7

What Tree-Ring Reconstruction Tells Us about Conifer Defoliator Outbreaks

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7.1 Introduction

Our ability to understand the dynamics of forest insect outbreaks is limited by the lack of long-term data describing the temporal and spatial trends of outbreaks, the size and long life span of host plants, and the impracticability of manipulative experiments at relevant temporal and spatial scales. Population responses can be studied across varying site and stand conditions, or for a few years under somewhat controlled circumstances, but it is difficult to study temporal variability for species that outbreak only two or three times a century. Fortunately, dendrochronology enables us to explore decadal- and century-scale outbreak dynamics at spatial scales ranging from within-tree to continental. Evidence of past insect defoliation can be identified, dated, and sometimes quantified using variation in the width and morphology of annual growth rings in trees (Plate 7.1). Mortality

Insect Outbreaks Revisited, First Edition. Edited by Pedro Barbosa, Deborah K. Letourneau and Anurag A. Agrawal.

events can be identified and dated by dating the last growth ring on dead trees, growth release events in survivors, and postdisturbance recruitment events. Insect defoliation can be distinguished from weather and other disturbance agents by comparing responses in host and nonhost trees.

A historical perspective increases our understanding of ecological disturbances and provides a reference for assessing modern disturbance events and ecosystem response to change. Dendrochronology enables the identification of outbreaks in times and places before the documentary period. This long-term perspective helps explain outbreak dynamics in forested ecosystems, and permits investigation of multiple factors interacting in space and time – time frames that encompass multiple events. It allows investigators to determine if observations made from contemporary events are unique to modern circumstances, perhaps influenced by anthropogenic factors, or are comparable to what occurred in the past. The role of insects as disturbance agents and regulators of forest ecosystems can be explored at the same scales at which the insect populations operate.

Tree-ring chronologies of insect outbreaks are proxy representations of population cycles. They excel at quantifying the temporal and spatial variability in events and at describing the nature of population oscillations – at determining how often outbreaks occur, the periodic nature of successive outbreaks, and the presence and strength of spatial autocorrelation. With other proxy or observational data, inferences can be made about associations with other disturbance regimes and climate. Tree-ring chronologies do less well at determining the precise timing of some types of events, particularly the onset of outbreaks that develop slowly, and at identifying causal relationships.

In this chapter I review the information gained through dendrochronologic study of coniferous forest defoliators, focusing on what has been learned through these studies. I provide brief summaries of species life cycles and biology to provide a context for the long-term record, and then summarize information learned from tree-ring studies. At the end of the chapter I review common themes emerging from dendrochronological study of insects, and the implications for our understanding of forest insect and disturbance ecology.

7.2 Methodological considerations

Dendrochronology is the science of dating wood material to the exact year and extracting from it information about events and environmental change. Tree growth reflects comprehensive integration of several processes and environmental conditions and is a reliable and robust indicator of environmental conditions (Pretzsch, 2009). Trees grow more slowly in periods of drought or other environmental stress than they do under favorable conditions, producing seasonal and annual variation in growth rings (Fritts, 1976). Because trees are long-lived organisms and because remnant material from dead trees may persist in the environment for long times and be incorporated into structures, wood material can be used to provide information about past environmental conditions.

Dendrochronology methodology is reliable, robust, and very well tested (Cook and Kairiudstis, 1990; Fritts, 1976; Schweingruber, 1996). Space does not permit a comprehensive review of the dendrochronology methodology used to develop insect outbreak chronologies. To obtain a good understanding of tree growth, how it is measured, and the influences of environmental factors on it, see Duff and Nolan (1953), Fritts (1976), Pretzsch (1996), Schweingruber (1996), and Telewski and Lynch (1990). Cook and Kairiudstis (1990), Schweingruber (1996), and Speer (2010) present the methodology of dendrochronology as it is used for a variety of disciplines. For methods related to detecting defoliator outbreaks, see Swetnam *et al.* (1985) and papers cited herein; for bark beetle outbreaks, see Berg *et al.* (2006) and Veblen *et al.* (1991), and papers cited therein.

Defoliation suppresses radial growth, and can affect the relative widths and physical characteristics of earlywood and latewood, wood density, cell structure, and chemistry (Cook and Kairudstis, 1990; Swetnam *et al*., 1985). These effects are often visible in raw wood samples (Plate 7.1). Using crossdated material, quantitative techniques can identify and separate variation in ring width related to climate, insects, fire, and other disturbances. The insect outbreak chronologies that are developed are long-term proxy data sets of insect population behavior that can be subjected to statistical analysis (Swetnam *et al*., 1985; Swetnam and Lynch, 1989, 1993; Speer, 2010; Volney, 1994). Dendrochronologic reconstruction of defoliator outbreak chronologies has been widely used, with refinements and adjustments for individual circumstances (Hadley and Veblen, 1993; Jardon *et al*., 1994; Morin and Laprise, 1990; Nishimura and Laroque, 2010; Swetnam *et al*., 1985, and papers cited herein).

Outbreak chronologies are usually analyzed by computing the intervals (length of the period between the beginnings of two successive outbreaks), duration (length of the period encompassing the beginning and end of outbreak-related growth suppression), and sometimes severity of growth suppression (determined by methods that vary considerably) on the basis of absolute numbers or the proportion of sampled sites involved in an outbreak at any given time, and for the presence and strength of periodic and synchronous patterns. Spectral analysis is used to identify cyclical components in chronologies by decomposing the time series into a spectrum of cycles of different lengths. Spatial autocorrelation analysis is used to quantify the degree of geographic dependency in outbreak chronologies and can be applied at any relevant scale. Significant autocorrelation values between time series suggest that observations in multiple areas are correlated with or even dependent on each other. Significant components found in insect chronologies may involve a single significant value (e.g., 36), a range of periods around a peak value (e.g., 34–38), or multiple periodicities (e.g., 25, 36, 48–51). For time series in which outbreaks have cyclical components, multiple components are somewhat analogous to variance components, in that components (significant periodicities) may account for certain proportions of the variance in temporal variation, say, 40% and 28% for the first and second periodicities. Multiple frequencies within the same system may be harmonic or nearly harmonic; this outcome appears to result from natural processes, but in some cases may be a mathematical artifact. Time series are analyzed for correlation with other time series, such as precipitation records or reconstructions. Investigators attempt to interpret causal relationships that produce periodic and synchronous patterns, perhaps as inherent to population dynamics or as entrained by climatic cycles, but while evidence may be strong, proof is usually lacking.

7.3 Reconstructions of outbreak histories

7.3.1 Spruce budworm

Spruce budworm (SBW) (*Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae)) and western spruce budworm (WSBW) (*Choristoneura occidentalis* (Freeman)) are closely related univoltine, wasteful early-season defoliators. Tree bud development and suitable weather in spring play important roles in budworm survival and population growth (Volney and Fleming, 2007). Outbreaks are generally extensive, often involving entire regions, and persist for many years. Balsam fir (*Abies balsamea*) and to a lesser extent white spruce (*Picea glauca*) are the most important SBW hosts, and Douglas-fir (*Pseudotsuga menziesii*) and true firs, especially white fir (*A. concolor*), are the most important WSBW hosts.

Tree-ring chronologies

Spruce budworm outbreaks are identified in the tree-rings primarily through numerous adjacent narrow rings (Plate 7.1) not observed in nonhost species. SBW reconstructions have been developed for many areas of eastern Canada and the United States (Table 7.1). One extraordinarily long chronology from Québec includes 13 outbreaks since the early 1500s. Outbreak initiation and duration vary considerably amongst trees and stands, and numerous missing rings occur during outbreaks (Blais, 1961; Morin and Laprise, 1990; Lemieux and Fillion, 2004). Chronologies show that intensity may decline during the course of the outbreak, but later resurge (Blais, 1983; Morin *et al*., 1993). Radial growth is usually suppressed for 11–14 years per outbreak, though duration is variable (Table 7.1). Growth suppressions detected in the tree-ring series begins 2–4 years after noticeable defoliation (Blais 1983). Mortality continues for up to 4 years after defoliation has ceased (Blais 1981a), which implies that growth suppression may persist for that long as well.

Tree-ring evidence indicates that outbreak extent and severity can be influenced by precedent landscape- and region-scale wildfires and SBW outbreaks (Blais, 1954; Bergeron and Archambault, 1993; Bergeron *et al*., 2001; Bouchard *et al*., 2006; Morin *et al*., 2007).

Associations with temperature and precipitation

Climate and SBW reconstructions longer than two centuries show that outbreaks tend to occur during periods of relatively dry, sunny, early-summer conditions (Blais, 1961, 1984; Morin *et al*., 1993), which result in more rapid larval development and increased fecundity as well as increased staminate flower production (staminate flowers are easily accessible, rich sources of nutrients for small larvae) (Greenbank, 1956; Pilon and Blais, 1961). In Minnesota, near the prairie-forest boundary where conditions for balsam fir are marginal, outbreaks are weakly

Table 7.1 For spruce budworm, location, sample size, initial year and length of chronology, number of outbreaks in the chronology (NOB), intervals, average interval length or significant periodicities from time series analyses (periods are indicated by square brackets [ ]; a number followed by parenthetical numbers indicates a peak periodicity within a range of significant period values), and duration or mean duration ± SD (DUR), as determined in dendrochronologically reconstructed chronologies. The interval just prior to the first twentieth-century outbreak is indicated in **bold**. Some statistics are computed from tabulated data or text references in publications. Information is presented in order of publication date, as dendrochronology and analysis methodologies have improved over time. See Blais (1983) for a figure depicting many of the eastern Canadian locations with respect to one another. Note that advances in methodology in the late 1980s improved the precision of subsequent chronologies.

General location	*No. sites (no. trees)*	*First year*	*Length*	*NOB*	*Intervals or [periods]*[1]	*DUR*	*Publication*	*Place name*
Northwest Ontario	81 (~800)	1802	170	3	average 93		Blais 1954, 1983	Lac Seul area
South-central Ontario	6 (300)	1704	268	3	average 93		Blais 1983	Lake Nipogen
Eastern Ontario		1802	180		**100**, 37		Blais 1983	Algoma
Southeast Québec	86 (430)	1812	140	2	**none**, 45	<21	Blais 1961	Gaspé Peninsula
Southeast Québec	32 (160)	1870	120	3–4	73, 35, **38**		Blais 1961	Lower St. Lawrence
Southern Québec and New Brunswick	37	1940	20	1		11	Blais 1964	Laurentide Park
Southern Québec	87	1680	281	6	44, 60, 25, **76**, 37	3–11	Blais 1965	Laurentide Park
Southwest Québec	18	1761	211	3	**127**, 28, 28		Blais 1981a	Ottawa River
Western Québec	(20)	1764	215	4	**127**, 30, 27		Blais 1981b	Dumoin and Coulonge Rivers
Southeast Québec		~1750	250	6	42, 75, **24**, 29, 27		Blais 1983	Eastern Townships, Lower St. Lawrence
Northeast Québec and Newfoundland	15	1810	162		**130**, 27		Blais 1983	North Shore
Southern Québec	8	1790	200	4	**76**, 36, 26	11.8 ± 2.8	Morin and Laprise (1990)	Lac Saint-Jean
Southwest Québec	30 (160)	1780	200	4	**109**, 11, 40	11–23	Morin *et al.* 1993	Lake Duparquet, Abitibi

Southern Québec	8 buildings (153)	1672	283	5–6	44, 57, 24, 33	3–11	Krause 1997	Chicoutimi, east of Lac Saint-Jean
Southern Québec	1 (121)	1859	130	4	**37**, 38, 23	7.3 ± 2.2	Filion *et al*. 1998	South of Lac Saint-Jean (highland sites with no history of wildfire)
Mid-latitude Québec	28	1847	152	1		10	Simard and Payette 2001	Eastern Laurentian Highlands
Northeast British Columbia	7	1817	176	0–6	26	6–17	Burleigh *et al*. 2002	Fort Nelson area
Southwest Québec	32	1875	130	5	[25–38, 29–34]		Jardon *et al*. 2003	Subregional collection
Northern and central New Brunswick	4	1940		1		9	Krause *et al*. 2003	Kedgewick
Southern Québec	7 buildings 1 stand	1513 1816	406 186	11	65, 36, 32, 42, 53, 27, 36, **46**, 33, 28	14.5 ± 5.7 (7–25)	Boulanger and Aresneault 2004	South shore of St. Lawrence River
Southern Québec	1 (25)	1859	141	3	38, 23	4–9	Lemieux and Filion 2004	Mount Mégantic
Western Québec	3	1820	180	5–6	180 yrs / 5 = 36		Bouchard *et al*. 2006	Témiscamingue region
Northern Maine	37	1700	300	5	53, 46, **106**, 62		Fraver *et al*. 2007	Big Reed Forest Reserve
Northwest Minnesota	5	1916	90	3–4	35, 38		Rauchfuss *et al*. 2009	Itasca State Park
Islandic Québec[2]	14	1850	152	4–7	26, 14, 11, **10**, 13, 8, 38		Barrette *et al*. 2010	Anticosti Island
Eastern Québec	9	1750			ca. **35, 35**, 30		Bouchard and Pothier 2010	North Shore

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[1] “**None**” indicates that no outbreaks are inferred in the chronology prior to 1900.

[2] SBW and hemlock looper outbreaks are not distinguished in this chronology.

associated with wetter-than-normal spring conditions (Rauchfuss *et al.*, 2009), similar to WSBW (discussed later). A change in outbreak frequency, extent, and severity in the twentieth century appears to be associated with a change in polar atmospheric circulation patterns (discussed later in this chapter).

Periodicity and synchrony

Tree-ring studies provide consistent evidence that periodic SBW outbreaks cycle synchronously at landscape and regional scales every 25 to 45 years (Table 7.1; Cooke *et al.*, 2007; Jardon *et al.*, 2003; Volney and Fleming 2007), similar to cycle lengths produced in modeled population dynamics (Royama *et al.*, 2005). Cycle amplitude varies considerably, and synchrony decays at very long distances (Gray *et al.*, 2000; Volney and Fleming, 2007). Time series analyses from southwestern Québec indicate a tighter signal of 25–38 years, with a true periodic component at 29–34 years, as well as quasi-periodic or complexly periodic components (Jardon *et al.*, 2003). Synchrony in SBW chronologies is attributed to moth migration (Jardon *et al.*, 2003). Tree-ring studies show that large SBW outbreaks usually develop over several years, and that outbreaks sometimes exhibit patterned, almost epicentric expansion, particularly during extreme events in which outbreaks envelop adjacent areas where conditions are marginal for SBW (Blais 1954, 1981b; Morin and Lapris, 1990; Morin *et al.*, 1993; Burleigh, 2002; Fraver *et al.*, 2007; Jardon *et al.*, 2003). Multicentury tree-ring studies and multidecadal survey data both indicate that areas less suited to budworm incur less frequent and less intense outbreaks (Blais, 1961, 1983; Burleigh *et al.*, 2002; Candau and Fleming, 2005; Gray *et al.*, 2000; Rauchfuss *et al.*, 2009; Williams and Birdsey, 2003).

Twentieth-century patterns

Outbreaks in the twentieth century have been synchronous (extensive) and severe, but not to the extraordinary degree indicated in the literatures. Such outbreaks occurred in the earlier dendrochronology record, but infrequently. If the Blais (1983) summary of his work from across eastern Canada is viewed as proportions of the number of areas in the chronologies at a given time, 70% were involved in an outbreak in the first decade of 1800. In later work, all chronologies that include the early nineteenth century show an outbreak in the first decade of 1800 (Elliott, 1960; Morin *et al.*, 1993; Krause, 1997; Bouchard and Pothier, 2010; Boulanger and Arsenault, 2004; Fraver *et al.*, 2007), except for one chronology (Morin and Laprise, 1990) in which the stands would have been too young in the 1800s to be susceptible to SBW.

There is a common (but not universal) pattern of a lengthy period without outbreaks prior to the first twentieth-century outbreak, followed by a dramatic increase in frequency and severity in the twentieth century (Table 7.1). In some cases, the first inferred or documented outbreak in an area occurred in the last half of the twentieth century, even though host trees were present earlier (Blais, 1961; Simard and Payette, 2001). The generally accepted interpretation of increased synchrony and severity in twentieth century SBW outbreaks has been that it is caused by human influences, particularly those of fire suppression and logging (which favored balsam fir abundance) and pesticide use (which maintained the forest in a budworm-susceptible condition), and less to natural changes in forest structure and species composition. Later developments have favored climate as the driving factor, perhaps exacerbated by human land use practices mentioned earlier. Coincidental reconstruction of fire history, SBW outbreaks, and climate have shown that fire frequency in eastern Canada dramatically decreased circa 1850, which was associated with changes in polar atmospheric circulation patterns and summer isolation (Bergeron and Archambault, 1993; Bergeron *et al.*, 2001; Carcaillet *et al.*, 2010). This favored increased balsam fir abundance over extensive areas; these forests matured into budworm-susceptible conditions at the turn of the twentieth century (Blais, 1954; Bergeron and Leduc, 1998; Morin *et al.*, 2007). It is interesting to note that all 81 sample sites in the Blais (1954) western Ontario chronology, which began in 1850, were of fire origin.

7.3.2 Western spruce budworm

Tree-ring chronologies

Several WSBW chronologies developed from Douglas-fir and white fir encompass 3–4 centuries and include 8–14 major outbreaks (Table 7.2). Two extraordinarily long chronologies from northern New Mexico and southern Colorado are from six to nearly eight centuries years long and include 17–20 outbreaks. The WSBW chronologies are characterized by temporal variability, missing rings during outbreaks, and mid-outbreak reprieves in outbreak intensity. Outbreak initiation and end are usually asynchronous, and there is considerable variability between outbreaks at multiple temporal and spatial scales (Swetnam and Lynch, 1989, 1993; Swetnam *et al.*, 1985; Ryerson *et al.*, 2003; Campbell *et al.*, 2006), though outbreak initiation is markedly synchronous in the Blue Mountains of northeast Oregon (Swetnam *et al.*, 1995), and for occasional outbreaks elsewhere (Swetnam and Lynch, 1989; Ryerson *et al.*, 2003). Radial growth response typically lags detectable defoliation by 1–3 years (Belyea, 1952; Kulman, 1971; Brubaker, 1978; Alfaro *et al.*, 1982; Swetnam *et al.*, 1985; Wickman *et al.*, 1980). Trees and stands also differ in post-outbreak rates of recovery, indicating that outbreaks may persist in some trees or stands longer than in others, or that damage severity or post-outbreak weather conditions influence the recovery period (Brubaker and Greene, 1979; Mason *et al.*, 1997).

Return intervals are commonly 32–40 years, and significant periodicities are 30–43 years (Table 7.2); in northern New Mexico, the strongest periods are 25 and 50 years. The mean duration of growth suppression is consistently between 11 and 15 years, though some inferred outbreaks in the southwestern reconstructions lasted two to several decades (Swetnam and Lynch, 1989). Years without evidence of infestation somewhere are rare in all regional chronologies. Outbreaks are neither more nor less frequent in old-growth stands than in younger stands (Lynch and Swetnam, 1992). Duration of growth suppression is generally longer in old-growth stands, but it is not clear if this is because WSBW population density persists longer in old stands, or if tree recovery is protracted in older stands (Lynch and Swetnam, 1992).

Table 7.2 For western spruce budworm and two-year cycle budworm, chronology length (years), number of outbreaks in the chronology (NOB), mean return intervals, significant periodicities from time series analyses, and mean duration of outbreaks, as determined in dendrochronologically reconstructed chronologies. The most significant of multiple periods are indicated with **bold** type. Some statistics are computed from tabulated data or text references in publications.

Location	*Length*	*NOB*	*Intervals*		*Periods*	*Publication*
Western spruce budworm						
Western Montana	100	3				McCune 1983
Western Montana	169	8	32–35		13.9 23.2 after 1910	Anderson *et al*. 1987
Southern Rocky Mountains	280	8	34.9		12.9	Swetnam and Lynch 1989
Northern New Mexico	389	9		**25** (20–33) 50 (30–11) 2 (2.0–2.1)		Swetnam and Lynch 1993
Northeast Oregon	300	8	21–47 average[a] 36 ± 10		13–17 average[a] 15 ± 2	Swetnam *et al*. 1995a
North-central Colorado	277	9			6.9	Weber and Schweingruber 1995
South-central Colorado	348	14	32–79 average 36 ± 10	25, **37**, 83		Ryerson *et al*. 2003
South-central British Columbia	300	8		**30**, **43**, 70		Campbell *et al*. 2006
Two-year cycle budworm						
Southern British Columbia	310	7	34 + 1.1	3–23		Parish and Antos 2002
Central British Columbia	278	7	32		10–16	Zhang and Alfaro 2002, 2003

Includes Douglas-fir tussock moth (*Orgyia pseudotsugata* (McDunnough) (Lepidoptera: Lymantriidae)).

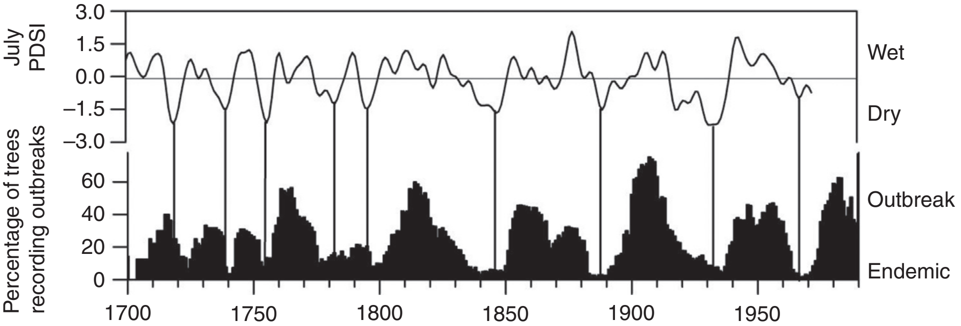

Figure 7.1 Western spruce budworm chronology (bottom) and Palmer Drought Severity Index (PDSI) (top) from the northern Blue Mountains, Oregon (T. Swetnam). Budworm outbreaks occur during relatively wet periods, and do not occur during droughts. Note that the PDSI cycle changes frequency about 1795, and the budworm cycle follows suit.

Associations with temperature and precipitation

WSBW outbreaks are positively associated with periods of increased spring and summer precipitation, and endemic periods are associated with drought conditions in the southwestern United States (Swetnam and Lynch, 1989, 1993; Ryerson *et al.*, 2003; Swetnam and Betancourt, 1998). These authors concluded that foliage production was abundant during pluvials, thereby supporting increased WSBW populations. Swetnam and Lynch (1993) also noted a weak pattern of cooler temperatures during periods of higher precipitation. Swetnam and Betancourt (1998) show a chronology from Oregon in which not only do WSBW outbreaks coincide with summer pluvials, but outbreak frequency decreases coincidentally with a decrease in pluvial frequency circa 1795 (Figure 7.1). This evidence strongly supports inferences that WSBW outbreaks in the southwestern United States occur during periods of increased moisture, and that the weakly or quasi-periodic population dynamics are entrained by climate.

WSBW outbreaks in British Columbia were associated with periods of average spring air temperatures after dry winters (Campbell *et al.*, 2006), a pattern more similar to those of SBW. Campbell *et al.* (2006) interpreted these circumstances as reflecting early spring conditions, which cued budworm emergence from hibernacula to coincide with the appropriate stage of bud development. The dissimilar findings from different regions are not incompatible, and regional differences should be expected.

Periodicity and synchrony

Some degree of synchrony is evident in the regional chronologies from each region, with significant periodicities of about 25, 30–43, and 70–80 (Table 7.2). Commonalities in periodicities from multiple regions, with multiple peaks in individual regions, indicate that WSBW population dynamics are at least inherently stable as periodic or quasi-periodic systems. Migration is an unlikely (but not impossible) mechanism to synchronize WSBW outbreaks because mountainous terrain and fire history cause host forests to be spatially discontinuous. Synchronization therefore requires exposure to one or more common factors able to harmonize the population oscillations. Given the demonstrated associations with climate, which is strongly periodic in western North America, it is implicated as the entraining factor.

Some WSBW cycles have unusually great amplitude, with a 70–80-year period (Table 7.2). This pattern is clearly evident in the south-central Colorado reconstruction (Ryerson *et al*., 2003) which shows fairly regular outbreaks, with every second or third outbreak being more extensive or severe. Whether these cycles occur when the maxima of all cycles coincide by chance (Campbell *et al*., 2006), are inherent in the population dynamics, or are driven by unknown exogenous factors is presently unknown. The temporal dynamics of root disease organisms should be examined as a possible factor affecting long-term cycles in western North American forests.

Twentieth-century patterns

The chronologies document changes in WSBW incidence in the twentieth century, including increased frequency, synchrony, duration, and severity. Of these, evidence is strongest for increased synchrony. Initiation of the 1940s–1950s and 1970s–1980s outbreaks across disjunct areas is notably synchronous in the Southwest, Oregon, and British Columbia (Campbell *et al*., 2006), as well as Montana for the 1970s–1980s outbreak. Synchronous outbreaks occurred in the past in all of these regions, but the two most recent regional outbreaks involved at least as many, if not more, sites than any earlier outbreak in the Southwest or British Columbia. The chronologies from northeast Oregon are notably synchronous throughout, especially for outbreak initiation.

Evidence of greater outbreak frequency in the twentieth century relative to the nineteenth century is found in several chronologies (Swetnam and Lynch, 1989, 1993; Swetnam *et al*., 1995), but not in others (Anderson *et al*., 1987; Ryerson *et al*., 2003). Conversely, interval length has varied considerably over time, and frequency during the twentieth century is within the reconstructed range of variability. There is consistent evidence of longer duration and increased severity, which is supported by well-documented high levels of tree mortality during the 1970s–1980s outbreaks. However, long, severe outbreaks occurred in the past in most of the chronologies.

The generally accepted interpretation of increased synchrony and severity in modern WSBW outbreaks pertains to the effects of fire exclusion, which fostered proliferation of shade-tolerant host species in multistoried canopies, thereby improving budworm habitat quality at large spatial scales (Fellin *et al*., 1983; McCune, 1983; Swetnam and Lynch, 1989, 1993; Swetnam *et al*., 1995). In much of western North America, fire exclusion began with livestock grazing, which reduced surface fuel amounts and connectivity. It became more comprehensive with changes in wildland fire suppression policies after devastating fires in the late nineteenth and early twentieth centuries, and improved fire-fighting technology increased the success of those policies (Swetnam, 1990; Keane *et al.*, 2002). Extensive forests that established after those fires would not have supported WSBW outbreaks for several decades, but later reached budworm-susceptible condition more or less simultaneously (Hadley and Veblen, 1993). A period of unusually low budworm activity can be seen in the early 1900s in several reconstructions (Swetnam and Lynch, 1989, 1993; Campbell *et al.*, 2006). Timing and duration of this period vary between regions, but the regional effects were to synchronize outbreaks in the latter half of the twentieth century over extensive areas. A second interpretation of increased synchrony and severity of modern WSBW outbreaks pertains to weather conditions suitable for population release. Ryerson *et al.* (2003) noted that if outbreaks are triggered by periods of increased moisture (as seen in most of the western chronologies), then synchrony of the 1970s–1980s outbreak might be associated with increases in precipitation, which is observed in the instrumental record and the dendrochronologic reconstructions. Probably both explanations are germane.

7.3.3 Two-year cycle spruce budworm

Biology

Two-year cycle spruce budworm (*Choristoneura biennis* (Freeman)) is semivoltine, overwintering as second and fourth instars. It is an early-season defoliator in both years of the life cycle, with heavy feeding on buds and new foliage in the second year, producing a distinctive tree-ring signal (Plate 7.1). Trees recover somewhat in alternate years, reducing the impact (Parish and Antos, 2002). It inhabits cold high-latitude high-elevation forests with Engelmann spruce (*P. engelmannii*), white spruce, and subalpine fir (*A. lasiocarpa*) as hosts.

Tree-ring chronologies

Our knowledge of the long-term patterns shown by this species was acquired by Parish and Antos (2002) and Zhang and Alfaro (2002, 2003) (Table 7.2). Suppression periods last 3–23 years (most last 7–16 years), about half of which may be a recovery period. Return intervals vary from 24 to 39 years, with averages of 32–34 years (Table 7.2). The initiation year, intensity, and extent of outbreaks vary spatially and temporally. Power spectra periods are significant at 6.8 and 43.6–45 years (Parish and Antos, 2002). The 45-year period and variability in outbreak extent and severity suggest quasi-periodic population dynamics influenced by a large-scale extrinsic factor, perhaps climate (Zhang and Alfaro, 2003). Some stands sampled by Parish and Antos (2002) were over 300 years old but did not incur an outbreak until almost 100 years into the chronology, indicating that stand structure and/or age are probably important features of susceptibility. In outbreak areas, tree growth over time is influenced more by two-year spruce budworm than it is by climate (Parish and Antos, 2002).

7.3.4 Larch sawfly

Biology

Larch sawfly (*Pristiphora erichsonii* Hartig (Hymenoptera: Diprionidae)) is usually univoltine, but pupation is sometimes prolonged to two winters. Males are rare, and most reproduction is parthenogenic. Adult emergence and egg-laying periods are nonsynchronous and long (up to 6 weeks), resulting in feeding throughout the summer. Populations do not develop in young stands. Due to the ability of larch (*Larix* spp.) to refoliate, and to sawfly preference for foliage on older twigs, impact is usually in terms of growth loss, but mortality can be severe in prolonged outbreaks (Drooz, 1971).

Tree-ring chronologies

Key attributes of tree-rings during larch sawfly outbreaks are the presence of pale latewood rings (which during the first year of the outbreaks may be of normal width), followed by radial growth suppression that is usually abrupt and synchronous amongst trees, and numerous (up to nine consecutive) missing or incomplete rings (Jardon *et al.*, 1994; Filion and Cournoyer, 1995; Girardin *et al.*, 2005; Nishimura and Laroque, 2010). Interval lengths vary considerably (6–56 years), but on average are between 25 and 35 years (Table 7.3). Data taken from the literature indicate that outbreaks generally last 6–10 years in individual stands, with a range of 2–18 years (Table 7.3). Once stands reach susceptible age, eastern larch (*L. laricina*) is defoliated on average 30–50% of the time (Girardin *et al.*, 2002; Jardon *et al.*, 1983). Both local and regional outbreaks are strongly synchronous (Girardin *et al.*, 2001, 2002; Nishimura and Laroque, 2010).

Dendrochronology studies indicate that larch sawfly is the most important regulator of eastern larch stand dynamics, influencing establishment dates and stand age structure (Girardin *et al.*, 2002; Busque and Arseneault, 2005). After severe outbreaks, larch establish from increased seed production on surviving trees (larch continues to reproduce during outbreaks) (Tailleux and Cloutier, 1993). After mild outbreaks, new stands establish from surviving advanced regeneration (Girardin *et al.*, 2002). In both cases, competition from shade-tolerant species is reduced.

Dendrochronologic investigations provided strong evidence that larch sawfly, once thought to be exotic, is native to North America. The evidence for this conclusion is the occurrence of numerous outbreaks since the early 1700s in Québec and Manitoba, established by Jardon *et al.* (1983) and Nishimura and Laroque (2010).

Twentieth-century patterns and associations with temperature

The 1894–1906 larch sawfly outbreak was probably the most severe and extensive disturbance event in eastern larch forests in 150 years (Arquillière *et al.*, 1990; Jardon *et al.*, 1994; Girardin *et al.*, 2002; Busque and Arseneault, 2005). Arquillière *et al.* (1990) and Nishimura and Laroque (2010) conclude that this mesocale event and other outbreaks between 1883 and 1911 are associated with a shift in sawfly disturbance regimes associated with warmer, improved conditions for larch growth and vigor. Investigators do not note periodic behavior associated with temperature or precipitation.

Table 7.3 For conifer-feeding defoliators other than SBW and WSBW: location, sample size, initial year and length (years) of chronology, number of outbreaks in the chronology (NOB), intervals or significant periodicities from time series analyses, and duration or mean duration ± SD (DUR) of suppressed growth, as determined in dendrochronologically reconstructed chronologies. Some statistics are computed from tabulated data or text references in publications.

Insect and general location	*Number of sites (trees)*	*First year*	*Length*	*NOB*	*Intervals or [periods]*	*DUR*	*Publication*
Cedar shoot moth, *Dichelia cedricola* (Diakonoff) (Lepidoptera: Tortricidae)							
Turkey	4 (17)	1954	48	3	30, 14	12, 6	Carus and Avci 2005
Epinotia subsequana (Hw). (Lepidoptera: Tortricidae)							
Northwest Spain	2 (10)	1900	100			3	Camarero *et al*. 2003
Hemlock looper, *Lambdina fiscellaria* (Guénée) (Lepidoptera: Geometridae), with SBW							
Eastern Québec	14	1846	160	4–7	26, 14, 11, 10, 13, 8, 38		Barrette *et al*. 2010
Larch budmoth, *Zeiraphera diniana* Guénée (Lepidoptera: Tortricidae)							
Switzerland	35	1503	488	57	8.6 ± 1.7		Weber 1997
French Alps	7	1800	190+	22	8.9 ± 1.0		Rolland *et al*. 2001
Northwest Italy	1	1760	240	19	[9, 23–28, ave. 27]	3.6 ± 1.3	Nola *et al*. 2006
European Alps	(180)	832	1173		[8.1–9.3]		Esper *et al*. 2007
European Alps	(70)	1700	300		9, varies with elevation		Büntgen *et al*. 2009
Larch sawfly, *Pristiphora erichsonii* Hartig (Hymenoptera: Tenthredinidae)							
Northern Québec	10	1596	391	2	35	4, 7	Arquillière *et al*. 1990
Northern Québec	1 (26)	1680	300	10	27 ± 9 (6–49)	9 (5–15)	Jardon *et al*. 1994
Southwest Québec	12	1858	142	5			Giardin *et al*. 2002
Manitoba	4	1880	200	5	35 ± 18 (12–56)	7 ± 3 (6–10)	Girardin *et al*. 2005
Western Labrador	12	~1720	280	8	25 ± 9 (14–36)		Nishimura and Laroque 2010

(*Continued*)

Table 7.3 (*Cont'd*).

Pandora moth, *Coloradia pandora* (Blake) (Lepidoptera: Saturniidae)							
South-central Oregon	14	1379	622	22	27 (8–44) [18–24, 37–41]	10 (4–18)	Speer *et al*. 2001
Pine butterfly, *Neophasia menapia* (C. Felder and R. Felder) (Lepidoptera: Pieridae)							
Idaho	(100)	1916	30	1		2	Evenden 1940
Pine false webworm, *Acantholyda erythrocephala* (L.) (Hymenoptera: Pamphilidae)							
Northern New York	21	1950	50	1		5	Mayfield *et al*. 2005
Pine sawfly, *Diprion pini* L. (Hymenoptera: Diprionidae)							
France	2	1953	31	2			Laurent-Hervouët 1986b
Southern Finland	1	1966	36	1			Kurkela *et al*. 2005
Processionary caterpillars, *Thaumetopoea pityocampa* Denis & Schiffermüller, *T. wilkinsoni* Tams., and *T. ispartaensis* (Doğanlar and Avcí)							
France	2	1959	25	1			Laurent-Hervouët 1986a
Turkey	1	1981	23	3–4	12, 7	6 ± 0	Carus 2004
Turkey	5	1947	57	4	8, 31, 13	5, 8, 5	Avcí and Carus 2005
Turkey	1	1985	20	3	5–7	4–7	Carus 2010
Western false hemlock looper, *Nepytia freemanii* Munroe (Lepidoptera: Geometridae)							
British Columbia	(200)	1880	105	1		5	Alfaro and MacDonald 1988

7.3.5 Pandora moth

Biology

The Pandora moth (*Coloradia pandora* (Blake) (Lepidoptera: Saturniidae)) is a large-bodied semivoltine insect that overwinters as second or third instars at the base of needles and as pupae in the soil (which may diapause up to 5 years). Large larvae occur early- to midseason every other year, heavily defoliating old foliage but not buds or new shoots. Adults are strong flyers. Outbreaks spread from centers, though centers may coalesce. Outbreaks collapse rapidly after 6–8 years from a nucleopolyhedrosis virus infection (Schmid and Bennett, 1986). Mortality to hosts ponderosa pine (*P. ponderosa*) and lodgepole pine (*P. contorta*) is generally low, because defoliation occurs only in alternate years, allowing some recovery, and because buds are not consumed (Schmid and Bennett, 1986).

Tree-ring chronology

Speer *et al*. (2001) developed a 622-year chronology of Pandora moth from ponderosa pine in central Oregon (Table 7.3). Radial growth in the first suppression year is sometimes a white ring, is reduced about 50%, and has very thin latewood (Plate 7.1). The pattern of narrow rings in alternate years found in two-year cycle budworm is absent in Pandora moth material, or at least is not striking. This difference is not discussed in the literature, but is probably related to feeding behavior. Both are early-season defoliators, but two-year cycle budworm feeds on buds and new foliage, while Pandora moth feeds on old foliage and not on buds or new foliage.

Initiation of the suppression periods are typically represented by a cluster of dates rather than a single year, originating in small groups of stands, consistent with a pattern of population spread from multiple initial locations over several years. Intervals between outbreaks range from 8 to 48 years, but are sometimes very long – up to 156 years. Time series analyses showed significant periods at 18–24 years and 37–41 years. Both periods are evident in the regional chronology, in which approximately a third of outbreaks were more extensive. The regional time series exhibited a striking episodic pattern with quasi-cyclic recurring outbreaks. Mean duration is 10 years (4–18 years). Twentieth-century outbreaks were not more synchronous, severe, or longer in duration than outbreaks in previous centuries, but there was an unusual 60-year reduction in regional activity during about 1920–1980 (similar to WSBW). Temporal variability of outbreaks does not appear to be associated with climate (Speer and Jensen, 2003), but variable amplitude and strengths of the cycles over centuries suggest that an exogenous process entrains population fluctuations (Speer *et al*., 2001). Nucleopolyhedrosis viruses persist in the environment for several years (Ghassemi *et al*., 1983; Olofsson, 1988) and might restrict cycle frequency at the short end, but once the virus degrades then other factors might influence periodicity.

Reduced fire frequency is associated with Pandora moth outbreaks (Speer *et al*., 2001), but it is not clear if this is because fine surface fuel accumulation is reduced because of needle consumption by larvae, thereby reducing fire frequency, or if Pandora moth survival is greater when fires are reduced.

7.3.6 Larch budmoth

Biology

Larch budmoth (*Zeiraphera diniana* Guénée) (Lepidoptera: Tortricidae)) (LBM) inhabits subalpine larch and larch-Swiss stone pine (*L. decidua* and *P. cembra*) forests of the European Alps. It is a univoltine early-season wasteful defoliator that pupates in the litter, though seasonality is variable (Baltensweiler and Fischlin, 1988). Larval eclosion is synchronized with host bud flush, and this coincidence is essential. Adults are strong fliers, and outbreaks can expand to less desirable habitats during intense outbreaks.

Tree-ring chronologies

LBM is detectable in the tree-rings by reduced ring width, reduced earlywood, reduced density of the latewood, and missing rings (Weber and Schweingruber, 1997; Esper *et al*., 2007; Nola *et al*., 2006; Rolland *et al*., 2001). Often so many rings are missing during suppression periods that wood cannot be cross-dated and is discarded by investigators (large numbers of missing rings also occur with Jack pine sawfly (*Neodiprion swainei* Midd., Hymenoptera: Diprionidae)) (O'Neil 1963). Growth is suppressed 3.6±1.3 years (computed from numbers presented by Nola *et al*. 2006), somewhat longer than the 2.9±0.2 years documented in the shorter historical record (Baltensweiler and Fischlin, 1988). Growth recovery is rapid, and is complete within 3 years (Rolland *et al*., 2001). Tree-ring reconstructions have confirmed a regular 8–9-year periodicity in the LBM population dynamics across the Alps that has persisted for 12 centuries (Table 7.3). LBM outbreaks are less frequent at lower elevations (Büntgen *et al*., 2009) and often exhibit an easterly expansion pattern across the Alps (Bjørnstad *et al*., 2002; Nola *et al*., 2006).

Associations with temperature and twentieth-century patterns

Tree-ring isotope chronologies found that the LBM cycle has been strongly coupled with cyclicity of below-average late summer temperatures for 300 years (Kress *et al*., 2009), and has persisted for 1200 years, through the Medieval Climate Anomaly and Little Ice Age, but ceased after 1981 (Esper *et al*., 2007). Degradation of the stable periodic pattern corresponds to regional warming that is exceptional in the last 1000+ years (Büntgen *et al*., 2009; Esper *et al*., 2007). Populations still exhibit synchrony at the local scale (Büntgen *et al*., 2009).

Periodicity and synchrony

LBM population dynamics are the best-synchronized oscillatory system observed in forest entomology. True periodicity in LBM cycles has been recognized for some time, and dendrochronology studies have established that epizootics have recurred with remarkable regularity every 8–9 years (Table 7.3). Rolland *et al*. (2001) and Nola *et al*. (2006) identified significant harmonic periods at 18 and 27 years, respectively. The most intense outbreaks in the time series are recorded in the years when short- and long-period cycles coincide (Nola *et al*., 2006). Synchrony, spread, and intensity are not uniform over the full LBM range (Bjørnstad *et al*., 2002; Nola *et al*., 2006; Cooke *et al*., 2007).

Synchrony is greater in the western Alps and in the valleys with continental climates (Nola *et al*., 2006). Outbreaks in suboptimal areas depend largely on immigration of moths from more optimal areas (Baltensweiler and Fischlin, 1988; Rolland *et al*., 2001).

7.3.7 Processionary caterpillars

Biology

Pine processionary caterpillars (*Thaumetopoea pityocampa* Dennis and Schiffermüller and *T. wilkinsoni* Tams) defoliate pines, cedars (*Cedrus* spp.), and larch in the circum-Mediterranean region and the Alps roughly corresponding to the distribution of *Pinus nigra*. They are univoltine, with all or part of populations exhibiting semivoltinism. Larval development and pupal diapause are variable, and adults emerge in summer. Pupal diapause may be extended for several years until weather conditions are suitable for adult emergence. Larvae feed on warm winter days and in the summer and autumn of alternate years, with maximum defoliation in February and March (Carus, 2004; Halperin, 1990; Masutti and Battisti, 1990), acting primarily as a dormant-season defoliator. Range expansion northward and to higher elevations in the last 3 years is associated with warmer winter temperature (Hódar *et al*., 2003; Battisti *et al*., 2005; Toffolo *et al*., 2006). The cedar processionary moth, *T. ispartaensis* (Doğanlar and Avcí), is a univoltine early-season defoliator of *Pistacia* spp., *Cypressus sempervirens*, and *Schinus terebinthifolius*, and a new threat on *Cedrus libani* in Turkey (Avcí and Carus, 2005).

Tree-ring chronologies

Dendrochronologic investigations have mostly been directed toward quantifying the impact of pine processionary caterpillars on timber impacts, but have also documented outbreak regimes. Tree-ring studies indicate a high frequency periodicity of 5–7 years in Turkey for pine processionary caterpillars (Table 7.3). Growth is usually suppressed for 4–6 years, reducing volume growth rate up to 45% over the long term. Trees barely recover from one outbreak before they incur another (Carus, 2004, 2009). Cedar processionary moth outbreaks exhibit a more variable return interval (Table 7.3) but outbreaks are of similar duration. Unusually long, large-scale outbreaks are followed by lengthy intervals before the subsequent outbreak. Outbreaks are associated with dry winter and spring weather prior to larval feeding (Avcí and Carus, 2005). Processionary moths on both pine and cedar in Turkey exhibited local- and regional-scale outbreaks (Carus, 2004, 2010; Avcí and Carus, 2005).

7.4 Conclusions

Using dendrochronology, researchers can date past forest insect disturbances with annual or near-annual precision and map their extent with considerable confidence. There is some loss of temporal precision because of delays between insect population increase, defoliation, and tree radial growth response, but the general timing of past outbreaks can usually be reconstructed with confidence.

Once developed, tree-ring chronologies of insect outbreaks provide proxy representations of population cycles. They are excellent for revealing the timing of events, quantifying the extent and strength of temporal and spatial variability in outbreak frequency and duration, determining the nature of population oscillations, and determining the presence and strength of spatial synchrony. With additional proxy or observational data, inferences are made about associations with other disturbance regimes and climate.

Tree-ring proxy records for many insects are several centuries long, and are composed of multiple outbreak events which occurred under variable forest and climatic conditions. Besides providing information about the ecology and population dynamics of individual species, these dendrochronology studies provide more broadly applicable insights into forest insect populations.

7.4.1 Insect outbreaks and forest health

Dendrochronology studies repeatedly show that host species and insects have coexisted for many centuries, surviving considerable variation in climate and many ecological upheavals. LBM/European larch, larch sawfly/eastern larch, Pandora moth/ponderosa pine, SBW/balsam fir, and WSBW/mixed-conifer systems have endured for centuries. This is evidence that insect outbreaks do not necessarily reflect unhealthy conditions or systems, and that alternating periods of outbreaks and non-outbreak conditions often represent stable systems. Ecosystems with natural cycles of perturbation and recovery may be highly resilient. It follows that many systems are self-regulating such that outbreaks modify stand or forest composition and structure such that reproduction of host species is favored in the long run, and natural development of forest structure and composition provides suitable habitat for the insect, as proposed by Mattson and Addy (1975). While tree-ring chronologies do not prove this hypothesis, they do provide evidence that it is so, since long chronologies identify repeated outbreaks, and recruitment dates make it clear that host species reestablish stands.

Forest ecosystems experience insect outbreaks much of the time. This fact seems self-evident, but the comprehensive nature of this observation can be startling. For some species, there are few years without an outbreak somewhere in the region. Other systems incur outbreaks 20–50% of the time. And in some systems, variation in tree growth is influenced more by insects than by climate, including two-year cycle budworm (Parish and Antos, 2002), larch sawfly (Girardin *et al.*, 2002; Busque and Arseneault, 2005), pine processionary caterpillars (Carus, 2004, 2009), and, though not explicitly documented, probably larch budmoth at higher elevations.

7.4.2 Outbreak periodicity and synchrony

The great length of tree-ring records provides an opportunity to study spectral properties of insect population oscillations. Esper *et al.* (2007) provide the best example of how informative, even profound, the results of such studies can be. All of the species for which multiple outbreak cycles have been reconstructed exhibit some degree of periodicity. Most of these systems are weakly periodic or quasi-periodic with local factors and exogenous Moran effects entraining persistent cycles, while other systems appear to be regulated by dispersal.

The dendrochronology record shows considerable evidence of large-scale synchrony in forest defoliator outbreaks, as well as indicating that synchrony is stronger is some places and periods than in others. There is consistent evidence that climate entrains the population dynamics of several species, especially for regional-scale events, acting as an exogenous Moran effect. SBW, WSBW, and LBM population fluctuations are closely associated with climate fluctuations. Evidence is particularly strong for WSBW and LBM. WSBW populations in geographically distant regions with different climate systems not only oscillate with precipitation (Ryerson *et al*., 2003; Swetnam and Betancourt, 1998; Swetnam and Lynch, 1989, 1993; Swetnam *et al*., 1995), but periodicity in the Oregon outbreak chronology changed frequency with a change in the precipitation cycle (Figure 7.1; Swetnam and Betancourt, 1998). LBM oscillated closely with late-summer temperatures for 1000+ years, and then abruptly lost regional synchrony when temperatures rose above those seen in the 1000-year record (Büntgen *et al*., 2009; Esper *et al*., 2007; Kress *et al*., 2009), though populations are still locally periodic (Esper *et al*., 2007). The chronologies also provide evidence that synchrony in some populations is associated with dispersal and natural enemy mechanisms.

Investigators speculate as to the mechanisms behind climatic influences on forest insect populations – food quality or quantity, larval development rates, overwintering survival, conditions promoting a good match between host and insect phenologic development, and so on – but causal relationships are difficult to discern through dendrochronology. The direct or indirect nature of climate-associated periodicity is not clear. Dendrochronologists tend to focus on information that can be extracted from the tree-ring record, and may overlook the many climate-related attributes that were not extracted in their analyses, such as flower events, phenology, and cold-season temperatures. Insect populations generally do respond to climate variability that can be quantified from tree-rings, but they also respond to climatic variability that cannot (so far) be reconstructed, such as bud phenology, and to nonclimatic variability. Identifying the coupled nature of insect and host-climate systems provides vital information to understanding ecosystem response to change, and other types of investigations can elucidate the nature of the relationship.

Cooke *et al*. (2007; see also Ranta *et al*., 1999; Royama *et al*., 2005) argue that periodicity and synchrony are inherent features of defoliator population dynamics that are determined by the ecological relationships among host plants, insect herbivores, and their natural enemies, and that variability in periodicity and synchrony is created through the influence of stochastic environmental variables. The dendrochronology record provides evidence that periodicity of is an inherent and strong characteristic of epizootic conifer defoliator population dynamics, and that exogenous factors often influence variability in the natural cycles. Climate is frequently implicated as an exogenous factor that influences cycle frequency and amplitude, including those of SBW, WSBW, and LBM. Dispersal is also implicated as a synchronizing force in SBW and LBM. In other cases, such as Pandora moth, periodicity persists with little change through long time frames that encompass considerable climate variability with little apparent change in outbreak periodicity. Dendrochronology studies also show repeatedly that synchrony is strongest in areas where habitat (including thermal habitat) is optimal for the insect, and that synchrony decays as habitat conditions become marginal. Relatively stable cycles with different characteristics amongst regions for the same insect species (Tables 7.1–7.3), and for the Oregon WSBW system, different cycle frequencies in different portions of the chronology (Figure 7.1) indicate that different environmental situations can create relatively stable, robust systems with different characteristics. Whether this means that periodicity in the insect cycle is inherently weak, that periodicity in the insect cycle is fairly strong but plastic, allowing adaption to various circumstances, or that strong periodicity in some other part of the system overwhelms the insect cycle, is not directly evidenced by the tree-ring record.

Some quasi-periodic populations exhibit multiple significant periodicities, with a high-amplitude long-period cycle harmonic with one or more shorter periods. It is not clear if harmonic cycles are inherent features of insect population dynamics or are due to exogenous factors such as climate or host population dynamics, but evidence indicates that such harmonics are not analytic artifacts, and that regional-scale outbreaks occur when multiple cycles coincide. There are several ways that harmonic periods could develop, including (1) the occurrence of fairly regular cycles, with a few outbreaks absent or of low intensity; (2) the occasional development of more extensive and/or severe outbreaks, resulting in greater numbers of trees or sites recording the outbreak (which subsequently might cause the next outbreak to be of low intensity if host-species survivors are immature or infrequent); or (3) the absence or diminution of entraining exogenous cycles (e.g., variability in climate cycles). High-amplitude events may result from the development of host forests to a mature condition over extensive areas (having once consisted of relatively immature stands over extensive areas because of a past large-scale disturbance), which may or may not be harmonic with the insect population cycles. Timing of the extraordinary event might be influenced by climate or other cyclic factors, but the size and severity of the event are influenced primarily by forest condition. The effects of tree pathogens, particularly those such as some root pathogens that have multidecadal residence on sites and function at large spatial scales, on insect defoliator periodicity and synchrony have not received much attention in tree-ring or population dynamic modeling studies.

The tree-ring proxy data strongly indicate that Moran effects, especially climate-related mechanisms, synchronize some forest insect systems, and that other systems are regulated by dispersal and natural enemies. Proving synchrony or its causes requires the manipulation or elimination of one of the synchronizing mechanisms (Hudson and Cattadori, 1999), so arguments about Moran effects, random effects, and the mechanisms of synchrony will likely never be satisfied. Further insights in insect disturbance ecology will require combining information from long-term proxy data and short-term population studies in carefully designed model systems, and using those models for carefully structured comparisons (Cooke *et al.*, 2007; Royama *et al.*, 2005). By definition models are imperfect representations of real systems, but they provide considerable insight into system behavior. In order to have the best chance of the model system elucidating causal mechanisms, knowledge of the real system should encompass (1) the entire range of the insect species habitat, or at least large portions of it in a reasonably continuous fashion; and (2) endemic and epizootic population phases.

There is much to be gained through a better understanding of the relationships between insect population density, defoliation, and radial growth, especially during the initial outbreak stages. In this regard, I suggest that effort might be better spent studying eruptive defoliators such as LBM, DFTM, larch sawfly, and processionary caterpillars before trying to quantify these relationships with the SBW and WSBW systems, for which outbreaks often develop so slowly that variability in tree radial growth associated with other factors obscures the initial tree response to insect population densities. Also, studying differential effects of early- and late-season defoliators, and by comparing responses between defoliated and defoliator-excluded treatments (i.e., Morrow and LaMarche, 1978), will provide insight into lagged responses and negative feedback mechanisms. It should be noted that dendrochronologic investigations of the type reported here are restricted in large part to ecological systems in which tree radial growth varies temporally with one or more climatic variables.

7.4.3 Changes induced by altered climate and large-scale antecedent events

Dendrochronology has demonstrated that relatively small changes in climate can dramatically alter forest insect disturbance regimes. A relatively small change in atmospheric circulation and solar insulation at the end of the Little Ice Age, circa 1850, is associated with a change in SBW outbreak regimes in eastern Canada (Bergeron and Archambault, 1993; Bergeron and Leduc, 1998; Bergeron *et al.*, 2001; Carcaillet *et al.*, 2010). Similarly, a mid-nineteenth-century warming trend is associated with altered larch sawfly regimes in Québec (Arquillière *et al.*, 1990; Nishimura and Laroque, 2010). Millennium-long, near-continental scale synchrony of LBM outbreaks in the European Alps has disintegrated, perhaps ended entirely, with regional warming that is unprecedented in 1000+ years (Büntgen *et al.*, 2009; Esper *et al.*, 2007). In eastern Oregon, WSBW outbreak cycle frequency decreased when frequency of precipitation cycles decreased (Swetnam and Betancourt, 1998). In each case, change in climate profoundly altered insect disturbance regimes.

Dendrochronology studies demonstrate that landscape-scale effects can induce similarly scaled changes in forest vegetation succession and subsequent insect outbreak regimes. These effects include climate change in the systems described above, and anthropogenic fire exclusion in the western North American mixed-conifer and WSBW system. Perturbing precedent events have brought about subsequent disturbances at the same scale, and synchronized future disturbances. For example, an unusually long period of reduced WSBW activity in the southwestern United States, and subsequent extensive severe outbreaks, is associated with anthropogenic fire exclusion (Anderson *et al.*, 1987; Campbell *et al.*, 2006; Hadley and Veblen, 1993; McCune, 1983; Swetnam and Lynch, 1989, 1993).

7.4.4 *Choristoneura*

SBW, WSBW, and two-year cycle budworm chronologies exhibited many similarities, with periodicity and duration generally within 25–46 and 11–15 years, respectively (though both are highly variable), strong local periodicity, regional (and for SBW, almost subcontinental scale) synchronicity, and occasional high-amplitude synchronous events. Though not in any way identical, gross similarity in outbreak regimes across different species at such long geographic distances, with vastly different climates, and with different host species (from relatively short-lived balsam fir to long-lived Douglas-fir), suggests that periodicity and synchrony are inherent characteristics of the population dynamics of conifer-feeding *Choristoneura*, though they may not be strong. It also suggests that cold system–inhabiting *Choristoneura* may be replaced by relatively warmer system–inhabiting *Choristoneura* species if climate warms, except of course in the warmest systems. Analyses of the chronologies indicate that common regional Moran effects (with climate-related effects implicated frequently) help synchronize outbreaks of conifer-feeding *Choristoneura*, and that migration is a synchronizing feature in some regions.

Significant periodicities at circa 25, 34–38, and 43–46 are frequently found in SBW, WSBW, and two-year cycle budworm chronologies from different areas (Tables 7.1 and 7.2). Repeatedly finding similar frequencies not only indicates that the systems are inherently periodic, but also indicates that ecological relationships among host plants, insect herbivores, their natural enemies, and climate can produce stable systems at different frequencies. Several possible factors may affect the frequency that each system acquires – habitat quality for host, herbivore, or natural enemies; fire regime; tree pathogen activity; climate; or other agents. But it appears that *Choristoneura* populations can adapt to different cycle frequencies.

7.4.5 Other implications

Outbreak regimes are characterized by temporal and spatial variability at many scales. Periodicity and synchrony are strong enough in several systems to provide guidance in ecosystem management. The information found in the tree-ring chronologies provides a better indicator of the potential range of variability than do historical records for many systems. However, no matter how strongly regulated, periodicity and synchrony are affected by many external forces, and it is unreasonable to expect perfect mathematical description and prediction of these systems. The tree-ring chronologies also provide indication that long-established patterns can be modified by external factors, and provide an indication of what factors have been related to shifts in system dynamics in the past (e.g., climate change, changes in fire regimes, and land use history). Predicting the timing, size, and severity of future events is likely to be successful in general terms, providing managers with a sense of how often serious events may occur, what precedent conditions might moderate or intensify outbreaks, and whether outbreak regimes are likely to be altered with climate change. Predicting precisely just when and where outbreaks will occur is less likely.

Of the many insect species that occur in forests, tree-ring chronologies have been developed for only a few. Chronologies usually encompass single-species systems (sometimes two insect species simultaneously) of native conifer defoliators. Only a few chronologies have been developed for hardwood defoliators, sap suckers, bark beetles, or pathogens. Chronologies are insect species–oriented rather than pertaining to ecosystem disturbance history. Studying the disturbance regimes of individual insect species helps us anticipate future outbreaks, develop an understanding of population behavior, and understand which climatic patterns and forest conditions are associated with outbreak oscillations, but developing an understanding of how ecosystems respond to changing conditions requires studying tree population demographic changes coincident with disturbance regimes of multiple agents – defoliators, bark beetles, pathogens, fire, and climate. The attributes of parasitoid and predator population dynamics are poorly known, but undoubtedly influence defoliator population behavior.

By understanding the record of past forest insect outbreaks that is found in tree-ring chronologies, we can better interpret short-term records and experimental results, determine the extent to which current trends have departed from past trajectories, and predict ecosystem response to future disturbance events. And, above all, we may ultimately understand the mechanisms driving ecosystem response to disturbance.

Acknowledgments

I wish to thank Thomas Swetnam and two anonymous reviewers for their helpful comments on an earlier version of the manuscript, and David Meko and Barry Cooke for helpful discussions. I also thank René Alfaro, Paul Shepperd, Jim Speer, and Thomas Swetnam for providing photographs and the charts used in Plate 7.1 and Figure 7.1.

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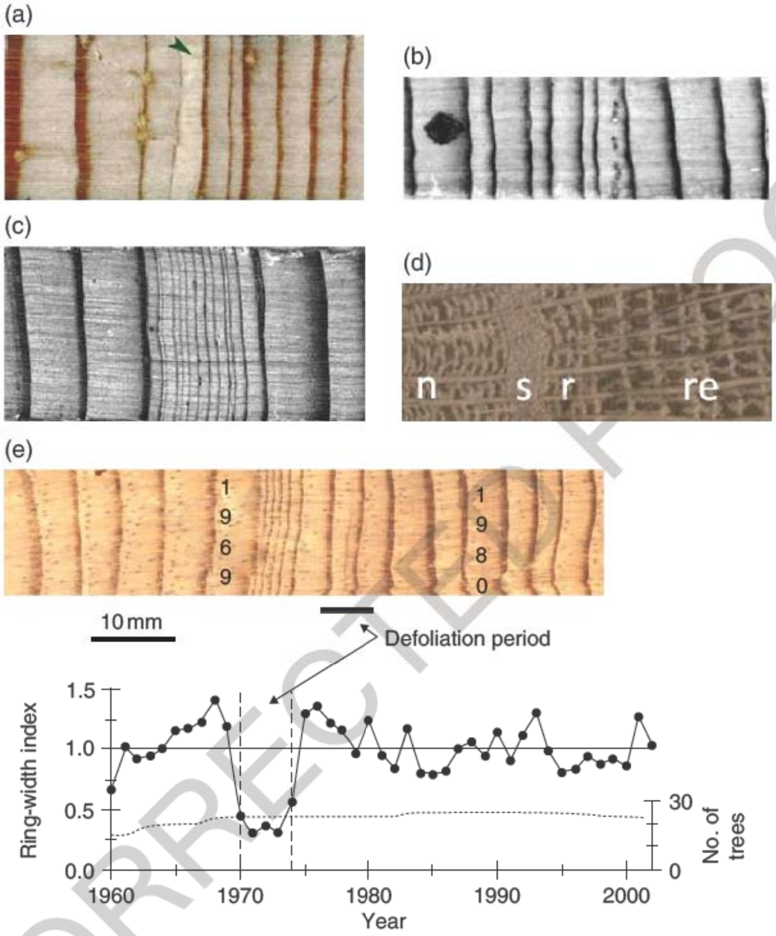

Plate 7.1 Examples of tree ring response to disturbance. (a) *Pinus ponderosa* defoliated by Pandora moth (J. Speer). Note that the ring formed the first year of defoliation is half the size of normal rings, followed by several small rings. The initial "white ring" and reduced latewood are also characteristic of Pandora moth defoliation: (b) *Abies lasiocarpa* defoliated by two-year cycle budworm (R. Alfaro). Note the alternating narrow and wide growth rings typical of this insect: (c) *Abies concolor* defoliated by western spruce budworm (T.W. Swetnam). Note that the 12 years of reduced growth are the width of 2 years of normal growth, (d) in *Quercus gambelii*; normal radial growth (n), probably in a closed-canopy situation, suppressed growth (s), followed by circa 4 years of recovery (r) and growth release (re) caused by defoliation and mortality associated with an unknown defoliator (R. Adams). (e) *Pinus leiophylla* defoliated by *Zadiprion falsus* Smith (Hymenoptera: Diprionidae) (photo) and standardized but uncorrected ring width series (chart) (P. Shepperd).