Ecology, 82(3), 2001, pp. 679–697

CHANGES IN PANDORA MOTH OUTBREAK DYNAMICS DURING THE PAST 622 YEARS

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Abstract. Episodic outbreaks of pandora moth (*Coloradia pandora* Blake), a forest insect that defoliates ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) and other pine species in the western United States, have recurred several times during the 20th century in forests of south-central Oregon. We collected and analyzed tree-ring samples from stands affected by recent outbreaks of pandora moth to develop a long-term record of outbreaks. Outbreaks were evident in tree-ring series as a characteristic ''signature'' of sharply reduced latewood width within a ring, followed by reduced ring widths lasting 4–20 yr. We verified that this tree-ring signature was unrelated to drought or other climatic fluctuations by comparing the timing of known and inferred outbreaks with independent climatic data. Using the pandora moth tree-ring signature, we reconstructed a 622-year record of 22 individual outbreaks in 14 old-growth ponderosa pine stands. This is currently the longest regional reconstruction of forest insect outbreak history in North America. Intervals between pandora moth outbreaks were highly variable within individual forest stands, ranging from 9 yr to 156 yr. Spectral analyses of a composite time series from all stands, however, showed more consistent intervals between outbreaks, suggesting quasicyclical population dynamics at regional and decadal scales. Waveforms extracted from the regional outbreak time series had periods ranging over ∼18–24 yr (39.7% variance explained) and ∼37–41 yr (37.3% variance explained). The periods and strengths of these cycles varied across the centuries, with the largest outbreaks occurring when relatively high-amplitude periods of the dominant cycles were in phase. Twentieth-century outbreaks were not more synchronous (extensive), severe, or longer in duration than outbreaks in previous centuries, but there was an unusual 60-yr reduction in regional activity during ∼1920–1980. The changing dynamical behavior of pandora moth populations highlights the need to evaluate historical factors that may have influenced this system, such as climatic variations, forest fires, and human land uses. Although cyclical dynamics in animal populations have most commonly been attributed to endogenous, ecological processes (e.g., ''delayed density dependence,'' predators, pathogens, and parasites) our findings suggest that exogenous processes (e.g., climatic oscillations) may also be involved.

Key words: dendroecology; density dependence; forest disturbance; insect outbreaks; Oregon; pandora moth (Coloradia pandora)*; ponderosa pine* (Pinus ponderosa)*; population cycles; quasicyclical population dynamics; spectral analyses; tree-ring width chronology.*

INTRODUCTION

Knowledge of natural and cultural disturbance history over broad temporal and spatial scales is essential for understanding the dynamics of ecosystems (Pickett and White 1985). By studying the history of disturbances, we may identify trends, ranges, variations, and periodicities of events and processes that sustain or change ecosystems (Foster et al. 1990, Wickman et al. 1994, Swetnam et al. 1999). Temporal and spatial variations over meaningful scales are often difficult to assess, except in those ecosystems that preserve the history of past disturbances. Forest ecosystems are unique, because high-resolution histories of disturbances and other environmental variations can be preserved for centuries in the tree-ring record (Fritts and Swetnam 1989). Fire is usually considered the most important natural disturbance in pine forests worldwide, and fire histories based upon tree-ring dating of fire-scarred trees have been central to developing this understanding (Agee 1993, 1998). Episodic outbreaks of insects, however, may be of equal or greater importance than fire in regulating the dynamics of some pine forests. Compared to the extensive knowledge of fire history in North American ponderosa pine forests (Agee 1993, Covington and Moore 1994, Swetnam et al. 1999), much less is known about the history or dynamics of insect outbreaks in this forest type.

A variety of dendroecological techniques have been used to distinguish the effects of climate from herbivory on tree-ring growth, and to reconstruct time series

Manuscript received 3 January 2000; revised 19 February 2000; accepted 2 March 2000.

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PLATE 1. Left: Pandora moth larvae eat the needles of ponderosa pine trees. Near the end of the summer, the larvae can be up to 6 cm in length and consume a large amount of foliage. (Photo printed with permission of Mike Wagner). Right: Ponderosa pine forest south of Bend, Oregon. This photo was taken in June of 1990, after severe defoliation from the pandora moth. All of these trees survived the outbreak. (Photo by Boyd Wickman).

of insect outbreaks over periods of centuries (Wickman 1963, Blais 1983, Swetnam et al. 1985, Veblen et al. 1991, Jardon et al. 1994, Weber and Schweingruber 1995; C. L. Fastie, E. E. Berg, and T. E. Swetnam, *unpublished manuscript*). For example, in studies of western spruce budworm (*Choristoneura occidentalis* Freeman) outbreaks in mixed-conifer forests, nonhost ponderosa pine tree-ring chronologies were used to identify and remove climatic signals in host Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco.) and true fir (*Abies* species) tree-ring chronologies (Swetnam et al. 1985, Swetnam and Lynch 1993, Swetnam et al. 1995). This technique was based on the assumption that, if nonhost and host trees responded in a similar manner to climatic variations, then the differences (or residuals) between standardized ring-width chronologies of nonhost and host trees will primarily reflect nonclimatic environmental variations, such as the effects of defoliating insects. In practice, this technique has been highly effective in reconstructing long histories, but imperfect because nonhost and host tree species do not have exactly the same response to climatic variations. Despite this limitation, tree-ring reconstructions of western spruce budworm outbreak patterns generally correspond to independently estimated 20th century defoliation records and insect population numbers (Swetnam and Lynch 1993, Swetnam et al. 1995, Mason et al. 1997).

A particular advantage of tree-ring reconstructions is that they provide the necessary temporal length for evaluating dynamical properties of insect populations characterized by long intervals between outbreaks. Robust statistical assessments of cyclical or more complex behaviors require time series with many iterations of outbreak and endemic phases. Adequate tests of association between population numbers and environmental factors, such as climate, may also depend on availability of time series with sufficient temporal length and spatial coverage. Twentieth-century population measurements of long-interval outbreak species, such as western spruce budworm and pandora moth, typically encompass only one to a few outbreaks. Tree-ring reconstructions can increase this number by a factor of $\geq$10. Although tree-ring reconstructions provide the longest available time series of insect populations from the same forests, they have rarely been used to evaluate or model population dynamics (Mason et al. 1997).

A variety of models involving endogenous (internal) processes have been proposed as explanations for population fluctuations and cycles in forest insect populations (Meyers 1993, Berryman 1996, Cappuccino and

Price 1995). Endogenous ecological processes most commonly investigated or speculated as being causes of cyclicity include delayed-density dependence, predators, parasites, and pathogens. The role and detection of delayed-density dependence in population dynamics has long been a subject of debate (e.g., Williams and Liebhold 1995, 1997, Berryman and Turchin 1997). Exogenous (external) processes, such as climate, have also been investigated as possible causes of insect population fluctuations and cycles (e.g., Greenbank 1956, Swetnam and Lynch 1993). Climatic causes have often been discounted because of statistically insignificant or weak correlations, but most of these analyses involved relatively short time series (<50 yr). It is also commonly assumed that climatic cycles are nonexistent or too weak to influence insect populations (Martinat 1987).

Pandora moth (*Coloradia pandora* Blake, Lepidoptera) is an indigenous phytophagous insect whose larvae consume the foliage of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), and lodgepole pine (*Pinus contorta* Dougl. ex Loud.; see Plate 1). Incidental host tree species include sugar pine *(P. lambertiana* Dougl.) and Coulter pine (*P. coulteri* D. Don.) (Patterson 1929, Wygant 1941, Furniss and Carolin 1977). Most studies have focused on pandora moth behavior and environmental impact during modern outbreaks, rather than long-term dynamics (Miller and Wagner 1984, Schmid and Bennett 1988, Wickman et al. 1996, Cochran 1998). Observations of 20th-century outbreaks and interviews with Native Americans who used the larvae and pupae as a food source (Patterson 1929, Massey 1940) suggest that outbreaks typically recur every ~20–30 yr and last ~6–8 yr. This inference, however, is based on only three or four outbreaks, and it is not clear whether outbreaks were aperiodic or cyclic over the long term. Changes in outbreak dynamics in the 20th century might be expected, because many ponderosa pine forests of eastern Oregon have been heavily harvested and fire regimes have been disrupted by livestock grazing and fire suppression (Lehmkuhl et al. 1994, Wickman et al. 1994, Heyerdahl 1997).

Tree-ring studies have suggested that increased severity of western spruce budworm outbreaks in the late 20th century might be related to land uses that led to forests that were more vulnerable to budworm outbreaks (Anderson et al. 1987, Swetnam and Lynch 1993, Hadley and Veblen 1993, Swetnam et al. 1995). Increased density of trees and development of multicanopy forests following fire suppression might be favorable to the spread and severity of outbreaks by providing a more abundant and spatially continuous food source for insects. Multicentury changes in pandora moth dynamics, however, have not been previously studied.

We sampled and analyzed the tree rings of ponderosa pine trees that were 200–600 yr old (or older) in areas that have been repeatedly defoliated by pandora moth during the 20th century. Our general objectives were to reconstruct the long-term history of pandora moth and to evaluate its temporal dynamics in ponderosa pine ecosystems of south-central Oregon. We compared historical patterns of outbreaks among a set of widely scattered ponderosa pine stands and analyzed changing periodicities in a regional outbreak time series using new spectral analysis tools. We discuss some of the theoretical implications of our findings for hypotheses and models of forest insect population dynamics, particularly temporal changes that may be related to human land use practices or climatic variations. Our study emphasizes the importance of long time series for evaluating exogenous vs. endogenous controls of forest insect dynamics.

Pandora Moth History and Tree-ring Impacts

Pandora moth has a patchy distribution that may be partly dependent on soil conditions; larvae seem to prefer loose soils developed from weathered granite or pumice into which they burrow to pupate (Furniss and Carolin 1977). Widely scattered outbreaks of substantial size (>1,000 ha) have occurred in Arizona, California, Colorado, and Oregon during the 20th century (Carolin and Knopf 1968). Outbreaks were documented in central Oregon during the 1890s (Keen 1937), 1918–1925 (Patterson 1929, Keen 1937), 1963–1968 (U.S. Forest Service reports, B. E. Wickman, *unpublished data*), and 1988–1996 (Wickman et al. 1996).

Pandora moth has a two-year life cycle that begins in July and August of the first year when females lay their eggs (Furniss and Carolin 1977). Larvae hatch in late August and September and begin to feed on mature needles of host trees, usually avoiding new foliage or buds (Carolin and Knopf 1968). Larvae overwinter at the base of needles during the second instar. With arrival of warm conditions in spring, larvae resume feeding on the foliage, reaching up to 6 cm in length by summer. In June and July, caterpillars move down the tree trunk, burrow into the soil, and pupate. Pupae remain in the soil for a second winter, finally emerging as moths in late June or July to continue the cycle. Some pupae can enter extended diapause and emerge in the third to fifth year (Carolin 1971). A nucleopolyhedrosis virus that kills mature larvae may act as a biological control of outbreaks (Schmid and Bennett 1988, Wickman et al. 1996).

Defoliation of ponderosa pine by pandora moth is often accompanied by reduction in ring widths (Patterson 1929, Keen 1937, Massey 1940, Wygant 1941, Miller and Wagner 1989). A study within one of our sampled areas (Pringle Falls) found 25%, 30%, and 63% reduction in basal area increment in three succeeding years of defoliation (1992–1994) (Cochran 1998). In a study of a 1978 outbreak on the Kaibab plateau in northern Arizona, Miller and Wagner (1989) found the 1980 ring to be present on all nondefoliated

TABLE 1. Site names, location, number of trees sampled, and earliest date in chronology for stands sampled for pandora moth defoliation in central Oregon.

Site name	Designation	Latitude N	Longitude W	Elevation (m)	No. trees cored	Inner date
Lookout Mountain Lower	LML	43° 45′30″	121° 39′00″	1320	12	1528
Pringle Falls Prescribed Fire	PPF	43° 44′00″	121° 39′00″	1320	40	1329
Experimental Forest	EF	43° 43′00″	121° 36′30″	1530	12	1333
Pringle Falls RNA	PF/RNA	43° 42′00″	121° 37′00″	1460	19	1504
Surveyor Flow	SVF	43° 37′00″	121° 18′30″	1550	5	1746
Deschutes	DES	43° 28′00″	121° 24′00″	1420	11	1574
Junction of Highways 51 and 97	JCT	43° 19′00″	121° 45′00″	1420	12	1412
Skookum Butte	SKB	43° 14′30″	121° 39′00″	1670	12	1639
Diamond Lake	DLK	43° 05′30″	121° 57′30″	1510	12	1512
Blue Jay Spring	BJS	42° 55′00″	121° 32′00″	1490	13	1422
Telephone Draw	TLD	42° 56′30″	121° 37′00″	1550	10	1493
Telephone Draw South	TDS	42° 45′30″	121° 31′00″	1550	7	1450
Crater Lake	CLK	42° 47′00″	122° 04′00″	1370	12	1572
Calimus Butte	CAB	42° 38′00″	121° 32′00″	2020	10	1652

trees, but missing in 83% of heavily defoliated and 24% of moderately defoliated trees. Mortality of mature trees is low, because new needles and terminal buds are rarely eaten, and the two-year life cycle results in most of the feeding in alternating years, allowing some respite from defoliation (Furniss and Carolin 1977). Subsequent infestations of bark beetles in weakened trees, however, sometimes lead to extensive mortality (Patterson 1929, Wygant 1941, Schmid and Bennett 1988).

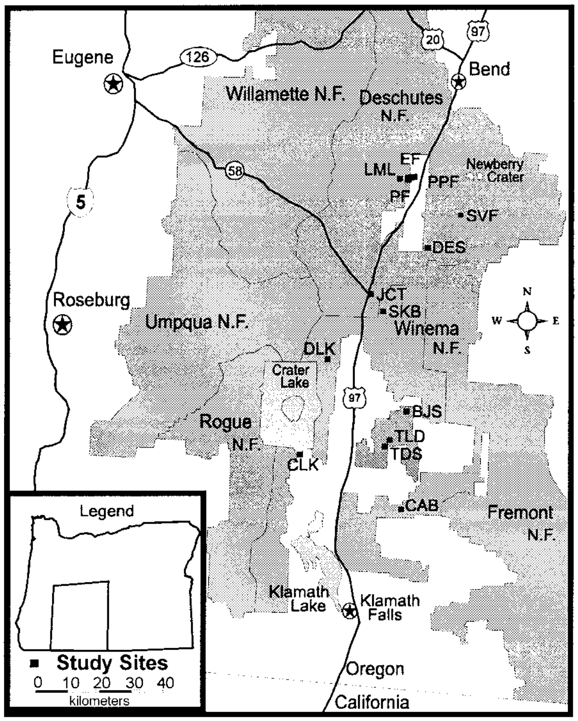

FIG. 1. Map of Oregon, USA, showing locations of old-growth ponderosa pine stands sampled in this study. See Table 1 for site descriptions.

METHODS

Tree-ring sampling, crossdating, measurement and standardization

Tree-ring cores were collected in 14 old-growth ponderosa pine stands (Table 1) dispersed throughout central Oregon (Fig. 1). All stands had a shrub understory (*Ceanothus velutina*, *Arctostaphylas patula*, or *Purshia tridentata*) and a thick accumulation of litter except the PPF and RNA stands, which had prescribed surface fires in 1992 and 1994, respectively. All stands are typical of old-growth ponderosa pine east of the Cascade Range in Oregon and northern California (Table 2). In general, stands were selected that had a substantial component of apparently old (>300 yr) ponderosa pine trees. Old-growth stands in this age range were not common in the study area and this precluded a random sampling of stands. Sampled stands were relatively easily accessible by road or walking. Individual trees were selected by systematically traversing the stand and choosing dominant trees that were approximately evenly distributed in the stand. The stand boundaries were defined by visible topographic features (e.g., ridge tops) and drastic canopy changes (e.g., along former harvesting boundaries). The size range of stands was ∼10–50 ha.

Two increment cores per tree were taken at breast height on opposite sides from ≥10 dominant ponderosa pine trees in each stand (except SVF and TDS stands, where fewer trees were sampled, Table 1). All cores were oven-dried for 24 h, sanded to enhance visibility of the cellular structure of the wood, and then crossdated by identifying key ring-width features (Stokes and Smiley 1968, Swetnam et al. 1985). We used the skeleton plot crossdating technique (Stokes and Smiley 1968) to develop a master chronology that recorded all narrow rings in the tree-ring series.

Ring widths were measured to the nearest 0.01 mm with an electronic microcaliper linked to a computer,

TABLE 2. Structural characteristics of nine of the sampled old-growth ponderosa pine stands.

Site	No. plots sampled†	Density (no. trees/ha) Mean	Density 1 SE	Basal area (m^2/ha) Mean	Basal area 1 SE	Tree species‡
BJS	9	1983	370	34.2	3.0	PIPO; a few POTR suckers
CAB	4	1525	46	81.8	2.4	PIPO + ABCO + PILA
CLK	12	2441	172	45.0	3.4	PIPO + ABCO
DLK	10	200	37	36.5	4.9	PIPO
LML	5	2800	128	46.6	1.5	PIPO + PICO
PPF	5	2700	95	46.7	1.2	PIPO + PICO seedlings
PF/RNA	8	869	81	23.2	1.0	PIPO + PICO; past burning
PPE	18	386	111	16.2	2.8	PIPO; past cutting and burning
SKB	14	2050	97	21.5	1.1	PIPO + PICO; past cutting

Note: Due to time constraints, comparable detailed measurements of the remaining five stands were not obtained.

† Number of 200-m^2 circular plots located at 50-m intervals along transects.

‡ Species codes are: PIPO, *Pinus ponderosa*; POTR, *Populus tremuloides*; ABCO, *Abies concolor*; PILA, *Pinus lambertiana*; PICO, *Pinus contorta*.

and the crossdating verified with the COFECHA program (Holmes 1986, Grissino-Mayer and Fritts 1997). The dated ring-width series from each core were then standardized with the program ARSTAN (Cook and Holmes 1986, Grissino-Mayer and Fritts 1997). Standardization of tree-ring width series is necessary to remove age-related trends in growth, so that other causes of growth variations can be evaluated separately (e.g., climate, insects). Standardization of the tree-ring series was accomplished by fitting flexible curves (cubic splines) to each measured ring-width series and then dividing the ring-width values by the value of the fitted curve to produce tree-ring indices. We standardized the ring-width series with 40-yr, 50% frequency response cubic splines (Cook and Peters 1981). Tree-ring indices computed using a cubic spline with this flexibility retain $>$90% of the variance in the original ring-width series with wavelengths of $\leq$20 yr. This means that almost all of the tree-ring width changes occurring over time scales of less than two decades were preserved in the index series, so most of the relatively short-term effects of individual pandora moth outbreaks should have been retained in the index series.

Detecting outbreaks and compiling results by tree, stand, and region

We first examined cores from stands known to have been heavily defoliated by the pandora moth during three documented outbreaks occurring ~1918–1925, 1963–1968, and 1988–1996 (Patterson 1929, Carolin and Knopf 1968). Flights of pandora moths were also observed in 1893 near Klamath Lake, but specific locations of defoliated stands were not documented (Patterson 1929, Carolin and Knopf 1968). We identified the characteristic ring-width pattern (or ‘‘signature’’) associated with pandora moth defoliation based on the timing, duration, and magnitude of ring-width reduction in stands, recording the three 20th-century outbreaks. The pandora moth signature was then used to infer past outbreak occurrences throughout individual tree-ring chronologies by assigning values to parameters in a computer program called OUTBREAK (Holmes and Swetnam, *unpublished operating manual* [on file at Laboratory of Tree-Ring Research, University of Arizona]; also see Swetnam et al. 1995).

The inputs to the OUTBREAK program were tree chronologies (i.e., the averaged ring-width index series from two cores for each tree). The program was run separately for each sampled stand. OUTBREAK works by sequentially reading the index values for each tree chronology, and by identifying years and periods (index values) that meet or exceed the assigned parameters. Identification of a pandora moth signature requires the following parameters simultaneously: (1) ring-width indices $\geq$1.28 standard deviations below the mean ring-width index (approximately the smallest 10th percentile values in the series), (2) growth reduction of this magnitude lasting $\geq$4 yr, and (3) the ring-width index for the first year of the inferred outbreak $\leq$50% of the previous year. These parameters were judged to adequately represent the general pattern of magnitude and duration of reduced growth observed in the tree-ring series during the known 20th-century outbreaks. This procedure provides a systematic and consistent rule set for rapidly analyzing a large number of tree-ring measurements for probable outbreak signals.

Using the selected ring-width index parameters, the OUTBREAK program identifies the timing (dates) of outbreaks and computed growth reduction, duration, percentage maximum annual growth reduction, and percentage mean periodic growth reduction for each outbreak in each tree chronology. Percentage maximum growth reduction for each outbreak was defined as the mean series index value minus the smallest index value during outbreak, multiplied by 100. Percentage periodic growth reduction for each outbreak is defined as the mean series index value minus the mean index value during outbreaks, multiplied by 100. In both cases, the ‘‘mean series index value’’ is usually ~1.0 in standardized ratio indices. After computing these values, the program computes the means of these values for all trees within the entire stand. The output of the program includes printable tables in text files that list the timing, growth reduction, and duration of detected outbreaks for each tree and the entire stand. Files are also produced in column format containing time series of the numbers of trees recording outbreaks each year and the number of trees sampled and with measured rings in each year.

We computed a regional time series of outbreaks by summing the numbers of trees recording an outbreak during each year of the entire record across all stands. Numbers of trees included in the record decreased with increasing time before the present, so we standardized the series by computing the percentage of trees recording outbreaks each year (i.e., we divided the number of trees recording outbreaks each year by the total number of trees with measurements for that year, and then multiplied by 100).

In addition to using the OUTBREAK program and the parameters based on total ring-width variations, we visually confirmed the timing of identified outbreaks by scrutinizing the dated tree-ring specimens. During known 20th-century outbreaks the total ring width was typically reduced during the first year of heavy defoliation, and the latewood was very thin or lighter in color than latewood formed during years without defoliation (Fig. 2) (Patterson 1929, Miller and Wagner 1989, Wickman et al. 1996). This pattern was also generally evident in our tree-ring specimens during the inferred, pre-20th-century outbreaks.

Distinguishing between droughts and outbreaks

In order to distinguish pandora moth herbivory from climatic events as causes of reduced growth, we compared the time series of known and inferred outbreaks with independent meteorological data and tree-ring based climate reconstructions. Climatic effects on tree growth are often accounted for in dendrochronological studies of insect outbreaks by using a local nonhost chronology for direct tree-ring chronology comparisons (e.g., Wickman 1963, 1980 , Swetnam et al. 1985, 1995, Hadley and Veblen 1993, Jardon et al. 1994). Most of our stands, however, were essentially pure ponderosa pine, and a suitable nonhost tree species was not locally available for control. Tree-ring growth of ponderosa pine trees in semiarid landscapes, such as eastern Oregon, tends to be correlated with interannual variations in seasonal precipitation or drought indices (Keen 1937, Fritts 1976, Garfin and Hughes 1996). Therefore, to distinguish defoliation from climatic effects we used 20th-century precipitation observations from central Oregon divisional meteorological data (National Climatic Data Center 1994). We also used a regional tree-ring reconstruction of annual precipitation and summer drought indices that was based predominantly on western juniper (*Juniperus occidentalis* Hook.) (Garfin and Hughes 1996).

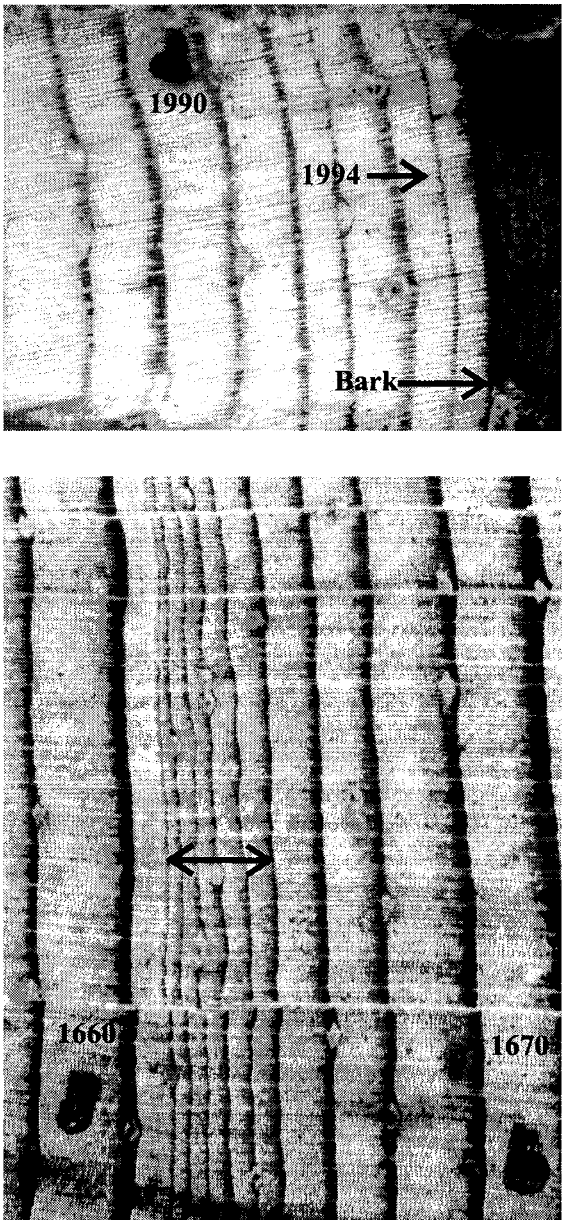

FIG. 2. Photographs of thin latewood during the initial year of defoliation for the most recent outbreak (1994; upper photo), and thin latewood (1661) and subsequent reduced growth (arrows) in a 17th-century outbreak (lower photo).

Western juniper is not a host for pandora moth, but western juniper and ponderosa pine have a similar growth response to severe and multiple-year droughts. For example, in a climate response analysis of western juniper chronologies using monthly and seasonal climate variables, Garfin and Hughes (1996) found that ring widths were most highly correlated with the total precipitation from October of the prior year to September of the current growing season, as well as with the August Palmer drought severity indices. Ponderosa pine tree-ring width chronologies from throughout the western United States are typically positively and significantly correlated with winter-to-spring seasonalized precipitation variables, or with integrated measures of temperature and precipitation during the growing season, such as June, July, or August Palmer drought severity indices (Fritts 1976, Cook et al. 1999). Thus, drought-induced growth reductions in our ponderosa pine chronologies should be consistent with the Garfin and Hughes (1996) regional, annual precipitation and summer drought reconstructions based on western juniper growth.

Spectral analyses

We used two advanced time series analysis tools, the maximum entropy method (MEM) and singular spectrum analysis (SSA), to assess possible oscillatory behavior and changing temporal patterns of reconstructed pandora moth populations. These relatively new spectral analysis techniques have been widely applied in paleoclimatology research, but infrequently in historical ecology or paleoecology (e.g., Swetnam and Betancourt 1998). The maximum entropy method is a high-resolution spectral estimating procedure that allows the user to investigate the strength of periodic behavior in a time series within a specified range of the spectrum (Burg 1978, Dettinger et al. 1995). Singular spectrum analysis is a nonparametric method for analyzing time series that employs a type of principal-components analysis (Vautard and Ghil 1989, Dettinger et al. 1995). Singular spectrum analysis enables the user to evaluate changing periodic behavior in a single time series by extracting pairs of ‘‘reconstructed components,’’ or ‘‘waveforms,’’ which represent the dominant periodic modes of the time series. These waveforms are essentially sine–cosine waves with wavelengths matching the dominant periodicities in the original time series. One advantage of SSA is that the waveforms retain the temporal character of the periodic behavior, so that it is possible to detect changes through time in amplitude and phasing of the dominant cycles. Software and additional information on these tools and their uses are available on the worldwide web (e.g., search for ‘‘Singular Spectrum Analysis Toolkit’’).

A distinct advantage of having a long time series for studying population dynamics is that multiple examples of cycles or other behaviors through time may be obtained, and it is also possible to assess how these dynamical characteristics changed through time. We used both MEM and SSA to assess temporal dynamics in the regional pandora moth time series. First, the MEM was applied to sequential, 200-yr segments of the time series overlapping by 100 yr. The spectral density functions for each 200-yr period were then overlaid on one another to assess temporal changes in periodicity. Second, waveforms from the SSA were extracted and plotted to evaluate the changing amplitude of the dominant periods and their relative phasing.

RESULTS

Modern outbreaks and the tree-ring signature

A total of 326 cores from 163 trees in the 14 sampled stands were dated and included in the host tree chronologies. Reduced ring-width indices in individual trees, and the mean indices for all trees in a stand, generally coincided with the timing of known, 20th-century outbreaks (e.g., Fig. 3). The OUTBREAK program, for example, identified the most recent outbreak in the LML, DES, and BJS (see Table 1 for site definitions) stands starting as early as 1989 in some trees, with distinct thin latewood in 1994 and an extremely narrow ring for 1995. This corresponds to the known timing of this outbreak, which occurred from ~1988–1996 (Wickman et al. 1996). The general pattern suggested by the documentary records was an advance outward from a central, initial location. A large larvae population was first observed in 1986 within a 1200-ha region near Bend, Oregon. By 1988, the population reached outbreak levels across 12 400 ha. In 1990, the first aerial survey mapped the defoliated area at 66 700 ha. This area expanded to 197 000 ha in 1992 and peaked at 864 000 ha in 1994, when virus-caused mortality of larvae was noted. Only 22 200 ha of total defoliation were mapped in 1996 (A. Eglitis, *personal communication* [Deschutes National Forest]).

The 1963–1968 outbreak was observed only at the SKB stand, where the beginning date is not precisely known. Radial growth was reduced at this site from 1967 to 1975. The 1967 ring was half the size of a normal ring and had very thin latewood; the latewood was thinner than normal throughout the entire period of growth reduction. A gradual return to the preoutbreak growth rate occurred during 1970–1975.

During the 1918–1925 outbreak, larvae were observed from the Sisters area south through the Deschutes and Winema National Forests and west to Crater Lake National Park, with patches of intense defoliation throughout the area (Patterson 1925). The peak defoliation occurred in 1919 east of Klamath Lake. Our tree-ring cores show thin latewood in 1920 and 1922, a signature consistent with that described by Patterson (1929). Ring-width reduction started in 1919 in the TDS stand, with growth reduction in the TLD and BJS stands in 1920 and 1921. The outbreak apparently moved north, with ring-width reduction first occurring in the LML stand in 1922, followed by occurrence in EF, PF, and PPF stands in 1923. Thin latewood was evident at each site, and the rings for 1922 or 1925 were often the narrowest in these chronologies. Growth reduction lasted until 1931 in the southern stands and 1934 in most of the northern stands. The first and last years were not synchronous between any two stands, suggesting that the trees responded to defoliation and not directly to variations in regional climate (e.g., drought).

Adult pandora moths were documented within our

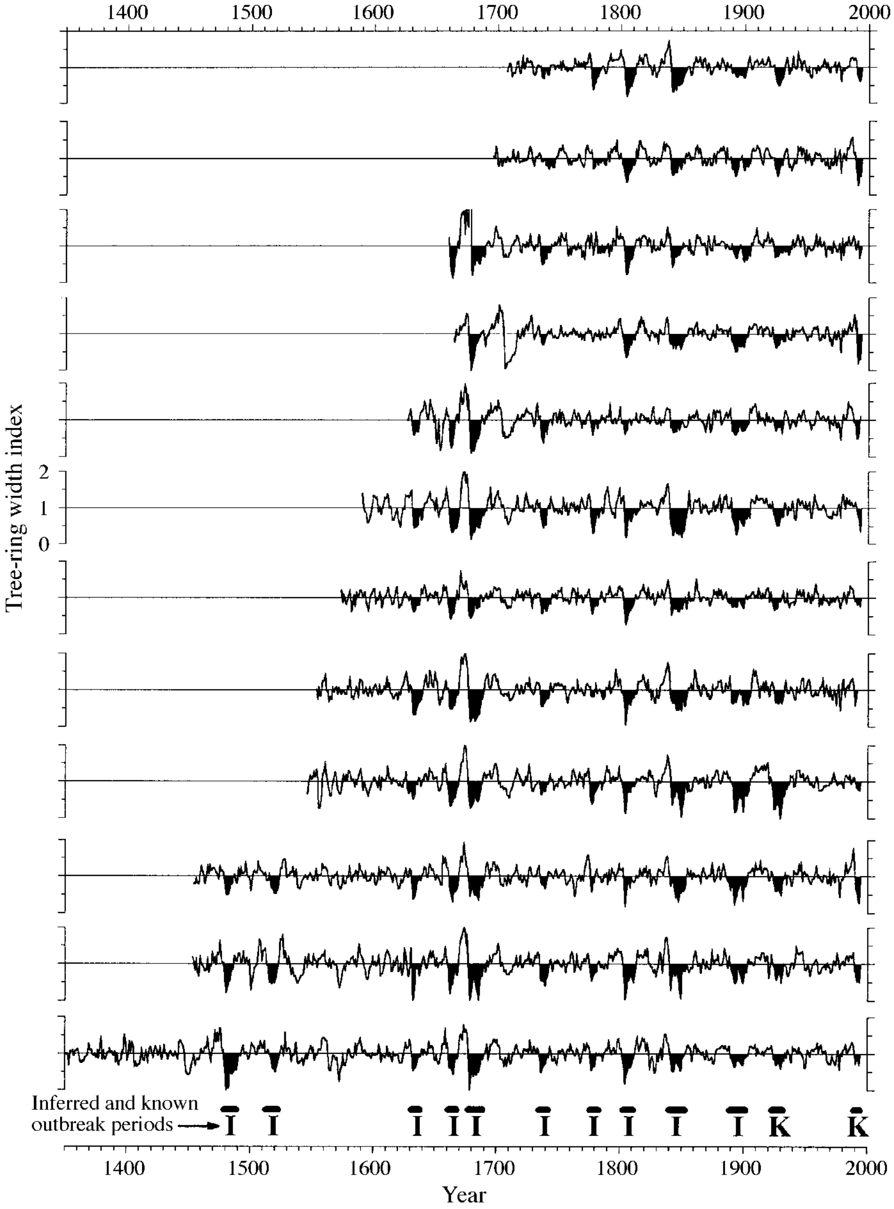

FIG. 3. Standardized ring-width indices for 12 old-growth ponderosa pine trees from the Experimental Forest (EF) stand, central Oregon. Shaded areas below each line represent periods of below-average radial growth that were known (K) or inferred (I) pandora moth outbreaks. Additional outbreaks may have occurred during the 1540s, 1570s, and 1710s, as indicated in the regional composite of stands (Fig. 4) and trees (Fig. 5).

study area at Fort Klamath (east of Klamath Lake) before 1893 (Patterson 1929, Carolin and Knopf 1968). Four chronologies from the northern stands (EF, PF, PPF, and DES) in the Deschutes National Forest (Fig. 1) had ring-width reductions beginning in 1889, while the LML stand first recorded a growth reduction in 1895. Return to mean growth at all these five stands occurred by 1903. Growth reduction was not evident in the southern stands (BUS, TLD, TDS, CAB) during this period, but all of these stands are >25 km from Klamath Lake (Fig. 1). It is possible, therefore, that the southern stands were outside the Klamath Lake outbreak area, and a separate outbreak center may have encompassed the northern part of our study area.

Outbreak timing, intervals, and duration

The combined history from all 14 stands reveals considerable synchrony of outbreaks among stands (Fig. 4), but only the mid-19th-century outbreak seemed to cover nearly the entire study area. The first year of each inferred outbreak appears as a cluster of dates rather than a single year, consistent with a pattern of

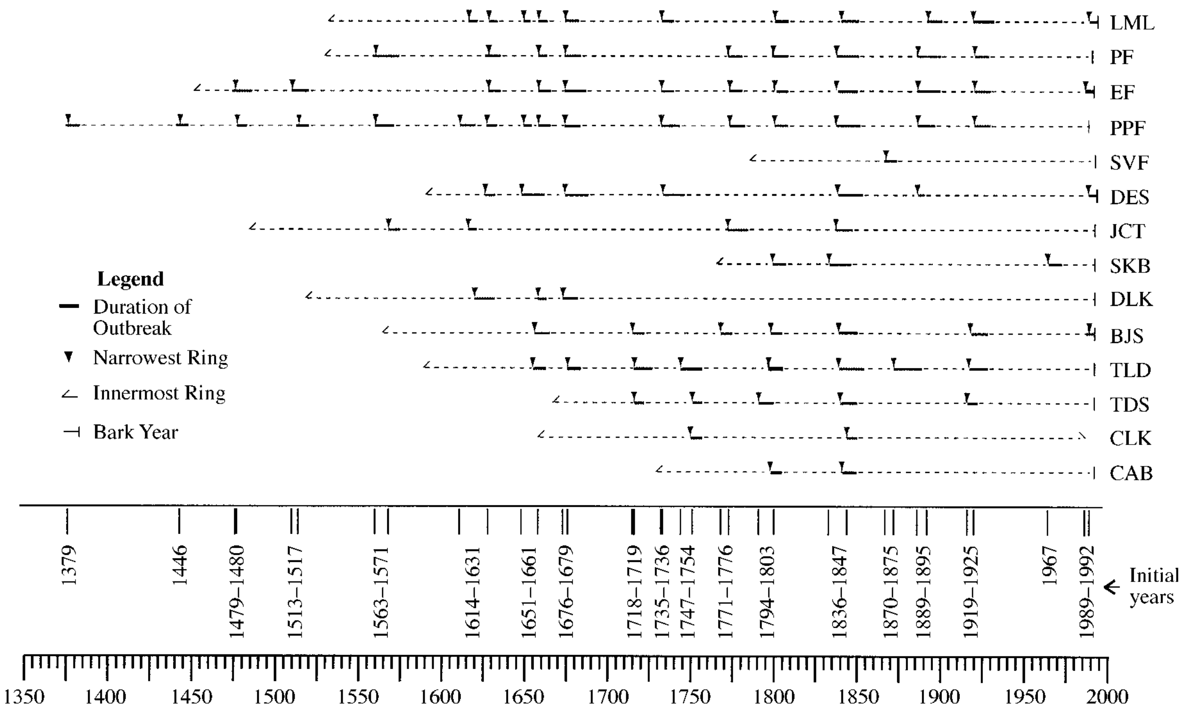

FIG. 4. Composite chronology of pandora moth outbreaks in 14 ponderosa pine stands in south-central Oregon. The arrowheads indicate the first years that outbreaks were recorded in the ring-width series from the sampled stands. The vertical lines and dates at the bottom are the first years of outbreaks composited across all stands.

population spread from an initial location outward to other stands over a period of several years. A total of 22 outbreak periods were identified over the 622-yr record from the clustering of growth reduction years in the composite record (Fig. 4).

The mean interval between outbreaks (i.e., between initial years) was 27 yr and ranged within 8–48 yr. The mean duration of outbreaks was 10 yr and ranged 4–18 yr. Dates of all inferred outbreaks, duration, intervals between outbreaks, and growth reduction estimates are listed in Table 3. Consistently narrow or locally absent rings were detected at the beginning of most outbreaks, particularly in the following two-year periods: 1480–1481, 1632–1633, 1662–1663, 1678–1679, 1803–1804, 1841–1842, and 1922–1923. The most consistent years with thin latewood were 1479, 1631, 1661, 1677, 1802, and 1840. The shortest inferred outbreaks, identified as one or two years of sharply reduced growth, followed by a few years of recovery, occurred at the PF/RNA site in ~1631, 1661, and 1677.

Climate comparisons

Several lines of evidence support our inference that the reduced growth periods we identified were caused directly by pandora moth defoliation rather than by drought. First, the ring-width signature identified for pandora moth is quite distinctive, particularly thin latewood appearing in the initial year of an extended reduced growth period (Fig. 2, and photographs in Patterson [1929]). So-called ''light rings'' (i.e., rings with thin latewood) have been linked to cold spells in northern latitudes, but sustained low growth in subsequent years does not seem to be a consistent characteristic of trees in these cases (Filion et al. 1986, Liang et al. 1997). Thin latewood and subsequent reduced growth, however, have been associated with tree defoliation by larch sawfly in Canada (Jardon et al. 1994, Liang et al. 1997).

Second, the duration of sharply reduced growth lasting ≥10 yr seems to be more characteristic of pandora moth defoliation than drought, in this portion of Oregon. The 275-yr precipitation reconstruction by Garfin and Hughes (1996) and 20th-century meteorological data show that multiple-year droughts of this length (or nearly this length) occurred only during the 1840s (1837–1844, 8 yr) and 1930s (1928–1937, 10 yr). During the 1840s, 12 of our sampled stands recorded growth reduction that was also consistent with pandora moth defoliation. Six of the stands also showed growth reduction during the long period of drought in the 1930s, which was the most severe drought in both the 20th-century meteorological records and the 275-yr tree-ring reconstruction (Garfin and Hughes 1996). In both cases (1840s, 1930s), however, the timing of inferred pandora moth outbreaks did not precisely match the timing of drought indicated in the independent climatic data. For example, growth reduction in

TABLE 3. Dates of inferred outbreaks, duration of ring-width reduction, interval between reductions, relative growth reduction for the reduction period, and the year of maximum reduction in old-growth ponderosa pine during 22 outbreaks of pandora moth, central Oregon, USA.

Site	Dates	Duration (no. years)	Interval (no. years)	Periodic growth reduction (%)	Smallest ring
LML	1619–1624	6	···	45.91	1620
	1631–1636	6	7	16.41	1633
	1652–1656	5	16	23.40	1653
	1661–1666	6	5	26.82	1662
	1677–1685	9	11	20.06	1680
	1735–1742	8	50	16.98	1739
	1803–1811	9	61	23.31	1804
	1843–1853	11	32	32.42	1845
	1895–1903	9	42	12.20	1899
	1922–1934	13	19	11.22	1930
	1991–1995	5	57	21.19	1995
PF	1563–1577	15	···	16.86	1565
	1631–1638	8	54	34.36	1632
	1661–1666	6	23	37.18	1662
	1677–1686	10	11	35.77	1678
	1775–1783	9	89	21.42	1777
	1802–1811	10	19	30.83	1804
	1840–1853	14	29	29.72	1841
	1889–1902	14	36	21.92	1893
	1923–1931	9	21	26.21	1925
EF	1479–1489	11	···	34.32	1480
	1513–1523	11	24	21.32	1520
	1631–1638	8	108	23.31	1632
	1661–1668	8	23	31.48	1662
	1677–1689	13	9	36.22	1678
	1735–1742	8	46	19.58	1736
	1776–1783	8	34	13.75	1777
	1803–1811	9	20	32.88	1804
	1840–1853	14	29	27.23	1842
	1889–1902	14	36	22.04	1893
	1923–1932	10	21	20.24	1926
PPF	1379–1386	8	···	27.54	1383
	1446–1451	6	60	29.36	1449
	1480–1486	7	29	36.42	1481
	1517–1523	7	31	25.31	1519
	1563–1574	12	40	13.95	1565
	1614–1623	10	40	17.51	1619
	1630–1636	7	7	19.61	1631
	1652–1657	6	16	27.00	1653
	1661–1668	8	9	25.02	1662
	1677–1686	10	49	31.02	1678
	1735–1746	12	30	12.95	1737
	1776–1785	10	18	13.84	1777
	1803–1811	9	29	31.28	1804
	1840–1854	15	35	20.49	1843
	1889–1899	11	24	15.25	1899
	1923–1932	10	···	17.68	1930
SVF	1870–1876	7	···	51.96	1871
DES	1629–1635	7	···	20.66	1631
	1651–1665	15	16	20.67	1652
	1677–1691	15	12	25.73	1687
	1736–1749	14	45	34.17	1741
	1841–1856	16	92	36.62	1846
	1889–1893	5	33	25.73	1890
	1991–1995	5	98	31.78	1995
JCT	1571–1578	8	···	19.39	1573
	1619–1624	6	41	19.83	1621
	1775–1787	13	151	14.59	1777
	1840–1850	11	53	17.59	1841
SKB	1802–1810	9	···	18.90	1803
	1836–1849	14	26	33.27	1845
	1967–1975	9	118	32.47	1969
DLK	1623–1635	13	···	17.87	1632
	1661–1666	6	26	25.33	1665
	1676–1685	10	10	25.46	1678
BJS	1659–1668	10	···	42.87	1660
	1718–1725	8	50	35.99	1720
	1771–1778	8	46	20.62	1772
	1801–1808	8	23	18.67	1802
	1842–1853	12	34	22.06	1843
	1921–1931	11	68	20.37	1923
	1992–1995	4	61	26.19	1992
TLD	1658–1666	9	···	40.85	1660
	1679–1687	9	13	26.42	1680
	1719–1730	12	32	30.81	1720
	1747–1760	14	17	21.84	1756
	1800–1808	9	40	24.40	1801
	1842–1854	13	34	36.75	1843
	1875–1892	18	21	26.13	1877
	1920–1931	12	28	43.45	1922
TDS	1719–1725	7	···	14.57	1721
	1754–1760	7	29	10.31	1756
	1794–1803	10	34	14.40	1802
	1843–1853	11	40	13.59	1851
	1919–1925	7	66	24.16	1922
CLK	1753–1760	8	···	24.19	1758
	1847–1853	7	87	24.80	1849
CAB	1801–1808	8	···	23.49	1802
	1844–1853	10	36	18.70	1845

the ponderosa pine chronologies persisted well into the 1850s (Figs. 3, 4), whereas the drought extended only until the mid-1840s. The documented 1920s outbreak began in some stands in the late 1910s, and growth reduction was evident in only a few of these chronologies after 1934. However, the drought began in the late 1920s and extended to ~1937. Overall, the mean reconstructed precipitation during all known and inferred outbreak years (303 mm) was only slightly lower than the mean precipitation of all other years in the reconstructed precipitation time series (312 mm) (one-sided Student's t test value, 1.49; $P = 0.14$).

Some of our sampled ponderosa pine stands did not show extreme growth reduction during the 1910–1920s outbreak or the severe 1930s drought. This suggests that these stands were not defoliated during this outbreak and that the sampled trees were insensitive to the regional drought conditions. Compared to most drought-sensitive chronologies used in dendroclimatic reconstructions, the year-to-year variability in our ponderosa pine chronologies was relatively low (mean sensitivity ranged 0.191–0.282) (see Fritts and Shatz [1975] for comparative statistics). Many of our ponderosa pine stands were on pumice-derived soils. The influence of droughts on trees growing in pumice may be moderated, because extensive root systems can develop in these loose soils and thereby capture moisture from large areas (Franklin and Dyrness 1988). This apparent low climate sensitivity of ponderosa pine growth at these sites increases our overall confidence

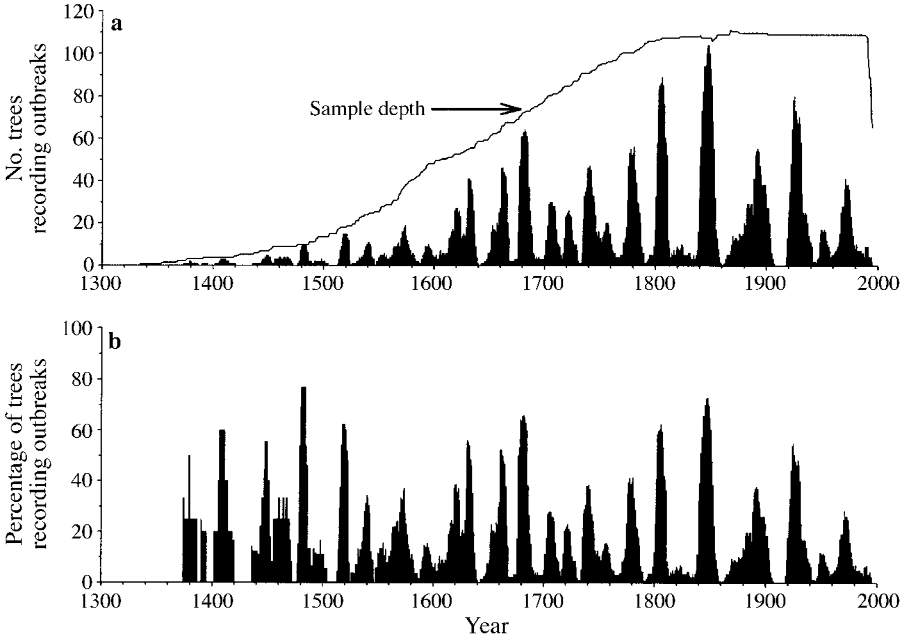

FIG. 5. (a) Time series of the number of trees recording outbreaks and the sample depth curve, and (b) percentage of trees recording outbreaks in old-growth ponderosa pine stands, central Oregon.

that defoliation rather than drought caused the sharp and persistent growth reduction periods we identified as pandora moth outbreaks.

Spatial patterns of initial growth reduction provide additional support for the timing of past pandora moth outbreaks. Although some years with thin latewood or missing rings closely coincided among stands, the initial outbreak years tended to originate in a single small group of stands, and other stands would show the indicators in subsequent years. This pattern is more consistent with the spreading pattern we would expect from a forest defoliator than for a regional drought effect, which is ordinarily marked by highly synchronized reduced growth among stands within a region (Fritts 1976).

Changing periodicity

The regional composite time series presented here (1374–1995) is the longest reconstruction of forest insect population dynamics yet developed for North America. Changing sample depth (i.e., number of trees included in the record) is responsible for the century-scale trend in the time series of decreasing numbers of trees recording outbreaks further back in time (Fig. 5a). The percentage time series (Fig. 5b) is more stationary, but probably has some bias before ~1600, because progressively fewer trees and stands are included in the composite.

A striking pattern evident in the regional time series was the episodic, quasi-cyclic recurrence of outbreaks. The maximum entropy method (MEM) and singular spectrum analyses (SSA) of the 622-yr record confirmed that strong but temporally changing cycles explained most of the variance in the time series (Figs. 6 and 7). Two cycles were dominant with wavelengths varying within ~18–26 and 35–41 yr (Fig. 6), depending upon the period of analysis. (Hereafter, we will refer to these combinations as the ''20-yr'' and ''40-yr'' cycles.) For example, the strength (i.e., power density, Fig. 6) of the 40-yr cycle was greatest during the late 1300s to ~1500, and from the 1700s to ~1900. Higher amplitudes of the 40-yr cycle were also evident during these periods in the SSA waveforms (Fig. 7b). The 20-yr cycle changed considerably in strength through time (Fig. 6), with three periods exhibiting amplitude maxima: ~1400s, 1600s, and 1750–1850 (Fig. 7c, d).

An advantage of the SSA, in addition to extracting time series that illustrated temporal changes in cycles (Fig. 7b–d), was that the percentage variance of the original time series explained by these cycles was estimated. The pair of reconstructed components with cycles ~40 yr in length (Fig. 7b), for example, explained 37.3% of the variance of the regional pandora moth time series (Fig. 7a). The combination of the pairs of cycles ~20 yr in length (Fig. 7c, d) explained 39.7% of the variance of the original time series. Overall, the combination of the 20- and 40-yr cycles explained ~77% of the variance in the original, regional time series.

Another observation is that the 40-yr cycle did not appear to be merely the first harmonic of the 20-yr cycle (i.e., a double 20-yr cycle). This can be seen by comparing the peaks (outbreaks) in the regional time series

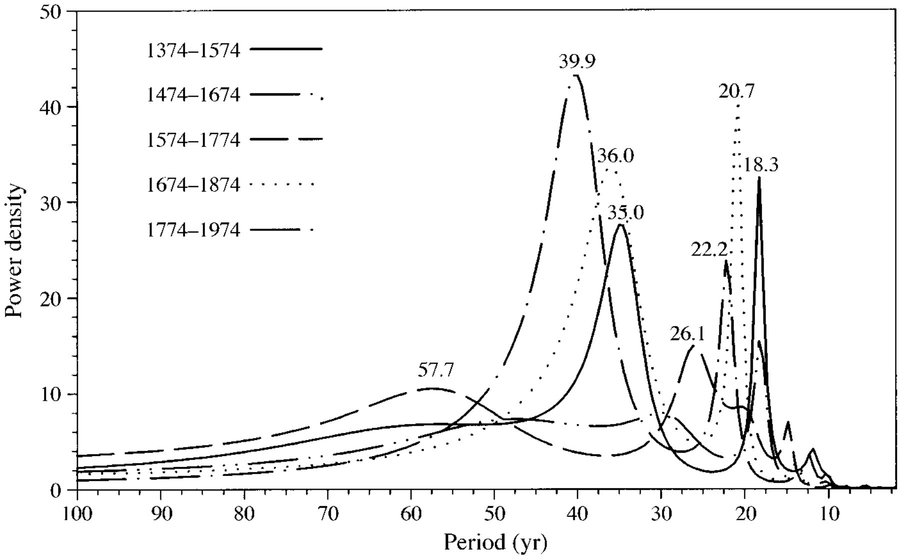

FIG. 6. Power spectral density plots for reconstructed, regional pandora moth time series (1374–1974) for 200-yr periods, overlapping 100 yr. The maximum entropy method (MEM) was used for a window of periods from 100 to 2 yr, and 50 lags.

(Fig. 7a) with the peaks in the 20- and 40-yr reconstructed components. Peaks in the 20-yr cycles coincide with peaks (or valleys) in the 40-yr cycles only during some periods, whereas during others they seem to be lagged with respect to each other. Both the 20-yr and 40-yr cycles were relatively quiescent (i.e., low amplitude) during the mid-1500s and late 1900s. The largest outbreaks (in terms of percentage of trees recording outbreaks and synchrony among the sampled stands) often occurred when the 40-yr and 20-yr maxima coincided, especially when maxima of all three pairs of waveforms were in phase (Fig. 7). Examples were the outbreaks of the 1910s–1920s, 1840s–1850s, 1800s, and 1670s–1680s.

DISCUSSION

Quality and reliability of the tree-ring reconstruction

We found a distinctive ring-width signature attributable to pandora moth defoliation similar to that described in previous pandora moth studies (Patterson 1929, Miller and Wagner 1989). In all documented outbreaks this signature started with thin latewood during the first year, followed by sharply reduced growth that persisted for 4 or more years (Fig. 2). Pandora moth larvae feed on older needles, which results in thinner latewood than that formed during years without defoliation (Wickman et al. 1996). The consistent recurrence of this signature in association with documented, 20th century outbreaks enabled us to reconstruct an exceptionally long outbreak history based on similar signatures extending back to AD 1379.

Our comparisons with independent climate reconstructions spanning the past 275 yr (Garfin and Hughes 1996) indicate that the growth reductions (signatures) we identified were not caused by drought. Climate response function analyses of western juniper in Oregon (Garfin and Hughes 1996) and ponderosa pine throughout the western United States (Fritts 1976, Cook et al. 1999) indicate these species have similar seasonal responses to precipitation and drought indices. However, there may be some important differences in climate response of these species that we have not measured, and climate responses might change through time. We have presented multiple lines of evidence that the pandora moth signatures are reliable, but we recognize that there remain some uncertainties about our reconstructions because of other unmeasured factors that might have caused some of these signatures.

Longer tree-ring reconstructions of drought from nonhost species in eastern Oregon are not currently available for direct comparison with inferred pandora moth outbreaks during the first half of our 622-yr reconstruction. However, the identified pandora moth signatures (i.e., thin latewood, reduced ring widths of particular magnitude and duration) in the early portion of the record were similar to those in the latter portion. New millennia-length dendroclimatic reconstructions from western juniper are currently being assembled for eastern Oregon (D. Meko, *personal communication*), and they should prove useful for further testing and comparison with our pandora moth reconstructions.

It is unlikely that other herbivorous insects caused the tree-ring signatures we identified as evidence of pandora moth outbreaks. Numerous insect species defoliate ponderosa pine trees, but only three are considered common or major pests: sawfly (*Neodiprion* and *Zadiprion* spp.), pine butterfly (*Neophasia menapia* Felder and Felder), and pandora moth. Pine sawfly outbreaks have not occurred in the 20th century in the Pacific Northwest. Based on the current distribution of

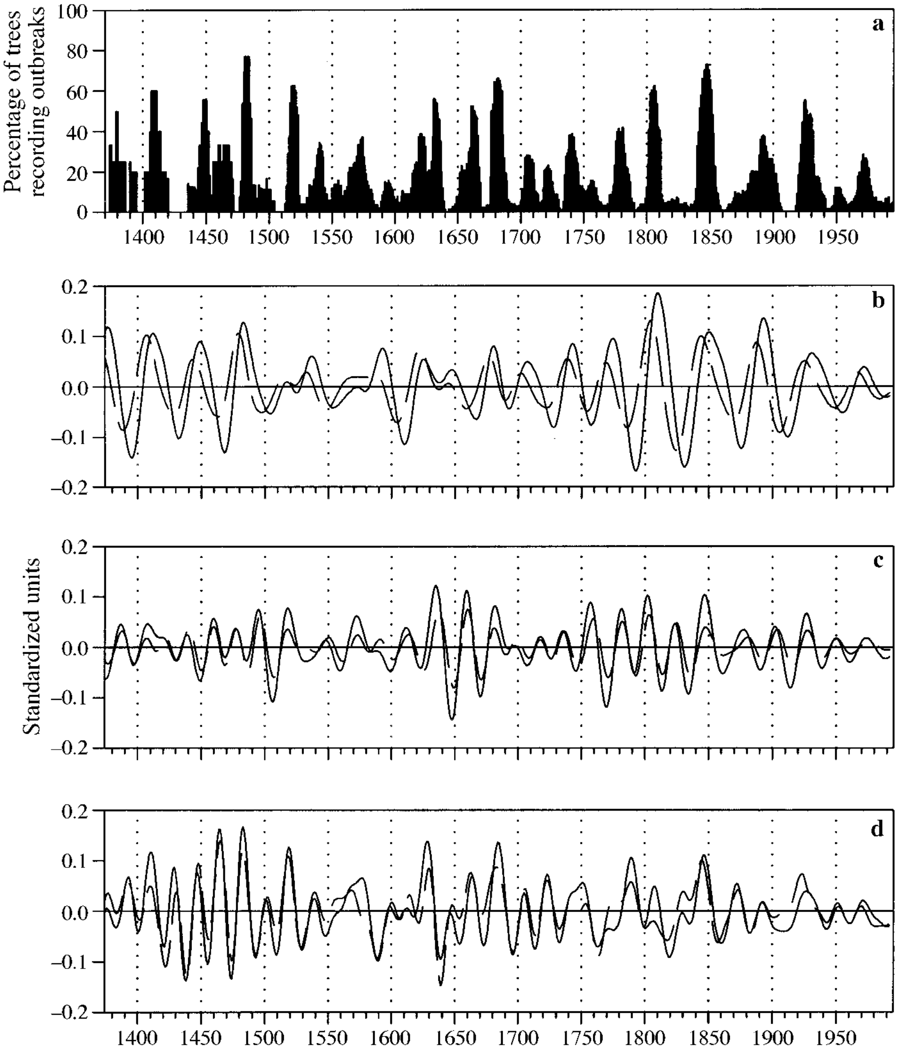

FIG. 7. (a) Singular spectrum analysis of regional pandora moth time series of the percentage of trees recording outbreaks per year. (b–d) Three pairs of waveforms (reconstructed components) are shown with periods clustered in the following ranges: (b) ~37–41 yr, (c) 24 yr, and (d) 18 yr. (b) The reconstructed component 1 (RC 1) had a period of 37.6 yr with 19.1% variance explained (solid line); RC 2 had a period of 40.7 yr with 18.2% variance explained (dashed line). (c) RC 3 had a period of 24.1 yr with 11.5% variance explained (solid line); RC 4 had a period of 24.1 yr with 11.5% variance explained (dashed line). (d) RC 5 had a period of 18.4 yr with 9.3% variance explained (solid line); RC 6 had a period of 18.0 yr with 18.2% variance explained (dashed line).

pine butterfly, it probably overlapped with the distribution of pandora moth in central Oregon. Flights of the pine butterfly have been observed near timberline in the Cascade Range, in the Blue Mountains of northeast Oregon, and near some of our northern stands (e.g., adults observed by B. Wickman in Pringle Falls area in 1996), but it apparently does not occur further south (Cole 1971). Pine butterfly, which has a one-year life cycle, usually occurs in cooler and more mesic regions than south-central Oregon.

Forest fires are a frequent disturbance in ponderosa pine forests of eastern Oregon (e.g., Heyerdahl 1997), but it is unlikely that they caused the tree-ring signatures we identified as pandora moth outbreaks. Surface fires can result in tree-ring growth reductions by scorching the canopies of trees or damaging stems and roots (Miller and Keen 1960). We reconstructed a surface fire history using fire-scarred trees in one of the sampled stands (PPF; see Table 1 for site definiition), and we found that ring growth reductions within individual fire-scarred trees were not consistently associated with fire scar dates (Speer 1997). This finding corresponds with observations of fire-scarred ponderosa pine specimens from elsewhere in the western United States, where ring growth reductions or increases sometimes immediately follow fire scars, but most commonly there are no obvious growth changes associated with most fire dates (T. W. Swetnam, *personal observation*).

Fire frequency at Pringle Falls was considerably higher than pandora moth outbreak frequency. Extensive fires burned through the study area at frequencies of about once or twice per decade during the 1700s, and once per 10 to 20 yr in the 1800s. No fires were recorded by fire-scarred trees after 1886 (Speer 1997), but three more outbreaks were detected after this date. Fire dates within the stand generally did not coincide with the pandora moth signatures, but we did identify an interesting pattern of reduced fire frequency during outbreaks, relative to non-outbreak periods. This is the opposite pattern of what would be expected if fires were directly causing ring growth suppressions via crown scorch or other types of damage. If this were the case, we should see more fires occurring during initial low-growth years identified as outbreaks than during other years, but we did not (Speer 1997).

Known pandora moth outbreaks during the 20th century were successfully detected in the ring-width series, but the timing of the tree-ring signature lagged the beginning of the regional outbreak by one to several years. During the most recent outbreak (1988–1996), for example, distinctive thin latewood marking the beginning of the ring-width signature occurred in most trees and stands in 1994, the year of greatest defoliation across central Oregon (Fig. 2). During the documented outbreaks of 1963–1968 and 1918–1925, the signature first appeared one to four years after the first year that defoliation was observed by forest managers within the region. Thus, tree rings sampled at scattered points across a region may primarily record years of heaviest defoliation, rather than a gradual transition from endemic to outbreak levels.

Studies of other conifers have also documented a lag of one to three years between initial defoliation by western spruce budworm and Douglas-fir tussock moth (*Orgyia pseudotsugata* McDunnough) and reduced tree-ring growth in the lower stem (Wickman 1963, Brubaker and Greene 1978, Wickman 1980, Alfaro et al. 1982, Swetnam et al. 1995, Mason et al. 1997). These lags may be related to physiological factors, such as stored food reserves from previous years that enable cambial growth in the lower stem of defoliated trees to be unaffected for a year or more (Koerber and Wickman 1970, Fritts 1976). Apparent lagged responses could also be due to insensitivity of tree-ring growth to initial low insect population numbers and defoliation levels. Estimates of pandora moth populations (e.g., numbers of egg masses, larvae) are incomplete or unavailable for our study sites, so we cannot evaluate the relations of tree rings, population, and defoliation levels at the tree or stand level, as has been done with western spruce budworm and Douglas-fir tussock moth (e.g., Alfaro et al. 1982, Swetnam et al. 1995, Mason et al. 1997).

Although physiological explanations of growth response lags are likely to be correct at the scale of trees, lags in timing at regional scales could also be due to insufficient sampling density or sampling bias. Modern defoliation records suggest that pandora moth outbreaks are initiated at the stand level and then spread outward to larger areas. If this was a typical historical pattern, then lags between observations of regional-scale defoliation patterns and the tree-ring dates of initial growth reduction could be the result of sampling outside of the stands where outbreaks began. We are also limited in making firm conclusions about spatial patterns, because our network of sites is nonrandomly sampled and is small relative to the size of the region and extent of historic outbreaks. These problems of spatial variability, scaling, and sampling are common in the study of insect population dynamics (Mason 1996, Ray and Hastings 1996), as well as paleoecology and landscape ecology (Swetnam et al. 1999).

Lags in detection of outbreak initiation years caused by physiological factors or sampling inadequacies have important implications for evaluating the dynamics of this system. Outbreak initiating events, for example, may have occurred one to several years before the trees recorded the effects of the outbreak. Delays in recovery of trees to ''normal'' growth levels following defoliation may also lag behind the actual collapse of insect populations (Wickman 1963, 1980, Swetnam and Lynch 1993). This delay might partly compensate for lags in detecting the beginning of outbreaks, so outbreak duration estimates may be fairly accurate, even if the estimated timing of outbreaks is imprecise. It is unclear how the lagged response of trees to defoliation might affect the cyclical properties of the reconstructed time series. We expect, however, that if initiating or terminating environmental factors were involved in outbreak dynamics (e.g., weather events, fires), the phase relations between the tree-ring reconstructions and independent time series of the initiating/terminating factors should reflect these lags. This kind of analysis is beyond the scope of this paper, but there is clearly a good potential to study such relations, because it is possible to develop independent reconstructions of climate, fire, and pandora moth outbreaks in the same stands and region.

Twentieth-century dynamics of pandora moth outbreaks in a multicentury context

One of the more important uses of multicentury reconstructions of insect outbreak histories is to evaluate the hypothesis that outbreaks have become more frequent, widespread, or severe during the 20th century. Much discussion in the ''forest health'' literature focuses on assumed or demonstrated changes in insect outbreak dynamics during the 20th century (e.g., Mutch et al. 1993). The causes of these changes have been attributed to past management practices and the effects of fire suppression on forest composition and structure

(Mutch et al. 1993, Langston 1995). Long-term reconstructions, however, have only been used in a few regions to assess these hypothesized patterns of change over periods of centuries (e.g., Blais [1983] for *Choristoneura fumiferana* in eastern Canada; Anderson et al. [1987], Swetnam and Lynch [1993], Hadley and Veblen [1993], and Weber and Schweingruber [1995] for *C. occidentalis* in the Rocky Mountains; and Swetnam et al. [1995] for the Blue Mountains of Oregon). Tree-ring studies in the western United States indicate that budworm outbreak frequencies have not increased in the 20th century. Outbreak extent (i.e., regional synchrony) and severity, however, may have escalated because of human-caused changes in forests, such as fire suppression and selective harvesting (Anderson et al. 1987, Swetnam and Lynch 1993, Hadley and Veblen 1993, Weber and Schweingruber 1995, Swetnam et al. 1995).

Our reconstruction of pandora moth population dynamics indicates that a broad range of outbreak duration, severity, and frequency has occurred over the past six centuries. The duration of the most recent outbreak, during 1988–1996 (nine years), fell within the multicentury historical range of 4–18 yr (Table 3). The severity (as estimated by percentage growth reduction) was also similar to previous outbreaks. Tree mortality is generally low during outbreaks (<2%), but higher levels sometimes occur when bark beetles attack weakened trees (Patterson 1929).

From a regional-scale perspective the mid-20th century appears to have been marked by an unusual absence of pandora moth activity. The interval between the most recent outbreak and the previous outbreak (1963–1968 outbreak in SKB) was ~19 yr, which was also within the historical range of 8–48 yr. However, the 1960s outbreak was very limited in extent compared to most of the outbreaks (Fig. 4). Before the 1980s outbreak, most stands had not been severely defoliated since the 1920s. Although intervals of this length (~60 yr) occurred between earlier outbreaks within individual stands, we found no other comparable intervals in earlier centuries (back to 1600) at the regional or subregional scale. The closest was the long interval between outbreaks in the late 1670s and the 1730s in a set of the northern stands (uppermost 5 stands shown in Fig. 4). Because relatively few old trees and stand chronologies extend back before 1600, our highest confidence in these regional patterns is for the post-1600 period.

The cause of the mid-to-late 20th-century lull in pandora moth activity is unknown. We suggest two possible explanations, both involving exogenous forcing factors. These hypotheses are speculative at this point, and clearly need further research: (1) 20th-century climatic changes may have caused an alteration in pandora moth dynamics through changing weather effects on tree or pandora moth physiology (or a combination of these effects), or (2) human land uses caused changes in the forest composition and/or structure that affected pandora moth dynamics. Evidence for unusual climate in the 20th century includes meteorological data and tree-ring reconstructions that show the 1930s drought (~1928–1937) was the deepest and longest drought of the past 275 yr. This drought was followed by exceptionally wet conditions in the 1940s (Garfin and Hughes 1996).

Human land uses have intensified greatly since the Euro-American settlement era began in the late 1800s (Langston 1995). Intensive livestock grazing, fire suppression, and timber harvesting are all implicated in changes in the structure and composition of forests during the 20th century (Lehmkuhl et al. 1994). This has led to a general decrease in numbers of large ponderosa pine trees in this region (Franklin and Dyrness 1988, Wickman et al. 1994), which may have affected pandora moth populations. Some of our sampled stands showing the long mid-20th-century interval between outbreaks, however, had not been harvested, and contained many old-growth ponderosa pines. Therefore, if the regional lull in pandora moth activity was related to harvesting practices during the 20th century, this was probably a broad-scale, regional effect. For example, heavy harvesting across the region might have prevented the 1960s outbreak from expanding from outbreak centers to the regional scale, because forest fragmentation could have limited the spread of these insects. The 1970s–1980s outbreak was more widespread than the 1960s outbreak, but apparently not as widespread as some earlier outbreaks (e.g., 1840s, 1800s). Overall, as previously acknowledged, these identified patterns in our data set are suggestive, but not conclusive, given the limited sample size and its nonrandom distribution.

Endogenous vs. exogenous forcing of insect population dynamics

The apparent cyclical nature of some forest insect populations has generally been interpreted as manifestations of endogenous ecological processes (e.g., density dependence, predators, pathogens, parasites), rather than responses to exogenous factors (e.g., climate, land use history), which are presumably noncyclical (Myers 1993, Berryman 1996). Many forest insect species are suspected of having cyclical or more complex population dynamics, but most 20th-century time series used to infer these dynamics encompass only one to a few outbreaks. An extensive and controversial literature focusing on theoretical explanations (particularly density dependence and other endogenous mechanisms) and empirical modeling of time series has developed (e.g., Myers 1993, Williams and Liebhold 1995, 1997, Berryman 1996, Mason 1996, Berryman and Turchin 1997). Statistical tests of models and theory with data, however, are seriously limited by the uncertainty associated with the short, noisy time series that are available from 20th-century records. Twentieth-century time series of long-interval outbreak species, such as budworms and pandora moths, contain too few oscillations for reliable statistical assessments of their dynamics.

Two examples where cyclicity is firmly established over long time periods and large regions include the larch budmoth (*Zeiraphera diniana* Gn.) (Baltensweiler et al. 1977) in Europe, and the western spruce budworm (Swetnam and Lynch 1993) in western North America. In the case of larch budmoth, the outbreak periods are short (8–10 yr) relative to 20th-century observational records, so a sufficient replication of the cycles (i.e., >10) has occurred for robust statistical analyses. Tree-ring reconstructions also confirm the cyclicity of larch budmoth populations over periods of many centuries (Schweingruber 1979, Weber 1997). Although cyclicity is clearly present in these series, this does not necessarily mean that these are fixed limit cycles reflecting simple population dynamics. As in the case of our regional pandora moth series, there is considerable variability in the amplitude and frequency of the larch budmoth and western spruce budworm ''cycles.'' For this reason, we refer to these dynamics as ''quasicyclical'' with explicit recognition that nonlinear dynamics may underlie these complex behaviors.

Statistical modeling of 20th-century insect population data as a test of hypotheses involving endogenous controls of population cycles (e.g., delayed density dependence) is based on an assumption that potential exogenous driving factors (e.g., climate) were purely stochastic and noncyclical. However, it has become increasingly clear in recent years that lagging and quasiperiodic behaviors in the global climate system are important to regional climates in the western United States (e.g., the El Niño–Southern Oscillation and Pacific Decadal Oscillation) (Hamlet and Lettenmaier 1999, McCabe and Dettinger 1999, Peterson et al. 1999). Analyses of some long climate time series demonstrate quasi-cyclic behavior, with changes in period, phase and amplitude over years and decades (e.g., Rasmusson et al. 1990, Ghil and Vautard 1991, McCabe and Dettinger 1999). Williams and Liebhold (1995) and Hunter and Price (1998) show that exogenous, autocorrelated forcing factors (such as quasi-cyclic climate patterns) can result in autocorrelated population time series that might be mistaken for density dependence.

Tree-ring reconstructions and independent climate data from the Southern Rockies show that strong, but temporally variable, western spruce budworm cycles were in phase with and perhaps entrained by weak precipitation cycles (Swetnam and Lynch 1993). Using contingency analyses Myers (1998) found that synchronous forest insect populations (in the family Lepidoptera) across the northern hemisphere were statistically associated ($P < 0.005$) with cold temperatures and low phases of the sunspot cycle (i.e., low numbers of sunspots). Dispersal is the other primary way that population fluctuations can be synchronized in space. However, this mechanism seems very improbable at continental or hemispheric scales. Myers speculated that such synchronous patterns might be caused by broad-scale climatic conditions favoring or disfavoring widely separated insect populations in a manner originally hypothesized by Moran (1953) for lynx (*Lynx canadensis*) populations. Another recent study found synchrony in ''crashes'' of insect populations across North America, and concluded that climatic causes were most probably involved at these very broad scales (Hawkins and Holyoak 1998).

The results of these broad-scale comparative analyses are intriguing and suggestive of underlying climatic causes, but strong experimental evidence in support of reasonable mechanisms is lacking. Experiments at broad spatial and temporal scales would be necessary for complete testing of possible mechanisms in these forest insect systems, but such experiments are clearly impractical or impossible at regional to global, or decadal to centennial, scales. Nevertheless, fruitful research might follow from interdisciplinary programs involving experiments at finer scales, coupled with realistic dynamical models, and model testing against historical time series and reconstructions.

Tree-ring reconstructions, like actual insect population measurements, are ''noisy'' (i.e., they contain variations unrelated to insect population changes). However, for purposes of empirical assessment and model testing, they have the distinct advantage of replication over large areas and long time periods. Our regional reconstruction includes progressively fewer trees and stands with increasing time before present, especially before ~1600 (Fig. 5). The trees used in these reconstructions also increased in age through time. It is possible, therefore, that some of the changes in cyclical behavior that we identified were related to changes in sample depth, spatial distribution of stands or trees, or changing relations as individual trees and stands increased in age. It seems unlikely, however, that these changes were causes of the general patterns of changing cyclicity that we identified. We base this conclusion on the facts that sample size was large and relatively constant (Fig. 5) after ~1800, and most sampled trees were already mature individuals after 1800, but we still detected variable 20- and 40-yr cycles during the post-1800 period, as well as some of the synchrony/asynchrony patterns in the waveform peaks (Fig. 7). Furthermore, we cannot detect clear or consistent patterns of temporal change in the waveforms associated with sample depth changes, except for the pre-1550 period. During this period, the very low numbers of trees and stands could be related to changes in the magnitude and variance of the percentage time series (Fig. 5b), and this might be related to the higher amplitudes in some of the waveforms before ~1550 (Fig. 7b, d).

Our spectral analyses indicate that pandora moth has quasicyclical dynamics. The dominant cycles of ~20 and 40 yr are relatively strong, but the phase (timing) of the cycles shifts through time. The autocorrelation function of the time series from these systems appears as a damped sine wave, with statistically significant ($P < 0.05$) negative and positive coefficients at the first half and full cycle periods, respectively (Speer 1997). Turchin and Taylor (1992) refer to these as ''phase forgetting'' cycles, or ''pseudoperiodic'' dynamics. The maximum entropy method (MEM) and singular spectrum analysis (SSA) provide a more time-specific perspective on these dynamics than simple autocorrelation functions, because they not only measure the average strength of the cyclic patterns over the entire length of the time series, but they also enable assessment of the historical and changing nature of these patterns. The extracted waveforms, for example, disaggregate the dominant cycles, and they indicate that during certain decades and centuries the amplitudes of these dominant cycles were unusually high or low, or in and out of phase with each other (Fig. 7).

Our results raise the classic and yet unanswered question of ecological population dynamics: Are the causes of animal population cycles endogenous (e.g., density dependence) or exogenous (density independent, e.g., climate)? Although we do not attempt to directly address this question here, we suggest that dendroecological reconstructions of insect populations provide rich opportunities for research. For example, detailed comparisons of regional outbreak time series with independent modern meteorological records and tree-ring reconstructions of precipitation and temperature are possible. Detailed reconstructions of fire history can also be assembled and compared with long histories of insect outbreaks, since fire-scarred trees are abundant in many forests, such as those we studied (Speer 1997). Experiments and mechanistic modeling will be essential for evaluating and confirming hypotheses suggested by broad scale observations and history. Long-term historical reconstructions may provide the best, if not the only, realistic test of dynamical models of forest–insect systems.

Whatever historical, experimental, or modeling analyses are undertaken, our results suggest that theoretical explanations of cycling populations must contend with the complexities of temporally changing periodicities. What endogenous or exogenous factors and mechanisms can explain such dynamics? We speculate that the answer will not reside in theoretical explanations relying solely upon endogenous or exogenous processes, but a more complex and interesting combination of the two. Long time series from tree rings and new spectral analysis techniques offer powerful data and tools for exploring these dynamics.

ACKNOWLEDGMENTS

We thank Chris Baisan for his advice and guidance in tree-ring dating and other aspects of the laboratory analyses, and we thank Andy Eglitis, Entomologist, Deschutes National Forest for providing aerial survey maps and information on the latest outbreak. Thanks also to two anonymous reviewers and Steve Jackson for very helpful reviews and editing of the manuscript. This project was supported by a cooperative agreement with the U.S. Forest Service, Pacific Northwest Research Station, and by the Laboratory of Tree-Ring Research, University of Arizona.

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