

TREE-RING RECONSTRUCTION OF WESTERN SPRUCE BUDWORM
OUTBREAKS IN THE RIO GRANDE NATIONAL FOREST, COLORADO

by

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ABSTRACT

Tree-ring records were used to reconstruct the spatial and temporal patterns of western spruce budworm (*Choristoneura occidentalis* Freeman) outbreaks in the Rio Grande National Forest (RGNF) of southern Colorado. Reconstructions at 11 host stands showed a synchronous pattern of outbreaks with a peak in the number of trees recording outbreaks over the entire RGNF on average every 24 years. These synchronous periods of outbreaks coincided with periods of increased moisture as indicated by an independently reconstructed summer Palmer Drought Severity Index, while relatively few trees recorded outbreaks during dry periods. The reconstruction on the RGNF does not support the hypothesis that human land use has significantly altered outbreak patterns. Tree response to outbreaks in the RGNF was different from prior studies as reductions in growth were typically detectable only when growth was compared to that of nonhost tree species.

CHAPTER 1: INTRODUCTION

Insects and pathogens are integral components of forest ecosystems with important roles in many ecosystem processes (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 species composition and structure of forests and redistribute biomass and resources (Schowalter 1981, Romme et al. 1986). Insect-caused disturbances interact with other disturbances by predisposing trees to attack by other insects (Schmid and Mata 1996), as well as to wind and fire. Insects can raise the potential of fire by increasing litter and woody fuels, but fire also influences insect populations by modifying habitat and directly impacting insects (McCullough et al. 1998).

Insect species that are particularly important in plant population dynamics are those that experience episodic outbreaks in population levels (Crawley 1989). Only a relatively small number of forest insect species exhibit these explosive increases in population densities (Furniss and Carolin 1977), but these species have particular importance. The extreme increases in populations can result in severe and relatively rapid changes in forest characteristics.

Budworms (*Choristoneura* spp.) are a widespread and influential group of insects in the forests of North America. These native defoliating insects affect forests throughout Canada and the United States, and in some 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* [Mirbel] Franco), the true firs (*Abies* spp.), Engelmann's spruce (*Picea engelmannii* Parry) and western larch (*Larix occidentalis* Nutt.) throughout the range of the insect from southern Arizona and New Mexico north to British Columbia (Harvey 1985, Hermann 1987). Reduced growth results from the decreased photosynthetic capacity of defoliated individuals (Van Sickle 1987). Extensive defoliation can result in top-kill and tree mortality (Ferrell and Scharpf 1982). Mortality is often variable and concentrated in the smaller age classes, altering the age structure toward older individuals (Van Sickle 1987).

Concern for outbreaks of western spruce budworm has centered primarily on its impacts upon timber harvesting, increased fire danger and degradation of aesthetically important areas (Fellin and Dewey 1986). With its widespread range and extensive impacts, the western spruce budworm has been labeled the most destructive insect pest of western coniferous forests (Fellin et al. 1983, Fellin and Dewey 1986). This description, however, ignores the long history of western spruce budworm in these forests and thus its role in their development.

Human activity has influenced western spruce budworm outbreaks both directly and indirectly. Due to the conflicting nature of outbreaks with some human uses, direct control of outbreaks has been accomplished using insecticides beginning in the late 1940's (Fellin 1983, Stipe 1987). Large scale suppression efforts have been discontinued because of the lack of long-term impact on outbreaks, the high cost, and environmental concerns (Fellin 1983). Human activity may have also indirectly altered outbreak patterns through forest use and management, including: grazing, timber harvesting, development and fire

suppression. Forest stand characteristics are important in determining the susceptibility to budworm defoliation (Wulf and Cates 1987). Of these characteristics, the density of the host tree species and structure of the forest are important characteristics determining the level of defoliation (Wulf and Cates 1987). Thus, by modifying forest structures, human management and use has had the potential of altering susceptibility to outbreaks.

Dendrochronological evidence has indicated that outbreak patterns have changed recently. The most common change noted is a trend toward more intense and widespread outbreaks in the 20th century (Anderson et al. 1987, Swetnam and Lynch 1993, Hadley and Veblen 1993).

These insights into temporal and spatial patterns of insect outbreaks have been revealed through the utilization of tree-ring records. No other method provides the long-term, annual resolution record of forest insect populations. Application of tree-ring studies to insects has long been an interest of dendrochronologists with investigations of insect influence on tree growth dating back to the 1920's (Dunning 1925, Perry 1925). Various procedures, from abrupt growth changes (Schweingruber 1986), insect specific ring signatures (Speer 1997), host/nonhost species comparisons (Carlson and McCaughey 1982, Swetnam et al. 1985), and suppression/release indices (McCune 1983, Veblen et al. 1991) have been used to identify and extract insect population signals from tree-ring records.

The goal of this research was to enhance our understanding of the temporal and spatial patterns of western spruce budworm outbreaks in the southern Rocky Mountains. I reconstructed and described outbreak regimes in the Rio Grande National Forest in the

San Juan Mountains using dendrochronological techniques. When characterizing disturbance regimes such as insect outbreaks, there are several primary characteristics that are important: frequency, distribution, predictability, size, magnitude and synergism (White and Pickett 1985). While not all of these characteristics of outbreaks can be determined from the tree-ring reconstruction presented here, tree-rings can provide valuable information on the temporal (frequency) and spatial patterns (distribution, size) as well as some level of information on duration and intensity (magnitude). Like many forests in the western U.S., the San Juan Mountains have experienced impacts resulting from human activities. Therefore, the potential exists for the altered outbreak regimes that have been found elsewhere. I analyzed the reconstruction to examine the outbreak patterns for any anomalous changes in the 20th century that may be related to past forest use and management.

During the development of the outbreak reconstruction, methodological issues pertaining to the use of the tree-ring series and the host/nonhost comparison technique were encountered. An important process when dealing with large numbers of tree-ring series is the standardization of the series to a common mean and variance for compilation of these series into chronologies and comparison between series. Standardization transforms data and thus can influence the outbreak reconstruction and its characteristics. I examined the potential impacts of standardization upon reconstruction techniques, with a focus on the detection and characterization of outbreak duration and growth reduction.

CHAPTER 2: TREE-RING RECONSTRUCTION OF WESTERN SPRUCE BUDWORM OUTBREAKS

Introduction

There is increasing evidence that characteristics of western spruce budworm outbreaks have changed within the past century. Many analyses of long-term outbreak patterns 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, Swetnam and Lynch 1993, Hadley and Veblen 1993, Weber and Schweingruber 1995, Swetnam et al. 1995). Spatial analyses have shown an increase in the synchrony of outbreaks during the 20th century compared to prior periods (Swetnam and Lynch 1989, Swetnam and Lynch 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 higher frequency in the Blue Mountains of Oregon (Swetnam et al. 1995).

These changes in outbreak patterns have been attributed to the greater abundance and continuity of host stands resulting from prior forest use and management. Timber harvesting beginning in the 19th century combined with later fire suppression efforts, has favored the establishment of shade tolerant species such as Douglas-fir and true firs in multiple crown level forests that are more susceptible to outbreaks of budworm (Carlson et al. 1983, Wulf and Cates 1987). The lack of fire has also shifted landscape structure

from a mosaic of patches of various ages and species to more contiguous and homogenous stands of susceptible species.

Western spruce budworm outbreak patterns have been shown to be associated with climatic patterns, therefore shifts in outbreak patterns could also be related to climate dynamics. 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 has been hypothesized to benefit insects through concentration of nutrients and compounds in plant tissues, lower resistance and reduced growth (Mattson and Haack 1987). More recent research, however, has shown that this is not true for all insects and instead there is a range of responses to water availability (Larsson 1989, Price 1991). Reconstructions of western spruce budworm outbreaks from New Mexico, Colorado and Oregon have shown a correspondence between outbreaks and periods of increased moisture availability, with few outbreaks occurring during droughts (Swetnam and Lynch 1993, Swetnam and Betancourt 1998).

Prior outbreak reconstructions in Colorado have focused primarily on the Front Range (Swetnam and Lynch 1989, Swetnam and Lynch 1993, Hadley and Veblen 1993, Weber and Schweingruber 1995). Outbreak patterns have not been examined in the southern Rocky Mountains west of the Front Range. This area contains large expanses of susceptible forest that have different characteristics than the Front Range. The different climate patterns and ecological communities of this area allow for potential differences in outbreak patterns. To evaluate this potential, I reconstructed outbreak patterns using a comparative growth technique. This technique uses the growth of nonhost tree species as

a reference level to which the growth of budworm affected host trees species are compared (Swetnam et al. 1985). One of the key assumptions of this technique is that the two groups of species should have similar climatic growth responses in absence of budworm defoliation. This assumption and the applicability of the host/nonhost comparison technique was tested by analyzing the climatic response of the host and nonhost species. In addition, graphical comparisons were used to evaluate the correspondence between the host and nonhost chronologies.

Basic characteristics of past outbreaks were described using the tree-ring reconstructions. Frequency and timing of outbreaks was examined through the use of spectral analysis and summary of outbreak return intervals. Spatial patterns were described through comparison of the individual site reconstructions across the RGNF. Outbreaks were characterized by determining the duration in the tree-ring record and the quantity of growth reduction. In addition to describing outbreak patterns, I evaluated the hypothesis that human land use has changed outbreaks by comparing outbreak patterns and characteristics in the 20th century to prior centuries. Timing of outbreaks was also compared to climate records to determine the relationship of outbreak with water availability.

Methods

Study area

The Rio Grande National Forest (RGNF) encompasses 794,000 hectares of the San Juan and Sangre de Cristo mountain ranges in southcentral Colorado. The majority 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 (Figure 2.1) with elevations ranging from 2560 to 3170 m. The headwaters of the Rio Grande are in the western portion of the RGNF, from which it flows east through the RGNF and into the San Luis Valley. Annual precipitation for the area ranges from 142 mm to 500 mm with an average of 310 mm (NOAA, National Climate Data Center, Colorado Division 5). 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 16.1 °C in July (NOAA, National Climate Data Center, Colorado Division 5).

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 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 and white fir (*Abies*

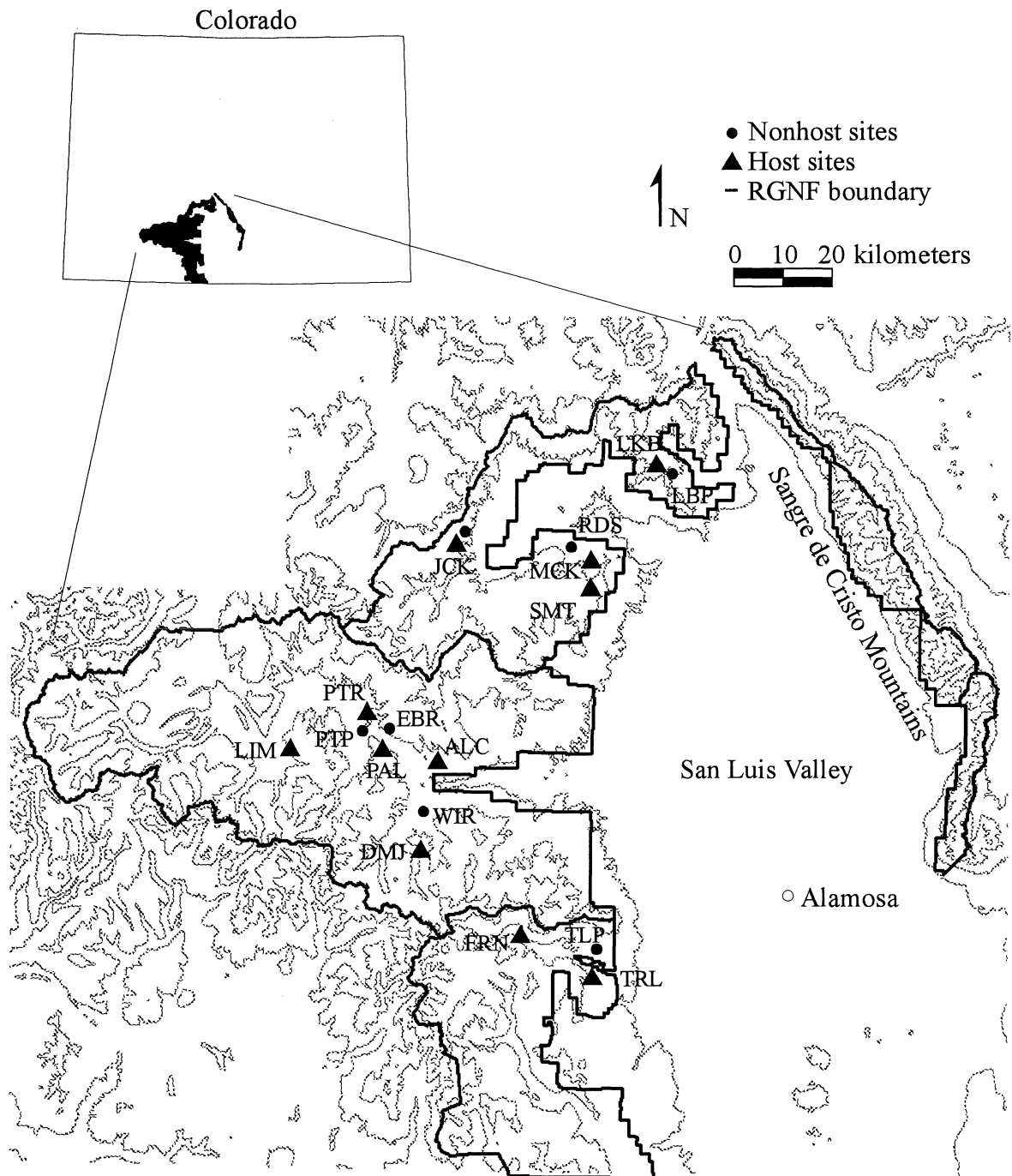


Figure 2.1. Study site locations for western spruce budworm outbreak reconstruction on the Rio Grande National Forest, Colorado.

concolor [Gord. & Glend.] Lindl. ex Hildebr.) and to a lesser extent Engelmann's spruce (*Picea engelmannii* Parry) (Schmid and Mata 1996).

Historical land use

Spanish settlers began to move into the San Luis Valley with livestock in the early 1600's, however most activity remained along the periphery of the mountains until the end of the 1800's (Griffiths 1984). Settlement in the San Luis valley accelerated in the 1850's and discoveries of gold in the San Juan drew people into the mountains (Simmons 1999). Settlers began to move into the Creede area beginning in the 1840's (Mumey 1949). The first major discovery of gold near the San Luis valley came in 1870 at what would become Summitville (Simmons 1999). By 1874 there were stagecoach stations every ten miles from Del Norte to Wagon Wheel Gap and onto Lake City (Mumey 1949).

The arrival of the Denver and Rio Grande Railway in the San Luis Valley over La Veta pass during the summer of 1878 enabled greater growth and movement of people into the area (Athearn 1962). In 1881 the railroad was extended west to Durango and a line was constructed from Alamosa up the Rio Grande to South Fork. Increasing mining activity and the development of the railroad drew people and development into many areas of the San Juan mountains. The D&RG completed the extension along the upper Rio Grande to Wagon Wheel Gap in December of 1891, however the company was reluctant to continue the line to the town of Creede. The president of the railroad, David Moffat, personally financed the extension of the railroad from Wagon Wheel Gap into Creede

which was completed in 1892 (Athearn 1962). The silver mining boom was in progress, and with the arrival of the railroad, Creede grew quickly.

To fulfill this need for building materials, the Creede Lumber Company was founded in January of 1892 (Mumey 1949). Mumey (1949) described the situation: “Tremendous demand for lumber during the ‘boom’ kept seventeen lumber yards busy day and night.” Some of the early lumber was shipped in on the railroad, but residents quickly began to take advantage of the trees in the area. Sawmills were established on East Willow Creek, Rat Creek, McCall Gulch, Bear Creek, South Fork and in Blue Park (Mumey 1949). Although the silver legislation of 1893 ended the silver rush, the silver boom and the railroad had brought accessibility to the area (Mumey 1949) and mining continued in Creede for nearly a century (Simmons 1999).

Field collections

Increment core samples were taken from 11 host stands and 7 nonhost stands during 1997 and 1998 (Table 2.1). Host stands were selected based upon: 1) presence of old individuals and 2) evidence of repeated budworm outbreaks. Prior research has shown that true fir species (*Abies* spp.) often show stronger growth responses to defoliation than Douglas-fir (Brubaker and Greene 1979, Swetnam 1987). White fir, however, is a minor component of the mixed-conifer forest in this region and only 3 of the selected sites contained white fir. Other tree species found in the host stands included: bristlecone pine (*Pinus aristata* Engelm.), Engelmann’s spruce, limber pine (*Pinus flexilis* James), ponderosa pine (*Pinus ponderosa* Lawson) and aspen (*Populus tremuloides* Michx.).

Table 2.1. Characteristics of sites used to reconstruct western spruce budworm outbreaks on the Rio Grande National Forest, Colorado. The lower size limit for stand description was 6.5 cm dbh.

Site		Elevation (m)	Aspect	Basal area (m ² /ha)	Density (trees/ha)	Percentage of total basal area ¹						
Name	Code					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°									

¹Species codes are: ABCO = *Abies concolor*, PIAR = *Pinus aristata*, PIEN = *Picea engelmannii*, PIFL = *Pinus flexilis*, PIPO = *Pinus ponderosa*, POTR = *Populus tremuloides*, PSME = *Pseudotsuga menziesii*.

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 5-10 hectares in size.

Continuous forest stands were sampled on linear transects, subjectively placed within stands along topographic contours. Typical transect lengths were 100 to 150 m long with 20 m intervals between points. At these points, two increment cores were taken 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). In addition, variable plot measurements 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 older 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. Within the patches, the older appearing Douglas-fir and white fir individuals were sampled and variable plot points were used to describe the patches. Due to the sampling differences, samples from these sites were mainly from the older age class, while the samples collected along transects included a greater variety of age classes. Cross-sections were taken from remnant wood (logs, snags, and stumps) where available.

Nonhost stands were selected based on the dominance of pine, proximity to the host stands, and climate sensitivity (principally precipitation). Stands separate from the host stands were selected in order 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 ten to thirty-five individuals at sites with these general characteristics.

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, Fritts 1976, Swetnam et al. 1985). Cores were mounted and surfaced so that individual tracheid cells were observable under magnification. The samples were crossdated (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 of each series were checked for errors with correlation analyses (COFECHA, Holmes 1986). All ring-width series were standardized with smoothing 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). The same standardization was used on both the host and nonhost series to preserve an equal amount of variance in all series (an analysis of standardization effects is presented in Chapter 3).

Series from two host sites, Palisades (PAL) and Pool Table Road (PTR), required special treatment due to impact of logging on the stands. Ring-width series showed large stand-wide releases that corresponded with cutting (death) dates on stumps sampled from the sites. Both sites showed physical evidence of logging, including stumps and old

logging roads. 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 removed prior to standardization.

Previous research has demonstrated that Douglas-fir and ponderosa pine growing in similar sites have comparable growth responses to climate (Fritts 1974, Swetnam 1987). This assumption is critical to the use of the host/nonhost comparison technique. I used graphical plots, correlation analyses and response function analyses to test this assumption. Response function analysis uses principal components to determine the months during which tree growth is most affected by climate variables. The months during which the trees were responding were compared between the host and nonhost chronologies.

Moving correlations of the pine and host chronologies were also used to analyze similarities and differences between the species over time. Due to the geographic grouping of the nonhost sites and the correlations between the chronologies, they were combined into 3 composite chronologies: north, central, and south. This also minimized any site specific, nonclimatic responses and enhanced the regional climate patterns.

Outbreak reconstruction

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

$$\text{Corrected Index} = I_{ht} - \frac{sd_h}{sd_n} (I_{nt} - \bar{I}_n),$$

where I_{ht} = host index at year t ,

sd_n = standard deviation of host for period common to both series,

sd_h = standard deviation of nonhost for period common to both series,

I_{nt} = nonhost index at year t , and

\bar{I}_n = mean of nonhost for period common to both series.

Each host tree composite series was corrected separately using the appropriate nonhost composite chronology (i.e. south, central or north)(Holmes and Swetnam 1996). The resulting corrected indices were records of host tree growth with little 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 1987, Swetnam and Lynch 1989). The corrected series were normalized by subtracting the mean and dividing by the standard deviation to bring the series to a common variance and facilitate outbreaks identification. 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 in the beginning and ending years of an outbreak

when larval populations are either increasing or decreasing (Swetnam et al. 1995).

In addition, this allows for brief declines in budworm populations that have been observed in some 20th century outbreaks (Swetnam et al. 1995).

3. A minimum of one year in the outbreak period was required to reach at least -1.28 standard deviation units.

Detected outbreaks during the twentieth century were compared to reports compiled on outbreaks in the RGNF and USDA Forest Service Region 2 (summarized in Appendix A) to verify identification of real outbreaks. The number of trees recording an outbreak at each site was plotted to provide an estimate of the severity and replication of the outbreak periods. These series were summarized using two minimum thresholds, 30 and 50%.

A composite series of the percentage of trees recording outbreaks for the entire study area was created by taking a ratio of the numbers of trees recording an outbreak to the total number of trees. The frequency content of this series was 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 3 and 5. 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, since the use of a “white noise” series is not appropriate to tree-ring studies (Meko et al. 1985).

Duration and growth reduction were summarized for periods at each site when 50% or more trees recorded a reduction in growth that met the outbreak criteria. The duration and quantity of growth reduction for the trees showing outbreaks were averaged together by site. I then grouped the outbreaks into the major outbreak periods as determined from the outbreak time series for the entire RGNF. I examined these characteristics for changes over time by pooling the outbreak periods into century length periods and testing for differences between these periods. Since the data were not normally distributed I applied a Kruskal-Wallis nonparametric ANOVA for significance and then performed Mann-Whitney two-sample tests to determine which centuries were different (Burt and Barber 1996, Wilkinson 1998). Only the Douglas-fir was tested for these changes as white fir was a minor component of the study with only a few samples. For testing of the duration I did not include the most recent outbreak as growth reduction was continuing at several sites. Relationships between outbreaks and climate were analyzed by comparing the regional outbreak series with summer tree-ring reconstructed and instrumental Palmer Drought Severity Indices (PDSI) (Cook et al. 1999).

Results

Host and nonhost growth responses

A total of 752 radial series from 397 trees were used in the outbreak reconstruction (Table 2.2). Mean sensitivity and autocorrelation values for the host and nonhost series were similar, but the nonhost series had slightly higher mean sensitivities and greater numbers of missing rings as expected for trees sampled on precipitation sensitive sites. The crossdating, correlation values, moving correlations and overlay plots indicated that the high frequency, inter-annual growth variation corresponded well between the host and nonhost chronologies. Pearson correlation coefficients between the host chronologies and the regional nonhost composites ranged from 0.48 to 0.86. Response function analysis showed that climate responses of the host and the nonhost trees to precipitation and temperature were similar (Figures 2.2 and 2.3). For all the chronologies there tended to be a positive response to precipitation in the fall prior to ring growth and in spring and summer in the year of ring growth. Significant response function coefficients are those where the 95% confidence interval does not include 0. Thus, for the northern chronologies, there was a significant response of the host and nonhost trees to precipitation during the months of May and June.

Comparison of the host and nonhost chronologies showed that although there was considerable similarity in the low frequency component of the series, differences were present. Filtering of the series with low-pass filters emphasized these differences (Figure 2.4). The correction procedure removed the high frequency information that was common to both series while emphasizing the low frequency differences (Figure 2.4).

Table 2.2 Summary characteristics for tree-ring series from the Rio Grande National Forest, Colorado.

Site	Species ¹	Length		Samples ²		Mean Sensitivity	Series Intercorr.	Auto- ³ correlation	Missing Rings	
		Start	End	Trees	n				%	n
Host										
ALC	ABCO	1736	1997	22	41	0.43	0.85	0.54	0.40	32
ALC	PSME	1693	1997	21	42	0.50	0.85	0.56	0.51	44
DMJ	ABCO	1840	1997	5	10	0.24	0.75	0.68	0.00	0
DMJ	PSME	1620	1997	17	30	0.28	0.76	0.69	0.04	3
FRN	PSME	1660	1997	21	39	0.37	0.82	0.60	0.10	8
JCK	PSME	934	1996	50	93	0.48	0.90	0.56	0.90	387
LIM	PSME	1411	1997	35	70	0.35	0.84	0.73	0.49	121
LKB	PSME	1515	1997	18	34	0.44	0.90	0.33	0.48	51
MCK	PSME	1693	1996	35	60	0.55	0.89	0.50	0.56	68
PAL	PSME	1600	1997	13	26	0.43	0.77	0.75	0.39	25
PTR	PSME	1480	1997	28	59	0.56	0.90	0.64	1.40	249
SMT	PSME	1659	1997	19	35	0.48	0.88	0.34	0.05	3
TRL	ABCO	1770	1997	15	27	0.47	0.86	0.60	0.18	7
TRL	PSME	1600	1997	17	35	0.56	0.89	0.67	0.98	73
Average of all host sites						0.44	0.85	0.59	0.46	
Nonhost										
EBR	PIPO	1610	1997	7	13	0.59	0.87	0.58	2.91	103
JCK	PIFL	1075	1996	10	21	0.45	0.89	0.49	0.69	69
LBP	PIAR	1380	1997	11	19	0.43	0.83	0.61	0.88	37
PTP	PIPO	1654	1997	12	23	0.41	0.85	0.72	1.37	86
RDS	PIPO	1605	1997	18	29	0.63	0.85	0.58	3.46	291
TLP	PIPO	1600	1997	11	23	0.60	0.85	0.63	2.30	150
WIR	PIPO	1675	1997	12	23	0.34	0.76	0.71	0.43	22
Average of all nonhost sites						0.49	0.84	0.62	1.72	
Total samples for all sites				397	752					

¹species codes are: ABCO = *Abies concolor*, PIAR = *Pinus aristata*, PIFL = *Pinus flexilis*, PIPO = *Pinus ponderosa*, PSME = *Pseudotsuga menziesii*

²n refers to the number of radial series

³average first order partial autocorrelation for undetrended series

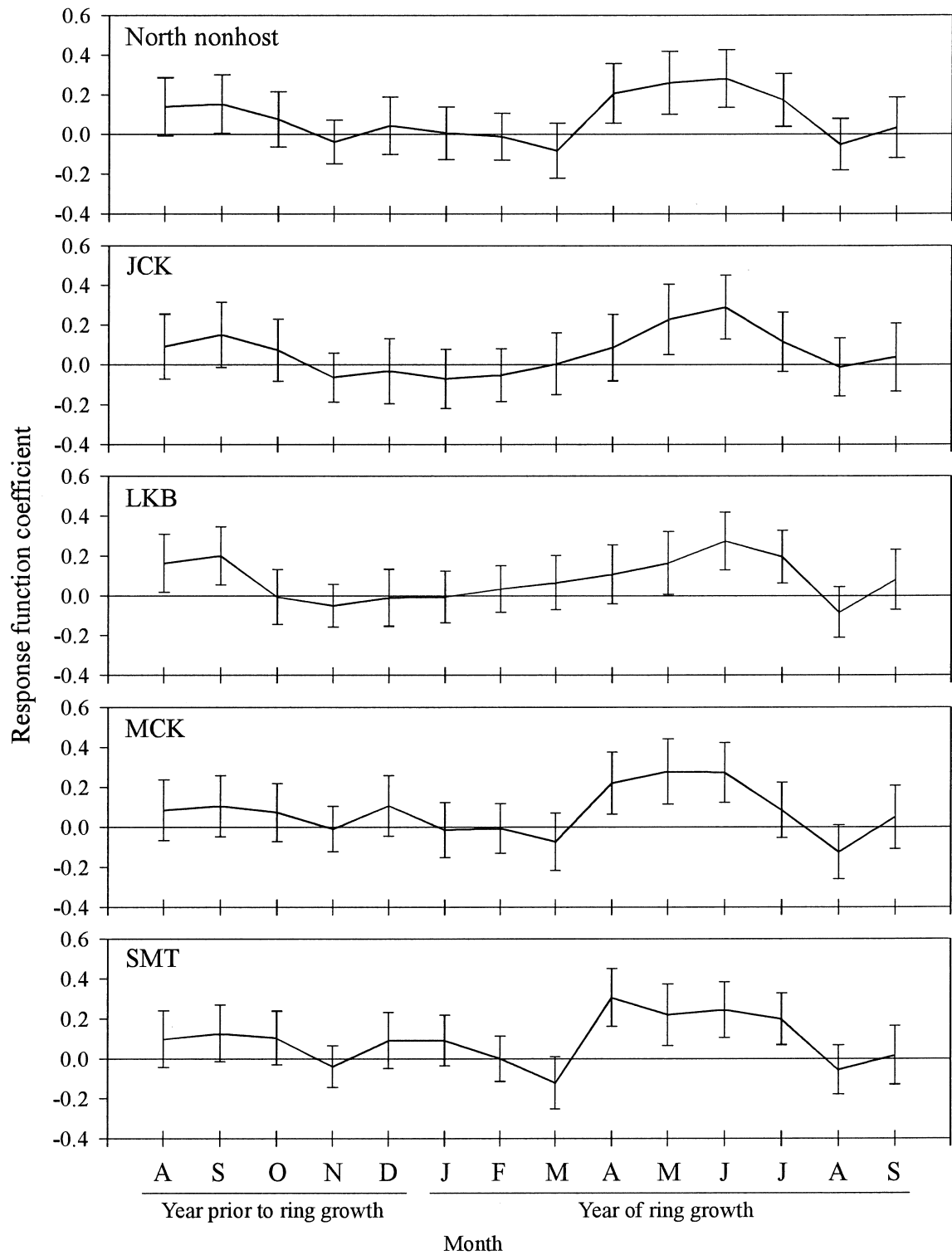


Figure 2.2. Precipitation response function curves for northern chronologies in the Rio Grande National Forest, Colorado. The north nonhost chronology is the composite of nonhost sites for the northern area. Error bars indicate the 95% confidence interval.

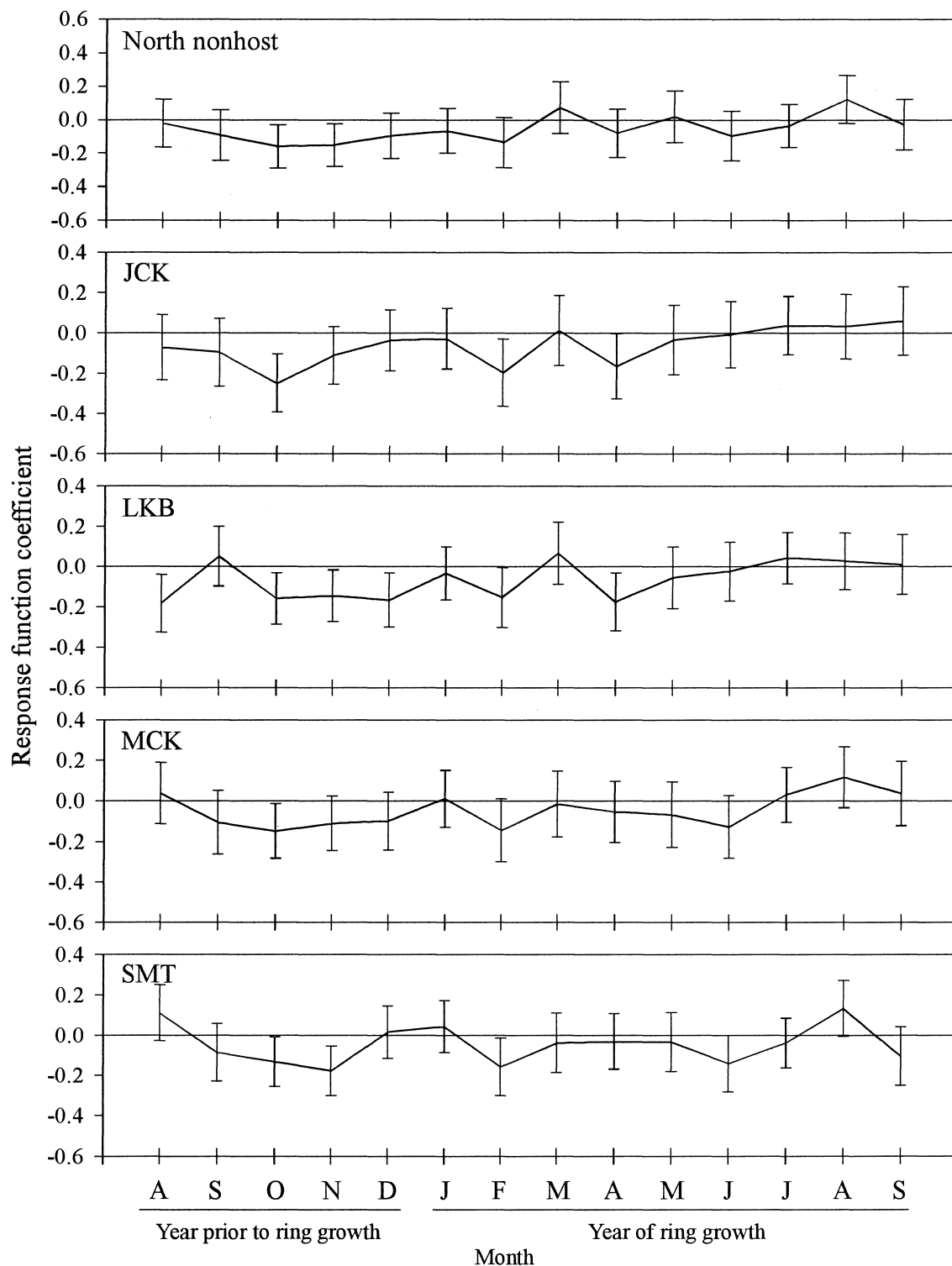


Figure 2.3. Temperature response function curves for northern chronologies in the Rio Grande National Forest, Colorado. The north nonhost chronology is the composite of nonhost sites in the northern area. Error bars indicate the 95% confidence interval.

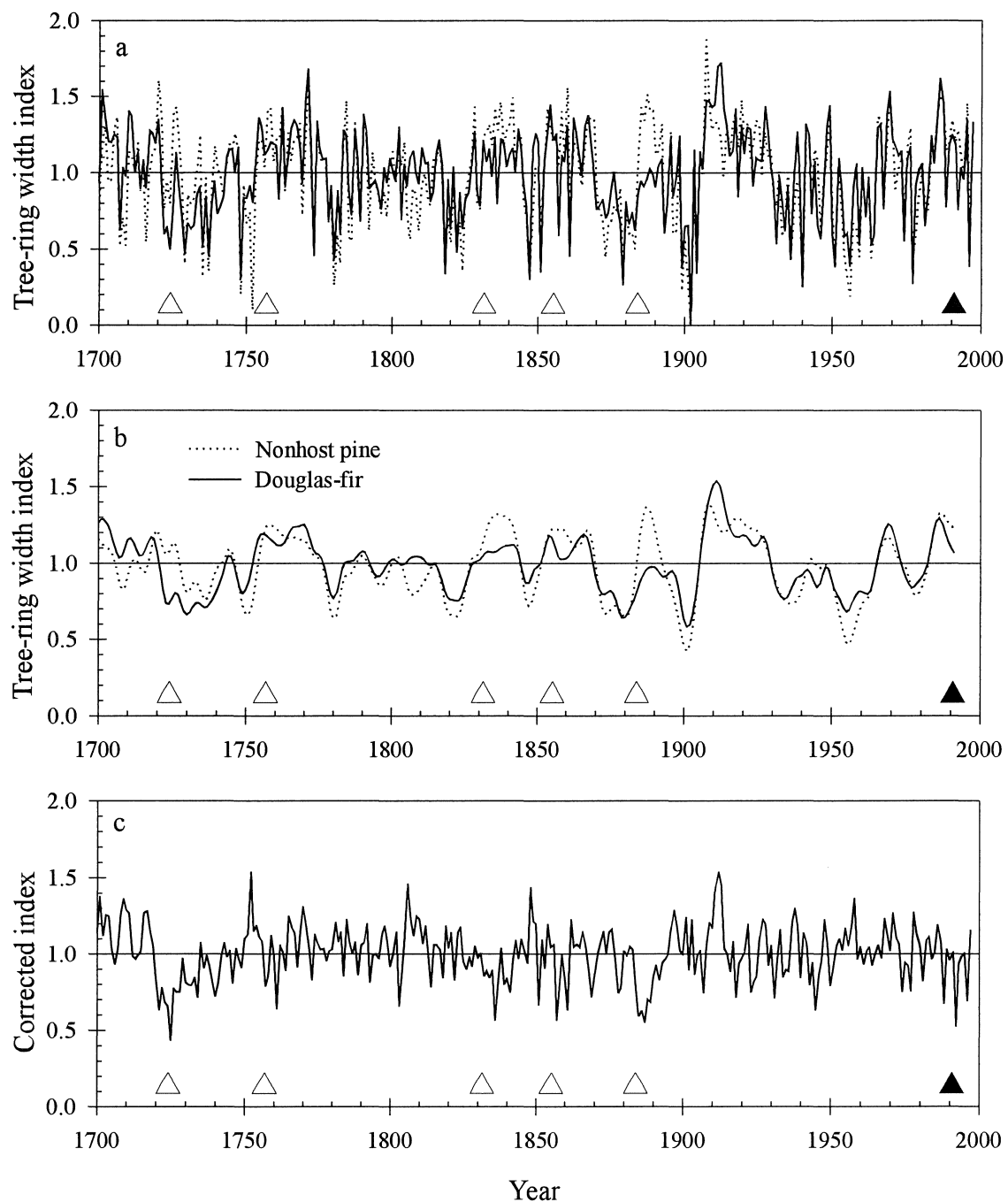


Figure 2.4. (a) Overlay plot of Lime Creek Douglas-fir and pine site chronologies. (b) Site chronologies smoothed with a digital filter to emphasize low frequency differences. (c) Corrected indices resulting from subtraction of pine chronology from Douglas-fir chronology. Filled arrows indicate documented outbreaks, open arrows indicate reconstructed outbreaks.

Tree-ring record of 20th century outbreaks

Records of three outbreaks on the RGNF from the 1940's to present were located in historical documentation (reports summarized in Appendix A). The first recorded outbreak was reported on the eastern and western slopes of the San Luis Valley from Villagrove to Poncha Pass in 1945 (McKnight undated) and the tree-ring reconstruction recorded an outbreak at the nearby, Lucky Boy Gulch site (LKB). The mean corrected series from this site showed an outbreak from 1941 to 1949 and individual trees in the site indicated constant budworm activity throughout the early portion of the 1900's up through the 1940's outbreak. The Jakes Creek site (JCK), located slightly south of the reported area, also recorded this outbreak. The two southernmost chronologies showed budworm activity throughout the early 1900's including the 1940's period, however, documented reports of the outbreak in the southern portion of the RGNF were not encountered.

The 1960's outbreak affected a greater portion of the RGNF. According to the records, the outbreak began in the late 1950's and continued through the 1960's. It was severe enough that 34,100 ha of infested forest were sprayed with insecticides in 1962 to control the outbreak (USDA 1963). The tree-ring record showed an outbreak at several sites with slightly different timing. Strongest responses were observed in the LKB, MCK, SMT and DMJ sites (Figure 2.5). The low percentage of trees affected in some sites might have resulted from the application of insecticides, however, reports did not have details on specific locations.

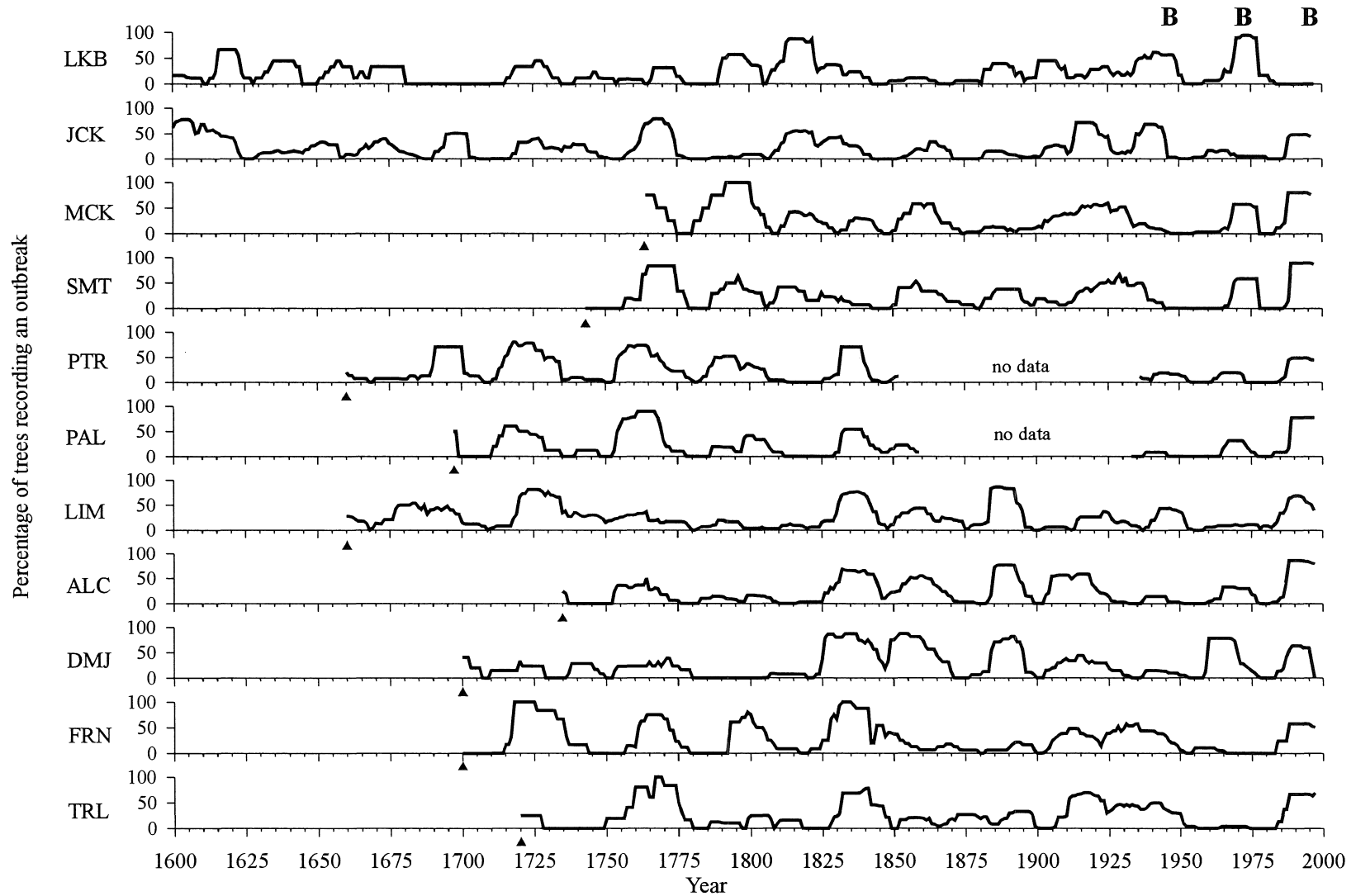


Figure 2.5. Percentage of trees recording an outbreak of western spruce budworm in the Rio Grande National Forest, Colorado. Sites are oriented from north (top) to south (bottom). Small triangles indicate beginning of the series, which were truncated when either the host or nonhost sample depth dropped below four trees. The letter “B” indicates documented outbreak periods. Data were removed from portions of PTR and PAL because of timber harvesting effects.

The most recent outbreak began in the 1980's. 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 1980's. The tree-ring record exhibited the start of the outbreak as around 1988, but with a typical response lag of 1 to 3 years (Belyea 1952, Alfaro et al. 1982, Mason et al. 1997) the beginning of strong defoliation would have occurred in the middle 1980's. Defoliation in the 1990's was moderate to heavy and widespread on the RGNF. In 1995 the continued budworm outbreak was described as a chronic condition 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. This outbreak was not identified at the Lucky Boy Gulch (LKB) site at the time of sampling (1998). These trees, however, were in the middle of a growth reduction, but had not yet met the minimum criteria for an outbreak. 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.

Outbreaks were typically not visible as suppressed growth in the increment cores themselves. A few cores showed single suppressions (such as the most recent outbreak in Figure 2.6), but the majority of cores showed no clearly discernible suppression during periods that were detected as outbreaks. The expected removal of drought periods, such as the 1950's drought, from the corrected series was evident (Figure 2.6).

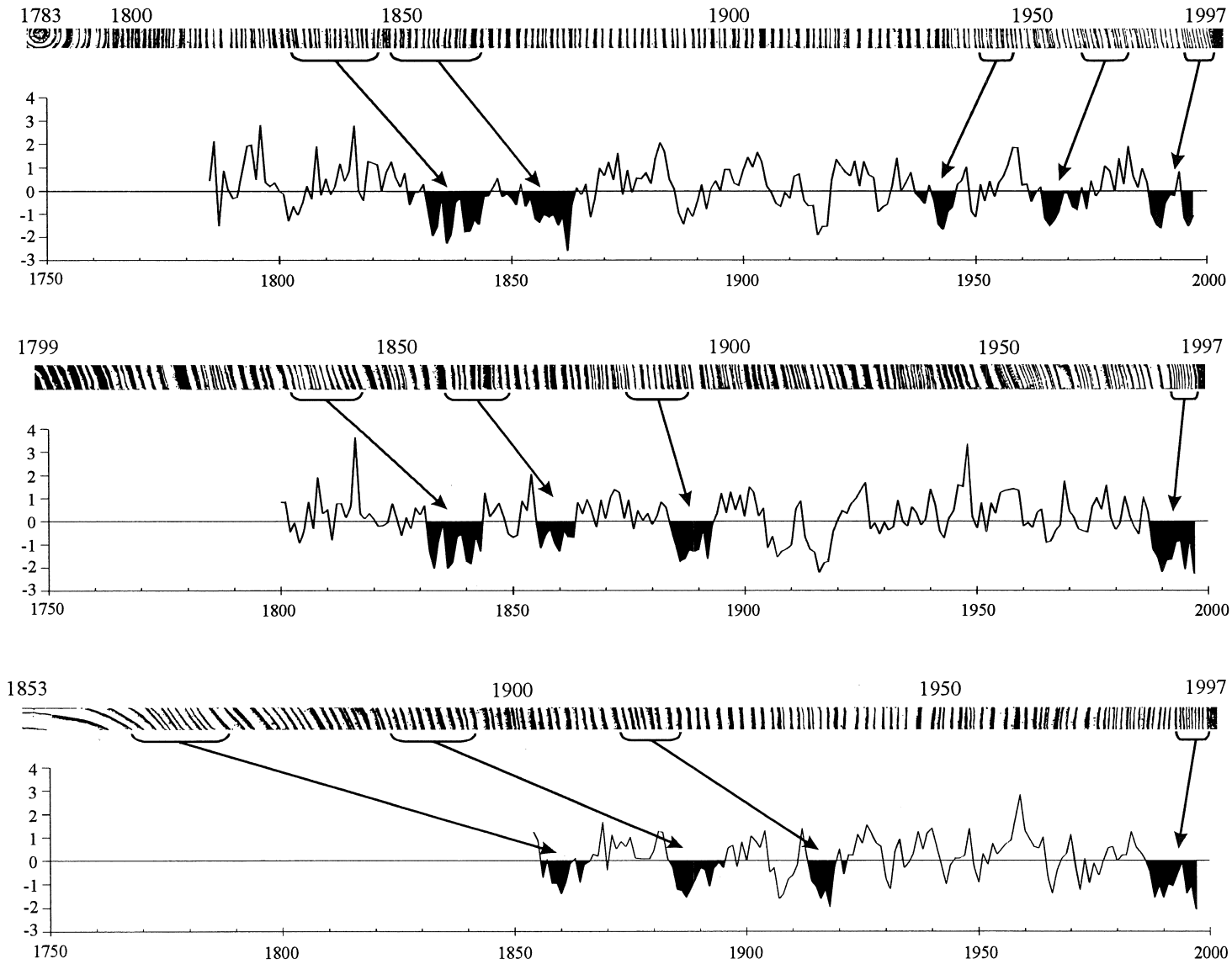


Figure 2.6. Increment cores and associated corrected series. Outbreak periods are bracketed on the core and correspond to the shaded portions in the corrected series.

Outbreak reconstruction

Outbreaks of western spruce budworm were identified over the past several hundred years (Figure 2.5). Although site specific patterns were evident, a high degree of synchronicity among sites was also noted. There are approximately 14 widespread outbreaks over the past 350 years (outbreak periods described in Table 2.3). The intensity of outbreaks varied within the study area; for example, in the 1750-1775 period, the north-central and far southern sites show stronger outbreaks while the remaining sites suggested lower levels of budworm defoliation. On a study area-wide level, there were few extended periods without outbreaks, however, within smaller areas, 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 outbreak periods. Summary of outbreaks at individual sites showed a range of return intervals from 30 to 60 years for events that affected at least 30% of the trees at a site (Table 2.4). As expected, those events that affected a greater percentage of trees (the 50% minimum threshold) occurred at longer return intervals.

Distinct patterns were evident in the outbreak time series for the entire study area (Figure 2.7). The spectrum of this outbreak series showed most of variance was concentrated at periods greater than 20 years (Figure 2.8). Peaks in relative variance were present at periods of approximately 25, 37 and 83 years. The dominant fluctuation observed at approximately 25 years in the outbreak time series (Figure 2.7) corresponds to the average interval between peaks (Figure 2.7). An average of the intervals between events that affected over 50% of the trees in the study area was 83 years. This suggests

Table 2.3. Description of the timing of western spruce budworm outbreaks on the Rio Grande National Forest, Colorado determined from tree-ring records. Dates for outbreak periods were determined from the regional outbreak series developed (Figure 2.7).

Documented outbreaks:	
1984 to 1997	Documented outbreak period from 1985 to 1997. Defoliation was described as moderate to heavy and chronic on the RGNF (Johnson 1996). Tree-ring evidence began in most sites in 1988. This was the most synchronous start outbreak between the sites. All but one site, LKB exhibited this outbreak. Trees at the LKB site showed a growth reduction during period, but it had not met the minimum criteria at the time of sampling. Approximately 65% of all the trees recorded the outbreak.
1960 to 1977	First noted in documentation in 1962. Concern for the outbreak led to application of insecticides to 84,285 acres on the RGNF (USDA 1963). Decreased defoliated was noted in the years following spraying. A resurgence and heavy defoliation was documented in 1968 (McKnight undated, USDA 1969). Activity in the tree-ring chronologies was found primarily in four stands (DMJ, LKB, MCK, SMT) with less impact at other stands. Beginning and ending periods were fairly synchronous within sites.
1936 to 1952	An outbreak in the area of Lucky Boy Gulch was documented in 1945 (McKnight undated). LKB and JCK sites clearly shows an outbreak during this period. In other sites, particularly the southern region, activity during this time span was an extension of the outbreak in the 1920's.

Inferred outbreaks:	
1903 to 1932	A period of moderate activity , more continuous activity with varied levels of trees affected. All sites (except PAL and PTR which do not cover this period) showed some evidence of an outbreak during this period.
1881 to 1898	A strong and synchronous outbreak in the central portion of the RGNF. High percentages of trees were affected at three sites (ALC, DMJ and LIM). There was high within and between stand synchrony for these sites.
1849 to 1876	Following a couple years of decline in activity from the prior outbreak, there was a resurgence at ALC, DMJ and LIM sites. The percentage of trees affected at the MCK and SMT was moderate.
1825 to 1846	A widespread outbreak which affected the central and southern portions of the RGNF. High levels of trees (up to 100% at some sites) were affected. Activity in northern region during this period appeared to be the continuation or a decline from the 1810 to 1824 outbreak.
1810 to 1824	An outbreak found exclusively in the northern chronologies. The strongest record was at the LKB site.

Table 2.3 *continued*

1785 to 1805	This outbreak period was variable across the forest. A high percentage of trees was affected at MCK, while other places showed moderate to low levels of trees affected. The outbreak was nearly nonexistent at sites south of the PAL site.
1753 to 1778	Evidence of this outbreak was exhibited in most stands. The percentage of trees affected was strong at most sites except for some of the sites in south central portion.
1715 to 1735	A widespread outbreak with activity shown in all stands that have records back this far. The timing between the stands varied from 5-10 years. The activity at the DMJ site was minor.
1689 to 1703	Period in which outbreaks affected moderate levels of trees at DMJ, JCK, LIM, PAL and PTR. The within stand synchrony observed here was primarily the result of the reduced sample depths during this early portion of most of the records.
1671 to 1685	A period of overlapping outbreaks between sites. Most central and southern sites showed some activity.
1650 to 1657	Earliest outbreak period with more than two sites recording. Moderate levels of trees were affected in LKB and JCK sites. PTR and LIM showed stronger responses, however this was the beginning of the record at these sites, thus sample depth was low during this period.

Table 2.4. Outbreak return intervals and duration estimates by site. 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 Figure 2.5).

Site	Start of record ¹	Min. Threshold	No. Outbreaks	Return Int. (years) ²		Duration (Years)			
				Mean	<i>s</i>	Trees		Site	
				Mean	<i>s</i>	Mean	<i>s</i>	Mean	<i>s</i>
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

¹lengths truncated when there were fewer than 4 trees in the host or nonhost sample

²return intervals are the number of years between the start dates of outbreaks

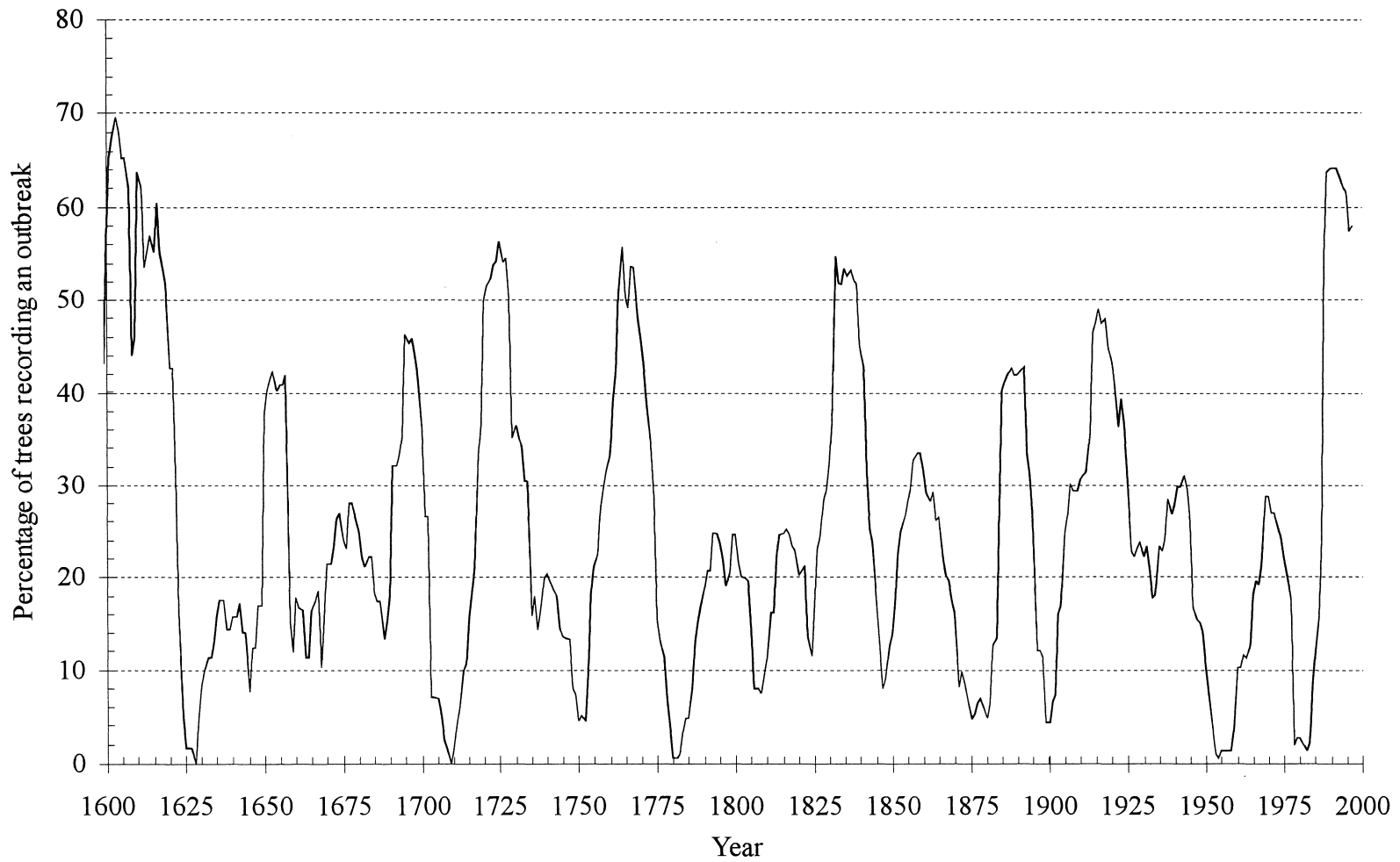


Figure 2.7. Composite time series of percentage of trees recording western spruce budworm outbreaks on the Rio Grande National Forest, Colorado.

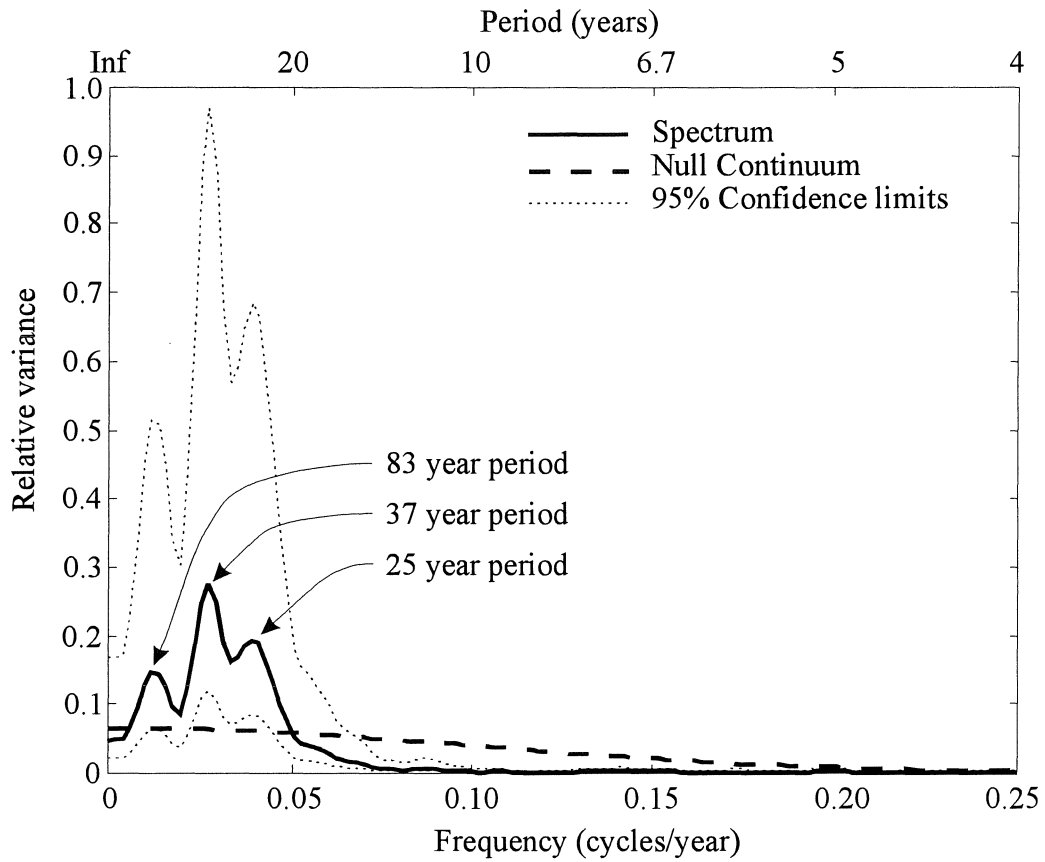


Figure 2.8 Smoothed periodogram of percentage of trees recording an outbreak from 1600 to 1997 for the Rio Grande National Forest.

that the peak at a period of approximately 83 years observed in the spectrum was related to these larger events.

Two outbreak periods exceeded the typical range: the early 1600's and 1990's. The higher percentage of trees affected in the 1600's was due to the decreased sample depth as only two sites had sufficient trees in both the host and nonhost chronologies to provide a valid reconstruction during this early period (see Figure 2.5). The higher percentage of trees affected in the 1990's outbreak was due to the synchrony across the sites. The percentage of trees affected at individual sites during the 1990's outbreak was not necessarily higher than prior outbreak periods, but the simultaneous outbreak at 10 of the 11 sites raised the total percentage of affected trees (Figure 2.7).

Synchrony in outbreak occurrence across the entire study area was evident over the entire length of the reconstruction. The exact starting and ending years of the outbreaks among stands, however, did not always coincide. The most recent outbreak was clearly unique in the strong synchrony in the starting year as indicated by the sharp increase in 1988 of the percentage of trees affected (Figures 2.5 and 2.7). This characteristic was visible at both the stand level and over the entire study area (Figures 2.5). Prior outbreaks exhibited occasional synchrony in starting years, but also exhibited outbreaks with gradual increases in the percentage of trees affected with a site and a range of starting dates between sites. The within stand synchrony found at the early portion of some series (Figure 2.5) was the result of low number of trees in these sites.

Growth reduction and duration values for the outbreak periods since 1600 were variable (Figure 2.9). There were no significant differences in the mean or maximum

growth reduction values between century periods ($P = 0.07$ and $P = 0.76$ respectively) (Table 2.5). Outbreak duration on a tree level was significantly shorter in the 20th century than the prior two centuries ($P < 0.001$) although it was not significantly different than duration in the 17th century ($P = 0.15$). An important note is that the 17th century had a reduced sample with fewer overall sites in the record during this period, which may have affected the duration during this period.

Jakes Creek

The Jakes Creek site contained the oldest trees sampled for this study. The oldest live 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. Remnant sections of wood extended the host chronology back to AD 934. In addition to the old Douglas-fir trees, the stand contained several old limber pine trees, the oldest dating to 1074. Although not truly separate from the host stand, and thus potentially influenced by defoliation of the host trees, these limber pine provided the only sufficiently long nonhost chronology available to correct the host chronology for climate. These two chronologies enabled the longest reconstruction of any of the sites (Figure 2.10).

Analyses of this long time series showed some of the longer period variation in the outbreak patterns. During the 1400's there was nearly constant defoliation with at least 20% of the trees exhibiting an outbreak for almost the entire period from 1400 to 1500. In contrast there was much reduced defoliation in the 1500's as indicated by the low level of trees affected. During this period, the percentage of trees affected rarely exceeded

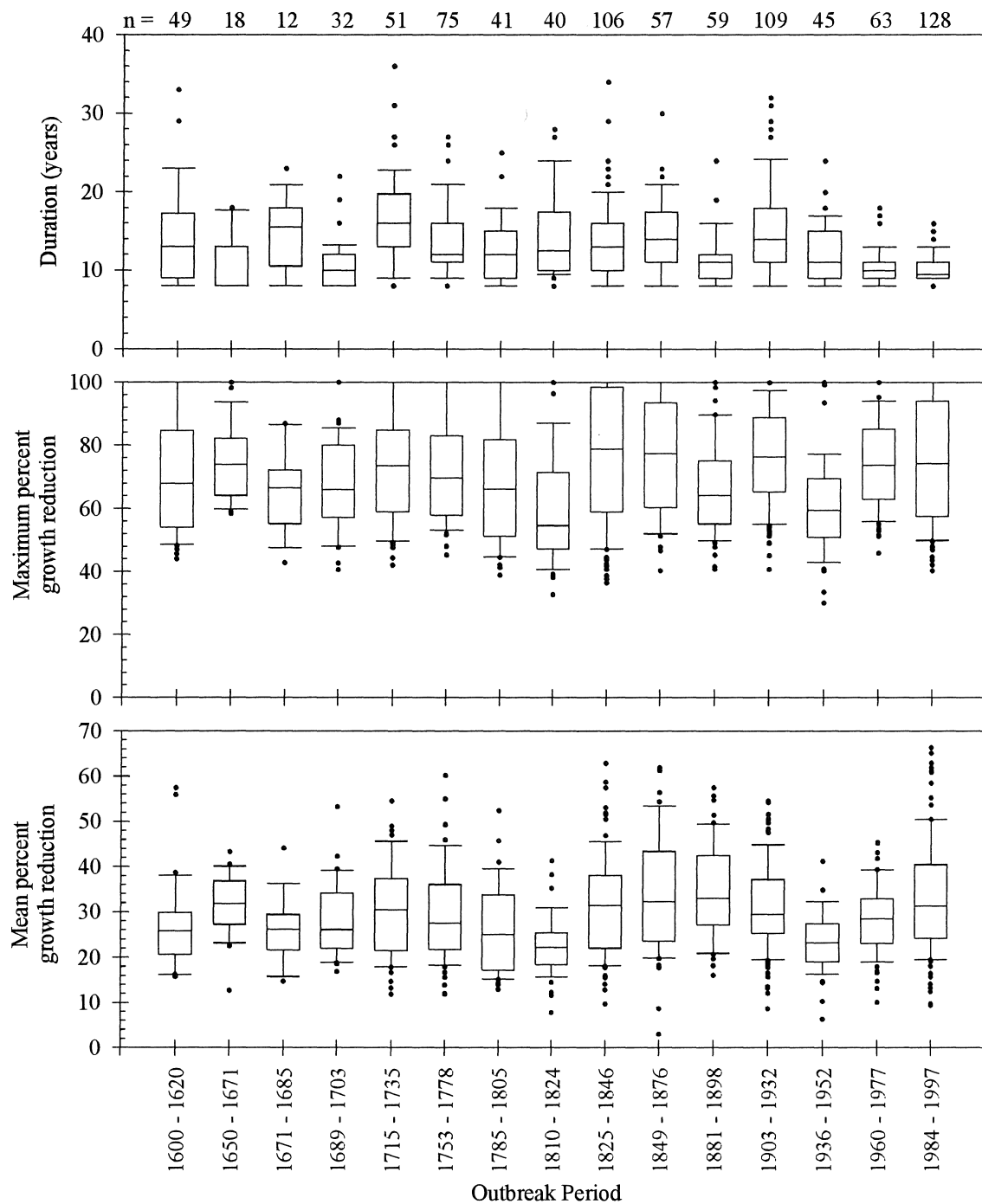


Figure 2.9. Box plots of characteristics of reduced growth periods in individual Douglas-fir trees. Trees are grouped into periods of increased activity over the entire RGNF. Trees were included only if at least 50% of the trees at the individual site exhibited growth reductions that met the outbreak 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.

Table 2.5. Descriptive statistics for outbreak characteristics on a tree level pooled across all sites on the Rio Grande National Forest. A minimum threshold of 50% trees affected was used at the site level to define an outbreak. Significant differences in medians ($P < 0.05$) between century periods are noted with a different superscript letter.

Period ¹	Duration (years)		Mean % Growth Reduction		Maximum % Growth Reduction	
	Median	<i>s</i>	Median	<i>s</i>	Median	<i>s</i>
1600 - 1703	11 ^a	5.1	27.0 ^a	9.0	67.1 ^a	16.0
1704 - 1805	13 ^b	5.1	27.5 ^a	10.5	69.7 ^a	17.4
1806 - 1899	12 ^b	4.5	30.8 ^a	11.4	69.7 ^a	19.4
1903 - 1997	10 ^a	3.1	26.4 ^a	7.7	68.0 ^a	16.4

¹Periods are not exact centuries because outbreaks overlapped centuries

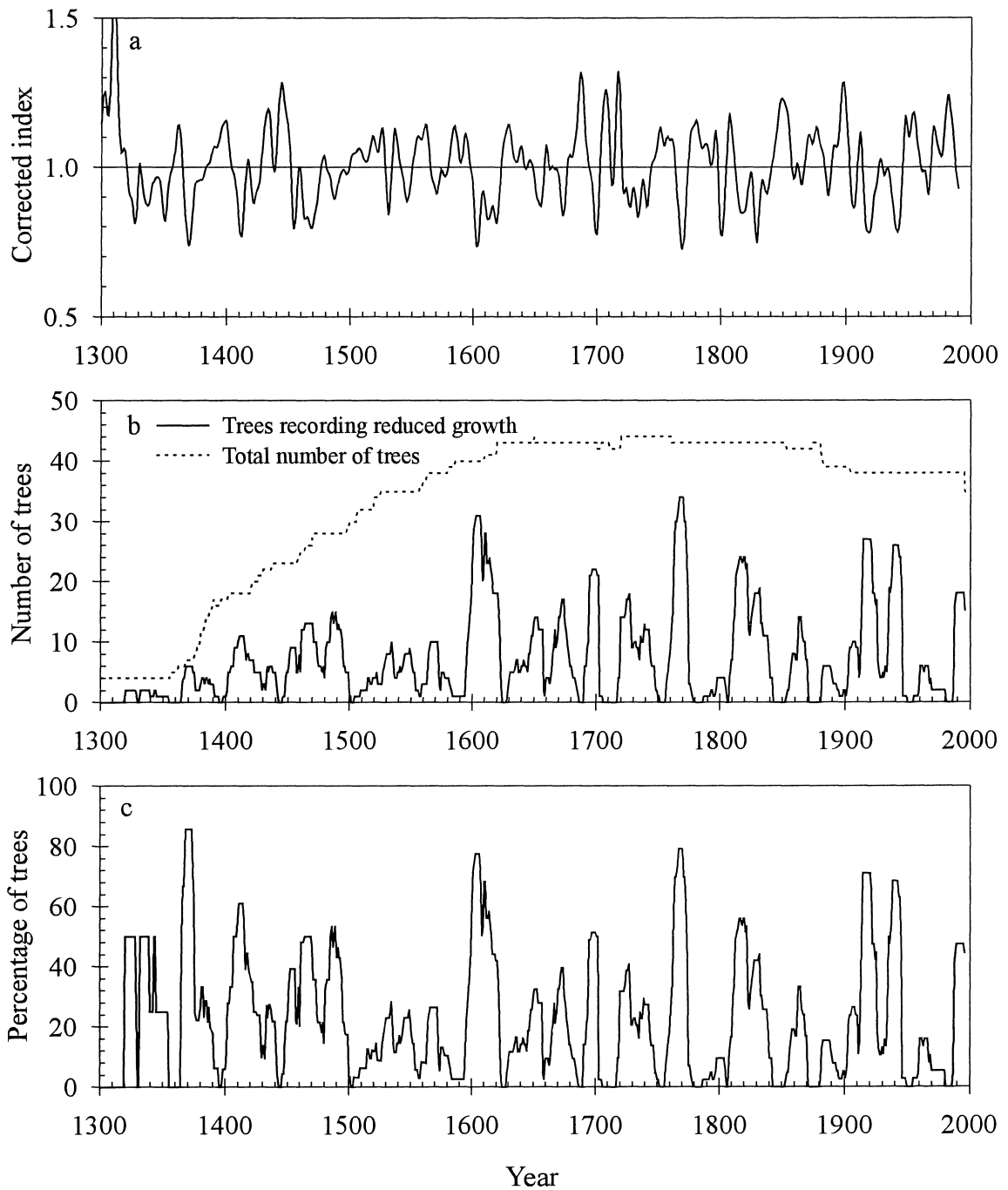


Figure 2.10. (a) Corrected chronology from Jakes Creek site in the Rio Grande National Forest, Colorado smoothed with a 13 year digital filter. (b) Sample depth of host trees and number of trees recording reduced growth. (c) Percentage of host trees recording reduced growth.

20%. This period of quiescence was followed by a large and relatively long outbreak in the early 1600's. There were a total of five outbreaks that affected high percentages of the trees in this stand: the two early outbreaks in the 1900's, the 1760's, the 1610's and potentially the outbreak in the late 1300's. Trends prior to the 1400's are difficult to interpret due to the decreasing number of samples.

Outbreak – climate relationship

Peaks in budworm outbreaks over the entire RGNF corresponded to average or above average (i.e. wet) periods in the tree-ring reconstructed summer PDSI (Figure 2.11). An even stronger relationship was observed between periods of low budworm populations and dry periods. For most major troughs in the PDSI time series, there was a corresponding depression in the percentage of trees recording an outbreak. There appeared to be a slight lagging effect in the budworm response as some dry periods tended to precede low outbreak levels.

Discussion

Detecting past outbreaks

Outbreak periods in this reconstruction, including documented periods, were not typically visible as reduced growth in samples or measured ring-widths. Brubaker and Greene (1979) found that the growth of Douglas-fir declined only slightly during budworm outbreaks and that grand fir (*Abies grandis*) had to be used in conjunction to confirm outbreaks. In this study, however, neither Douglas-fir nor white fir series showed

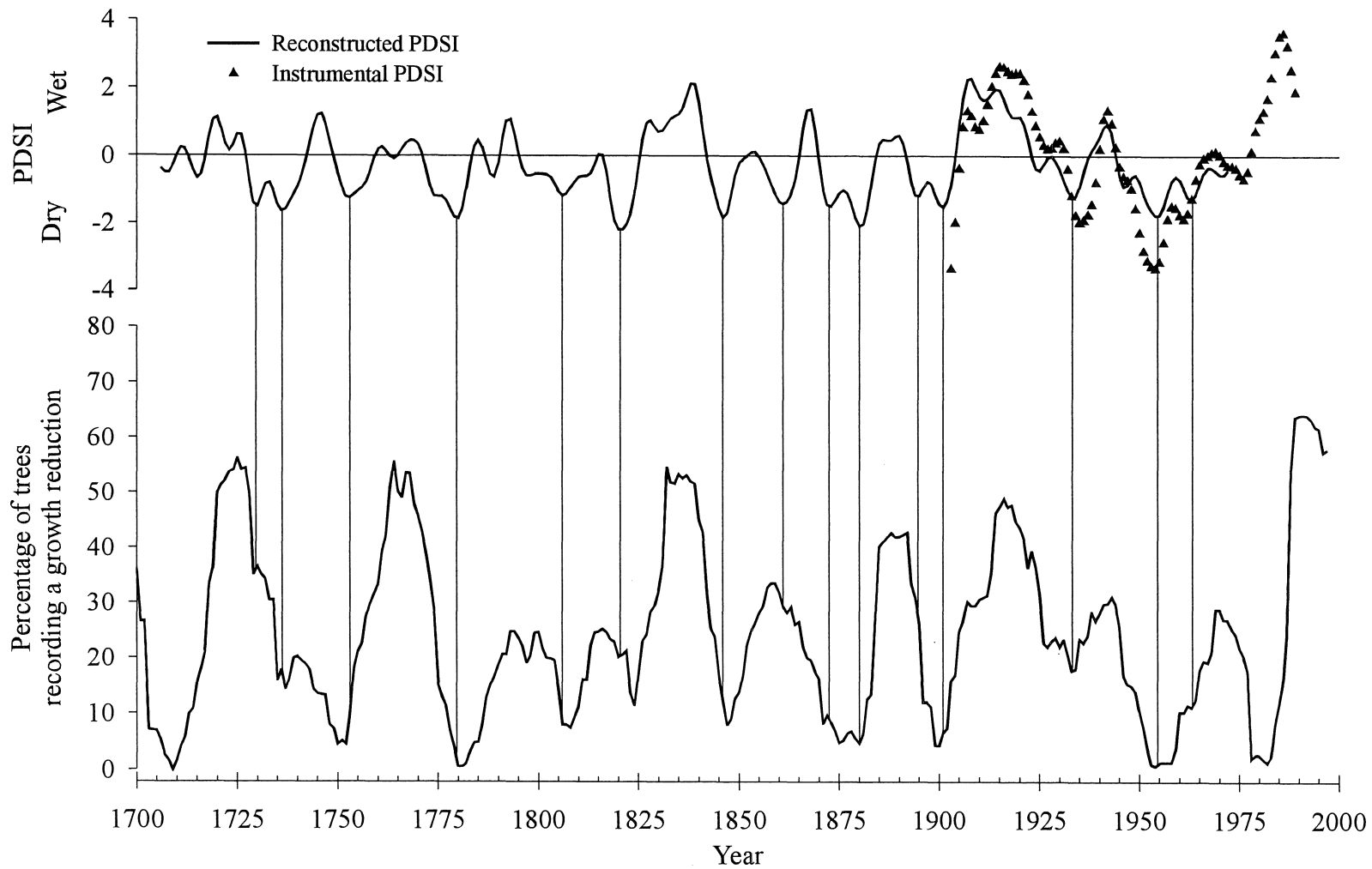


Figure 2.11. Instrumental and tree-ring reconstructed Palmer Drought Severity Index (PDSI) and percentage of host trees recording a reduction in growth on the Rio Grande National Forest, Colorado. PDSI series are smoothed with a 13 weight digital filter. Vertical lines are placed at minimums of the tree-ring reconstructed PDSI series which exceed -1.

strong declines in growth with the exception of a small number trees during some outbreaks (such as the most recent outbreak). In contrast, considering only the host trees, growth during outbreaks was usually average or above average relative to long-term growth. Reduced growth effects were detected typically only when growth was compared to that of the nonhost trees. The lack of clearly definable suppressions in the host cores was unexpected based on results of other tree-ring studies where the effects of insect outbreaks were clearly visible in the ring series (for example Alfaro et al. 1982, Swetnam and Lynch 1993, Weber and Schweingruber 1995). One explanation is that historical outbreak severity in this area was lower compared to other regions. Another possibility is that the trees might have been able to partially compensate for the lost foliage.

It is also possible that the inferred “outbreaks” were actually an artifact of the correction procedure and were caused by inherent systematic differences in sensitivities of trees in the host and nonhost sites to precipitation. Differences between the host and nonhost sites were evident: host sites were on more mesic sites and had higher tree densities; nonhost sites were in more exposed, southerly facing slopes with lower tree densities. During periods of increased moisture, the nonhost trees might have a greater growth than the host trees; trees at host sites might have encountered limiting factors such as competition for nutrients and light earlier than nonhost trees. During dry periods, the host sites would be buffered against the decreased moisture in comparison to the nonhost sites. Higher mean sensitivities and missing rings were observed at the nonhost sites. The overall climatic response, however of the two types of sites was equivalent as shown by the response function coefficients.

The problem might arise when the growth from these two types of sites is compared. The nonhost series is scaled using the standard deviation of the series to account for any differences in sensitivity. If differences remained, however, 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. Interestingly, this was the relationship observed between the reconstructed outbreaks and PDSI.

Although this hypothesis provides a potential explanation of the lack of clearly visible suppressions, the technique of correcting the host series with nonhost series has been used in other reconstructions. These reconstructions have been shown to correspond well with detailed documentation including time series of larvae densities (Mason et al. 1997) and annual defoliation levels (Swetnam and Lynch 1993, Swetnam et al. 1995). The reconstruction by Swetnam and Lynch (1993) used similar site selection strategies and yet were able to show associated suppressions in samples suggesting that the hypothesized site related differences in growth were not important in the sampled areas. The reconstructions for the RGNF did not show consistent visually obvious suppressions in the samples, but the tree-ring record of 20th century outbreaks was consistent with the documented outbreaks. The three documented outbreaks in the RGNF were all reflected in the reconstruction and no outbreaks were detected in the reconstruction within the past 50 years that did not coincide with one of these documented periods.

The response of the host trees to budworm on RGNF has implications for future reconstruction of insect outbreaks. Outbreak patterns can be quite subtle in ring-width series and may be masked by climatic responses of the trees. Therefore, samples from some regions cannot be visually scanned and assessed for prior outbreaks as has been done in other areas. Weber and Schweingruber (1995), for example, used visual assessment alone to reconstruct outbreaks along the Colorado Front Range. Although the technique worked in that region, it would have created erroneous results in the RGNF.

Limitations of tree-ring reconstruction

There are limits to the level of information that this reconstruction can provide. Sites cannot be considered to be representative of most mixed-conifer stands on the RGNF due to subjective selection for sites with the presence of old host trees that had survived past outbreaks. Thus, certain spatial patterns, such as synchrony and study area trends could be influenced by site selection. By selecting for these types of sites, I may have inadvertently selected sites with similar responses and susceptibilities to budworm defoliation in the most recent period. Thus, the increased synchrony in the start year of the most recent outbreak could result from the site selection.

As shown by the aggregate model of tree-ring growth (Cook 1987), ring growth is the result of several factors and thus extracting any single factor can be difficult. Even though I have attempted to remove age-related growth, climate factors and some endogenous disturbances through various analytical techniques, some influence from these factors still remain. Standardization techniques, for example, are essential to the analysis

of large numbers of tree-ring series. These same techniques also influence outbreak detection and characterization, particularly the duration and growth reduction of outbreaks (see Chapter 3).

Reconstructing outbreak severity is less precise than reconstructing outbreak frequency. The impact of an outbreak also includes the level of mortality, which was not reconstructed. Growth reduction of surviving trees can provide some idea of 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. Secondly, surviving trees will not show the high degree of growth reduction that results 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.

Outbreaks and land use history

Changes in forest structure, particularly a shift toward greater abundance of host tree species resulting from human land use have been hypothesized as the reason for the changes in outbreak patterns observed in some regions (Swetnam and Lynch 1989, Swetnam and Lynch 1993). Although the San Juan Mountains have a slightly different land use history than the Front Range and New Mexico, this area has also experienced significant human impacts. As described, mining and timber harvesting began in the late 1800's in the study area, particularly along the Rio Grande. The sample sites in the central portion of the RGNF lie within this area of high historical use. Two host sites showed evidence of timber harvesting during the late 1800's. Utilizing stumps it was determined

that timber harvesting was occurring in the Palisades (PAL) site around 1887 and at the Pool Table Road Site (PTR) in the late 1870's. Other evidence, a flume in the Terrace Lake site (TRL) were observed. Tree response along the remnants of the flume indicate an approximate construction date of 1907. Grazing, fire suppression and continued timber harvesting have all influenced on forest structure, creating conditions considered to be more favorable to budworm outbreaks.

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, other reconstructions have shown an increase in the severity of outbreaks (Swetnam and Lynch 1989, Swetnam and Lynch 1993, Hadley and Veblen 1993, Weber and Schweingruber 1995). Duration of growth reduction has also been reported to be longer in the 20th century (Anderson et al. 1987). In contrast, periods of growth reduction on the RGNF have been shorter in the 20th century compared to the 18th and 19th centuries (Table 2.5). Duration was not different that in the 17th century, however the lower sample size in this early period of the record undoubtedly accounted for some of the variation.

Another change in outbreak patterns noted elsewhere is the increased synchrony of outbreaks. It has been hypothesized that the larger, more homogenous stands of Douglas-fir and true firs have allowed for a synchronization of outbreaks (Swetnam and Lynch 1989, Swetnam and Lynch 1993). Synchrony of outbreaks between sites on the RGNF has been high throughout the length of the record. Therefore, changes in synchrony were

harder to observe in the RGNF compared to other reconstructions, where the outbreaks prior to the last few events were less synchronous. The most recent outbreak on the RGNF was unique in the high degree of synchronicity in the starting year of the outbreak within and between sites. This outbreak was recorded by 10 of the 11 stands and the single remaining stand showed a growth reduction, which had not met the minimum criteria at the time of sampling. It is hard to determine from this single event if outbreak synchrony has changed. In addition, climate patterns appear to have a key role in synchronizing outbreaks patterns.

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 (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 by wind long distances (Dobesberger et al. 1983, Carolin 1987). Even though individuals can move long distances, outbreaks of the eastern species of spruce budworm are generally not considered to be spread by dispersal (Royama 1984). In addition, outbreaks expanding due to dispersal should proceed like a wave through the forest (Berryman 1987). Tree-ring records from widely scattered stands (such as this reconstruction) are probably too coarse in resolution to discern such a pattern.

Extrinsic factors can also have 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. The western spruce budworm outbreaks typically corresponded to periods of increased moisture availability, further confirming the range in insect response to water availability (Larsson 1989, Price 1991). The correspondence of outbreak periods with periods of normal to wet conditions as shown by the PDSI record suggests that climate might be synchronizing budworm populations (Swetnam and Lynch 1993, Swetnam and Betancourt 1998). Since 1976, the southwestern United States had experienced an increased 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 middle 1970's (NOAA, National Climate Data Center, Colorado Division 5). If outbreaks are associated with wetter periods (Swetnam and Betancourt 1998), it is possible that the increased moisture has further synchronized budworm populations.

The exact mechanisms of how increased moisture facilitates increases in budworm populations is not well understood. It is hypothesized that folivores benefit through changes in the nutrient or water content of plant tissue, the larger size of plant tissues and reduced cuticle production during periods of increased moisture availability (Larsson 1989). Experimental evidence and direct observations of insect populations will be necessary to identify these causal mechanisms between outbreaks and climate.

Jakes Creek

During sampling for their outbreak reconstructions, Lynch and Swetnam (1992) found unusually old stands that provided the longest records of repeated defoliation by western spruce budworm. The Jakes Creek (JCK) stand in this study was similar in many respects to these stands. The most noticeable similarity being the old, extremely slow growing trees. 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 exceptionally harsh locations, such as a forest border, where slower growth would be expected. All sites showed both tree-ring and physical evidence (spike tops, crooked stems, dead leaders) of repeated spruce budworm defoliation. Thus, the Jakes Creek stand may provide further additional evidence for the hypothesis that western spruce budworm and Douglas-fir may have developed a mutualistic relationship which allows stands to persist for extraordinary lengths of time by maintaining low levels of productivity (Swetnam and Lynch 1993).

Conclusion

Tree-ring records showed that western spruce budworm has a long history of coexistence with forests in the Rocky Mountains. Regular outbreaks have occurred on the forests of the San Juan mountains for at least the past 600 years. There is a high synchrony of outbreaks across the RGNF, with peaks in activity on average every 24 years. Larger events occurred approximately every 83 years. 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 are capable of surviving multiple outbreaks. No significant changes in growth reduction were observed from one century to another, although duration in the 20th century has been significantly shorter than the prior two centuries.

CHAPTER 3: EFFECTS OF STANDARDIZATION TECHNIQUES UPON OUTBREAK IDENTIFICATION

Introduction

The linear aggregate model of tree-ring growth expresses ring growth as the result of five factors: (1) age-size related trend, (2) climatic conditions, (3) endogenous disturbances, (4) exogenous disturbances and (5) unexplained variability (Cook 1987). To examine the influence of one factor on ring-width variation, the contribution to radial growth by the other factors must be removed or minimized. The process of standardization allows for the comparison of growth patterns of different aged trees by removing the age-related growth trend. This trend is a decline in the rate of ring growth due to geometry and limitations in physiological and environmental conditions (Fritts 1976). Standardization is accomplished by fitting a curve of the expected ring growth through the series and then computing the ratio or difference between the observed and expected growth. Depending upon the type of curve fit to the series, a different combination of factors can be removed from the series. The resultant indices are transformed to a uniform mean, that allows trees of different ages to be averaged together into chronologies (Fritts 1976).

Standardization also enables the comparison of growth patterns as in the host/nonhost technique used in this reconstruction of western spruce budworm outbreaks. Depending upon the type of standardization technique used, different quantities and types of information, including budworm induced growth patterns, can be removed from the

series. This analysis was performed to determine which techniques might be best suited for use in the outbreak reconstruction and to evaluate the extent to which standardization techniques can influence the reconstruction.

Both the host and nonhost series had age-size related growth trends that had to be removed. The host samples also contained fluctuations in growth resulting from the interior forest environment of these stands. Competition and gap dynamics create surges in growth of these individuals (Fritts 1976, Cook 1987). The age-related growth trends common to both sets are typically removed with most standardization techniques, thus the main concern was to select a standardization technique that would remove the low frequency growth pulses in the host series without removing or overly distorting the signal caused by defoliation.

Smoothing splines (Cook and Peters 1981) provide a way to remove a variable quantity of low frequency information from the series depending upon the flexibility of the spline that is used. The more flexible a spline is, the more closely it tracks variation in the series. When the series is standardized by computing a ratio index of the series and the curve, the variation contained in the curve is removed from the standardized series. For example, very flexible splines that closely track decade scale variation will result in the removal of that variation when the ratio index is computed. The flexibility of cubic splines utilized in tree-ring research is defined by a frequency response at particular wavelength (Cook and Holmes 1986). The frequency response refers to the percentage of the variation will be retained. For example, a spline with a 50% frequency response at 100 years will retain 50% of the variation of a wavelength of 100 years. Above wavelengths

of 100 years, a lower percentage of variation is retained while below 100 years, a greater percentage of variation is retained.

Historical records of western spruce budworm in the 20th century show most outbreaks last at least 4-9 years (Campbell 1987). The minimum defined length for an outbreak in this reconstruction is eight years (see chapter 2 discussion for criteria). Longer documented outbreaks range from 25 to 30 years (Johnson and Denton 1975). A large outbreak (~ 800,000 ha) in the northern Rocky Mountains is reported to have persisted for 35 years (Fellin et al. 1983), however, estimated duration of large outbreaks can be deceiving as they are scale dependent. The actual outbreak lengths in any individual stand may be shorter. Therefore, the outbreak duration of interest ranges from a minimum of 8 years up to approximately 30 years. Since outbreak duration is half the wavelength of a full cycle of outbreak/nonoutbreak years, the full wavelengths of interest are from 16 to 60 years. The standardization technique chosen should preserve most of the variance in this range.

I analyzed series from five of the host sites to assess the impacts of using different standardization techniques upon outbreak detection and characterization. A range of standardization techniques was used to evaluate the influence of standardization upon the corrected site tree-ring series and the outbreak periods. I hypothesized that the use of more flexible standardizations would result in fewer outbreaks being detected as the variation of budworm signals would be reduced.

Methods

Five Douglas-fir host tree sites (DMJ, FRN, LIM, MCK and SMT) were selected from the entire sample collection. I selected a range of standardizations based on the types considered for the outbreak reconstruction (Figure 3.1). Both the host and nonhost series needed to be standardized, therefore I evaluated six pairs of nonhost and host standardizations. The paired standardizations selected were as follows:

(nonhost standardization listed first/host standardization second, all splines refer to a 50% frequency response at the given wavelength)

- 1.) negative exponential or linear regression/negative exponential or linear regression
- 2.) negative exponential or linear regression/100 year smoothing spline
- 3.) negative exponential or linear regression/40 year smoothing spline
- 4.) 150 year smoothing spline/150 year smoothing spline
- 5.) 100 year smoothing spline/100 year smoothing spline
- 6.) 40 year smoothing spline/40 year smoothing spline

The individual unstandardized ring-width series were plotted overlaid with the various standardization curves to visually evaluate how well growth was modeled. In addition, this allowed for identification of individual tree growth patterns and stand wide growth suppressions and surges. The host and nonhost series were standardized with the pairs listed above (Cook and Holmes 1986). Corrected tree indices were produced (as discussed in the outbreak identification section) to remove the climatic information

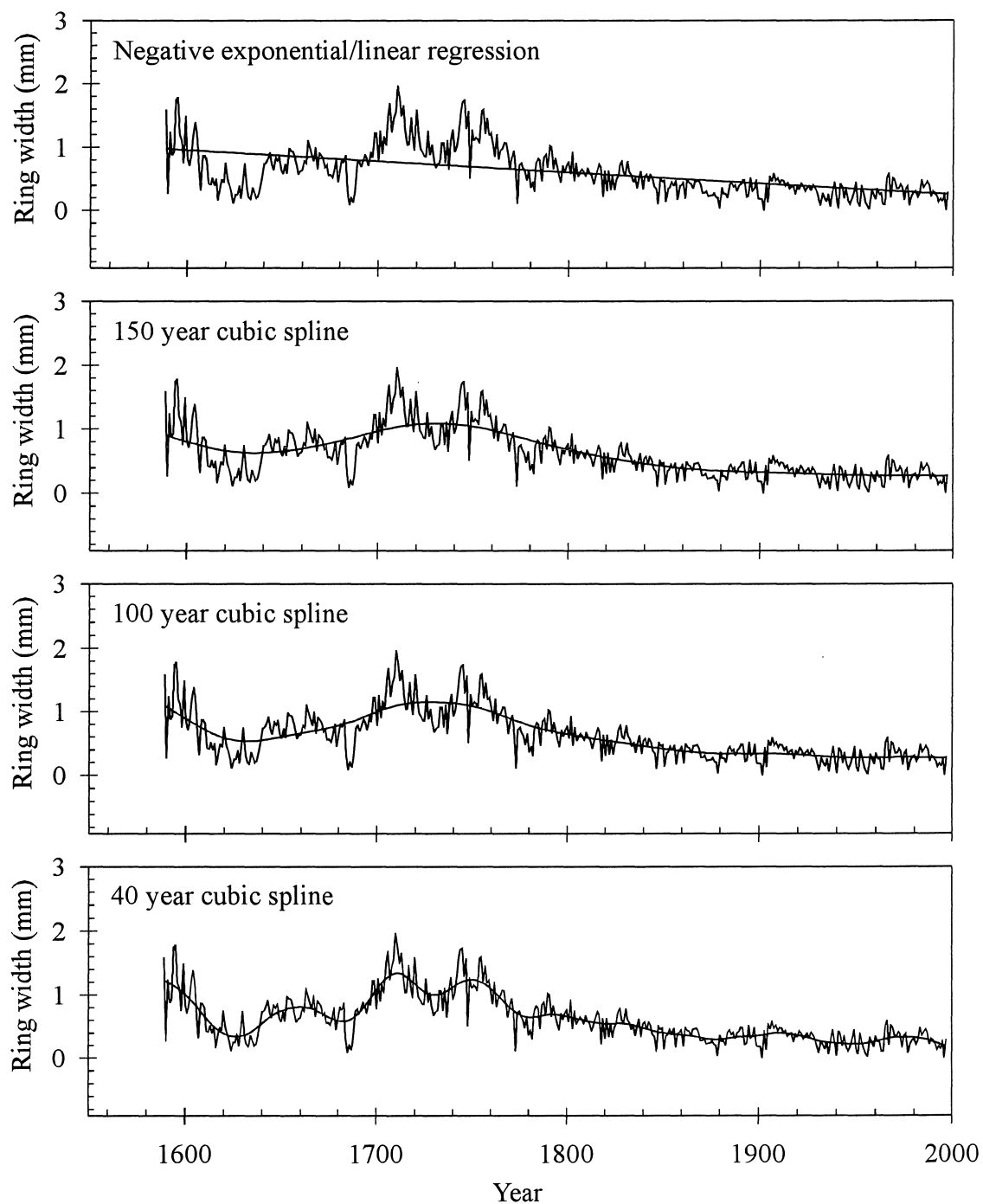


Figure 3.1. Single tree-ring width measurement series from Lime Creek site (LIM) fit with the four standardization techniques used in this analysis. The negative exponential/linear regression option fits the data with either a negative exponential curve or a linear regression depending upon the series.

contained in the nonhost series from the host series (Holmes and Swetnam 1996). The corrected series were analyzed with the same outbreak criteria used in the final reconstruction: a minimum length of eight years of growth reduction with one positive exception allowed before and after the year of maximum growth reduction and a growth reduction of at least 1.28 standard deviations for one year (Swetnam et al. 1995).

Corrected site chronologies were plotted to visually evaluate changes resulting from the standardization selections. Particular attention was paid to the variability in detection of outbreaks among the standardizations. The number of outbreaks detected using each standardization pair was recorded. Characteristics for a single outbreak at each site were summarized to evaluate the variability of duration and growth reduction values among the different standardizations.

Results

The normalized corrected series (mean chronologies from DMJ and LIM shown in Figures 3.2 and 3.3) show that different standardizations result in both obvious and subtle differences in tree-ring indices. The series standardized with more flexible techniques (for example, standardizations 5 and 6) had fewer extended departures from 0 than the other techniques. This reduction in extended departures resulted in a reduction of the number of detected outbreaks. For example, an outbreak was detected from approximately 1750 to 1770 at the Demijohn Peak site (Figure 3.2). In the first four standardization pairs, this period was negative and thus detected as an outbreak. In series transformed with more

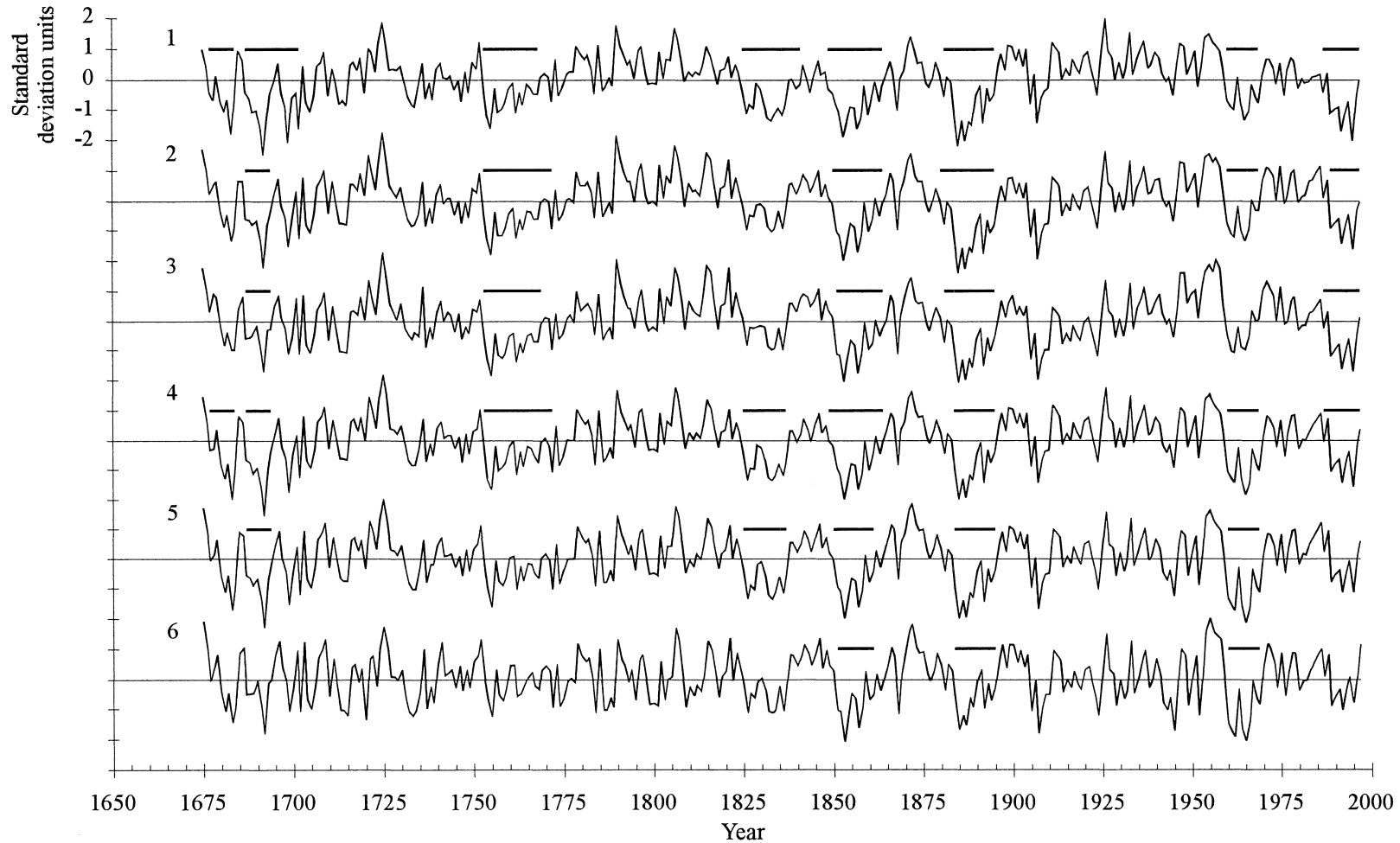


Figure 3.2. Normalized corrected series for Demijohn Peak (DMJ) site standardized with different techniques (1 = ne/lr and ne/lr, 2 = ne/lr and 100 year spline, 3 = ne/lr and 40 year splines, 4 = 150 year splines, 5 = 100 year splines, 6 = 40 year splines). Horizontal bars indicate detected outbreaks.

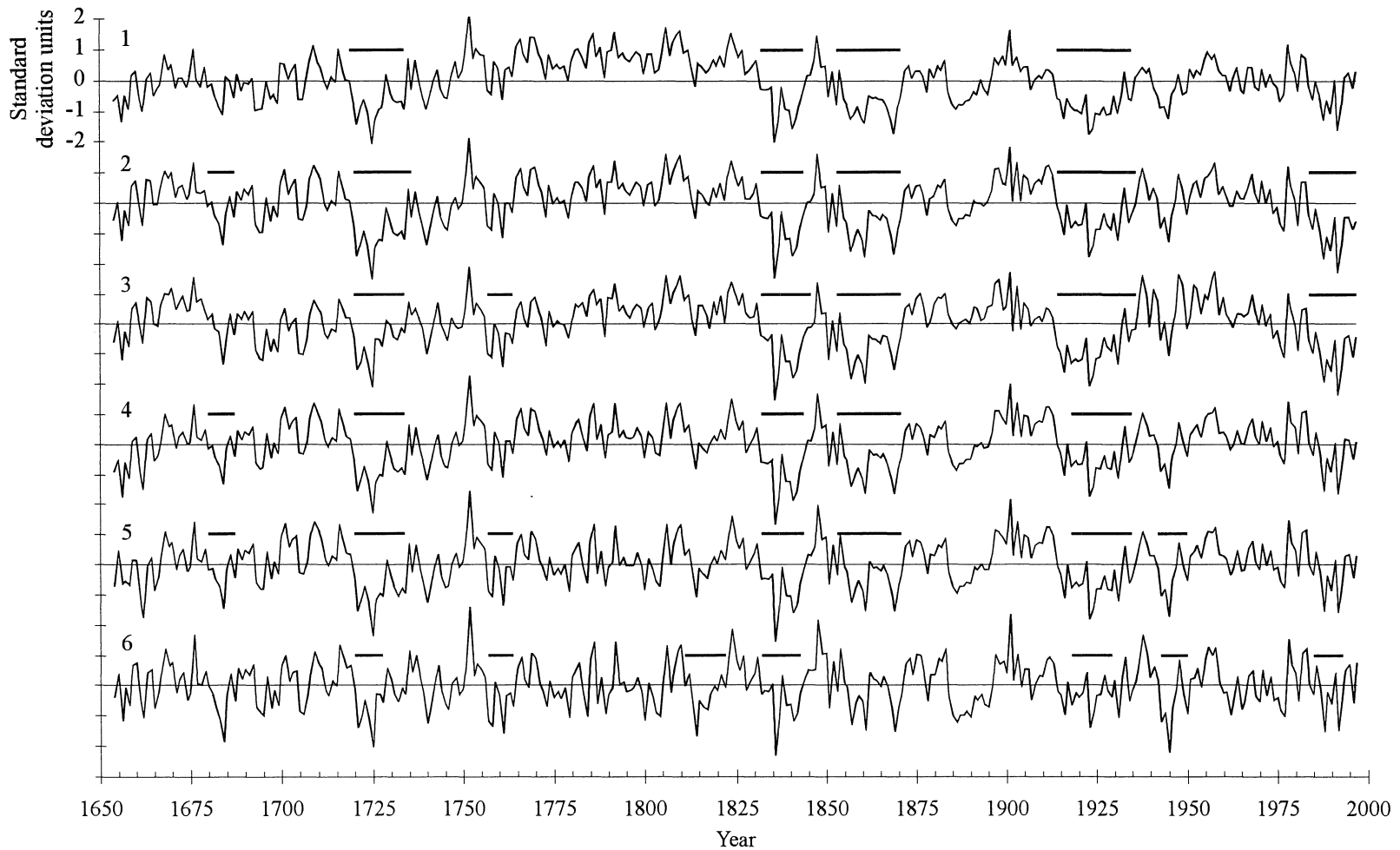


Figure 3.3. Normalized corrected series for Lime Creek (LIM) site standardized with different techniques (1 = ne/lr and ne/lr , 2 = ne/lr and 100 year spline, 3 = ne/lr and 40 year splines, 4 = 150 year splines, 5 = 100 year splines, 6 = 40 year splines). Horizontal bars indicate detected outbreaks.

flexible standardizations (standardizations 5 and 6), this period varied about zero and the outbreak was no longer detected.

At the Lime Creek site (Figure 3.3), three of the nine potential outbreak periods in the series were found in each series, regardless of the standardization technique used. Compared to these common outbreaks, the other six outbreaks tended to be shorter in length and/or have less growth reduction, and therefore, they were closer to the minimum criteria. The detection of these lower severity events was more affected by standardization. The series from the Demijohn Peak site (Figure 3.2) showed a similar response with two of the eight outbreak periods being detected in all standardizations. The total number of outbreaks detected (Table 3.1) was remarkably similar except for standardization 6, which had the lowest number of outbreaks detected. Thus, except for the use of the more flexible techniques, such as the 40 year spline (standardization 6), there were only minor differences between techniques in detecting outbreaks.

Although most of the same potential outbreak periods were identified in all the standardization pairs at a site, the duration and quantity of growth reduction estimates were highly variable among the different standardization techniques (Table 3.2). Mean growth reduction for the 1925 outbreak at the Lime Creek site (Table 2.2) varied from a low of 7.3% up to 31.5% as in the outbreak around 1925 in the LIM site (Table 3.2). In addition, the relative relationships between outbreaks did not necessarily remain constant. For example, at the Demijohn Peak site (Figure 3.3), the relative intensities of the 1960's and 1990's outbreaks shifted. In standardization 1, the 1990's outbreak exhibited greater growth reduction, suggesting a more intense defoliation than the

Table 3.1. Number of outbreaks detected for each site with the six different standardizations. Standardization pairings are described in the text.

Standardization	Number of outbreaks					
	1	2	3	4	5	6
DMJ	8	6	5	8	5	3
FRN	5	6	5	6	7	3
LIM	4	6	6	5	7	7
MCK	9	6	8	5	6	7
SMT	6	7	6	7	5	4
Total	32	31	30	31	30	24

Table 3.2. Duration and percent growth reduction are given for a single outbreak period at each site. The outbreak for which the characteristics are given is listed following the site code. Standardization pairings are described in the text.

Site/characteristic	Standardization						Average	Range
	1	2	3	4	5	6		
DMJ (1965)								
Duration (yrs)	10	10	7*	10	10	10	9.5	3
% Growth Reduction	32.1	26.1	26.9*	37.4	40.7	35.0	33.0	14.6
FRN (1720)								
Duration (yrs)	22	21	18	21	18	15	19.2	7
% Growth Reduction	41.4	39.4	25.2	40.4	39.1	22.3	34.6	19.1
LIM (1925)								
Duration (yrs)	22	23	23	18	18	12	19.3	11
% Growth Reduction	31.5	14.7	22.6	15.6	15.5	7.3	17.9	24.2
MCK (1920)								
Duration (yrs)	11	11	13	11	11	8*	10.8	5
% Growth Reduction	7.3	28.0	36.0	21.6	18.3	12.7*	20.6	28.7
SMT (1675)								
Duration (yrs)	9	9	4*	9	9	9	8.2	5
% Growth Reduction	31.7	23.2	15.2*	29.7	28.0	25.7	25.6	16.5

* denotes that period no longer meets the minimum criteria for an outbreak

outbreak in the 1960's. In contrast, standardization 2 showed the two outbreaks to be of a similar growth reduction. Then in standardizations 5 and 6, the 1960's outbreak appeared much stronger and the 1990's suppression was reduced to a level such that it no longer met the minimum criteria.

Discussion

Standardization is an essential process in the analysis of tree-ring series. This transformation, however, also influences the detection and characterization of outbreaks. The more conservative techniques examined here were similar in the detection of outbreaks, but all the standardization techniques effected the growth reduction and duration estimates of the outbreaks. It is important, therefore, to understand how estimated characteristics of past outbreaks can be modified by standardization of the original tree-ring series.

The hypothesis that the use of more flexible spines would result in fewer outbreaks being detected was confirmed as the most flexible standardization pair (6) had the lowest number of outbreaks detected and typically showed lower amounts of growth reduction. On an site level there were specific individual responses, however, as standardization 6 showed the highest number of outbreaks detected at the Lime Creek site. In addition when only the host series was subjected to this flexible standardization (3), the number of outbreaks detected was not noticeably less than the other series. Thus, the relationship between standardization and outbreak detection is a combination of variance removed in both the host and nonhost series. Overall, the more flexible techniques, such as the 40

year spline used here, are less suitable as they remove more of the low frequency information of interest.

Based on these results, I decided to use cubic splines of relatively low flexibility for the reconstruction of western spruce budworm outbreaks on the RGNF. These were cubic splines with a 50% frequency response at a wavelength of 150 years (standardization 4). Using these splines, 97.5% of the variance of wavelengths of 60 years was retained in the series. Thus, outbreak signals, including those of longer suppressions, were maintained in the series. The selection of the standardization technique was a compromise between maintaining important low frequency signals in the series and removing unwanted endogenous responses resulting from forest dynamics. The same length spline was used on all series to avoid problems with different frequency responses of separate standardization techniques.

Standardization is an essential process in examining tree-ring series, however it can result in important changes in time series. The use of different standardizations revealed relatively variable values of growth reduction and duration. Since outbreaks were defined using a minimum duration and growth reduction, detection was also influenced. On an individual site level there were differences in outbreak detection between the standardizations, but for most of the standardizations there was no overall bias toward detecting a greater or lower number of outbreaks. Excessively flexible standardizations, however, reduced detection of outbreaks as more variance of interest was removed. Thus the most rigid standardization that adequately modeled the unwanted growth trends was used in the reconstruction.

CHAPTER 4: SUMMARY

Western spruce budworm has a long history as a disturbance agent in the mixed-conifer forests of western North America. Outbreaks have impacts on forest structure, succession and species composition. Tree-ring reconstructions have elucidated some of the long-term population dynamics of western spruce budworm such as the frequency, extent and duration of outbreaks. Prior reconstructions have found altered outbreak patterns in the 20th century including greater levels of growth reduction, longer duration and increased spatial synchrony. These changes have been hypothesized to be the result of human land use and management which has increased host tree abundance. To evaluate basic outbreak characteristics in the San Juan Mountains of the Southern Rocky Mountains, I reconstructed outbreak patterns using 11 host sites on the Rio Grande National Forest. In addition, some methodological questions were investigated during the reconstruction process.

An examination of the effects of standardization techniques on tree-ring series has shown that standardization can influence the detection of outbreaks by removing variations with certain frequency content from the series. Comparison of results from different standardization techniques showed an overall similarity in the number of outbreaks detected by the relatively conservative techniques. The more flexible standardizations, such as the 40 year splines examined, are less suitable to western spruce outbreak studies because these techniques remove more variations of interest from the series. Characterization of outbreaks was also affected by standardization, with the greatest effect on estimates of growth reduction. Based on these results, I selected the

least flexible spline (50% frequency response at a wavelength of 150 years) that was still able to remove the long-term growth fluctuations that are typical of trees growing in an interior forest stand and applied it to all series used in the reconstruction.

The other methodological issue encountered was the growth response of the host trees to defoliation on the RGNF. Typically tree growth is reduced severely from the defoliation that occurs during an outbreak (Van Sickle 1987). This response has been so striking in some areas that visual assessment of samples for suppressions has been utilized to reconstruct outbreaks (Weber and Schweingruber 1995). On the RGNF tree growth responses to budworm defoliation did not show this level of growth reduction. Visible periods of suppressed growth in the samples during outbreaks were rare. More typically, growth appeared relatively normal with no striking changes from the ring patterns before and after the outbreak period.

Relatively reduced growth was detected, however, when host ring-width indices were compared with nonhost ring-width indices. I hypothesize that since outbreaks were occurring during wet and thus favorable growing periods, host trees partially compensated for the lost foliage. Extreme suppressions in growth were not observed because of the overall favorable moisture conditions during outbreaks. It is also possible that budworm population numbers or defoliation levels are lower in this region than in other regions where extreme growth suppressions are common. This response highlights the ability of the host/nonhost comparison technique to detect outbreaks that are masked by other influences on growth. In addition, it prevents misidentification of suppressed growth resulting from other influences, particularly climate, as an outbreak. Thus, a primary

assumption of this technique is that the growth of the two species and sites is quite similar in the absence of any external disturbances, such as the outbreaks studied here. The climatic response of the host and nonhost species were partially tested and shown to be quite similar.

The changes observed during the 20th century in many other reconstructions have been attributed to changes in forest composition and density as a result of human land use and management. The San Juan Mountains have experienced extensive human impacts, including mining and timber harvesting that began in the middle of the 19th century. The reconstruction for the RGNF, however, did not reflect obvious changes in outbreak dynamics. No significant changes in the level of growth reduction during outbreaks was observed and duration was shorter in the 20th century compared to the prior two centuries. Considerable variation over time, however was evident in both duration and growth reduction.

Increased synchrony has been noted in several reconstructions, including New Mexico and Colorado (Swetnam and Lynch 1989, Swetnam and Lynch 1993). For the past three centuries, outbreaks have been rather synchronous across the RGNF, with peaks in activity occurring approximately every 24 –30 years. These periods of synchronized outbreak activity coincide with above average moisture availability. The most recent outbreak had increased synchrony in the initiation of growth reduction, however it is unclear if this signals a change in the outbreak pattern. Overall the outbreak patterns in the RGNF do not support the hypothesis that land use has significantly altered outbreak patterns in this area.

Western spruce budworm is an important disturbance agent with a long history in the ecology of coniferous forests throughout western North America. Reconstruction at a single old-growth stand showed a 600+ year history of repeated outbreaks. These repeated outbreaks have undoubtedly impacted the development of these forests. The lack of clearly discernable suppressions and the absence of some of these 20th century changes indicate that forest – outbreak dynamics in this area may differ from that of the Front Range and other regions in the Rocky Mountains.

APPENDIX A

Compilation of western spruce budworm outbreaks for USDA Forest Service Region 2 and Rio Grande National Forest from annual insect reports and miscellaneous reports and maps. Only relevant portions of the records were included in this compilation. Consult original documentation for complete records.

Year	General USDA Forest Service Region 2	Rio Grande National Forest
1945		"The susceptible host types in Colorado and southern Wyoming were inspected for budworm outbreaks in 1945. The eastern and western slopes of the San Luis Valley were damaged from Villagrove to Poncha Pass." (McKnight undated)
1955		"By 1955 the activity of the budworm was increasing in the forests of Colorado adjacent to epidemic areas in New Mexico. It was reported that the infestation on the Del Norte District, Rio Grande National Forest, had been active since 1943." (McKnight undated)
1956		"Budworm damage on the San Juan and Rio Grande National Forests increased to 39,423 acres in 1956 and 89,500 acres in 1957. Most of the damage was described as light; local centers were widespread across the southern forests." (McKnight undated)
1962	"A reversal occurred in the trend of spruce budworm infestations in the mixed conifer forests in Colorado. Instead of the increase in acreage and severity of infestations noted in 1961 and prior years, a decline in scope and intensity of defoliation occurred in 1962. On the basis of budworm egg mass surveys in affected areas, the downward trend of infestations is expected to continue in 1963." (USDA 1963)	"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. The other, encompassing but 600 acres, was in the vicinity of Ouray, Grand Mesa-Uncompahgre National Forests. Fixed wing aircraft and helicopters were used to spray infested areas adjacent to streams so as to minimize possible adverse effects to fish and fish food organisms." (USDA 1963)
1963	"The scope and severity of spruce budworm infestations decline materially throughout the Central Rocky Mountains. Area of defoliation in 1962 was 718,300 acres. In 1963 it totaled 46,800 acres. On the basis of information obtained from budworm	Aerial survey indicates 640 acres defoliated in the RGNF. (Minnmeyer 1971)

APPENDIX A *continued*

Year	General USDA Forest Service Region 2	Rio Grande National Forest
1963 <i>cont.</i>	egg-mass surveys in July, it seems likely that the severity of tree defoliation in current infestation areas will be less in 1964. The decline of populations was due to unknown natural control factors.” (USDA 1964)	
1964	“Spruce budworm populations increased sharply along the eastern slope of the Sangre de Cristo Mountains, San Isabel National Forest, Colo. The infestation was estimated to involve 80,000 acres. Egg mass surveys made in August indicated that defoliation in this area will be moderate to heavy in 1965. In other forest areas of Colorado, spruce budworm populations remained endemic. Defoliation, heavy enough to be seen from the air, covered 97,800 acres or about two times more than the number of acres reported in 1963.” (USDA 1965)	Aerial survey indicates 300 acres defoliated in the RGNF (Minnemeyer 1971).
1965	“Infestations persist in southern Colorado on some 79,600 acres of fir type. Heaviest defoliation occurred in the Vallecito Reservoir, Florida River and Little Sand Creek areas, San Juan Forest; eastern slope of the Sangre de Cristo Mountains, San Isabel Forest; and Soap Creek drainage, Gunnison Forest. Although damage was heavy with more than 60 percent of the current foliage destroyed, it was not severe enough to cause top-killing or tree mortality. Defoliation is expected to remain heavy in 1966. There are no plans to suppress infestations in 1966.” (USDA 1966)	“Infestations persist in southern Colorado on some 79,600 acres of fir type.” (USDA 1965) Aerial survey indicates 1,300 acres defoliated in the RGNF. (Minnemeyer 1971)

APPENDIX A *continued*

Year	General USDA Forest Service Region 2	Rio Grande National Forest
1966	<p>“Infestations occur on 80,000 acres of mixed-conifer forest in Colorado. The largest and most continuous infestation (about 75 percent of total acreage) is east of the Sangre de Cristo Range on the San Isabel Forest. Here, defoliation has been heavy during the past 3 years, but permanent damage has not yet occurred. The remaining infested acreage consists of small, isolated, moderate outbreaks on the Rio Grande, San Juan, Gunnison, Grand Mesa-Uncomphgre, and Roosevelt National Forests. No suppression work is planned in 1967.” (USDA 1967)</p>	<p>“The remaining infested acreage consists of small, isolated, moderate outbreaks on the Rio Grande, San Juan, Gunnison, Grand Mesa-Uncomphgre, and Roosevelt National Forests.” (USDA 1967)</p> <p>Aerial survey indicates 2,700 acres defoliated in the RGNF. (Minnemeyer 1971)</p>
1967	<p>“Infestations total about 100,000 acres. The largest area, on the eastern side of the Sangre de Cristo range on the San Isabel National Forest, remains at about 50,000 acres. Heaviest defoliation appeared on Corral Mountain on the San Juan National Forest. Other small infestations are on the Rio Grande, Roosevelt, and Gunnison National Forests. No suppression projects are planned during 1968.” (USDA 1968)</p>	<p>“Other small infestations are on the Rio Grande, Roosevelt, and Gunnison National Forests.” (USDA 1968)</p> <p>Aerial survey indicates 2,700 acres defoliated in the RGNF. (Minnemeyer 1971)</p>
1968	<p>“Areas of budworm defoliation have increased by approximately 75,000 acres in 1968, making a total of over 175,000 acres. The heaviest defoliation was on the San Isabel, San Juan, and Rio Grande National Forests. Other infestations were scattered throughout Colorado.” (USDA 1969)</p>	<p>“The heaviest defoliation was on the San Isabel, San Juan, and Rio Grande National Forests.” (USDA 1969)</p> <p>“Budworm-damaged acreage increased in 1968 mainly in southern Colorado on the San Isabel, San Juan and Rio Grande National Forests.” (McKnight undated)</p> <p>Aerial survey indicates 8,320 acres defoliated in the RGNF. (Minnemeyer 1971)</p>

APPENDIX A *continued*

Year	General USDA Forest Service Region 2	Rio Grande National Forest
1969	<p>“Infestations dramatically decreased in severity and acreage. The decrease was caused by subnormal temperatures accompanied by snow in the early summer; and by increased parasitism.” (USDA 1970)</p> <p>“In 1969 no defoliation due to the budworm was recorded in Colorado or Wyoming for the first time since aerial surveys were initiated in 1955. Low temperatures accompanied by snow killed the new shoots of the host trees in late June and, in some areas, in early July. However, enough budworms survived to produce egg masses sufficient to indicated possible light defoliation in 1970 in some areas in Roosevelt, San Isabel, and San Juan National Forests.” (McKnight undated)</p>	
1970	<p>“Defoliation has increased from no observable defoliation last year to about 32,000 acres in 1970 on the San Isabel National Forest.” (USDA 1971)</p>	
1971	<p>“Defoliation on the San Isabel National Forest increased from 32,000 acres in 1970 to 113,000 acres in 1971. Sampling during 1971 indicates that, at the most, moderate (35 to 65 percent) defoliation can be expected in 1972; therefore, no control is being considered.” (USDA 1972)</p>	
1972	<p>“Budworm defoliation dropped from 113,000 acres in 1971 to 90,500 acres in 1972. In the San Isabel National Forest, defoliation decreased by 50,000 acres with the intensity of defoliation remaining about the same, mostly moderate. Some moderate defoliation is expected in 1973 along the Sangre de Cristo Range, with light feeding in the Wet Mountain Range. A new infestation area was discovered near</p>	<p>“Increased defoliation of 7,500 acres was observed in the Rio Grande National Forest along the Conejos River.” (USDA 1973)</p>

APPENDIX A *continued*

Year	General USDA Forest Service Region 2	Rio Grande National Forest
1972 <i>cont.</i>	Bear Creek north of the Spanish Peaks, primarily on private lands and extending into the San Isabel National Forest. Light defoliation occurred on 10,000 acres of the Roosevelt National Forest and adjacent lands west of Boulder, Colo. Increased defoliation of 7,500 acres was observed in the Rio Grande National Forest along the Conejos River." (USDA 1973)	
1973	"The San Isabel National Forest, which ordinarily experiences the heaviest budworm defoliation of any area in the region, sustained light to moderate defoliation." (USDA 1975)	
1974	"Budworm, a perennial defoliator of fir and spruce in Colorado, caused generally light defoliation in 1974. Moderate defoliation occurred on less than 10,000 acres, a slight increase over 1973. Light defoliation is predicted for 1975." (USDA 1977)	
1975	"While defoliation from this insect was detected over a large area of Colorado, the host species was not a major component of the forest stand, and the damage was not severe." (USDA 1977)	
1977	"This insect defoliated Douglas-fir, spruce, and true fir forests on all National Forests in the Region except the Black Hills and Nebraska. Aerial surveys indicated more than 650,000 acres were defoliated this year compared to 517,500 acres last year. Defoliation was most extensive on the Colorado National Forests." (USDA 1978)	"A ground survey in the Beaver Creek and Alder Creek area did not detect any evidence of budworm activity. Defoliation in 1977 was undetectable. The forecast for 1978 is undetectable defoliation." (Linnane 1977)

APPENDIX A *continued*

Year	General USDA Forest Service Region 2	Rio Grande National Forest
1978	<p>“The western spruce budworm remained a serious defoliator in Douglas-fir and white fir stands in Colorado and Wyoming. Over 900,000 acres of forest land exhibited various levels of defoliation in Colorado this year, with most severe damage on the Arapaho and Roosevelt National Forests. These populations are expected to increase slightly next year. Lighter outbreaks occurred on the San Juan National Forest, where populations are declining, and on the Pike National Forest where populations are increasing.” (USDA 1980)</p>	
1980	<p>“Defoliation was detected on 1,052,000 acres in Colorado. This is a slight increase over that reported in 1979.” (USDA 1981)</p> <p>Defoliation map for the year shows activity primarily along the Front Range and some in southwestern Colorado, near the San Juan National Forest. (USDA 1980)</p>	
1981	<p>“In 1981 1,768,000 acres were infested.” (USDA 1982)</p> <p>Map shows infestations along Front Range and in the San Juan National Forest. (USDA 1982)</p>	
1982	<p>“Budworm continues widespread in the Region. Intensity of feeding is down on the Front Range of Colorado.” (USDA 1983)</p> <p>500,843 acres were defoliated on the San Juan NF. (Raimo 1982)</p>	
1983	<p>“Western spruce budworm is building momentum in 1983 after a small decline in 1982. Moderate defoliation was mapped on 2,750,311 acres. Egg mass survey results indicate there should be moderate to heavy</p>	<p>The defoliation map for the state shows no large defoliation in the San Juan portion of the RGNF. (Lister and Hildebrand 1983)</p> <p>“Aerial surveys indicated that approximately</p>

APPENDIX A *continued*

Year	General USDA Forest Service Region 2	Rio Grande National Forest
1983 <i>cont.</i>	defoliation in the same area in 1984.” (Lister and Hildebrand 1983)	20,458 acres were defoliated on National Forest (RGNF) and adjacent lands in 1983. Most of the defoliation occurred east of Great Sand Dunes National Monument between Mosca Pass and Medano Pass. No egg mass density data was gathered from this area.” (Raimo 1983)
1984	<p>“Extensive areas of moderate defoliation continued to occur throughout central and northern parts of the Front Range. The most prominent, continuous defoliation, however, occurred on a 923,000-acre area in southern Colorado.” (USDA 1985)</p> <p>“Western spruce budworm remained the most widespread defoliator in the Region. Again, defoliation damage was mapped from the air and resulting estimates were 2,210,924 acres of defoliation activity in Colorado and Wyoming combined. This is a reduction of 539,387 acres from 1983 acreage estimates. Regionwide, the severity of defoliation remains classed as moderate.” (Sharon and O’Neil 1984)</p> <p>“The egg mass survey results for 1984 indicate the overall infestation will be moderate in 1985 where the budworm is present.” (Sharon and O’Neil 1984)</p>	<p>“Approximately 64,066 acres were infested on National Forest (RGNF) and adjacent lands in 1984. Egg mass density and defoliation data was collected in 1984 for the first time in several years. This year’s data indicate that the area suffered light to moderate defoliation in 1984 and that moderate to severe defoliation can be expected in 1985.” (Ramio 1984)</p> <p>Defoliation map shows only small defoliated areas on the RGNF south of the Rio Grande. Activity is concentrated in the San Juan National Forest and in the Sangre de Cristo mountains. (Sharon and O’Neil 1984)</p>
1986	<p>“The area of visible defoliation in the Region continued to decline from 1.6 million acres in 1985 to 1.1 million acres in 1986. Despite the decline, there were several areas of extreme defoliation scattered throughout the Region. The decline in the area of visible defoliation is expected to continue.” (Lessard et al. 1987)</p>	
1988	<p>“Western spruce budworm populations continued their overall decline in the Region. Visible defoliation on federal and</p>	

APPENDIX A *continued*

Year	General USDA Forest Service Region 2	Rio Grande National Forest
1988 <i>cont.</i>	private lands was at the lowest level in nearly 15 years. Between 11,000 and 12,000 acres of visible defoliation on the Dolores Ranger District, San Juan National Forest created public concern. An egg mass survey and evaluation were conducted. It indicated budworm population levels will be less in 1989 than that observed in 1988. Significant deoliation occurred in the area of the Divide West into southern South Park, Colorado also. About 600 acres of Douglas-fir were sprayed in the Mueller Ranch State Park near Divide and Salida, Colorado.” (Johnson et al. 1989)	
1989	“Western spruce budworm populations continued their overall decline in the Region. About 50,000 acres were infested in Colorado.” (Pasek and Angwin 1990)	
1990	“Western spruce budworm remains low in Colorado except for a small infestation of 52,000 acres at Kauffman Ridge on the San Isabel National Forest where defoliation was again heavy in 1990 acres.” (Lundquist and Lister 1991)	
1991	“In Colorado, the area infested by the western spruce budworm is estimated to be 509,000 acres. Moderate to heavy defoliation occurred on the San Juan, San Isabel, Rio Grande, Gunnison, White River, and Pike National Forests. The outbreaks in these areas are expected to increase in 1992.” (O’Neil 1993)	“Moderate to heavy defoliation occurred on the San Juan, San Isabel, Rio Grande, Gunnison, White River, and Pike National Forests.” (O’Neil 1993)
1992	“Defoliation occurred on approximately 262,000 acres of mixed conifer and subalpine forests on the San Juan, Rio Grande, Gunnison, and White River National Forests as well as private land in	“Western spruce budworm populations have been at outbreak levels throughout much of the mixed conifer type on the Creede and Del Norte Districts of the Rio Grande National Forest since the early 1980’s.” (Raimo 1992)

APPENDIX A *continued*

Year	General USDA Forest Service Region 2	Rio Grande National Forest
1992 <i>cont.</i>	Gunnison County, Colorado. The activity is expected to continue into 1993. Areas along the Front Range and adjacent intermingled state and private lands experienced moderated defoliation." (Blunt 1993)	"In 1992, an estimated 50,000 acres of primarily mixed conifer forests were defoliated by the budworm on the two districts. Defoliation range from less than 1 percent of the 1992 needles at Aqua Ramon to 55 percent of the 1992 needles at the Haney Canyon area. Egg mass counts indicate that the western spruce budworm populations will remain at outbreak levels in all of the samples areas through 1993." (Raimo 1992)
1993	"Defoliation of mixed conifer and subalpine forests continued in the Gunnison zone in 1993. Most of the defoliation occurred on the Salida District of the San Isabel NF, on the Creede and Del Norte Districts of the Rio Grande NF, the Rifle District of the White River NF, and on National Park Service lands in Gunnison County. The activity in these areas is expected to continue into 1994." (Blunt 1994)	"Most of the defoliation occurred on the Salida District of the San Isabel NF, on the Creede and Del Norte Districts of the Rio Grande NF, ..." (Blunt 1994)
1994	"Aerial surveys on the Pike National Forest detected 101,761 acres of older budworm mortality. New defoliation was negligible. Defoliation of mixed conifer and subalpine fir continued in the Gunnison zone in 1994. Most of the defoliation appeared on the Salida District of the San Isabel National Forest, on the Creede and Del Norte Districts of the Gunnison National Forests, and on the Rifle District of the White River National Forest. Aerial survey of the San Isabel National Forest revealed 9,690 acres of old heavy mortality." (USDA 1995)	"Most of the defoliation appeared on the Salida District of the San Isabel National Forest, on the Creede and Del Norte Districts of the Gunnison National Forests..." (USDA 1995)
1995	"Widespread defoliation of Douglas-fir, true firs and spruce continued throughout the forests of southern Colorado. Douglas-fir and true fir mortality is common in areas that have been repeatedly defoliated	"Widespread defoliation of Douglas-fir, true firs and spruce continued throughout the forests of southern Colorado. Douglas-fir and true fir mortality is common in areas that have been repeatedly defoliated for almost a decade.

APPENDIX A *continued*

Year	General USDA Forest Service Region 2	Rio Grande National Forest
1995 <i>cont.</i>	for almost a decade. Activity appears to be chronic in many areas, particularly on the Rio Grande NF. Defoliation has increased sharply on the Uncompahgre Plateau, indicating expanding populations.” (Johnson 1996)	Activity appears to be chronic in many areas, particularly on the Rio Grande NF.” (Johnson 1996)
1996		Aerial defoliation maps showed current defoliation by western spruce budworm through the RGNF. Light to heavy defoliation from budworm was noted along the south side of the Rio Grande between Wagon Wheel Gap and South Fork. Budworm induced defoliation was also noted in the area of the Palisades (PAL) and Alder Creek (ALC) sites. (Aerial defoliation maps from RGNF)
1997	“Currently, there are no major outbreaks of western spruce budworm within southern or south-western Colorado, although there are areas with significant “chronic” budworm activity. There are a number of stands scattered throughout the mixed conifer type of the San Isabel, Grand Mesa-Uncompahgre-Gunnison, Rio Grande, and San Juan National Forests, which have had many consecutive years of defoliation by budworm. This activity is thought to be a direct result of stand conditions complicated by fire exclusion. Budworm defoliation is expected to continue in these susceptible stands until these stand conditions change.” (USDA 1998)	“There are a number of stands scattered throughout the mixed conifer type of the San Isabel, Grand Mesa-Uncompahgre-Gunnison, Rio Grande, and San Juan National Forests, which have had many consecutive years of defoliation by budworm. This activity is thought to be a direct result of stand conditions complicated by fire exclusion. Budworm defoliation is expected to continue in these susceptible stands until these stand conditions change.” (USDA 1998)

APPENDIX B

Summary of reconstructed outbreak periods for the 11 host stands. Outbreaks were summarized from the time series of the percentage of trees recording outbreaks at each site using a minimum threshold of 30% (Figure 2.5). A lower threshold of 15% was used to define the start and end dates of the outbreaks.

Outbreak Period		Return ¹ Interval	No. of years in period	Growth Reduction	
Start	End			Mean %	Maximum %
Alder Creek (ALC)					
1753	1771	-	19	23.9	67.6
1826	1845	73	20	38.6	81.9
1848	1869	22	22	29.2	72.8
1884	1896	36	13	36.2	69.1
1903	1924	19	22	39.8	84.8
1965	1976	62	12	28.4	68.1
1987	1997	22	11	43.1	83.6
Demijohn Peak (DMJ)					
1720	1728	-	9	25.4	74.6
1753	1779	33	27	25.7	59.1
1825	1869	72	45	36.3	85.7
1884	1895	59	12	30.9	65.9
1905	1925	21	21	24.4	63.9
1960	1974	55	15	31.5	73.3
1986	1996	26	11	27.1	59.4
Fern Creek (FRN)					
1715	1743	-	29	45.7	94.6
1761	1775	46	15	31.2	76.3
1793	1808	32	16	27.8	70.6
1825	1855	32	31	33.2	93.1
1905	1921	80	17	32.8	82.4
1923	1948	18	26	29.3	81.0
1984	1997	61	14	35.1	85.7
Jakes Creek (JCK)					
1402	1428	-	27	25.2	69.5
1448	1479	46	32	19.8	60.0
1481	1499	33	19	22.4	60.2
1595	1622	147	28	23.8	64.2
1646	1657	51	12	23.9	61.0

APPENDIX B *continued*

Outbreak Period		Return ¹	No. of years in period	Growth Reduction	
Start	End	Interval		Mean %	Maximum %
<i>Jakes Creek (JCK) continued</i>					
1665	1678	19	14	18.3	58.3
1693	1702	28	10	24.5	62.7
1720	1744	27	25	22.8	69.8
1759	1774	39	16	24.4	63.2
1809	1839	50	31	21.3	57.1
1858	1870	49	13	17.4	59.0
1912	1926	54	15	27.4	69.5
1934	1945	22	12	23.9	58.9
1988	1996	54	9	34.3	86.1
<i>Lime Creek (LIM)</i>					
1673	1700	-	28	25.4	62.6
1718	1749	45	32	28.2	70.0
1751	1768	33	18	26.8	72.0
1825	1844	74	20	22.9	55.1
1851	1874	26	24	23.4	58.4
1883	1895	32	13	33.5	66.0
1914	1927	31	14	25.9	57.8
1940	1952	26	13	17.4	49.8
1984	1997	44	14	21.2	60.4
<i>Lucky Boy Gulch (LKB)</i>					
1587	1604	-	18	24.3	63.5
1615	1624	28	10	28.5	79.3
1632	1644	17	13	31.3	73.2
1653	1662	21	10	21.5	52.8
1669	1680	16	12	29.4	61.6
1718	1731	49	14	36.1	83.1
1767	1774	49	8	29.1	60.1
1790	1804	23	15	28.6	69.4
1808	1839	18	32	28.1	66.6
1882	1895	74	14	24.9	56.9
1901	1910	19	10	24.2	63.0
1918	1951	17	34	22.7	61.8
1966	1981	48	16	27.9	75.8

APPENDIX B *continued*

Outbreak Period		Return ¹ Interval	No. of years in period	Growth Reduction	
Start	End			Mean %	Maximum %
Mill Creek (MCK)					
1781	1805	-	25	33.8	83.9
1813	1827	32	15	28.5	77.2
1835	1844	22	10	26.7	61.4
1852	1870	17	19	32.3	67.7
1903	1933	51	31	29.9	76.1
1968	1977	65	10	28.0	75.1
1986	1996	18	11	29.7	65.5
Palisades (PAL)					
1711	1728		18	33.6	86.9
1754	1772	43	19	39.9	86.9
1798	1807	44	10	25.6	54.4
1832	1845	34	14	24.0	69.6
Break in series					
1965	1974	-	10	21.2	66.7
1988	1997	23	10	40.9	78.6
Pool Table Road (PTR)					
1690	1702		13	33.9	73.5
1713	1734	23	22	25.8	68.3
1754	1777	41	24	31.4	77.0
1786	1805	32	20	19.2	55.4
1832	1841	46	10	29.4	83.8
Break in series					
1988	1997	-	10	30.6	68.2
Spruce Mountain (SMT)					
1757	1778	-	22	41.0	85.9
1787	1804	30	18	29.4	76.6
1809	1830	22	22	30.9	74.6
1852	1868	43	17	32.5	78.3
1882	1895	30	14	19.0	63.8
1913	1941	31	29	27.5	73.7
1968	1977	55	10	27.0	72.4
1988	1997	20	10	37.0	86.9

APPENDIX B *continued*

Outbreak Period		Return ¹ Interval	No. of years in period	Growth Reduction	
Start	End			Mean %	Maximum %
Terrace Lake (TRL)					
1750	1779	-	30	33.3	69.7
1829	1848	79	20	44.7	98.3
1887	1898	58	12	30.2	75.7
1906	1950	19	45	31.3	76.1
1986	1997	80	12	42.6	84.0

¹return interval is the number of years between start dates of outbreaks

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