. and Glend.] Lindl.), subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), and Engelmann spruce (*Picea engelmannii* Parry). Nonhost species in the sampled stands were ponderosa pine (*Pinus ponderosa* Laws.), and trembling aspen (*Populus tremuloides* Michx.). Less frequent species were limber pine (*P. flexilis* James), bristlecone pine (*P. aristata* Engelm.), Colorado blue spruce (*Picea pungens* Engelm.), Rocky Mountain maple (*Acer glabrum* Torr.), and Gambel oak (*Quercus gambelii* Nutt.).

METHODS

Field methods

Old-growth stands were selected with both Douglas-fir and white fir present and with little or no evidence of past logging (i.e., most stands contained few or no stumps or old logging roads). This enabled us to compare the response of the two main host species and also to maximize the length of reconstructed budworm history. In stand 13 (Rito Claro) too few white fir were present to develop a tree ring chronology for that species (minimum of ≈10 trees), but this stand contained the oldest sampled Douglas-fir trees. In most watersheds it was difficult to find old-growth stands that had not been partially cut, and even the virgin stands we sampled were usually surrounded by forest lands with a long history of logging. Four stands (17, 22, 23, and 24) were sampled in 1985 for an earlier study (Swetnam and Lynch 1989). A variety of mixed-conifer habitat types (sensu Moir and Ludwig 1979, DeVelice et al. 1986) were sampled (Table 1).

Approximately 5 ha were sampled within each stand in 1987 and 1988 (except the four stands mentioned above). Three evenly spaced transects were located parallel to the topographic contour. Three to five evenly spaced sample points were located on each transect, for a total of 9–15 points per stand. Stocking (basal area, in square metres per hectare) and density (stems per hectare) were estimated by species and diameter class at each point with a prism or relascope and variable plot techniques (Husch et al. 1982). Spiked (dead) and crooked tops were noted when present, as they can indicate past insect damage (Ferrell and Scharpf 1982).

Increment cores were taken at each sample point from the nearest Douglas-fir and white fir >20.3 cm in diameter at breast height (dbh, measured at 1.3 m above the ground surface). Cores were taken from at least two radii per tree and parallel with the contour of the slope. An additional 10 or more of the oldest appearing host trees within the stand were cored to obtain the longest record possible. A total of 692 Douglas-fir trees and 336 white fir trees from 24 mixed-conifer stands were used in the analysis (Table 2).

Increment cores were also taken from 215 nonhost trees (ponderosa pine, limber pine, or piñon [*Pinus edulis* Engelm.]) in 13 nearby stands (Table 2, Fig. 1). These stands were located at similar or slightly lower elevations (2450–2750 m) than the host stands, and were selected because they were monospecific, or nearly so, and therefore could not have been affected by defoliation of competing host trees.

Tree ring analyses

Dendroecology procedures and techniques for analyzing radial growth in budworm-defoliated trees were described and illustrated by Swetnam et al. (1985) and Swetnam and Lynch (1989), and are summarized here. Host and nonhost increment core samples were cross-dated, ring widths were measured on a sliding-stage micrometer, and then transformed to growth indices by fitting curves to the ring width series and dividing the ring widths by the values of the fitted curves (Fritts 1976). This "standardization" procedure was followed to remove age-related growth trends in the raw tree ring width series. Depending on the shape of the age-related growth trend, a negative exponential curve, a straight line of negative slope, or a cubic spline was fit to each core series (Graybill 1979, Cook and Peters 1981, Cook and Holmes 1986, Cook and Kairiukstis 1990). Only relatively "stiff" cubic splines were used (50% frequency response, with minimum 100-yr lengths [see Cook and Peters 1981]). Thus, virtually all variations on annual to decadal scales, and most low frequency trends of less than century length, were preserved in the index series. Tree and stand chronologies were derived by simple averages of the core indices. A total of 45 host (24 Douglas-fir, 21 white fir) and 13 nonhost tree ring index chronologies were developed.

Host and nonhost 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. The statistical comparisons consisted of correlation analysis of host and nonhost chronologies for entire common periods and for shorter "moving" periods (Swetnam 1987*a*). In earlier work a dendroclimatic response function analyses demonstrated that host and nonhost tree ring width chronologies from this region contained similar climatic response (Swetnam 1987*b*).

Graphical comparisons included overlay plotting of host and nonhost tree ring series. Pronounced and persistent differences between host and nonhost chronologies were taken as preliminary evidence of past infestations. Procedures originally developed by Nash et al. (1975) were used to "correct" the host tree ring series for climatic and other nonbudworm environmental signals. Nonhost series were rescaled to approximately the same variance of the host series by taking the product of each yearly nonhost index value and a ratio of standard deviations (standard deviation of nonhost series divided by standard deviation of host series). The rescaled nonhost indices were then subtracted from the host indices (see Swetnam et al. [1985] for equations). If host and nonhost trees were responding similarly to climate, then the differences between the two chronologies (called "corrected indices") preserve the variation due primarily to the effects of budworm defoliation or other nonclimatic environmental variations. Mean ring width index chronologies for individual trees (two cores per tree) and mean chronologies for all trees within sites were corrected and plotted together on the same graph.

Comparison of the corrected series from the 1920s to present with independent records of budworm infestations was an important aspect of the analysis. This comparison provided a test of the assumption that the corrected series contained mainly a budworm infestation signal. We compared the corrected index series with 20th century records in forest entomology and aerial survey reports (on file at U.S. Department of Agriculture Forest Service Southwestern Region Office, Albuquerque, New Mexico). Low growth periods in the corrected series corresponding to recent infestations were the basis for criteria used to identify infestations in the period preceding forestry records. These criteria were: periods in the corrected series during which the indices were less than expected growth (1.0) for three or more consecutive years, and the lowest growth value during this period was more than 1.28 standard deviations below the mean of the series (approximately the 10th percentile of smallest ring index values). These criteria emphasized persistent and high magnitude growth reduction in corrected host indices.

TABLE 2. Numbers of trees sampled in each site. Two cores were taken from each tree.

Watershed name Stand no. and name	Number of trees sampled		
	Douglas-fir	White fir	*Pinus*
Jemez River watershed			
1 Peralta West	17	11	...
2 Peralta High	15	16	...
3 West Vallecitos	18	18	...
4 Los Griegos High	16	8	...
5 Los Griegos Low	15	12	...
6 Fenton Lake	17	12	...
7 East Fork	15	19	...
8 Lower East Fork	15	13	...
9 Barley Ridge	15	14	...
P1 Baca	...	...	19
P2 Fenton Lake	...	...	12
P3 Abouselman Spring	...	...	17
P4 Cat Mesa	...	...	13
Rio Grande watershed			
10 Frijoles Canyon	14	19	...
Cabresto Creek watershed			
11 Bonita Canyon	19	15	...
12 Singing River	16	17	...
13 Rito Claro	47	...	...
14 Cabresto Canyon	90	...	...
P5 Italian Canyon	...	...	38
P6 Cabresto pinyon	...	...	20
Red River watershed			
15 Fawn Lakes	17	18	...
16 Red River	19	17	...
P7 Elephant Rock	...	...	16
Rio Vallecitos watershed			
17 Burned Mountain	45	22	...
P8 Burned Mountain Pine	...	...	14
Rio Pueblo watershed			
18 Policarpio Canyon	17	15	...
19 Flechado Canyon	16	13	...
20 Alamitos	20	15	...
21 La Junta	15	12	...
P9 Rio Pueblo	...	...	15
P10 Boca de la Junta	...	...	10
Rio de Taos watershed			
22 Capulin Canyon	60	25	...
23 Garcia Park	48	25	...
P11 Capulin Canyon Pine	...	...	13
P12 Garcia Park Pine	...	...	12
Coyote Creek watershed			
24 Osha Mountain	106	...	...
P13 Osha Mtn. Pine	...	...	16
Totals	692	336	215

Budworm defoliation effects on radial growth generally differ from effects due to other environmental disturbances in the tree-to-tree synchrony, duration, and intensity of the response. The initial and terminal growth reduction years caused by defoliation often differ by one to a few years among trees in a stand. Growth responses due to drought tend to be synchronized between trees within and among stands, with some effect evident in all species (Fritts 1976). Budworm infestations usually last 5–20 yr (Perry 1925, Lessard 1975, U.S. Department of Agriculture Forest Service records), but infestations of other defoliators in northern New Mexico are typically shorter. For example, *Orgyia pseudotsugata* McDonnough and *Epinotia meritana* Heinrich in northern New Mexico have been limited to short-term (<5 yr), small infestations (<400 ha) (e.g., see Shepherd et al. 1988) with white fir as the principal host (Wickman et al. 1971, Furniss and Carolin 1977, Wickman 1980).

Estimates of duration and intensity of infestations were compiled for all stands for different time periods. Duration was the period when growth was below the mean value of the corrected index series (≈1.0), and intensity was measured as the maximum single-year growth reduction during an infestation. The corrected growth index value minus the chronology mean and multiplied by 100 provided an estimate of percentage growth reduction relative to expected growth.

Differences in means of duration or intensity between different time periods, pooled across all stands, were tested with a one-way analysis of variance (ANOVA). All comparative groups, for these tests and those described below in the climate analyses, were first tested for normality (Kolmogorov–Smirnov tests) and homogeneity of variance (Bartlett tests). Transformations (logarithmic, square root, etc.) of some groups was attempted to more closely approximate normal distributions. Some combinations met the assumptions of normality and homogeneous variance, but others did not (with or without transformations). Therefore, we used the nonparametric Kruskal–Wallis one-way ANOVA (Wilkinson 1990).

A regional outbreak chronology was computed by summing the number of chronologies recording an infestation each year among all corrected host tree ring chronologies. This series has an increasing trend from earlier to later periods because the number of chronologies included in the series increases with time (i.e., fewer chronologies extend back to earlier times). Thus, to produce a time series with long-term stationary mean and variance the regional series was detrended by fitting a 100-yr, 50% frequency response cubic spline (Cook and Peters 1981) to it and then dividing by the fitted curve. The detrended series was then standardized by subtracting the mean and dividing by the standard deviation. This standardized regional outbreak chronology (standard normal variates) was used to classify the years as "release," "outbreak," and "endemic." These three groups of years may correspond to the "classic" phases of insect outbreak (Martinat 1987). A fourth phase, termed "collapse," is included in our grouping of "outbreak" years. We decided not to classify these years (i.e., declining values following the maximum values) separately because it is likely that the negative effects of defoliation introduced some lag in the recovery of trees following outbreak collapse, and so this would be the least precisely identifiable set of years. Values greater than zero (the mean of the series) persisting >5 yr were classified as "outbreak." Three to six years of values prior to each outbreak were classified as "release." If consistently ascending values (less negative) were observed prior to the outbreak, these years plus three previous years were classified as "release" years. If no consistently ascending (less negative) values were observed prior to the outbreak, the 3 yr preceding the 1st yr (first positive value) of an outbreak were classified as the "release" years. Other negative value years were classified as "endemic" years.

Experiments on detrending the original summed regional outbreak series by dividing the values by other stiff cubic spline fits, moving averages, or with the sample depth (total number of chronologies in the data set each year) had relatively small effects on the classification of release, outbreak, and endemic years. Usually only 1 or 2 yr at the beginning or end of some outbreaks were affected by the different standardizing approaches.

Climatic analyses

Monthly total precipitation and monthly mean temperature data from New Mexico Division 2 (National Climate Data Center, Karl et al. 1983) from 1895 to 1990 were used to assess weather patterns during and between outbreaks. This division encompasses most of north central New Mexico and all of our study area. The precipitation and temperature data were seasonalized into winter (November through February), spring (March through June), and summer–fall (July through October). The spring season encompasses the entire normal period of emergence and feeding by the larvae. The summer–fall season encompasses the normal period of pupation, adult emergence, egg laying, emergence of instar I larvae, and beginning of hibernation as instar II larvae in overwintering hibernacula. Generally, no defoliation takes place during this period. The winter season encompasses the remainder of the hibernation period.

Scatter plots of precipitation vs. temperature, sorted by release, outbreak, or endemic years were first used to identify visual patterns. The one-way ANOVA (Kruskal–Wallis) was used to test differences in mean precipitation or temperature between the groups of years. The null hypotheses stated that differences in any of the possible comparisons between groups of years in mean precipitation or temperature (i.e., outbreak years vs. endemic years, outbreak years vs. release years, and release years vs. endemic years), did not occur. We rejected the null hypothesis for all tests at the $P < .05$ level.

A long-term reconstruction of spring precipitation was developed from the mean tree ring series from two limber pine sites (Elephant Rock, stand P7, and Italian Canyon, stand P5, Fig. 1) (H. D. Grissino-Mayer et al., *unpublished manuscript*). To the best of our knowledge, limber pine has no major insect pest problems in this region. Standard dendroclimatic procedures were used in the reconstruction, including model calibration (linear regression) with a meteorological data set, and verification of the selected climate–tree growth model with a reserved portion of the meteorological data set (Fritts 1976, Fritts 1991). The meteorological data were from Red River, New Mexico (1906–1990), which is located ≈5 km from the Elephant Rock site and 8 km from the Italian Canyon site. Red River is also near the same elevation (2650 m) as the limber pine sites.

Fortuitously, the best seasonal climate reconstruction obtained with these data was for total March through June precipitation. The climate tree growth model was a simple linear regression with ring width indices and March through June precipitation (1906–1989). The transfer function producing reconstructed precipitation series as a function of tree ring indices explained 68% of the variance in the modern meteorological data set (calibration period: 1948–1989, three outlier years removed, R^2 adjusted = 0.68, $F = 78.6$, $P = .0001$; verification period: 1906–1947, $r = 0.59$, reduction of error = 0.30, product means test t value = 2.78, see Fritts [1976, 1991] for descriptions of these methods and statistics). This reconstruction was used to test for possible association between the long-term regional outbreak record and spring precipitation. This was accomplished by graphically comparing the two time series, by computing correlation coefficients, and by testing for differences in mean reconstructed precipitation during release, outbreak, and endemic years.

Standard normal variates of both the detrended regional outbreak chronology and the reconstructed precipitation time series were computed and plotted together. The reconstructed precipitation series was smoothed with a symmetrical 13-weight low pass filter (Fritts 1976) to emphasize long-term variations ($> \approx 10$ yr) in the series. Pearson correlation coefficients were computed for the smoothed and unsmoothed time series. The one-way ANOVA test (Kruskal–Wallis) was used to test for differences in means of reconstructed precipitation during release, outbreak, and endemic years identified in the regional outbreak series back to AD 1700. This test was applied to the unsmoothed precipitation series only.

Two of the longest host tree chronologies (stands 11 and 13) were initially corrected with the limber pine chronologies used to reconstruct the March through June precipitation series. To preserve independence these sites were not included in the regional series used in the statistical analyses described above. Total sample sizes were too low before 1700 (especially after removing stands 11 and 13) to place much confidence in the comparisons of earlier periods, so the statistical tests were applied only to the data after 1700.

Spectral analysis

We analyzed the periodic behavior of the detrended regional outbreak series and the reconstructed precipitation series by applying univariate and bivariate spectral analysis techniques (Jenkins and Watts 1968, Sowell and Lough 1984). This analysis provided a more in-depth assessment of the time series properties of the data, including measurements of cyclicity, and correlation between the budworm and precipitation time series. The analysis used the lag–covariance method, Fourier transform, and Hamming spectral window. Univariate power spectra for each series were computed from the Fourier transform of the autocovariance functions computed with different lags (30, 50, and 100 yr). The longer lag functions provide greater resolution of spectral variations, but lower statistical confidence than shorter lag functions. A population spectrum (or null continuum) was estimated as a first-order autoregressive red noise stochastic process, and 95% confidence intervals around the spectra were estimated using the chi-square distribution (Jenkins and Watts 1968, Sowell and Lough 1984).

A bivariate, or "cross-spectral" analysis, was also conducted. This procedure examines the strength of the association, and any phase-lagged relationships, between two time series across all frequencies. The cross spectrum of the two series was computed from the Fourier transform of the cross-covariance function of the two time series. The coherency-squared spectrum provides an estimate of the proportion of variance in common between two time series across all frequency bands.

RESULTS

Evidence of multiple infestations

Host trees in the stands often displayed evidence of past budworm infestations by the presence of spike (dead) tops. Topkilling is a well-known effect of budworm defoliation (Ferrell and Scharpf 1982). Some older trees had as many as four old spike tops with crooked stems just below each weathered spike, indicating that a new terminal leader had assumed apical dominance following each infestation.

Multiple periods of obvious reduced growth were evident in many, but not all cores (Fig. 2). Identification of probable budworm-caused reduction sometimes required comparison of individual host tree chronologies (two core series averaged) (Fig. 3). The impacts of infestations were sometimes pronounced in some trees within the stand, but were not noticeable in other trees (Figs. 3 and 4).

The crossdating (synchronization) of year-to-year variations in the uncorrected data reflected primarily the influence of climate on tree growth, as evidenced by the absence of many of these high frequency patterns in the data corrected with the pine chronology (Fig. 3). The corrected tree chronologies had approximately half of the variance of the uncorrected chronologies (Fig. 3), indicating that a substantial common signal was removed. Some low frequency variations (longer term trends) common to both the Douglas-fir and pine series were also removed. For example, a period of low growth in the late 1770s and 1780s was common to both the uncorrected Douglas-fir and pine series and was generally absent from the corrected Douglas-fir set. This was probably caused by a drought episode. Independent dendroclimatic reconstructions confirm a severe drought in the 1770s to early 1780s (Rose et al. 1981,

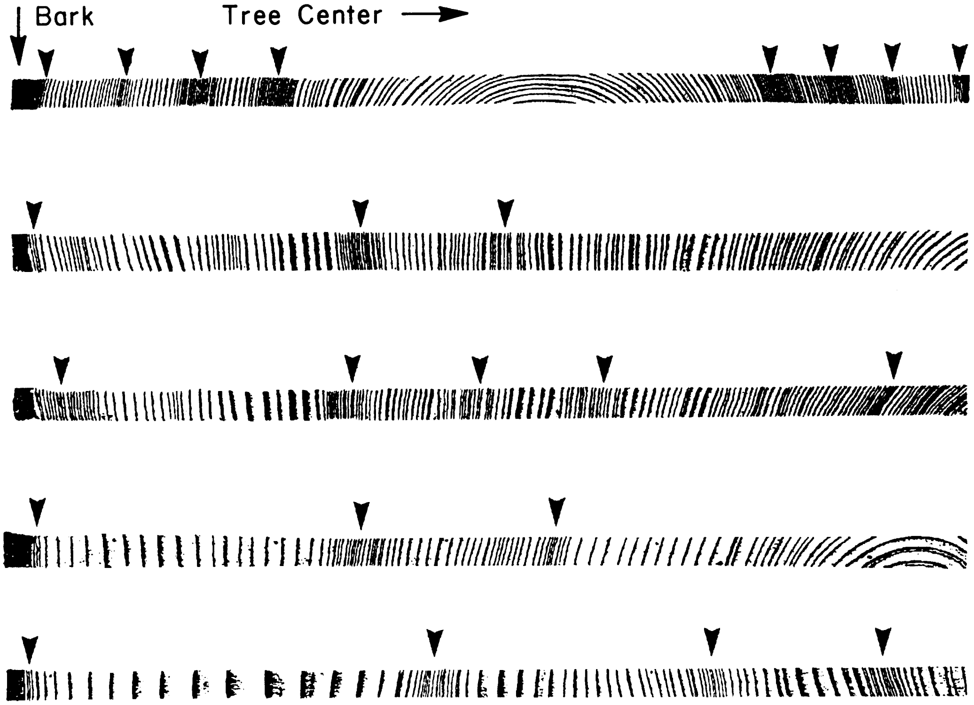

FIG. 2. Increment cores from five trees in stand numbers 2 and 20 with periods of pronounced and sustained growth reductions due to defoliation by western spruce budworms (arrows). Increased growth is also evident following many of the reduced growth periods.

Stockton et al. 1984, Fritts 1991). However, an inferred infestation with variable timing and effects among the trees appeared in the late 1760s to early 1770s and overlapped the onset of the drought.

Corrected white fir tree chronologies from stand 2 exemplified a different result of the correction procedure (Fig. 4). The uncorrected series had very little high frequency variation, and were dominated by de-

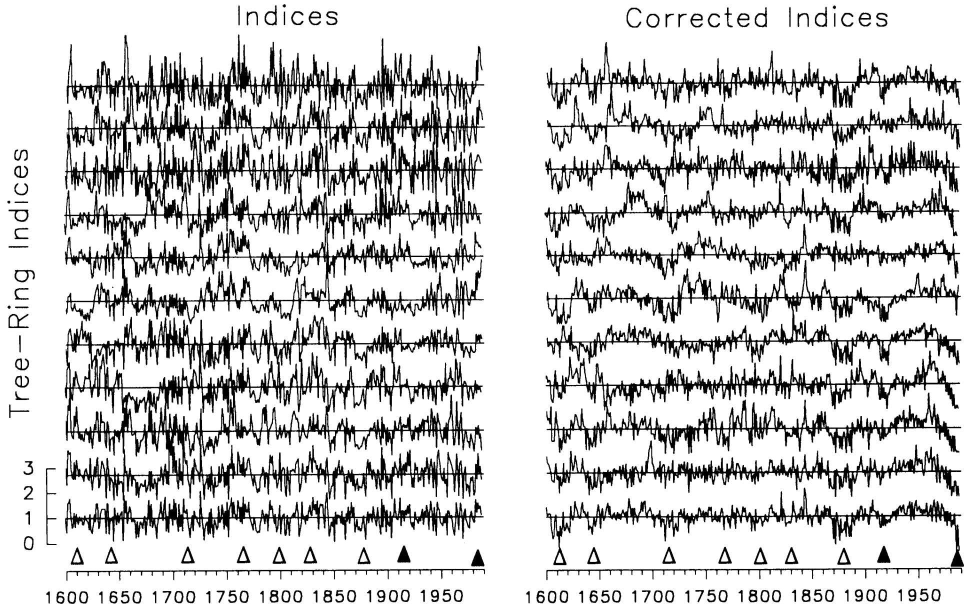

FIG. 3. Tree ring growth indices for 10 Douglas-fir trees from stand number 13 (1600–1989). The plots on the left are standardized indices (two cores averaged per tree), and the plots on the right are the same series after being "corrected" with the local pine chronology. The lowermost line plots are the mean chronologies from all trees at this site. ▲, budworm infestations confirmed by United States Forest Service records; △, inferred infestations.

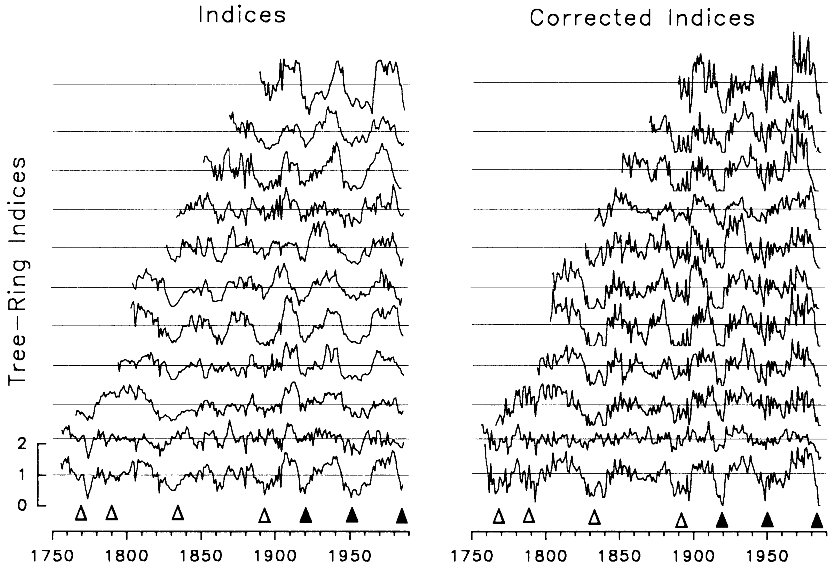

FIG. 4. Tree ring growth indices for 10 white fir trees from stand number 2. Data presentation as in Fig. 3. In this example the variance of the corrected series is increased relative to the uncorrected series, but long-term negative growth departures corresponding to budworm infestations (arrowheads) are still visible. ▲, budworm infestations confirmed by United States Forest Service records; △, inferred infestations.

cade-length periods of severe growth reduction interspersed with periods of growth recovery. Subtraction of the local pine chronology (stand P4), which contained much more high frequency variation, added variation to the corrected white fir set. Nevertheless, the corrected series still retained the decade-length growth reduction and increase periods, indicating that these patterns were not a common signal (e.g., climate) between the white fir and pine series. The correction procedure usually reduced the variation in the host series, and the exceptions tended to be old white fir with low year-to-year ring width variation and a pronounced pattern of repeated and severe budworm infestations.

This difference in results of the correction procedure was the primary reason we decided to develop the regional budworm infestation chronology as a simple sum of the number of corrected chronologies recording an infestation in each year (rather than the average corrected ring width indices for all chronologies). We have greatest confidence in our ability to determine whether or not an infestation occurred within a stand in a given year, but less confidence in the corrected tree ring indices as a measure of the intensity of past infestations. Thus, the regional chronology is primarily a measure of the spatial extensiveness of budworm activity through time.

Comparison of U.S. Forest Service and tree ring records

Comparison of infestation timing as recorded in the U.S. Forest Service documents and in the tree ring series confirmed that the tree ring series were good indicators of past infestations. The forestry records extended back to 1924 and for the early period (1924–1960) consisted primarily of annual forest pest and disease condition reports. These documents verbally summarized annual observations of insect activity on each national forest, with occasional references to specific ranger districts and watersheds. Continuous and reliable quantitative records of estimated defoliated areas were only available for some areas after ≈1960.

The early 1920s reports described severe defoliation in large areas of the Carson and Santa Fe National Forests. Comments in the 1924 Annual Insect Condition Report (Southwest Regional Office document sent to the Washington, D.C. office) included: ". . . budworm is in its third year of heavy infestation, with the heaviest this year . . . prevalent around the Halleck and Howard Sale [El Rito ranger district, west division of Carson National Forest]," ". . . budworm on Santa Fe . . . especially on Cuba district [Jemez Mountains] . . . a good deal of it." The Jemez chronologies indicate this infestation began in the late 1910s and persisted into the early 1920s (Figs. 4 and 5). This infestation also occurred on the Questa district, with variable timing in these stands between 1910 and 1930 (Fig. 6). Apparently, a small infestation of short duration occurred somewhat earlier (1900s) in the Rio Pueblo Watershed of the Camino Real district (Figs. 1 and 6, stands 18, 19, and 21) and was less widespread. Neither this short event, nor the longer lasting 1910s to 1920s outbreak, was recorded by the trees in other watersheds sampled on the Camino Real district in our earlier study (Fig. 1, stands 22, 23, and 24) (Swetnam and Lynch 1989).

An extensive outbreak in the mid-1940s to early or mid-1950s was also noted in the forestry documents

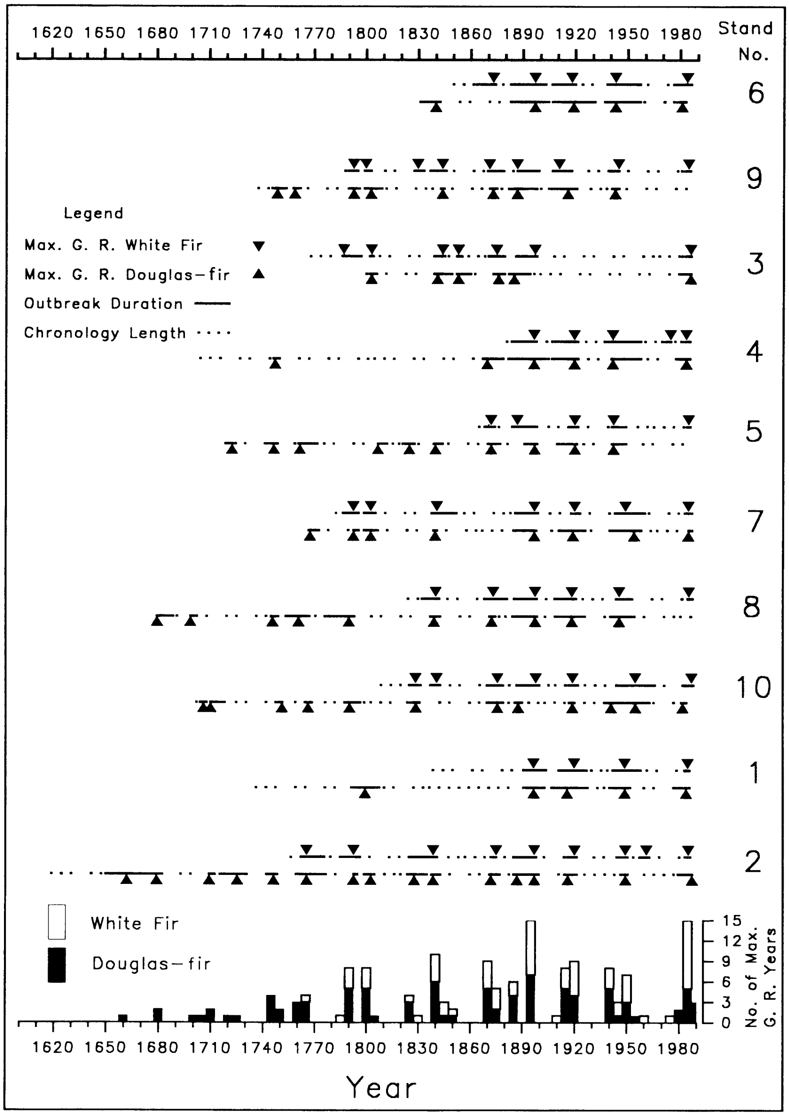

FIG. 5. Spruce budworm outbreak timing and duration in mixed-conifer stands from the Jemez Mountains, New Mexico from 1600 to 1989. Maximum growth reduction years (Max. G. R., arrowheads) and duration of infestations (—) inferred from Douglas-fir and white fir trees are plotted separately for each stand. The bar graph at the bottom is the total number of maximum growth reduction years per 5-yr interval.

in several of our sampled watersheds. For example, the Rio Pueblo watershed including the Alamitos (stand 20) and Policarpio (stand 18) areas were specifically mentioned. Stands on the Jemez district also recorded this outbreak, but stands on the Questa district did not. In many stands this outbreak appeared as two major episodes of growth reduction, the first in the mid-1940s and the second in the early-to-mid-1950s. This was consistent with the forestry documents that referred to severe defoliation in many areas of the two national forests in 1944 or 1945, some abatement of defoliation in the late 1940s, then a resurgence of defoliation from ≈1950 to 1955. A severe drought also occurred in the region during the 1950s (Bowen 1989, New Mexico Climate Division 2 data). The pine chronologies document this event as sustained low growth through the 1950s, but the defoliated host trees had sharply reduced growth beginning in the relatively wet early 1940s (Fig. 4). Many of the host trees sustained low growth through the 1940s and 1950s, and usually the low growth in the 1950s was still lower than growth of the pines.

Aerial and ground surveys of defoliation became more frequent and systematic in the 1960s and estimates of annual area defoliated in the Southwestern Region (all of Arizona and New Mexico) were available after ≈1960, although incomplete records prevented us from sorting the data by national forest. Comparison of the 1960–1989 defoliation estimates with the tree ring de-

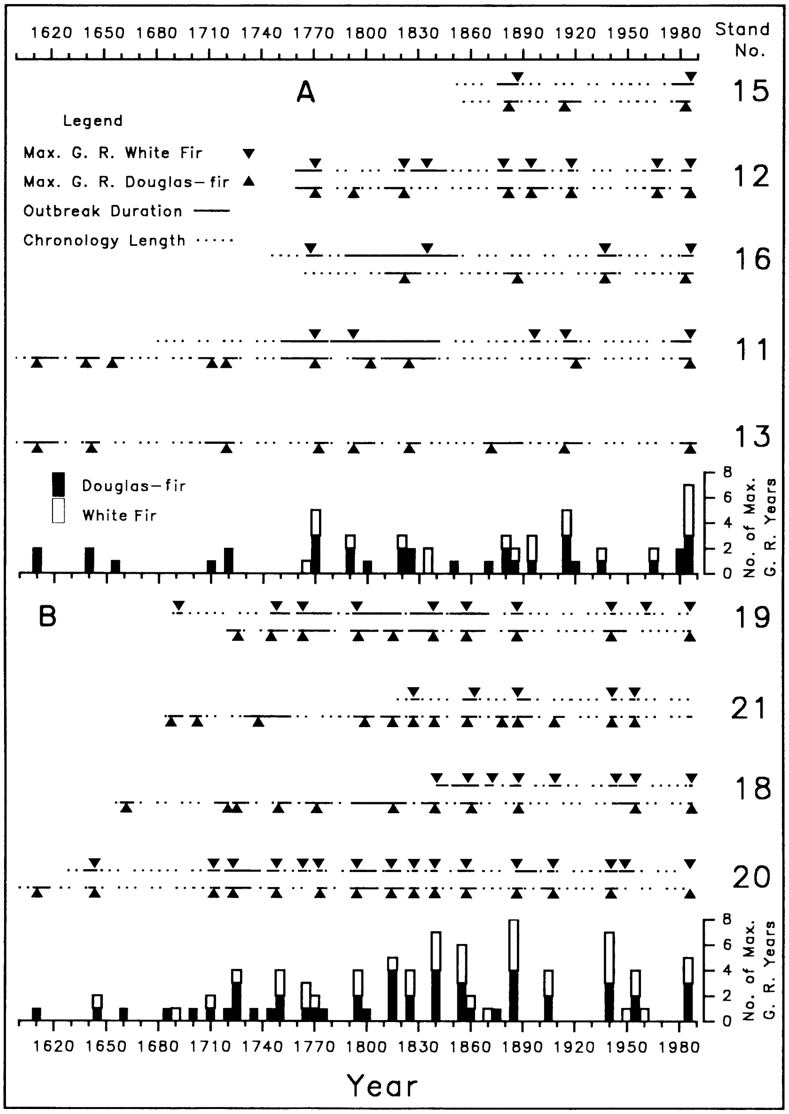

FIG. 6. Spruce budworm outbreak timing and duration in mixed-conifer stands from the Sangre de Cristo Mountains, New Mexico. (A) Stands on the Questa ranger district. (B) Stands on the Camino Real ranger district. Data presentation for each stand as in Fig. 5.

rived budworm record shows a good match for the 1970s–1980s outbreak (Fig. 7). The 1960s event was evident in the stands sampled in the Rio Fernando de Taos watershed (stands 22 and 23) and in the Osha Mountain stand (24) (Swetnam and Lynch 1989). Only a few stands on other districts had relatively minor growth reduction during this period. Large areas were also defoliated in the early 1960s on national forests to the south of our study area (Cibola and Lincoln National Forests), which might explain the difference in amplitude between the regional record and our record from the Carson and Santa Fe National Forests. It is also worth noting that at least 100 000 ha of budworm-infested area on the two national forests were aerially sprayed with DDT in each of the years 1955, 1962, and 1963 (U.S. Forest Service documents). Thus, it is possible that reduced spread or severity of infestations during this period may account for the muted response in the tree ring record. Other aerially applied insecticide treatments (carbaryl or *Bacillus thuringiensis*) were also applied to smaller areas during the late 1970s to mid-1980s (<15 000 ha were sprayed per year).

The 1970s–1980s outbreak was the best documented. Correspondence between maps of defoliation estimates from aerial and ground surveys of these infestations and the tree ring measurements was good, with ring growth (dbh) reduction beginning in the same year of first recorded defoliation, or sometimes lagging by one year. For example, growth reductions were obvious

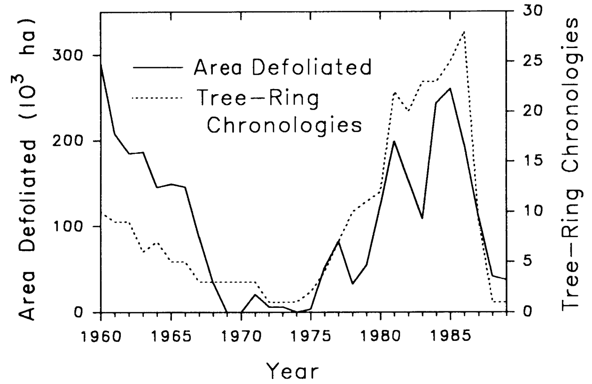

FIG. 7. Estimated annual area defoliated by western spruce budworm in Arizona and New Mexico compared with the number of Douglas-fir and white fir tree ring chronologies from northern New Mexico recording an infestation (1960–1989).

in stands from the Cabresto and Red River watersheds by 1981. Severe defoliation (estimates of >66% of needles consumed) was first recorded in this watershed in 1980. The Rio Pueblo stands did not exhibit growth reduction until 1985 or later. Annual aerial and ground survey maps from the 1980s clearly show that this infestation spread eastward up this watershed, with first detection of defoliation in the vicinity of our sampled stands in 1985.

Regional-scale outbreak patterns

At least nine regional-scale budworm outbreaks occurred during the past three centuries (Fig. 8). Roughly, these outbreaks lasted from: 1710–1735, 1745–1775, 1790–1840, 1850–1860, 1870–1880, 1885–1900, 1910–1925, 1940–1965, 1975–present. Since 1800 widespread infestations were recorded in all three districts during most major outbreaks. Exceptions were a brief outbreak in the late 1850s to early 1860s on the Jemez and Camino Real districts, an outbreak in the 1870s on the Jemez and Questa districts, and from the 1940s to 1960s when only one sampled stand on the Questa district had evidence of defoliation (Fig. 6). Forestry documents did not specifically mention budworm activity on this district during this period.

Our earlier compilation of outbreak history from both Colorado and New Mexico showed an increase in synchrony of infestations among stands during the late 20th century. This was manifest as relatively close temporal clustering of minimum growth years during outbreaks in the 1940s and 1980s as compared to earlier outbreaks. Our larger data set from New Mexico also reflects this pattern (Fig. 8), as evidenced by clustering of infestations in the 20th century, with relatively long periods of lower budworm activity between the major outbreaks. The mid-1920s to late 1930s and mid-1960s to late 1970s were years of particularly low budworm populations. The larger numbers of chronologies recording infestations during the last two outbreaks was at least partly a function of a larger number of stands in the data set in this period relative to earlier times (Fig. 8).

The number of chronologies in the sample declines steadily before the mid-1800s, so confidence in the reconstruction of regional patterns also decreases with increasing time before present. Nevertheless, clustering of infestation years back to the late 1600s (Fig. 8) provides evidence that episodic, regional-scale budworm outbreaks, interspersed with more quiescent periods, have been a common spatial–temporal pattern for at least three centuries.

Some of the periods (e.g., 1790s–1840s, 1870s–1890s, 1940s–1960s) have a pattern of high activity, decline, and then resurgence. This pattern was also apparent in descriptions of outbreak intensity and extent in forestry

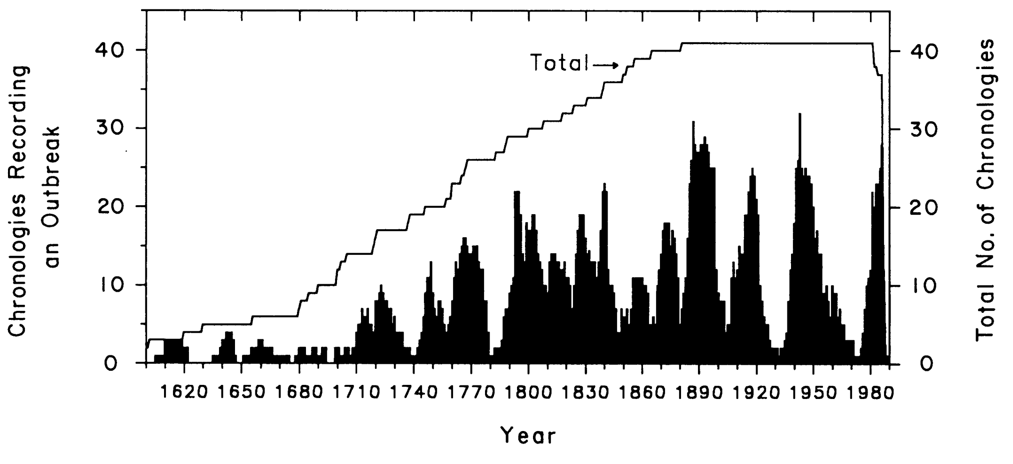

FIG. 8. Regional western spruce budworm outbreak occurrence in northern New Mexico, 1600–1989. The number of tree ring chronologies recording an outbreak were summed for each year to produce this series. The line above the area graph is the total number of chronologies sampled.

TABLE 3. Duration and severity of budworm outbreaks during different time periods, as estimated from ring-width reductions in corrected tree ring chronologies. Means followed by a different superscript letter within columns are significantly different (one-way ANOVA, $P < .05$).

		Duration (yr)		Maximum growth reduction (%)	
Period		Douglas-fir	White fir	Douglas-fir	White fir
1680–1779	Mean	9.8^{a}	12.0^{a}	62.3^{a}	61.5^{a*}
	SD	6.0	7.2	18.3	16.7
	n	38	11	38	11
1780–1879	Mean	10.6^{a}	10.2^{a}	51.2^{b}	56.6^{a}
	SD	6.4	5.9	13.7	17.1
	n	45	34	45	34
1880–1969	Mean	11.8^{a}	10.8^{a}	55.6^{ab}	57.0^{a}
	SD	5.8	5.7	15.1	19.0
	n	43	41	43	41
1970–1988	Mean	…	…	76.7^{c}	82.8^{b}
	SD	…	…	19.8	17.2
	n	…	…	14	13

documents for the 1940s–1960s period. There were no zero values in the summary outbreak series (Fig. 8) back to 1600. The Forest Service entomology reports confirm this pattern: western spruce budworm has been a chronic pest in the Southern Rockies, with some defoliation probably taking place somewhere in the region nearly every year.

A long episode of increased budworm activity extended from the late 1700s through the early 1800s (Fig. 8). Budworm populations appear to have waned and resurged several times during this 60-yr period. At individual sites two or three infestations occurred, lasting from 5 to 25 yr each, and separated by only a few years with radial growth at or above the expected growth level. At other sites, especially on the Questa district, growth was reduced for the whole period.

No clear change in duration or intensity of infestations during the past three centuries was evident (Table 3), except that the most recent infestations (1970s–1980s) were more intense than infestations in earlier centuries ($P < .03$). The century-length intervals were placed so as to begin and end approximately during low budworm activity periods evident in Fig. 7. Duration of the most recent infestation was treated separately because it was ongoing in many of the stands at the time of sampling.

Maximum 1-yr growth reductions and duration of infestation for all identified infestations were 56 ± 17.6% growth reduction (mean ± 1 SD, $n = 140$) and 10.8 ± 6.0 yr ($n = 126$) in Douglas-fir, and 60 ± 20.0% growth reduction ($n = 99$) and 10.7 ± 5.9 yr ($n = 86$) in white fir. Thus, white fir may have sustained slightly greater maximum 1-yr growth reduction ($t = 1.73$, $P = .08$), but duration of infestations was similar in the two species ($t = 0.11$, $P = .91$).

Exceptionally long chronologies

The Rito Claro stand in the Cabresto watershed contained many very old Douglas-fir. The oldest tree sampled at this site had a pith date of AD 1210. From a total of 64 trees sampled at this site, 4 trees dated before 1230, and 10 other trees dated before 1300. A search for old pines to serve as a climatic control for this site resulted in discovery of two ancient stands of limber pine in the Cabresto and Red River watersheds (P5—Italian Canyon and P7—Elephant Rock, respectively). Many living pines at these sites exceeded 900 yr in age, and the oldest was 1670 yr old (inner ring date of AD 320). Tree rings in a remnant log on the ground surface dated back to AD 93. These sites contain the oldest known living trees in the Southwestern U.S. (i.e., Arizona and New Mexico) (Swetnam and Brown 1992). The oldest known bristlecone pine (*Pinus aristata*) in the Colorado Rocky Mountains has an inner ring date of 442 BC (Brunstein and Yamaguchi 1992).

The Rito Claro Douglas-fir chronologies were corrected using the Italian Canyon limber pine series. The two series had a Pearson correlation coefficient of $r = 0.803$ ($P < .001$), indicating that they shared a substantial common year-to-year variance. The corrected series (not shown), however, indicates that the longer term variations in the two series diverged during many periods. A total of 20 past budworm infestations were inferred; 12 occurred from 1210 to 1600 (first half of the series) and eight occurred from 1601 to 1989. Duration of infestations during the earlier part of the record tended to be relatively short (5–10 yr), especially during the period from ≈1360 to 1520. Outbreaks since 1600 lasted from ≈10 to 30 yr.

Positive departures from expected growth were almost as frequent as the negative departures in the Rito Claro and other site chronologies (Figs. 3 and 4). These variations were probably due to growth release of sampled trees that survived the outbreaks and benefited from reduced competition or an influx of nutrients via insect frass. The growth releases were obvious following infestations on the core samples (Fig. 2). This phenomenon has also been reported by researchers in other

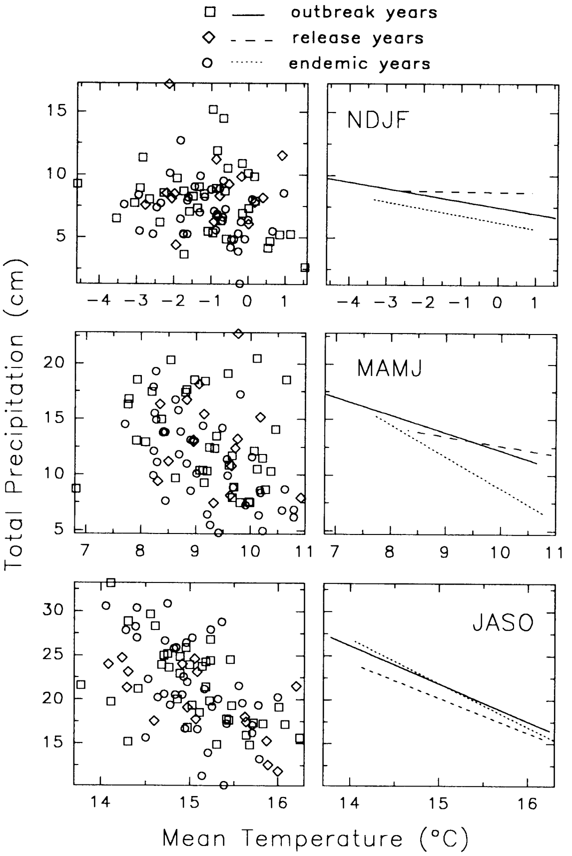

FIG. 9. Scatter plots of New Mexico Climate Division 2 precipitation vs. temperature (1895–1990). Total precipitation and mean temperature were seasonalized into November (prior year) through February (current year) (NDJF), March through June (MAMJ), and July through October (JASO). Years classified as release, outbreak, and endemic were plotted with different symbols (left side of figure). Plots on the right side are the linear regressions of the different groups of years.

regions under different insect defoliation regimes (e.g., Wickman 1980, Alfaro et al. 1982, Carlson and McCaughey 1982, Carlson et al. 1985).

Interactions of climate and budworm outbreaks

A weak inverse relationship existed between regional seasonal precipitation totals and mean temperature from 1896 to 1988 (i.e., higher precipitation corresponded to lower temperatures) (Fig. 9). The linear regression lines summarize the patterns of precipitation and temperature during endemic, release, and outbreak years for the last four major outbreaks, except for the release years of the 1890s–1900s outbreak. The most obvious pattern of higher precipitation in the release and outbreak years relative to the endemic years occurred for the March through June (MAMJ) season. MAMJ precipitation averaged 13.2 ± 4.1 cm (mean ± 1 SD, $n = 38$) during release years, 13.7 ± 4.6 cm ($n = 39$) during outbreak years, and 11.1 ± 3.9 cm ($n = 16$) during endemic years. Only outbreak years were significantly wetter than endemic years ($P = .03$). November through February (NDJF) precipitation was also significantly greater ($P = .04$) during the release years (8.7 ± 2.9 cm, $n = 16$) than during endemic years (6.9 ± 2.1 cm, $n = 39$). No significant differences were detected in the mean temperatures between the groups of years (all P levels $> .80$).

Long-term variations in MAMJ precipitation and regional-scale budworm outbreaks appear to be related from 1600 to 1980 (Fig. 10). The Pearson correlation coefficient of these two series from 1700 to 1988 was $r = 0.30$ for the unsmoothed precipitation vs. unsmoothed outbreak series, and 0.38 for the smoothed precipitation (low pass filtered) vs. unsmoothed outbreak series. Correlations between the regional outbreak series and New Mexico division 2 spring precipitation (1895–1988) were $r = 0.22$ for the unsmoothed series, and $r = 0.40$ for the smoothed series. Unfortunately, standard tests of the significance levels of these correlations are unreliable because the time series are highly autocorrelated, except the unsmoothed precipitation series. The regional outbreak series has significant ($P < .05$) autocorrelation at lags 1 to 5 and 11 to 16 yr (Fig. 11). Removal of this autocorrelation via autoregressive–moving average modeling (Box and Jenkins 1976) is not justified because the autocorrelation itself is a manifestation of the long-term outbreak trends, which are the focus of our interest. Hence, the correlations must be considered descriptive only. Nonetheless, the graphical comparison of the reconstructed regional outbreak and precipitation series (Fig. 10), and the ANOVA tests are compelling evidence that a climate–budworm association has existed for at least three centuries.

The one-way ANOVA was applied to test differences in reconstructed spring precipitation (unsmoothed) during the groups of years classified as release, outbreak, and endemic series back to 1700. Mean reconstructed spring precipitation was 17.4 ± 3.5 cm (mean ± 1 SD, $n = 50$) during release years, 18.5 ± 4.6 cm ($n = 170$) during outbreak years, and 15.7 ± 4.1 cm ($n = 171$) during endemic years. Thus, release and outbreak years had greater mean rainfall amounts than during endemic years ($P = .03$ and $P = .001$, respectively), and mean rainfall during outbreak and release years were similar ($P = .22$).

Spectral and cross-spectral analyses

The autocorrelation function and power spectrum of the regional budworm outbreak series (Fig. 11A, B) clearly indicated that moderately strong cycles were present in this time series. Power spectra computed at different lags identified significant ($P < .01$) cycles with periods varying between 20 and 33 yr. The percentage of the total variance of the time series explained by the combination of these harmonics was at least 50% (Fig.

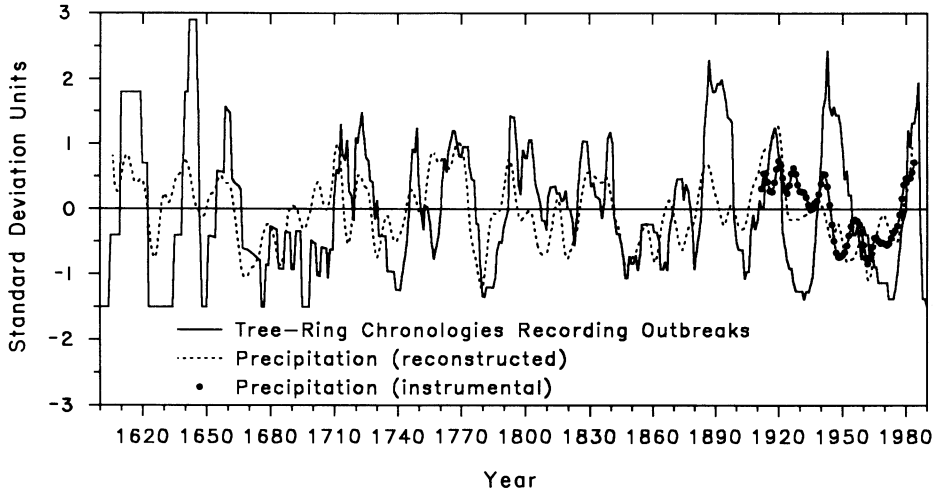

FIG. 10. The detrended regional outbreak series (——) is compared to tree ring reconstructed March through June (MAMJ) precipitation (– – –), and actual Red River, New Mexico MAMJ precipitation (●).

11B). The strongest cycle had a period of 25 yr (20.4% of the total variance in the 50-yr lag analysis). This appears to be the first statistical evidence that regional western spruce budworm populations have long-term cyclical dynamics, as opposed to other possible behaviors, such as stable-point equilibrium or aperiodic dynamics (see *Discussion* section).

The variance spectrum of the Red River reconstructed precipitation also had significant ($P < .025$) but relatively weak cycles with periods that varied between ≈30 and 100 yr (Fig. 11B). The percentage of the total variance in the time series explained by these harmonics was < 18%. The strongest cycle had a period of ≈50 yr (6.5% of the total variance in the 50-yr lag analysis). The precipitation series also had significant ($P < .025$) cycles with periods slightly greater than 2 yr. Meko (1992) reported similar weak periodicities in many tree ring chronologies in the western U.S. (especially periods ≈50–60 yr, and 2–10 yr). The shorter period cycles may be associated with the El Niño–Southern Oscillation, but causes of the longer period cycles (climatic or otherwise) are unknown.

The cross-correlation function (Fig. 11C) indicated that the budworm and precipitation time series had the strongest positive association at the zero lag, i.e., their simple year-to-year correlation ($r = 0.30$) was higher than any of the lagged correlations. Persistent positive correlations were also evident with the outbreak series lagging the climate series up to ≈12 yr (negative lags, Fig. 11C), with the highest negative lagged correlation at minus 3 yr ($r = 0.28$). This lagging relationship can be discerned in the plots of the budworm and precipitation time series (Fig. 10). This pattern occurred frequently in what appears to be both a delayed positive response of budworms to increased precipitation prior to outbreaks and a delayed negative response of budworms to decreased precipitation prior to the end of outbreaks (Fig. 10).

The "significant" correlations at positive lags 1 and 2 (Fig. 11C) seem illogical (i.e., budworms leading climate), but we note these correlations were actually quite weak ($r < 0.2$), and we suspect they may be related to inaccuracies in the identification of the timing of the beginning or ending dates of some of the inferred outbreaks. For example, significant but low correlations at positive lags could occur if the beginning and ending dates of some of the inferred outbreaks were occasionally dated too early. The estimated significance levels of the cross-correlations in general should be viewed with caution because, as mentioned earlier, the budworm series is highly autocorrelated.

The coherency spectra show the strength of the association between the two time series across the spectrum (Fig. 11D). The coherency squared (y axis) is the analog of the squared correlation coefficient (or the coefficient of determination, r^2). Hence, the coherency squared indicates the amount of variance in common between harmonics of a given frequency (or period) of the two time series. The highest and only significant ($P < .05$) coherency-squared harmonic was at a period of 25 yr (a value of 0.61, $P < .05$). Another output of the cross-spectral analysis (phase angle, not shown) also confirmed that the two series were slightly out of phase at the 25-yr period, with the precipitation cycle leading the budworm cycle by ≈3 yr.

Twenty-five years is also the approximate period of the strongest cycle in the power spectra of the regional outbreak series, but is somewhat shorter than the most statistically significant periodicities in the precipitation series (Fig. 11B). The 25-yr cycle in the precipitation series explained ≈4% of the total variance ($P = .06$), as compared to ≈5% for the 33-yr cycle ($P = .04$).

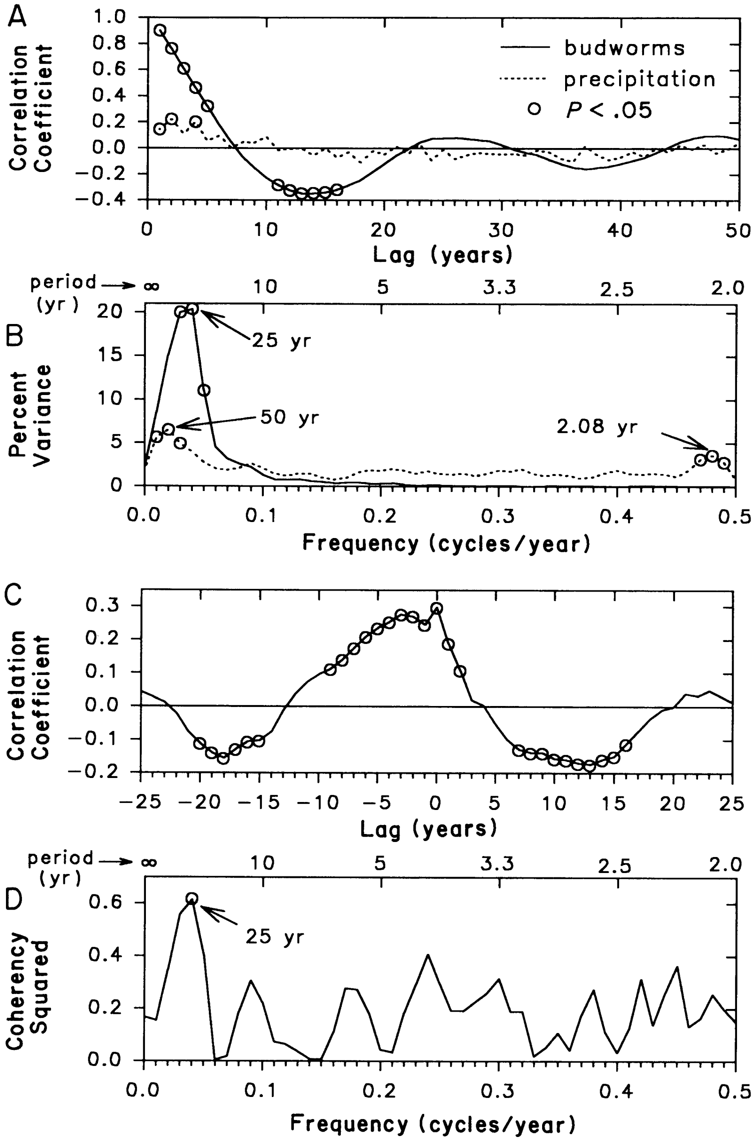

FIG. 11. (A) Autocorrelation functions of reconstructed regional budworm time series and spring precipitation (1600–1989), (B) univariate power spectra of the two time series, (C) cross-correlation function of budworms and precipitation, and (D) coherency squared spectra from the bivariate spectral analysis of budworms and precipitation. Circled values were significant at $P < .05$.

Thus, we conclude that weak long-term cycles in spring rainfall were statistically associated with moderately strong 25-yr cycles in regional budworm outbreaks.

DISCUSSION

Reliability of tree ring reconstructions

Interpretations of the temporal and spatial variations of past budworm regimes recorded by tree rings must be tempered with recognition of shortcomings of these data. These include: (1) Only surviving trees were sampled so measures of outbreak severity do not include past mortality. (2) The sample sizes within and among the stands decreased with time before present. Thus, less confidence can be placed in variations identified in earlier periods. (3) The corrected index chronologies contain some variations due to nonbudworm sources because the nonhost chronologies were not perfect "climatic controls" for variations in the host chronologies. (4) Identification of infestations within sites may be limited to the moderate to severe occurrences because very low levels of defoliation may not be distinguished from other variations that remain in corrected indices (Swetnam and Lynch 1989). (5) Lags in response of tree growth to onset and cessation of defoliation may be expected. This would lower the temporal precision of our estimates of outbreak timing, especially in the release and collapse phases.

Given the problems listed above, we cannot be entirely certain of our "inferred" outbreak reconstructions prior to the 20th century. Two lines of evidence, however, suggest that overall the tree ring data have good fidelity in recording past spatial and temporal infestation patterns. The first was the good verification of reconstructions in the 20th century and in earlier centuries with multiple sets of independent observations. The second is replication of results within our data set.

The outbreak timing observed within individual stands and in the regional summary closely matched forestry records of budworm activity in this century (Fig. 7). Our tree ring records consistently identified infestations occurring in specific watersheds or stands in the same year, or within one year of first reported occurrence in the documents. Even without the tree ring record we would have chosen a similar pattern of release, outbreak, and endemic years after the 1920s from the forestry documents. The meteorological data show that relatively wet conditions prevailed during the major outbreak years of this century. The use of nonhost species (pines) to correct the host tree ring chronologies provided an objective means of accounting for the effects of climate variation on tree growth in our assessment of pre-1922 outbreak timing and intensity. Replication of outbreak observations was evident in synchrony of outbreaks among widely separated stands, while using many different host and nonhost tree ring combinations. Furthermore, evidence of repeated infestations were obvious in the field as trees with multiple spike tops, and in the laboratory as periods of sharply reduced ring widths in host tree increment cores (Fig. 2). These observations were independent of our specialized data transformations and statistical analysis.

The March through June precipitation reconstruction from limber pine was based on a localized data set (two tree ring chronologies and model calibration with one weather station), however, year-to-year and long-term patterns coincide with regional reconstructions. For example, 19th and 20th century periods of long-term wetter conditions (annual precipitation) reconstructed from a grid of 96 tree-ring sites in the western U.S. were: early 1830s to early 1840s, 1870s, early 1880s to early 1890s, 1910s to 1920s, and 1940s (reconstructions end in 1970) (Fritts 1991). Similar long-term patterns of wet and drought periods were reported in other dendroclimatic grid studies from northern New Mexico (Rose et al. 1981, Stockton et al. 1984, D'Arrigo and Jacoby 1991). Individual meteorological station and divisional data also confirmed these climate variations in the 20th century. These variations closely matched wet and dry periods we have reconstructed (Fig. 10).

Budworm outbreaks and land use history

During the past three centuries the 20th century had the longest intervals of reduced budworm activity, and the most recent outbreak (1970s–1980s) resulted in the largest mean growth reduction. These observations agree with our earlier findings (Swetnam and Lynch 1989), i.e., budworm infestations and endemic periods in the 20th century appear to have been more synchronous than during earlier centuries, and the most recent outbreak was unusually severe.

A difference between these expanded data and those from the original 10 chronologies we compiled for the Southern Rockies of Colorado and New Mexico (Swetnam and Lynch 1989) was the record of a major outbreak in the 1900s–1920s. This outbreak was missing in most of our stands from the Colorado Front Range and Sangre de Cristo Mountains, and thus a long gap appeared in the record during the early 20th century. Our interpretation was that this gap was linked to rapid changes in Southern Rockies mixed-conifer forests during the early 20th century. Extensive logging and fires in the previous decades of the settlement era had reduced forest density. Subsequent favorable climate (Schulman 1956, Rose et al. 1981, Bowen 1989), fire suppression, and reduced sheep grazing in the 1920s (Carlson 1969, Baker et al. 1988) allowed host tree seedlings to become established. During the first half of the century stands were less susceptible or vulnerable to outbreaks because they had few mature host trees and the open stand conditions limited opportunities for insect dispersal. By the 1940s mixed-conifer forests had greater canopy closure within stands, mature host trees were an important stand component, and forests were more continuous across the landscape than during presettlement times. Thus, budworm outbreaks have been more widespread and intense than during earlier periods.

The larger and spatially concentrated data set reported here generally supports this historical hypothesis. For example, a new finding was the occurrence of a synchronous and intense 1900s–1920s outbreak in the Jemez Mountains (Figs. 2, 3, and 5). This outbreak did not occur in most of the Colorado Front Range and New Mexico Sangre de Cristo Mountain stands, but these areas were much more exploited during the 19th century than the Jemez Mountains. Logging for railroad ties, mine timbers, and other building lumber was extensive in the Front Ranges during the late 1800s and around the turn of the century (Veblen and Lorenz 1986), and very extensive timber cutting for railroad ties took place on the Camino Real district during the 1910s and early 1920s (Korstian 1914, Cook 1954, DeBuys 1985). Some logging on the periphery of the Jemez Mountains began in the late 1890s, but cutting in the interior part of the mountain, where our sampled stands were located, was not extensive until after ≈1930 (Allen 1989). Thus, the relatively undisturbed Jemez mixed-conifer forests probably had greater canopy closure early in this century than the harvested forests to the east, and therefore were more susceptible to an outbreak.

The importance of land use history and considerations of spatial scale are evident in these comparisons. Regional patterns of budworm outbreaks are observed as synchrony among widely dispersed stands, but local patterns differ in some particulars from the overall regional patterns. One implication of this is that changes in regional outbreak history are generally not resolvable in records from single stands, watersheds, or even entire mountain ranges. At these smaller spatial scales unique site characteristics and land use history may override larger scale exogenous influences (e.g., regional climatic fluctuations). Nevertheless, exceptionally long records from single stands can be insightful regarding the potential stability of the forest–budworm system.

The Rito Claro stand

Several observations support the general inference that the Rito Claro stand was subject to chronic stress from repeated outbreaks. Although the site was not particularly dry or otherwise obviously harsh (elevation is 2870 m), the average dbh for 700+ yr old Douglas-fir trees was only 44.4 cm. No white fir trees over ≈100 yr old were found on the site. Many of the Douglas-fir trees had multiple old spike tops on their stems, indicating repeated top-killing by budworm. The ring series had numerous periods of extreme growth suppression followed by surges of increased growth. The 790-yr tree ring chronology suggests that budworm regimes in this stand shifted from more frequent and relatively short infestations before AD 1600 to less frequent but longer infestations after 1600. Since this pattern was observed only in this ancient stand we cannot extrapolate to the region as a whole.

Although this stand sustained many infestations during its lifetime (at least 20), no clear evidence was present on the site that indicated the stand had undergone drastic changes in the past seven or eight centuries. For example, there was not a large abundance of dead standing trees, or logs on the ground that would be indicative of major mortality events or progressive stand dieback, as often observed in old-growth forests. Given the great age of many dominant canopy trees it is apparent that some form of a stable forest–budworm regime existed for centuries.

We cannot quantify actual biomass changes from our radial growth data to determine if productivity losses during outbreaks were completely compensated by subsequent growth releases in survivors. Nevertheless, the amazing persistence of this stand in the face of repeated budworm infestations over seven centuries seems to lend some support to Mattson and Addy's (1975) hypothesis that insects may act as cybernetic regulators of some natural ecosystems. In this case, over the long term budworms may have ensured consistent, albeit suppressed output of biomass production. Sustained low levels of productivity (i.e., reduced living and dead fuels) and reduced stand density (i.e., spatial discontinuity of the tree canopy) may be a stabilizing condition where the probabilities of episodic stand-replacing fires or budworm infestations are greater than zero. This potential parallel (and interaction) between the dynamics of fires and budworm infestations has been noted before (Holling 1981, Stocks 1987).

Interestingly, the Rito Claro stand currently has one of the highest stand densities (stems per hectare) among the sampled stands, and one of the highest proportions of Douglas-fir relative to white fir (Table 1). Much of this high density is due to smaller diameter white fir trees that established since fire suppression began ≈80 yr ago (observations from increment cores). Dominance by the ancient Douglas-firs in the overstory may be due to the long-term selective pressure by budworm against the more shade-tolerant white fir, since true firs (*Abies*) are generally preferred hosts and often have greater budworm-caused mortality than Douglas-fir (Perry 1925, Williams 1967, Carlson et al. 1983). The apparent increased stand density in this century has probably increased the hazard of a stand-replacing fire or budworm outbreak, a catastrophe that the Rito Claro stand has escaped for at least the past 790 yr.

The exceptionally long history revealed at the Rito Claro site suggests that in some circumstances Douglas-fir trees and budworms can coexist in a relatively stable state for many centuries. Douglas-fir and white fir coexist on the larger regional scales in mixed-conifer forests, but it appears that long-term displacement of white fir may occur within long-lived, episodically defoliated stands. Speculating a bit further, the long-term persistence of episodically defoliated trees and stands in this fire-prone environment may indicate that Douglas-fir and western spruce budworm have developed a kind of mutualistic relationship, and therefore, it is likely that they have a long co-evolutionary history. This is in marked contrast to the typically fatal outcome of spruce budworm infestations (*C. fumiferana*) in balsam fir [*Abies balsamea* (L.) Mill.] forests of northeastern North America, where forest–budworm interactions may have begun in the Holocene (Volney 1985).

Outbreaks and climatic variation

Our climate–budworm comparisons show a positive relationship between spring and early summer precipitation and regional-scale outbreak occurrence. Experimental work on chemical ecology of the forest–budworm system within our study area generally seems to contradict our results and to support the plant stress hypothesis (Cates et al. 1983, Redak and Cates 1984, Cates et al. 1987). These studies reported increased budworm larval survival and adult masses on drought-stressed (trenched) Douglas-fir trees relative to control trees. Reciprocal treatments (i.e., watering) were apparently not conducted. Changes in distribution and concentrations of specific foliar terpenes and productivity of trees appeared to be important factors affecting budworms.

Differences between these experimental results and our tree ring observations may be due to differences in the spatial and temporal scales that were studied. The trenching experiments were conducted in two stands in the Jemez Mountains (one control stand and one treatment stand) and the insect populations were observed for ≈1 yr. Thus, relative to the tree ring reconstructions, the spatial scale of the experiments was small and the time perspective short. Similar limitations in temporal perspectives exist in extrapolation of results from most weather–budworm studies in that most have tracked patterns only over short time spans of months to a few decades at best. This may be insufficient to clearly identify "climatic" patterns relevant to forest–budworm regimes operating over regional areas and periods of years to centuries, particularly if the climate–budworm associations are weak to moderate, or change through time.

On the other hand, while the large space and time scales encompassed in the tree ring reconstructions helps identify climate–budworm patterns, the exact mechanisms remain unknown. Many other potential climate-sensitive factors may be involved in budworm population dynamics, such as parasites, predators, viral diseases of budworms, host tree and budworm phenologies, and dispersal (e.g., convective storms that loft insects [Greenbank 1957]). None of these factors have been intensively investigated in our region in the context of weather–budworm hypotheses. For a mechanistic understanding of the forest–budworm system it will be necessary to try to isolate the effects of environmental factors on plants and insects. This can only be accomplished in field and laboratory experiments designed to study such interactions (Larsson 1989).

Long- and short-term environmental conditions at the stand level and plant adaptedness to climate-related stress are probably also very important in determining the response of an insect population to tree stress. Hypotheses of nonlinear responses of insects across continua of plant stress have been proposed to explain observed differences in results from plant stress/herbivore studies (e.g., Bultman and Faeth 1987, Mopper and Whitham 1992). For example, in certain environments insects may be most successful at intermediate plant stress levels and less successful at low and high plant stress levels (i.e., a dome-shaped response curve across the plant stress continuum). Thus, for a given forest stand the response of herbivorous insects to changes in climate may depend upon whether short-term increased or decreased tree stress is toward or away from intermediate stress levels. In this model, insect populations would tend to increase during droughts within stands that are ordinarily at relatively low moisture stress levels. In contrast, insect populations may increase during wet periods within stands that are ordinarily at relatively high moisture stress levels.

We may have identified a regionally specific climate–budworm response that is quite different from the response observed at higher latitudes in North America. Our study region is essentially arid to semiarid, especially in comparison to most of the range of western spruce budworm in North America. Hence, most of our stands are often nearer to the high end of a stress continuum than to the low end. Using the model described above, a mechanism of improved budworm performance in this region during wet climatic episodes may involve increased tree vigor (i.e., decreased stress), which would generally result in more rapidly growing, larger, and more numerous leaves, conditions that are particularly favorable to some leaf-eating insects (Price 1991).

Another conceptual model derived from experimental work on pine sawflies (*Neodiprion* spp.) offers a somewhat different explanation for shifting responses of forest insects to climate changes (Wagner 1990, 1991). This model posits that increased precipitation would lead to shifts in carbon allocation from belowground to aboveground biomass, and decreased thickening of leaf cuticles, which are primarily an adaptation to limit moisture loss. Greater leaf biomass and thinner leaf cuticles benefit defoliator populations, especially in arid to semiarid environments. In such environments, long-term dry conditions ordinarily forces trees to invest heavily in belowground biomass (i.e., roots), and only the episodic wet conditions result in temporary relative increases in aboveground biomass.

An important commonality among these models is the implicit recognition that plant stress is a relative condition that is contingent on both long- and short-term environmental conditions. Thus, the diversity of plant responses to stress (and indirectly, insect responses) may be a function of conditions that constitute unusual stress, or lack of stress, in a particular site.

Although our results may be specific to the relatively dry southwestern U.S., two of the longest weather–budworm studies in other regions suggest that some of the patterns we observe may not be entirely unique. Thomson et al. (1984) reported that warm/dry years generally preceded budworm (*C. occidentalis*) outbreaks (1912–1978) in British Columbia, and like others (e.g., Mattson et al. 1991), they emphasized the importance of synchrony in larval emergence and bud flush in the release or collapse of outbreaks. Their scatter plots of precipitation vs. temperature sorted by type of year (analogous to our Fig. 9) also show that many of the wettest and coolest years occurred during outbreaks. In a regional study of jack pine budworm (*Choristoneura pinus* Freeman) in Canada (1937–1986) Volney (1988) reported that the largest fire years in the region (inferred drought years) occurred between major outbreaks, whereas low fire activity (inferred wetter conditions) generally occurred during outbreaks.

Volney (1988) and others (e.g., Wellington 1950, Greenbank 1956, Mattson et al. 1991) suggested that drought conditions preceding outbreaks might be important as a release mechanism because water stress has a stimulating effect on staminate flower production in conifers. "Release" years in our data tend to be wetter than endemic years. Because of lag times in the buildup of budworm populations and in the tree ring response to significant defoliation, our identification of the critical years may not have sufficient resolution to observe a drought-flowering-release effect. However, the lagged positive correlations, with precipitation leading budworms by several years to about a decade (Fig. 11C), suggest that drought is an unlikely outbreak "trigger" in the southwestern U.S.

Dynamics of the western spruce budworm

A variety of other forest insects have oscillatory population dynamics (Meyers 1988, Turchin and Taylor 1992). The *Choristoneura,* however, appear to have much longer periodic fluctuations than other Lepidopteran genera. Typical periods of population oscillations (time lag between population maxima or minima) of forest Lepidopterans ranges from ≈6 to 12 yr, but western and eastern spruce budworm periodicity ranges from ≈13 to 35 yr (Meyers 1988). These longer periods have hampered the quantitative study of budworm dynamics because they are often longer than the careers of observers or funded research projects. Thus, very few long-term data sets of budworm population numbers exceeding more than one period are available (e.g., Morris 1963, Royama 1984). Clearly, time series long enough to contain many outbreaks are needed to confidently identify the character of population dynamics. Proxy time series of forest insect populations, such as defoliation observations or tree ring reconstructions, may be noisier than actual observations of insect numbers. However, centuries-long reconstructions provide a chance to identify and characterize even weak to moderate insect population signals because they contain numerous observations of the release, outbreak, and decline phases.

Meyers (1988) pointed out that decline phases of Lepidopteran populations across regions were often more synchronous than release phases. This suggests that regional factors synchronizing insect populations were more important during the later stages of outbreaks than during release years. Such factors could include regional weather fluctuations directly influencing insect populations, their food resources, or changes in regional populations of predators, parasites, and pathogens. Explanations of insect population fluctuations involving pathogens have been particularly popular (e.g., Anderson and May 1980, Ewald 1987, Sheppard et al. 1988). We plotted separately the beginning and ending dates of inferred infestations in all stands (not shown) and did not detect any clear visual patterns of greater synchrony in beginning or ending dates.

The dynamics of fluctuating animal populations may be categorized as stable point equilibria, limit cycles, pseudo- or quasiperiodic, or aperiodic chaos (Shaffer and Kot 1985, Logan and Allen 1992, Turchin and Taylor 1992). Such distinctions are not trivial because these patterns are indicative of underlying mechanisms of the fluctuations. For example, relatively simple dynamics, such as stable limit cycles, may suggest that one or relatively few endogenous interactions are important in driving the population fluctuations. (Following Turchin and Taylor [1992], "endogenous" refers to dynamical feedbacks affecting the system, including those that involve a time lag. "Exogenous" refers to density-independent factors that are not a part of the feedback loop.) If a system fluctuates with a stable limit cycle, obviously there is good potential for predicting future population trends. On the other hand, highly complex dynamics, such as quasiperiodicity or chaos indicate there could be few or many interacting endogenous or exogenous factors (or both) producing the fluctuations. In these cases there is little or no potential for predicting the precise timing of future outbreaks, particularly outbreaks beyond the next one (Logan and Allen 1992). Nevertheless, empirical descriptions and modeling of these dynamics can help provide estimates of the bounds of variability of the system.

The significant lagged values and damped oscillations in the budworm autocorrelation function (Fig. 11A) suggest this is a "phase forgetting" oscillatory system, i.e., cyclicity is present but phases of the cycles shift through time (Turchin and Taylor 1992). The spectral analysis (Fig. 11B) and a phase portrait of lagged values of the regional outbreak series (not shown) confirms that the cycles varied through time with periods never exactly repeating. The regional series does not appear to be chaotic (estimated Lyapunov exponent was less than zero; P. Turchin, *personal communication*). Hence, this regional series may be categorized as "pseudoperiodic" (Poole 1977, Turchin and Taylor 1992). (The term quasiperiodic is usually reserved for the behavior of similar dynamical systems without noise.) Differentiating between the mathematically distinct behaviors of limit cycles, pseudoperiodicity (or quasiperiodicity), and aperiodic chaos in noisy, short time series (i.e., series with less than thousands of data points) is a fundamental methodological problem in nonlinear analysis of ecological data (Shaffer and Kot 1985, Logan and Allen 1992).

Key issues in the interpretation of the results we have so far are the relative roles and importance of endogenous vs. exogenous factors as mechanisms of the observed dynamics. The existence of a general synchrony of infestations among stands dispersed across a large region may be indicative of an important exogenous controlling factor or factors (Meyers 1988). Furthermore, the fact that the long-term budworm and precipitation series were correlated indicates that climate was one of these exogenous factors. However, the precipitation cycles were much weaker and had somewhat longer periods than the budworm cycles. Although statistically significant the correlation and ANOVA tests indicated the year-to-year climate–budworm associations were fairly weak. Thus, it seems unlikely that climatic variations could be solely responsible for the relatively strong cyclic behavior of the regional budworm outbreaks.

We hypothesize that both endogenous and exogenous time-varying factors control this system. One of these factors may be the rate and duration of lagged recovery of the forest canopies following defoliation. This would be consistent with the famous Ludwig et al. (1978) model of spruce budworm dynamics (*C. fumiferana*), which produces a limit cycle from three equations governing (1) a slow response variable (the forest canopy), (2) a fast response variable (the budworms), and (3) the energy potential of the forest. In a simulation we added the tree ring reconstructed precipitation as an exogenous pulse to the forest canopy equation, and the model produced a time series closely resembling the actual regional budworm time series. Addition of the precipitation pulse to either the budworm equation or the energy equation had little effect on the basic limit cycle produced by the model (T. W. Swetnam et al., *unpublished manuscript*). These preliminary findings lead us to hypothesize that climate operates as an exogenous factor in this system primarily through its direct influence on the production of foliage. Addition of this exogenous (i.e., density-independent) pulse to a fundamental delayed density-dependent system may have produced the observed pseudoperiodicity. Furthermore, we speculate that the observed association between weak precipitation cycles and the stronger budworm cycles may represent a type of coupled-oscillatory system, since it has been demonstrated that relatively weak interactions can result in synchrony of oscillating systems (Winfree 1980). Testing of these ideas will require further investigation of the dynamical behavior of long budworm and climate time series, preferably from both the Southern Rockies and other regions where episodic budworm outbreaks occur.

CONCLUSION

A range of observations across spatial scales, from individual trees (Figs. 2–4) to stands and watersheds (Figs. 5 and 6) to the region (Fig. 10), enabled us to identify both unique local-scale patterns, and the larger regional-scale patterns in which they were embedded. These embedded patterns were partly related to historical land use practices and climatic variability. In particular, historical impacts of timber harvesting and fire suppression in southwestern forests appear to have altered the timing and impacts of infestations in some areas, but overall regional occurrences of outbreaks were still at least partly driven by spring precipitation amounts. At the same time, the temporal–dynamical behavior of the system also suggests that endogenous factors (perhaps delayed-density dependence) may also be at play. Thus, combinations of small and large-scale processes, endogenous and exogenous factors, and chance and necessity interact to produce the forest–budworm dynamic.

A unique long-term perspective was also provided by discovery of a long-lived stand of Douglas-fir trees that sustained at least 20 outbreaks over a period of seven centuries. The existence of such a stand indicates that some overstory trees can coexist with budworms for extraordinary lengths of time. This disturbance regime may be analogous to long-lived ponderosa pine stands of the southwestern U.S. that sustained climate-linked fire regimes of episodic, low intensity surface fires for many centuries (Swetnam and Betancourt 1990). Even though the dynamics of these presettlement forests were complex, due to the disturbance-sustained low fuel (food) levels within stands, the system trajectories rarely fluctuated so violently that the dominant overstory trees were eliminated by catastrophic disturbance events (Holling 1981). Unfortunately, the analogy may extend further because both systems (ponderosa pine and mixed-conifer forests) may have become less dynamically stable in the 20th century due to human-caused changes in the fuel–food base. Hence, catastrophic events may have become more likely (see Wickman [1992] and Mutch et al. [1992] for discussions of this problem in eastern Oregon).

"Natural trajectory experiments," such as our tree ring reconstructions, can encompass large spatial and temporal scales (Diamond 1986). Thus, the strength of our historical–regional approach is that observations match the temporal and spatial scales of important processes influencing the system (Ricklefs 1987). Limitations of this approach include the lack of control of some of the interacting variables (e.g., biotic and abiotic factors, other trophic levels, etc.). The tree ring record is also inherently noisy and diminishing sample sizes with increasing time before present lowers the reliability of estimates in earlier periods. These problems prevent us from exactly identifying the specific mechanisms of climatic influence on budworm populations. More controlled experimental studies are needed to test the importance of climate variations on budworms and trees. A focus on testable hypotheses and questions deriving from new theoretical constructs (e.g., Wagner 1991, Mopper and Whitham 1992, Price 1991) is particularly needed. For example, does increased seasonal moisture improve budworm performance only in relatively dry sites? If moisture is important to budworm performance does it mainly operate through effects on the trees (e.g., tree stress or vigor), the budworms, or other components of the system (e.g., predators, parasites, and pathogens), or certain combinations of the above? Studies involving simultaneous observations of insect numbers, defoliation amounts, and tree ring growth parameters would improve our abilities to interpret the tree ring record.

Finally, the detection of pseudoperiodicity in long-term western spruce budworm time series suggests this is a complex nonlinear system. We hypothesize that this complexity is the result of a combination of time-lagged responses to external forces and inherent structural characteristics of the forest–budworm system. One implication of these dynamics is that long-term prediction of future regional outbreaks may not be possible, but forest–budworm models incorporating previous years' precipitation and forest canopy variables might be able to anticipate with reasonable precision (i.e., within a few years) the timing of the next endemic, release, or outbreak phase.

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