Swetnam

A DENDROCHRONOLOGICAL RECORD OF PANDORA MOTH (*COLORADIA PANDORA*, BLAKE) OUTBREAKS IN CENTRAL OREGON

by

James Hardy Speer

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STATEMENT BY AUTHOR

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SIGNED: James H. Speer

APPROVAL BY THESIS ADVISOR

This thesis has been approved on the date shown below:

Thomas W. Swetnam
Associate Professor of Dendrochronology

8/8/97
Date

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DEDICATION

This thesis is dedicated to my family for all of their support and all that they have taught me. Thank you Collie, Jenna, and Chuck.

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ABSTRACT

Pandora moth (*Coloradia pandora* Blake) is a phytophagous insect, defoliating ponderosa pine trees in the western United States. However, long-term studies of this insect and its effects on the forest ecosystem have not been conducted. Using dendrochronological techniques, I examined past timing and intensity of defoliation through its effects on radial growth of trees in the forests of south central Oregon. Pandora moth leaves a distinctive ring-width "signature" that was easily identifiable in the wood. The growth for the first year of the signature was half the normal ring-width with narrow latewood. The following two years produced extremely narrow rings, with the entire suppression lasting from 4 to 18 years.

Twenty-two individual outbreaks were reconstructed from this 620 year chronology. I found that pandora moth outbreaks were episodic on individual sites, with a return interval of 9 to 156 years. Conversely, on the regional scale of south central Oregon, outbreaks demonstrated a 37-year periodicity. On average, pandora moth defoliation caused a 29% mean periodic growth reduction in defoliated ponderosa pine trees. Spread maps of the first year that sites demonstrated suppression were plotted revealing an apparent annual spread of the outbreaks. Examination of a fire history on one pandora moth outbreak site suggested that pandora moth outbreaks delay fire by interrupting the needle fall needed for fire spread. Superposed epoch analysis showed that the year that the outbreak was first recorded was significantly dry and the fourth year prior

was significantly wet. Therefore, climate may be a triggering factor in pandora moth outbreaks. The stem analysis demonstrated that the percent volume reduction was greatest at the base of the tree and declined further up the bole. The percent volume reduction in the canopy of the trees was variable with outlying high and low values. The mean volume reduction per outbreak was .053 m^3 per tree.

Although this insect is considered a forest pest and causes inconvenience for people living nearby, pandora moth is not as widespread and damaging as some other phytophagous insects. However, its very distinctive ring-width signature and the length of the ponderosa pine record enables reconstruction of very long outbreak histories, which may deepen our understanding of the interaction between defoliating insects and their ecosystem.

CHAPTER 1

INTRODUCTION

1.1 Pandora Moth

Pandora moth (*Coloradia pandora* Blake) (Fig. 1.1) is an endemic phytophagous insect whose larvae feed on the foliage of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), and lodgepole pine (*Pinus contorta* Dougl. ex Loud.). Other incidental host tree species include sugar pine *(P. lambertiana* Dougl.) and coulter pine (*P. coulteri* D. Don.) (Patterson 1929; Wygant 1941; Carolin and Knopf 1968; Furniss and Carolin 1977). Outbreaks have occurred throughout the western United States mostly in Arizona, California, Colorado, and Oregon (Carolin and Knopf 1968) (Fig 1.2).

A current outbreak of pandora moth in the Deschutes National Forest of Oregon has been active for 10 years, providing the impetus for this study. Historical records document the occurrence of past defoliation events in the 1890s (Keen 1937; Carolin and Knopf 1968), 1918 to 1925 (Patterson 1929; Keen 1937), and 1963 to 1968 (B. Wickman, pers. comm.), as well as the modern outbreak of 1988 to 1996 (Wickman *et al.* 1996). However, nothing is known about earlier occurrences of pandora moth outbreaks, and very little is understood about the magnitude of the impact of outbreaks on ponderosa pine tree growth and health.

Understanding disturbance factors that influence forest ecosystems over long

Figure 1.1. Mature pandora moth larvae feeding on ponderosa pine foliage. The mature larvae can achieve 6 cm in length (Photograph from Blake and Wagner 1981).

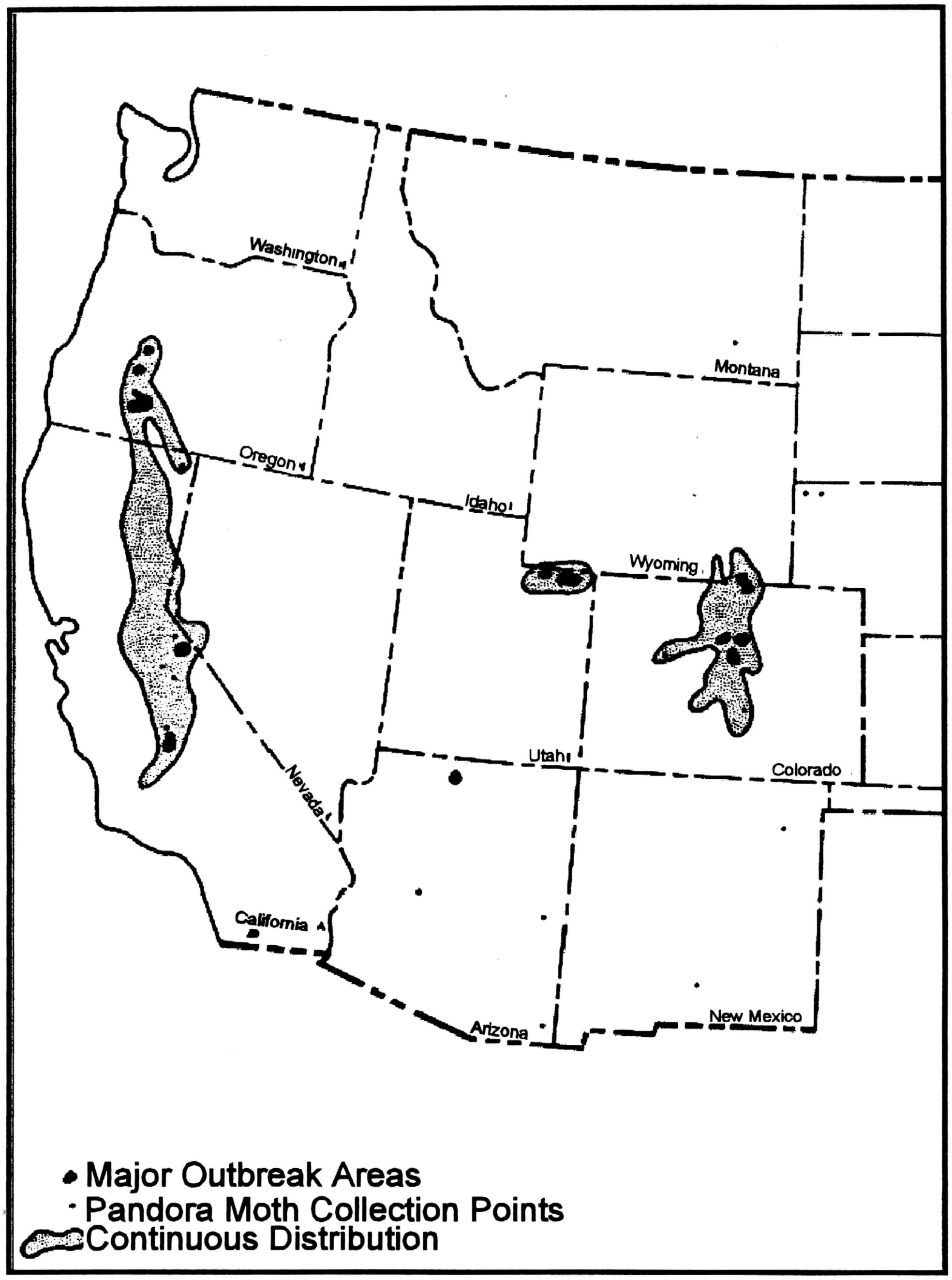


Figure 1.2. Distribution of pandora moth in the Western UnitedStates (Carolin & Knopf 1968).

periods and large areas (*e.g.* climate, fire, or past insect outbreaks) is of considerable interest today. Baseline data are needed to provide a historical perspective of current forest conditions and to enhance understanding of the interaction between different processes (Wickman 1992; Swanson *et al.* 1994). By studying the history of ecosystem processes, we may determine their typical range of variation (Morgan *et al.* 1994) and possibly identify the conditions that sustained or changed the system. Such knowledge could indicate if recent or current changes are normal or atypical, with associated implications for forest management policy and practices. Long-term records would enable us to examine the synergism between natural phenomena, such as the climate-fire-insect system, and to study the impact of cultural phenomena, such as variations in land use.

This study will address several important questions concerning the dynamics of the pandora moth and its effects on the ponderosa pine forests of central Oregon. Specifically:

- *When did pandora moth outbreaks occur in the past?* The temporal patterns of past pandora moth outbreaks could be reconstructed with a multi-century history. The duration and frequency of past pandora moth outbreaks could then be quantified. Also the possible cyclicity of outbreaks could be examined. If outbreaks were periodic, it may provide a predictive tool for future outbreaks. If outbreaks were episodic, it may be possible to determine if they were triggered or controlled by exogenous factors such as climate conditions or fire occurrence.

- *What is the spatial pattern of past outbreaks?* With a long record of outbreaks reconstructed across a spatial network of sites, it should be possible to determine the distribution of outbreaks across the landscape and the typical spread pattern of an individual outbreak.

- *What is the effect of insect defoliation on wood volume in affected trees?* Quantifying the reduction in growth suffered by host trees during each outbreak would permit a more accurate assessment of aggregate impact of outbreaks on forest productivity and health. The cost-effectiveness of alternative techniques for controlling or suppressing infestations could also be evaluated relative to the potential loss in wood volume with no intervention.

- *How have the dynamics of pandora moth outbreaks changed through time?* The temporal perspective provided by a long record of outbreaks can help identify trends in the occurrence of outbreaks, as well as any areas where forest health may have declined as a result. This would assist forest managers in developing and targeting more effective strategies for protecting and improving forest health and managing for sustainable resources.

1.2 Study Objectives

The specific objectives of this study were as follows:

- Determine if pandora moth outbreaks caused a distinguishable suppression pattern in ponderosa pine tree-ring width.
- Reconstruct pandora moth outbreaks over multi-century time scales.
- Investigate the spatial dynamics of past outbreaks.
- Investigate the development of a single insect outbreak by examining the spatio-temporal aspects of the modern outbreak (1988-1996).
- Evaluate the effects of pandora moth on radial growth throughout the tree stem.
- Investigate the effect of surface fires on ring-width patterns and study the fire-insect system.
- Investigate the effects of climate on the ring-width patterns and study the climate-insect system.

1.3 Overview of Methodology

To reconstruct a record of past pandora moth outbreaks increment cores were collected from 163 trees at 14 sites in central Oregon. The cores were then crossdated and measured. I identified ring-width suppressions in the wood that were associated with documented outbreaks at two sites (the Experimental Forest (EF) and Pringle Falls (PF) sites). These inferred and known outbreaks periods were used to calibrate the OUTBREAK program (Holmes and Swetnam unpublished), so that it consistently identified the same periods using the ring-width measurements as were visually identified. Data from the remaining sites was then entered into the OUTBREAK program, which identified the inferred outbreaks.

Confounding factors, such as fire, climate, and other insects, were examined. I reconstructed the fire history of one site to examine fire-insect interactions, and examined climate effects on all the insect outbreak sites using a regional climate reconstruction (Garfin and Hughes 1996). I also sampled four trees for a stem analysis study to determine the effect of pandora moth defoliation on the entire tree. This is the first study to reconstruct a history of past outbreaks of pandora moth and to compare this history with fire and climate histories. This is also the first stem analysis of trees defoliated by pandora moth.

1.4 Area Description

1.4.1 Study Area

The study area is located on the east side of the Cascade mountains in south central Oregon. It is situated on a plateau punctuated by cinder cones. The area is designated by Franklin and Dyrness (1988) as the High Lava Plains Province and the Basin and Range Province. The study area encompasses 3.12 million ha (240 km north-to-south and 130 km east-to-west) (Fig. 1.3) and ranges in elevation from 1320m to 1670m. It includes most of the known range of pandora moth in Oregon, a range

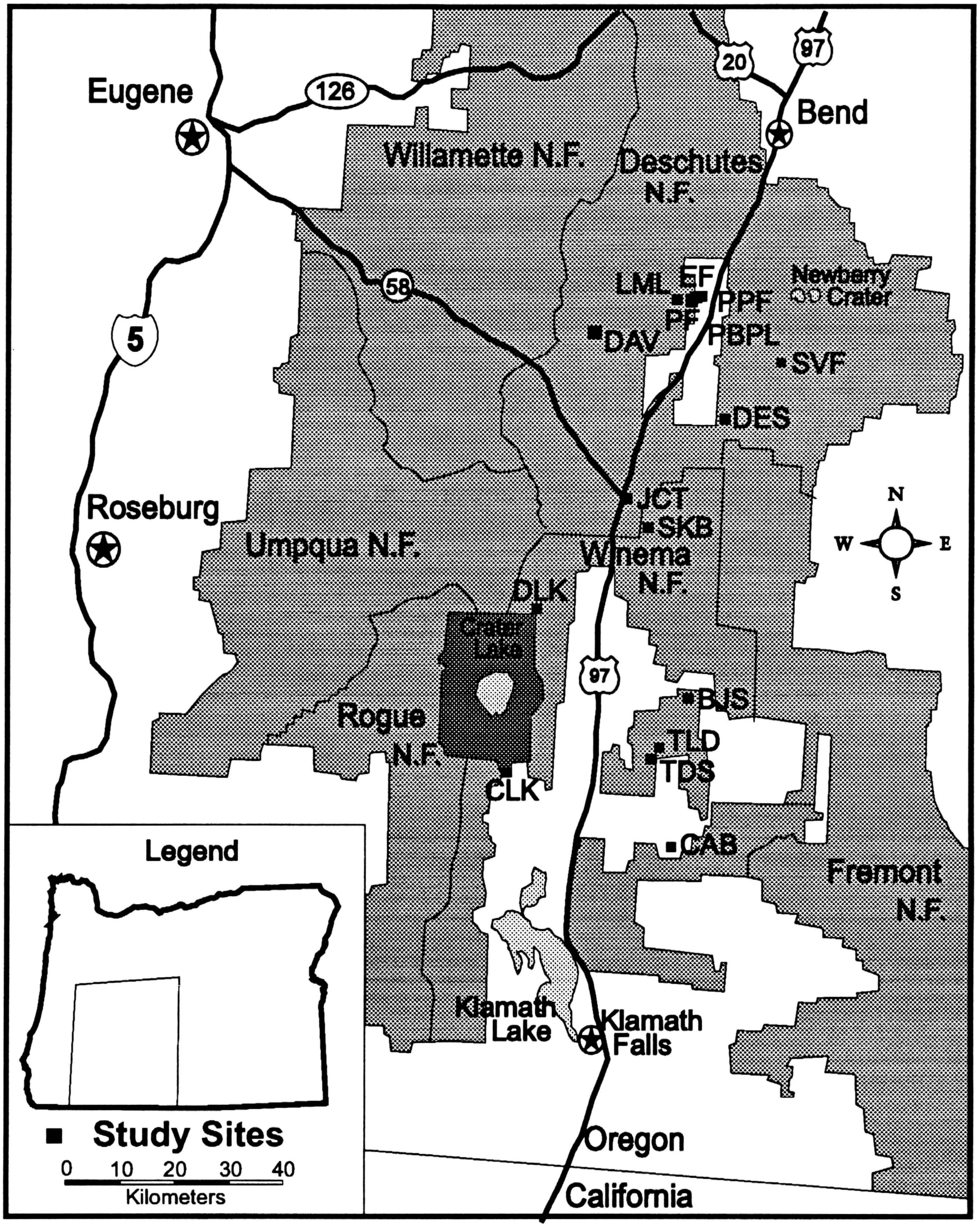


Figure 1.3. Site map for pandora moth project in south Oregon. The field area was on the east side of the Cascade Mountain Range covering a rectangle 240 km by 130 km.

roughly defined by the zone of ponderosa pine and lodgepole pine (pandora moth host species) and the layer of pumice soil deposited by the eruption of Mt. Mazama (Patterson 1929; Massey 1940) (Fig. 1.4).

1.4.2 Geology

The Cascade Range is a chain of volcanic and granitic mountains with active volcanism continuing today. This is evident by the repeated eruptions of Mt. St. Helens between A.D. 1470 and A.D. 1875 and again in A.D. 1980 (Findley 1981; Yamaguchi *et al.* 1990; Yamaguchi 1993; Yamaguchi and Hoblitt 1995). This volcanism has shaped the landscape throughout the Pacific Northwest. Mt. Mazama erupted approximately 6,600 years ago, ejecting a large amount of volcanic ash and pumice that now blankets the east side of the Cascades. This layer varies between 0.5m and 1.0m in thickness atop a basalt bedrock or buried soil layers (Franklin and Dyrness 1988). The volcanic ash and pumice provide a loose porous soil conducive to pandora moth pupation (Patterson 1929; Massey 1940; Carolin and Knopf 1968).

1.4.3 Vegetation

The study sites are dominated primarily by old growth ponderosa pine, with an understory of snowbrush ceanothus (*Ceanothus velutinus* Dougl. ex Hook) or bitter-brush (*Purshia tridentata* Pursh.). Old-growth ponderosa pine stands are now rare on the landscape, due to extensive logging. Lodgepole pine is more frost tolerant than

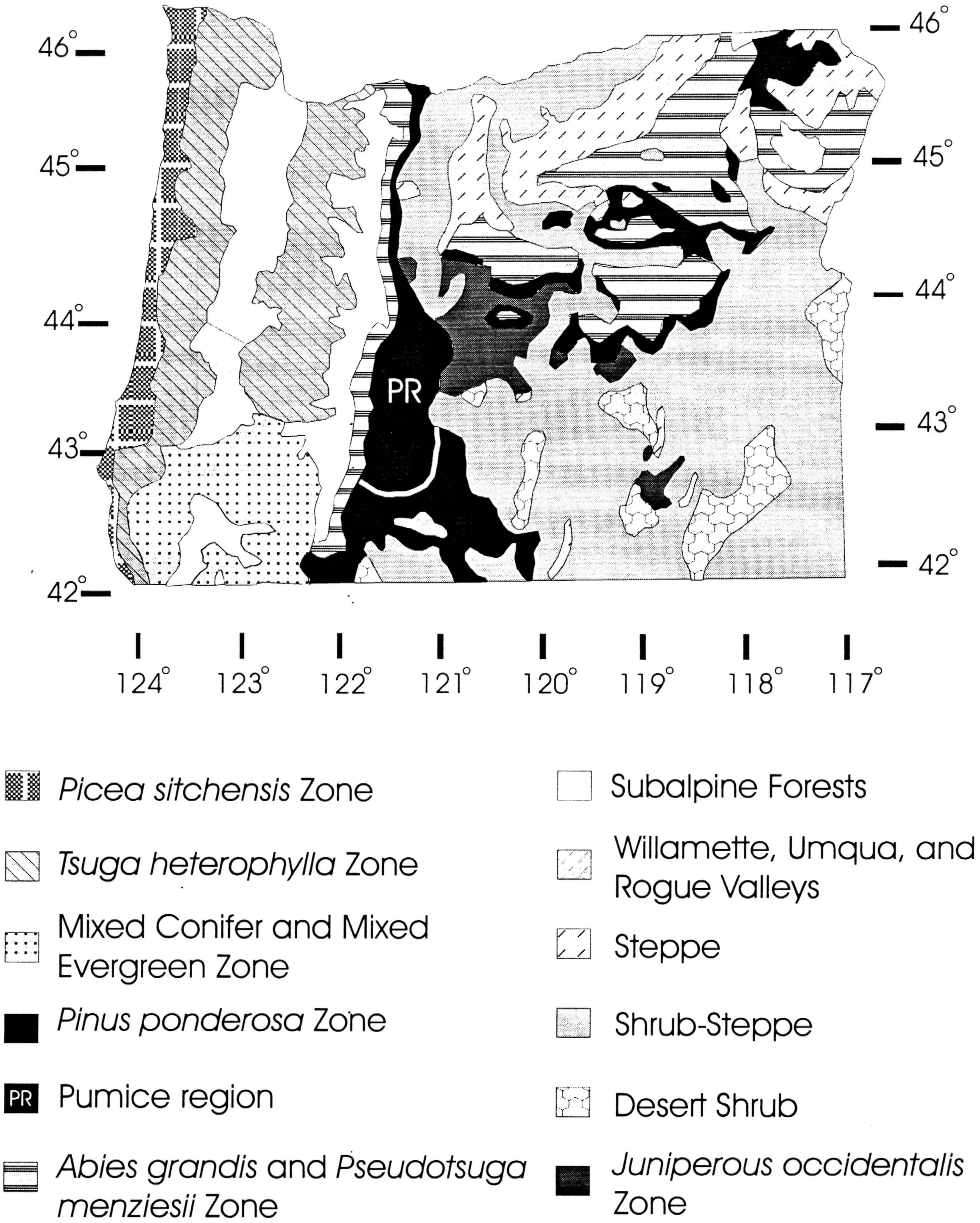


Figure 1.4. Vegetation map of Oregon (adapted from Franklin and Dyrness 1988).

ponderosa pine and, therefore, maintains dominance in cool air drainages where more frequent frosts occur (Franklin and Dyrness 1988). Ponderosa pine stands are found on the hills and ridges emerging from this continuous lodgepole pine forest.

1.4.4 Climate

The climate of the sampled area is semi-arid, relative to the west side of the Cascades mountain range. According to dendroclimatic reconstructions, this area experienced occasional periods of drought, usually lasting from 3 years to 10 years (Keen 1937; Garfin and Hughes 1996). An orographic rainshadow effect from the Cascade Range restricts rainfall to between 500mm and 1,000mm a year, most of which (75 percent) falls in the winter months as snow. July, August, and September are the driest months of the year, receiving about 10 percent of the annual precipitation. June, July, and August are the only months where the average temperature is above 15.6° C (Fig. 1.5). Defoliation by pandora moth in Colorado was found to be negligible when average daily air temperatures dropped below 15.6° C (Massey 1940). Large diurnal temperature fluctuations occur in summer, with hot days and cold nights, and, in many areas, frost may occur any night of the year (Franklin and Dyrness 1988).

Pumice soils effectively retain moisture, providing productive growing conditions for ponderosa pine (Franklin and Dyrness 1988). Persistent snow pack during the winter and snow melt during the spring typically maintains damp soils until June.

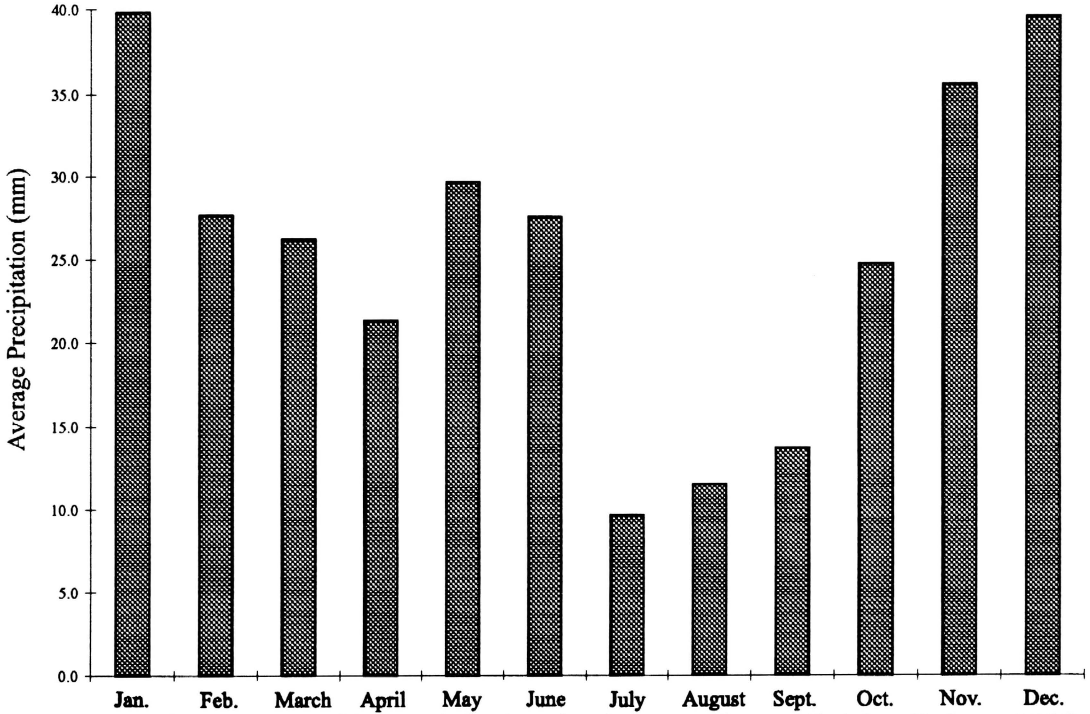


Figure 1.5. Average monthly precipitation for Oregon climate division 7, from 1930 to 1979.

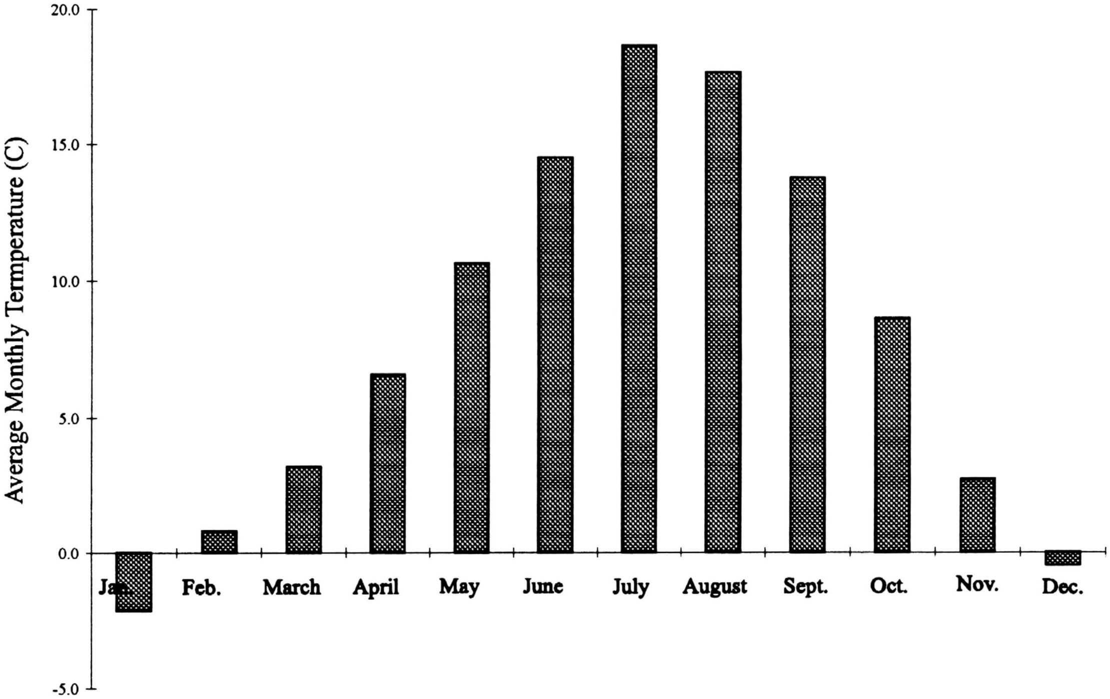


Figure 1.5(Continued). Average monthly temperature for Oregon's climate division 7 from 1930-1979.

Thus, the natural fire season in the central Oregon ponderosa pine forests is restricted to the late summer and fall, the hottest and driest period of the year (Bork 1984; Agee 1993; Heyerdahl and Agee 1996; Wright 1996).

1.4.5 Past Land Use

1.4.5.1 Klamath Indians

Small bands of Paiute and Tenino Indians resided in the Deschutes River Valley prior to the arrival of Euro-American settlers. The Klamath Indians occupied much of the land to the south. Following the wars of the 1850s, Native American groups were confined to reservations (Oliphant 1968). The Klamath Indian Reservation, located in what is now the Winema National Forest, covered 427,393 ha in 1880 (Oliphant 1968). Prior to their confinement on reservations, Native Americans had been hunter-gatherers adept at using whatever resources were available to them. They used fire, for example, to aid in hunting, to improve grasslands, and in warfare (Stewart 1936; Shinn 1978). The Klamath and Paiute Indians used the pandora moth larvae and pupae as a traditional food source when it was available, indicating they had knowledge of its life cycle. This led early forest entomologists to speculate that pandora moth outbreaks had often recurred in the past (Aldrich 1912, 1921; Patterson 1929; Blake and Wagner 1987).

1.4.5.2 Forest Service

The first Euro-Americans to arrive in southern Oregon were trappers in 1825, followed by the first immigrant wagons in 1845. By 1880, settlers were established throughout the Deschutes Valley (Vaughn 1981). On September 28, 1893, President Grover Cleveland withdrew from public domain the original forest land that included the Deschutes National Forest (A. Eglitis, pers. comm.). The forest boundaries have since changed and new National Forests added. Around 1909, logging began near the study area, and the first large mills in Bend were built in 1915 by the Shevlin-Hixon and Brooks-Scanlon Companies (A. Eglitis, per. comm.). Ponderosa pine was, and has remained, the major harvested timber species in the area.

Besides logging, the most significant impact on the study area has been fire suppression. Forest fires had always been a natural occurrence in Oregon pine forests, where forest litter and vegetation provides ample fuel and lightning serves as an ignition source (Agee 1993). During the past 80 years, the Forest Service has been suppressing fire in what was viewed as an effort to stop the destruction of valuable timber and protect public resources. Although successful in achieving these objectives, the practice resulted in unintended consequences creating a buildup of fuels and leaving the system susceptible to catastrophic fires in recent decades (Agee 1993; Mutch *et al.* 1993). Some of the sampled areas are now choked with underbrush and dense thickets of young ponderosa pines. There are few remaining sites with the open stands and grass understory characteristic of presettlement ponderosa pine forests (Weaver 1959, 1961; Glauert and Kunz 1976).

1.4.5.3 Grazing

In 1869, the transcontinental railroad opened northern Oregon's Columbia River Basin to Euro-American settlers. By 1903, almost 700,000 cattle were grazing on Oregon grasslands, a nearly seven-fold increase over the number in 1850. The cattle population peaked in 1971 at 1.6 million head before declining to the present 1.4 million. The number of grazing sheep likewise increased between 1875 and 1903, peaking at 3.6 million head--a more than five-fold increase--before gradually declining to 345,000 head in 1990 (U.S. Dep. of Agriculture 1863-1987; U.S. Dep. of Agriculture 1896-1902; U.S. Dep. of Agriculture 1936-1993).

Cattle and sheep grazing, coupled with fire suppression practices, has also altered the vegetation composition throughout Oregon. Grazing reduces the fine fuels that support efficient fire spread (Savage and Swetnam 1990; Agee 1993; Belsky and Blumenthal 1997). The resulting lack of fires allows shrub species to dominate grasses and shade tolerant trees to out-compete mature ponderosa pine stands (Leopold 1924). Fire history studies have shown that wildfires in Oregon ceased around the turn of the century, coincident with the introduction of large scale grazing (Bork 1984; Heyerdahl and Agee 1996; Wright 1996). This same spatio-temporal pattern has also been found in numerous fire history studies of the Southwestern United States (Baisan and Swetnam

1990; Savage and Swetnam 1990; Grissino-Mayer and Swetnam 1995) and the Sierra Nevada of California (Swetnam 1993; Caprio and Swetnam 1995). In these areas, cessation of widespread natural fires typically occurred two or more decades before the beginning of government organized fire suppression practices, but closely coinciding with the advent of intensive livestock grazing.

CHAPTER 2

BACKGROUND

2.1 Dendrochronology and Crossdating

Dendrochronology was developed by A.E. Douglass, founder of the first laboratory entirely devoted to tree-ring research at the University of Arizona (Robinson 1990). Douglass's initial interest was the impact of solar cycles on the Earth's climate. While working in Flagstaff, Arizona, he noticed a distinct annual ring pattern in the stems of many ponderosa pine trees, a repeated signature of narrow and wide rings. This now famous pattern, which Douglass subsequently found in trees throughout the region, became known as the Flagstaff signature. Ring-width patterns enable dendrochronologists to precisely and accurately date every individual tree ring in a chronology (Stokes and Smiley 1968; Fritts 1976).

When all trees on a site are limited by a common factor, such as inter-annual variability in climate, the size of their annual growth rings is affected in a similar manner, and a common ring-width pattern emerges across the site or region (Douglass 1941; Stokes and Smiley 1968; Fritts 1976). Crossdating; *i.e.,* matching the ring patterns in tree-ring samples across a site, can provide a reliable chronological record of the natural history of the stand. As a result, dendrochronology is the most accurate tool available for dating natural phenomena in forest systems; among other applications, it has been used to date archeological ruins (Douglass 1935; Dean 1978), treeline fluctuation

(LaMarche 1973; Lloyd and Graumlich 1997), fire scars (Dieterich and Swetnam 1984; McBride 1983), and insect outbreaks (Wickman 1963; Brubaker and Greene 1978; Swetnam *et al.* 1985; Hadley and Veblen 1992; Swetnam and Lynch 1993; Wickman *et al.* 1994; Swetnam *et al.* 1995). It can also provide an annual record of climate in any place having dateable tree-rings (Fritts 1976), thereby enabling dendrochronologists to compare multiple processes and patterns in the ecosystem, such as climate, insect outbreaks, and fire.

2.2 Tree-ring Reconstructions of Other Defoliating Insects

Outbreaks of phytophagous insects can cause reduced radial growth in forest trees through severe defoliation. By applying dendrochronological methods to the study of defoliating forest insects, particularly western spruce budworm and Douglas-fir tussock moth, researchers have identified defoliation-related ring-width suppressions produced by peak insect populations (Wickman 1963; Koerber and Wickman 1970; Brubaker and Greene 1978; Wickman *et al.* 1980; Swetnam *et al.* 1985; Swetnam and Lynch 1989, 1993; Swetnam *et al.* 1995; Weber and Schweingruber 1995).

Calibration of the tree-ring record with historical documentation of past insect outbreaks has been very helpful in determining the insect's effects on the trees (Brubaker and Greene 1978; Wickman *et al.* 1980; Swetnam *et al.* 1985; Wickman *et al.* 1994). Comparisons of ring patterns during periods of known outbreaks in a study area can identify a tree-ring signature specific to that insect species. By examining the defoliation effects of tussock moth and spruce budworm in the same tree, researchers have in some cases been able to differentiate between the signature of the two species and subsequently document past outbreaks of each species (Brubaker and Greene 1978; Wickman *et al.* 1994; Mason and Wickman 1997). Douglas-fir tussock moth produced a 4 to 5 year signature of sharply reduced growth, while the western spruce budworm entailed a more gradual but longer outbreak periods (often 10 years), leaving a signature of less abrupt but more persistent growth reduction (Wickman 1963; Brubaker and Greene 1978). This aptly demonstrated the effectiveness of dendrochronology in identifying specific ring signatures for phytophagous insects throughout the length of the tree-ring chronologies. Although western spruce budworm and Douglas-fir tussock moth create different signatures, they cannot always be differentiated in trees and stands that were defoliated in the past by both species. This is especially true when the outbreaks of the two species occurred simultaneously or closely spaced in time (Swetnam *et al.* 1995).

Reduction in tree growth reflects the period when defoliation significantly impacts tree health and does not usually begin precisely with the onset of the insect population's increased growth (Swetnam and Lynch 1993; Mason and Wickman 1997). Stored food reserves can delay defoliation-induced growth loss by one or more growing seasons (O'Niell 1963; Kulman 1971; Brubaker and Greene 1978; Wickman *et al.* 1980; Mason and Wickman 1997). Since a tree requires time to replace lost foliage following severe defoliation, its growth may be inhibited for several years after the insect populations have crashed (Duff and Nolan 1953; Mott *et al.* 1957; Wickman 1963;

Brubaker and Greene 1978; Wickman *et al.* 1980; Alfaro *et al.* 1984; Lynch and Swetnam 1992).

Researchers have developed techniques for differentiating climate-related ring-width suppressions in the host trees from those produced by some species-specific factor, such as defoliation (Wickman 1963; Koerber and Wickman 1970; Brubaker and Greene 1978; Swetnam *et al.* 1985). Variations of this technique have been developed and widely-tested in studies of the western spruce budworm (Brubaker and Greene 1978; Swetnam *et al.* 1985; Swetnam and Lynch 1993; Wickman *et al.* 1994; Swetnam *et al.* 1995; Weber and Shweingruber 1995). In the Swetnam *et al.* 1985 approach, a non-host "control" tree species is collected from the same or an adjacent site as the host species and its tree-ring chronology compared to the host chronology. The common “signal” can be then subtracted from the host chronology, thereby isolating the species-specific factors for further study. However, some error (or “noise”) may be introduced into the analysis due to differing responses to climate between the host and non-host tree species (Swetnam *et al.* 1985).

The outbreak history of an insect can be further understood by determining if the outbreaks are episodic or periodic. When outbreaks occur due to some triggering factor that is not cyclical, the outbreaks can be termed episodic. Conversely, if the outbreaks occur with regular cyclic behavior, they are termed periodic. Episodic outbreaks are likely to be triggered by some exogenous factor such as climatic conditions that provide an advantage for the insect (Koerber and Wickman 1970; Mason and Wickman 1988).

Koerber and Wickman, in their examination of climatic factors (1970), hypothesized that warm dry conditions, by increasing larvae feeding activity and depressing the activity of disease organisms, may lead to insect outbreaks. Larvae, being cold blooded, may increase their activity and feed more heavily on warmer days, thereby enhancing survivorship and speeding up their life cycle. Additionally, viral agents may be slower to develop and spread through the insect population, thereby delaying larvae mortality (Koerber and Wickman 1970).

The chemical ecology of the host trees also responds to climatic variables in ways that may trigger episodic insect outbreaks. Dry climatic conditions can induce stress, making host trees less able to defend themselves with naturally produced terpenes (Cates *et al.* 1983; Thomson *et al.* 1984; Kemp *et al.* 1985; Mason and Wickman 1988). Stressed plants appear to have higher food quality, probably due to greater amounts of soluble nitrogen and carbohydrates or reduced defensive secondary compounds (White 1976; Matson and Haack 1987a,b). Although cambium feeding insects typically favor stressed trees, phytophagous insects sometimes have a weak or even negative response to stressed trees (Matson and Haack 1987b; Larsson 1989). Furthermore, long records (*ca.* 300 years) of spruce budworm outbreaks in New Mexico, when compared to precipitation reconstructions, show a consistent relationship between the beginning of outbreak episodes and high precipitation in spring and early summer (Swetnam and Lynch 1993). If a climatic trigger can be reliably associated with specific insect outbreaks, it could provide a means for predicting outbreaks, as well as provide insight into a controversial issue of which climate conditions are more favorable for defoliating insects.

Periodic outbreaks are likely due to processes intrinsic to the system such as nutrient cycles, predator-prey interactions, and delayed density dependent responses (Clendenen *et al.* 1978; Haukioja 1980; Berryman 1983; Hassell 1985; Mason and Wickman 1988). Clendenen *et al.* (1978) found just such a cyclic phenomenon in outbreaks of tussock moth, which occur every 8 to 9 years in the interior Pacific Northwest. A density dependent argument for cycles in outbreak occurrence holds that growth of the insect population will be limited by a superabundance of individuals. One mechanism of density dependence is that extreme populations will completely defoliate the trees, thereby creating a shortage of food (Mason and Wickman 1988). Given the improbability of instantaneous population response to this feedback mechanism, oscillation in population will likely occur (Hassell 1985; Mason and Torgensen 1987). Insect population oscillations can also occur as a result of interaction with a destructive virus, in which case the system would manifest a predator-prey type of oscillation. Thompson (1978) argues that, although virus-caused diseases are commonly associated with the decline of an outbreak, they are usually triggered suddenly in stressed populations rather than built up gradually in a density-dependent situation. Climate has also been noted to be weakly cyclical (Fritts 1976; Grissino-Mayer 1995). It is possible that such weak climate cycles could also entrain the cyclical insect outbreak system if the periods of the two cycles are similar (Swetnam and Lynch 1993). This could be an example of a higher order process (climate) entraining a lower order process (Holling 1993)

Many spruce budworm studies, having noted an increase in severity and synchrony of outbreaks during the 20th century (Blais 1983; Carlson *et al.* 1985; Fellin *et al.* 1983; Swetnam *et al.* 1985; Swetnam and Lynch 1989; Wickman 1992; Hadley and Veblen 1993; Wickman *et al.* 1994; Swetnam *et al.* 1995; Weber and Schweingruber 1995), postulate an increase in forest vulnerability due to past harvesting and fire control practices, insecticide use, and logging. These practices create dense multiple-storied stands with higher densities of shade tolerant tree species favored by spruce budworm. Such changes in forest composition could inversely affect pandora moth outbreaks. Because ponderosa pine, a major timber species, is the main host of pandora moth, its removal through logging may decrease food availability and continuity for pandora moth across the landscape. In the Blue Mountains of Oregon, Wickman *et al.* (1994) found, for the period between 1936 and 1960, commercial ponderosa pine acreage decreased from 80% to 40% of all commercial holdings. Stand fragmentation by roads, logging, and other development might also retard spread of pandora moth. Therefore, if stand species composition and continuity is a factor in pandora moth dynamics, we would hypothesize that 20th century pandora moth outbreaks would be smaller and less severe than prior outbreaks.

The possible interactions between an insect population and its environment are many, varied, and potentially complex. Long-term records of insect outbreaks would allow researchers to study such interactions over time scales much longer than single outbreak cycle of the insect. Examination of multiple outbreaks could provide opportunities for improved understanding of these important ecosystem processes.

2.3 Life History & Ecology of Pandora Moth

Pandora moth has a two-year life cycle that begins in July and August of the first year when the females lay their eggs. The larvae hatch in late August and September and begin to feed on the mature needles of the host trees, usually avoiding new foliage or buds. The larvae over-winter at the base of the needles during the second instar. With the arrival of warm conditions in spring (March and April), the larvae resume feeding on the foliage, reaching up to 6 cm in length by summer. In June and July, the caterpillars move down the trunk of the tree, burrow into the soil, and pupate. The pupae remain in the soil for their second winter, finally emerging as moths in late June or July to continue the cycle (Patterson 1929; Massey 1940; Carolin and Knopf 1968; Fitzgerald 1992). Some pupae can go into extended diapause and emerge on the third year (Carolin and Knopf 1968).

Pandora moths are preyed upon by many different organisms. Squirrels eat the pupae and moths, bears eat the pupae, and birds eat the caterpillars and eggs (though the caterpillars are not a favored food source of the birds). Parasites infest both larvae and eggs (Patterson 1929; Massey 1940; Schmid and Bennett 1988). The main mortality agent, however, may be a nucleopolyhedrosis virus that kills mature caterpillars

(Patterson 1929: Massey 1940; Wygant 1941; Carolin and Knopf 1968; Blake and Wagner 1987; Schmid and Bennett 1988; Wickman *et al.* 1996). When the virus is active, larvae can be observed hanging limp at the ends of branches. The spread of the virus is thought to be density-dependent, occurring when the population of pandora moth is sufficiently large to cause increased contact between larvae.

Extremes in temperature greatly affect pandora moth. The pupae cease to feed at temperatures below 15.6° C (Massey 1940; Schmid and Bennett 1988), and extremely cold weather may kill many caterpillars during their first winter (Massey 1940). High soil temperatures, such as those created by fire, can kill the pupae in the ground (Massey 1940), although Schmid and Bennett (1988) found that prescribed burns resulted in negligible mortality of pandora moth pupae.

Soils conditions are also a factor in Pandora moth outbreaks: pandora moth prefers areas with weathered granite or pumice soil, which are loose enough to permit the larvae to easily burrow into them (Patterson 1929; Massey 1940; Carolin and Knopf 1968; Furniss and Carolin 1977). In the absence of such soils, the larvae may die before finding a suitable place for pupation, preventing a population from attaining sufficient momentum for outbreak on that site. Without such soils even endemic populations are rarely sustained therefore soils seem to determine the distribution of pandora moth.

2.4 Pandora Moth Studies

Two studies have shown that defoliation of ponderosa pine trees by pandora moth caused suppressions in tree-ring widths (Patterson 1929; Miller and Wagner 1989). In their study of the 1978 outbreak on the Kaibab plateau in northern Arizona, Miller and Wagner (1989) found the 1980 ring to be present on all non-defoliated trees, but missing in 83% of heavily defoliated and 24% of moderately defoliated trees. On average, studies have found only 2% mortality of mature trees in stands associated with pandora moth defoliation, since new needles and buds were not eaten (Patterson 1929; Massey 1940; Bennett *et al.* 1987). However, subsequent bark beetle infestations of weakened trees may cause mortality (Patterson 1929; Schmid and Bennett 1988).

Most pandora moth studies have focused on modern outbreaks to better understand the insect's behavior and environmental impact for immediate management purposes (Miller and Wagner 1984; Schmid and Bennett 1988; Wickman *et al.* 1996). Based on interviews with Native Americans and direct observations of a few historical outbreaks, entomologists have estimated that outbreaks were typically 6 to 8 years in duration and occurred approximately every 20 to 30 years (Patterson 1929; Massey 1940; Coulson and Witter 1984). Given the considerable age of ponderosa pine stands where mature trees may survive 4-6 centuries and the estimated time between outbreak periods, these historical records encompass a comparatively short period (the past 100 years), with only three or four outbreak episodes.

The closely-observed Kaibab Plateau outbreak in northern Arizona, which lasted from 1978 to 1984, provided forest managers and researchers an opportunity to test pandora moth control techniques as well as document the activity of the insect (Schmid *et al.* 1981; Schmid *et al.* 1982; Schmid and Bennett 1988; Miller and Wagner 1989). Researchers tested the effect of pesticides, observed the distribution of egg masses, and evaluated the efficacy of fire in killing pupae. Schmid and Bennett (1988) concluded prescribed burning produced too low mortality of the pupae to justify it as an efficient control technique. Pesticides were also found to be ineffective at ending the outbreak. In all studies, natural biological agents ended the outbreaks, making artificial control unnecessary (Massey 1940; Carolin and Knopf 1968; Schmid and Bennett 1988).

Although the detailed observations and experiments on modern outbreaks are informative, they do not evaluate patterns and processes occurring over long time scales. Long-term reconstruction of past fires at pandora moth outbreak locations would provide a better understanding of fire-insect interactions and the possible effectiveness of fire as a control technique. Furthermore, a precise determination of the degree to which pandora moth defoliation inhibits tree growth would enable evaluation of the cost effectiveness of control techniques relative to reduced forest productivity and wood "loss" due to outbreaks.

2.5 Confounding Factors in Determining Insect Outbreaks

The rate of radial growth in trees, reflected in the width of tree rings, will vary with the quality and quantity of nutrients provided by photosynthesis in the needles and raw materials brought in through the roots. Narrow rings can result from either a lack of photosynthetic potential, due to foliage loss, or a deficit in the supply of water or soil-derived minerals (Koerber and Wickman 1970; Fritts 1976). Because the width of the tree ring is dependent upon the factor most limiting to tree growth, ring-width thus serves as a measure of these parameters. Any process that disturbs this food cycle, such as climate, or physical damage by other insects or fire, can suppress ring-width. Such confounding factors must be considered when attempting to deduce pandora moth outbreaks from the tree-ring record.

2.5.1 The Role of Climate

Climate is an exogenous process that affects tree growth over large areas and can therefore coordinate responses in an ecosystem (Fritts 1976). Climatic effects on tree vigor can be accounted for in dendrochronological studies of insect outbreaks by using a non-host chronology for direct ring-width comparison. It is not feasible, however, to apply this technique in all habitats. Ponderosa pine often grow in pure stands, and a non-host tree species may not be available for control. Miller and Wagner (1989) used ponderosa pine trees from nearby unaffected stands as a climatic control. This technique is only applicable to a modern outbreak, where larvae populations can be directly observed and the absence of larvae in the control stand reliably confirmed. For past outbreaks, researchers cannot discount the possibility of past low levels of insect infestation affecting tree growth in nearby stands selected as controls.

Dendrochronology has been used very successfully to reconstruct, over long periods of time, the annual values of precipitation and temperature in a climatic region. Tree-ring records from a network of sites in a given climatic region are compared to climate records for the 20th century (Fritts 1976; Graumlich 1987; Meko *et al.* 1993; Garfin and Hughes 1996). From this long-term reconstruction, drought periods can be identified throughout the length of the tree-ring record (Meko 1991). Therefore, it should be possible to use a regional climate reconstruction to control for drought effects in the insect outbreak sites. Garfin and Hughes (1996) reconstructed precipitation back to A.D. 1705 as a companion project to this research. The reconstruction was based predominantly on western juniper (*Juniperus occidentalis* Hook.) trees growing throughout south-central Oregon. Western juniper is not a host for pandora moth. This climate reconstruction will be used to evaluate the effects of climate versus pandora moth defoliation on the ring-width pattern in ponderosa pine trees. Although different tree species have somewhat different climatic responses (Fritts 1976), it is likely that severe and multiple-year droughts (which could be confused with defoliation episodes in pine) will be evident in both pine and juniper.

2.5.2 Other Insects

Approximately 200 insect species utilize ponderosa pine trees as a host, 60 of these specifically affect the foliage (Schmid n.d.). The three major defoliators of ponderosa pine are pine butterfly (*Neophasia menapia* Felder and Felder), sawfly (*Neodiprion* and *Zadiprion* spp.), and pandora moth (Schmid n.d.), but only pandora moth and pine butterfly could have caused enough damage to greatly suppress radial growth in the Pacific Northwest. Pine butterfly, which has a one-year life cycle, appears to prosper in colder climate regions than pandora moth, having been observed at the snow line of Mt. Hood and in the Blue mountains of Oregon, but not in southern Oregon (Hopkins 1908; Cole 1971). It defoliates both Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and ponderosa pine, causing ring-width suppressions during its outbreaks similar to those of pandora moth (Evenden 1940). The entomologist for the Deschutes National Forest and other research entomologists have never observed pine butterfly outbreaks in this area (Wickman and Eglitis, pers. comm.). Thus, lack of 20th century observations of pine butterfly and sawfly in the study area suggests these insects probably did not occur here in the past, but this remains an assumption of this study.

2.5.3 Fire History

Fire can cause injury through scorching the needles or directly damaging the tree stem or roots by heating the cambium to lethal temperatures. The resulting damage is capable, in come cases, of suppressing tree growth for many years (Sutherland *et al.*

1991; Mutch 1994; Peterson *et al.* 1994). Since this phenomena has been observed in some fire history studies (Bork 1984), it is important that this study not incorrectly attributed fire-related growth suppression to pandora moth outbreaks. Thus, the ring-width pattern associated with fire scars was examined in one of the studied stands to establish the effect of fire on ponderosa pine growth.

Fire could interact with pandora moth in several possible ways: (1) fire could trigger insect outbreaks by stressing and consequently weakening the host trees (*i.e.*, the stress hypothesis); (2) fire could suppress or extinguish an insect outbreak by killing a substantial number of the pupae while they over-winter in the soil or by heat/smoke effects on feeding larvae; or conversely (3) pandora moth could alter the fire regime by interrupting needle fall, thereby removing this fine fuel component needed for fire spread. Finally, fire may have no detectable effect on the tree-ring structure and/or no interaction with pandora moth outbreaks.

A fire history reconstruction on a host site will help determine what role fire plays in the pandora moth-fire system. Such studies quantify the fire type (*i.e.* ground, surface or stand replacing fire regimes), frequency, and seasonality of a given fire regime (Heinselman 1981). Surface fire regimes are common in ponderosa pine forests (Wright and Bailey 1982; Bork 1984; Agee 1993), with fires frequently burning through stands at low intensities, removing forest litter but not destroying mature trees. The past occurrence of surface fires can be reconstructed by obtaining fire-scarred specimens from stumps, logs, snags, and living trees. A surface fire scars trees by killing the cambium on an area of the trunk close to the ground. Once this initial wound is formed, without its protective bark covering, it is likely to re-scar in subsequent fires. Thus, after a tree is scarred the first time, it can become a consistent recorder of even very low intensity fires (Arno and Sneck 1973; Dieterich and Swetnam 1984; Baisan and Swetnam 1990).

In addition to accurate calendar dates achieved through crossdating, scar position within the ring can be used to estimate the season of past fires (Dieterich and Swetnam 1984; Baisan and Swetnam 1990; Orloff 1995). A scar in the early, middle, or late part of the earlywood was formed in the beginning or middle portion of the growing season, while a scar in the latewood occurred at the end of the growing season. Scars located between the latewood cells of one ring and the earlywood cells of the next formed during the tree's dormant season, *i.e.*, during either the late summer and early fall of one year or the spring of the following year.

With knowledge of cambial phenology for a specific area and tree species, it is possible to use the position of the fire scar within the ring to deduce the actual time (within approximately a month) that the fire occurred. During the summer of 1995, Wright (1996) made a set of observations at the Teanaway River drainage in central Washington, coring a set of ponderosa pine trees every two weeks to track the growth of that year's annual ring. By mid-June to late July, the earlywood had begun to grow. The earlywood was formed during the month of August, and, within a week of September 1, the latewood started to form. The tree entered dormancy in mid- to late September. (Wright notes that, since his study was limited to only one growing season, replication of the study in other years would help identify year-to-year variability in cambial phenology.) Wright found that the boundary between earlywood and latewood defines the beginning of the main fire season in his study area, with more than 80% of the fire scars occurring after this boundary. According to Agee (1993), the relatively wet winter and spring weather in the Pacific Northwest, followed by extended summer drought conditions, restricts the typical fire season to late August and September. In the Cascades, abundant snow during the winter and snow melt in the spring and summer keep fuels moist until late summer.

As a result, most fire scars in the region occur in the latewood portion of the annual ring. It is reasonable to infer that most dormant season scars occurred in the fall and to assign them to the calendar year of the adjacent latewood cells (Agee 1993; Wright 1996). A similar convention has been followed in the Sierra Nevada of California (Caprio *et al.* 1995) and far northern California (Brown and Swetnam 1994). This contrasts with the convention in the Southwestern United States of assigning the dormant season scar to the calendar year of the adjacent earlywood cells (*i.e.* the spring of the following year) (Swetnam and Baisan 1990). In the Southwest, the spring and early summer are relatively dry, while the late summer is characterized by monsoon storms, which bring a large portion of the total annual precipitation. Consequently, fires in the Southwest occur predominantly in the spring or early summer and most dormant season scars are formed during this time.

2.6 Stem Analysis

Potential wood volume increases of a forest stand can be reduced during insect outbreaks through both mortality of the host trees or suppression of radial growth. Pandora moth outbreaks typically cause almost no loss due to mortality. However, the amount of volume reduction due to the effects of defoliation can be quite substantial and should be considered in the management of ponderosa pine forests in affected areas (Massey 1940; Wickman 1963; Koerber and Wickman 1970). Growth loss during outbreaks may be offset by a growth increase after the insect population has crashed, a phenomenon observed with spruce budworm and Douglas-fir tussock moth outbreaks (Wickman 1980; Alfaro *et al.* 1985; Swetnam and Lynch 1993). This effect may be attributable to factors such as reduced competition among trees for resources and nutrient cycling associated with frass accumulation.

Stem analysis has been used extensively to investigate the effects of insect defoliation on growth allocation. The standard technique, with refinements by Duff and Nolan (1953 and 1957), involves taking multiple cross-sections along the stem of the tree. Duff and Nolan (1957) and LeBlanc (1990) suggested a section midway between each internode to allow for quantification of height and radial growth in every year. For trees a few centuries in age, it is very difficult or impossible to identify internodes on the external surfaces of the main stem. Thus, with increasing age it becomes impractical to determine all of the height increments. LeBlanc *et al.* (1987) note the added accuracy in determining the overall tree response to disturbance, but mentioned the added effort might preclude widespread application of stem analysis. They also mentioned the added difficulty when studying older/larger trees.

The amount of radial growth reduction from insect defoliation can vary throughout the bole of the tree. Greater growth reduction in the crown of the tree, where the defoliation actually occurs, has been documented with spruce budworm and Douglas-fir tussock moth outbreaks (Mott *et al.* 1957; Wickman 1963; Koerber and Wickman 1970; Alfaro *et al.* 1985). It is also theoretically possible that the growth reduction could be greater at the base of the tree, furthest away from the site of auxin (a growth hormone) production (Onaka 1950; Fritts 1976). Understanding the effect of defoliation on radial growth throughout the tree will enable us to determine whether measurements of cores taken at breast height are a good representation of the overall growth reduction in ponderosa pine stems.

Several researchers have used stand projection and prognosis models to quantify wood volume reduction from insect defoliation and its impact on forest growth and yield (Watt 1964; Wycoff *et al.* 1982; Beveridge and Cahill 1984; Maclean and Erdle 1984; Nichols 1984). Wood volume production under normal conditions was compared to production under conditions of episodic defoliation by insects. Maclean and Erdle (1984) found that severe defoliation by spruce budworm caused 46% to 64% volume reduction in the maximum sustainable harvest. A model of this type, which could evaluate the effect of pandora moth outbreaks on yields from ponderosa pine forests, has not yet been developed. Accurate volume reduction estimates for individual trees may assist in development of such a model.

CHAPTER 3

METHODS

3.1 Introduction

Remnant stands of old-growth ponderosa pine trees, a rarity in central Oregon, were located through discussions with foresters and B. Wickman. Tree-ring cores were collected from a total of 24 sites. B. Wickman collected samples at the Crater Lake (CLK) site in 1992 and, with G. Paul, the Pringle Falls (PF), Experimental Forest (EF), and Pringle Prescribed Fire (PPF) sites in 1994; these were chosen to determine if pandora moth produced a consistent ring-width signature, which would make a broader scale study feasible. The Pringle Butte Sugar Pine (PBPL) site was also sampled in 1994 to determine its potential as a non-host species in tree-ring comparisons with ponderosa pine. An additional 11 pandora moth sites were located and sampled in the summer of 1996. Fire-scarred crossections were also collected at the Pringle Falls site to investigate fire effects within this stand. Finally, four dominant wind-thrown ponderosa pine trees in the Research Natural Area (RNA) of Pringle Butte were sampled to examine the effect of defoliation by pandora moth on the entire tree (Table 3.1).

3.2 Insect Outbreak Site Collections

3.2.1 Site Description

Each of the 14 insect outbreak sites was a disjunct stand of old-growth ponderosa pine, covering 5-10 ha (sites are listed in Table 3.2, beginning with the northernmost and

Table 3.1. Tally of all sites collected for the pandora moth project. Over all 187 trees were sampled with some of these cross sections for fire history and stem analysis. Otherwise two cores were taken per tree.

Site Name	Number of Trees	Tree Species	Type of Chronology	Inner Date	Outer Date
EF	12	PIPO	Host	1333	1993
LML	12	PIPO	Host	1528	1995
BJS	13	PIPO	Host	1422	1995
DES	11	PIPO	Host	1574	1995
DLK	12	PIPO	Host	1512	1995
SKB	12	PIPO	Host	1639	1995
CAB	10	PIPO	Host	1652	1995
CLK	12	PIPO	Host	1572	1990
TLD	10	PIPO	Host	1493	1995
TDS	07	PIPO	Host	1450	1995
SVF	05	PIPO	Host	1746	1995
JCT	12	PIPO	Host	1412	1995
PF/RNA	19	PIPO	Host/Stem Analysis	1504	1993
PPF	40	PIPO	Host/Fire History	1329	1991
TOTAL	187				

Table 3.2. Site names and descriptive characteristics.

Site Name	Designation	Longitude	Latitude	Elevation
Lookout Mountain Lower	LML	121 39’00”	43 45’30”	1320m
Pringle Falls Prescribed Fire	PPF	121 39’00”	43 44’00”	1320m
Experimental Forest	EF	121 36’30”	43 43’00”	1530m
Pringle Falls	PF/RNA	121 37’00”	43 42’00”	1460m
Surveyor Flow	SVF	121 18’30”	43 37’00”	1550m
Deschutes	DES	121 24’00”	43 28’00”	1420m
Junction of Roads 51 and 97	JCT	121 45’00”	43 19’00”	1420m
Skookum Butte	SKB	121 39’00”	43 14’30”	1670m
Diamond Lake	DLK	121 57’30”	43 05’30”	1510m
Blue Jay Spring	BJS	121 32’00”	42 55’00”	1490m
Telephone Draw	TLD	121 37’00”	42 56’30”	1550m
Telephone Draw South	TDS	121 31’00”	42 45’30”	1550m
Crater Lake	CLK	122 04’00”	42 47’00”	1370m
Calimus Butte	CAB	121 32’00”	42 38’00”	2020m

moving southward). All sites had a brush understory (*e.g. Ceanothus velutina* and *Purshia tridentata*) and a thick accumulation of litter except the RNA and PPF sites which had been recently burned under prescription. The overstory was mainly ponderosa pine, with occasional sugar pine or lodgepole pine. Many saplings and young trees were growing on most sites. Most of the stands generally comprised an "island" located within a contiguous lodgepole pine forest, with the exception of the mixed conifer CLK site. Older trees, identifiable by their large size, platy bark, and heavy limbs, were sampled to obtain the longest possible tree-ring chronology (Fig. 3.1). Every site was blanketed with a loose pumice soil.

3.2.2 Field and Laboratory Methods

Cores were collected from a minimum of 10 dominant ponderosa pine trees at each site. Two increment cores were taken at breast height on opposite sides of each tree, with general information about site and tree characteristics noted on sample cards. All cores were oven-dried for 24 hours, then mounted with white glue on prefabricated wood core mounts, taking great care to vertically align the tracheids. Once dried, the cores were sanded with a belt sander using a series of increasingly finer grits (180, 220, 320, 400), producing a well-polished surface on which the cellular structure of the wood could be observed (Stokes and Smiley 1968; Swetnam *et al.* 1985). The cores were then crossdated by identifying key features (*i.e.* narrow rings and thin latewood boundaries) in the wood.

Figure 3.1. Characteristics of an old growth ponderosa pine tree. There are large plates of bark, heavy limbs, and a spike top. Photograph taken at the JCT site.

Using the skeleton plot crossdating technique (Stokes and Smiley 1968), I developed a master chronology that recorded all of the narrow rings in the tree-ring series. Calendar dates were then marked on the specimens with pinprick holes for decades and centuries. After measuring all tree-rings to the nearest .01 mm, I verified the dating with the COFECHA program (Holmes 1986). COFECHA partitioned the series into 50-year segments and statistically searched for dating and measuring errors in every tree-ring series. Cross correlation is the primary statistical method used by COFECHA. Each segment was compared against a master chronology composed of all cores excluding the core being tested. If a low correlation existed between a series and the master, COFECHA flagged the questionable segment and suggested an alternate dating position, if one existed. Dating errors were typically only +/- 1 or 2 years over fairly short intervals, while measurement errors consisted of an occasional ring with a spurious measurement value. Once these corrections were made and verified by visual re-examination of the cores, crossdating and measurement accuracy was ensured.

The dated ring-width series were entered into the program ARSTAN to standardize the series (Cook and Holmes 1985). ARSTAN uses linear, negative exponential, and spline-fitting routines to remove growth trends and long-term fluctuations specific to individual trees. Because historical information suggested that pandora moth outbreaks lasted for less than 12 years, I retained 100% of the signal that was 12 years or less. I chose a 40-year cubic spline that retained 99% of the variance at 13 years and 50% of the variance at 40 years. Index values for each series were determined by dividing the actual ring-width value by the value of the fitted cubic spline. ARSTAN then used a mean value function to calculate annual averages for each year for all cores within each site. These indices were plotted and examined, then subsequently used as input for the program OUTBREAK.

OUTBREAK (Holmes and Swetnam unpublished; Swetnam *et al.* 1995) provides a means to automate outbreak identification and to quantify the amount of growth reduction for each outbreak, permitting the operator to specify and subsequently refine the parameters, or criteria, for outbreaks. Prior to running the program, the wood was examined to assess the effects of defoliation by pandora moth on the ring-width pattern. A review of historical data for all known pandora moth outbreaks in Oregon documented four outbreaks occurring around 1893, 1918-1925, 1963-1968, and 1988-1996 (Patterson 1927; Keen 1937; Carolin and Knopf 1968; Wickman pers. comm.). I compared these with the timing and duration of ring-width suppressions at the sites recording these outbreaks and was able to identify the typical ring-width signature associated with pandora moth defoliation. This signature was then used to infer past outbreak occurrences throughout the chronology by assigning values to parameters (described below) in the OUTBREAK program. The program flagged as outbreak periods those sections meeting the given parameters. The dates of the suppressions due to outbreaks, which had been determined from visual examination of the wood, were compared to the periods identified by the OUTBREAK program. If OUTBREAK did not identify the same visually observed period, the parameters were changed accordingly and the output checked in an iterative process until OUTBREAK replicated, as closely as possible, the results of visual identification. Once the appropriate parameters had been established, OUTBREAK generally identified the same periods of suppression as those determined by visual examination of the wood.

For pandora moth outbreaks, the following parameters were chosen: 1) growth reduction must reach 1.28 standard deviations below the mean (values below this amount are approximately in the smallest 10th percentile values in the series), 2) growth reduction must last between 4 years and 20 years (this span should encompass the range of duration of all past outbreaks), and 3) the beginning year of the outbreak must have a growth reduction of at least 50% that of the previous ring. Using these parameters, OUTBREAK computed the timing of the suppression, the duration, the year of maximum growth reduction, and the percent mean periodic growth reduction. These aspects of the outbreaks were determined for each tree, and then summed or averaged (as appropriate) across sites and across the whole study area.

These methods describe the automated computer identification of outbreaks based on total annual ring widths. But, throughout the entire process, the most important method for identifying past outbreaks, and for assuring the computer programs were correctly identifying outbreaks, was visual notation of the past occurrences of the distinct ring-width signature formed by pandora moth defoliation. This signature of thin latewood and ring-width reduction was noted by previous researches and confirmed in this study (Patterson 1929; Miller and Wagner 1989).

In summary, past outbreak periods were inferred by four methods:

- the plotting of the standardized ring-width indices developed in ARSTAN,
- the suppression periods chosen by OUTBREAK, and
- most importantly, visual examination of the wood.

When all of these methods identified a series of ring-width suppressions as a possible outbreak in the majority of the trees at an individual site, the suppressions were judged to be attributable to defoliation by pandora moth.

To examine the time series for cyclic behavior relating to defoliation events, an autoregressive model was fit to the time series of percent of trees recording outbreak. This method noted the correlation coefficient between percent of trees recording outbreaks in the year of analysis and the percent of trees recording outbreaks in each of the 50 individual prior years. If the outbreak series had cyclic behavior, the autoregressive function should reflect this periodicity with oscillating, alternatively positive and negative values (Swetnam and Lynch 1993).

Histograms were used to quantify the range of values recorded for the mean periodic growth reduction and the duration of outbreaks. Basic descriptive statistics such as the minimum, maximum, and mean values were used to show historical range of variation and central tendency.

3.3 Mapping the Modern Outbreak and Inferred Outbreaks

The most completely recorded pandora moth outbreak in Oregon was the most recent, beginning in 1988 and lasting until 1996. The availability of data made it possible to examine the evolution of the outbreak and its relationship to the tree-ring signature. After acquiring aerial survey maps of pandora moth defoliation for the years 1990, 1992, 1994, and 1996 (unpublished data collected by the Deschutes National Forest in Oregon), I digitized and plotted them. I then evaluated how this particular outbreak spread from an initial area before finally collapsing after about five insect generations.

The area covered by inferred outbreaks and inferred outbreak spread maps were also examined in comparison to the modern outbreak. These maps were constructed by drawing a line enclosing recording sites and excluding non-recording sites. The areas were arbitrary with no definite correlation to the actual area of defoliation. But they were, however, useful for relative comparison among outbreaks and enabled visualization of the apparent spread of the inferred outbreaks.

3.4 Stem Analysis

3.4.1 Site Description

In 1994, 15 dominant ponderosa pine trees were cored at the Pringle Falls (PF) site. In 1996, I returned to this site to collect samples for a stem analysis, using the site name "RNA" after the "Pringle Falls Research Natural Area" (Fig. 3.2). The RNA site was a pure ponderosa pine forest with most of the underbrush removed by prescribed burns in 1989 and 1994. Char was still evident on most of the tree trunks, and pine regeneration was patchy. Destructive wind storms in the winter of 1995/1996 blew down a few dominant ponderosa pine trees in this area. The Forest Service permitted me to remove half sections of wood from four of these trees for the stem analysis.

3.4.2 Field and Laboratory Methods

The trees selected had no external evidence of fire damage or other injury and were, on average, 40 meters tall and greater than one meter diameter at breast height (DBH). Using a chain saw, five-centimeter-thick cross-sections were cut at three-meter intervals along each tree (Fig. 3.3), beginning at three meters height above the root crown in order to avoid the fractured bases of the fallen trees. The cross-sections were allowed to dry for one month then were surfaced using a belt sander and progressively finer grits of sandpaper (60, 120, 240, 320, 400).

I drew three radii 90° apart on each sanded section, placing each radii in the same orientation up the tree. Each radii was crossdated and its ring-widths measured, then the width of each ring averaged for all three radii on a section using the TREEGROW program (developed by Richard L. Holmes of the Laboratory of Tree Ring Research, The University of Arizona). The average ring widths were plotted in stem profiles to evaluate how pandora moth outbreaks affected growth over the entire tree. The periods of ring-growth suppression due to outbreaks were initially identified from

Figure 3.2. Stem analysis site. Four wind thrown trees were selected with no external evidence of fire or lightning damage.

Figure 3.3. A crossection was cut every three meters along the stem of the tree.

cores taken at breast height.

The effects of these outbreak periods were also examined by evaluating the volume growth reduction throughout the tree and the percent growth reduction on each individual disc along the tree. TREEGROW averaged the multiple radii from each disc to approximate a basal area increment. Using the basal area increment at each 3-meter cross-section interval along the tree, the volume of the entire tree was estimated using a simplified, stacked cylinder model (Fig. 3.4). The hypothetical volume of the tree without insect defoliation was estimated by extrapolating a curve (fit to the basal area increment chronology developed from each disc) through the period of outbreak-related suppression based on the mean of the rest of the series. This value was compared to the volume of wood at the end of each outbreak, with the difference being the volume reduction associated with each outbreak. The formula used to determine the amount of volume reduction for each outbreak was:

$$V = (R_n^2 H_n - R_o^2 H_o)\pi/3 \qquad [1]$$

Where:

V = Volume Reduction.

R_n = Radius if no outbreaks; $R_n = (R_o)$ + Radial reduction due to outbreak.

R_o = Radius after outbreak.

H_n = Height if no outbreak; $H_n = H_o * R_n / R_o$.

H_o = Height after outbreak.

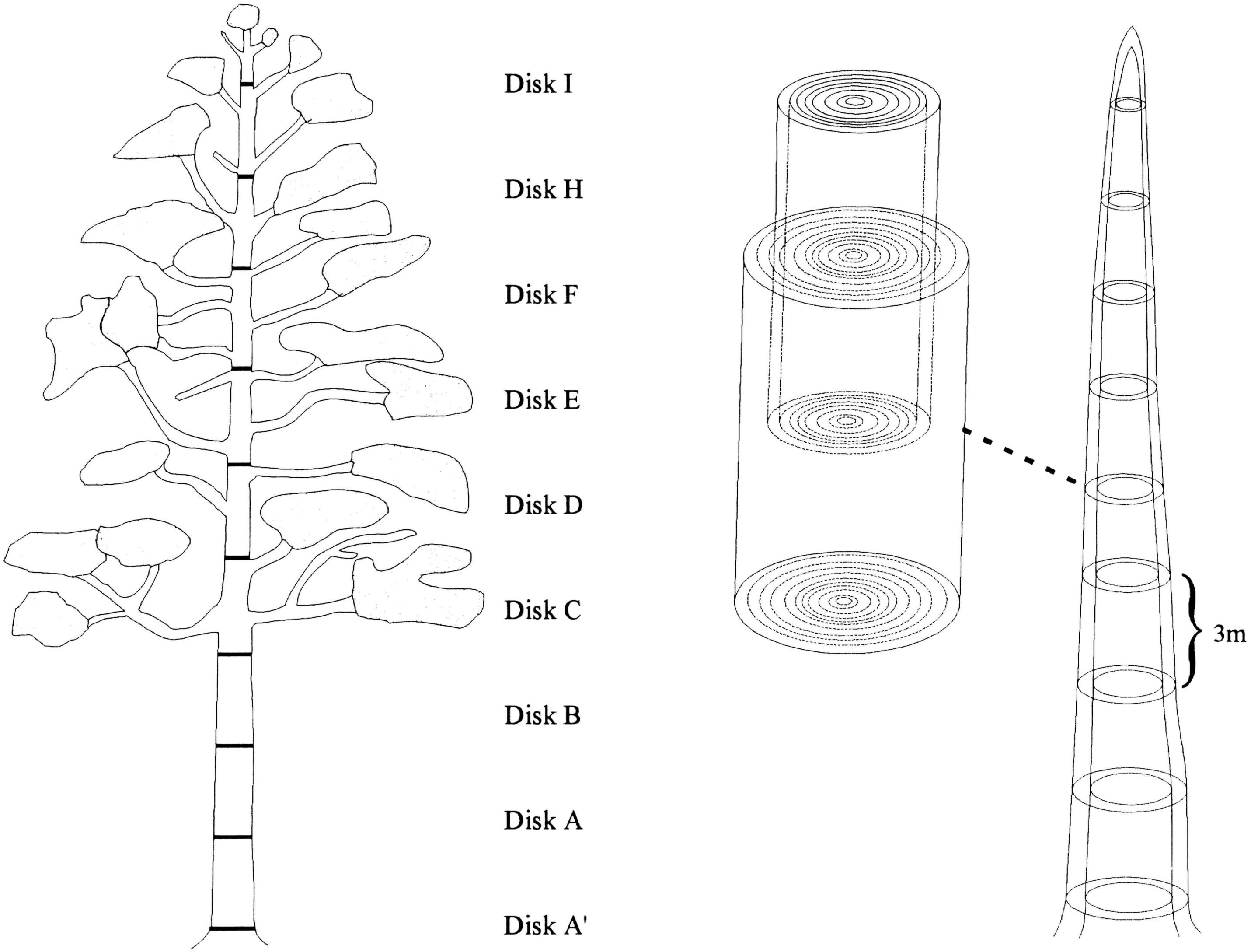


Figure 3.4. A. Sampling technique for the stem analysis. A crossection was takenevery three meters along the main stem of the ponderosa pine trees. B. For the volume calculation the trees were assumed to be a set of stacked cylinders with each cylinder centered on a crossection. (This graphic is modified from Raske pers. comm.).

To account for tree-specific variation, all volume reduction measurements for a given outbreak period were averaged to yield a mean volume reduction, which represents the relative severity of the particular outbreak. The mean volume reduction was then divided by the number of years in the outbreak period to determine the total annual volume reduction. This provides a measure of outbreak severity independent of the length of the outbreak.

3.5 Non-host chronology

Although sugar pine has been described as an incidental host to pandora moth (Patterson 1929; Carolin and Knopf 1968), Forest Service entomologists in Oregon have never observed pandora moth defoliation of sugar pine trees in their area (Wickman and Eglitis, per. comm.). Therefore, sugar pine trees were sampled to determine if this species could be used as an independent climatic control. Twenty sugar pine trees were cored at the PBPL site by B. Wickman in 1994 for comparison with the ponderosa pine collection (EF). Two cores were taken from each tree at breast height. The cores were prepared, crossdated, and measured using techniques described in Section 3.2.2. The index chronology was compared to the ponderosa pine index chronology from the EF site. I focused particularly on the possible outbreak periods documented from the EF site to determine if the sugar pine chronology showed any evidence of the pandora moth outbreaks.

The regional climate reconstruction developed by Garfin and Hughes (1996) was used to evaluate climatic variations in the insect outbreak chronologies. After a ten-year running average was applied to the precipitation reconstruction to accentuate log-term droughts, it was then compared to the host chronologies. A Student's t-test was also used to test if the precipitation value for all years of inferred outbreaks was statistically different from all other years.

The climate chronology was then tested against the outbreak periods to identify any possible climate relations. A superposed epoch analysis was used to determine average precipitation values around the beginning year of the outbreaks. The first years of all of the inferred outbreaks were entered into the EVENT program (Holmes 1986), as were the precipitation values from the climate reconstruction. EVENT then averaged the precipitation values from the 10 years preceding and 5 years following the first years recording the outbreaks. These averaged values were plotted to see if any years were consistently wet or dry when compared to the pool of precipitation values.

3.6 Fire History

3.6.1 Site Description

The fire history site (PPF) was located on the Pringle Falls Experimental Forest (Fig. 3.5). This area was thinned and burned by prescription in 1992. It is now an open ponderosa pine stand closely resembling the natural ponderosa pine forests that existed at the turn of the century (Franklin and Dyrness 1988). The area is still surrounded by

Figure 3.5. Photograph of the fire history site. Crossections were cut from snags, stumps, logs, and a few living trees.

dense stands of young ponderosa pine regeneration. The prescribed fire left many stumps and a few snags, but it had a tendency to burn hot within the existing cat faces, often burning off old fire scars. Nevertheless, numerous trees with well preserved fire scars were located and sampled.

3.6.2 Field and Laboratory Methods

At the PPF site, all trees, snags, stumps, and downed logs within a 10 ha area were examined for external evidence of fire scars. Twenty-seven specimens containing the largest number and the best preserved fire scars were sampled (Dieterich and Swetnam 1984; Baisan and Swetnam 1990). To obtain the record of fires during the 20th century, partial sections were cut from three living fire-scarred trees, which were left standing and intact (Arno and Sneck 1977) (Fig. 3.6). All sections were allowed to dry for a month and were then sanded with successively finer grits of sand paper (60, 180, 220, 320, 400).

The sections were crossdated using total ring widths and the pandora moth outbreak signatures as a key dating features. The fire events were identified by the presence of characteristic, fire-damaged cambial material (Dieterich and Swetnam 1984) and subsequent curled growth and charred surface. The FHX2 program (Grissino-Mayer 1995) graphed the master chronology of the fire scars from all of the trees in the site, and to compute descriptive statistics for the fire interval (the time span between two consecutive fires) data and the seasonality of the scars.

Figure 3.6. Photograph of a "cat face" of a living tree, showing the successive scars left by fire.

The fire dates were noted and compared with the occurrence of inferred pandora moth outbreaks. I used a Student's t-test to determine if mean fire intervals during outbreaks were statistically different from all other intervals. I also quantified the number of fires before, during, and after outbreaks.

CHAPTER 4

RESULTS

4.1 Introduction and Overview of Results

The initial objective of this thesis was to reconstruct the occurrence of past pandora moth outbreaks. In this effort, historical records of the known outbreaks were examined and the spread of the modern outbreak mapped. Comparisons with historical data enabled identification of the typical tree-ring pattern, or "signature", of growth reduction and altered wood structure caused by pandora moth outbreaks. Once this signature was noted, possible confounding factors (climate, other insects, and fire) were examined to determine if they, rather than pandora moth outbreak, could have caused similar ring-width growth patterns.

From the samples collected at 14 sites, a 620-year record of 22 pandora moth outbreaks was developed. With this record, I examined the spread of outbreaks across the landscape, the trend of occurrence of outbreaks through time (specifically looking for change in the 20th century), and the historical range of variability in duration, frequency, severity, and extent of pandora moth outbreaks. Long dendrochronologically-dated climate and fire records enabled accurate comparisons with the insect outbreak history, providing insights into the climate-fire-insect system. Finally, a stem analysis revealed the amount of volume reduction due to pandora moth outbreaks and the effect of defoliation throughout the stem of the tree.

4.2 Identification of the Suppression "Signature"

Four, historically documented, pandora moth outbreaks were used to identify the suppression signature and provide insight into the spatial and temporal characteristics of inferred outbreaks. The most recent pandora moth outbreak was documented from 1988 to 1996 (Wickman *et al.* 1996) (Fig. 4.1; Table 4.1). Larvae in abundance were first observed in the Deschutes National Forest in 1986, distributed across 1,200 ha. By 1988, the population had spread across 12,400 ha, at which time the forest entomologists classified this as an outbreak and began monitoring the population (A. Eglitis, pers. comm.). In 1990, the first aerial survey mapped the defoliated area, which by then encompassed 66,700 ha. It expanded to 197,000 ha in 1992, then peaked at 864,000 ha in 1994. At that time, many dead larvae were noted hanging from the ends of branches, the cause being attributed to a nucleopolyhedrosis virus. By 1996, the population had crashed, and only 22,200 ha were defoliated. The outbreak was patchy across these sites, with the trees and stands in the defoliated areas being affected at different levels of severity. The OUTBREAK program showed suppression in four sites starting as early as 1989, but all four sites had distinct thin latewood in 1994 and an extremely narrow ring for 1995 (Fig. 4.2). The general pattern described by the modern outbreak was an advance outward from a central location, overlapping some of the previously defoliated areas.

The 1963-1968 outbreak was only observed at the Skookum Butte site in the Winema National Forest, the beginning date not being precisely known (B. Wickman,

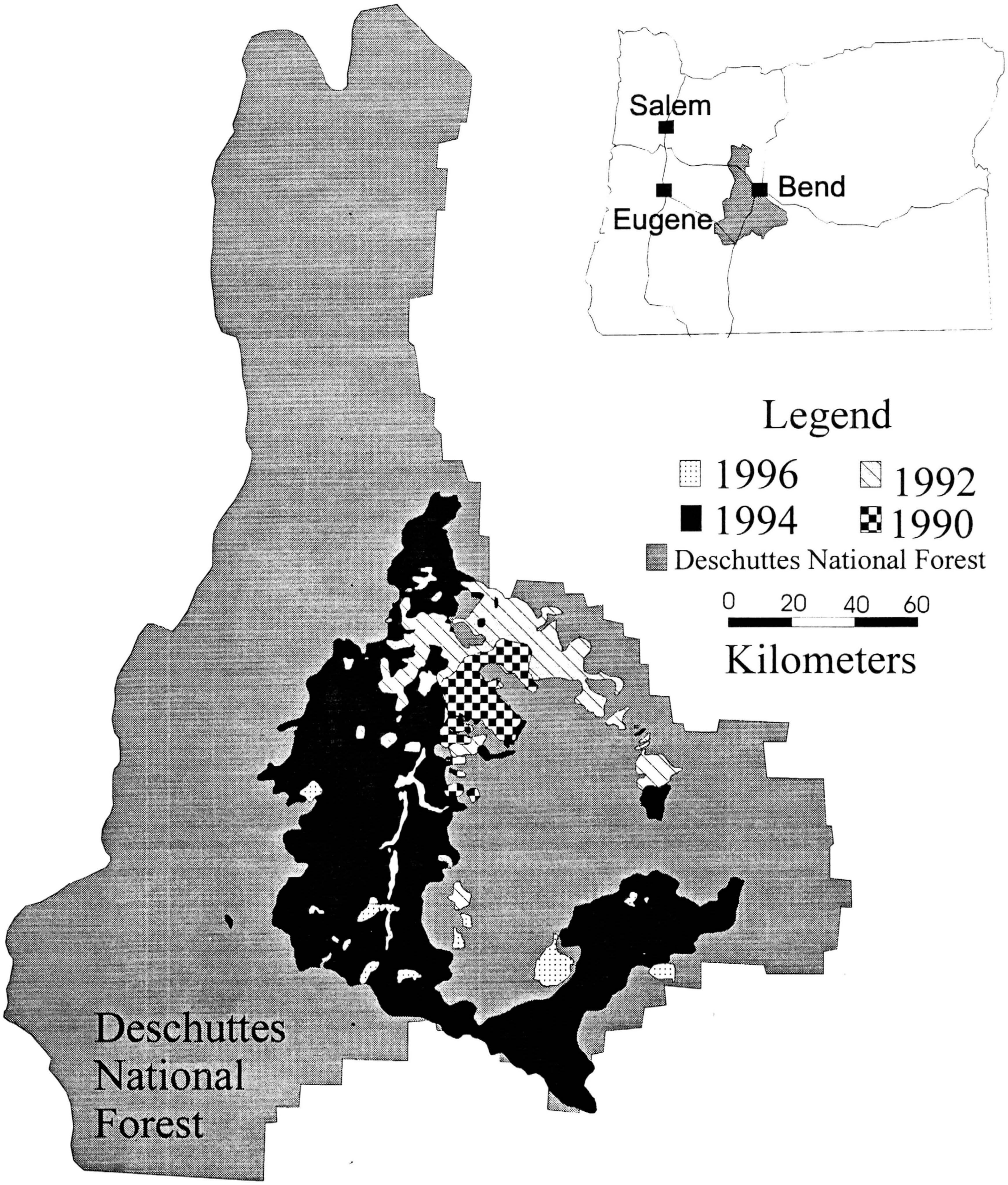


Figure 4.1. The modern outbreak which started in 1986 and is still active but declining.

Table 4.1. Acres defoliated by pandora moth during the current outbreak (unpublished data collected by the Deschutes National Forest).

Year	Hectares	Arial Maps of Defoliation
1986	1,200	No
1988	12,400	No
1990	66,700	Yes
1992	197,600	Yes
1994	864,500	Yes
1996	22,200	Yes

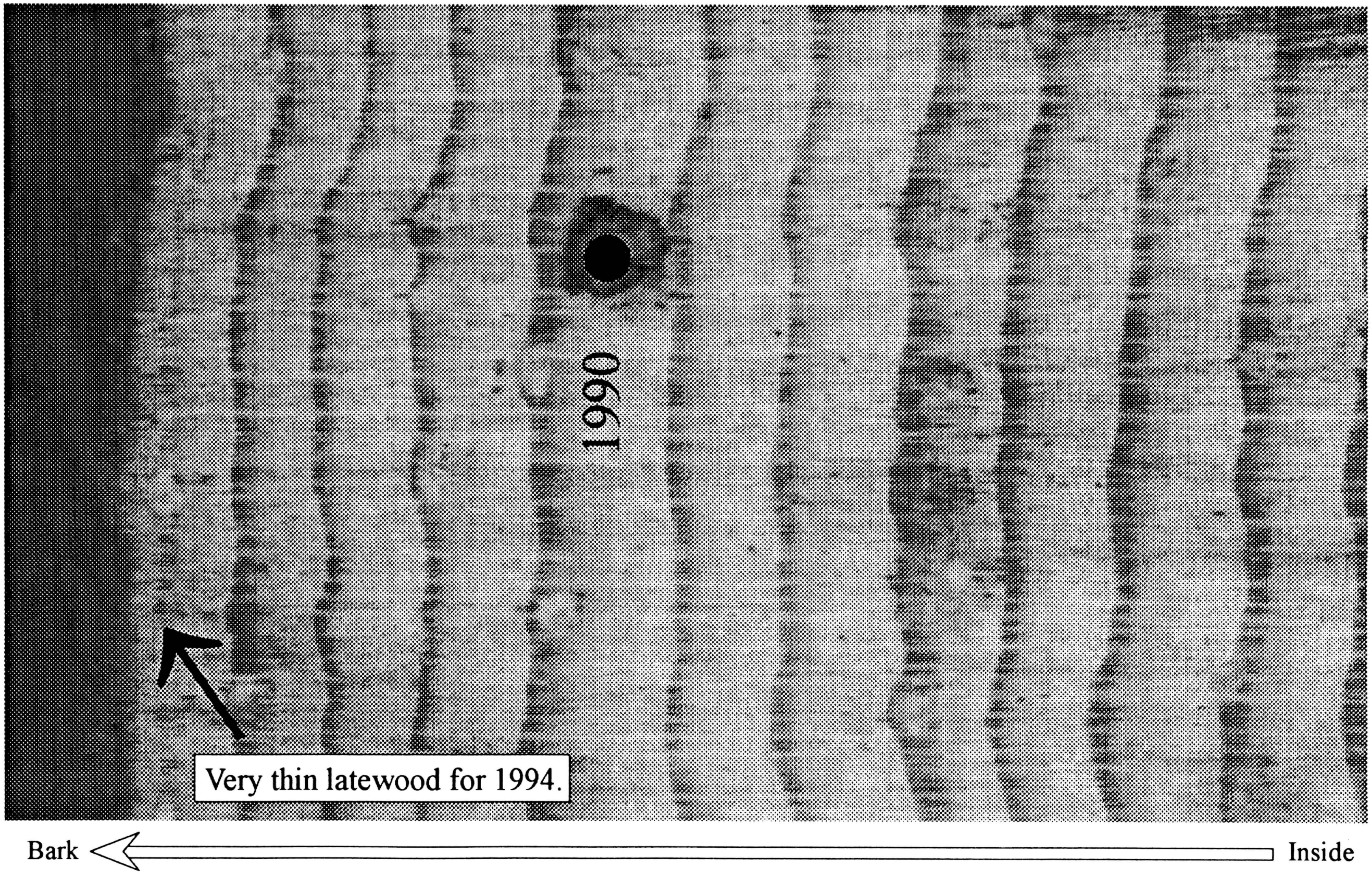


Figure 4.2. Ring pattern for the modern outbreak from the sample RNA03bb. The inside complete ring is 1984 and the outside is 1995 with very thin latewood in 1994. This is the beginning of the "signature" of pandora moth after the massive defoliation event in 1994.

pers. comm.). The radial growth in affected sites was suppressed 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 suppression (Fig. 4.3). The rings gradually began returning to normal size around 1970 requiring five years to regain normal growth.

In the 1918-1925 outbreak, the larvae were evident from the Sisters area south through the Winema National Forest and west to Crater Lake National Park, with patches of intense defoliation throughout the area (Patterson 1925). The peak defoliation occurred in 1919 near Klamath Lake. Patterson's core samples show a thin latewood signature in 1920 or 1922 (Patterson 1929). My own findings were similar. Ring-width suppression started in 1919 at the TDS site, then at two other southern sites in 1920 and 1921. A northern site first exhibited ring-width suppression in 1922, followed by three more sites in 1923. Thin latewood was evident at the beginning of the growth reduction at each site, and the rings for 1922 or 1923 were often the narrowest in these chronologies. The suppression lasted until 1931 in the southern sites and 1934 in the northern sites. The first and last years were not synchronous between any two sites, suggesting that the trees responded to the specific effects (*i.e.* defoliation) in the immediate area and not a regional factor like drought.

Several references mention the existence of pandora moths around the Klamath Lake area a few years before 1893 (Patterson 1929; Keen 1937; Carolin and Knopf

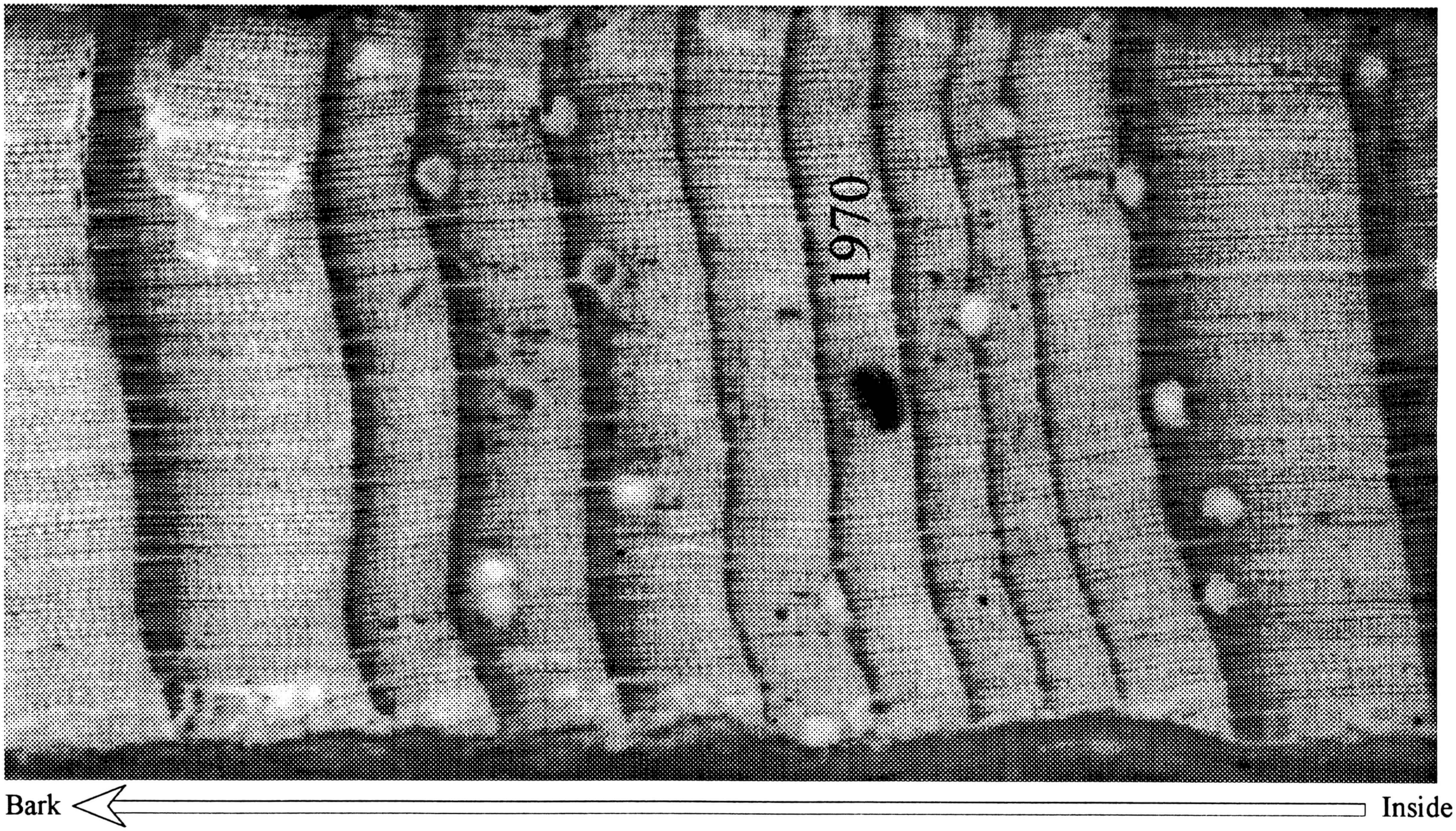


Figure 4.3. .A pandora moth outbreak occurred at Skookum Buttes from1963-1968. The suppression appears from 1967-1975.

1968). Four ring-width chronologies from the northern sites in the Deschutes National Forest had suppressions starting in 1889, and one northern site first recorded suppression in 1895, with growth returning to normal at all these sites by 1902 or 1903. The southern sites, however, did not exhibit any suppressions during this period.

In all documented outbreaks, the distinctive ring signature associated with pandora moth defoliation started with the first year of the suppression having reduced latewood and a ring-width that was less than 50% the mean ring-width. Rings for the following two years were extremely narrow or absent, with an overall pattern of reduced ring-width that lasted 4 to 18 years. Furthermore, all suppressed rings had relatively thin latewood. Pandora moth larvae feed on old needles; this results in the generally lighter color and very thin latewood of rings formed during outbreaks (Wickman *et al.* 1996). This lack of darkening of the rings can be attributed to removal of the photosynthetic area in the latter part of the growing season when these latewood cells are formed (Fritts 1976). The beginning year of the ring-width suppression consistently lagged the documented beginning of the corresponding insect outbreak. The trees recorded the period during which they suffered severe defoliation, which began sometime after the insect population started to grow to outbreak levels. Throughout this text, the term "the beginning year of an inferred outbreak" refers to the first year the tree recorded a suppression. The tree-ring record consistently recorded a sustained period of suppression longer than the actual insect outbreak. This was presumably due to the slow recovery of the tree after the defoliation had ceased, a pattern often observed in insect outbreak studies (Table 4.2) (Koerber and

Table 4.2. Calibration of the tree-ring record with historically documented outbreaks. Historical information comes from Patterson (1929), Keen (1937), and B. Wickman. pers. comm.

Sites	Outbreak Records		Length of Outbreak		Max. Year of
	Historical	Tree-Ring	Historical	Tree-Ring	Defoliation
LML, EF, DES, BJS	1988-1996	1989-????	9	?	1994
SKB	1963-1968	1967-1975	6	9	1967
LML, EF, PF, PPF, TLD, TDS, BJS	1918-1925	1921-1931	8	11	1921
LML, EF, PF, PPF	?1893 ?	1889-1902	?	14	1893

Wickman 1970; Swetnam and Lynch 1993). I found the distinctive pandora moth signature occurring repeatedly throughout the tree-ring chronologies in this study, which cover a period of more than 620 years (Fig. 4.4).

4.3 Inferred Outbreaks

A total of 326 cores from 163 trees on the 14 host tree sites were dated and included in the host tree chronologies. The ARSTAN program computed ring-width indices for each tree sampled. Inferred periods of suppression due to pandora moth defoliation were observed on all host tree sites (Appendix A, Figs. 1-14). The OUTBREAK program compiled a continuous time series of the number of trees recording ring-width suppressions associated with inferred outbreaks. The record extended as far back as A.D. 1329 and included a minimum sample depth of four trees in A.D. 1375. The greatest sample depth of 140 trees lasted from A.D. 1800 to A.D. 1995 (Fig 4.5). Using a continuous time series of the percent of trees recording suppressions (Fig. 4.6), twenty-two individual periods of suppression were identified throughout the 620-year record. Some rings were consistently narrow or locally absent at the beginning of these suppression periods (*e.g.*, 1480-1481, 1632-1633, 1662-1663, 1678-1679, 1803-1804, 1841-1842, and 1922-1923). Many years within the outbreak periods consistently had thin latewood due to defoliation (1479, 1631, 1661, 1677, 1802, 1840), a corroboration of the pattern observed in the ring-width signatures for the documented

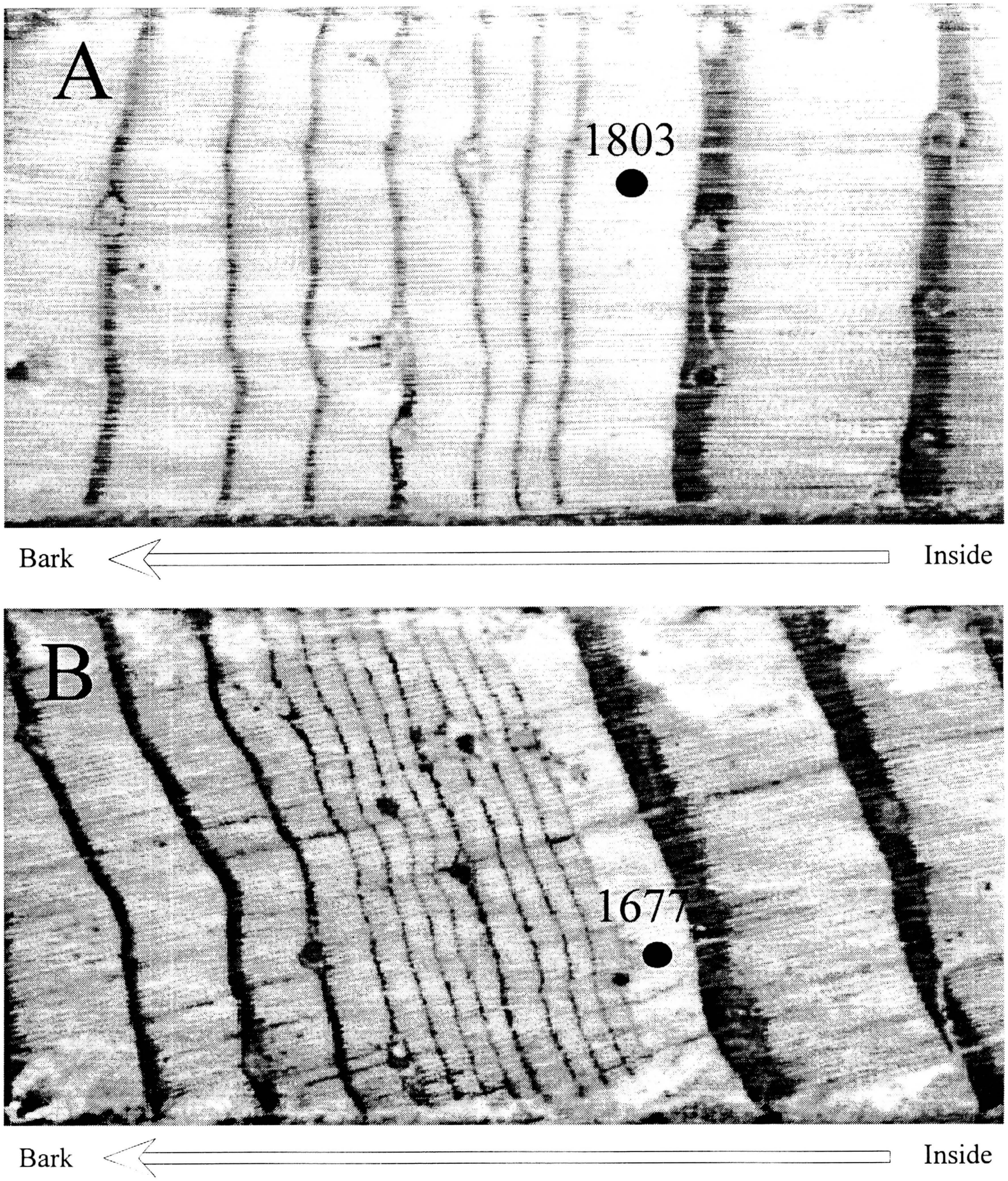


Figure 4.4. A: Pandora moth signature for the 1803-1811 inferred outbreak. The signature starts with thin latewood and contains small rings for 9 years. The rings resume the preoutbreak width in 1812, which is not in the graphic. B: Pandora moth signature for the 1677-1688 inferred outbreak, showing the same signature.

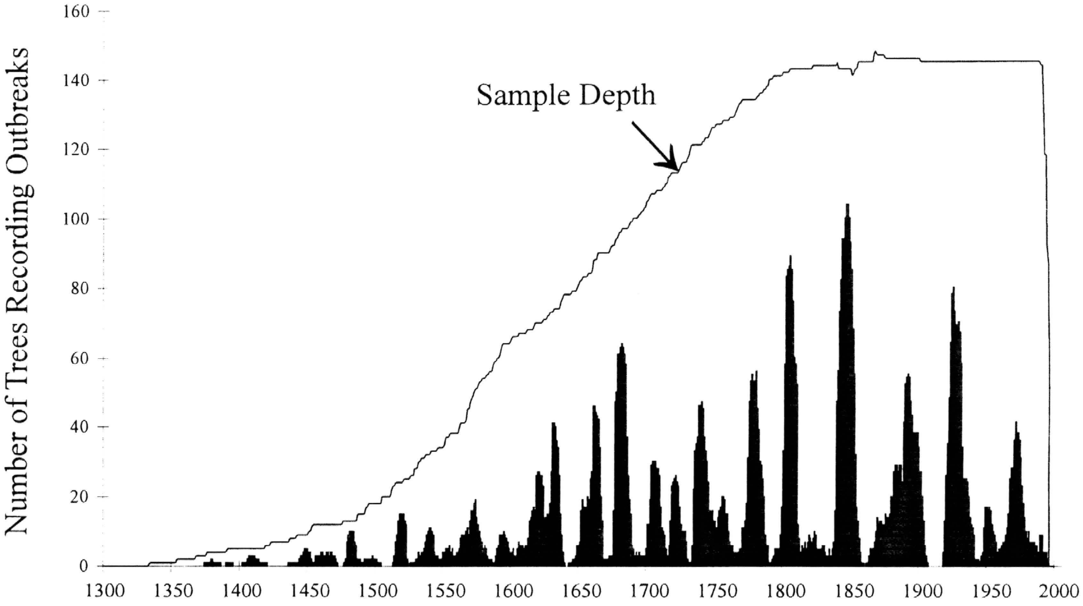


Figure 4.5. Time series of the number of trees recording outbreaks and the sample depth curve.

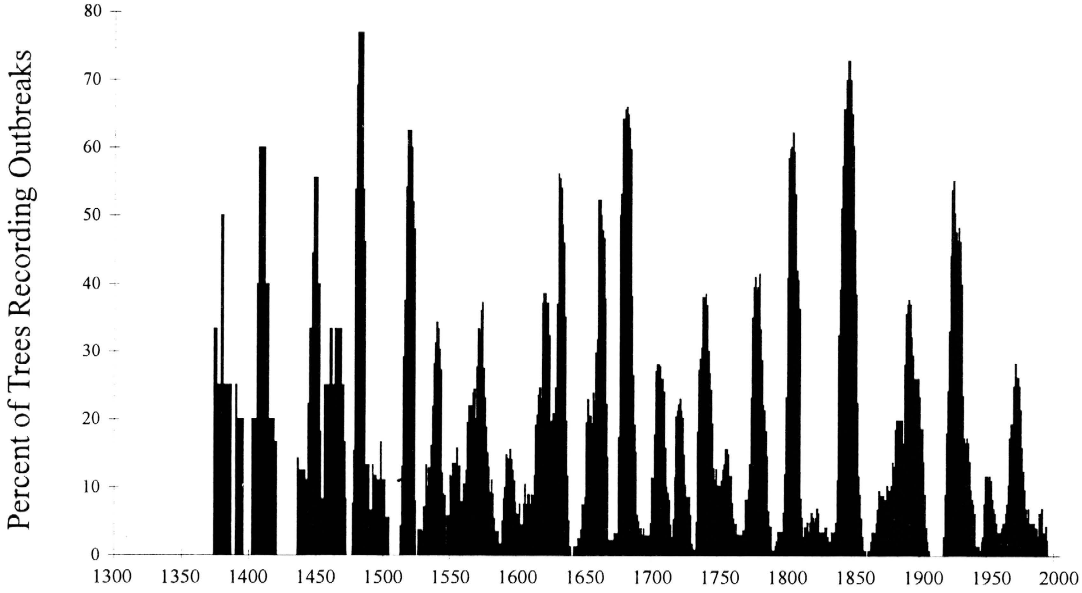


Figure 4.6. Percent of trees recording pandora moth outbreaks through time, for all sites.

outbreaks. The shortest outbreak signatures represented a year or two of heavy defoliation followed by a few years of recovery. This signature, showing only six years of suppression, was evident in the 1631, 1661, and 1677 outbreaks recorded at the PF/RNA site.

Over the 620-year period, the outbreaks appeared spatially dispersed throughout the sample area, affecting only a few of the tree-ring sites at any given time (Fig. 4.7a,b). Only one outbreak seemed to cover nearly the entire study area (in 1836). A compilation of all sites in the region showed the beginning year of each inferred outbreak to be a cluster of dates rather than a single year (Fig. 4.8). The spatial distribution of the beginning dates provided a picture of the propagation of an outbreak, beginning at an individual site and generally spreading out concentrically from this initial point (Fig. 4.9, 4.10, 4.11, 4.12, 4.13, and 4.14). This pattern was observed in the modern outbreak of 1988-1996. It was not clear if the insects actually spread from this initial site, or whether favorable climate conditions in subsequent years enabled the resident population at other sites to be released.

Interval, duration, and mean periodic growth reduction were used to describe the dynamics of the inferred pandora moth outbreaks (Appendix B). The intervals between outbreaks on individual sites ranged from 9 to 156 years, with a mean of 46 years (Fig 4.15). The composite of all sites showed a minimum of 8 years and a maximum of 48 years between outbreaks, with a mean of 25 years (Table 4.3). The autocorrelation function suggested cyclical or quasi-cyclical behavior, with periods around 20 and 40 years (Fig. 4.16). These results indicate that outbreaks were episodic on specific sites, but

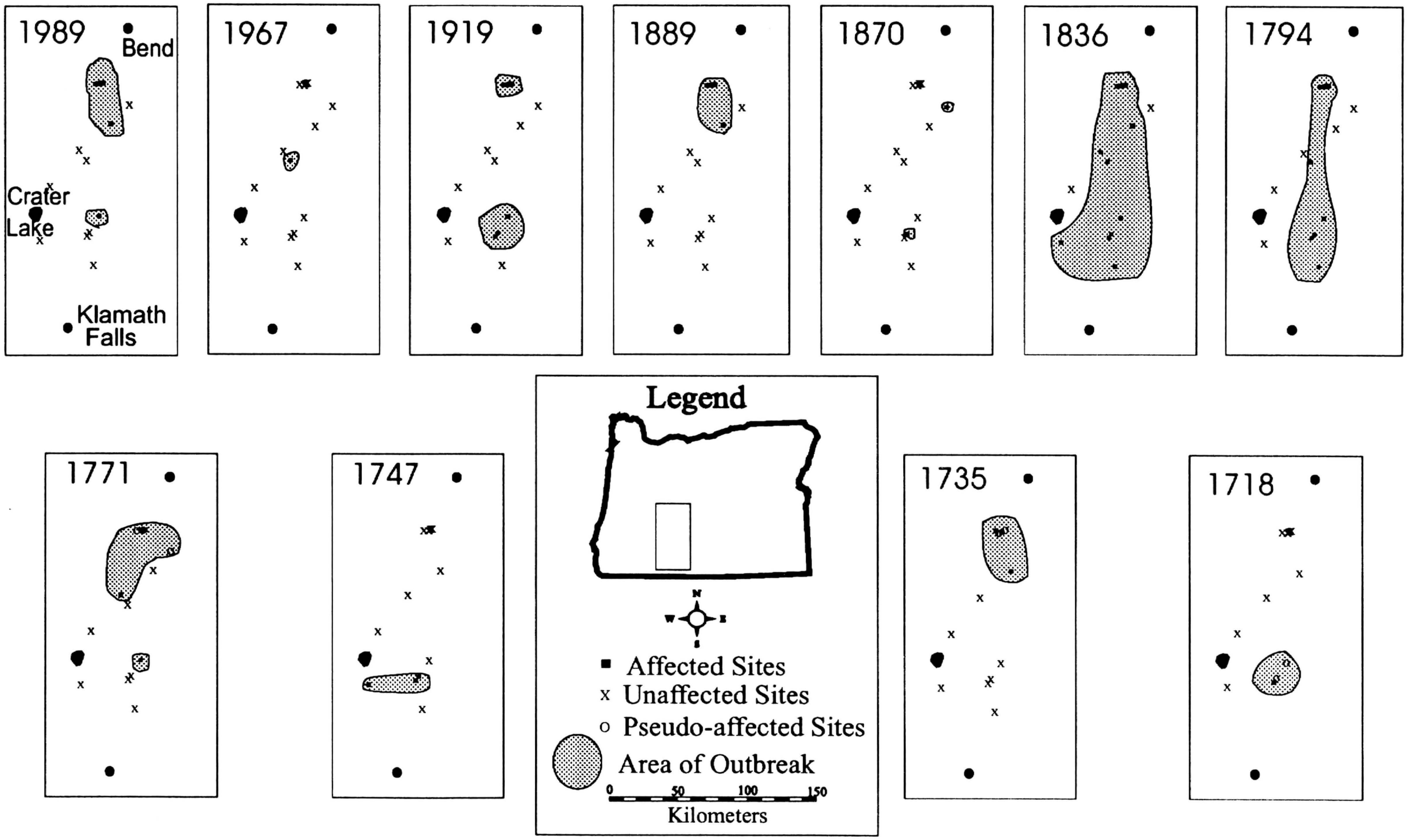


Figure 4.7a . Distribution of pandora moth outbreaks for the entire tree-ring chronology. A pseudo-affected site was one that corroborated a recorded outbreak but was not originally recorded because of low sample depth.

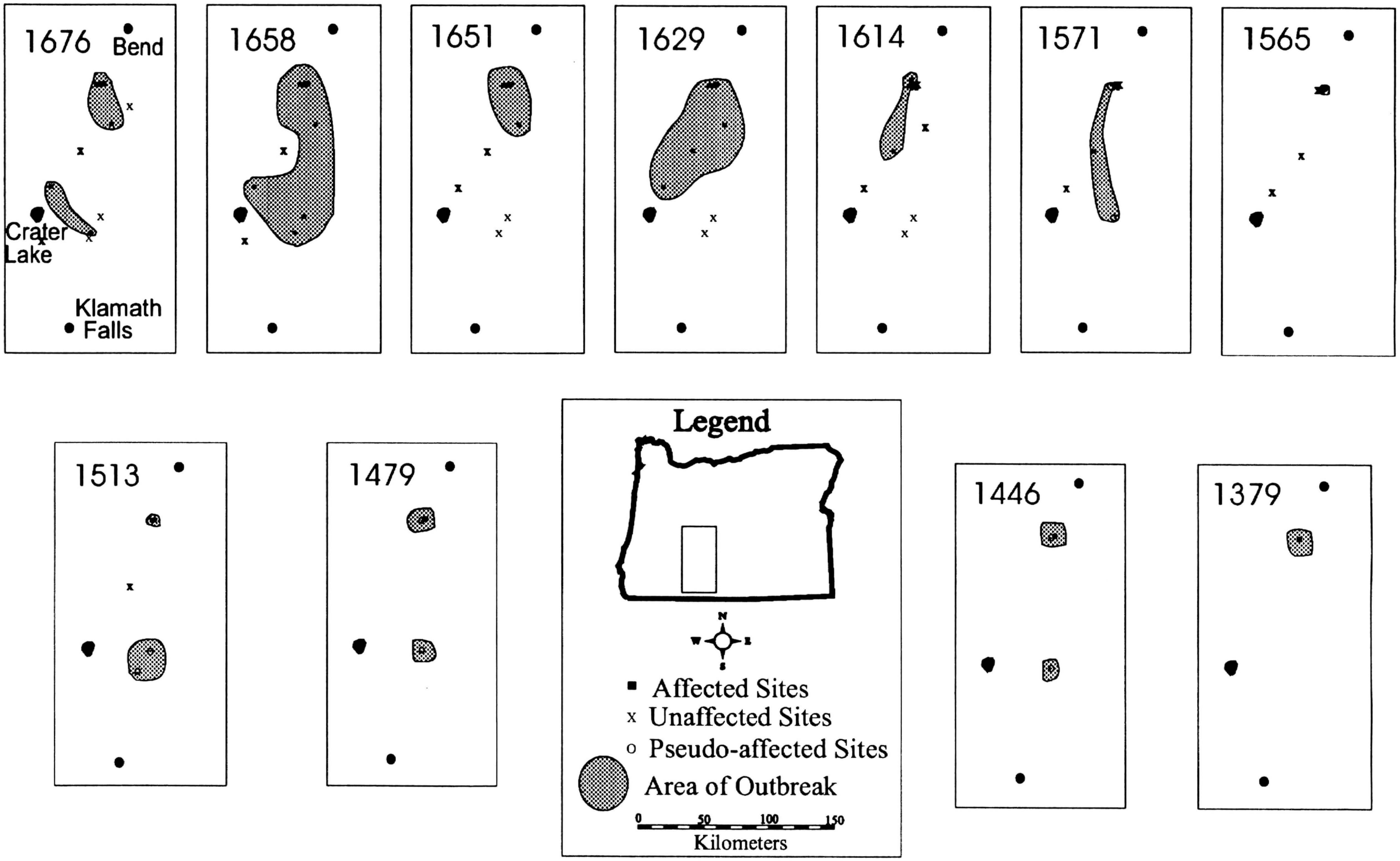


Figure 4.7b (Continued). Distribution of pandora moth outbreaks for the entire tree-ring chronology. A pseudo-affected site was one that corroborated a recorded outbreak but was not originally recorded because of low sample depth.

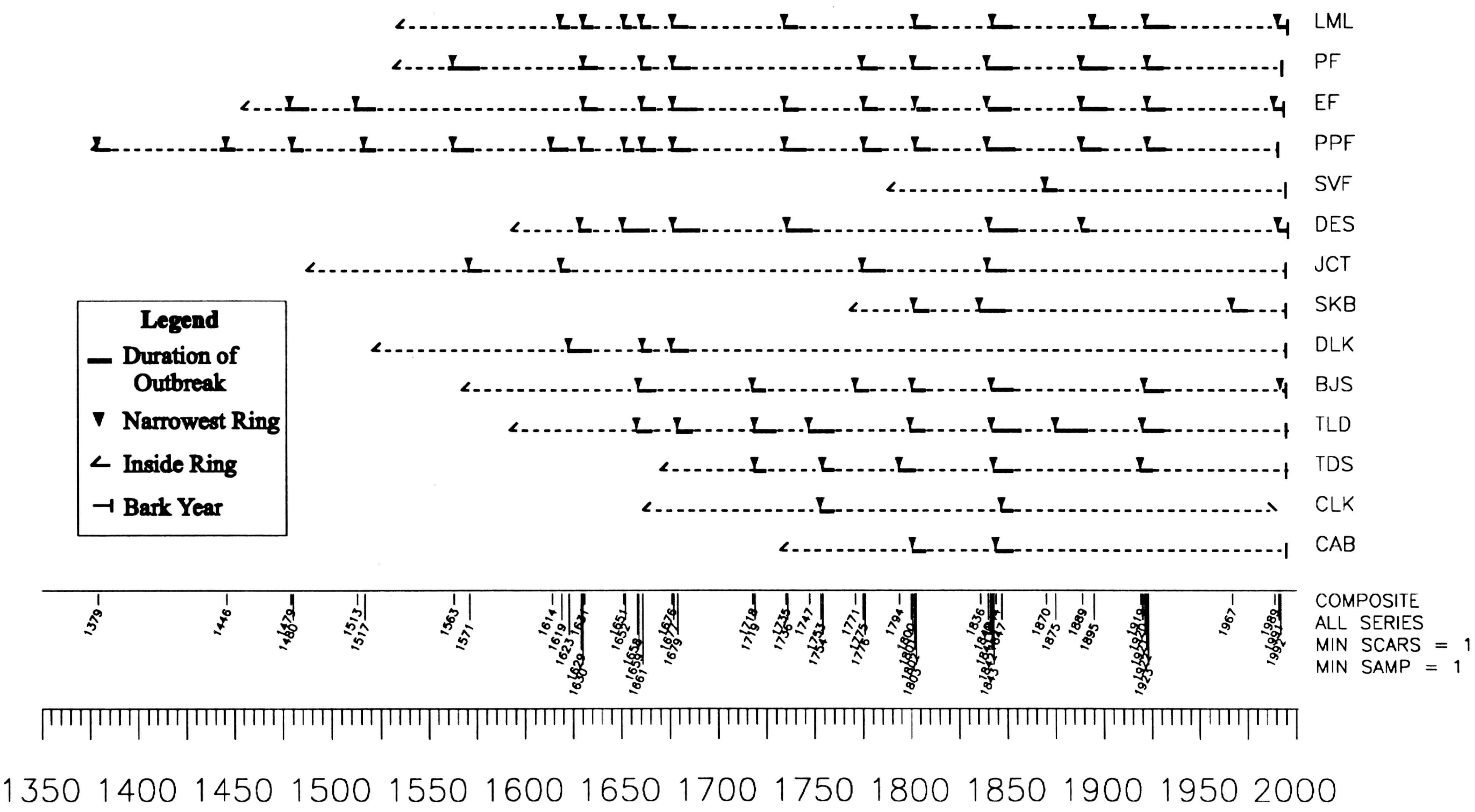


Figure 4.8. Composite of the sites showing outbreaks. The arrow designates the first year that the site records the outbreak. The composite represents all of the first recording years for the outbreaks.

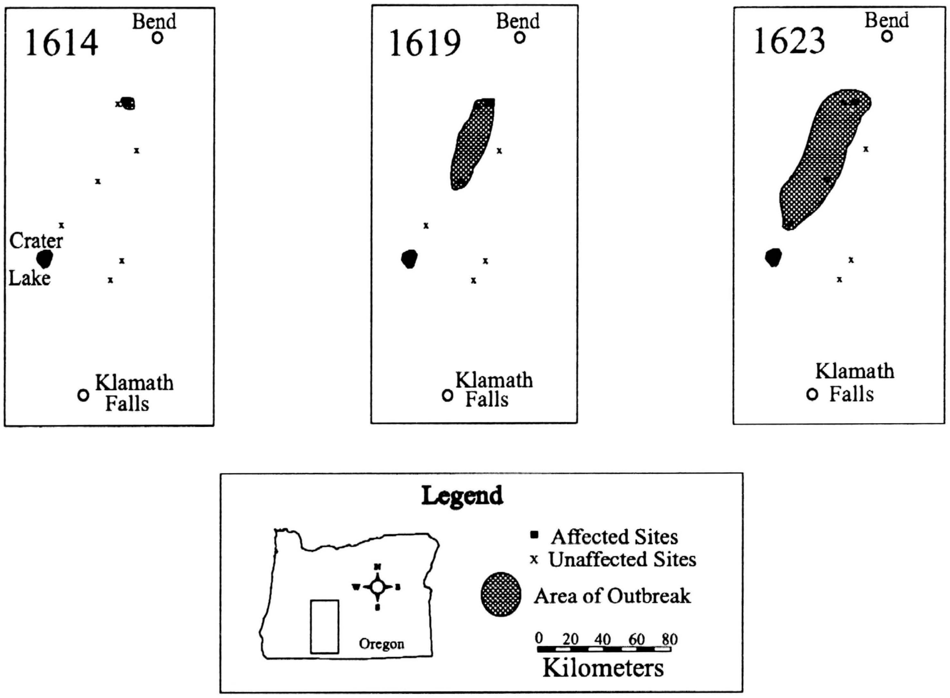


Figure 4.9. Spread of the 1614 pandora moth outbreak. The black squares mark recording sites and the shaded area is the estimated area of effect.

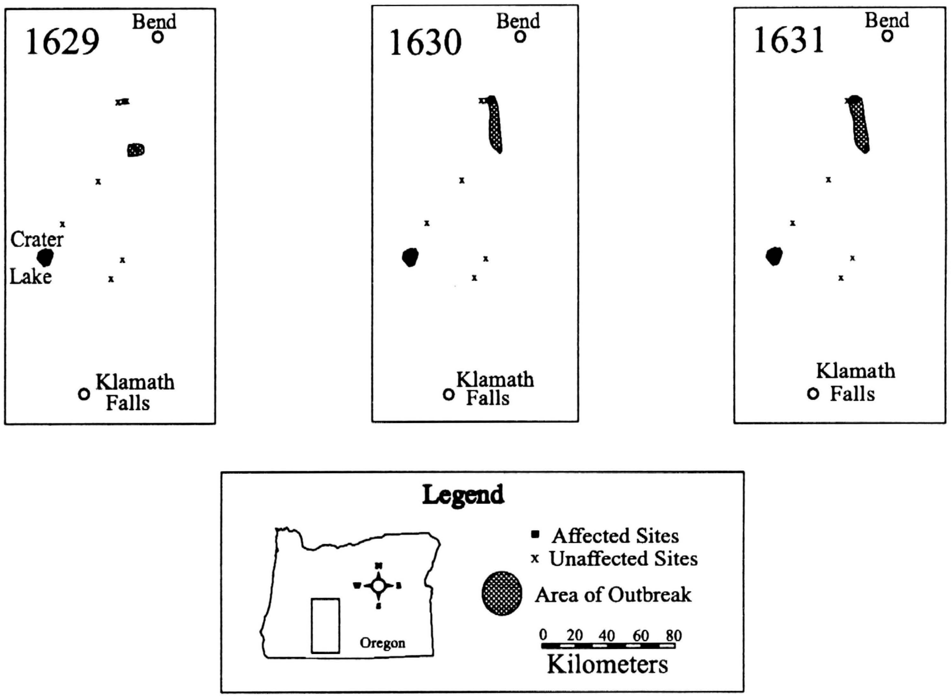


Figure 4.10. Spread of the 1629 pandora moth outbreak. The black squares mark recording sites and the shaded area is the estimated area of effect.

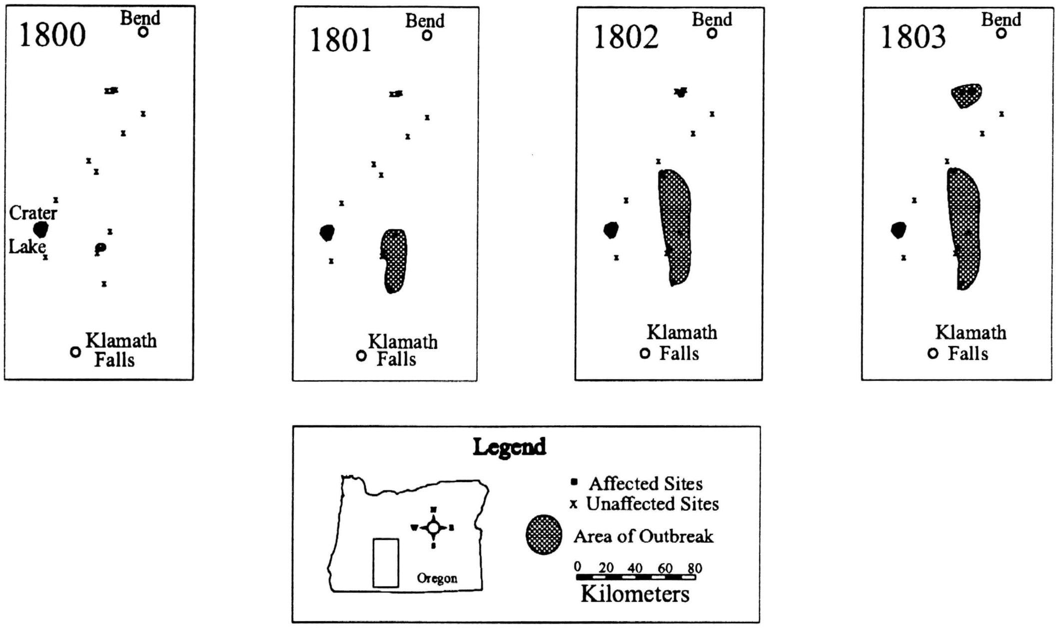


Figure 4.11. Spread of the 1800 pandora moth outbreak. The black squares mark recording sites and the shaded area is the estimated area of effect.

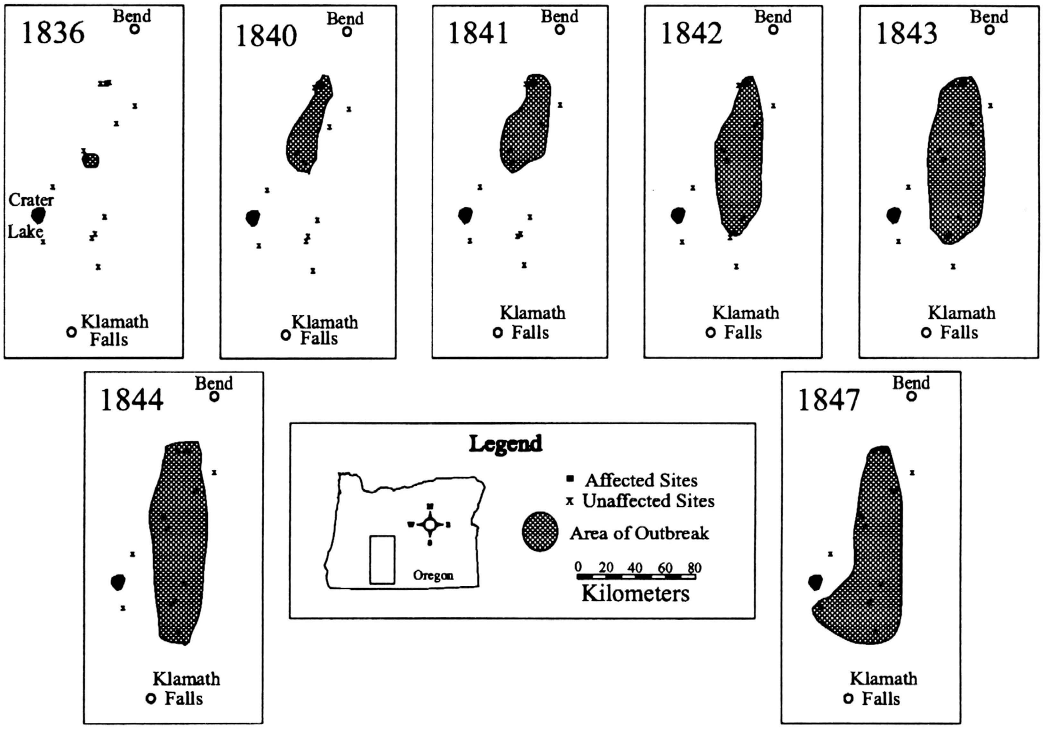


Figure 4.12. Spread of the 1836 pandora moth outbreak. The black squares mark recording sites and the shaded area is the estimated area of effect.

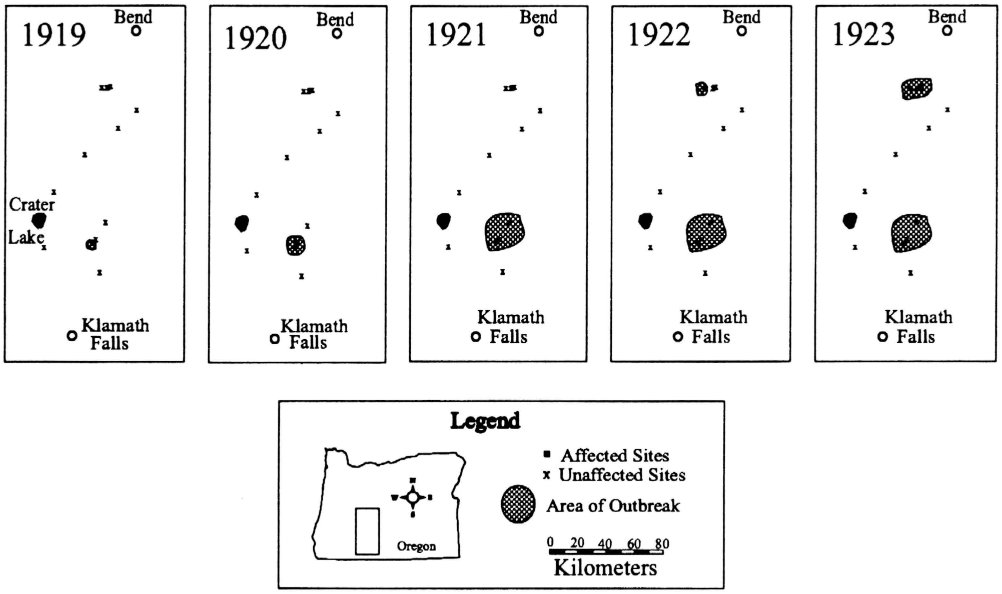


Figure 4.13. Spread of the 1919 pandora moth outbreak. The black squares mark recording sites and the shaded area is the estimated area of effect.

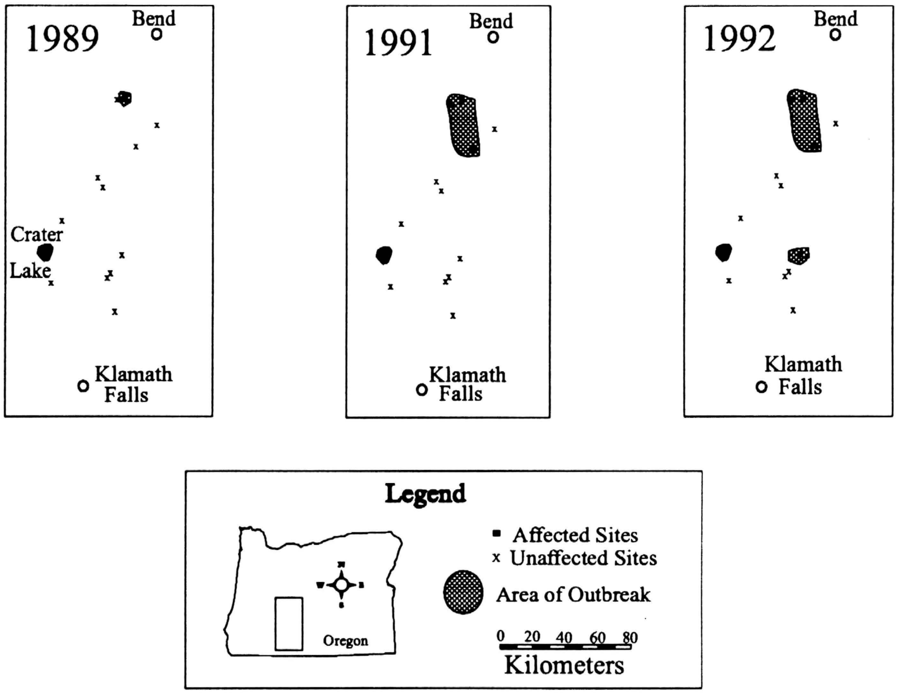


Figure 4.14. Spread of the 1989 pandora moth outbreak. The black squares mark recording sites and the shaded area is the estimated area of effect.

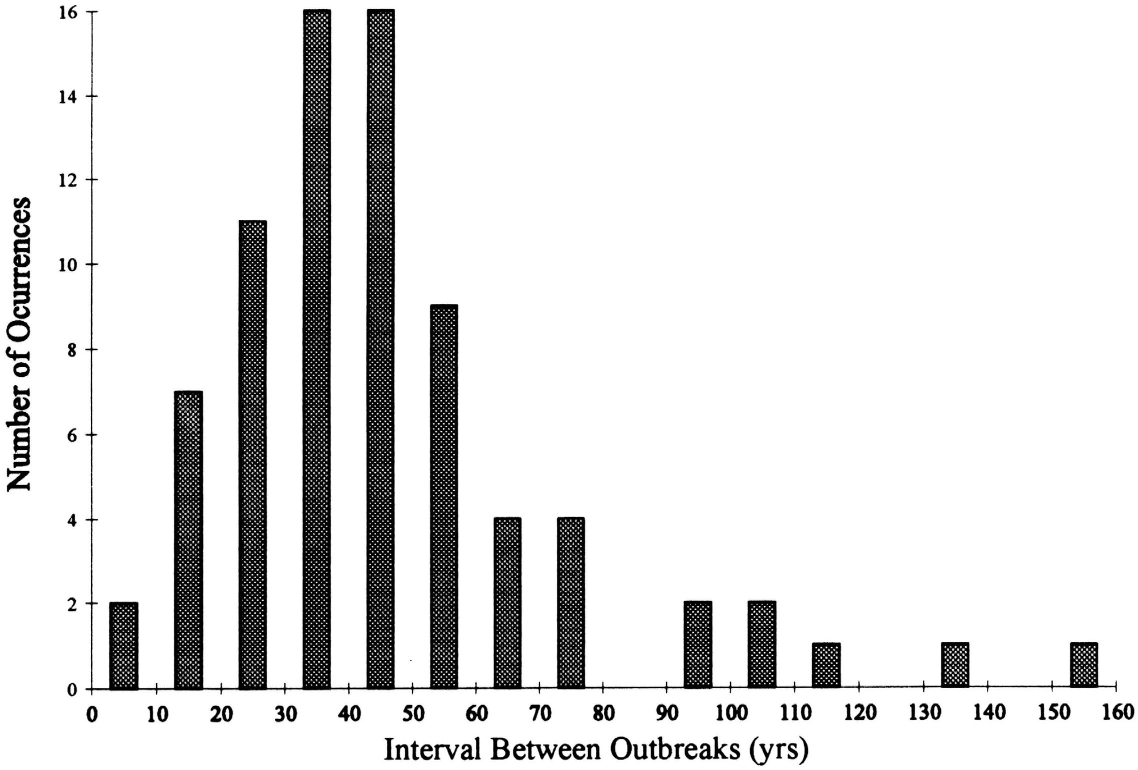


Figure 4.15. The frequency of the intervals between outbreaks. Values are binned into 10 year groups, with the first barrepresenting intervals 0-9. The mean is 46.4 year and the standard deviation is 28.2.

Table 4.3. Interval statistics for the pandora moth sites with more than one interval. The first record, All, is the composite of all of the sites.

Site	Min interval(yr)	Mean interval(yr)	Max interval(yr)
All	8	27.30	48
LML	9	37.5	65
PF	16	45	99
EF	16	46.64	112
PPF	9	36.47	66
DES	21	60.7	105
JCT	48	89.3	156
SKB	42	83	124
DLK	13	23	33
BJS	30	55.33	80
TLD	20	37.43	45
TDS	35	50.25	71

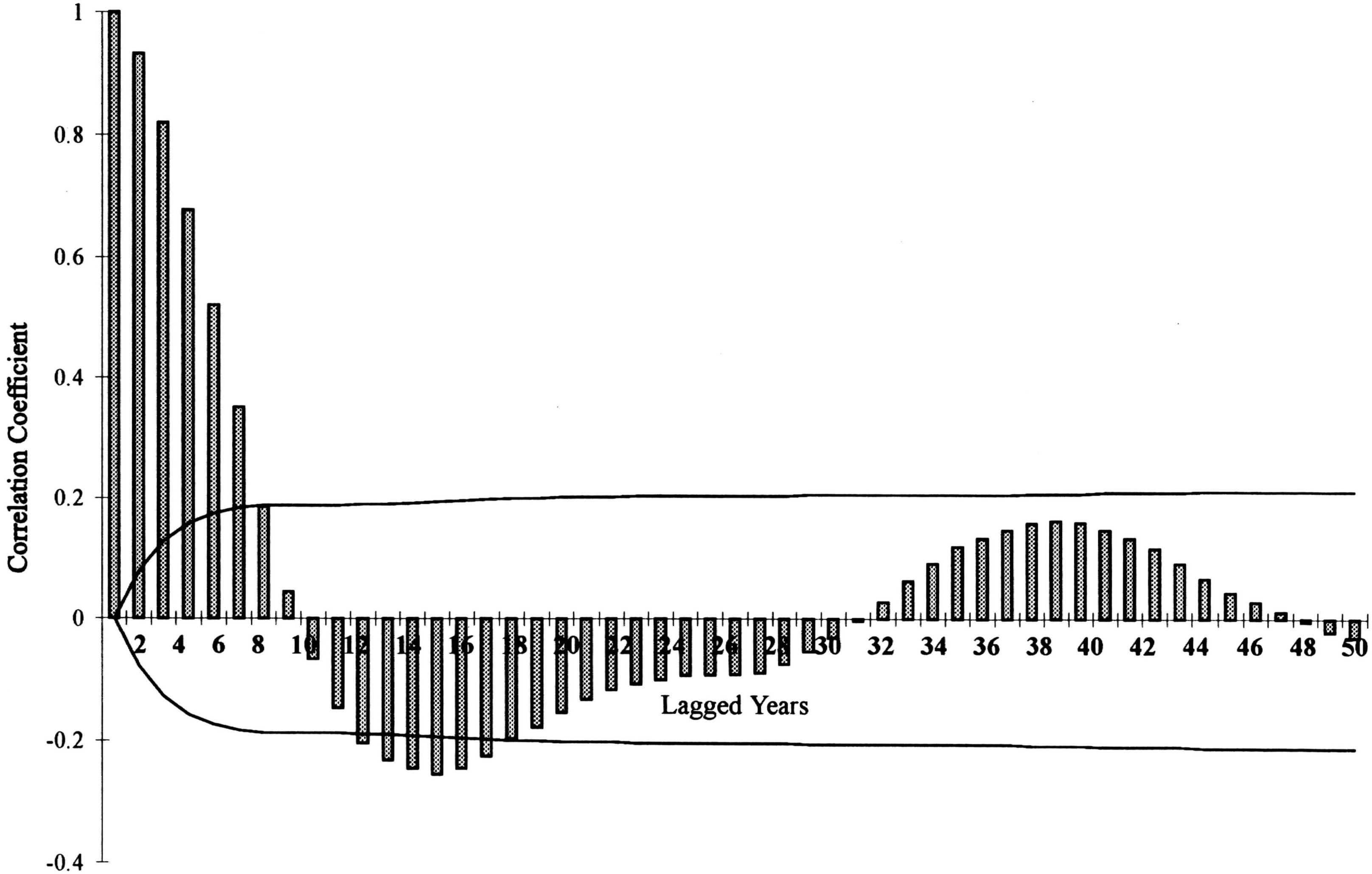


Figure 4.16. The autocorrelation function for pandora moth outbreaks through time. The time series appears to have cycles at around 20 and 40 years. The confidence intervals shown are 2 standard deviations from the mean.

somewhat periodic over the whole sampled range of pandora moth in Oregon.

The duration of each inferred outbreak, that is, the period over which tree-ring growth was suppressed, ranged from 4 to 18 years, with a mean of 10 years (Fig 4.17). The cumulative growth reduction in the tree rings associated with an inferred outbreak ranged from 12.5% to 57.5%, with a mean growth reduction of 29% (Fig. 4.18).

4.4 Climate

Twenty-eight sugar pine trees were cored as a possible non-host tree species to be used as a climate control in this study. The chronology was examined to determine if the ring-widths were affected during actual or inferred pandora moth outbreaks, as documented by an adjacent host tree site (EF). In two instances (1738 and 1802), the sugar pine trees showed a marked reduction in ring-width with thin latewood, the signature characteristic of pandora moth outbreaks. This suggests that sugar pine trees in south central Oregon were occasionally damaged by pandora moth outbreaks and, therefore, they were deemed not reliable as a non-host comparison in this study.

Because no other suitable non-host tree species could be located close to the pandora moth outbreak collection sites, a regional precipitation reconstruction from tree rings was used to control for climatic effects on tree growth. The 275-year-long regional precipitation reconstruction by Garfin and Hughes (1996) was used to determine regional periods of drought (Fig. 4.19). A ten-year running average indicated extended dry

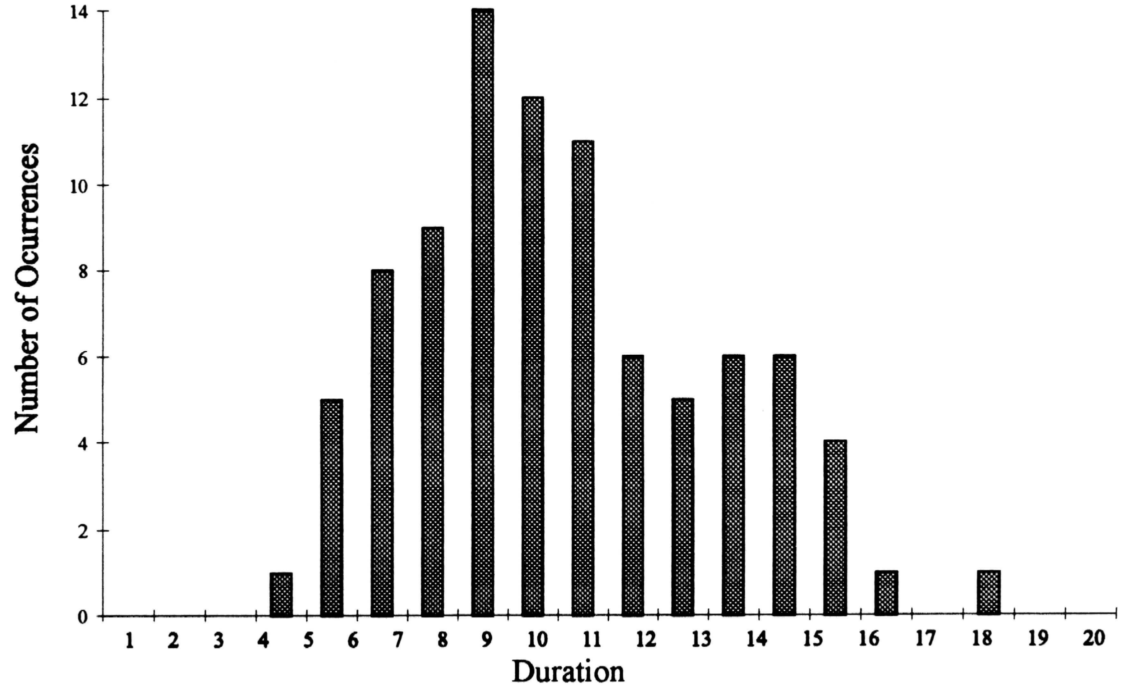


Figure. 4.17. Frequency distribution of the duration of outbreaks.

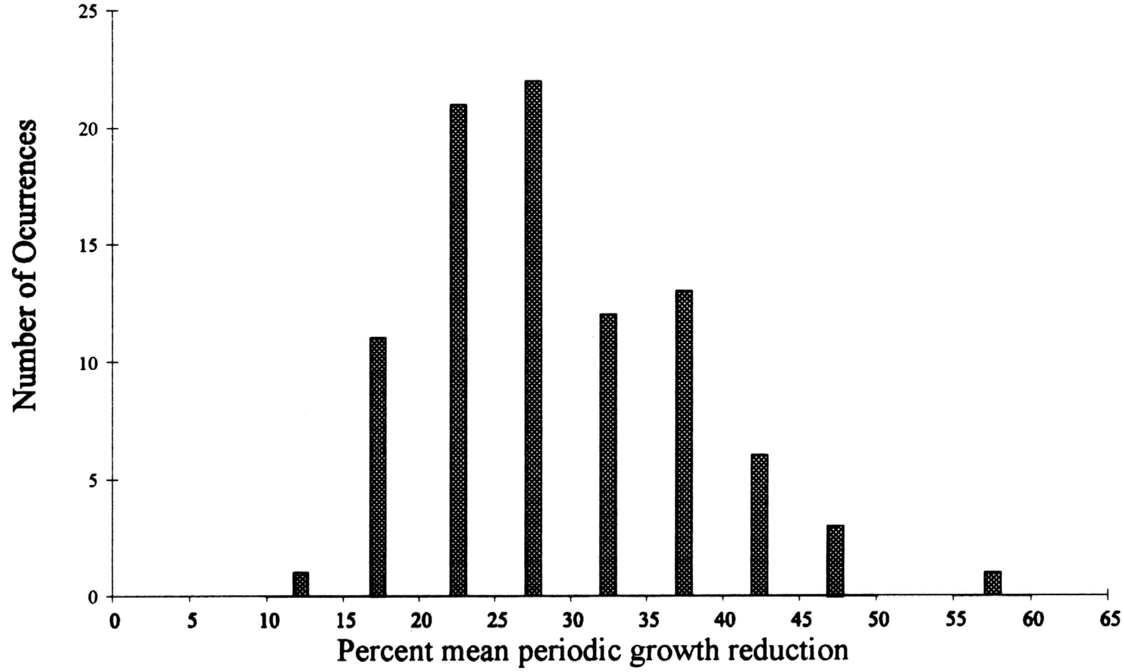


Figure 4.18. Frequency of the percent mean periodic growth reduction. This is a measure of the amount of growth reduction due to pandora moth outbreaks. Each bar represents a binned value of 5%, with the first bar including the values 10-14. The mean value is 25% and the standard deviation is 13%.

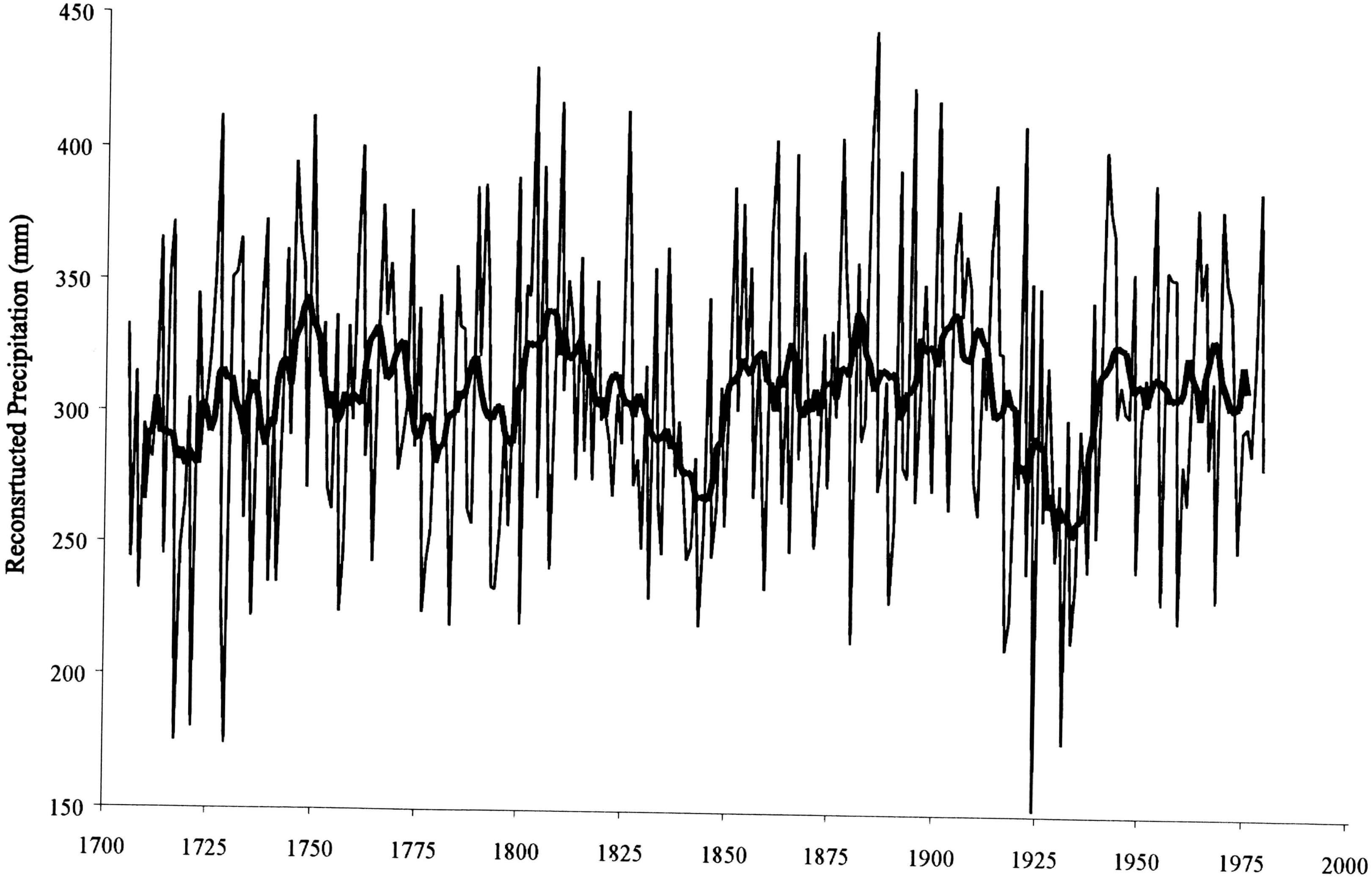


Figure 4.19. Reconstructed precipitation values for Oregon climate division 7 (Garfin and Hughes 1996).

periods in the 1840s and again in the 1930s. Twelve out of 14 tree-ring sites in this study recorded suppressions during the 1840s drought, all having the characteristic sharp decline in ring-width and thin latewood signature associated with pandora moth outbreaks. During the long period of drought in the 1930s, one of the most severe on record (Keen 1937), six of my tree-ring chronologies showed the distinct pandora moth suppression signature associated with the 1918-1925 documented outbreak (Patterson 1929). However, no suppressions were evident in these chronologies after 1934, and all other host trees in the outbreak area exhibited no ring suppressions during this dry period.

Garfin and Hughes (1996) also delineated 11 periods of drought that lasted from 3 to 10 years (Table 4.4). These dry periods showed no consistent relationship with the 12 periods of documented or inferred pandora moth outbreaks (Fig. 4.20). Furthermore, a Student's t-test indicates that the periods of outbreaks were not drier than periods between outbreaks (Table 4.5). This supports my conclusion that the suppressions inferred as pandora moth outbreaks were not due to drought.

The year-to-year variability in the tree-ring series was typically low, suggesting very little climate signal was present in these chronologies (Fritts 1976). It was common to only have four or five reliable narrow rings in a 600-year series. Common narrow rings were 1500, 1606, 1925, 1977, and 1989. This was reflected in the extremely low values for mean sensitivity. However, the series intercorrelation was relatively high for this species in the Pacific Northwest, and was probably due to the common signal of the outbreaks (Table 4.6).

Table 4.4. Dry periods for three years or greater compiled from a climate reconstruction for division 7 in Central Oregon (Modified from Garfin and Hughes 1996). Each dry year is chosen for having less than 100% of the mean of precipitation. Severity is defined as the cumulative level of the percent of precipitation over the duration of the dry period.

First Year	Last Year	Duration	Severity
1708	1711	4	356
1717	1719	3	224
1739	1742	4	344
1776	1778	3	235
1793	1798	6	515
1827	1829	3	262
1837	1844	8	684
1870	1872	3	263
1917	1920	4	325
1928	1937	10	829
1959	1961	3	251

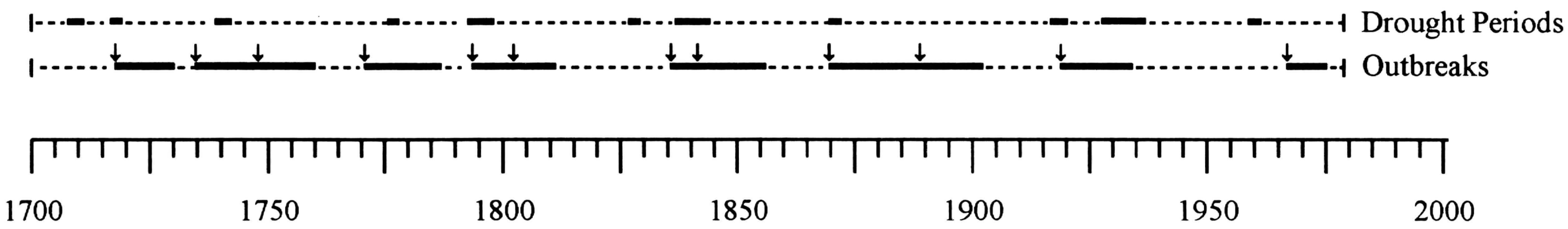


Figure 4.20. Comparison between drought periods and suppression periods. The arrows mark the beginning of inferred outbreaks.

Table 4.5. Results from Student's t-test for years during suppression with precipitation from Garfin and Hughes (1996) climate reconstruction.

Statistical Test	Mean (mm)	Standard Deviation	T value	P value	Interpretation
Years during suppression	303.1	57.2	1.49	.14	Not Significant
All other years	312.8	50.3			

Table 4.6. Fourteen outbreak sites listing the duration of the chronology, the mean sensitivity of the chronology, and the series intercorrelation

Site	Duration	Mean Sensitivity	Series Intercorrelation
LML	1529-1995	.203	.500
PF	1476-1993	.237	.514
EF	1334-1993	.207	.548
PPF	1354-1991	.228	.413
SVF	1747-1995	.217	.537
DES	1574-1995	.227	.599
JCT	1419-1995	.209	.441
SKB	1850-1995	.198	.491
DLK	1513-1995	.191	.478
BJS	1423-1995	.229	.510
TLD	1570-1995	.282	.534
TDS	1442-1995	.261	.487
CLK	1572-1990	.247	.513
CAB	1700-1995	.207	.519

The beginning years of the inferred outbreaks were compared to the regional precipitation reconstruction to ascertain a possible climatic triggering factor. The superposed epoch analysis demonstrated that the fourth year prior to an outbreak and the 2nd year after the beginning of the outbreak were wetter, while the year coincident with the start of the outbreak and the first year following it tended to be dry (Fig. 4.21). These values were based on only 12 occurrences of outbreaks during the period of record for the precipitation reconstruction. This is an interesting first look at climate phenomena versus pandora moth outbreaks but much more work needs to be done before any robust conclusions about climate as a triggering factor for outbreaks can be made.

4.5 Fire

Based on 30 fire-scarred sections from 25 trees, representing a chronology dating from A.D. 1350 to A.D. 1991, I identified 206 fire scars that occurred during 60 separate years (Fig. 4.22). The majority of the fire scars were in either the latewood or the dormant period, indicating that the fires burned at the end of the growing season, in late summer or fall (Fig. 4.23). The number of samples available to record the occurrence of widespread fires decreased drastically before 1652 and such fires ceased after 1886. Thus I have limited the period of analysis for these types of fires to that period. Only one widespread fire occurred at the beginning of a period of ring-width suppression identified as an outbreak period. Seventeen other suppression periods were not associated with any indication of past fires. Some local growth suppression occurred

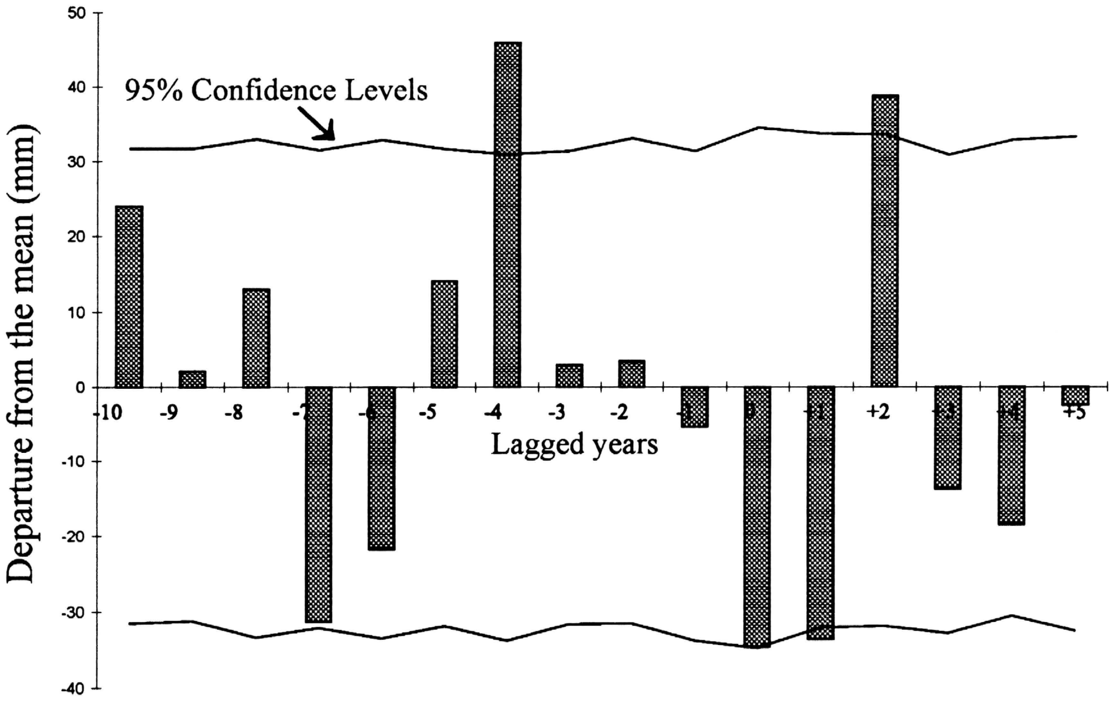


Figure 4.21. Superposed epoch analysis comparing average precipitation in years preceeding and following the onset of the outbreaks. The mean for precipitation values for all years is 305.5 millimeters.

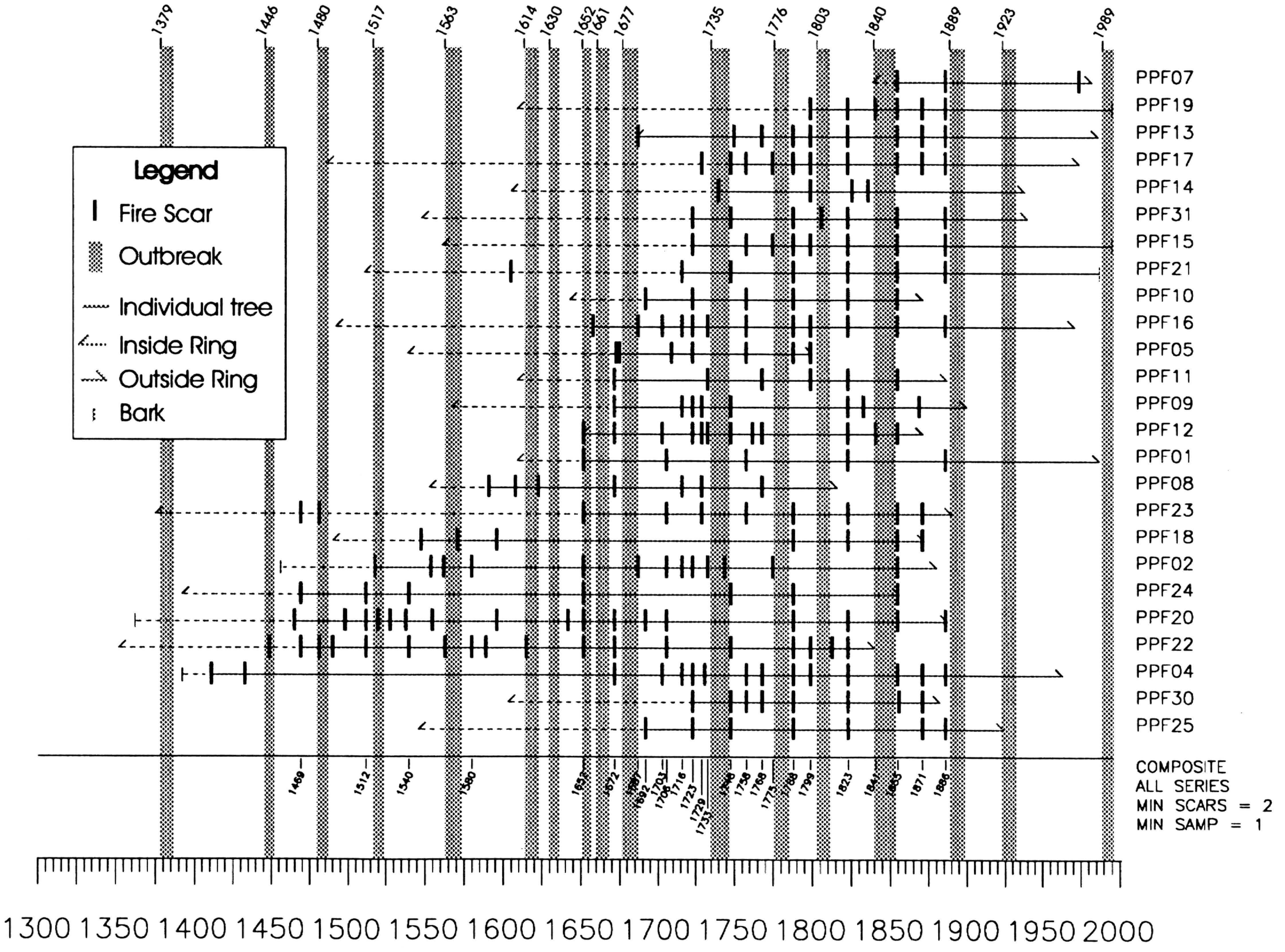


Figure 4.22. Fire history and outbreak record for site PPF.

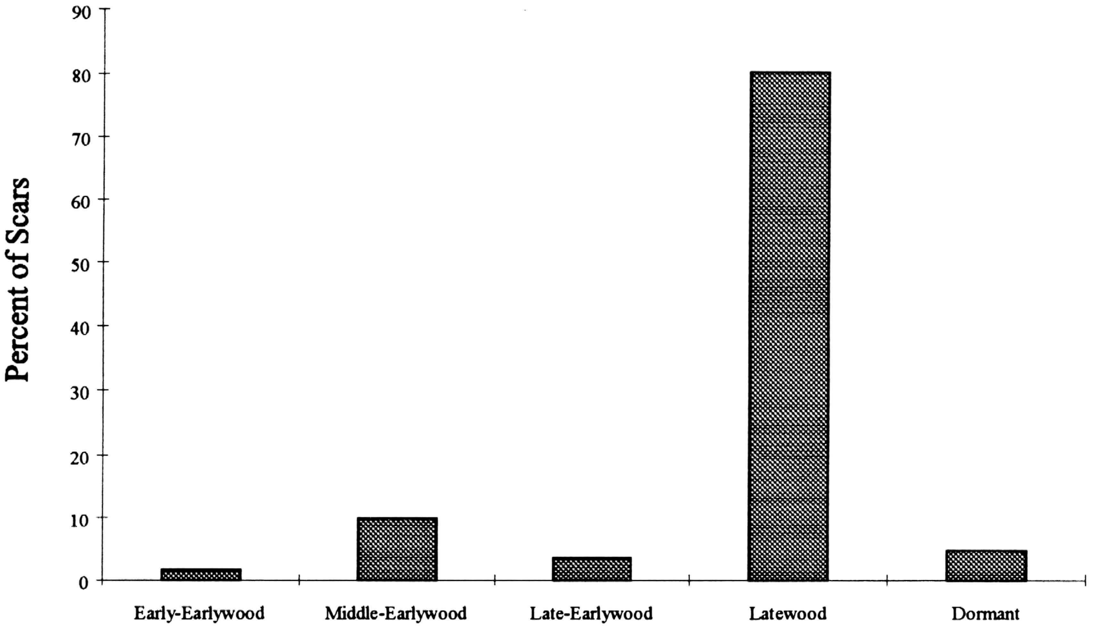


Figure 4.23. Position of the fire scars within the tree-rings, representing seasonality of the fires.

adjacent to the fire scars but did not continue more than a few centimeters from the scarred area (Fig. 24). Therefore, fire was not associated with the suppressions in the ponderosa pine trees, at least on the PPF site. There was also no consistent pattern of fire occurrence just prior to the beginning or prior to the end of an outbreak (Tables 4.7 and 4.8). From this I conclude that fire was not important in triggering or ending pandora moth outbreaks at the PPF site.

To examine what effects pandora moth outbreaks had on the fire regime, three different aspects of fire occurrence were evaluated, with consistent results. First, fires were five times more frequent during years that had no outbreaks, with a total of 17 fires during the 176 non-outbreak years, as compared to only two fires during the 91 cumulative years of outbreak (Fig 4.22). Second, fire occurrence tended to increase following the end of the outbreak period (Table 4.8). Finally, fire intervals (the period between fires) during outbreaks were significantly longer than intervals between outbreaks (Table 4.9). Thus, it appears that pandora moth may interfering with fire spread by interrupting needle fall.

4.6 Stem Analysis

The four trees used in this stem analysis ranged from 371 years to 569 years of age, with as many as ten outbreaks recorded on a single tree. Ring-width suppressions were evident throughout the entire stem on all trees (Fig. 4.25, 4.26, 4.27, and 4.28). For

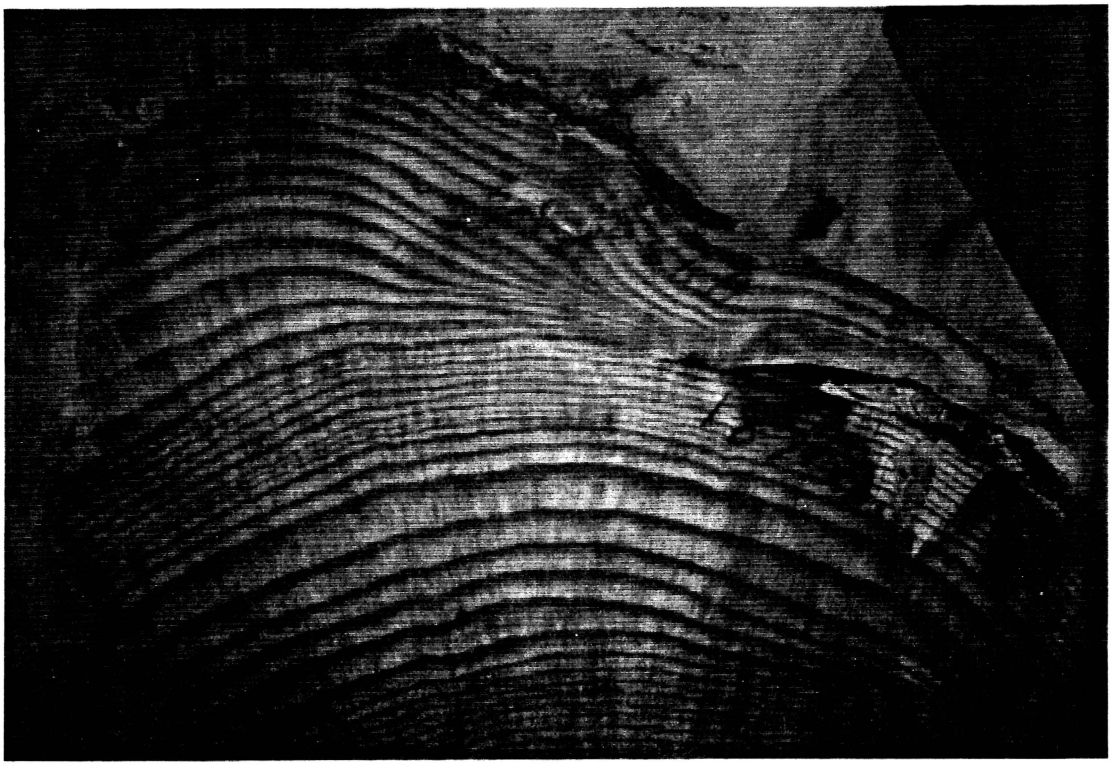


Figure 4.24. There was some local suppression due to cambial damage from past fires, but the suppression did not occur away from the scar.

Table 4.7. Occurrence of widespread fires (those that scar at least two trees in the study area) before the beginning of the outbreak. 1 designates the presence of a fire, 0 designates the absence of a fire, and * designates no data.

Lagged Years											**Year Beginning Outbreak**
t-10	**t-9**	**t-8**	**t-7**	**t-6**	**t-5**	**t-4**	**t-3**	**t-2**	**t-1**	**0**	
*	*	*	*	*	*	*	*	*	*	1	**1652**
0	1	0	0	0	0	0	0	0	0	0	**1661**
0	0	0	0	0	0	0	0	0	0	0	**1677**
0	0	0	0	1	0	0	0	1	0	0	**1735**
0	0	1	0	0	0	0	0	0	1	0	**1776**
0	0	0	0	0	0	1	0	0	0	0	**1803**
0	0	0	0	0	0	0	0	0	0	0	**1840**
0	0	0	0	0	0	0	1	0	0	0	**1889**
0	0	0	0	0	0	0	0	0	0	0	**1923**
0	1	1	0	1	0	1	1	1	1	1	**Total**

Table 4.8. Occurrence of widespread fires (those that scar at least two trees in the study area) at the end of the outbreaks.

Lagged Years											**Year Ending Outbreak**	**Lagged Years**			
t-10	**t-9**	**t-8**	**t-7**	**t-6**	**t-5**	**t-4**	**t-3**	**t-2**	**t-1**	**0**		**t+1**	**t+2**	**t+3**	**t+4**
0	0	0	0	0	1	0	0	0	0	0	**1657**	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	**1668**	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	**1686**	1	0	0	0
0	0	0	0	0	0	0	0	0	0	0	**1746**	0	1	0	0
1	0	0	0	0	0	0	0	0	0	0	**1785**	0	0	1	0
0	0	0	0	0	0	0	0	0	0	0	**1811**	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	**1854**	1	0	0	0
0	0	0	0	0	0	0	0	0	0	0	**1899**	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	**1932**	0	0	0	0
1	0	0	0	0	1	0	0	0	0	0	**Total**	2	1	1	0

Table 4.9. Fire intervals during outbreaks were significantly longer than fire intervals between outbreaks.

Fire intervals between outbreak	**Duration (years)**	**Fire intervals during outbreak**	**Duration (years)**
1687-1692	5	1652-1672	10
1692-1703	11	1672-1687	15
1703-1706	3	1733-1748	15
1706-1716	10	1775-1785	10
1716-1723	7	1799-1823	10
1723-1729	6	1823-1841	18
1748-1758	10	1841-1855	14
1768-1775	7	Mean	13
1788-1799	11	STD	3.18
1855-1871	16		
1871-1886	15	T=2.31	
Mean	9	p=.035	
STD	4.05		

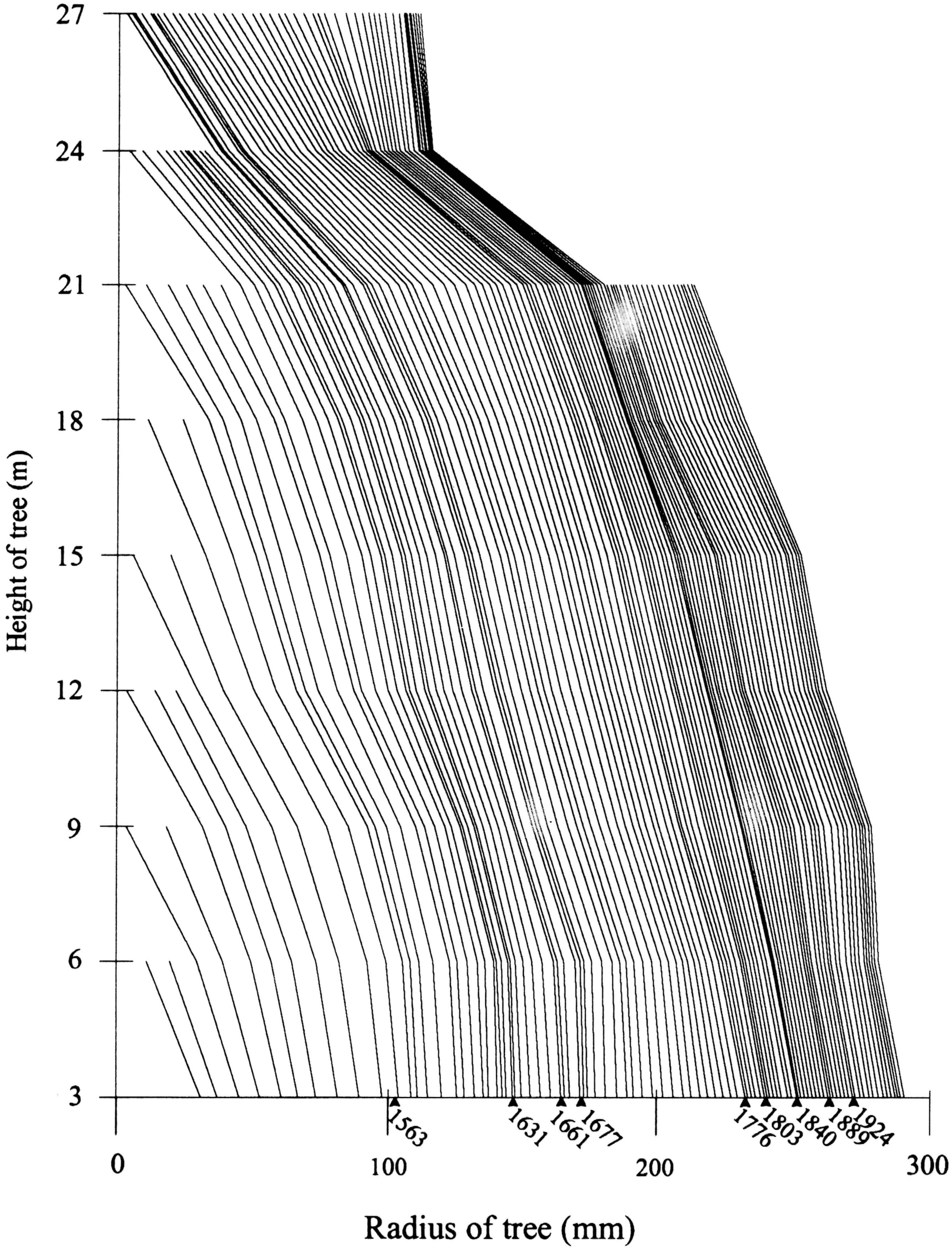


Figure 4.25. Stem profile of RNA01 with ring-widths summed every five years. The outbreaks are evident as areas of tight growth with the dates labeled at the bottom of the graph. The inside ring is dated at 1497.

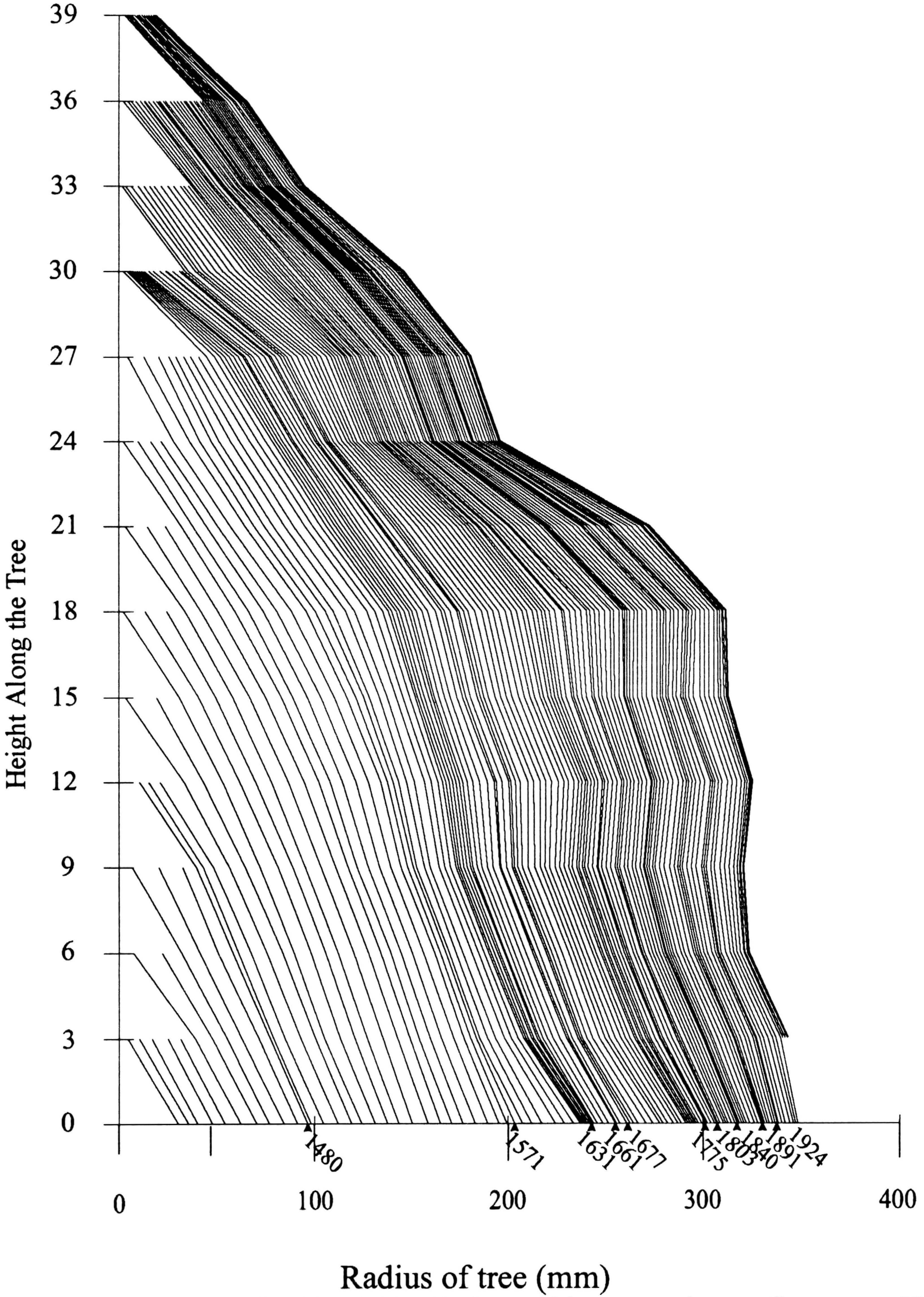


Figure 4.26. Stem profile of RNA02 with ring-widths summed every five years. The outbreaks are evident as areas of tight growth with the dates labeled at the bottom of the graph. Inside ring is dated at 1428.

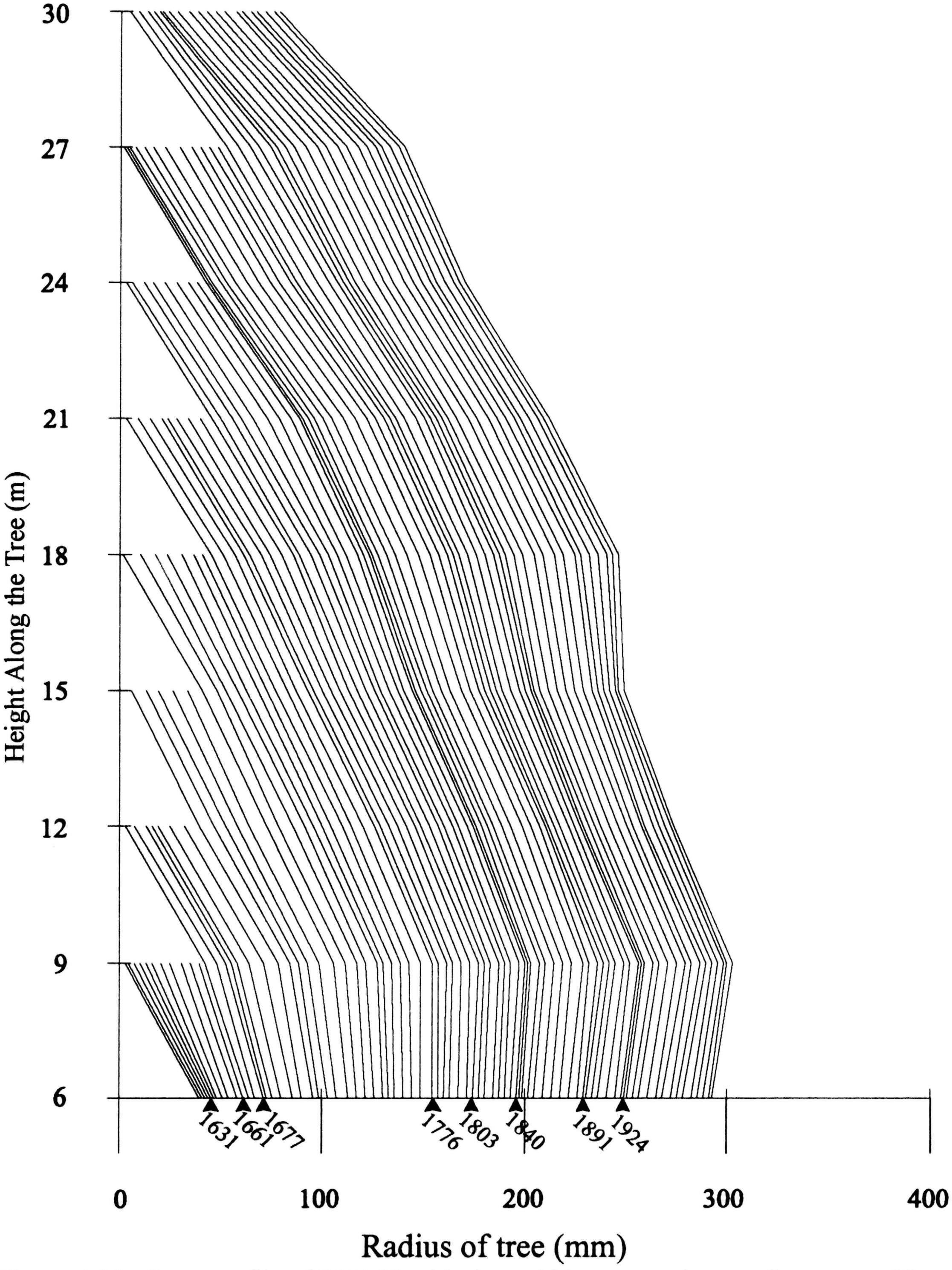


Figure 4.18. Stem profile of RNA03 with ring-widths summed every five years. The outbreaks are evident as areas of tight growth with the dates labeled at the bottom of the graph. The inside ring is dated at 1607.

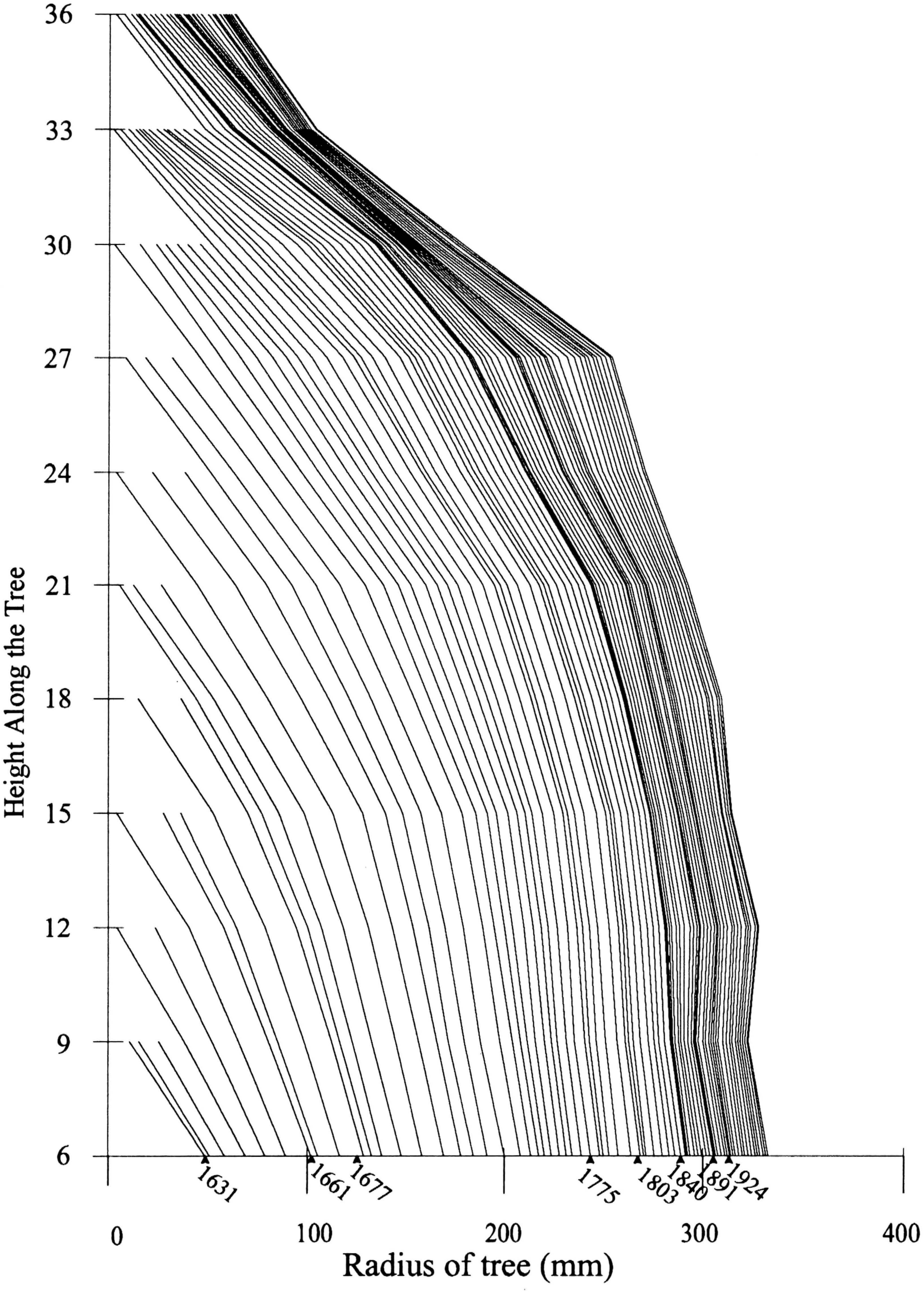


Figure 4.28. Stem profile of RNA04 with ring-widths summed every five years. The outbreaks are evident as areas of tight growth with the dates labeled at the bottom of the graph. The inside ring is dated at 1626.

a single outbreak, the volume reduction ranged from .001 to .146 m^3, with a minimum reduction of .026 m^3 for a mature tree (a tree producing growth on all crossections taken for the stem analysis). The average reduction for a single outbreak was .057 m^3 for a mature tree (Fig. 4.29). Variations occurred among the trees in cumulative volume reduction for all outbreaks, with two trees having less than half the overall volume loss of the other two trees (Fig. 4.30; Table 4.10), suggesting individual tree response to defoliation was dependent on stored food reserves, vigor of the tree, and the intensity of defoliation. The amount of volume loss within a given tree also varied along its length. The percent radial growth reduction tended to be greatest at the base of the tree, gradually decreasing along the stem with increased variability in the crown (Fig. 4.31).

Based on total annual volume reductions per outbreak, no temporal trend was apparent in the severity of outbreaks (Fig. 4.32). Neither was there any increase in the length of the outbreaks. The most severe outbreak occurred in the 1840s, whereas the 20th century outbreaks appeared to be within the range of severity and extent of prior recorded outbreaks (Fig. 4.6).

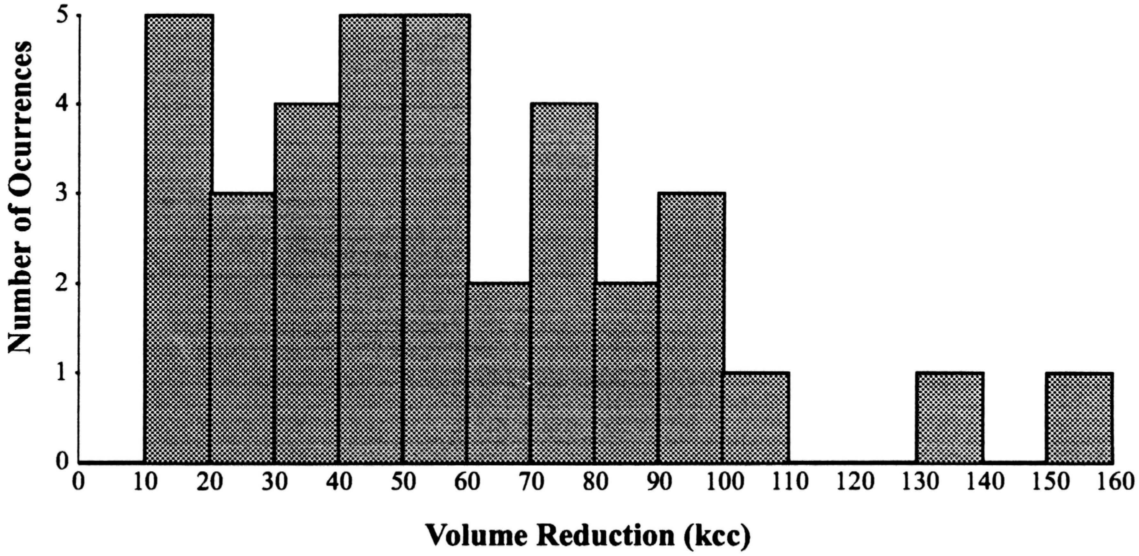


Figure 4.29. Frequency distribution of the amount of volume reduction in the stem analysis trees due to defoliation by pandora moth outbreaks.

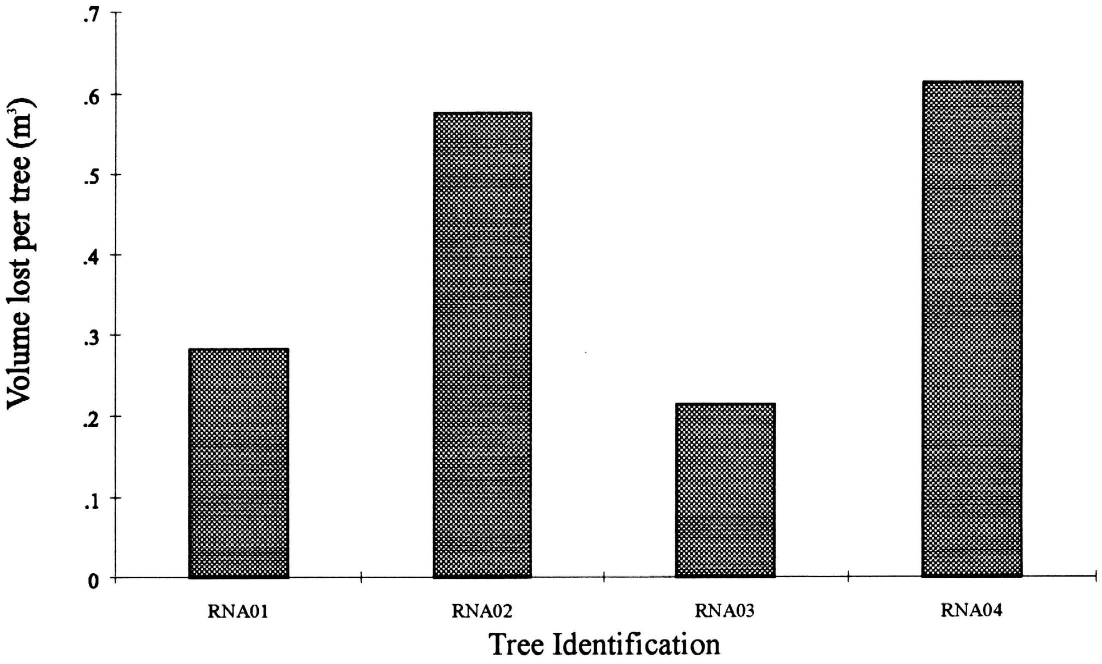


Figure 4.30. Total volume lost per stem analysis tree for all outbreaks.

Table 4.10. Volume of growth reduction within each tree due to each outbreak.

Outbreak	RNA01 Volume(m^3)	RNA02 Volume(m^3)	RNA03 Volume(m^3)	RNA04 Volume(m^3)
1479-1489	****	.039	****	****
1563-1577	.040	.077	****	****
1631-1638	.022	.030	.001	.007
1661-1666	.029	.043	.002	.034
1677-1686	.052	.064	.009	.091
1775-1783	.032	.036	.017	.080
1802-1811	.026	.038	.013	.124
1840-1853	.044	.082	.062	.146
1889-1902	.022	.061	.048	.072
1923-1931	.014	.071	.060	.059
Total	.281	.541	.212	.613

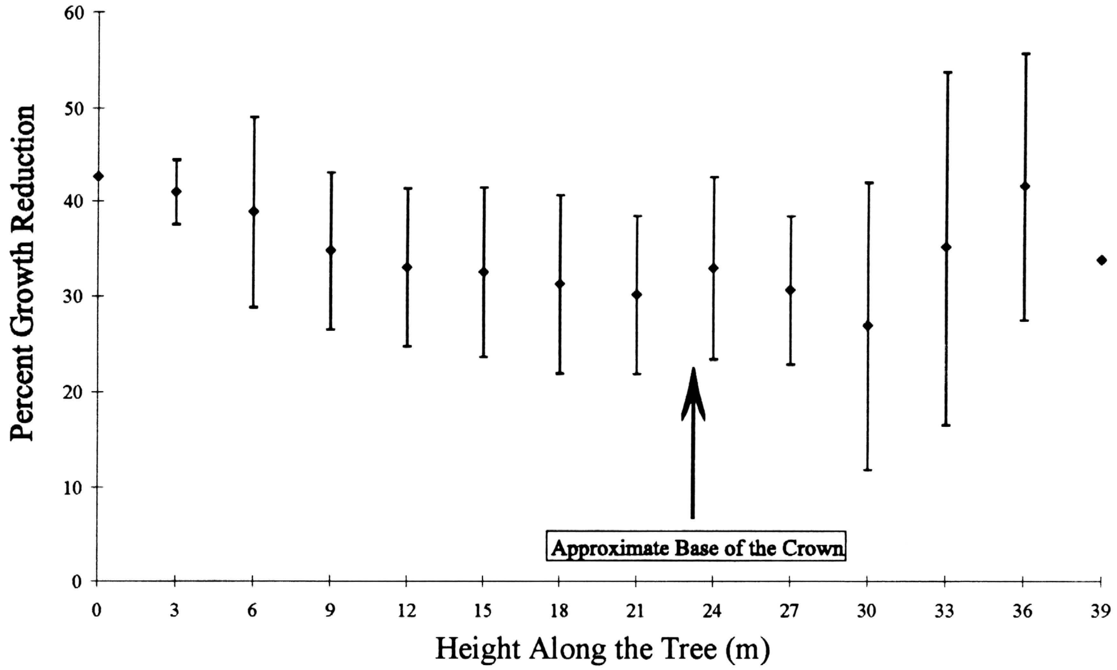


Figure 4.31. Percent radial growth reduction along the stem of the tree. This is the composite of all four trees for all outbreaks recorded by each tree.

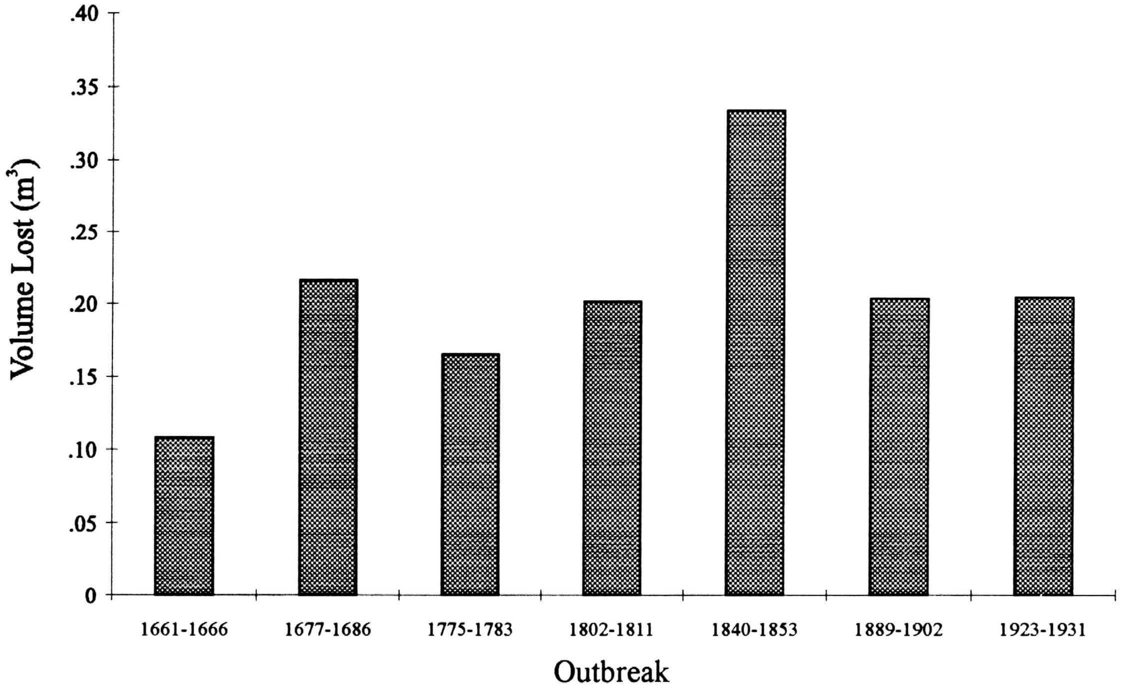


Figure 4.32. Average volume reduction per stem analysis tree for each outbreak.

CHAPTER 5

DISCUSSION

5.1 Identification of the Pandora Moth Signature

This study found a distinctive ring-width signature attributable to pandora moth defoliation. This pattern was similar to that found in previous pandora moth studies (Patterson 1929; Keen 1937; Miller and Wagner 1989). It was more distinct than signatures noted for spruce budworm and tussock moth (Wickman 1963; Brubaker and Greene 1978; Swetnam and Lynch 1993), but very similar to that of the pine butterfly (Evenden 1940). The consistent recurrence of this signature, as demonstrated in the comparison with independent, 20th century entomology records, enabled me to confidently identify specific occurrences of pandora moth outbreak throughout the 620-year tree-ring record.

Although the incidence of outbreak was reliably recorded, the 20th century comparisons indicate that the appearance of the signature lagged the beginning of the actual insect outbreak by one to several years. The tree rings tend to record the first years of highest insect population, and hence heavy defoliation, rather than the years in which the growth of the insect population began to accelerate. For example, in the modern outbreak, the distinctive thin latewood marking the beginning of the ring-width signature was concurrent with the year of maximum area defoliated in the region (1994). In the other well documented outbreaks of 1963-1968 and 1918-1925, the signature first appeared 1 to 4 years after the documented first year of the outbreak. (The beginning of the ca 1893 outbreak was not documented.) This lag can have important implications when searching for a climatic triggering factor, as any triggering factor could have occurred as much as 4 to 6 years before the trees recorded the effects of the outbreak.

Spruce budworm and Douglas-fir tussock moth studies have noted a lag between heavy defoliation and the first evidence of its effect on tree growth (Blais 1961; O'Niell 1963; Wickman 1963; Kulman 1971; Rook and Whyte 1976; Brubaker and Greene 1978; Wickman *et al.* 1980). The lag effect was attributed to stored food reserves in the tree. The impact seems to be fairly immediate with pandora moth, however, due to their quick removal of all old foliage, which only occurs in a year of extremely large population. For the modern pandora moth outbreak, the four tree-ring sites recording the outbreak show the distinct thin latewood marker ring in 1994, the year of peak insect population and heaviest defoliation. Only the modern outbreak was sufficiently documented, regarding peak population year and specific sites affected, to permit such comparisons.

There was insufficient historical information to permit comparison of the numbers of pandora moth larvae to amount of growth reduction, as was done in a number of spruce budworm and Douglas-fir tussock moth studies (Wickman 1963; Wickman 1980; Wickman *et al.* 1980; Swetnam *et al.* 1995; Mason *et al.* 1997). While aerial maps of the modern outbreak do show areas of light, moderate, and heavy defoliation, it will be a few years before the ring signature is complete and a comparison similar to those in previous studies (Miller and Wagner 1989) can be attempted. A study at that time may establish a relationship between the degree of defoliation and the resultant effect on the tree.

The tree-ring record did not always corroborate the historical documentation of whether a site was part of an observed outbreak. Some tree-ring sites outside the documented outbreak areas exhibited ring-width suppressions identical to the distinctive pandora moth ring-width signature. These suppressions also occurred around the time of the documented outbreaks. Consequently, I am confident these represent pockets of pandora moth defoliation that probably went undetected because all of the forest area could not be continually surveyed. Although the Klamath Lake outbreak around 1893 was recorded in the tree-ring record of the northern sites, the southern sites had no evidence of this in their tree-ring records. It is possible that these southern sites were simply not in the right locations to detect the outbreak signal.

5.2 Possible Confounding or Interacting Factors

5.2.1 Climate

Several lines of evidence lead me to conclude that drought did not directly cause the ring-width suppressions identified as pandora moth outbreaks in these ponderosa pine chronologies:

(1) The ring-width pattern identified for pandora moth is very distinctive and has persistent thin latewood. The overall ring pattern is complex and would be unlikely to form as a result of climate.

(2) Long-term droughts (*i.e.* lasting 10 years or more) were rare in the region, only two (the 1840s and 1930s) being recorded in the precipitation reconstruction of Garfin and Hughes (1996). Suppression from a documented pandora moth outbreak was recorded from 1922 to about 1931. The tree-ring series showed the distinct pandora moth suppression signature a few years prior to the main period of drought. During the 1840s drought, the ring-width suppressions again had the distinct ring-width signature associated with pandora moth outbreaks.

(3) The Student's t-test demonstrated that the periods during which outbreak inferred growth suppressions were recorded in the ponderosa pine tree record were not significantly drier than all other years in the precipitation reconstruction based on a regional set of juniper tree-ring chronologies.

(4) The outbreak spread maps illustrate dissemination from a central area and propagation through time which would be expected from outbreaks but not climate.

Using the principle of uniformitarianism ("the present is the key to the past"), this conclusion should hold true for this region in the past. I would further postulate that, in this part of central Oregon, the ponderosa pine chronologies' weak response to drought was due to the loose pumice soil on which the trees grow. This soil has unusually high water retention, providing enough available moisture to sustain the tree through periods of limited precipitation (Franklin and Dyrness 1988). Consequently, throughout the length of the chronologies, the tree growth was relatively complacent. A lack of response to climate, normally a curse to dendrochronologists, is a boon in this instance, since climate did not complicate the signal of past outbreaks.

The output from the EVENT program suggests two possible climate triggers for pandora moth outbreaks: wet periods may help trigger initial outbreaks of the insect, and a dry year during active outbreaks may release resident populations. These opposite forcing factors might act on different parts of the moth's life cycle. Moth survivorship could be enhanced by wetter periods, stimulating pandora moth egg laying resulting in growth to outbreak levels. Larvae survivorship could be enhanced by dry climate conditions, resulting in a high moth population. These preliminary findings are interesting but may not provide the full picture. The insects might be responding to short-term (daily to weekly) weather fluctuations (Koerber and Wickman 1970), and the annual values used here could confuse the issue. Therefore, careful study of climate variability at various time scales may provide insight into possible climate triggering mechanisms. The two most important time periods are about 4 to 6 weeks of larval feeding in the early summer and several weeks of mating, flight, and oviposition (B. Wickman, pers. comm.).

5.2.2 Fire

I initially hypothesized that fire could be a confounding factor in determining past pandora moth outbreaks. After comparison of the fire dates with the beginning of the suppression periods at one site, I am confident that fires did not cause the ring-width suppressions interpreted as outbreaks. Some suppression was concurrent with the fire events but was confined to the local area of cambial damage (Fig 4.8). This contradicts findings in a previous study that associates ring-width suppressions with fire scars in the Pringle Falls area (Bork 1984). Bork (1984) conducted a climate reconstruction and concluded the suppressions were not due to climate, but were attributable to fire. I would speculate that this conclusion was reached without knowledge of recurring pandora moth outbreaks on the site.

From the lack of synchroneity between the occurrence of fire and the first year that the trees record pandora moth outbreaks, I conclude that fire did not trigger outbreaks. There was no increase in the number of fires before the outbreaks began. Furthermore, over half the outbreaks commenced without any evidence of a fire occurring up to 10 years prior to the outbreak. Neither did the occurrence of fire terminate the outbreaks. There was no pattern of increased fires in the 10 years prior to the end of each outbreak, with widespread fires preceding outbreak termination in only 2 out of 9 cases. This conclusion is supported by Schmid and Bennett (1988), who found that prescribed burns during the 1978 Kaibab Plateau outbreak in Northern Arizona did not reduce the number of pupae sufficiently to alter the course of the outbreak.

Several findings suggest that defoliation by pandora moth affected fire spread in the past. Five times fewer fires occurred when the trees were experiencing ring-width suppression due to pandora moth defoliation. The inferred outbreaks were associated with significantly longer intervals between fires. An increase in the number of fires occurred following the end of the suppressions in tree growth due to pandora moth. Therefore, I hypothesize that pandora moth outbreaks delayed the occurrence of fire by interrupting needle fall. A reduced amount of needles on the forest floor in years during outbreaks may have been sufficient to inhibit fire ignition and spread. This conclusion may be unique to the pandora moth system, in which little tree mortality occurs from outbreaks and, hence, the heavy fuels (dead wood) that characterize other types of insect outbreaks do not accumulate. The constraint on fire spread due to the lack of needle fall may not hold true during the fire suppression era (*i.e.* the past 80 years) when fuels have been allowed to accumulate. The lack of needle fall during modern outbreaks would have relatively little influence on the overall fuel load. These conclusions were based on findings from a fire history study on one pandora moth outbreak site. Further work should be conducted to test this hypothesis more broadly by studying the occurrence of widespread fires on many more insect defoliation sites.

5.3 Reconstruction of Pandora Moth Outbreaks

Based on the calibration of tree-ring chronologies with documented outbreaks of pandora moth, the tree rings record the first year that the specific trees were heavily defoliated, which lags, by 1 to 4 years, the first year that insect populations grew to outbreak levels. Furthermore, the recovery time of the tree was somewhat longer than the time required for the insect population to rise from initial outbreak levels to peak population. Consequently, the tree-ring signatures of the outbreaks were consistently longer than the documented outbreaks, complicating estimates of past outbreak length.

Given these conditions and uncertainties, the tree-ring suppressions can be used to reconstruct some aspects of past pandora moth outbreaks:

- They will enable determination of the year of peak defoliation during past outbreaks, but probably not the initial phase during which the insects began multiplying to outbreak populations.
- The approximate length of the insect outbreak will be a few years (2-3) less than the length of the suppression period in the tree-ring record.

5.3.1 Spatial Pattern in Outbreaks

An interesting pattern presents itself in the spread maps of the individual outbreaks in the outbreak history. Because the pandora moth has a two year life cycle, trees would most likely suffer severe damage in the second year of the cycle, and a pattern of outbreaks at new sites every other year would be expected. However, the peak years for most outbreak across the study sites were generally one year apart (*e.g.* Figs. 4.13 and 4.14). Stored food reserves could enable a defoliated tree to persist one more year with normal growth before showing the effect of defoliation. If the majority of trees in a particular stand were healthy enough to postpone the effect of defoliation, perhaps because of slightly better growing conditions at that site, their lagged response would produce a suppressed tree-ring a year later than a less robust stand, giving the appearance of a one-year spread pattern. A second hypothesis would be that the diapause of the insect enabled emergence of the moth to occur every year, a phenomena not observed in the 20th century. Because most of the spread maps show this one-year spread pattern, I do not believe that this was the explanation in the past. A third possible explanation concerns the first year of the pandora moth life cycle, when only first and second instar larvae feed on needles. Although the larvae are much smaller than during the second year, and presumably consume a smaller quantity per individual, at high enough populations they may be capable of major defoliation causing tree-ring suppression. Trees at these sites would then begin recording in the first rather than second year of the cycle, giving the appearance of a one-year spread pattern. None of these hypotheses were tested here but are put forth as possible explanations.

5.4 Modern versus Past Outbreaks

The insect outbreak history developed for this study encompasses a wide range of lengths and severities of outbreaks. The modern outbreak of 1988-1996 was examined against the outbreak history to determine if it fell within the range of historical variability. When the range of all suppressions periods, 4 to 18 years, was discounted by a few years to account for the previously noted difference between outbreak duration and suppression period, the 9-year length of the modern outbreak fell well within this historical range. The interval between the modern outbreak and the prior one, 27 years, was also within the historical range of 8 to 48 years. The area of effect, as mapped from recording sites, was within the natural range of variability. Also the severity on individual trees seems to be no greater than in the past. These findings contrast with many spruce budworm studies that have found an increase in severity and extent of 20th century outbreaks (Blais 1983; Swetnam *et al.* 1995).

I suggest that pandora moth would respond to logging, which removes its primary food source and fragments ponderosa pine stands, in a manner opposite that of the spruce budworm, with the result of smaller outbreaks and less severe outbreaks. This is a much more difficult signal to discern than the increased severity and expanse of modern spruce budworm outbreaks, with their higher mortality rates, often as much as 80%, in heavily defoliated stands (Swetnam *et al.* 1995). Therefore, a pattern of change for pandora moth outbreaks may not yet be apparent on the landscape.

A trend towards smaller and less severe pandora moth outbreaks would be more difficult to establish, since the outbreak history contains earlier periods of less severe outbreaks occurring over longer intervals. This may, in fact, be occurring at present, but the system is still within its historical range of variability, and no striking sign of change in this system is yet evident. It is also possible that current land use practices have no effect on pandora moth outbreaks. Because pandora moth is a strong flyer, fragmentation by logging and the introduction of roads may not have a significant effect on the outbreak dynamics.

5.5 Stem Analysis

The stem analysis indicated that the percent volume reduction due to pandora moth defoliation was greatest and most consistent at the base of the tree. These findings agree with that of Alfaro *et al.* (1985) but are contrary to those of Wickman (1963) and Mott *et al.* (1957). Alfaro *et al.* (1985) contend the discrepancies with other studies were probably due to a difference in methods. Our two studies being based on percentage of potential growth rather than actual increment of radial growth. When I analyzed the stem profiles in this study using incremental radial growth, my measurements also showed less radial growth in the crown of the tree than the base. But this was due to the tree producing less radial increment in the crown even under normal circumstances.

Aside from methodological differences, greater growth loss in the canopy could result from the stem die-back that accompanies spruce budworm infestation. In this study, the phenomenon of die-back was not observed in trees that had experienced pandora moth defoliation; therefore, it would be quite possible that these trees would not exhibit greater growth loss in the canopy.

A lag between growth reduction in the canopy of the tree and the base of the tree was noted in other stem analysis studies (Wickman 1963; Mott *et al.* 1957). This lag throughout the tree was not noticed with pandora moth, possibly because pandora moth feed on old needles, and the first instance of heavy defoliation is usually abrupt, with severe defoliation occurring in one year. The conclusion of a lag between the canopy and the base of the tree within a single year of growth also seems to violate basic tree physiology; if a tree shows the effect in the canopy in a particular ring, the effect should be evident in the same year at the base of the tree. Actually, the effect of reduced growth due to limited resources, such as drought, is usually accentuated at the base of the tree. If the supply of the growth hormone auxin, produced in the foliage, is limited, it could be exhausted by the time the tree ring forms at the base (Onaka 1950; Fritts 1976). Also, Mott *et al.* (1957) did not crossdate the specimens for their stem analysis, therefore, the apparent lag in ring-growth response between canopy and base could be simply a mis-interpretation of the year the tree rings formed on the cross-sections under comparison.

The work done in this stem analysis determined the range of volume reduction due to pandora moth defoliation that occurred in four ponderosa pine trees. Should these trees prove to be representative of the population of ponderosa pine trees, they may provide a useful estimate of the amount of volume reduction likely in future outbreaks. At this time, the amount of volume reduction cannot be directly related to the mean periodic growth reduction obtained from a core at breast height. However, sampling at breast height does yield an accurate record of past pandora moth outbreaks and may be a good relative measure of the impact of the defoliation.

5.6 Need for Multi-Regional Pandora Moth Outbreak Study

This study has identified interesting interactions between pandora moth outbreaks, fire, and climate on the regional scale of central Oregon. It would be of further interest to study the dynamics of pandora moth outbreaks in other areas to ascertain if there is a multi-regional dynamic. The next closest population of pandora moth is 400 kilometers away in California, with other populations as far away as Colorado. The next obvious step in expanding this research is a study of the long-term history of this insect throughout all of its range in the western United States. This may enable a better understanding of the interaction between climate and pandora moth outbreaks.

The economic impact of pandora moth is not as significant as that of some other insect species. Western spruce budworm and Douglas-fir tussock moth both cause more damage to the forests and are more widespread. However, this study's finding that pandora moth leaves a very distinct ring-width signature raises the possibility of studying past pandora moth outbreaks to determine the interaction between defoliating insect outbreaks and the ecosystem in which they operate, a broad area in great need of further work and deeper understanding.

One of the more interesting findings of this study is the effect of pandora moth on the spread of fire. This should also be further studied, for if it can be clearly demonstrated to be true, it will be the first definite evidence of synergism between fire and insect outbreaks over century time scales.

CHAPTER 6

CONCLUSIONS

Pandora moth proved to leave a distinctive signature in the ring-width series of the defoliated ponderosa pine trees. The signature from defoliation could be discerned from suppressions left by drought or fire. This distinctive signature combined with the old age of the trees enabled a long-term reconstruction of pandora moth outbreaks.

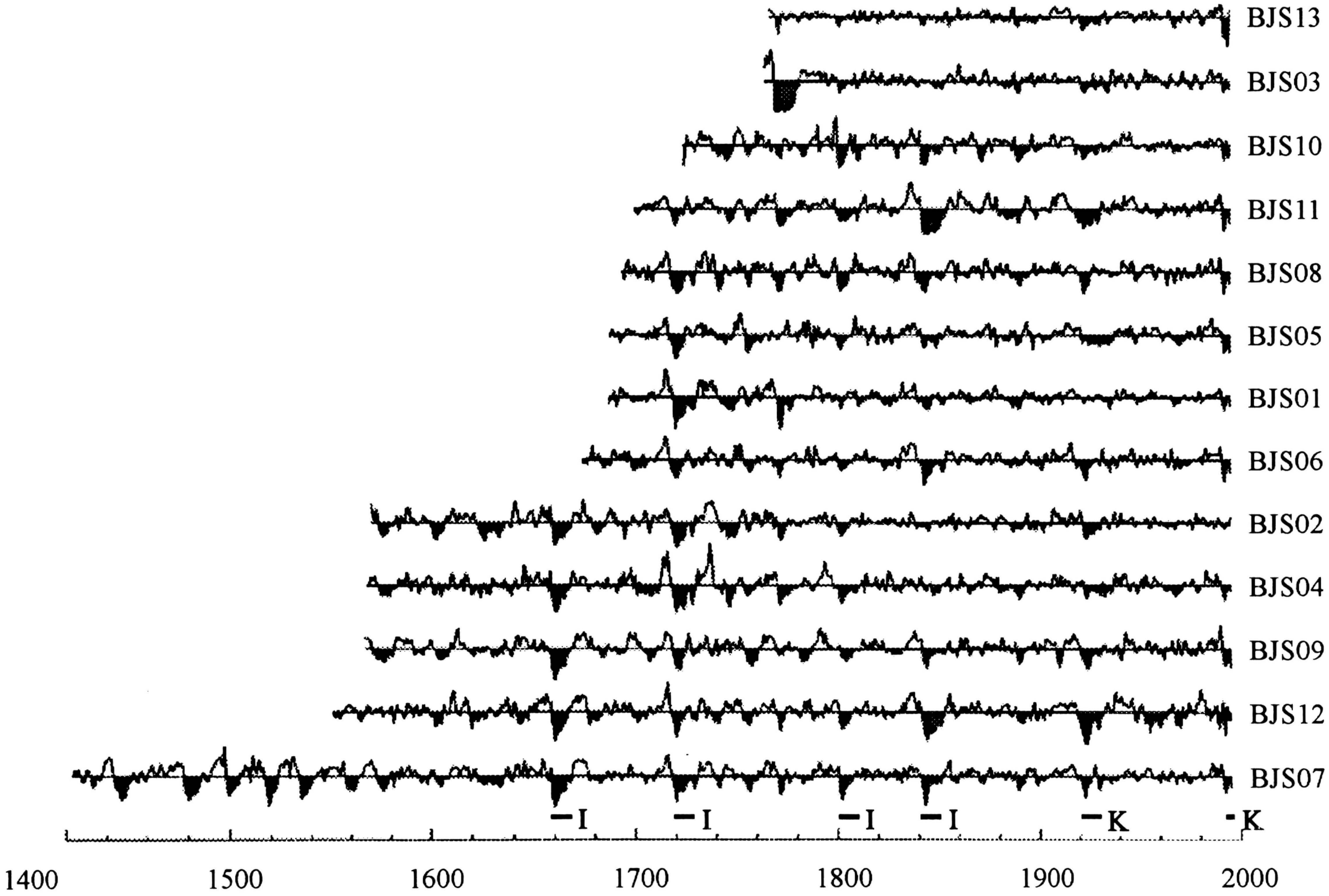
The signature left by pandora moth outbreaks lasted from 4 to 18 years, with an average duration of 10 years, suggesting that the modern outbreak of 9 years was within the natural range of variability. The interval between outbreaks was episodic on individual sites but somewhat periodic on the regional scale. This suggests that the population in Oregon behaves as one population, moving from one site to another. The periodic growth reduction for an outbreak ranged from 12.5% to 57.5%, with mean of 29%.

The spread maps of the inferred outbreaks revealed spread similar to that observed in the modern outbreak, but new sites were affected usually every year. This was thought not to be possible because of the two year life cycle of pandora moth. Three possible explanations are suggested: 1) lagged tree response to defoliation could cause an artificial propagation signal for the beginning of the outbreaks; 2) the first and second instar larvae (that feed in the first year of the life cycle) could cause more damage than was expected, producing growth reduction in the same year as a moth flight; or 3) diapause of the pupae in the ground could allow mature larvae to be feeding every year during an outbreak.

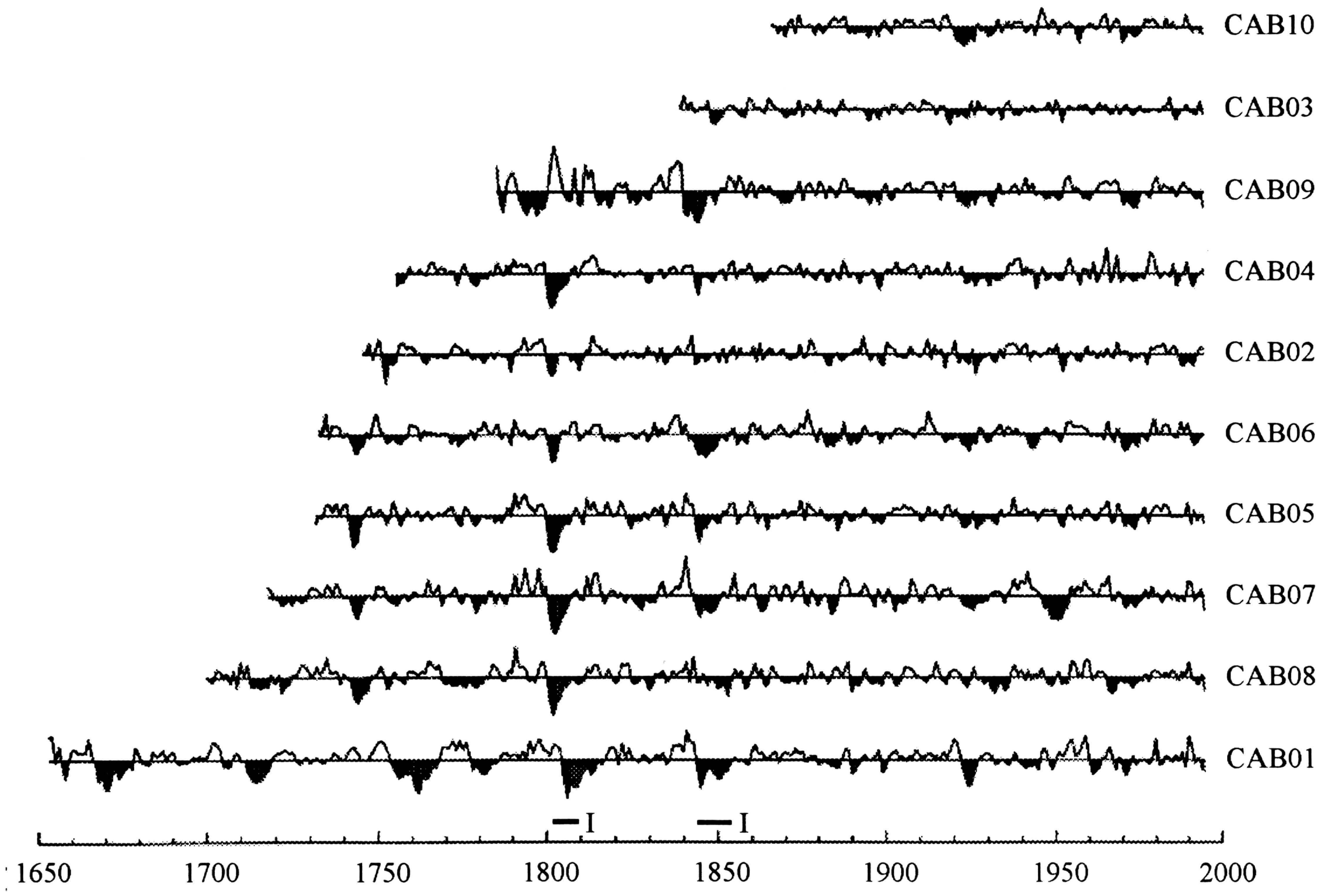
Defoliation by outbreak populations of pandora moth interrupted needle fall needed for fire ignition and spread. Therefore, pandora moth seems to be affecting the fire regime. Although fire does not seem to trigger or end pandora moth outbreaks, precipitation does seem to affect the occurrence of outbreaks. The first year that the outbreak was recorded tended to be dry while the fourth year prior tended to be wet. This could be due to precipitation having differing effects on the stages of pandora moth's life cycle. Additional insight could be gained by studying weekly precipitation values instead of the water year (October through September) values examined here.

The stem analysis was the first conducted on pandora moth defoliated trees. I found that the effect of defoliation was greatest at the base of the tree. This differed from findings for stem analyses on spruce budworm and Douglas-fir tussock moth defoliated trees, which demonstrated a greater effect in the canopy of the trees. This discrepancy could be due to differences in quantifying this effect. I measured the percent of volume reduction, while the researchers with different findings measured radial increment. I suggest that percent volume reduction is a more accurate measure of the effect of defoliation because it accounts for the normal tree growth pattern of less volume of wood produced in the crown (as demonstrated by the stem profiles Figs. 4.25, 4.26, 4.27, and 4.28).

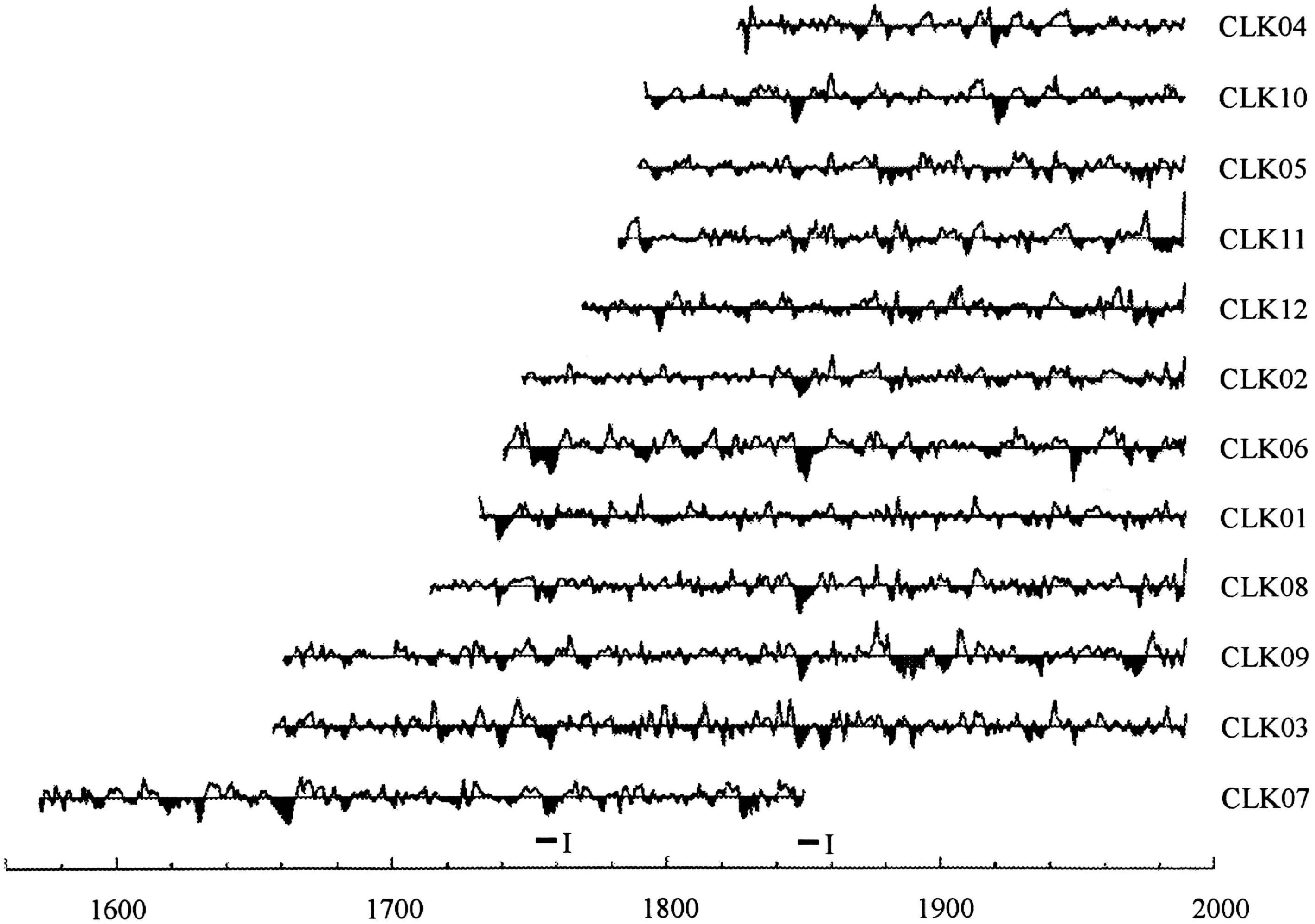
This study of pandora moth outbreaks has provided a clear picture of some disturbance processes in the ponderosa pine forests of south central Oregon. It has reconstructed an unprecedented long-term record of pandora moth outbreaks, and also identified a possible synergism between insect outbreaks and fire.



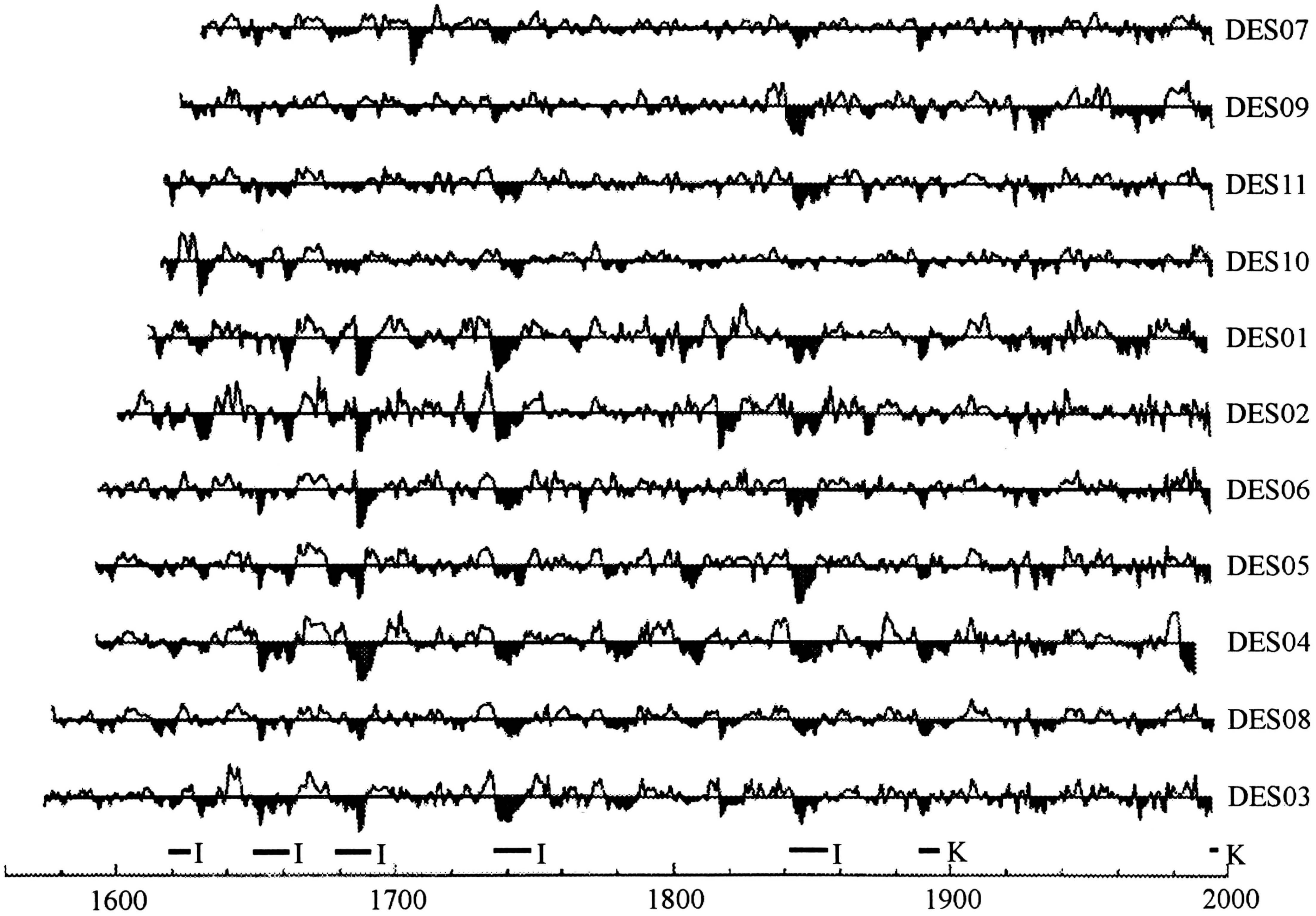
Appendix A, Figure 1. Plot of the ring-widths for the Blue Jay Spring (BJS) site. The shaded area are the below average ring-widths. Insect defolitation causes long periods of suppression. (K stand for known outbreaks, I stand for inferred outbreaks).



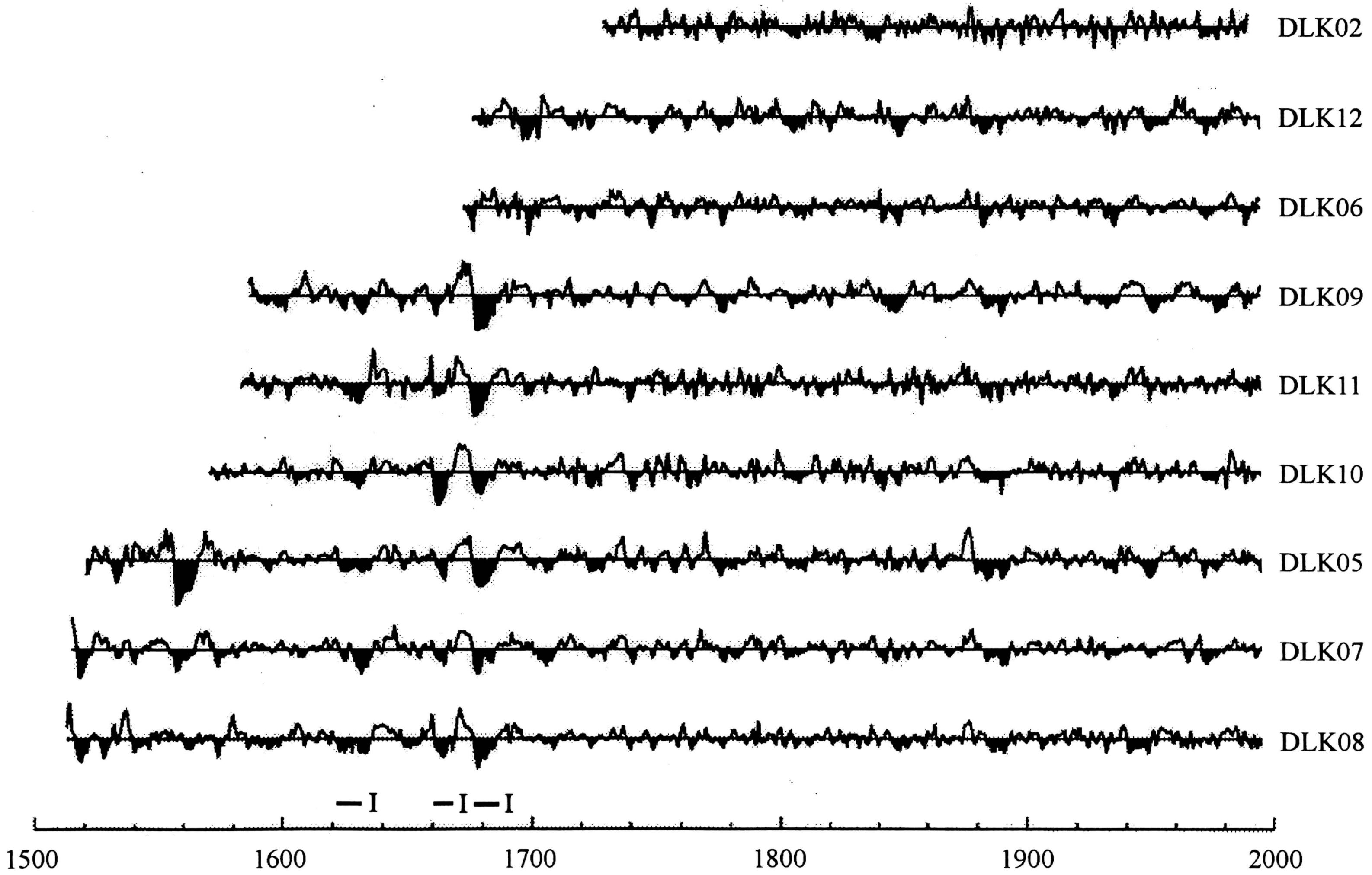
Appendix A, Figure 2. Plot of the ring-widths for the Calimus Butte (CAB) site. The shaded area are the below average ring-widths. Insect defolitation causes long periods of suppression. (K stand for known outbreaks, I stand for inferred outbreaks).



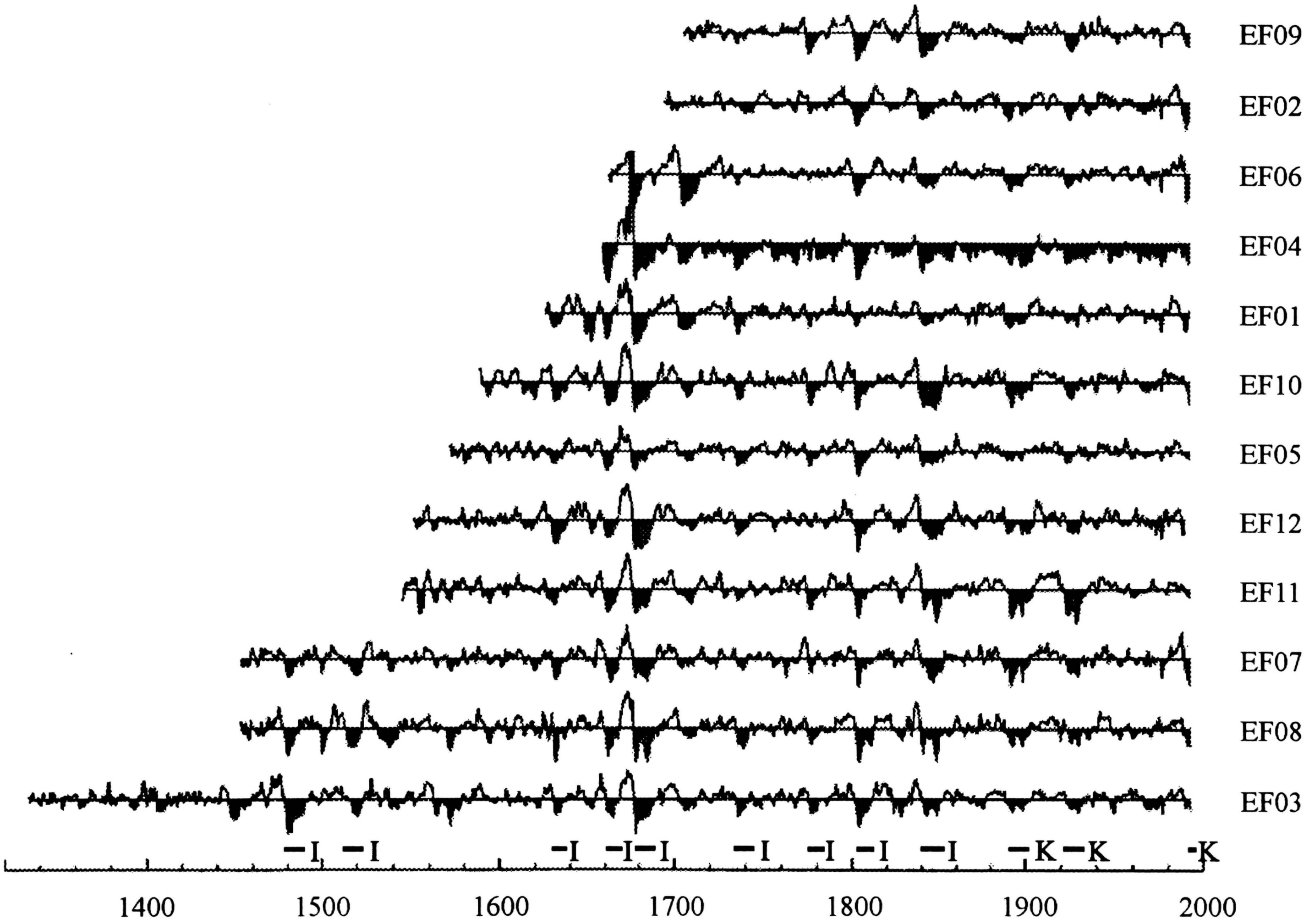
Appendix A, Figure 3. Plot of the ring-widths for the Crater Lake (CLK) site. The shaded area are the below average ring-widths. Insect defolitation causes long periods of suppression. (K stand for known outbreaks, I stand for inferred outbreaks).



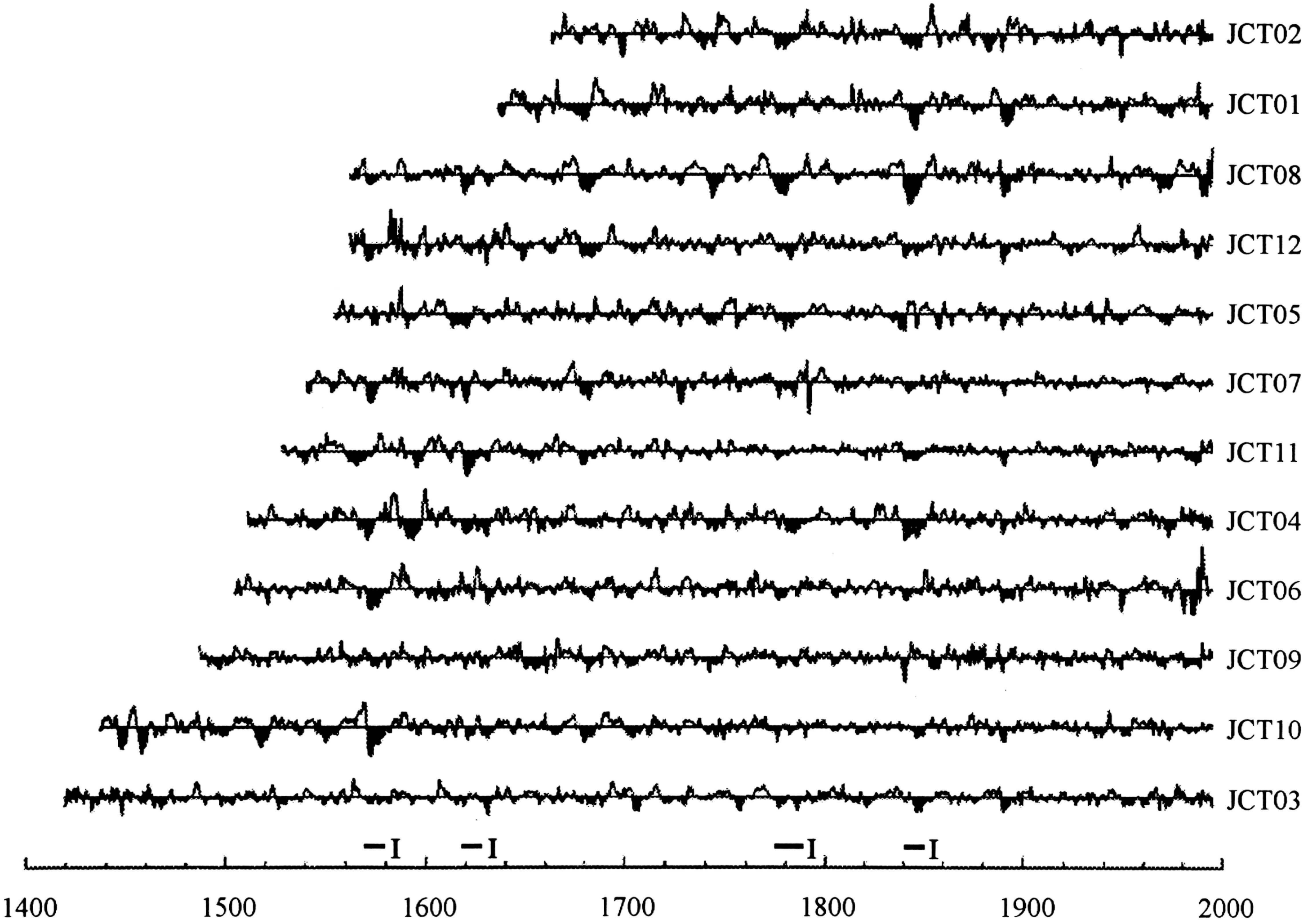
Appendix A, Figure 4. Plot of the ring-widths for the Deschutes (DES) site. The shaded area are the below average ring-widths. Insect defolitation causes long periods of suppression. (K stand for known outbreaks, I stand for inferred outbreaks).



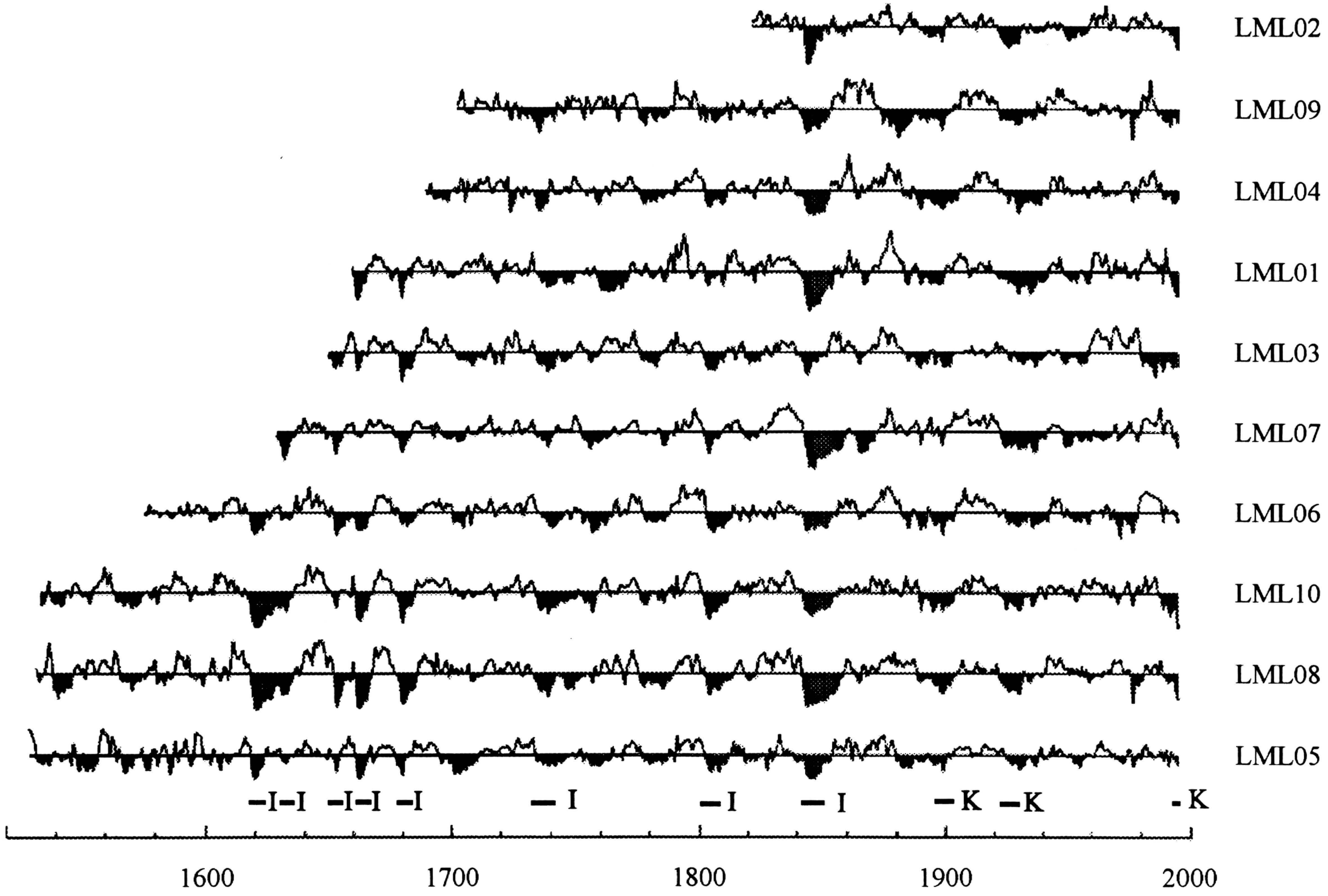
Appendix A, Figure 5. Plot of the ring-widths for the Diamond Lake (DLK) site. The shaded area are the below average ring-widths. Insect defolitation causes long periods of suppression. (K stand for known outbreaks, I stand for inferred outbreaks).



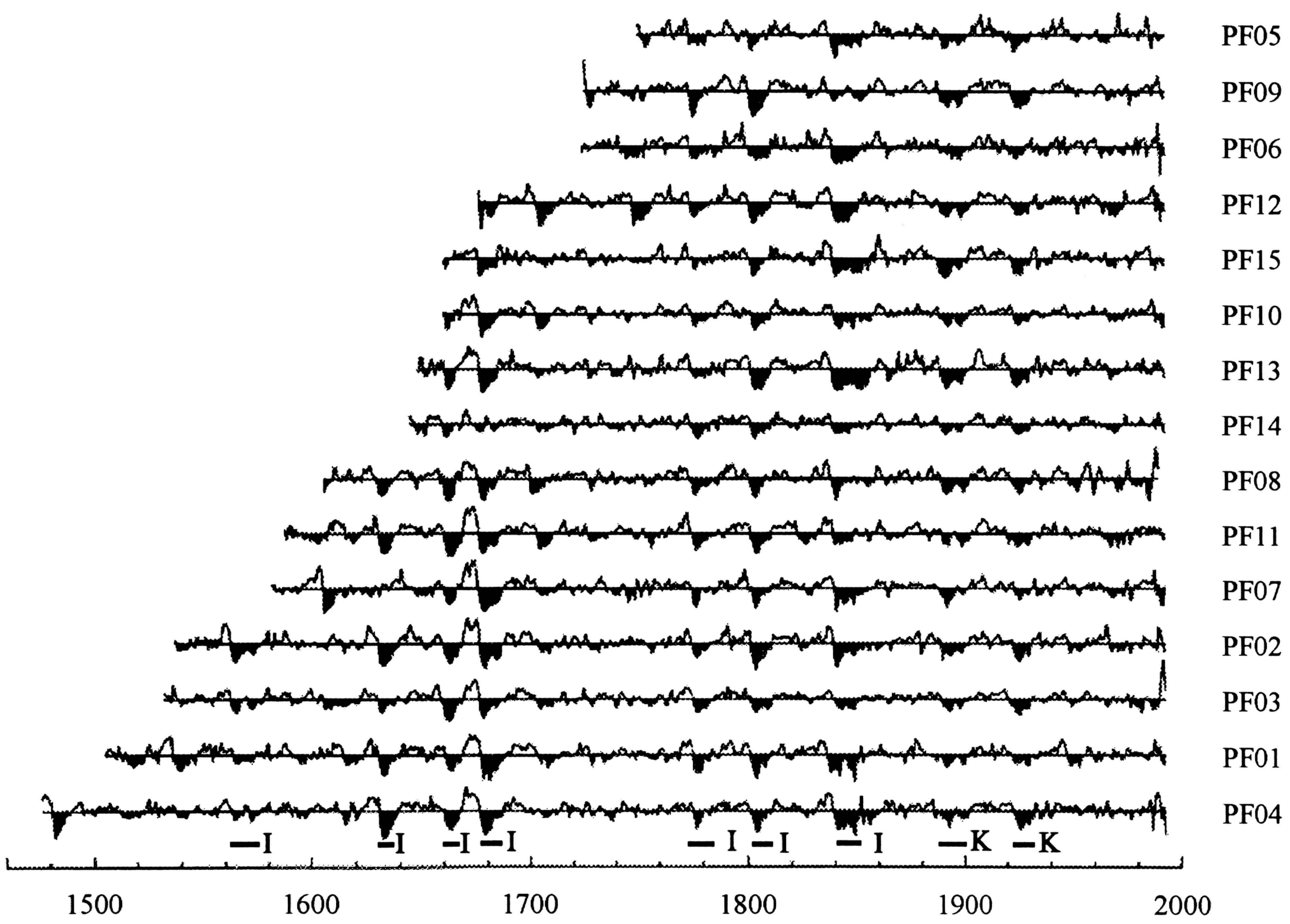
Appendix A, Figure 6. Plot of the ring-widths for the Experimental Forest (EF) site. The shaded area are the below average ring-widths. Insect defolitation causes long periods of suppression. (K stand for known outbreaks, I stand for inferred outbreaks).



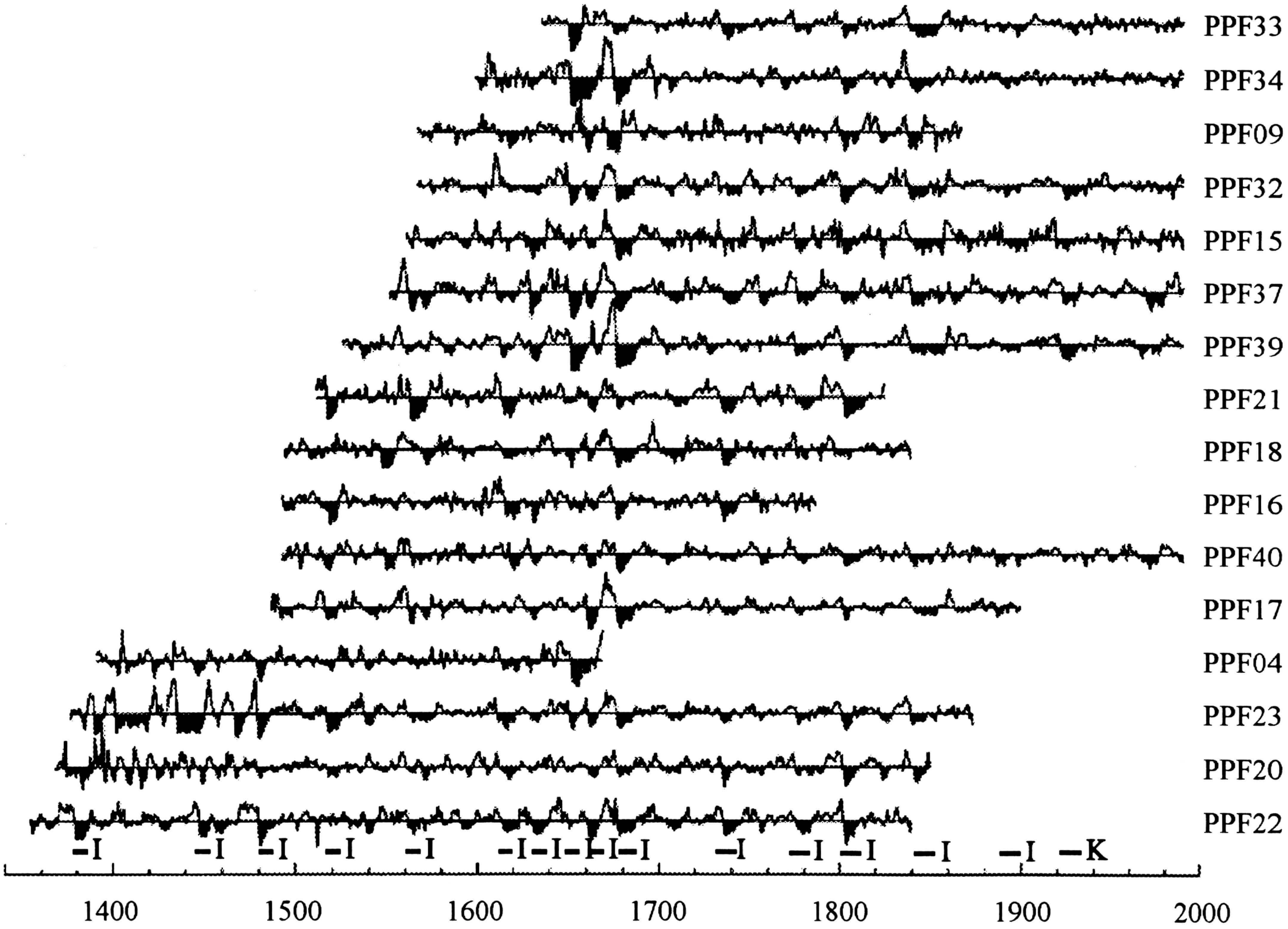
Appendix A, Figure 7. Plot of the ring-widths for the Junction (JCT) site. The shaded area are the below average ring-widths. Insect defolitation causes long periods of suppression. (K stand for known outbreaks, I stand for inferred outbreaks).



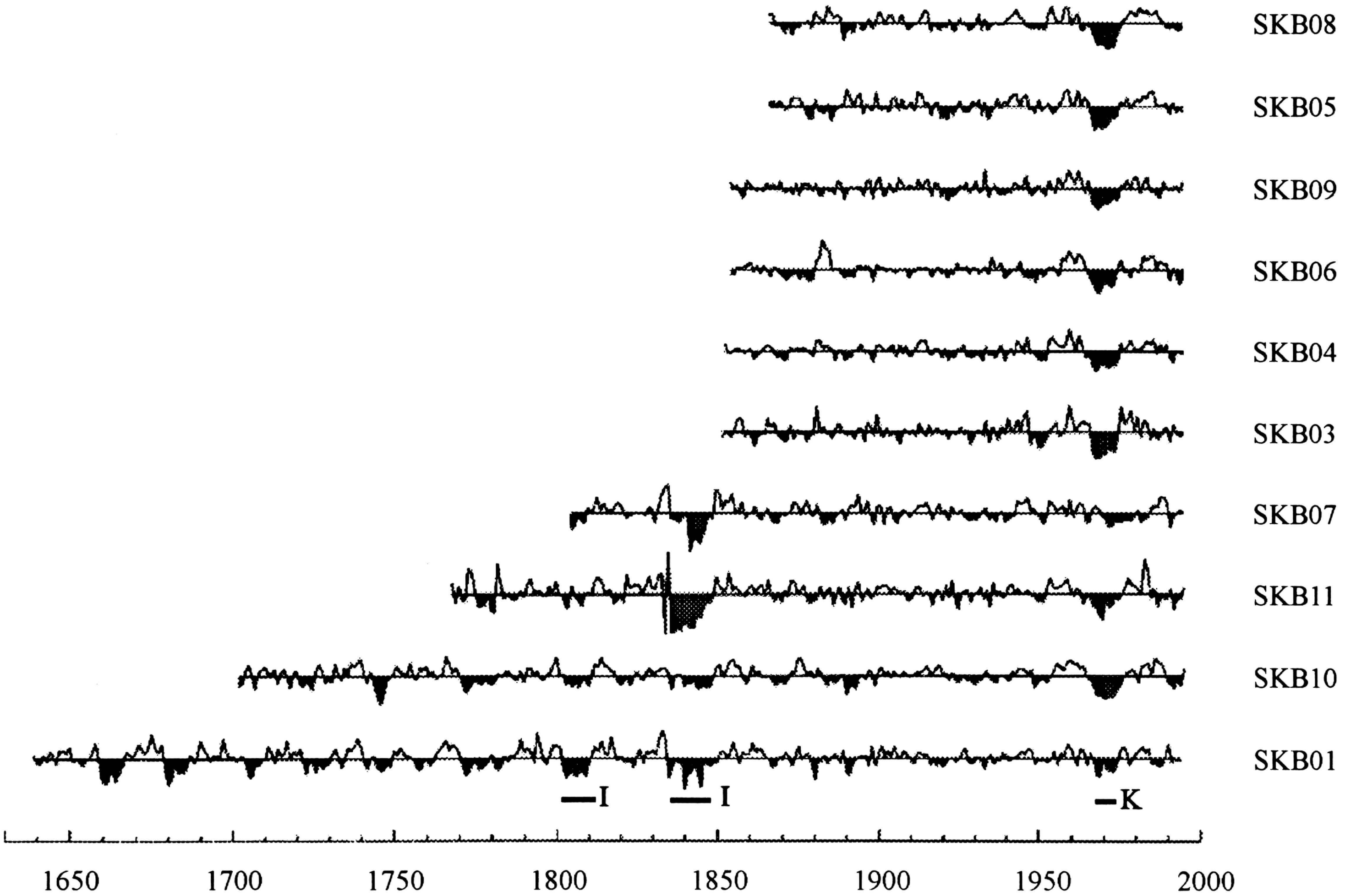
Appendix A, Figure 8. Plot of the ring-widths for the Lookout Mountain Lower (LML) site. The shaded area are the below average ring-widths. Insect defolitation causes long periods of suppression. (K stand for known outbreaks, I stand for inferred outbreaks).



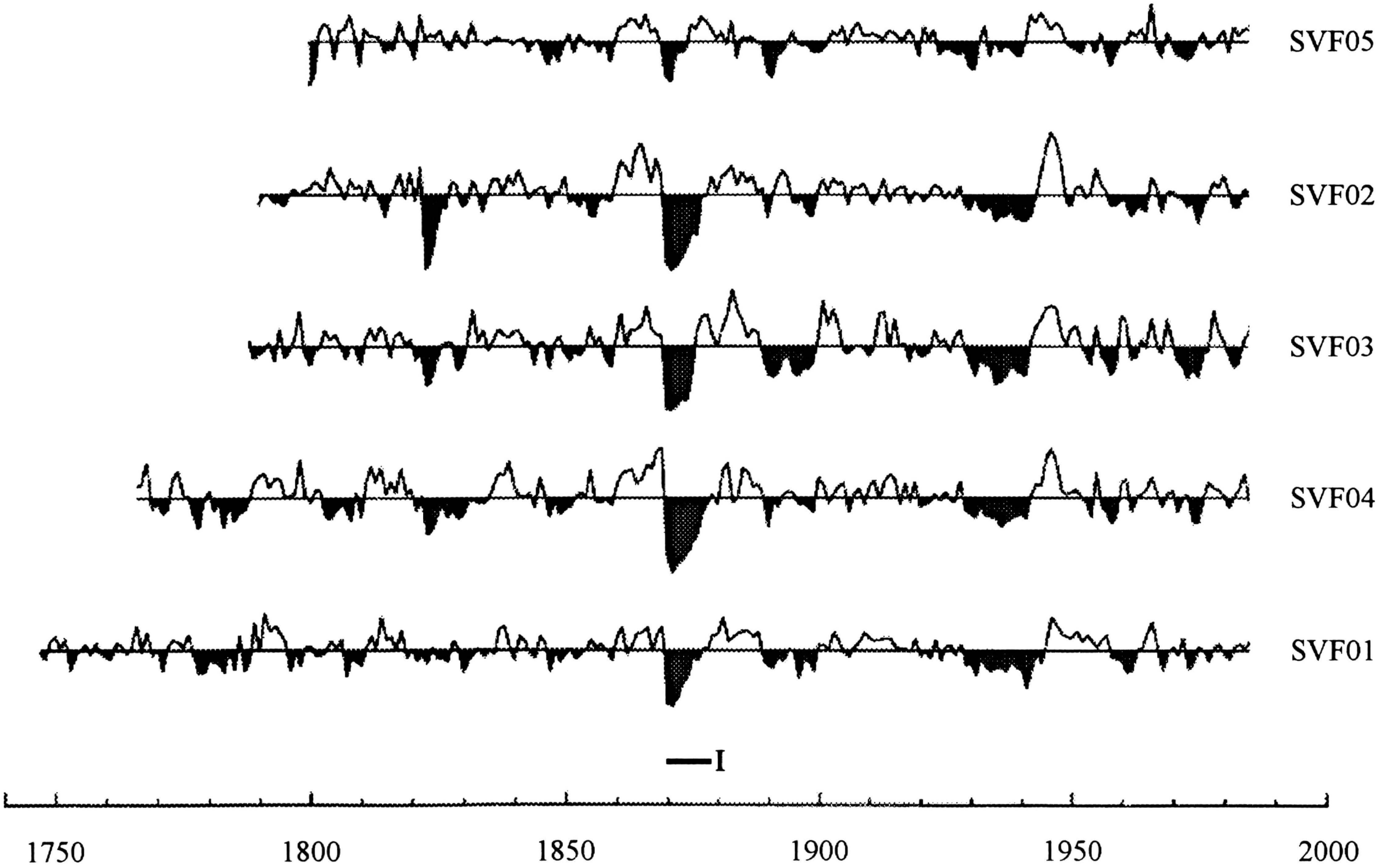
Appendix A, Figure 9. Plot of the ring-widths for the Pringle Falls (PF) site. The shaded area are the below average ring-widths. Insect defolitation causes long periods of suppression. (K stand for known outbreaks, I stand for inferred outbreaks).



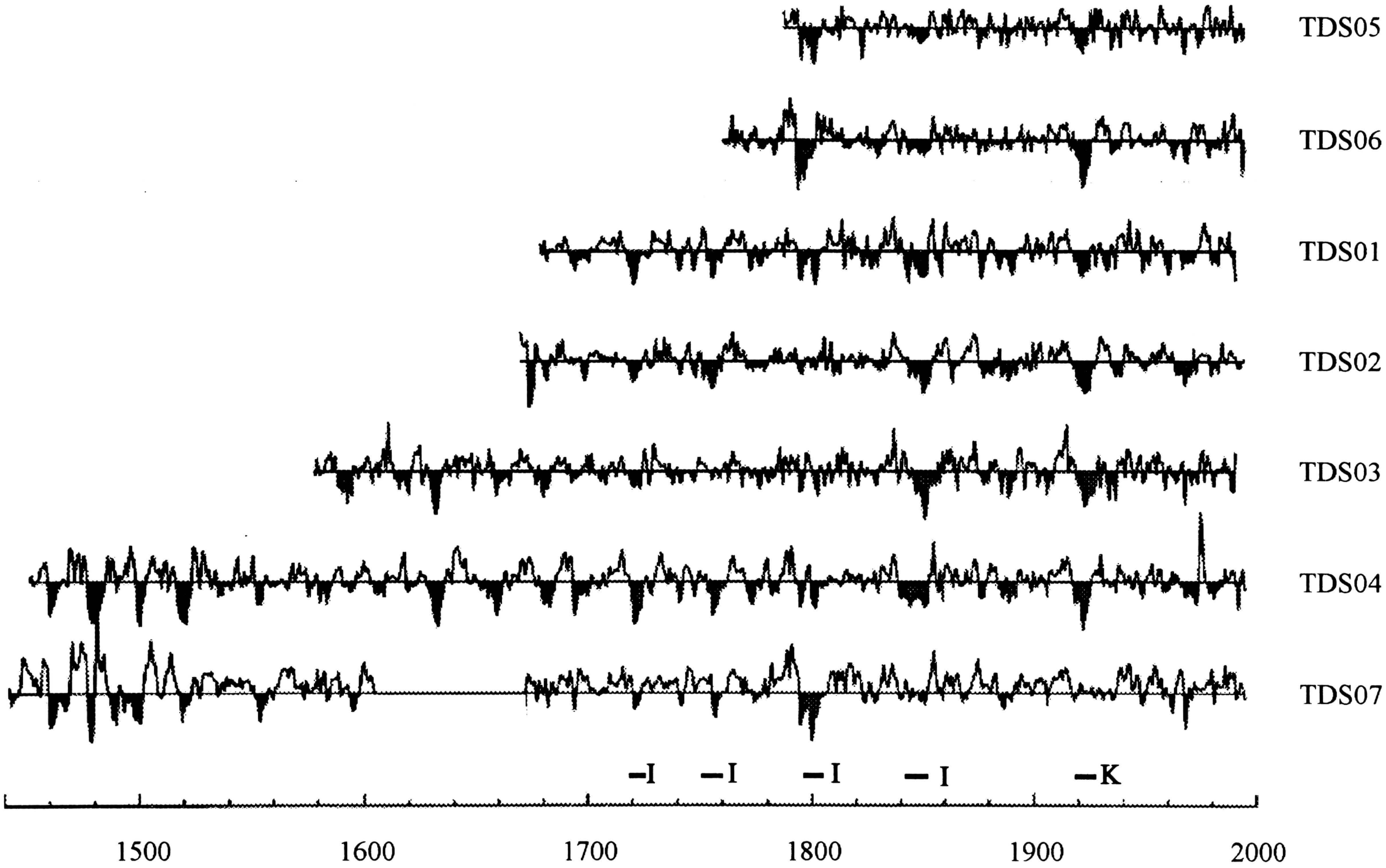
Appendix A, Figure 10. Plot of the ring-widths for the Pringle Prescribed Fire (PPF) site. The shaded area are the below average ring-widths. Insect defolitation causes long periods of suppression. (K stand for known outbreaks, I stand for inferred outbreaks).



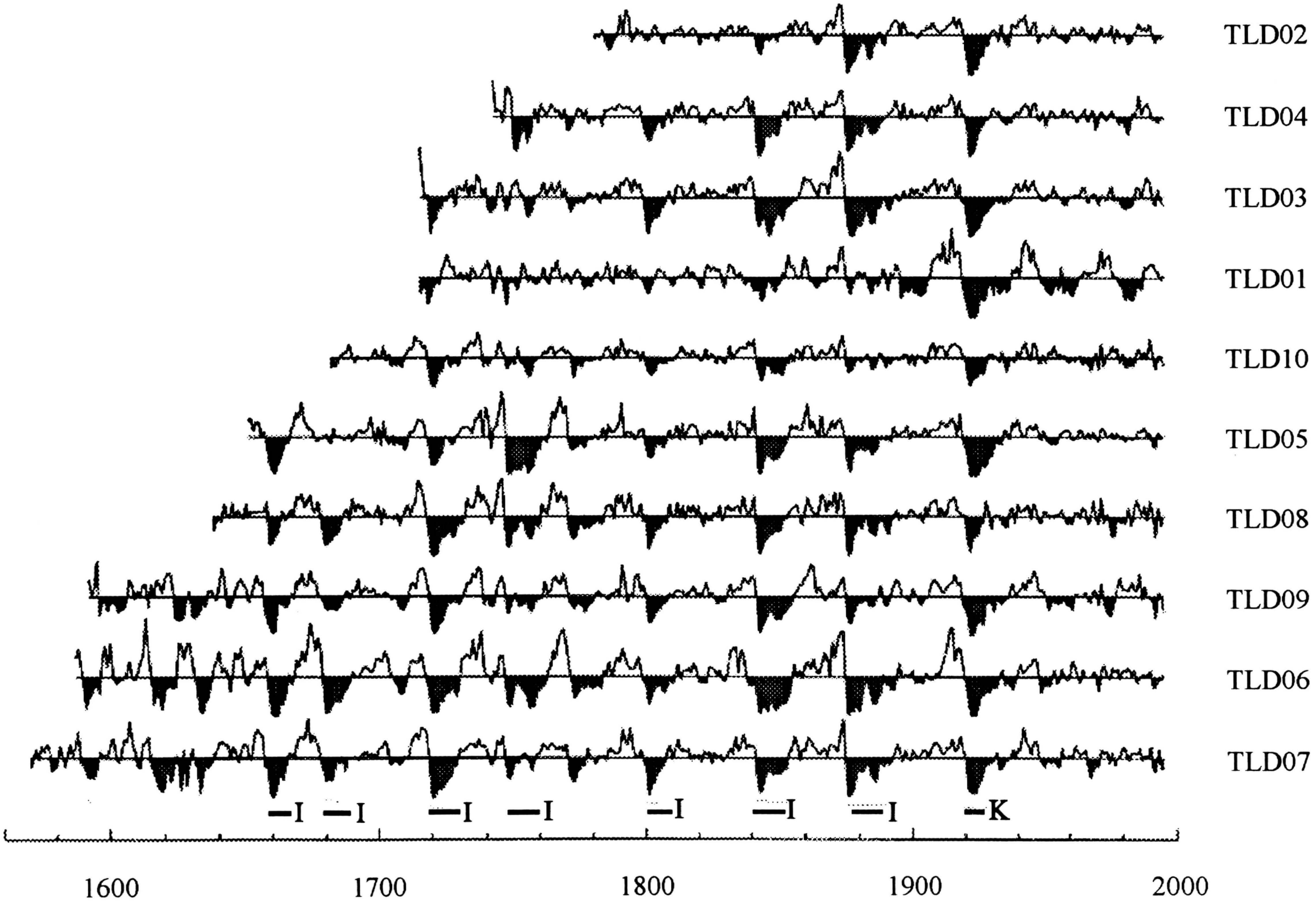
Appendix A, Figure 11. Plot of the ring-widths for the Skookum Butte (SKB) site. The shaded area are the below average ring-widths. Insect defolitation causes long periods of suppression. (K stand for known outbreaks, I stand for inferred outbreaks).



Appendix A, Figure 12. Plot of the ring-widths for the Surveyor Flow (SVF) site. The shaded area are the below average ring-widths. Insect defolitation causes long periods of suppression. (K stand for known outbreaks, I stand for inferred outbreaks).



Appendix A, Figure 13. Plot of the ring-widths for the Telephone Draw South (TDS) site. The shaded area are the below average ring-widths. Insect defolitation causes long periods of suppression. (K stand for known outbreaks, I stand for inferred outbreaks).



Appendix A, Figure 14. Plot of the ring-widths for the Telephone Draw (TLD) site. The shaded area are the below average ring-widths. Insect defolitation causes long periods of suppression. (K stand for known outbreaks, I stand for inferred outbreaks).

APPENDIX B

Fourteen outbreak sites listing the period of suppression, the duration of the suppression, the interval between suppressions, the percent growth reduction for the suppressed period and the year of maximum growth loss in the 22 identified outbreaks. Overlap between separate inferred outbreaks occasionally occurred due to the recovery time of the trees.

Site	Dates	Duration	Interval	% Growth Reduction	Smallest Ring
LML	1619-1624	6		45.91	1620
1534	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
1532	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
1454	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
1376	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	4	25.02	1662
	1677-1686	10	9	31.02	1678
	1735-1746	12	49	12.95	1737*
	1776-1785	10	30	13.84	1777*
	1803-1811	9	18	31.28	1804
	1840-1854	15	29	20.49	1843
	1889-1899	11	35	15.25	1899
	1923-1932	10	24	17.68	1930
SVF	1870-1876	7		51.96	1871
1788					

DES	1629-1635	7		20.66	1631
1593	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
1487	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
1768	1836-1849	13	26	33.27	1845
	1967-1975	9	118	32.47	1969
DLK	1623-1635	13		17.87	1632
1521	1661-1666	6	26	25.33	1665
	1676-1685	10	10	25.46	1678
BJS	1659-1668	10		42.87	1660
1567	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
1592	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
1670	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
1661	1847-1853	7	87	24.80	1849
CAB	1801-1808	8		23.49	1802
1732	1844-1853	10	36	18.70	1845

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