

A tree-ring reconstruction of western spruce budworm outbreaks in the San Juan Mountains, Colorado, U.S.A.

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Abstract: Tree-ring records were used to reconstruct spatial and temporal patterns of western spruce budworm (*Choristoneura occidentalis* Freeman) outbreaks in mixed conifer forests of southern Colorado. Reconstructions in 11 host stands showed a regionally synchronous pattern of at least 14 outbreaks during the past 350 years. Intervals between outbreaks were highly variable within stands, but at the regional scale outbreak intervals were more consistent. Spectral analyses of regional outbreak time series confirmed periodicities at about 25, 37, and 83 years. Comparison with an independent drought reconstruction indicated that outbreaks typically corresponded to increased moisture, while relatively little budworm activity occurred during dry periods. In contrast to other published reconstructions in Colorado and New Mexico, reconstructions from this study area did not exhibit significant 20th-century changes in the frequency of outbreak occurrence or magnitude of growth reduction. Sharply reduced growth during outbreaks was not clearly visible on the increment core samples, and budworm-induced reductions in tree-ring growth were usually detectable only after comparison with nonhost tree-ring series. This finding emphasizes that defoliation effects on ring growth can be highly relativistic. Hence, caution should be exercised in reconstructing insect outbreak histories based only on visual detection approaches, or without comparison with nonhost or nondefoliated tree-ring control series.

Résumé : Des données dendrochronologiques ont été utilisées pour reconstituer la distribution spatiale et temporelle des épidémies de la tordeuse occidentale de l'épinette (*Choristoneura occidentalis* Freeman) dans les forêts mixtes de conifères du Sud du Colorado. Les reconstitutions effectuées dans 11 peuplements hôtes révèlent qu'au moins 14 épidémies synchrones à l'échelle régionale sont survenues au cours des 350 dernières années. Les intervalles entre les épidémies ont été très variables dans les peuplements mais plus consistants à l'échelle régionale. Selon les analyses spectrales des séries temporelles, les épidémies régionales avaient des périodicités d'environ 25, 37 et 83 ans. La comparaison avec une reconstitution indépendante des périodes de sécheresse montre que les épidémies correspondent typiquement à une augmentation des précipitations alors que la tordeuse a été relativement peu active pendant les périodes de sécheresse. Contrairement à d'autres reconstitutions au Colorado et au Nouveau-Mexique, les reconstitutions effectuées dans cette zone d'étude ne révèlent aucun changement significatif dans la fréquence des épidémies ou l'importance des réductions de croissance au cours du 20^e siècle. Aucune réduction évidente de croissance associée aux épidémies n'était visible sur les carottes échantillonnées. Les réductions dans la croissance des cernes annuels dues à la tordeuse ne pouvaient être détectées qu'en effectuant des comparaisons avec les séries dendrochronologiques des arbres non hôtes. Ces résultats mettent en évidence le fait que les effets d'une défoliation sur la croissance des cernes peuvent être très relatifs. Par conséquent, on devrait être prudent dans la reconstitution de l'historique des épidémies d'insecte basée seulement sur des approches de détection visuelle ou sans effectuer de comparaison avec les séries dendrochronologiques d'arbres non hôtes ou non défoliés.

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Introduction

Insects and pathogens are integral components of forest ecosystems with important roles in forest dynamics (Haack and Byler 1993). Insects regulate primary productivity through consumption of photosynthetic tissue (Mattson and

Addy 1975; Morrow and LaMarche 1978) and increased nutrient cycling and availability (Schowalter et al. 1986). By inducing species-specific mortality, insects modify both the composition and structure of forests and redistribute biomass and resources (Schowalter 1981; Romme et al. 1986). In addition, insect-caused disturbances can interact with other bi-

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otic and abiotic disturbances. For example, attack by one species of insect can predispose trees to attack by other insects (Schmid and Mata 1996), and climatic variations (e.g., wet and dry episodes) may increase or decrease tree vulnerability to attack by insects (White 1976; Larsson 1989). Insect-caused mortality of trees can increase the probability of subsequent forest fires by increasing dead fuel loads (McCullough et al. 1998).

A widespread and influential group of insects in the forests of North America are the budworms (*Choristoneura* spp.). These native defoliating insects influence ecosystems throughout Canada and the United States, and in some forested regions may be the most important biotic disturbance agent (Filion et al. 1998). The western spruce budworm (*Choristoneura occidentalis* Freeman) defoliates Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), the true firs (including white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.)), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and western larch (*Larix occidentalis* Nutt.). The range of western spruce budworm extends from southern Arizona and New Mexico north to British Columbia (Harvey 1985; Hermann 1987). Because of its extensive geographic range and impacts on timber resources, the western spruce budworm has been labeled the most destructive insect pest of western coniferous forests (Fellin et al. 1983; Fellin and Dewey 1986). Like forest fires, however, outbreaks of native insect species can be considered "natural" or even necessary ecological events. Therefore, the impacts of modern forest insect outbreaks should be considered in light of their long-term history and ecological role.

Several independent tree-ring reconstructions of western spruce budworm outbreak history have indicated a trend toward more severe outbreaks in the 20th century, with the most recent event in each record being the most severe (McCune 1983; Anderson et al. 1987; Swetnam and Lynch 1989, 1993; Hadley and Veblen 1993; Weber and Schweingruber 1995; Swetnam et al. 1995). Spatial analyses in the Front Range of Colorado and in northern New Mexico have shown an increase in the synchrony of outbreaks during the 20th century compared with prior periods (Swetnam and Lynch 1989, 1993; Hadley and Veblen 1993; Weber and Schweingruber 1995). Other changes in outbreak patterns in the 20th century relative to earlier centuries include increased duration in the northern Rocky Mountains (Anderson et al. 1987) and possibly a higher frequency in the Blue Mountains of Oregon (Swetnam et al. 1995).

These changes in outbreak patterns have been attributed to a greater abundance and continuity of host trees within forest stands resulting from prior forest use and management. Livestock grazing and timber harvesting beginning in the 19th century and later fire suppression efforts favored the establishment of shade-tolerant species such as Douglas-fir and true firs in multiple crown level forests. Thus, land uses have shifted landscape structure from a fine-grain spatial mosaic of various tree ages and species to a coarse-grain pattern with more contiguous and homogenous tree ages and species. These forests are probably more susceptible and

vulnerable to outbreaks of budworm (Carlson et al. 1983; Wulf and Cates 1987).

Changing climate patterns may also contribute to altered outbreak patterns. Outbreaks of phytophagous insect populations, including budworm, have typically been associated with drought periods (White 1976; Mattson and Haack 1987). Physiological stress in plants during droughts apparently benefits some insects through increased concentration of favorable nutrients and compounds in plant tissues, or lowered resistance due to the reduction of defensive compounds and resin flow (Mattson and Haack 1987; Cobb et al. 1997). However, a range of insect responses to water availability and stress in trees has been noted, with some populations increasing in response to reduced tree stress (Larsson 1989; Wagner and Frantz 1990; Price 1991; Mopper and Whitham 1992). Centuries-long reconstructions of western spruce budworm outbreaks from New Mexico, Colorado, and Oregon have identified a correspondence between regional-scale outbreaks and decadal-scale periods of increased moisture availability, with very few outbreaks occurring during droughts (Swetnam and Lynch 1993; Swetnam and Betancourt 1998).

Our goal in this research was to reconstruct and evaluate outbreak history on the western side of the southern Rocky Mountains in Colorado. We anticipated that outbreak patterns might be different in this area relative to other study areas because of differences in climate patterns, ecological communities, and land-use histories. We examined basic outbreak characteristics, including frequency, timing, and spatial patterns. Outbreak patterns were also examined for changes in the 20th century relative to prior centuries. Finally, we evaluated possible relationships between outbreaks and climatic patterns.

Materials and methods

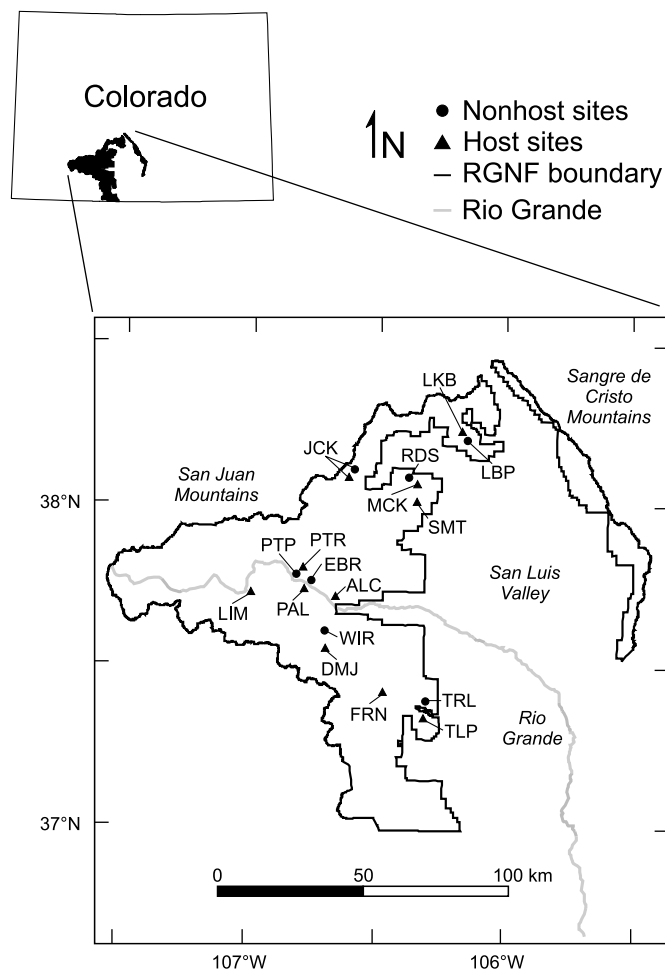
Study area

The study area is in the Rio Grande National Forest (RGNF) located in the San Juan and Sangre de Cristo mountain ranges in south-central Colorado (Fig. 1). Most of the forest is located in the San Juan Mountains west of the San Luis Valley. Elevations of the region range from 2100 m in the San Luis Valley to peaks over 4200 m in the Sangre de Cristo and San Juan mountains. Study sites were widely distributed throughout the San Juan portion of the RGNF with site elevations ranging from 2560 to 3121 m (Table 1). Annual precipitation for the area ranges from 142 to 500 mm with an average of 310 mm (NOAA, National Climate Data Center, Colorado Division 5³). Most precipitation falls in the summer, with 44% of annual precipitation occurring during May to August. The mean monthly temperature during January is -8.8°C and during July is 16.1°C (NOAA, National Climate Data Center, Colorado Division 5³).

The topographic diversity of the region supports a range of vegetation communities. Shrub-steppe communities exist along the lower foothills and in the San Luis Valley. Moving up from the foothills, a typical sequence of vegetation communities is piñon-juniper woodlands, ponderosa pine – oak

³National Oceanic and Atmospheric Administration (NOAA), National Climate Data Center. State divisional data available online at <http://lwf.ncdc.noaa.gov/oa/ncdc.html>

Fig. 1. Study site locations in southwestern Colorado in the Rio Grande National Forest (RGNF).



communities, mixed conifer, spruce–fir, and alpine vegetation along the peaks. Sampling for this research was concentrated in the ponderosa pine and mixed conifer communities. The primary hosts for western spruce budworm within the southern Rocky Mountains are Douglas-fir, white fir, and to a lesser extent, Engelmann spruce (Schmid and Mata 1996).

Human history has impacted the area in the past several centuries. Although Spanish settlers began to move into the San Luis Valley with livestock in the early 1600s, most human activity remained along the periphery of the mountains until the end of the 1800s (Griffiths 1984). Increased settlement in the San Luis Valley in the 1850s, discovery of gold in the San Juan Mountains in 1870 (Simmons 1999), and the arrival of the railroad in the Creede area in 1892 (Athearn 1962) brought greater human impact to this region. The mining boom in the late 1800s generated a demand for forest products, particularly timber. Extraction of natural resources and the resultant impacts upon the ecosystem have continued to the present (Simmons 1999).

Field collections

Increment core samples were taken from 11 host stands and 7 nonhost stands during 1997 and 1998 (Table 1). Host stands were selected based upon (i) the presence of old indi-

viduals and (ii) evidence of repeated budworm outbreaks (e.g., dead leaders and numerous dead branches on living trees). Prior research has shown that true fir species (*Abies* spp.) often show stronger growth responses to defoliation than Douglas-fir (Brubaker and Greene 1979; Wickman et al. 1980; Swetnam 1987). White fir, however, is a minor component of the mixed-conifer forest in this region, and only three of the selected host stands contained white fir. Other tree species found in the host stands included bristlecone pine (*Pinus aristata* Engelm.), Engelmann spruce, corkbark fir (*Abies lasiocarpa* var. *arizonica* (Merr.) Lemm.), limber pine (*Pinus flexilis* James), ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.), and aspen (*Populus tremuloides* Michx.). Stands with no evidence of human influence were preferred for sampling; however, many stands had some level of prior timber harvesting as indicated by the presence of stumps. The sampled areas ranged from about 5 to 10 ha in size.

Continuous forest stands were sampled on linear transects, subjectively placed along topographic contours. Typical transect lengths were 100 to 150 m with 20-m intervals between points. At these points, two increment cores were taken from opposite sides of each tree at or below 1.3 m above the ground from each of the two nearest host trees over 20 cm in diameter at breast height (DBH). Increment cores were preferentially taken perpendicular to the slope. In addition, variable plot measurements (using a prism or relascope) with a minimum tree size of 6.5 cm DBH were used to describe the species basal areas and stem densities of the stands. Additional increment cores were taken from oldest appearing host trees near the transect to maximize the length of the tree-ring record. In stands with discontinuous or patchy distributions of host trees, the linear transect strategy was found to be inefficient in sampling host trees. At these sites the older appearing Douglas-fir and white fir individuals within the patches were sampled, and variable plot points were used to describe the patches.

Nonhost stands were selected based on the dominance of pine, proximity to the host stands (typically within about 5 km of at least one host stand), and climate sensitivity (principally to precipitation). Pine-dominated stands were selected to avoid the potential for increased growth during outbreaks when competing host trees were defoliated. Trees that are sensitive to precipitation in the northern hemisphere are typically on southern-facing slopes with relatively shallow substrates and are near lower forest boundaries (Fritts 1974). Two increment cores were taken from opposite sides of each tree, sampling perpendicular to the slope. Ten to 35 trees were sampled per site.

Laboratory analysis

Methods used for the reconstruction of outbreaks have been described by Swetnam et al. (1985, 1995) and are briefly summarized here. Samples were processed according to standard dendrochronological procedures (Stokes and Smiley 1968; Swetnam et al. 1985). Cores were mounted and surfaced so that individual tracheid cells were observable under magnification. The samples were cross-dated (Stokes and Smiley 1968), and ring widths were measured using a sliding-stage incremental micrometer with a precision of 0.01 mm. The dating and ring-width measurements

Table 1. Characteristics of sites used to reconstruct western spruce budworm outbreaks on the Rio Grande National Forest, Colorado.

Site name	Code	Elevation (m)	Aspect (°)	Basal area (m ² /ha)	Density (trees/ha)	Percentage of total basal area*						
						ABCO	PIAR	PIEN	PIFL	PIPO	POTR	PSME
Host												
Alder Creek	ALC	2713	20	22.2	410	36	—	—	3	12	2	47
Demijohn Peak	DMJ	2902	180	33.6	291	8	—	—	5	15	5	67
Fern Creek	FRN	2853	245	28.9	229	—	—	7	—	—	—	93
Jakes Creek	JCK	3085	340	32.5	447	—	—	—	52	—	—	48
Lime Creek	LIM	3048	350	25.2	605	—	—	21	—	—	—	79
Lucky Boy Gulch	LKB	3121	230	29.3	239	—	18	—	15	—	—	68
Mill Creek	MCK	2755	0	17.9	255	—	—	—	—	13	—	87
Palisades	PAL	2591	25	22.9	219	—	—	20	—	—	—	80
Pool Table Road	PTR	2896	300	27.9	455	—	—	—	—	—	—	100
Spruce Mountain	SMT	3048	70	31.0	950	—	—	14	—	3	25	58
Terrace Lake	TRL	2670	195	11.0	199	67	—	—	—	4	—	29
Nonhost												
East Big River	EBR	2652	200									
Jakes Creek	JCK	3085	340									
Lucky Boy Pines	LBP	2926	140									
Pool Table Pines	PTP	2877	230									
Roadsite	RDS	2621	280									
Terrace Lake Pines	TLP	2658	340									
Wilson Ranch	WIR	2560	340									

Note: The lower size limit for stand description was 6.5 cm DBH.

*Species codes are as follows: ABCO, *Abies concolor*; PIAR, *Pinus aristata*; PIEN, *Picea engelmannii*; PIFL, *Pinus flexilis*; PIPO, *Pinus ponderosa*; POTR, *Populus tremuloides*; PSME, *Pseudotsuga menziesii*.

of each series were checked for errors with time series correlation analyses (Holmes 1986; Grissino-Mayer 2001). All ring-width series were standardized with cubic splines with 50% frequency responses at wavelengths of 150 years to remove the influences of age-related growth and stand dynamics (Cook and Peters 1981; Cook and Holmes 1986).

Series from the Palisades (PAL) and Pool Table Road (PTR) host sites required special treatment because of the impact of logging on the stands. Both sites showed physical evidence of logging, including stumps and old logging roads. Ring-width series showed large standwide releases that corresponded with cutting (death) dates on stumps sampled from the sites. To separate this human-caused effect on ring widths from effects of defoliation by budworm, the measured ring-width series were truncated at the probable date of timber harvest, and affected portions of the data were removed prior to standardization.

The nonhost chronologies were clustered in three geographical groups (see Fig. 1), and chronologies within these groups were well correlated with each other (minimum r value = 0.66, $p < 0.001$). The individual nonhost chronologies were combined into three composite chronologies: north (LBP, RDS, JCK-pine), central (EBR, PTP, WIR), and south (only one chronology, TLP). This compositing of nonhost chronologies (except for the single chronology in the south) minimized site-specific, nonclimatic responses of the nonhost chronologies and enhanced the subregional climate patterns in the nonhost series that were used for comparisons with (and correction of) the host series.

Previous research demonstrated that Douglas-fir and ponderosa pine growing in similar sites and regions tend to have similar growth responses to climate (Fritts 1974; Swetnam 1987). Similarity in host–nonhost climate response is necessary for effective application of the correction procedure (Swetnam et al. (1985), see details of this method below). We used graphical plots, correlation, and response function analyses to assess the host–nonhost climate responses in the RGNF. Response function analysis uses principal components to estimate the response of tree growth to climate variables (Fritts 1974). The climate variables we used were monthly total precipitation and monthly average temperature for the period 1895 to 1998 (NOAA, National Climate Data Center, Colorado Division 5³). We utilized divisional data because this record was longer than individual stations near the study sites, and Colorado Division 5 covers an area just slightly larger than our study area. Colorado Division 5 includes the Rio Grande Basin and encompasses the RGNF and the San Luis Valley. We examined response functions from August in the year prior to the year of ring growth through September of the year of ring growth. This window of months has been commonly found to include all or most of the climate variables in prior and current years that are most important to conifer tree-ring growth in the southwest (Fritts 1974, 1976). Response function analyses were completed for all individual host chronologies and nonhost composite chronologies for both temperature and precipitation. The resulting monthly climate response coefficients of the host and nonhost tree-ring-width chronologies were directly compared.

Outbreak reconstruction

Climatic variation contained in the host index series was removed (“corrected”) through subtraction of the nonhost index series following the strategy developed by Nash et al. (1975) and extended to insect outbreak investigations by Swetnam et al. (1985). The corrected series were calculated with the following equation:

$$[1] \quad \text{Corrected index} = I_{ht} = \frac{SD_h}{SD_n} (I_{nt} - \bar{I}_n)$$

where I_{ht} is the host index at year t , SD_h is the standard deviation of the individual host tree series for the period common to both series, SD_n is the standard deviation of the nonhost composite chronology for the period common to both series, I_{nt} is the nonhost index at year t , and $\bar{I}_n$ is the mean of the nonhost index for the period common to both series.

A computer program automates the correction procedure and applies a set of user-defined criteria for identifying outbreak patterns in measured ring-width series (OUTBREAK, Holmes and Swetnam (1996);⁴ see Swetnam et al. (1995) and Speer et al. (2001) for more descriptions of this program and examples of its application). The individual host tree chronologies (two standardized ring-width series averaged per tree) from each site were corrected separately using the corresponding nonhost composite chronology for that area (i.e., south, central, or north). The resulting corrected indices were records of host tree growth with reduced or no influence of climate. Values less than 1.0 in the corrected series indicated reduced growth with respect to potential growth, while values greater than 1.0 indicated increased growth. Criteria used to identify outbreaks were developed based on the characteristics of 20th-century outbreaks (Swetnam and Lynch 1989; Swetnam et al. 1995).

The corrected series were normalized by subtracting the mean and dividing by the standard deviation. The following criteria were applied to the normalized corrected series to identify outbreaks:

- (1) A minimum of 8 years of negative values in the normalized corrected series.
- (2) Two positive excursions (one before and one after the year of maximum growth reduction) were allowed. The positive excursions were allowed to include potential increased growth years during the beginning and ending years of an outbreak when larval populations may have declined and then surged again — a pattern that has been observed in some 20th-century outbreaks (Swetnam et al. 1995).
- (3) A minimum of 1 year in the outbreak period was required to reach at least -1.28 standard deviation units. This value delineates the approximate smallest decile of the ring-series values. This particular threshold value is somewhat arbitrary (just as statistical confidence limits are arbitrary), but from experience has proved to be effective in correctly identifying known outbreak periods recorded in documentary sources (i.e., insect survey reports and maps).

⁴R.L. Holmes and T.W. Swetnam. 1996. Program OUTBREAK users manual. Unpublished paper, on file at the Laboratory of Tree-Ring Research, University of Arizona, Tucson, Ariz.

After carrying out the tree-ring correction procedures and tentatively identifying outbreaks, we verified outbreaks in the 20th century with USDA Forest Service records. We located various types of reports from the Forest Service that contained information on historical outbreaks at regional, National Forest, and individual site levels. These reports included annual National Forest and Regional insect and disease summary reports, National Forest reports on western spruce budworm outbreaks, and annual detection survey maps. From these reports, a yearly summary of budworm activity was generated, recording available information, such as specific geographic location (i.e., place names) of outbreak, size, and intensity. The tree-ring-reconstructed outbreaks were compared with this annual summary of reported outbreaks to test whether the reconstructions correctly identified historically documented outbreaks.

Because the outbreak reconstructions often show some percentage of trees recording an outbreak, a threshold was set to identify outbreaks at a site from these apparent smaller events (or background noise). Certain characteristics, such as outbreak return interval and duration, however, depend upon the threshold utilized. For example, a lower threshold will show a shorter return interval than a higher threshold. To highlight the differences between lower- and higher-intensity events, characteristics for the outbreak series at each site were summarized using two minimum thresholds of trees recording an outbreak: 30 and 50% of the composite tree series present in each year.

Duration and growth reduction were summarized for periods at each site for outbreaks with 50% or more trees recording a reduction in growth. The duration and quantity of growth reduction for the trees showing outbreaks were averaged together by site. We examined these characteristics for changes over time by pooling the outbreaks into century-length periods and testing for differences. Because the data were not normally distributed, we applied a Kruskal–Wallis nonparametric ANOVA to test for overall significance of the differences among centuries, and then we performed Mann–Whitney two-sample tests to determine which centuries were different from each other (Burt and Barber 1996; Wilkinson 1998). Only Douglas-fir was tested for these changes because white fir was a minor component in most of our sampled stands. For testing of outbreak duration, we did not include the most recent outbreak because growth reduction was continuing at several sites at the time of sampling (1997 and 1998).

A composite time series for the entire study area was created by computing the ratio of the numbers of trees recording an outbreak to the total number of trees in the data set for each year. The spectral (or periodic) characteristics of this time series were examined using a smoothed periodogram (Bloomfield 1976). The estimated spectrum was obtained by smoothing a periodogram computed from the discrete Fourier transform with two Daniell filters with lengths three and five. The 95% confidence interval around the spectrum was calculated using the chi-square distribution (Bloomfield 1976). A null continuum was created by smoothing the periodogram further, because the use of a “white noise” series is not appropriate to tree-ring studies (Meko et al. 1985).

In addition to the periodogram analysis we performed a singular spectrum analysis (SSA) (Vautard and Ghil 1989;

Speer et al. 2001). SSA is a nonparametric method for analyzing time series that employs a type of principal components analysis. An output of this analysis is a listing of the principal components (and their eigenvalues, percent variance explained, and period) representing the dominant periodicities (waveforms) contained in the original time series. We used this analysis to compare with the results of the periodogram analysis and to estimate the percent variance explained by the dominant periodicities identified in both analyses.

Relationships between outbreaks and climate were analyzed by comparing the regional outbreak series with summer (June, July, August average) tree-ring-reconstructed and instrumental Palmer drought severity indices (PDSI) (Cook et al. 1999). The grid point in southwestern Colorado (representing a $1^\circ \times 1^\circ$ latitude–longitude area) was used from the Cook et al. (1999) coterminous United States PDSI network. The coincidence of budworm outbreak–endemic periods (in the regional budworm series) and wet–dry episodes (in the PDSI series) was examined with a two-way contingency analysis. The PDSI series was filtered with a symmetrical 13-weight digital filter to emphasize decadal-scale variations (Fritts 1976). Periods in the filtered PDSI series with values higher than 0.5 or lower than –0.5 were defined as “wet” or “dry”, respectively. Maximums of 25% of trees recording outbreaks or greater in the regional outbreak series were classified as outbreaks. Minimums of 25% or less were classified as endemic periods. Because the total number of events tested in this contingency analysis was small, a Fisher two-tailed exact test was used (Zar 1999).

Results

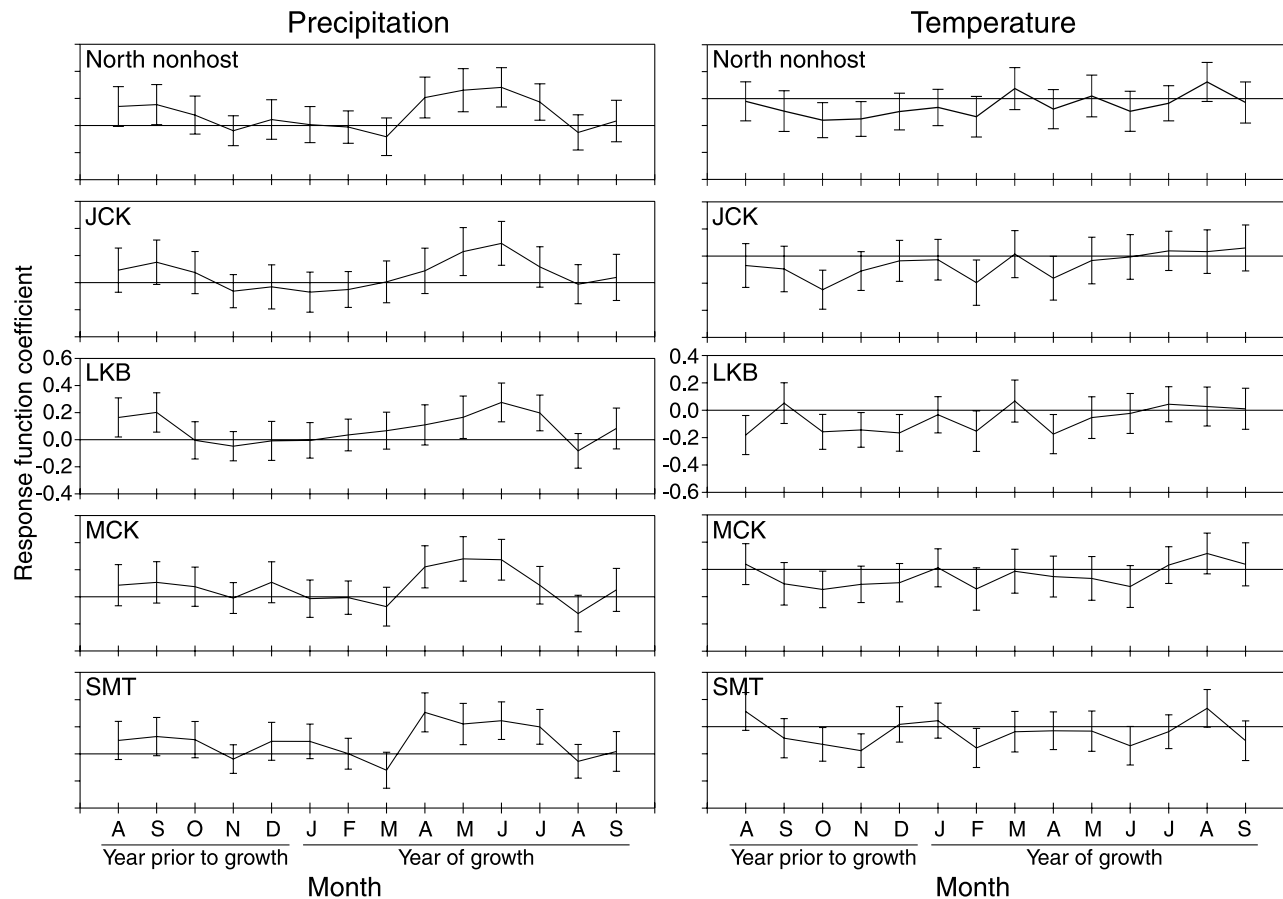
Dendrochronological characteristics

A total of 752 radial series from 397 trees (316 host, 81 nonhost) was used. Mean sensitivity and autocorrelation values for the host and nonhost series were similar, but the nonhost series had higher mean sensitivities and greater numbers of missing rings because of their more xeric locations. The cross-dating, correlation values, moving correlations, and overlay plots indicated that the high-frequency, interannual growth variation corresponded well between the host and nonhost chronologies. Pearson’s correlation coefficients between the host chronologies and the regional non-host composites ranged from 0.48 to 0.86.

Response function analysis revealed that the host and non-host chronologies had similar responses to precipitation and temperature. The results from the northern chronologies are shown as examples (Fig. 2). Results for the other subregions were similar and are described only. In the northern chronologies, ring growth in both host and nonhosts responded positively to precipitation occurring in the spring and summer of the year of growth. The ring-width chronologies showed a negative response to temperature in October and November of the year prior to growth.

The central chronologies showed a similar but less pronounced response to both precipitation and temperature. The central nonhost chronology had a positive response to precipitation in June and July of the year of ring growth. The host chronologies also responded to June precipitation, with some sites showing responses to precipitation in May. Growth

Fig. 2. Precipitation and temperature response function curves for the northern portion of the Rio Grande National Forest, Colorado. The north nonhost chronology is the composite of nonhost sites for the area. Error bars indicate the 95% confidence interval.



of the central chronologies (host and nonhost) responded negatively to temperature in November prior to growth and in June during the year of growth. The response of the southern chronologies to precipitation (host and nonhost) was primarily in the fall (August and September) prior to growth, with a response in some chronologies to precipitation during the summer of growth. The temperature response of the southern chronologies was mixed, but again, was similar between host and nonhost chronologies. Positive responses to temperature in both host and nonhost chronologies occurred in March, and negative responses in both species occurred during the early summer, primarily June.

A few differences did appear between monthly variables in some comparisons, but overall there was a broad similarity in the shapes of the host and nonhost response functions (i.e., the ups and downs in the coefficients through the course of the prior and current year were similar; see example of Fig. 2). Another general observation was that the climate – tree growth relationships were not very strong in most cases, in either host or nonhost chronologies. Typically only one to five monthly variables were significantly related to tree growth (i.e., values with 95% confidence interval bars completely above or below the zero line in Fig. 2) in each chronology, and these significant ($p < 0.05$) months were

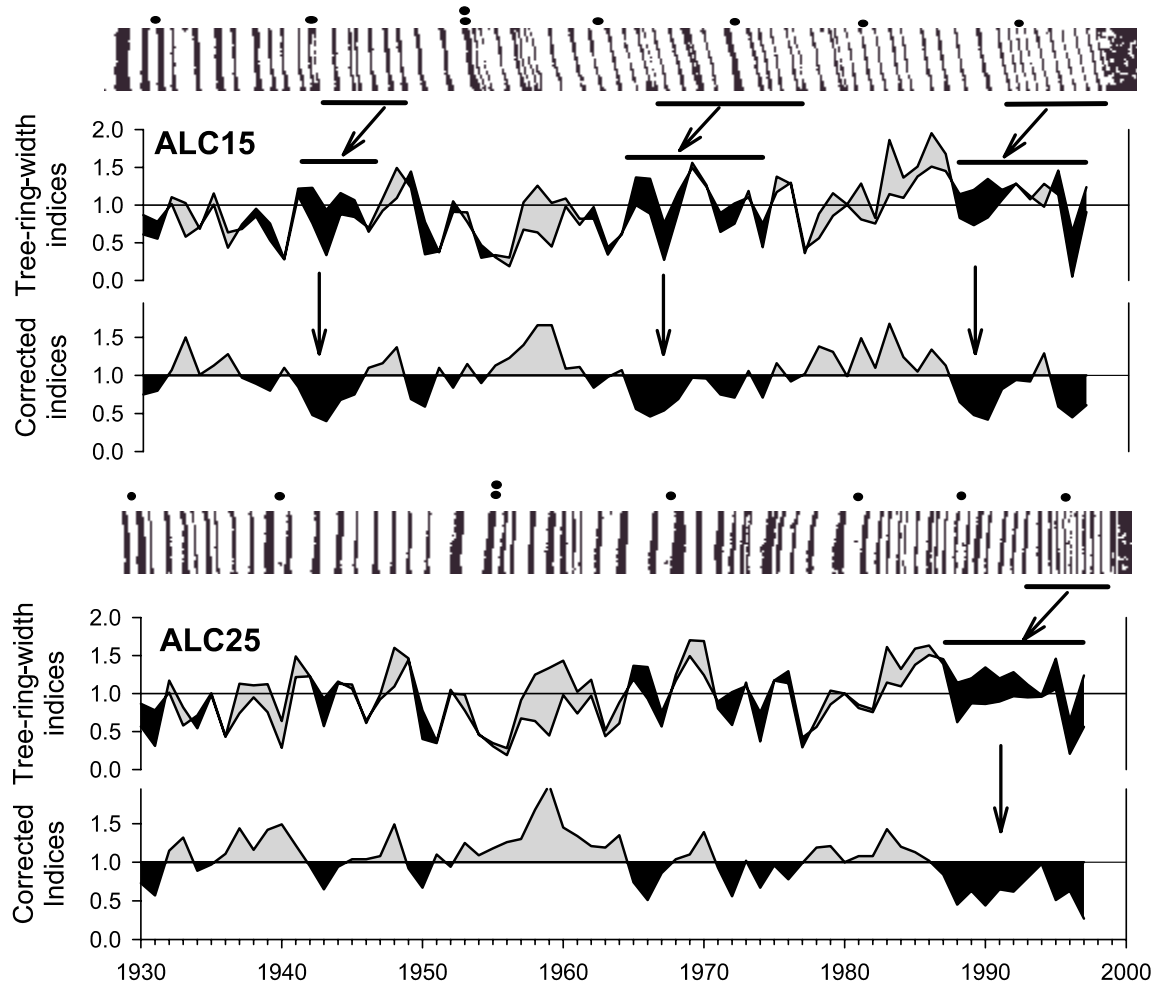
usually shared between hosts and nonhosts. For example, 24 of 29 (83%) significant precipitation variables in host response functions matched significant variables in the nonhost response functions. Eleven of 19 (58%) of the significant temperature variables in host response functions corresponded with significant variables in the nonhost functions.

Tree-ring record of 20th-century outbreaks

Reconstructed outbreaks were compared with historical documentation. Three general outbreak periods on the RGNF from the 1940s to present were recorded in historical documentation: 1940s, late 1950s to late 1960s, 1980s to 1990s. All three outbreak periods were reflected in the tree-ring reconstructions (Figs. 3 and 4). Part of one of these outbreaks evident in the tree-ring series (the late 1960s), however, was not well confirmed by the documentary records (maps and survey reports), as discussed below. The first recorded outbreak was reported on the eastern and western slopes of the San Luis Valley from Villagrove to Poncha Pass in 1945 (M.E. McKnight, unpublished manuscript⁵). This area is in the northern portion of the RGNF and includes the Lucky Boy Gulch site (LKB), which recorded an outbreak during this period. The mean corrected series from

⁵M.E. McKnight. Undated. Outbreaks of the western spruce budworm recorded in the central and southern Rocky Mountains. Unpublished manuscript, on file at the Laboratory of Tree-Ring Research, University of Arizona, Tucson, Ariz.

Fig. 3. Two examples of host and nonhost tree-ring comparisons from the Alder Creek site. The upper graph in each set shows the ring-width indices from a white fir tree overlaid on the ring-width series from the nonhost composite chronology from this subregion. The gray shading shows periods when the host tree chronology exhibited higher growth than the nonhost composite chronology, and the black shaded areas show the periods of lower host ring growth. The lower plots in each set show the corrected series derived by subtracting a rescaled version of the nonhost chronology from the host chronology. Horizontal lines and arrows show the correspondence of documented 20th-century outbreaks in the measured chronologies and in the scanned images of the actual cores from these trees. Note that the late 1960s to early 1970s outbreak evident in the ring series is not well confirmed in the documentary record, but we have reasons to believe that this outbreak did in fact occur (see text). Despite this uncertainty, the well-confirmed outbreaks (1940s and 1980s to 1990s) are clearly evident only in the corrected series and are generally too subtle to be identified by only a visual inspection of the cores or the measured host ring-width series. Although the 1940s and 1960s outbreaks did not reduce growth in the lowermost tree (ALC25) by a sufficient magnitude or duration to be identified as outbreaks with the criteria that we used, slightly reduced growth during these periods suggests that this tree may also have experienced some defoliation at those times.

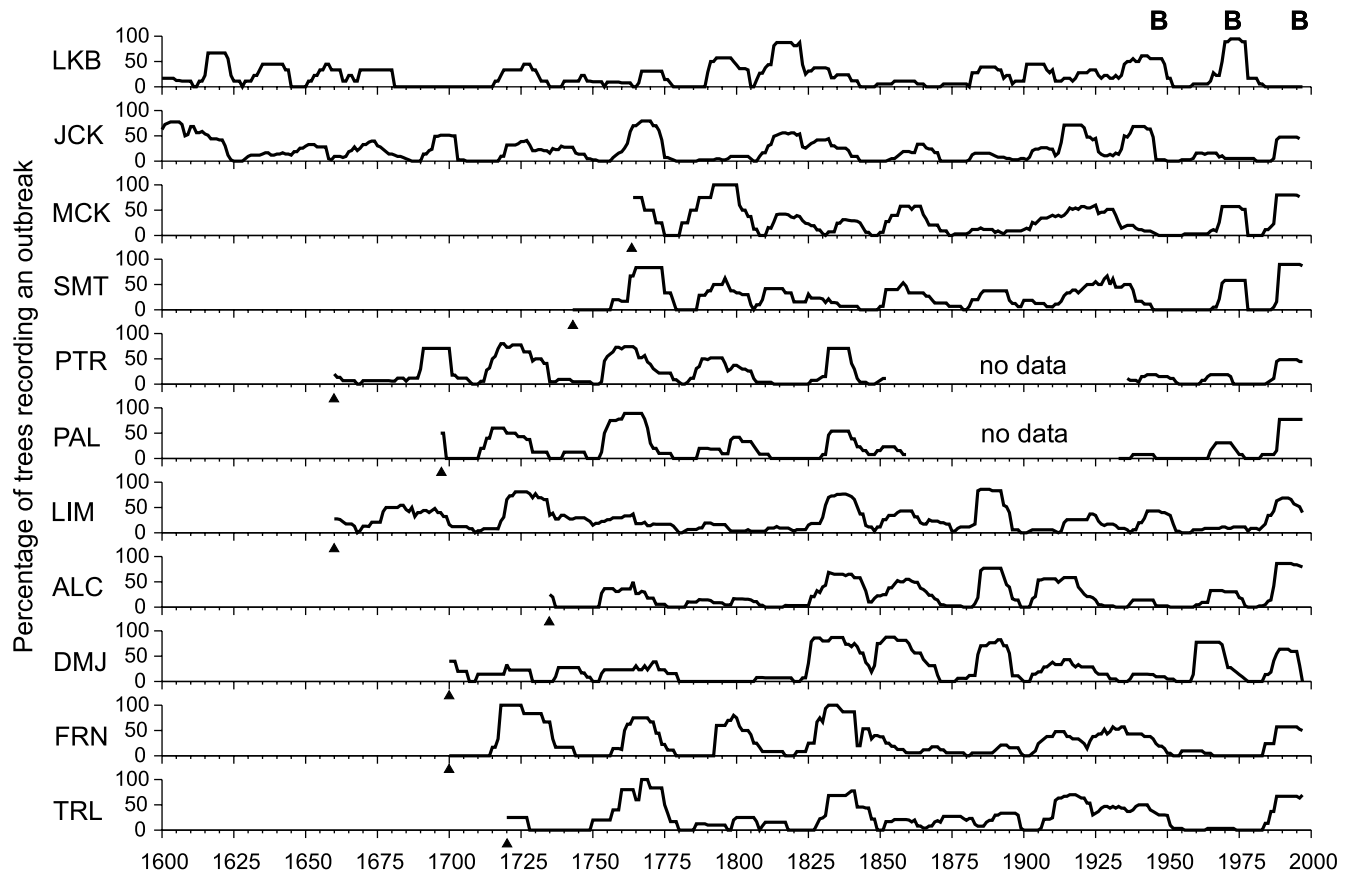


the LKB site indicated a pronounced outbreak occurred from approximately 1935 to 1949. Some individual tree corrected series at this site indicated constant budworm activity throughout the early portion of the 1900s and up through the 1940s outbreak.

Outbreaks were better documented in maps and written records after the 1950s compared with previous decades, but the post-1950 documentary records were not complete either. Regional reports stated that “budworm damage on the San Juan and Rio Grande National Forests increased to 39,423 acres in 1956 and 89,500 acres in 1957” (M.E. McKnight, unpublished manuscript⁵). Aerial detection survey maps for 1955 showed a large outbreak in the area encompassing the Demijohn Peak site (DMJ). The outbreak

was mapped with medium- to high-activity areas. The DMJ tree-ring chronology recorded an outbreak beginning in 1959, and growth was affected through the early 1970s (Fig. 4). This outbreak affected approximately 75% of the trees sampled at the site. Hence, the record in the tree-ring chronology lagged 4 years behind the first report of the outbreak in aerial surveys for this general area (i.e., 1955 to 1959). This is not unusual because the lag in response of tree-ring growth to defoliation is typically 1 to 3 years (Belyea 1952; Alfaro et al. 1982; Swetnam and Lynch 1989; Mason et al. 1997). Moreover, the aerial survey maps were coarsely drawn and did not show pockets of nondefoliated areas within larger polygons of defoliated areas. Therefore, it is quite possible that the specific area of sampling at DMJ (less

Fig. 4. Percentage of trees recording an outbreak of western spruce budworm in the Rio Grande National Forest, Colorado. Sites are oriented from north (top) to south (bottom). Small triangles indicate the beginning of the series that were truncated when either the host or nonhost sample depth dropped below four trees. The letter “B” indicates documented outbreak periods. Data were removed from portions of PTR and PAL because of timber harvesting effects.



than 10 ha) was, in fact, not defoliated until one to a few years after the 1955 survey. The regional report by M.E. McKnight also emphasized the later surge in defoliated area (i.e., 1956 and 1957) on the Rio Grande National Forest.

The aerial surveys showed the outbreak spreading during the late 1950s northwest along the Rio Grande and reaching the area around the Palisade site (PAL) in about 1958. Aerial survey maps show continued western spruce budworm activity through 1962. A regional report on conditions during 1962 reported that “two spruce budworm outbreaks in southern Colorado were successfully controlled in June 1962. The largest, on the Rio Grande National Forest, involved aerial spraying on 84,285 acres” (USDA 1963). It is not clear, however, what occurred in 1963 and 1964, because no maps were found for these years. Maps from 1965 to 1968 show defoliation present in the southeast part of the study area (to the west of Antonito, Colorado), but apparently expanding in 1967 and 1968 with more defoliated areas mapped to the north (and closer to more of our sample sites). The PAL site chronology shows an outbreak from about 1964 through 1976. Outbreaks during this period were also reconstructed in the LKB, MCK, and SMT chronologies (Fig. 4), but the 1965 to 1968 maps do not show defoliation specifically within these areas during this period.

In general, the late 1960s part of this outbreak that is evident in the tree-ring reconstructions (i.e., PAL, LKB, MCK,

SMT) is not well verified by the documentary records (but there is correspondence with the early 1960s outbreak at DMJ). There are reasons, however, to have some confidence in the tree-ring-reconstructed outbreaks in the late 1960s to early 1970s. For one thing, the aerial survey maps were drawn with low spatial resolution (polygons are usually greater than about 100 ha in size), and these surveys could have missed smaller defoliated patches the size of our sampled stands (about 10 ha) or low to moderate levels of defoliation not visible from aircraft over flights. Moreover, as mentioned, some maps could not be found for the early 1960s (1963 and 1964) or for the post-1968 period. It is possible, therefore, that defoliation occurred during these missing years in the documentary record, and defoliation may have occurred at finer spatial scales than was typically mapped in aerial surveys. The 1967 and 1968 maps suggest an expanding population (relative to previous years), and so the late 1960s to early 1970s peaks in some of the tree-ring sites (Fig. 4) may reflect this expansion. We speculate that the 1962 insecticide spraying (with DDT) may have delayed the outbreak that began in the early 1960s and is reflected in some of our sites (e.g., at DMJ), but by the middle to late 1960s budworm populations surged again. In sum, we suspect that relatively low levels of defoliation or small patches of defoliation in the middle to late 1960s may not have been detected by aerial surveys, or otherwise mapped by entomologists.

The most recent outbreak began in the 1980s, and this event corresponds well between the documentary and tree-ring records. Reports in 1992 stated that budworm populations in the Creede and Del Norte districts of the RGNF had been at outbreak levels since the early 1980s. The tree-ring record exhibited the start of the outbreak in some trees and sites in 1983 or 1984 (e.g., PAL, DMJ, FRN, LIM, MCK, TRL), with a maximum surge in the percentage of trees recording the event from about 1986 to 1988. Defoliation in the 1990s was moderate to heavy and widespread on the RGNF. In 1995 the continued budworm activity was described as “chronic” on the RGNF (Johnson 1996). This was reflected by the relatively high percentage of trees affected in nearly all of the host sites in the reconstruction. In addition to the generalized reports, available aerial defoliation maps of portions of the RGNF in 1996 confirmed outbreaks on or near the Palisades (PAL) and Alder Creek (ALC) sites.

An important point to note here is that the outbreaks that were detected using the corrected tree-ring series (i.e., using the nonhost correction procedure) and that were also clearly confirmed through documented reports and aerial surveys (i.e., 1940s, early 1960s, 1980s) did not usually appear as visually obvious periods of ring growth reduction in the uncorrected tree-ring series. There were a small number of trees in some stands showing clearly visible growth reductions on the increment core samples and in the measured ring-width series; however, they were not sufficient in number to develop an outbreak chronology. The majority of increment cores samples had no clearly discernible suppression in ring-width during periods that were subsequently detected in the corrected ring series and then confirmed as late 20th-century outbreaks in the documentary records (Fig. 3).

Outbreak reconstruction

Outbreaks of western spruce budworm were identified over the past several hundred years (Fig. 4). Although site-specific patterns were evident, a high degree of synchronicity among sites was evident. There were approximately 14 widespread outbreaks over the past 350 years. The intensity of outbreaks varied within the study area. For example, during the 1750–1775 period, the north-central and far southern sites had stronger outbreaks, while the remaining sites had lower levels of budworm defoliation. Over the entire study area, there were few extended periods without outbreaks. Within smaller areas, however, periods with no activity did occur. For example, the period from 1775 to 1825 was a quiescent period for the central and southern sites, while the northern sites exhibited two outbreaks. A summary of outbreaks at individual sites showed that intervals between outbreaks ranged from 30 to 60 years for events that affected at least 30% of the trees at a site (Table 2). Outbreaks affecting a greater percentage of trees within sites (a 50% minimum threshold) occurred at longer return intervals (i.e., about 50 to 80 years).

Distinct periodic patterns were evident in the outbreak time series for the entire study area (lower portion of Fig. 5). The dominant fluctuations observed in the time series (Fig. 5) occurred at intervals ranging from about 25 to 40 years (Table 2). The spectrum of this outbreak series confirmed periodicities of about 25, 37, and 83 years (Fig. 6). A simple average of the intervals between events that affected over

50% of the trees in the study area was 83 years, suggesting that the spectral peak at approximately 83 years was related to these larger events. The singular spectrum analysis (SSA, graphics not shown) confirmed these approximate periodicities, with the dominant waveforms in the regional series having periods of 38.7 years (principal components (PC) 1 and 2, 35% variance explained), 83.7 years (PC 3, 16% variance explained), and 26.5 years (PCs 4 and 5, 25% variance explained).

Two outbreak periods exceeded the typical level of trees affected: the early 1600s and 1990s. The higher percentage of trees affected in the 1600s, however, was due to the decreased sample depth (47 host trees), as only two sites had sufficient trees in both the host and nonhost chronologies to provide a valid reconstruction during this early period (Fig. 4). The higher percentage of trees affected in the 1990s outbreak reflects the high degree of synchrony across the sites during this event (10 of 11 sites). Some degree of synchrony in outbreak occurrence across the study area was evident over the entire length of the reconstruction. The exact starting and ending years of most outbreaks among stands, however, did not usually coincide. The most recent outbreak was clearly unique in the strong synchrony of the beginning years among the sampled stands. Some prior outbreaks exhibited synchrony in beginning years, but the beginning of other outbreaks were usually characterized by relatively gradual increases in the percentage of trees affected within and between sites.

Growth reduction and duration values for the outbreak periods since 1600 were variable (Fig. 7). Differences in the mean or maximum growth reduction values between century periods were not very large ($p = 0.07$ and 0.76 , respectively) (Table 3). Outbreak duration at the tree level was shorter in the 20th century than during the 18th or 19th centuries ($p < 0.001$), but not during the 17th century ($p = 0.15$). The 17th century had a reduced sample with fewer overall sites in the record during this period, which may have affected the duration estimates.

Jakes Creek site

The oldest sampled trees were at the Jakes Creek site (Fig. 8). The oldest living Douglas-fir in this stand had an inner date of AD 1225, and 14 of the living Douglas-fir trees had inner dates prior to AD 1400. Cross-section samples from dead trees extended the host chronology back to AD 934. In addition to many old Douglas-fir trees, the stand contained several old limber pine trees; the oldest dated to AD 1074. Although the limber pine were growing within the host stand, and thus potentially influenced by defoliation of the host trees, they provided the only sufficiently long non-host chronology available to use in correcting the host chronology for climate variations. These two chronologies provided the longest reconstruction of any of the sites (Fig. 9).

Analyses of this long time series revealed long-period variation in outbreak patterns. The 1400s were a period of relatively high budworm activity, with typically at least 20% of the trees exhibiting an outbreak. In contrast, reduced defoliation occurred in the 1500s as indicated by the low number of trees affected (Fig. 9). During this period, the percentage of trees affected rarely exceeded 20%. This pe-

Fig. 5. Instrumental and tree-ring-reconstructed summer Palmer drought severity index (PDSI) (top) and percentage of host trees recording a reduction in growth on the Rio Grande National Forest, Colorado (bottom). PDSI series were smoothed with a 13-weight digital filter. Vertical shaded lines were aligned with troughs in the outbreak series that had less than 25% of trees recording an outbreak.

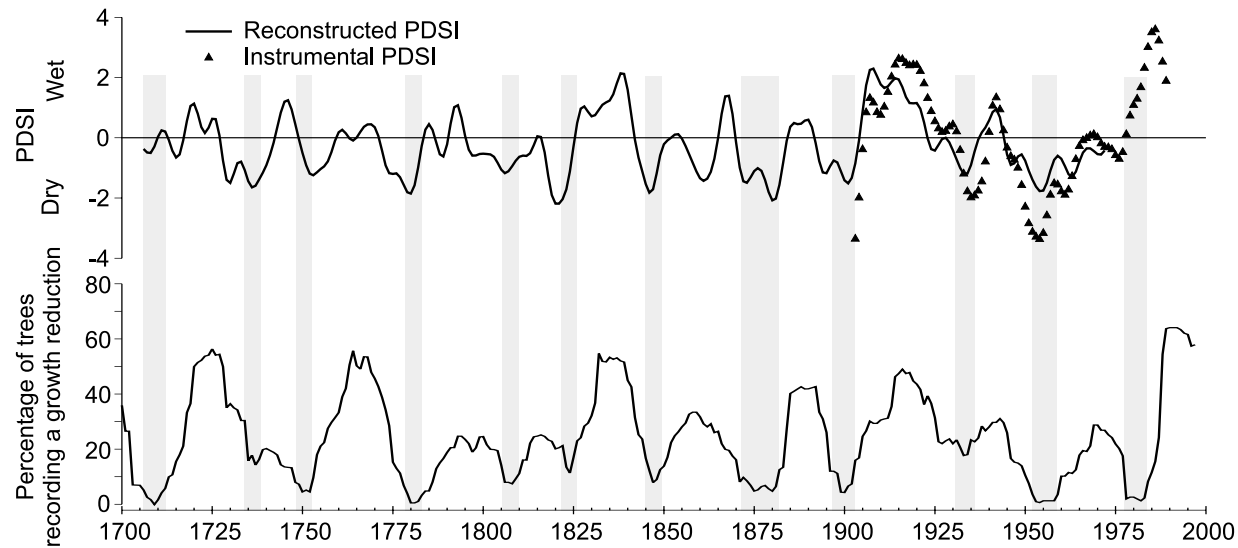


Table 2. Outbreak return intervals and duration estimates by site.

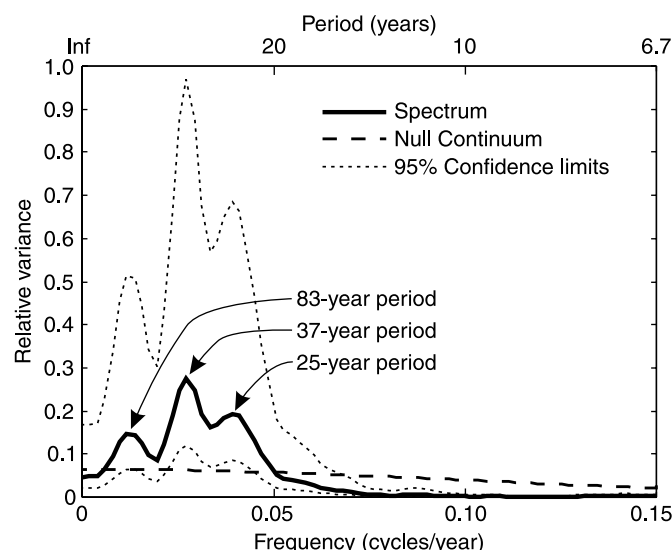
Site	Start of record* (year)	Minimum threshold (%)	No. of outbreaks	Return interval† (years)		Duration (years)			
						Trees		Site	
						Mean	SD	Mean	SD
ALC	1735	30	7	39.0	23.1	12.8	3.7	17.0	4.8
		50	6	46.8	29.9	12.8	3.8	17.8	4.7
DMJ	1700	30	7	44.3	20.5	15.5	9.1	20.0	12.7
		50	4	53.7	25.4	16.1	9.9	11.0	16.3
FRN	1700	30	7	44.8	22.6	15.4	6.2	20.9	7.6
		50	6	53.8	27.5	15.2	6.2	21.5	8.1
JCK	1380	30	14	44.3	24.2	12.5	5.0	18.8	8.1
		50	9	72.9	34.6	13.3	5.2	21.1	8.5
LIM	1660	30	9	38.9	15.9	13.5	4.8	19.6	7.0
		50	5	77.8	30.9	13.7	5.1	21.4	8.4
LKB	1565	30	13	31.6	18.8	12.5	4.7	15.8	8.1
		50	6	75.8	66.0	13.3	5.5	20.8	9.8
MCK	1764	30	7	34.2	19.7	12.7	5.4	17.3	8.2
		50	5	51.3	23.7	13.0	5.7	19.2	9.0
PAL	1697	30	6	36.0	9.8	11.9	4.1	13.5	4.2
		50	4	60.5	24.7	12.4	4.4	15.3	4.1
PTR	1660	30	6	35.5	10.1	13.2	4.6	16.5	6.3
		50	5	35.5	10.1	13.7	4.7	17.8	6.0
SMT	1743	30	8	33.0	12.2	11.8	4.2	17.8	6.5
		50	6	46.2	20.0	11.6	4.2	17.7	7.3
TRL	1720	30	5	59.0	28.5	15.9	7.7	23.8	14.0
		50	4	78.7	1.5	16.4	7.9	26.8	14.2

Note: Outbreaks were determined from percentage of host trees recording an outbreak using two minimum thresholds. Duration estimates are presented two ways: the average of the individual trees and the average duration at the site based on the percentage of trees recording an outbreak (see Fig. 4).

*Lengths truncated when there were fewer than four trees in the host or nonhost sample.

†Return intervals are the number of years between the start dates of outbreaks.

Fig. 6. Smoothed periodogram of percentage of trees recording an outbreak from 1600 to 1997 for the Rio Grande National Forest. Periodicities labeled with arrows are cases where the spectral peaks and their 95% confidence limits exceed the null continuum line.



riod of quiescence was followed by a large and relatively long outbreak in the early 1600s. There were a total of four outbreaks that affected high percentages of the trees in this stand. These outbreaks occurred in the early periods of the 20th and 19th centuries, the middle 16th century, and the early 17th century. Trends prior to 1400 are difficult to interpret because of the decreasing number of samples.

Outbreak – climate relationship

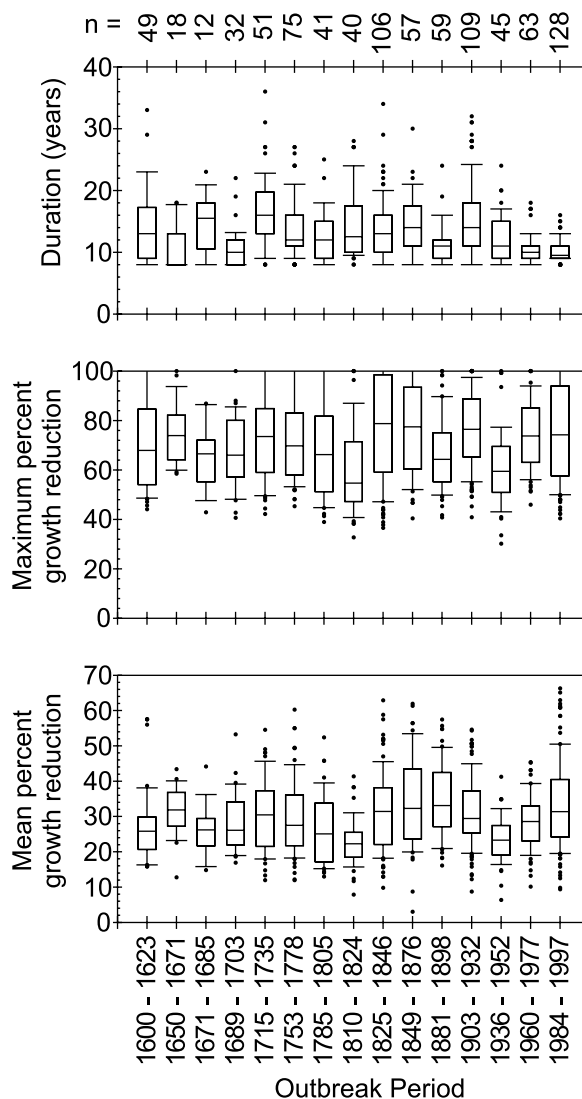
Outbreak and endemic periods were statistically associated with wet and dry episodes, respectively (Fig. 5). Since 1700, 8 of 11 outbreaks coincided with wet episodes, and 11 of 12 endemic periods coincided with dry episodes. The probability of obtaining such a coincidence of events by chance was very low (Fisher's exact test, $p = 0.011$).

Discussion

Detecting past outbreaks

In contrast with most previous tree-ring studies of western spruce budworm, where the effects of outbreaks were often clearly visible in uncorrected ring-width series (e.g., Wickman et al. 1980; Alfaro et al. 1982; Swetnam and Lynch 1989, 1993; Hadley and Veblen 1993; Weber and Schweingruber 1995), outbreaks in our study area were not typically visible as sharply reduced tree-ring growth. Brubaker and Greene (1979) also found that the growth of Douglas-fir in northeastern Oregon declined only slightly during budworm outbreaks. They concluded that tree-ring-width patterns in grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), which tends to be more severely defoliated than Douglas-fir, had to be studied from some stands to confirm the timing of outbreaks in Douglas-fir. Swetnam and Lynch (1989, 1993) observed that although outbreaks in the Colorado Front Range and northern New Mexico often could be detected by visual

Fig. 7. Box plots of the characteristics of reduced growth periods in individual Douglas-fir trees. Trees were grouped into periods of increased activity over the entire Rio Grande National Forest. Trees were included only if at least 50% of the trees at the individual site exhibited growth reductions that met the outbreak criteria. The number of trees meeting this criteria is shown at the top. The boxes represent the 25th, 50th, and 75th percentiles, while the tails represent the 10th and 90th percentiles.



examination of increment cores or of raw ring-width measurements, the effects of some defoliation events were much more subtle. They found that the "correction" procedure involving the use of a nonhost tree-ring chronology as a climatic control was necessary to consistently and confidently identify outbreaks within and among trees and stands. Mason et al. (1997) found that insect population data in northeastern Oregon were a better predictor of host tree radial growth when using corrected indices than when using uncorrected tree-ring indices as measures of host tree growth. Weber and Schweingruber (1995), in contrast, relied entirely on visual detection of outbreaks in host tree-ring samples and measured series from the Colorado Front Range, and asserted that this was the most efficient and reliable approach.

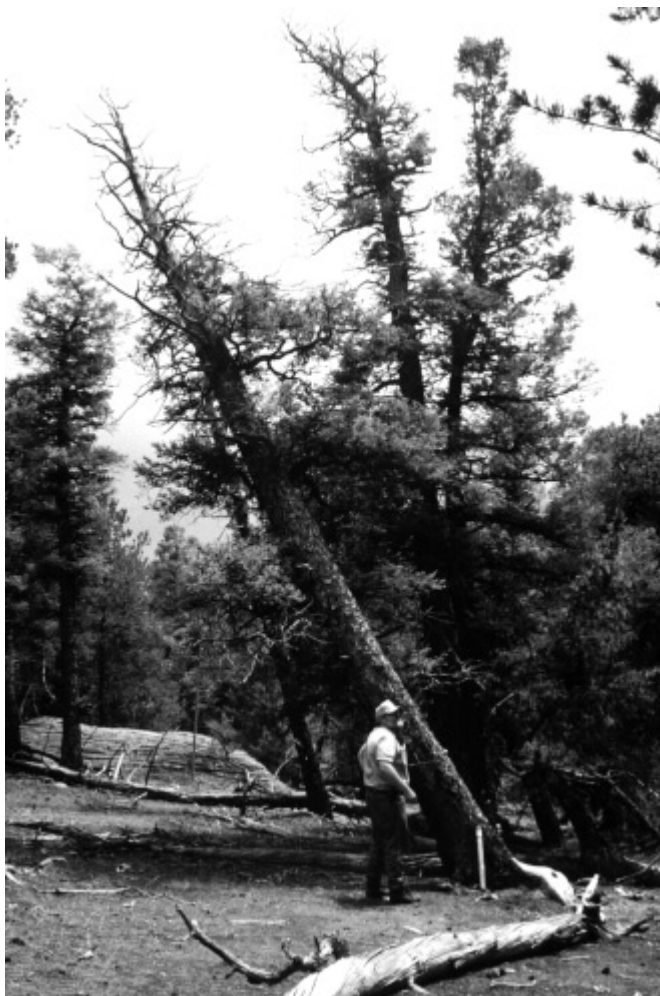
Table 3. Descriptive statistics for outbreak characteristics on a tree level pooled across all sites on the Rio Grande National Forest.

Period*	Duration (years)		Mean % growth reduction		Maximum % growth reduction	
	Median	SD	Median	SD	Median	SD
1600–1703	11a	5.1	27.0a	9.0	67.1a	16.0
1704–1805	13b	5.1	27.5a	10.5	69.7a	17.4
1806–1899	12b	4.5	30.8a	11.4	69.7a	19.4
1903–1997	10a	3.1	26.4a	7.7	68.0a	16.4

Note: A minimum threshold of 50% trees affected was used at the site level to define an outbreak. Medians followed by different letters are significantly different ($P < 0.05$) between century periods.

*Periods are not exact centuries because outbreaks overlapped centuries.

Fig. 8. Photograph of Jakes Creek site. Several ancient Douglas-fir trees (400 to 600 years old) are in the center of this view. All four trees on the skyline exhibit the typical characteristics of host trees that have been repeatedly defoliated, including multiple crooks in their main stems, old spike tops, and killed branches.



In this study, neither the Douglas-fir nor the few white fir raw ring-width series showed consistent, sharply reduced growth periods. We did observe sharp growth reductions in a small number of tree-ring samples (<20 trees) during some

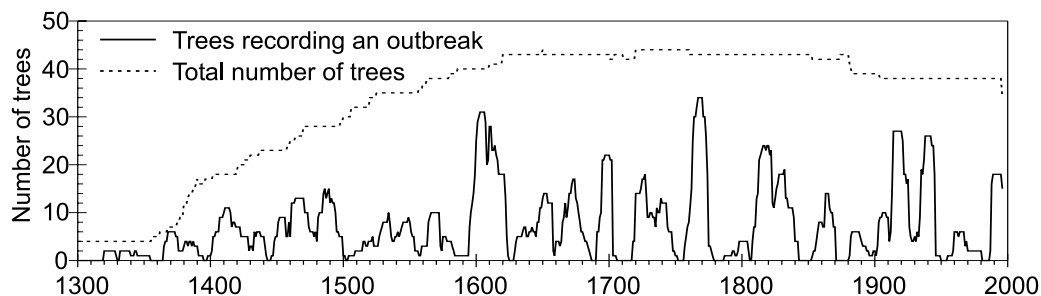
of the known and inferred outbreaks in some of the sampled stands. It is important, however, to recall that late 20th-century outbreaks identified in the corrected series were generally confirmed by independently documented outbreaks in aerial surveys and entomological reports. The late 1960s outbreak evident in some stands was not well confirmed, but this does not change the fact that the other good matches between the documents and the tree rings (e.g., 1940s, early 1960s, 1980s) clearly showed that defoliation events did occur within our sampled stands, but radial growth effects were clearly and consistently detectable only in the corrected host tree-ring width series (e.g., Fig. 3).

Possible explanations for these observations are that historical outbreak severity (amounts of defoliation per tree) in this area of southwestern Colorado may have been relatively low compared with other regions. Host trees may also have been more resilient and (or) more productive in this region than in other areas of the southern Rockies. The host trees might have been able to partially compensate for the lost foliage during the relatively wet periods that coincided with outbreaks. We suspect that some combination of these explanations is probably correct. Testing of these hypotheses will require continuous monitoring of insect populations, defoliation amounts, and tree growth in comparative analyses with other budworm outbreak regions.

A key point here is that the effects of defoliation by insects on tree-ring widths, like most other environmental effects on tree rings, should be considered to be relativistic. Absolute values of tree-ring widths are functions of multiple factors, including tree age, climate variations, endogenous and exogenous disturbances, and genetics (Fritts 1976; Cook 1987). This is why dendrochronologists standardize tree-ring widths (i.e., remove age trends) prior to other quantitative analyses. It is recognized that the relative effects of age trends must be removed prior to other statistical treatments or interpretations; otherwise the relative changes in other factors can be masked. There is no a priori reason to believe that the annual- to decadal-scale effects of defoliation must always result in variations and trends in tree-ring series that will overwhelm (or exceed) the variations and trends induced by other factors, such as climatic influences. Hence, defoliation by western spruce budworm in our study area apparently does reduce tree-ring growth of host trees, but this is a relative reduction in growth. This growth reduction is typically detected only when compared with growth that was expected during those periods, as estimated by nonhost tree-ring growth.

An additional implication of these findings is that tree-ring studies aimed at reconstructing past climate variables from budworm host species (e.g., Douglas-fir and white fir) should be particularly cautious in using these species from this region of Colorado. A recent experimental study by Trotter et al. (2002) on chronically infested pinyon pine (*Pinus edulis* Engelm.) trees in northern Arizona suggested that herbivore effects may commonly confound dendroclimatic reconstructions. Although we agree that dendroclimatologists should carefully avoid this possibility (e.g., by judicious site and species selection), we doubt that insect outbreak signals are a confounding problem in the vast majority of existing tree-ring climate reconstructions. This is because most climate reconstructions are based on trees

Fig. 9. Number of Douglas-fir trees recording budworm outbreaks at the Jakes Creek site (solid line) and sample depth (dotted line).



growing in extremely dry or cold environments where episodic or chronic insect defoliators are rare to nonexistent. Moreover, based on our experience, and that of most dendroecologists who have studied insect outbreaks, the type of subtle effects of episodic defoliation on ring widths we have noted in this study is unusual. In most cases past insect-caused defoliation episodes are noticeable as sharply reduced and sustained low-growth periods, and these periods do not usually coincide with droughts or cold periods.

Does the correction procedure create “false” outbreaks?

We have carefully considered the possibility that the correction procedure may somehow create “false” outbreaks (i.e., artifacts), but this appears to be highly unlikely. The most logical way that the correction procedure could introduce outbreak artifacts would be if the climatic responsiveness or sensitivities of the host and nonhost trees were systematically different. Some differences between the host and nonhost site characteristics were evident. In particular, host sites tended to be in more mesic locations with higher tree densities than nonhost sites. Nonhost sites (primarily ponderosa pine) were typically located on more exposed southerly facing slopes with lower tree densities. It is possible that during periods of increased moisture the nonhost trees could have had a more positive response than the host trees, whereas host trees might have encountered limiting factors such as competition for nutrients and light earlier than nonhost trees. If these differences existed, host growth during wet periods would tend to be less than the nonhost growth, and these differences might have been detected as outbreaks. During dry periods, the nonhost growth levels would have declined further than host levels, and detection of outbreaks might have been less probable. In this scenario, spurious outbreaks would be detected during wet periods with a lack of outbreaks during dry periods, as we observed in our comparison between the reconstructed outbreaks and PDSI.

However, the climate – tree growth response function analyses showed that the host and nonhost series were generally quite similar during the 20th century (Fig. 2). Moreover, the strength of the precipitation or temperature responses, as reflected in the magnitude of response function coefficients, were not measurably greater in nonhost trees versus host trees. The highest and most statistically significant coefficient values, for both monthly temperature and precipitation variables, were usually in the 0.2 to 0.4 range (and –0.2 to –0.4 range for negative responses) in both host and nonhost species (see Fig. 2 example). Because of the relatively broad confidence intervals on these coefficient values they were

generally not statistically distinguishable between hosts and nonhosts. Thus, the possible explanation that the nonhosts may have been more responsive to precipitation variables is not supported. About 83% of all significant precipitation variables in host response functions were also significant in nonhosts response functions. Overall, our statistical results indicate that the host and nonhost trees share many more similar climatic responses than differences.

It remains plausible that there were short-term differences (i.e., decadal) in climatic responses between the host and nonhost species that were not apparent in the average responses estimated over the 20th century. Assessing changing climate – tree growth responses on decadal scales, however, is problematic because such reduced-period analyses would necessarily result in small sample sizes in response function or other time series analyses and hence less confidence in mean values or in difference tests. This kind of assessment can be quite complex and would involve an in-depth study on its own.

Although we acknowledge the possibility that the correction procedure may have created outbreak artifacts, we point to four lines of evidence that indicate this scenario is highly unlikely, and that our reconstructions are generally reliable. First, as previously mentioned, response function analyses (including more detailed climate – tree growth assessments in Ryerson (1999) and Swetnam (1987)) have shown that the overall climatic responses of host and nonhost species from nearby areas were generally quite similar, despite some differences in site characteristics. Second, we confirmed with independent documentary evidence (i.e., maps and reports) that most outbreaks identified during the late 20th century in the corrected series were indeed increased defoliation periods within the region and specific areas of the sampled stands (e.g., Fig. 3). Third, within all host stands we observed at least a few examples of the classic morphological features that are indicative of past defoliation events. These features are commonly reported in the literature (e.g., Wickman 1980; Alfaro et al. 1982; Swetnam and Lynch 1989), and include: (i) crooked stems with old spike tops emerging (sometimes two or three on a single tree), resulting from past top killing during defoliation episodes, (ii) numerous dead branches persisting on main tree stems, and (iii) evidence of epicormic sprouting of new branches from stems on some trees (Fig. 8). (It should be noted that these features were present on some trees in the stands, but were not clearly present on most of the sampled trees.) These observations provide additional evidence that multiple past outbreak events occurred within the sampled host stands where we detected outbreaks in corrected ring-width series.

A fourth line of evidence that the relative reduced growth periods in the corrected series were indeed budworm outbreaks, and not artifacts, was the presence of strong periodicities in the regional event time series. As noted in the results of the spectral analyses, periods of about 25, 37, and 83 years were detected in the regional series using two different techniques (periodogram and singular spectrum analysis). The SSA showed that the two strongest periodic components (about 27- and 39-year periods) explained about 60% of the total variance in the regional time series of percentage of trees scarred per year (1600 to 1997). These are remarkably strong quasi cycles (i.e., “quasi” because the periods between peaks and valleys vary somewhat from period to period). Quasi cycles of this strength and consistency are virtually unknown in climatic time series of this type, but they are known or strongly suspected in forest insect population biology and particularly in the case of the eastern spruce budworm (*Choristoneura fumiferana* (Clemens)) (e.g., Royama 1984). The two strongest periodicities we detected (i.e., about 25 to 27 and 37 to 39 years) conform to what is known about the approximate periods between budworm outbreaks in eastern and western North America. Other tree-ring studies (Swetnam and Lynch 1993) found similar periodicities, and host trees in these regions often showed sharp reductions in raw tree-ring widths during outbreaks confirmed with documentary records in the late 20th century.

Given the presence of these strong quasi cycles in the outbreak reconstructions, it is evident that there is a glaring inconsistency in the alternative explanation that a difference in host–nonhost climate response is the cause of outbreak artifacts in the corrected ring series. If a systematic difference in host–nonhost tree-ring responses to climate was a common cause of spurious outbreaks in the reconstructed time series, this would imply that an underlying climate variable (or variables), to which the host and nonhosts were both responding, must itself be strongly quasi-cyclical. This conclusion is not supported. Spectral analysis of reconstructed precipitation time series that were positively correlated with budworm activity (e.g., see Swetnam and Lynch 1993) indicates that there were only weak periodicities in this climatic variable. Summer PDSI is a good integrator of temperature and precipitation variables that Douglas-fir (host) and ponderosa pine (nonhost) trees are responsive to in the western U.S. (Fritts 1976; Cook et al. 1999). SSA of the summer PDSI series we used in this study indicates that several decadal periodic components were present (i.e., periods ranging from about 10 to 30 years), but the cumulative variance explained by these weak quasi cycles was less than 30% of the total variance in the original time series. The potential synchronization of weak climate and strong budworm quasi cycles (i.e., “coupled oscillators”) is a fascinating topic and certainly worthy of future research.

Considering all of the four lines of evidence listed above, the simplest and most parsimonious explanation for our detection of quasi-cyclic relative growth reductions in host trees is that these patterns were due to outbreaks of western spruce budworms. An alternative explanation — that our outbreak reconstructions are largely artifacts due to systematic differences in climatic responses of host and nonhost trees — would require the acceptance of a rather incredible

and unsupported conclusion, i.e., that heretofore unknown, strong climatic cycles are somehow revealed by our procedures.

Outbreak synchrony and climate

Spatial synchrony of population dynamics is often attributed to rapid migration of individuals (Smith 1974) and (or) extrinsic factors, such as climate variations (Moran 1953). Long-range dispersal of budworm is possible; larvae can be moved by wind (Carolin 1987), and adults of both the eastern spruce budworm and western spruce budworm have been observed to fly or to be blown long distances by wind (Dobesberger et al. 1983; Carolin 1987). Even though individuals can move long distances, outbreaks of the eastern species of spruce budworm are generally not thought to commonly spread by long distance dispersal (Royama 1984). In addition, outbreaks expanding due to dispersal should proceed like a wave through the forest (Berryman 1987). The high synchrony between the sites observed in the RGNF argues against a wavelike pattern.

Extrinsic factors can also play a role in synchronizing populations over large regions. Moran (1953) hypothesized that a similar climatic pattern over a region could bring independently oscillating populations into phase with each other. In a regression–interpolation study that used historical western spruce budworm defoliation and climate data from Oregon, Williams and Liebhold (1995) found that when temperature and precipitation variables were increased budworm populations expanded (but not when these variables were decreased). The correspondence of outbreaks with periods of normal to wet conditions in our study area (Fig. 5) suggests that climate might be synchronizing budworm populations. From the mid-1970s to late 1990s, the southwestern United States experienced a high frequency of El Niño events, resulting in mild, wet winters and springs (Swetnam and Betancourt 1998). Regional climate records for the San Juan Mountains also show an increase in total precipitation beginning in the mid-1970s (NOAA, National Climate Data Center, Colorado Division 5³). If outbreaks are triggered somehow by periods of increased moisture, the 1970s–1990s increase in precipitation might be involved in the high degree of synchrony of the recent outbreak.

The mechanisms of temperature or moisture control over budworm populations are not well understood, particularly at the regional and decadal scales. It is hypothesized that folivores benefit through changes in the nutrient or water content of plant tissue. For example, better quality and quantity of plant production during periods of increased moisture availability could be beneficial to defoliators (Larsson 1989). Long-term observations of insect populations, experiments, and modeling at a range of scales, from trees to regions and months to decades, will be necessary to evaluate possible causal mechanisms of budworm population responses to climatic variations.

Jakes Creek

During sampling for their outbreak reconstructions, Lynch and Swetnam (1992) found unusually old stands in northern New Mexico that provided the longest records of repeated defoliation by western spruce budworm (>600 years). The Jakes Creek (JCK) stand in this study was similar in many

respects to these stands. The most noticeable similarity was the old, extremely slow growing trees and open-stand conditions (Fig. 8). The average DBH for ≥ 700 -year-old Douglas-fir trees in a stand in New Mexico was 44.4 cm (Swetnam and Lynch 1993), while at Jakes Creek the average DBH for ≥ 600 -year-old Douglas-fir trees was only 38.8 cm. These sites were not found in noticeably harsh locations, such as a forest border, where slower growth would be expected. All sites showed both tree-ring and physical evidence in some living trees (spike tops, crooked stems, and dead leaders) of repeated budworm defoliation (Fig. 8). The great age of the Jakes Creek stand may provide support for the hypothesis that western spruce budworm and Douglas-fir may have developed a kind of mutualistic relationship that allows some stands to persist for extraordinary lengths of time (Swetnam and Lynch 1993). By maintaining low levels of productivity in overstory trees, budworm might help maintain open canopy conditions that are less conducive to stand-replacing fires.

Outbreaks and land-use history

Changes in forest structure resulting from human land use have been hypothesized as a chief reason for the changes in outbreak patterns observed in some regions (Fellin et al. 1983; Anderson et al. 1987; Wulf and Cates 1987; Swetnam and Lynch 1989, 1993). These changes include a shift toward greater abundance of host trees within mixed conifer stands. Although the San Juan Mountains have a somewhat different land-use history than the Front Range and New Mexico, this area has also experienced significant human impacts. Mining and timber harvesting began in the late 1800s in the study area, particularly along the Rio Grande (Simmons 1999). The sample sites in the central portion of the RGNF lie within this area of human use and impacts. Two host sites showed evidence of timber harvesting during the late 1800s. Utilizing stumps we determined that timber harvesting occurred in the Palisades (PAL) site around 1887 and at the Pool Table Road Site (PTR) in the late 1870s. Other evidence of land uses included a water carrying flume in the Terrace Lake site (TRL). Tree-ring responses along the remnants of the flume indicate an approximate construction date of 1907. Grazing, fire suppression, and continued timber harvesting have all influenced forest structure, creating conditions that are likely to be more favorable to budworm outbreaks.

Despite these forest changes, outbreak patterns of western spruce budworm in the San Juan Mountains did not exhibit the obvious changes in the 20th century that have been found elsewhere. No changes in mean or maximum growth reduction were observed relative to the prior two centuries. In contrast, reconstructions from the Front Range have suggested an increase in the severity of outbreaks (Swetnam and Lynch 1989, 1993; Hadley and Veblen 1993; Weber and Schweingruber 1995). Duration of growth reduction has also been reported to be longer in the 20th century in Montana (Anderson et al. 1987). Periods of growth reduction on the RGNF were shorter in the 20th century than in the 18th and 19th centuries (Table 2). Duration in the 20th century was not significantly different than that in the 17th century; however, the lower sample size in this early period of the record decreases our confidence in this pattern.

Another change in outbreak patterns noted in the Front Range was increased synchrony of outbreaks. It was hypothesized that the larger, more homogenous stands of Douglas-fir and true firs resulted in a greater apparent synchronization of outbreaks in the late 20th century (Swetnam and Lynch 1989, 1993). Synchrony of outbreaks among sites on the RGNF has been high throughout the length of the record with no obvious changes. The most recent outbreak on the RGNF, however, was unique in the high degree of synchrony in the beginning years of the outbreak within and among sites. The single remaining stand showed a growth reduction that did not meet the minimum criteria for classification as an outbreak at the time of sampling.

Uncertainties and limitations

As previously discussed, we recognize that the host–nonhost correction procedure is imperfect, and it remains plausible that short-term differences in climatic responsiveness or sensitivities of the tree species has introduced some spurious outbreaks as “artifacts” in our reconstructions. We have argued, however, that it is unlikely that this effect has created the basic historical features of our regional reconstruction, particularly the periodic character of this time series. Nevertheless, research is needed to further test the fidelity of the host–nonhost correction approach in reconstructing past outbreaks. Additional work involving direct comparisons and experiments of insect population and defoliation time series with tree-ring time series is needed (e.g., Mason et al. 1997; Trotter et al. 2002).

Other limitations of the tree-ring data presented here should also be kept in mind. First, the sampled sites may not be representative of all mixed-conifer stands on the RGNF because we selected them partly on the basis of the presence of old host trees that had survived past outbreaks. These sites may show more uniform responses and susceptibilities to budworm defoliation than would a random sample, particularly in the most recent period. Tree-ring growth is the result of several environmental factors, including age trends, climate variations, and disturbances (Fritts 1976; Cook 1987). Even though we have attempted to remove age-related growth, climate factors, and some human-caused disturbances effects (e.g., a possible logging event) through various analytical techniques, some influence from these factors may still remain.

Tree-ring reconstructions of outbreak severity (or magnitude) and duration is probably less precise than estimates of overall outbreak frequency (i.e., number of events per time period). Severity of an outbreak includes the levels of mortality that occurred, and this impact was not assessed. Growth reduction of surviving trees can provide some idea of outbreak intensity, but it is constrained by two thresholds. First, the criteria used to detect outbreaks establish a lower boundary for the duration and growth reduction of outbreaks. Second, surviving trees will not show the high degree of growth reduction that result in death of the tree. The effect of these two constraints was visible in the low overall variation in some characteristics, such as the maximum percent growth reduction. Our estimated growth reductions were also based only on outbreaks in trees that met our detection criteria hence these estimates are for affected trees only and not the sampled stands as a whole.

Conclusions and summary

Western spruce budworm has a long history of coexistence with its primary host trees in the southern Rocky Mountains. Regular outbreaks have recurred in the forests of the San Juan Mountains for at least the past 600 years. The outbreaks have been regionally synchronous across the RGNF, with peaks in activity at approximately 25- to 40-year intervals. Larger events occurred at approximately 83-year intervals. Greater variation in intervals and duration of outbreaks occurred at the stand level.

The peaks in activity across the RGNF typically corresponded to increased moisture, while periods of low activity corresponded to dry periods. The most recent western spruce budworm outbreak was unusually synchronous in the starting year of the outbreak. Although the mortality caused by these outbreaks was not studied, records from living trees showed that these stands were capable of surviving multiple outbreaks. No significant changes in growth reduction were observed from one century to another, although duration in the 20th century was shorter than the prior two centuries.

An important implication of our finding that host tree growth was typically reduced only in a relative sense during outbreaks is that tree-ring samples cannot always be simply visually assessed to identify past outbreaks. In the absence of comparison with nonhost ring-width series, host ring-width series may not show obvious evidence of past outbreaks if (i) defoliation coincides with relatively favorable climatic conditions and (or) (ii) defoliation levels are not extreme and (or) (iii) the defoliated trees are highly productive and resilient to the effects of defoliation (including branch and top killing). This suggests that dendroecological studies aimed at reconstructing insect outbreaks should utilize non-host control chronologies whenever possible. Dendroclimatologists should not assume that the absence of visually obvious, sharply reduced and sustained low-growth periods in tree-ring series guarantees that insect outbreak effects were not present.

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