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DECOUPLING TREE-RING SIGNATURES OF CLIMATE VARIATION, FIRE, AND INSECT OUTBREAKS IN CENTRAL OREGON

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ABSTRACT

Dendroecological methods play a critical role in developing our understanding of forest processes by contributing historical evidence of climate variability and the temporal characteristics of disturbance. We seek to contribute to these methods by developing a research protocol for decoupling radial-growth signatures related to climate, fire, and insect outbreaks in central Oregon. Our methods are based on three independent, crossdated tree-ring data sets: 1) a 545-year tree-ring climate reconstruction, 2) a 550-year fire history, and 3) a 250-year pandora moth outbreak history derived from host (*Pinus ponderosa*) and non-host (*Abies grandis-Abies concolor*) tree-ring chronologies. Based on these data, we use visual criteria (marker and signature rings), statistical comparisons, and Superposed Epoch Analysis (SEA) to identify the timing of growth anomalies and establish the temporal relationships between drought, climate variation (ENSO and PDO), fire events, and pandora moth (*Coloradia pandora*) outbreaks. Our results show pandora moth outbreaks generally coincide with periods of below-average moisture, whereas fire in central Oregon often follows a period of wetter than average conditions. Fire events in central Oregon appear to be related to shifts in hemispheric climate variability but the relationship between fire and pandora moth outbreaks remains unclear.

Keywords: dendroecology, disturbance interactions, pandora moth, insect, disturbance, Newberry National Volcanic Monument.

INTRODUCTION

Predicting the influence of global climate change on disturbance regimes requires an *a priori* understanding of the relationship between climate variability and disturbance agents (Dale *et al.* 2001; McKenzie *et al.* 2004). The influence of climate variability on fire regimes has become an important research topic in the Pacific Northwest (PNW) (*e.g.* Heyerdahl 2002; Norman and Taylor 2003; Hessl *et al.* 2004) yet little is known about the temporal effects of climatic variation on other types of forest disturbance such as insect outbreaks (Dale *et al.* 2001; Logan *et al.* 2003). Disturbance agents often interact with each other (*e.g.* Knight 1987; Anderson *et al.* 1987; Hadley 1994), confounding our understanding of climate-disturbance relationships (*e.g.* Speer *et al.* 2001; Dale *et al.* 2001) and little previous research has examined

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the interrelationships of more than two of these processes (but see Geiszler *et al.* 1980; Veblen *et al.* 1994; Kramer *et al.* 2001).

Fire is typically considered the most important disturbance agent in the PNW (Agee 1993) where successive dry years may lead to fuel load desiccation between fire events (Mote *et al.* 1999). This contrasts with the American Southwest, where successive wet years increase surface fuels and single dry years can promote fire conditions and where there is a strong link with El Niño/ Southern Oscillation (ENSO) (Swetnam and Betancourt 1992, 1998). Although drier conditions are more likely to occur in the PNW during El Niño conditions (Redmond and Koch 1991), the historical link between fire and ENSO is generally weak (Heyerdahl *et al.* 2002; Pohl *et al.* 2002; Hessl *et al.* 2004; Knapp *et al.* 2004) and the Pacific Decadal Oscillation (PDO) appears to have a stronger influence on the regional climate (Pohl *et al.* 2002; Knapp *et al.* 2004). Warm (positive) phases of the PDO typically cause drier than average conditions in the PNW and have been linked to more severe fire conditions in eastern Washington (Mote *et al.* 1999; Hessl 2004).

Episodic outbreaks of defoliating insects are important components of disturbance regimes in many inland forests of the American West (*e.g.* Swetnam and Lynch 1989; Hadley and Veblen 1993; Speer *et al.* 2001). Pandora moth (*Coloradia pandora*) is one of the dominant defoliators of ponderosa pine (*Pinus ponderosa*) in central Oregon (Carolin and Knopf 1968). Pandora moth rarely causes host-tree mortality (Furniss and Carolin 1977) but can result in severe defoliation and corresponding radial growth reductions (Speer and Holmes 2004). Pandora moth outbreaks in central Oregon typically exhibit irregular spatial distributions reflecting the distribution of loose pumice soils required for pupation (Furniss and Carolin 1977; Speer and Jensen 2003). Research by Speer (1997) suggests that wet periods may trigger initial outbreaks of pandora moth in central Oregon, but short-term drought conditions may increase populations. Because of their short life cycle, high-frequency climate variation (daily-weekly) may be more influential on pandora moth populations than annual or interannual climate variations (Speer 1997).

These complex interactions between climate and insect outbreaks are confounded by fire. Fire can have an immediate impact on insect populations, causing mortality or initiating favorable conditions for outbreaks, and is strongly influenced by climate conditions (*e.g.* Swetnam and Betancourt 1998; Veblen *et al.* 2000). Conversely, insect outbreaks influence tree mortality and fuel loads (*e.g.* Knight 1987; Hadley and Veblen 1993), which can alter the timing or severity of fire. Speer *et al.* (2001) suggest that pandora moth outbreaks may alter the frequency and timing of fire by interrupting needle fall; fire could also trigger pandora moth outbreaks by weakening trees and making them more susceptible to infestation.

Recent scenarios of global climate warming suggest that climate variation may become more intense and climate extremes more frequent, affecting forest ecosystems directly by changing patterns of tree establishment and growth and indirectly by altering the timing, magnitude, and intensity of forest disturbance processes (Trenberth and Hoar 1997; Mote *et al.* 1999; Urban *et al.* 2000; Cole 2001; Dale *et al.* 2001; McKenzie *et al.* 2004). Many types of forest disturbance, including fire and insect outbreaks, are dependent on seasonal patterns of moisture availability and are directly related to patterns of interannual (*e.g.* ENSO) and interdecadal (*e.g.* PDO) climatic variation (*e.g.* Swetnam and Betancourt 1998; Mote *et al.* 1999; Veblen *et al.* 2000; McKenzie *et al.* 2004).

Tree-ring records provide a unique proxy for extending the historic climate record (Fritts 1976) and for identifying and characterizing a wide range of forest disturbance regimes (Fritts and Swetnam 1989). Nonetheless, serious methodological challenges remain, especially for dendroecologists seeking to understand local-scale processes that require the separation and correct identification of growth patterns resulting from multiple causes (Trotter *et al.* 2002). Our research objectives reflect these challenges. Specifically, we seek to: 1) develop a methodological protocol for decoupling the tree-ring signatures caused by drought, fire, and insect outbreaks in the tree-ring record, 2)

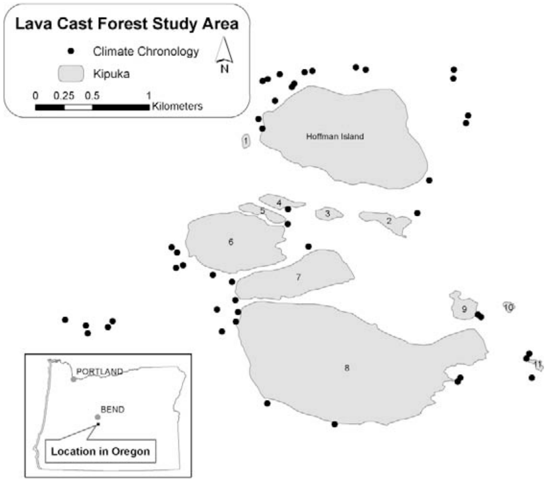

Figure 1. Lava Cast Forest study area. Numbers identify forest isolates (kipukas). Black dots represent one or more trees isolated in lava flows that were sampled in the climate chronology.

compare the timing of climate variation to the timing of fire history and insect outbreaks, and 3) examine the interactions among these disturbance agents in central Oregon.

STUDY AREA

Our study site is located at Lava Cast Forest (LCF) in Newberry National Volcanic Monument in central Oregon (43.69°N, 121.25°W, 1500 m a.s.l.) (Figure 1). This site is characterized by shallow Holocene-aged lava flows (6,200 and 5,800 cal y BP) (Peterson and Groh 1969) surrounding 11 forested habitat islands (kipuka) (Figure 1). The kipukas range in area from 0.3 to 113 ha and retain conditions unaltered by human activity beyond recent fire suppression activity and other management activities in the surrounding forest (Figure 1).

Climate conditions are characterized by a short growing season (May to August) with the majority of precipitation occurring as snow during the winter (October–March). Average annual precipitation (1961–1990) at the nearest meteorological station in Bend, Oregon (44.06°N, 121.28°W) is 297 mm (Taylor and Hannan 1999). The moisture regime is semi-arid, consistent with the strong rainshadow effect of the Cascade Mountains to the west.

Vegetation at LCF is dominated by pure and mixed stands of ponderosa pine, lodgepole pine (*Pinus contorta*) and (*Abies grandis/Abies concolor* hybrid). Forest dominance varies by aspect and topoedaphic conditions. The soils at LCF are young and weakly-developed, primarily derived from deposits of Mazama pumice (MacLeod *et al.* 1981; Franklin and Dyrness 1988).

We chose LCF as our study site for four reasons. First, the naturally fragmented landscape allows sampling of isolated ponderosa pine trees that share a low probability of experiencing fire, pandora moth defoliation, or mistletoe infection, and lack resource competition with other trees. Second, the grand fir-white fir hybrid at Lava Cast Forest provides a potential non-host species for our pandora moth analysis. Third, minimal human disturbance ensures the availability of old-growth (300+ years) ponderosa pine for our climate reconstruction.

METHODS

Our climate, pandora moth host and non-host tree-ring chronologies (Table 1) were developed from tree cores extracted from ponderosa pine and the grand fir-white fir hybrid. We prepared all samples following standard procedures (Stokes and Smiley 1968). All tree-ring samples were visually crossdated using the list method (Yamaguchi 1991) by noting marker years identified by their consistently narrow rings. Tree cores were measured to the nearest 0.001 mm using a Velmex measuring system. We used the program COFECHA (Holmes 1983; Grissino-Mayer 2001a) as a quality control measure to ensure the accurate dating of each series. Following crossdating, each series was detrended as described below.

Dendroclimatic Reconstruction

The dendroclimatic reconstruction is from Pohl *et al.* (2002) and was developed from a chronology of 50 increment cores taken from 35 isolated ponderosa pines distributed within the lava flows at LCF. Trees with evidence of fire or lightning scarring, visible dwarf mistletoe (*Arceuthobium* spp.) shoots, or deformities were not sampled.

Table 1. Tree-ring chronologies and fire history data used in this study.

Name	Sample Size	Year Range	Species	Use in this Study
Climate Chronology[1]	50 cores from 35 trees	1455–2000	Ponderosa pine	Reconstructing climate, correcting for climate in Pandora moth reconstruction
Fire History[2]	85 partial cross-sections, 98 unique fire events	1458–2001	Ponderosa pine, Lodgepole pine	Reconstructing fire events
Pandora Moth Host Chronology	26 trees	1750–2000	Ponderosa pine	Reconstructing pandora moth history
Non-Host Chronology	17 trees	1750–2000	Grand fir-White fir hybrid	Correcting for climate in pandora moth chronology and comparing to climate chronology

[1] From: Pohl *et al.* 2002.
[2] From: Arabas *et al.* 2006.

We detrended each crossdated ring-width series with a curve of best fit (negative exponential or linear regression line) and a 50-year cubic smoothing spline (Cook and Peters 1981). This procedure retained 75% of the variance within the series and yielded the highest correlations with historical climate records. The reconstructed Palmer Drought Severity Index (PDSI) was verified with independent historical records and other regional dendroclimatic reconstructions (Keen 1937; Holmes *et al.* 1982; Holmes *et al.* 1983; Oregon Climate Service 2001).

We used two additional reconstructions to examine the relationship between disturbance events and hemispheric climate variability. First, we compared our climate chronology to the Southern Oscillation Index (SOI) from instrumental records (1900–1999) (NCEP 2001) and regionally averaged tree-ring records to compare the El Niño/Southern Oscillation (ENSO) to disturbances (Stahle *et al.* 1998). We then used Gedalof and Smith's (2001) tree-ring reconstructed PDO to compare to the timing of fire and pandora moth events with reversals in the PDO.

Pandora Moth Outbreak Data

Chronology Development

We developed our pandora moth outbreak history using three independent chronologies (Table 1): (a) a pandora moth *host-chronology* created from 26 ponderosa pine trees opportunistically collected from the largest and presumably oldest trees found on the kipukas and in surrounding forest; (b) a *non-host chronology* derived from 17 of the oldest grand fir-white fir trees growing on the kipukas, and (c) the *climate chronology* described above. The non-host and climate chronologies served as controls for our comparison with the pandora moth host-chronology. These chronologies were used to identify and isolate the pandora moth tree-ring signal in the host chronology by eliminating climate-related or other growth conditions.

We detrended the host chronology using ARSTAN (Cook and Holmes 1983), by applying a 40-year, 50% frequency response cubic smoothing spline (Cook and Peters 1981) to amplify the variance associated with outbreaks of pandora moth (Speer *et al.* 2001). The selected cubic smoothing spline retained 99% of the variance at a frequency of 13 years, the average frequency of pandora moth outbreaks. We then detrended the non-host chronology by applying the ARSTAN parameters used in our climate reconstruction to ensure the replication of the climate signal. We then compared our non-host chronology to the filtered fire records to identify and remove any growth anomalies (suppressions or releases) related to known fire events.

Dating Outbreaks

We used a three-step procedure to determine the onset and duration of pandora moth outbreaks. First, we visually identified outbreaks by noting the unique tree-ring signature identified by Speer (1997) in each core using in our host chronology. Second, we used the program OUTBREAK (Holmes and Swetnam 1996) to statistically identify periods of growth reduction. This procedure entailed subtracting the values of the non-host and climate chronologies from our host chronology and correcting for differences in standard deviations (Swetnam *et al.* 1985; Holmes and Swetnam 1996). Based on the documented effect of pandora moth on radial tree growth (Keen 1937; Carolin and Knopf 1968; Speer 1997; Speer *et al.* 2001), we established growth reductions criteria for OUTBREAK at ≥1.28 standard deviations below the mean that lasted between 4 and 20 years, and began with a year having a ≥50% reduction in ring-width compared to the previous year (Speer 1997). We then examined the statistical similarity among the chronologies using Pearson's correlation coefficient. Our third step entailed the application of OUTBREAK to our host and climate chronologies to independently verify the presence of growth reductions in our host chronology, and the absence of defoliation-related growth reduction in our climate chronology. Final identification of outbreaks was made by comparing the results of each of the steps identified above. Where two of the three steps overlapped in identification of outbreaks, we inferred an outbreak.

We confirmed the accuracy of our inferred outbreaks by comparing them to outbreaks documented in the 20th Century and reconstructed outbreak history by Speer (1997), Speer *et al.* (2001), and Speer and Jensen (2003). We then used Pearson's correlation coefficient to compare growth rates for our three chronologies during and between outbreaks. Stronger positive correlations between (versus during) outbreaks indicate little or no defoliation within our two control (non-host and climate) chronologies (Swetnam *et al.* 1985).

Fire History Data

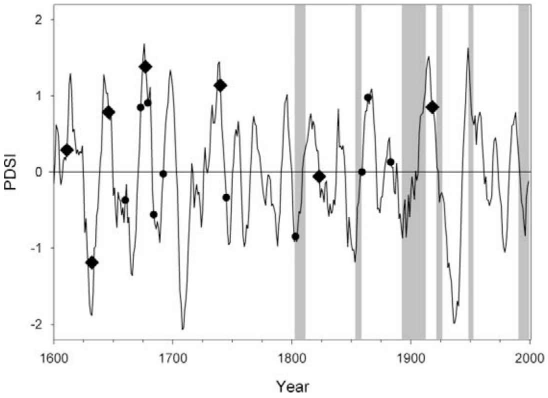

Figure 2. Reconstructed PDSI, fire events, and pandora moth outbreaks, 1600–2001. Solid line represents 8-year running average of tree-ring reconstructed PDSI. Small circles represent fire events that scarred ≥10% of trees (n = 17); large diamonds represent fire events that scarred ≥25% of trees (n = 7). Grey bars represent pandora moth outbreaks. Pandora moth reconstruction only extends back to 1750; fire events to 1600.

The fire history reconstruction is from Arabas *et al.* (2006) and derived from fire-scarred trees sampled on the kipukas and in the adjacent surrounding forest. This reconstruction extends from 1458–2001, contains 98 unique fire events, and has a MFRI of 5 years for the study area. Because we were interested in fires related to climate variation, we filtered the Arabas *et al.* (2006) fire chronology to capture only those fires that had a large, relative extent or synchrony across the study area. The filters include only those fires that scarred 10% and 25% of our samples (with a minimum of 2 trees scarred). Filtering reduced the length of the fire history by 142 years (to 1600–2001). The 10% filter yielded 17 unique events with a MFRI of 19 years; the 25% filter yielded 7 unique events with a MFRI of 51 years (Figure 2).

Comparing Disturbance to Climate

We compared the timing of fire and pandora moth outbreaks to climate variability graphically and by conducting separate superposed epoch analyses (SEA). SEA superimposes all disturbance events into a composite history and averages the climate characteristics prior to, during, and after all disturbance events into a common window (Grissino-Mayer 2001b).

Using the SEA module of the FHX2 software

Table 2. Standardized chronology statistics. The three chronologies have a common interval of 1750–1998.

	Pandora Moth	Non-Host	Climate
Number of Series	26	17	50
Length in Years	299	298	555
Interseries Correlation	0.478	0.529	0.522
Standard Deviations	0.585	0.450	3.674
Autocorrelation	0.841	0.842	0.625
Mean Sensitivity	0.220	0.217	0.243
Pearson's R (all correlations are significant at p ≤ 0.01)			
Pandora Moth	1.00	0.470	0.663
During Outbreaks		0.479	0.653
Between Outbreaks		0.507	0.694
Non-Host	0.470	1.00	0.503
During Outbreaks	0.479		0.495
Between Outbreaks	0.507		0.501

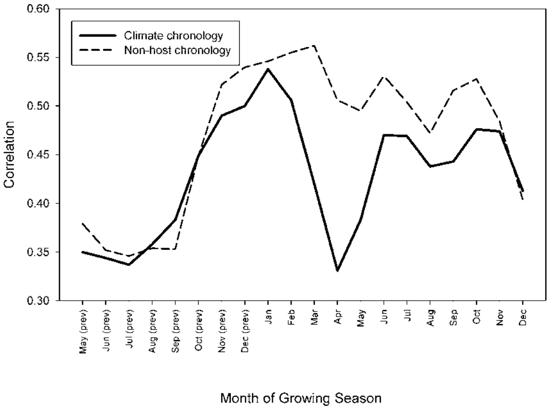

Figure 3. Monthly correlations of Climate (ponderosa pine, solid) and Non-host (fir, dashed) chronologies with Palmer Drought Severity Index. All values significant at $p \leq 0.001$.

(Grissino-Mayer 2001b), we compared the timing of drought from reconstructed PDSI with fire events comprising each of our filtered fire histories. We used 15-year windows (ten years before and four years after the fire event) to examine climate in the years immediately around fire events. We then compared the timing of fire to ENSO and PDO using SEA. This procedure compared the filtered fire events to: 1) tree-ring reconstructed winter (December–February) SOI values (Stahle *et al.* 1998) in 15-year windows, and 2) a graphic comparison of filtered fire events to tree-ring reconstructed reversals in the PDO (Gedalof and Smith 2001).

The timing of pandora moth outbreaks and climate were compared using SEA in the Dendrochronology Program Library software, EVENT (Holmes and Swetnam 1994). We centered 20-year windows on the first year of inferred outbreaks. The occurrence of pandora moth outbreaks were also graphically compared to the timing of fire events to determine if the two disturbances are temporally related.

RESULTS

Pandora Moth Outbreak History

The three chronologies used to determine periods of pandora moth outbreaks share similar interseries correlations, autocorrelation, and mean sensitivity statistics (Table 2). The climate chronology has higher mean sensitivity and lower autocorrelation, reflecting the greater sensitivity of this chronology. The host chronology was most strongly correlated to the climate chronology ($R = 0.663$, $p \leq 0.01$). The seasonal response of the climate chronology exhibited a bimodal relationship, unlike the non-host chronology, and peaked in both the preceding winter and the summer of tree growth (Figure 3).

Visual identification of the pandora moth signature in the host chronology cores reveals six outbreaks during the extent of the reconstruction, from 1750 to 1999 (Figure 4). These outbreaks were also identified in our OUTBREAK (Holmes and Swetnam 1996) results and our growth reduction comparisons between the host and non-host chronologies, and our host and climate chronologies. Comparison of our reconstructed outbreak periods to the timing of fire events indicates that host growth reductions and growth releases are unrelated fire-caused trauma and reduced post-fire competition among neighboring trees (Goldblum and Veblen 1985). Only two fire events occurred during the early portion of outbreaks in the non-host chronology: 1803 (outbreak from 1803–1811) and 1883 (outbreak from 1880–1886). The 1803 fire event was not evident in the growth of the non-host chronology and occurred in a portion of

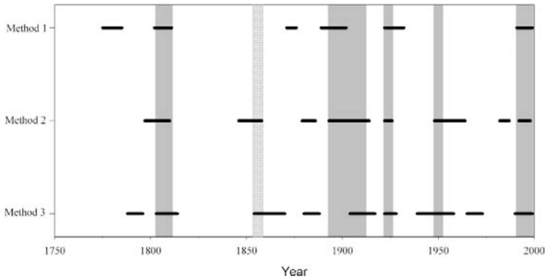

Figure 4. Pandora moth outbreaks. Method 1: visual identification of pandora moth ring-width signature in host cores. Method 2: OUTBREAK analysis of pandora moth chronology corrected for climate with non-host chronology. Method 3: OUTBREAK analysis of pandora moth chronology corrected for climate with climate chronology. Outbreaks were inferred where at least two methods overlap, shown by vertical grey bars. Dashed vertical bar indicates growth suppression from a fire event.

the contiguous forest lacking non-host samples. The 1803–1811 pandora moth outbreak was also reconstructed by Speer *et al.* (2001). The 1880–1886 pandora moth outbreak has not been documented in other outbreak reconstructions and corresponds to a period of rapid growth in our non-host sample. This outbreak may have been erroneously identified because of growth releases following the 1883 fire and was removed from our final reconstruction (Figure 4).

We confirmed our inferred periods of outbreak by comparing the host, non-host, and climate chronologies using Pearson's correlation coefficients for periods during and between outbreaks (Table 2). In all cases, the host chronology correlated more strongly with the control chronologies (both non-host and climate chronologies) between outbreaks than during outbreaks, indicating that periods identified as outbreaks contained different ring-width signatures between the pandora moth chronology and the control chronologies.

We confirmed the absence of a pandora moth response in the climate chronology in three ways. First, the program OUTBREAK failed to identify any 20th Century pandora moth outbreaks using the climate chronology as a ''host'' and the non-host chronology as a control. Second, each of the inferred outbreak periods identified in the climate chronology, except 1854–58 (Table 3), had the lowest percentage of trees recording each outbreak. Third, visual examination of the climate cores confirmed the absence of the requisite pandora moth signature for all outbreak periods.

The most severe inferred outbreak occurred in the 1990s, as indicated by the high percentage of trees recording the outbreak (Table 3) and high frequency of missing rings visually observed in the pandora moth chronology. The 1803–1811 outbreak also appears to have been severe, although sample depth was smaller during this period. The six outbreaks we inferred agree with historical documentation of outbreaks (Keen 1937; Carolin and Knopf 1968; Cochran 1998) or reconstructions of pandora moth outbreak for central Oregon by Speer (1997; Speer *et al.* 2001; Speer and Jensen 2003), except the 1949–1952 outbreak. The 1854–1858 outbreak was designated based on the ring-width departures between the host and non-host

Table 3. Year of maximum growth reduction and percentage of trees recording pandora moth outbreaks. See Table 1 for chronology definitions and Table 2 for chronology statistics.

		Year of Maximum Growth Reduction			Percentage of Trees Recording Outbreak		
	Host:	Host Chronology	Host Chronology	Climate Chronology	Host Chronology	Host Chronology	Climate Chronology
Inferred Outbreaks	Control:	*Non-Host Chronology*	*Climate Chronology*	*Non-Host Chronology*	*Non-Host Chronology*	*Climate Chronology*	*Non-Host Chronology*
1803–1811		1803	1808	1804	68%	75%	64%
1854–1858		1854	1855	1854	50%	44%	82%
1893–1912		1900	1908	1899	51%	49%	41%
1922–1926		1925	1923	1925	35%	33%	17%
1949–1952		1950	1952	1950	58%	50%	22%
1991–1999		1996	1997	1995	40%	65%	11%

Table 4. Methods to decouple the tree-ring signatures of drought, fire, and pandora moth outbreaks. Each field explains how climate, fire, and pandora moth signals (columns) were unlikely to be included or erroneously attributed in each reconstruction (rows).

	Climate Signal	Fire Signal	Pandora Moth Signal
Climate Reconstruction		Isolated sampled trees unlikely to experience fire. Sampled trees exhibit no external fire scars.	Isolated trees unlikely to experience infestation. Ring-width signature of pandora moth not observed samples. Program OUTBREAK did not detect same outbreaks as other chronologies.
Fire Reconstruction	All fire events were dated from scars exhibiting visible cambium damage		All fire events were dated from scars exhibiting visible cambium damage
Pandora Moth Reconstruction	Outbreaks identified by unique ring-width signature Climate was controlled for using a non-host and a separate host reconstruction.	Trees sampled did not have external evidence of fire Chronology was compared to fire history to examine periods of overlap.	

and climate chronologies. This outbreak period corresponds to a period of growth reduction but the lack of the visual signature of pandora moth defoliation in the climate chronology. This outbreak immediately follows the large 1840–1853 outbreak identified by Speer and Jensen (2003) representing a later initiation or an initially low pandora moth population density during the first few years of the outbreak (Speer and Jensen 2003).

Disturbance and Climate Variation

Superposed epoch analysis revealed that PDSI values do not statistically differ during fire years, but are significantly higher in the years preceding our filtered fire events (five and two years preceding fire events that scarred 25% of trees; four years preceding fire events that scarred 10% of trees; Figure 5). Our SEA comparison with reconstructed SOI values and our filtered fire events (not shown) revealed a statistically significant relationship ($p \leq 0.01$) between fire and winter SOI the year following small fire events (10% filter). We also found that three of our four large-area fires (25% filter) occurred during the negative (cool) phases of the PDO (Figure 6) identified in the Gedalof and Smith (2001) 400-year, regional tree-ring reconstruction of PDO reversals.

Graphic analysis of pandora moth outbreaks and climate variation show the majority of outbreaks occurred during dry periods (below average reconstructed PDSI) (Figure 2). Superposed epoch analysis of climate variation and the first year of insect outbreaks also show outbreak initiation is not correlated to individual dry years, but years of maximum growth reduction immediately follow dry years ($p \leq 0.01$). Graphic analysis of the fire history and pandora moth outbreaks showed no consistent pattern (Figure 2).

DISCUSSION

Previous research has explored the role of climate on individual disturbance agents (*e.g.* Swetnam and Betancourt 1992; Veblen *et al.* 1999, 2000; Heyerdahl *et al.* 2002) or examined interactions among forest processes without incorporating climate variation (*e.g.* Geiszler *et al.* 1980; Hadley and Veblen 1993; Veblen *et al.* 1994). Other work has attempted to incorporate climate variation, fire, and insect outbreaks, but has yielded generally qualitative results or had difficulty sep-

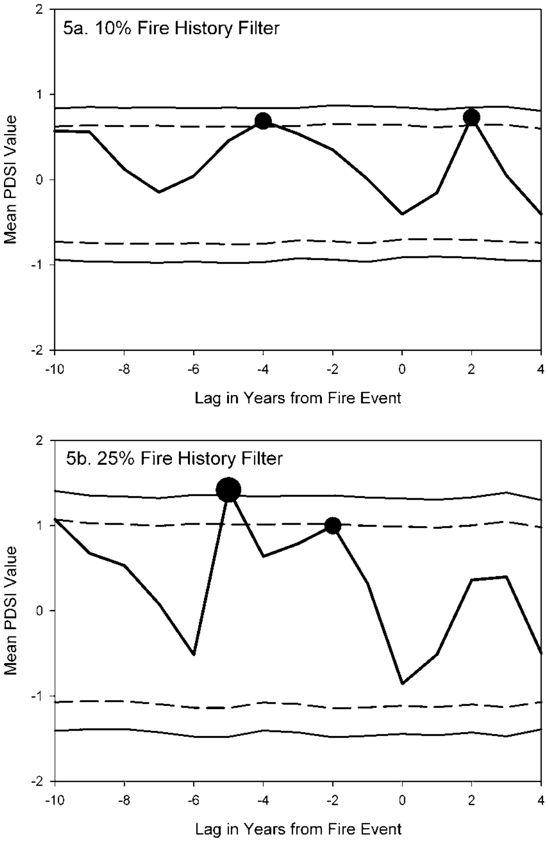

Figure 5. Superposed epoch analysis of fires scarring 10% (a) and 25% (b) of trees and reconstructed Palmer Drought Severity Index (PSDI). X-axis is the lag from a fire event, with the year of the fire at 0. Y-axis is the mean difference between PDSI during the year in the window and the average of all years. Dashed horizontal lines represent 95% confidence limits. Solid horizontal lines represent 99% confidence limits. Years when the plotted line extends outside the confidence limits (dots) indicates climate conditions were statistically different from the average.

arating the tree-ring signals of disturbances (Swetnam and Betancourt 1998; Speer *et al.* 2001). While this body of research has made important contributions toward our understanding of how forest processes respond to environmental conditions, it has also raised new methodological questions and concerns regarding the accuracy and precision of their results (Trotter *et al.* 2002). Our results indicate that highly selective sampling and the use of multiple verification procedures allows researchers to consider both abiotic (*i.e.* climate) and biotic (*i.e.* herbivory and species-specific responses to climate) factors in our insect outbreak reconstruction.

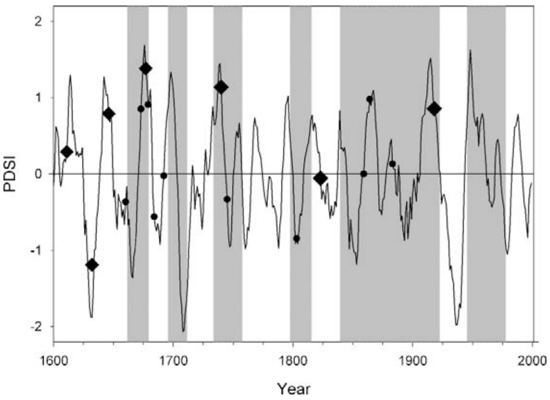

Figure 6. Pacific Decadal Oscillation (PDO), reconstructed PDSI, and fire events. Grey bars represent cool (negative) phases of the PDO; white bars represent warm (positive) phases (Gedalof and Smith 2001). Solid line is PDSI reconstructed from tree rings. Small circles represent fire events that scarred ≥10% of trees; large diamonds represent fire events that scarred ≥25% of trees.

Decoupling Drought, Fire, and Pandora Moth Tree-Ring Signatures

Decoupling growth reductions resulting from pandora moth outbreaks versus those caused by drought was the greatest challenge we encountered during our disturbance history reconstructions. These difficulties stem from the requisite comparisons of the host chronology with our two "control chronologies," each of which possesses its own limitations: a non-host chronology containing a different climate signal, and a host species climate chronology that may have contained the pandora moth signal. We minimized the probability of sampling defoliated trees used in our climate chronology by sampling ponderosa pine isolated in lava flows where low tree densities and soils conditions are unlikely to support large pandora moth populations. We verified this assumption by examining and noting the absence of the unique pandora moth ring-width signature (Speer 1997) during our construction of the climate chronology. We then compared the drought record reconstructed in our climate chronology with other drought reconstructions for central Oregon to ensure these growth suppressions were climate-related. This procedure included a comparison of our drought episodes with regional reconstructions using the non-host western juniper (*Juniperus occidentalis*) (Pohl et al. 2002). This procedure provided independent identification and verification of fire-, drought- and defoliation-induced growth variations. It did not, however, allow us to remove the influence of microsite differences between the growth conditions inherent to lava flows (climate chronology) and the surrounding forests (host and non-host chronologies).

Despite considerable differences in substrate (pumice soils versus lava), our non-host chronology demonstrates a relatively strong relationship with local PDSI values. We attribute this to Lava Cast Forest's location near the northern distributional limit of white fir and its presumed tolerance to environmental conditions. In contrast, the ponderosa pine climate chronology exhibits a higher mean sensitivity and lower series autocorrelation, both indicators of a more sensitive climate signal. These tree species exhibit a weak but statistically similar response to climatic variation with their primary growth departures occurring during the early growing season.

The low interseries correlation (R = 0.663) between the ponderosa pine-based pandora moth host and climate chronologies appears related to growth differences caused by pandora moth defoliation and additional site factors including microclimatic differences between the lava (climate chronology) and the forest environment (host-chronology), and other environmental conditions such as competition and soil moisture not considered in this study. The pandora moth host ponderosa pine and non-host fir chronologies share similar sample sizes and autocorrelation, mean sensitivity, and standard deviation statistics, providing a statistically sound comparison of these chronologies with the ponderosa pine climate chronology. Differences among the three chronologies illustrate the importance of comparing host chronology to a climate chronology derived from the same species and to a non-host chronology exhibiting a similar sensitivity and persistence to local environmental conditions (Swetnam *et al.* 1985). Used in combination, this multiple chronology protocol minimizes the likelihood of a Type II error inherent to insect outbreak reconstructions based on a single non-host species or same species comparison alone (Trotter *et al.* 2002).

Disturbance Interactions

Graphic comparisons and the superposed epoch analysis of fire events and the climate reconstruction show that the years preceding fire are statistically wetter than average, peaking at five years prior to fire events. This pattern is similar to those found in the American Southwest, where wet periods, such as those associated with ENSO, precede dry years. These conditions enhance tree vigor and increase fuel accumulation, resulting in widespread fires during subsequent drought (*e.g.* Swetnam and Betancourt 1998). Fire years at LCF are not associated with prolonged drought, as has been hypothesized more generally for the Pacific Northwest (Agee 1993; Mote *et al.* 1999) and suggest a climate-fire pattern more similar to the American Southwest, and northern (Norman and Taylor 2003) and southern California (Keeley 2004) where antecedent moisture exceeds the role of drought as a contributing factor influencing the probability of fire.

Our comparison of fire occurrence and decadal variations in climate revealed small area fires, those scarring 10% of trees in a given year, precede a positive to negative phase switch in PDO values. We also found that the three large area fires, those scarring at least 25% of trees, occurred more frequently during negative (cool) phases of the PDO. While these results are inconclusive because of the small number of large local fires and few phase changes (four) documented in the PDO reconstruction, they are consistent with the shift from growing season to dormant season fires at Lava Cast Forest during a negative phase of the PDO between 1880 and 1950 (Arabas *et al.* 2006). These conditions suggest: 1) the relationship between fire and reversals in the PDO may be related less to precipitation patterns than to other factors such as increased lightning ignitions as storm tracks migrate during switches of the PDO, and 2) additional research is needed to understand of how climate at the local, regional, and hemispheric scales interact to drive fire (Arabas *et al.* 2006).

Our results show pandora moth outbreaks are temporally related to drought. Graphic analysis shows five of the six outbreaks we identified occurred during periods of below average reconstructed PDSI (Figure 2). Superposed epoch analysis also indicates significantly drier conditions the year preceding maximum growth reduction. Typically, maximum growth reductions occur at the beginning or end of outbreaks and may reflect the combined and lagged stress of dry conditions following the onset of defoliation (Speer 1997). Alternatively, drought conditions may promote the intensity of herbivory in response to a decrease in host fitness or higher pandora moth survivorship or reproduction during drought years (Speer and Jensen 2003). These interpretations are consistent with the stress hypothesis (White 1976; Mattson and Hack 1987) which posits drought conditions increase susceptibility to defoliation by herbivorous insects. We found no relationship between fire and pandora moth outbreaks (*cf.* Speer 1997) suggesting that regional influences including climate and the episodic life-cycles of pandora moth are better predictors of outbreaks.

CONCLUSIONS

Linking climate variation to forest disturbance is critical to our understanding of forest processes and the development of appropriate forest management strategies (Dale *et al.* 2001; Logan *et al.* 2003; McKenzie *et al.* 2004). Tree-ring research has and will continue to play an important role in developing this understanding through methodological improvements that aid in our accurate and precise identification of climate patterns, forest processes, and their interaction.

Our research presents a case study from central Oregon to introduce a research protocol for reconstructing, decoupling, and identifying the interactions among multiple disturbance agents. Using three tree-ring based reconstructions for climate, fire, and insect outbreaks we demonstrate how unique tree-ring patterns can be decoupled to minimize the confounding influences of different processes. This protocol emphases the importance of sampling trees sensitive to each factor (*cf.* Fritts 1976) and making direct comparisons of multiple chronologies. Our results show careful sampling techniques reduced the likelihood of erroneously attributing growth suppressions to drought, fire, or insect outbreak. We also find that by comparing defoliating insect host and non-host chronologies to a climate-sensitive but non-defoliated host chronology, we can mitigate the effects of different species responses to climate. Lastly, we find that a comparison of multiple chronologies provides independent confirmation of disturbance events that can occur simultaneously or overlap in their occurrence. This allows researchers to isolate the cause of growth variations and to attribute them to one or multiple possible causes. While our protocol may be impractical in some locations, careful sampling techniques and comparisons between host, non-host, and climate reconstructions are essential to correctly identify each of these events.

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