

Climatic Inferences from Dendroecological Reconstructions

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9.1 Introduction

Dendroecology – the application of tree-ring analysis to ecological questions – is a rapidly expanding subfield of dendrochronology with increasing relevance to the study of past and present ecosystems and climatic variations. Ecologists have typically focused on short-term studies (<10 yrs) at fine spatial scales (<1,000 m²), but the importance of long-term and broad-scale processes is increasingly appreciated (Ricklefs 1987; Levin 1992; Turner et al. 1993; Brown 1995). Many ecosystem processes, especially those affected by climate changes, only manifest themselves over longer time periods and broader spatial scales than what can be studied in typical ecological studies. Understanding the dynamics of long-lived organisms and ecosystems - and the role of climate in controlling these dynamics - requires decadal to centennial and landscape to regional-scale perspectives. Various types of tree-ring data can provide the type and depth of temporal and spatial information needed for multi-scale, comparative analyses to fully evaluate climatic effects on ecosystems (Fritts and Swetnam 1989; Schweingruber 1996; Swetnam et al. 1999).

The most common types of dendroecological datasets with relevance to studies of climate effects are disturbance histories (e.g., chronologies of forest fires and insect outbreaks) and demographic histories of tree populations (chronologies of tree natality and/or mortality). For both of these types of datasets, there are - or there is the potential for development of – broad networks of data from multiple sites that allow for regional-scale analyses. Disturbance and demographic processes are driven by both internal system dynamics (e.g., species life histories and community dynamics, such as competition) as well as by external factors such as climate. Generally, evidence for climate effects only emerges at larger spatial and longer temporal scales because of the “noise” introduced by local, internal ecological processes and effects. There have been a variety of dendroecological studies that primarily focused on internal stand or community ecological dynamics (e.g., Spencer 1964; Clark et al. 1975; Morneau and Payette 2000; Lorimer 1985; Frelich and Graumlich 1994; Kneeshaw and Bergeron 1998). These

studies were carried out at the stand or watershed scales and climatic analyses were not included, or were limited because of the fine spatial scale of the datasets. In contrast, broader studies examining climate effects on ecosystem dynamics have used network-based approaches involving many sites distributed across mountain ranges or regions (i.e., 10^4 to $>10^6$ km²; e.g., Swetnam and Betancourt 1998; Veblen et al. 1999, 2000; Kitzberger et al. 1997, 2007; Kitzberger and Veblen 1998; Villaba and Veblen 1997a; Brown and Shepperd 2001; Sibold and Veblen 2006; Brown 2006).

Networks of well-dated disturbance and demographic chronologies can be aggregated at multiple spatial scales to enhance common patterns, just as is done in regional networks of ring-width or ring-density chronologies. Climatic influence emerges as patterns of synchrony (or asynchrony) of events, oscillations, or trends. Very broad-scale synchrony (at $>10^4$ km² scales) is typically related to climate variability affecting the co-occurrence of ecological events in many places, because most ecological disturbances or processes are not capable of physically spreading over such large areas. For example, fires generally can not burn across the enormous desert valleys and canyons that separate forested mountain ranges in the American Southwest. Therefore, synchrony of annual fire events (or absence of fire events) among these widely dispersed mountain ranges has to be related to regional-scale fire-inducing (or suppressing) climatic conditions, such as regional drought (wet) events (Swetnam and Baisan 1996).

In general, synchrony of disturbance events and demographic processes at regional or broader scales can be inferred to reflect climatic influences. An apt analogy is crossdating of tree-ring measurements among trees and sites. In the case of tree-ring widths or densities, it is understood that numerous unique or local factors (e.g., soils, competition, genetics, human land uses, etc.) at the scales of trees and forest stands may affect cambial growth and thereby introduce non-synchronous, non-climatic signals in tree-ring time series (Cook 1990). However, when sites and trees are carefully selected to maximize climatic sensitivity and ring series from many locations are combined, the existence of broad-scale crossdating (i.e., synchrony) of ring patterns across regions is logically and demonstrably related – both statistically and mechanistically - to climatic variations (e.g., Fritts 1976). Likewise, disturbance and demographic events are affected by numerous local factors, but if common, synchronous patterns emerge across broad-scale networks, those ecological patterns are most probably climatic in origin, especially when coupled with mechanistic understanding of climate/ecological relationships, such as the fact that regional droughts affect dry fuels that result in regional fire years (e.g., Swetnam and Betancourt 1998).

Assembly of regional to continental-scale networks of disturbance and tree demographic histories is just beginning (see the International Multiproxy Paleofire Database at: <http://www.ncdc.noaa.gov/paleo/impd/>). Analogous development of tree-ring width networks in North America and South America began in the 1950s with Edmund Schulman's work (Schulman 1956), and continued through the 1970s and 1980s with Harold Fritts' efforts (Fritts 1976, 1991). Many other dendrochronologists have assembled tree-ring data networks at continental to global scales and contributed these to publicly-accessible databases (see the International Tree-Ring Data Bank at <http://www.ncdc.noaa.gov/paleo/treering.html>). These datasets have been applied in broad-scale dendroclimatic reconstructions (e.g., Fritts 1991; Briffa et al. 1994; Mann et al. 1998, 1999; Cook et al. 1999, 2004). In addition to providing an example for

dendroecology of the power of the network approach, dendroclimatic networks also provide a tremendous source of comparative data. Replicated time series of reconstructed hydro-climate variables or global circulation indices are often used to evaluate the effects of annual to multi-centennial climate variability and change on ecosystems. The easy availability of these climate reconstructions is now stimulating a surge of dendroecological research with a climatic focus.

The fact that synchronous ecological processes occur at very broad spatial scales (e.g., Koenig and Knops 1998; Hawkins and Holyoak 1998), and that this synchrony is driven in part by climatic variability (e.g., Swetnam 1993; Villalba and Veblen 1997a; Swetnam and Betancourt 1998; Brown and Wu 2005), raises important questions for both ecology and climatology:

- *How can chronologies and networks of ecological patterns be used to study past climate variability and change?*
- *How does climate entrain ecological disturbance events and population dynamics (natality and mortality) at regional and broader scales?*
- *When and in what manner do externally forced effects from climate over-ride internal or local factors (e.g., competition, predation, random variations) in determining the dynamics of ecosystems?*
- *How can we use our understanding of past climate influences on ecosystems at long-term and broad-scales to predict impacts of future climate change on ecosystem structure, function, and disturbance dynamics?*

In this chapter we describe several examples of ecological disturbances and population dynamics that are influenced by climatic variations. In particular, we illustrate how spatial networks are useful for evaluating climatic and ecological relationships by drawing upon our own fire history, insect outbreak, and tree population studies in the western United States. In addition to describing and discussing the ecological insights and implications of these tree-ring studies, we also focus on their relevance for climatological investigations. We compile both regional tree recruitment and fire occurrence data to highlight an unusual hiatus of forest fire occurrence in the western U.S. and southern South America during the early 1800s as an example of what we term here as an “ecologically effective climate change”.

9.2 Examples of dendroecological-climate reconstructions

9.2.1 Fire history and fire climatology

Fire history studies using crossdated fire-scarred trees are the most common type of dendroecological analysis involving assessments of climatic effects. There are numerous examples of sub-regional to continental (and even inter-continental) studies of fire climatology using fire-scar chronologies and various hydroclimatic reconstructions (e.g., see summaries in Veblen et al. 2003). Fire-scarred trees are a fortuitous ecological and physical phenomenon, whereby past fire events (primarily low-intensity surface fires) create very distinctive lesions within tree-ring series (Fig. 9.1). The ubiquitous presence of fire-scarred trees in many forests worldwide has provided evidence to

reconstruct detailed chronologies of fire history in hundreds of forest stands (e.g., Kitzberger et al. 2007). Fire history networks are now the most developed among dendroecological data networks, with more than 350 fire-scar time series included in the International Multi-Proxy Paleofire Database (<http://www.ncdc.noaa.gov/paleo/impd/>).

The power of a dendroecological network for assessing fire/climate relationships is illustrated here with an example from the southwestern US. At present, there are a total of 120 crossdated fire-scar chronologies that have been compiled from sites in Arizona and New Mexico (Fig. 9.1). Site chronologies typically are composed of sets of 20 or more fire-scarred trees sampled in forest stands of about 10 to 100 hectares in size (see Swetnam and Baisan 1996, 2003, and references therein for details of site selection and other details). Compilation of fire dates recorded in individual sites results in a regional fire chronology, which documents years when both highly synchronous fires were burning in many sites across the region as well as years when few fires occurred (Fig. 9.2).

The regional fire chronology documents strong relationships both with hydroclimatic variables and with ocean-atmosphere indices, such as the El Niño-Southern Oscillation (ENSO; Figs. 9.3, 9.4). Regional fire years – defined as years when fire scars were recorded on trees at more than 20 sites – mainly occurred during relatively dry years of a set of gridded, independently derived reconstructions of summer Palmer Drought Severity Indices (PDSI; Cook et al. 2004; Fig. 9.3, top panel). In contrast, years during which almost no fires were recorded around the region tended to occur during relatively wet years. Regional fire years also tended to occur during years of cool sea surface temperature conditions (low NINO3, an index of ENSO, which are La Niña years), while all but one of the small fire years occurred during warm sea surface temperatures conditions (Fig. 9.3, bottom panel; El Niño years).

These patterns are supported by superposed epoch analyses (SEA; Fig. 9.4). SEA is used to compare average annual climate anomalies for the set of regional fire years to climate for the entire period of the climate reconstructions (Swetnam 1993). SEA also is used to compare climate during years prior to fire years to assess antecedent conditions that may have been important for fire occurrence. Significant climate anomalies are assessed using bootstrapped confidence intervals based on distributions of annual climate values. SEA results from the Southwest regional data confirm that on average the larger fire years occurred during drought years and La Niña events, and that the small fire years occurred during the opposite patterns of pluvial years and El Niño events (Fig. 9.4). Interestingly, SEA also often shows that there were significant lagging relationships in climate/ecosystem dynamics, with fire years typically following one to three years of wet conditions. These fires were mainly surface fires, burning in grasses and herbaceous fuels, and wet conditions would have resulted in more continuous and denser fuels that would have burned more readily and widespread during subsequent drought years (e.g., Brown and Wu 2005).

Overall, the Southwest climate and fire comparisons (Figs. 9.3, 9.4) illustrate not only the close coupling between wet/dry patterns and fire in this region, but they also provide a strong confirmation of the high fidelity of these two types of dendrochronological reconstructions. The regional reconstructed climate and fire time series are based on independently collected and quite different types of tree-ring data. The climate-sensitive trees used to develop the drought and NINO3 reconstructions

generally come from dry, rocky sites where fire spread is unlikely, and ring widths are the measured variable. The fire scar records generally come from ponderosa pine and mixed conifer forests in the same region, but typically in sites where grass and pine needle under stories could carry widespread fires. Fire scars are the primary observed variable in these time series. Despite these differences, the remarkable coincidence of extreme regional dry (wet) years and high (low) fire occurrence suggests that the two kinds of network-based reconstructions are accurately identifying ecological effective climatic conditions at annual resolution.

9.2.2 Western spruce budworm outbreaks and climatic entrainment

One of the most widespread forest defoliators in the western United States is the western spruce budworm (*Choristoneura occidentalis*). During its larval stage, this Lepidopteran moth is a voracious feeder on the buds and needles of true firs (*Abies* species) and Douglas-fir (*Pseudotsuga menziesii*) trees. The name “spruce” budworm is a bit of a misnomer, because although spruce trees (*Picea* spp.) are minor hosts, the true firs and Douglas-fir typically suffer much heavier defoliation and higher mortality rates than spruces. Another closely related budworm species (*Choristoneura fumiferana*) occurs throughout eastern Canada and parts of the Northeastern US, where it is the most widespread and important defoliator of conifers. Numerous tree-ring studies have reconstructed outbreak histories of eastern and western spruce budworm (e.g., Blais 1981; Morin et al. 1993; Swetnam and Lynch 1993; Hadley and Veblen 1993; Krause 1997; Jardon 2001; Ryerson et al. 2003), making this an excellent candidate for development of regional (and perhaps continental) networks of outbreak chronologies.

The tree-ring basis for developing outbreak chronologies is the observation of very sharply reduced ring growth in the host species during the defoliation episode, which typically lasts for a decade or longer (Fig. 9.5). The methods are rather involved for confidently identifying reduced growth periods as outbreaks (involving distinguishing the outbreak signals from potentially confounding climate effects, e.g., droughts), and compiling the observations into stand-level chronologies of outbreak events and sub-regional composites (see Swetnam et al. 1985; Swetnam and Lynch 1993; and Ryerson et al. 2003). In general, the process we have followed includes: (1) the separate development of “host” and “non-host” tree species ring-width chronologies from nearby sites, (2) detailed graphical and statistical comparisons of these chronologies against each other and with independent instrumental climate data, (3) the use of the non-host chronologies (if comparison tests are satisfactory) to “correct” the host chronologies (i.e., to remove most or all of the climate effects from the host chronologies), and (4) validation of the corrected chronologies with independent forest entomology records (e.g., maps and observations of defoliation and/or insect population measurements). The correction procedure involves subtraction of a variance re-scaled version of the non-host chronology (index values) from the host chronology.

Resulting “corrected” budworm-affected chronologies from individual trees or stand averages can then be combined into network composites for sub-regions. Our original work on this focused primarily on stand-level averages of corrected host ring-width chronologies, and the sub-regional composites were expressed as “number of chronologies (stands) recording outbreaks” each year (Fig. 9.6). In subsequent work we

found that an “epidemiological approach”, focusing more on the responses of individual trees and their collective responses, rather than solely on stand averages, was more effective in revealing outbreak timing and magnitudes. Composites of these data are expressed as numbers or percentages of trees (by site or in the whole network) recording an outbreak each year (Fig. 9.6).

One of the consistent findings of our western spruce budworm studies in four sub-regions of the western United States is a general correspondence between budworm outbreaks and wet periods, coupled with reduced budworm outbreaks (endemic periods) during drought episodes (Fig. 9.6). In detailed analysis of precipitation and temperature variables in the Southern Rocky Mountains of New Mexico, Swetnam and Lynch (1993) found that a wetter spring through early summer season (March to June) was best correlated with the regional budworm composite record. In addition to concurrence of wet periods and outbreaks, in cross-correlation and cross-spectral analysis we found that increased wet conditions usually preceded the outbreaks by several years up to a decade. These findings suggest that wet conditions predispose trees and forests to budworm outbreaks.

The subject of potential climate entrainment of insect outbreaks - and on animal population dynamics in general - has been debated in the ecological literature for decades (e.g., White 1976; Royama 1984; Martinat 1987; Mattson and Haack 1987). A variety of theories have emerged, including the famous “Moran Effect”, based on Moran’s theorizing about the oscillatory behavior and regionally synchronized lynx-hare populations of Canada (Moran 1953). In the case of western spruce budworm, it seems likely that favorable moisture conditions may act through an increase in the quantity and improvement in the quality of tree foliage, the food base for these defoliators (Swetnam and Lynch 1993). Although the mechanisms remain unclear, we think the consistent, coincident patterns in the tree-ring data of wet periods/outbreaks, and droughts/endemic phases over multiple centuries and large regions are quite compelling evidence that decadal moisture variability is an important driver of budworm populations.

Notable features of forest insect outbreak reconstructions from tree-rings are the remarkable cycles or quasi-cycles that are evident in these time series. The famous larch budmoth (*Zeiraphera diniana*) of central Europe is the clearest example of relatively fixed-period (cyclic) outbreaks. These outbreaks produce a distinct tree-ring signature of defoliation events, evident as sharply reduced ring widths and densities, that have allowed for reconstructions of up to 1,200 years in length (Weber 1997; Esper et al. 2007). The recent work of Esper et al. (2007) demonstrates a remarkable regularity and stability of larch budmoth cycles in the European Alps over the past millennium, with an average period of 9.3 years between outbreaks. Perhaps the most notable finding in this paper is that the larch budmoth reconstruction (832 to 2004 C.E.) shows that the recent period (since 1981) is the most unusual in the entire reconstruction, with an unprecedented absence of outbreaks. Esper et al. (2007) show that this period corresponds to an unprecedented (over the same time period) increase in temperatures in this region (from an independent tree-ring reconstruction), and conclude that nutrient cycling and other ecosystem processes operating in the Alps may be undergoing a drastic alteration. Although the exact mechanisms of this change are not known, Esper et al. (2007) speculate that warming winter temperatures may have led to earlier emergence of larvae from their eggs in the late winter or spring before larch tree needles have emerged,

leading to starvation and failure of the larch budmoth populations to enter an outbreak phase.

Our regional time series of western spruce budworm typically show more variable oscillatory behaviors than is the case with larch budmoth, with considerable variability in the periods between budworm outbreaks. Hence, budworm population fluctuations appear not to be very strongly cyclic. Nevertheless, as much as 50 to 60% of the variance of the regional composite time series is explained by cycles of about 25 to 35 years (Swetnam and Lynch 1993; Ryerson et al. 2003). Considering that these data are derived from tree-rings, where cycles of this strength are virtually never observed in raw ring-width series from non-host trees, this in itself is a remarkable characteristic of defoliated host trees. Moreover, in cross-correlation and cross-spectral analysis there appears to be some coherence of these moderate strength outbreak periodicities, and much weaker but similar periodicities in climate reconstructions (Swetnam and Lynch 1993).

A notable example of the use of tree rings in evaluations of animal population dynamics and cyclic environmental variables are the studies of Sinclair et al. (1993, 1997) of hare populations, climate, and sunspot cycles in Canada. Unfortunately, the physical tree-ring basis of the hare population reconstructions (feeding scars on aspen stems) seems obscure and is not well illustrated or described in these papers. Some of the quantitative time series analyses are also problematic and difficult to evaluate. More research in this area, particularly with employment of more rigorous dendrochronological sampling and analysis procedures, may be fruitful in evaluating previous findings, and shedding light on the role of climate and animal population dynamics. New and powerful statistical-analytical tools that are increasingly employed by dendrochronologists and paleoclimatologists might be usefully employed in this endeavor (e.g., univariate and bivariate singular spectrum analysis, wavelet analysis, e.g., Speer et al. 2001; Esper et al. 2007).

The periodic and aperiodic behaviors evident in tree-ring based insect outbreak reconstructions, and their potential coherence with climate deserves much more study. Most insect population dynamics studies have relied on much shorter observational data sets, which in some cases include only one to a few insect outbreaks (e.g., Royama 1984; Myers 1998) or population “eruptions” (e.g., Ranta et al. 1997). Tree-ring based insect outbreak and climate reconstructions for population dynamics research is of potentially great value because numerous population oscillations over periods of centuries can be identified at numerous locations over regions, and even continents. We think there are opportunities here for breakthroughs in our understanding of how climatic variations and oscillations act as potential synchronizing (e.g., the Moran Effect) or disrupting factors in plant and animal population dynamics. Given recent enormous outbreaks of bark beetles in concert with climatic changes in North America (e.g., Logan et al. 2003; Breshears et al. 2005), and Esper et al.’s (2007) findings about changes in larch budmoth and temperature in the Alps, the importance of this topic is likely to increase in coming years.

9.2.2.1 Confounding of dendroclimatic signals by insect outbreaks?

One final point regarding insect outbreaks is important in the context of this chapter and book, i.e., the potential confounding influence of insect outbreaks/defoliation on dendroclimatic interpretations from host trees. Dendroclimatologists are certainly

aware of this as a potential problem (e.g., Morrow and LaMarche 1978), and as a general practice they seek to avoid sampling sites and trees that have a known history of past outbreaks (Fritts 1976). A recent paper by Trotter et al. (2002) evaluated this issue in some detail in pinyon pine (*Pinus edulis*) stands near Flagstaff, Arizona defoliated by pinyon pine needle scale (*Matsucoccus acalyptus*). They concluded that, indeed, chronic or episodic effects of this insect could alter the dendroclimatic estimates of drought if one were to use tree-ring width series from affected trees.

It is our opinion that the large majority of tree-ring width series that have been sampled and measured for dendroclimatic studies in the western United States do not have a great risk of being confounded with insect outbreak (or chronic insect feeding) signals. This is because most of the major episodic defoliators of conifers (e.g., western spruce budworm and Douglas-fir tussock moth) generally tend to feed in stands that have relatively closed-canopy conditions, in moderate to highly mesic sites, and at mid-elevations. Stands with *Abies* as a dominant or co-dominant species, for example, are more vulnerable than pure Douglas-fir stands. In general, these kinds of stands are infrequently sampled for dendroclimatic purposes. The classic western U.S. drought-sensitive site is an open-canopy conifer stand, in a xeric site, at the lower forest border, with steep slopes and shallow soils (Schulman 1956; Fritts 1976). These are typically the least-likely stands to be attacked by western spruce budworm. High elevation, near-treeline stands that are sampled for temperature reconstructions also are generally not affected by budworm or other major defoliators. Although some insect defoliators and stem feeders (e.g., bark beetles) can affect large areas, to the best of our knowledge, past outbreaks have tended to occur in a relatively small proportion of the range of host species.

In addition to the reasons listed above, episodic or chronic defoliation, or past insect induced mortality within stands is usually visually obvious within the stands themselves, or in the sampled ring-width series (e.g., Fig. 9.6; but see Ryerson et al. 2003 for a case study where outbreak signals were not often visually obvious in the “uncorrected” ring-width series). Within stands, past defoliation events are usually apparent in the presence of trees with old dead tops (spikes), and new dominant crown leaders, and many old dead branches which are not simply the result of great age. Also, dead trees from past killing events may be present, and in the case of bark beetles, tell-tale feeding and egg-laying galleries may be visible on the stems of dead trees for many years after the event (e.g., Perkins and Swetnam 1996).

In summary, the potential confounding effects on tree-ring series of past insect attacks – and other disturbances such as fires – are an important consideration that dendroclimatologists should be more keenly aware of than they generally are. Precautions should be taken to investigate what is known from documentary sources and local experts about the potential occurrence of past outbreaks in areas to be sampled. Dendroclimatologists should have some field and laboratory training and experience in identifying signs of past outbreaks within stands and on tree-ring specimens. We encourage greater awareness of this issue by dendroclimatologists. We also recommend further study of the potential “contamination” of dendroclimatic databases with insect and other disturbance signals. Perhaps a screening of existing dendroclimatic databases is warranted for potentially unknown insect outbreak signals that may exist in some

chronologies from host species in areas with known outbreaks. However, it is our expectation that if there are any such problem chronologies, they are likely to be few.

9.2.3 Regional tree demography and climate effects

Ecologists have long recognized that time series of tree births and deaths are of fundamental value for understanding forest and woodland dynamics (Blackburn and Tueller 1970; Henry and Swan 1974; Harper 1977). Estimating the age of a tree by counting its annual rings is probably the best known tree-ring application in history, extending at least back to the writings of Aristotle. However, from a dendroecological perspective, the determination of tree ages is more complex than simply counting rings, and understanding forest demographic patterns requires much more than merely sampling what one suspects are the oldest trees in a forest. Because rigorous dendroecological analyses of tree demography are somewhat less well described in the literature than disturbance history methods (e.g., fire scar and fire history methods) we briefly describe here some key aspects of this tree-ring application in the context of studies that are relevant to climatic influences on forests and woodlands.

There are several important considerations in determining ages of individual trees and hence the age distribution of a forest stand or landscape. First, obtaining accurate dates for tree-ring sequences is of primary importance for ecological and climatic studies since identification of synchrony of events and processes requires high temporal resolution (Baumgartner et al. 1989; Fritts and Swetnam 1989). Dendrochronological crossdating of ring sequences (Stokes and Smiley 1968; Swetnam et al. 1985) should always be used (or at least attempted) to derive absolute dates for tree-ring sequences. Even in studies where temporal precision of recruitment dates is on the order of 10-20 years, it is usually impossible to know how much error is involved in ring-counted data without first crossdating at least some of the tree-ring sequences. Crossdating is particularly critical for demographic studies in forests that have been selectively harvested (Brown and Cook 2006). Sampling of only living trees in harvested stands may give a biased perspective on the age distribution of the historical forest as larger (and, hence, generally older) trees are often removed in selective harvest procedures.

In practice it is difficult to determine the exact germination dates of trees. This is due both to limitations in the ability to obtain ring series at the exact point of seedling germination (the “root-shoot” boundary) and typically indistinct growth patterns in the very earliest years of seedling growth that make identification of annual ring boundaries difficult. Using the most intensive techniques and under the best circumstances, annual or nearly annual resolution of tree germination dates is possible using destructively sampled trees (Savage et al. 1996; League and Veblen 2006). However, most studies are limited to pith dates on ring sequences taken from some height above the original germination point, i.e., above the root/shoot boundary (e.g., Villalba and Veblen 1997b; Brown and Wu 2005; Brown 2006). These studies have generally used the terms “tree establishment” or “tree recruitment” to refer to the date or period when a tree became successfully rooted as a seedling, rather than the exact date of germination. Often establishment periods of 5 to 20 years resolution are used to reflect the relatively low precision in estimates of tree ages.

It is also often difficult to obtain exact death dates of remnant trees. Reasons include difficulties in obtaining usable tree-ring samples from often highly decayed wood, and irregular ring characteristics near the outside, especially in very old trees that were stressed at the time of death. Death dates on remnant trees are also often difficult to determine because sapwood typically decays rapidly after tree death (especially in logs on the ground), which removes an unknown number of rings from the outside of the stem. Again, however, using the most intensive techniques and with careful consideration of available evidence, annual or near-annual resolution of death dates can be obtained for examination of stand to landscape-scale mortality events (e.g., Margolis et al., in review).

Another requirement of tree demographic studies is an adequate sample size. However, no studies have addressed exactly how many trees may be needed to adequately characterize population age structure in varying forests, and more work is needed in this regard. In old, uneven-aged forests sometimes hundreds of trees must be sampled to obtain adequate characterization of age structure distributions. This is mainly due to the decline in survivorship of trees as they age (often following an inverse J-shaped curve). This is what has been referred to as the “fading-record” problem, which is common, in varying degrees, to all paleoecological studies. The oldest trees that represent germination pulses, or “cohorts”, in the earliest periods may not be detected unless numerous trees are sampled, but few studies have addressed this question in any type of systematic manner (but see Johnson et al. 1994). Furthermore, many studies have found relatively poor relationships between tree size and age. Therefore, some sort of systematic sampling procedure should be used to select trees for aging rather than merely selecting the largest trees in a stand.

Similar to tree recruitment dates, preservation of dead trees is a declining function with time before present, and obtaining estimates of past mortality events depends both on persistence of woody material and the ability to adequately sample the material to obtain death dates. Old forests usually contain complex recruitment and mortality patterns, and to temporally resolve the different pulses and hiatus periods of establishment and mortality events requires very large sample sizes and careful sample techniques, particularly with sampling difficulties of obtaining the bark rings on dead trees.

However, despite these and other difficulties in obtaining high-resolution tree demographic data, concentrated efforts have resulted in very useful time series for evaluating population dynamics related to climatic influences. One of the most successful of these studies to date is the work of Villalba and Veblen (1997a) on *Austrocedrus chilensis* woodlands in Argentina. They demonstrated a clear set of linkages between favorable moisture conditions promoting regional tree cohort establishment, and unfavorable (drought) conditions promoting reduced tree establishment and mortality (Fig. 9.7). Another successful example is a recent study by Brown and Wu (2005) that illustrated the contingent effects of climate and fire occurrence on tree establishment in a ponderosa pine (*Pinus ponderosa*) forest in southwestern Colorado (Fig. 9.8).

Examples of regional- to landscape-scale tree natality, mortality, and climate associations found by Villalba and Veblen (1997a), Brown and Wu (2005) and Brown (2006) inspired us to undertake a “meta-analysis” of regional tree establishment data in

ponderosa pine forests from the Southwestern United States. For this analysis, we compiled data from 12 studies that sampled hundreds of ponderosa pine trees distributed around the Southwest (Fig. 9.9). Some of these studies estimated stand densities (number of stems or trees per hectare) from a sampling of trees, while others reported total counts of trees establishing by date or period over a certain size class within fixed plots or belt transects. There were also differences in the establishment date (period) resolution in the data sets, including 5, 10, and 20 year periods.

Regional patterns of synchrony emerge in an overall compilation of the 12 time series in a ponderosa pine “establishment index” (Fig. 9.10). This time series was derived from the logarithms of the time series values (tree numbers and tree densities; 1.0 added to all values so that logarithms could be computed for years/decades with zero values) and the ratio of each log transformed value to the mean of the entire log transformed series. The regional time series is the average of all the establishment indices computed for each series (site). Logarithmic transformations are useful here because there is a strong tendency for recent periods (especially after 1900) to have one to several orders of magnitude more trees establishing (or surviving) than before this period. Hence, to evaluate relative patterns the log transform and ratio index helps to standardize all data sets for visual comparisons and combination in the regional index time series.

Overall, the regional composite (Fig. 9.10) shows that ponderosa pine forests are typically uneven-aged and the age structures are often dominated by episodes of tree establishment (cohorts) that alternated with multi-decade periods when relatively fewer trees established in the stands. Moreover, the composite suggests that there was substantial regional synchrony of these episodes of establishment (and lack of trees establishing), indicating the likely influence of broad-scale climate forcing. In general, the largest cohorts correspond with wetter conditions, as shown in the comparison with dendroclimatic reconstructions of drought indices (Cook et al. 2004) from the region (Fig. 9.10). In particular, the 1810s-60s and 1890s-1930s cohorts coincide with exceptional wet periods. Decreases in establishment of trees also appear to approximately coincide with drier periods in the 1750s-1760s, 1850s-1860s, and 1950s-1960s. Note also that a most recent cohort in the 1980s-1990s also coincides with a wet period in the Southwest that occurred from approximately 1977 to 1992 (Swetnam and Betancourt 1998), although many of the data sets used here lack measurements of tree seedlings and saplings in these recent decades. Earlier wet periods (1610s-1640s and 1690s-1710s) may coincide with very slight establishment episodes, but these cohorts are not well resolved, probably because fewer trees overall are included in this earlier part of the record.

Although this is a relatively coarse-scale spatial and temporal analysis of ponderosa pine age structure patterns in the Southwest, the results (Fig. 9.10) suggest there are several key features of local to regional recruitment dynamics that were responsive to climatic variability. It is well known that ponderosa pine produces large cone crops only erratically, and that successful germination of the seeds is enhanced by warm, wet summers (Pearson 1950; Savage et al. 1996). Successful establishment and survival of seedlings into saplings is dependent on (1) favorable moisture conditions (i.e., lack of drought), (2) the absence of surface fires for a sufficient length of time to allow the saplings to develop thicker, more heat resistant bark (e.g., Brown and Wu 2005; Fig 9.8), and (3) for meristems to be elevated above grasses and other surface fuels. Hence, it

seems quite likely that historically, the favorable germination and establishment periods of ponderosa pine in the Southwest corresponded with wetter conditions for the reasons described above, i.e., more successful germination and survival during these periods, and relatively longer intervals between fires during these wet periods (see also Fig. 9.8). It is likely that climate affected recruitment in many of these forests both through direct effects on demographic processes (seed production, germination, and seedling growth) as well as by modifying fire frequency and timing (and perhaps other disturbances, such as insect outbreaks; e.g., Fig. 9.6). In a later section of this chapter, we will discuss timing of longer fire-free intervals, and their relationships to both climate and patterns of regional tree recruitment shown in Fig. 9.10.

As in most dendrochronological studies involving networks of chronologies, regional-scale emergent patterns of ecological synchrony may be reasonably interpreted to reflect, at least in part, the important role of climatic variability. This is not to discount the important role of local factors in causing unique disturbances or demographic peculiarities at the tree or stand level. Interactions between disturbances and demography (e.g., fire, insect outbreaks, and tree mortality and subsequent natality) can add multiple layers of complexity and non-climatic signals in composite, ecological time series. Nevertheless, depending on the extent and degree of spatial coherence and synchrony of disturbances or demographic patterns, the relative role of climate can be assessed by the nature of the aggregated time series, and their relations to independent climate reconstructions. The moderate degree of regional synchrony in Southwestern U.S. ponderosa pine establishment over the past several centuries, and approximate correspondence with reconstructed drought indices (Fig. 9.10), suggests that climate is at least partly controlling. We recognize, however, that multiple other environment factors probably also determine the non-synchronous variations, especially at finer spatial scales of individual stands.

9.3 The late-18th century, early-19th century fire gap

We close our discussion of dendroecological and climate reconstructions with a specific example of an interesting climatic episode that has been identified in multiple fire chronologies. Fire historians in North and South America have long recognized a very interesting “gap” or hiatus in fire events during the period from ca. 1780 to 1840. The gap appears as an unusually long interval (relative to average intervals in the rest of the chronologies) between fire events. This gap is evident in many forest stands from the Southwest (e.g., Swetnam and Dieterich 1985; Fig. 9.11; see also Fig. 9.8 from Brown and Wu 2005), Baja California (Stephens et al. 2003; Fig. 9.12), and northeastern Oregon (Heyerdahl et al. 2002). The gap seems to be detectable primarily in the intermediate fire frequency fire regimes (i.e., mean fire return intervals between about 7 to 15 years). The timing and length of the gap varies somewhat from area to area, starting or ending some years earlier or later, but generally within the period from the late 1700s through to the middle 1800s.

Kitzberger et al. (2001) noted that a similar gap of reduced fire frequency was present during approximately the same time period (i.e., 1780s-1840s) in fire histories from *Austrocedrus chilensis* woodlands in northern Patagonia, Argentina (Fig. 9.13). Perhaps most remarkably, the regional fire-scar time series from the Southwest and

Patagonia were statistically coherent (i.e., synchronous), especially in the frequency range of about 2 to 7 years (determined in an evolutive bivariate spectral analysis). Kitzberger et al. (2001) hypothesized that the common response of fire regimes in the Southwest and Patagonia to the El Niño-Southern Oscillation (Swetnam and Betancourt 1990; Kitzberger et al. 1997; Veblen et al. 1999, 2000; Veblen and Kitzberger 2002) was likely to be the reason for coherence of the two fire occurrence time series from different hemispheres. Moreover, they proposed that the hiatus during the late 18th and early 19th centuries could be due to a combination of (1) reduced amplitude and/or frequency of ENSO events (especially La Niña events) during this period (Fig. 9.14; see also Brown and Wu 2005, Fig. 9.8), and (2) a coincidence of this period with a major global cooling phase in the early 1800s (i.e., 1810s to 1820s), that might be associated with volcanic eruptions, and is clearly indicated in northern hemisphere temperature reconstructions (e.g., Mann et al. 1998, 1999).

Additional detailed analysis of the Southwest regional fire-scar series (Fig. 9.2), and a sub-set of this series, offers further insight on the nature and possible causes of the gap. Swetnam and Baisan (1996) found that an index of regional fire occurrence in the Southwest based on 63 fire-scar sites was highly correlated with tree-ring width based Palmer Drought Severity reconstructions from the region during the early to mid 1700s and after the mid 1800s (Pearson's $r > 0.8$). However, this correlation declined precipitously during the late 1700s and early 1800s ($r < 0.3$) before rising again after about 1850. This finding seems to support the interpretation that inter-annual climate variations were reduced, perhaps associated with a quiescent ENSO, and this may have caused an uncoupling from the fire occurrence pattern in the Southwest (see also Fig. 9.8, and Brown and Wu 2005 findings of reduced "biennial" oscillations during this period).

Other dendroecological evidence also points to possible shifts in fire regimes during the late 18th and early 19 century period. An analysis of a sub-set of fire-scar chronologies from the El Malpais area of west central New Mexico indicated that the seasonal timing of fires also shifted during the late 18th century (Grissino-Mayer and Swetnam 2000). This analysis of the distribution of fire-scar seasonality found that late season scars were more prevalent in the period before the late 1700s than after. In this remote and rugged area (with impassable lava flows in places) human-set fires were unlikely. It is probable that climate shifts were responsible for a change in seasonal timing of fires. Grissino-Mayer and Swetnam (2000) hypothesized that the arid fore-summer/monsoon pattern may have strengthened after the late 1700s, resulting in more fires during the early to mid growing season (i.e., the arid fore-summer, May and June), but fewer fires during and after the late summer monsoon (July to August). Prior to this time, a weaker monsoon may have persisted for some decades (early to mid 1700s) allowing more fires to occur later in the growing season (i.e., July to August).

Other synoptic climate patterns also may have played a role in the fire gap. In a recent multi-variate and contingency analyses of 238 fire scar chronologies from across western North America, extending from southern British Columbia to northern Mexico, Kitzberger et al. (2007) showed that the most coherent regional signal in the fire scar data set was well correlated with ENSO (Pearson $r = -0.47$, $p < 0.001$, between the 1st principal component of the 238 series and the D'Arrigo et al. [2005] reconstruction of the NINO3 sea surface temperature index). An independent tree-ring reconstruction of the Pacific Decadal Oscillation (D'Arrigo et al. 2001) was weakly correlated with the 2nd

principal component ($r = 0.17$, $p < 0.01$). Moreover, an independent tree-ring width reconstruction of the Atlantic Multidecadal Oscillation (Gray et al. 2004) appeared to be associated with periods of maximum coherence (cross correlations) among the fire-scar chronologies during warm phases of the AMO, and minimum coherence during cool phases. The longest and coldest AMO phase occurred during the period 1750 to 1849, encompassing the fire scar gap observed in many of the sites in the network. These findings corroborate and expand a growing list of tree-ring studies demonstrating fire-climate teleconnections at mountain range to sub-regional scales in the western U.S. involving ENSO (e.g., Swetnam and Betancourt 1990; Veblen et al. 1999, 2000; Donnegan et al. 2001; Heyerdahl et al. 2002; Norman and Taylor 2003; Schoennagle et al. 2005), PDO (e.g., Westerling and Swetnam 2003; Norman and Taylor 2003; Hessl et al. 2004; Taylor and Beaty 2005; Schoennagle et al. 2005), and AMO (Sibold and Veblen 2006; Brown 2006).

9.4 Ecologically-effective climate change

It appears likely that changes in both fire regimes and increases in tree recruitment during the early 19th century in western North America and South America are related to changes in timing and strength of ENSO events (Brown and Wu 2005), with further possible modulation of the effects of ENSO (at least in North America) by the AMO (Kitzberger et al. 2007). The early 1800s regional cohort synchrony (Fig. 9.10) may be the best example of the contingency of favorable regional climate and fire conditions occurring together to promote successful establishment, i.e., wetter conditions and longer fire intervals (e.g., Figs. 9.8, 9.11, and 9.12). We suggest that overall, these findings and the widespread occurrence of the “gap” in fire-scar chronologies in North and South America are compelling examples of an “ecologically effective climate change” deserving of more focused analysis by paleoclimatologists and others. In particular, we posit that these ecological responses that occurred at the turn of the 18th to 19th centuries reflect one of the most important and ecologically-effective climatic changes in the past three centuries in western North America and southern South America, causing changes in forest structure that persist to the present.

Most dendroecological studies involving climatic analysis, and most of the preceding examples in this chapter, focus primarily on the ecological implications of the responses of disturbances or demographic processes to climate variations and changes. This is natural and appropriate as a focus of dendroecological research. However, now that numerous case studies have been conducted demonstrating and evaluating ecological responses to climate, and broad-scale network approaches using dendroecological data are increasingly feasible (and with regional data sets starting to become available), we propose that such dendroecological data sets and analyses be used more broadly for identifying important climatological events and processes. Glacier and lake level fluctuations are commonly used by dendroclimatologists and paleoclimatologists as corroborating lines of evidence for identifying climate events and changes. Fire and other dendroecological evidence are used less frequently for such validation (but see Cook et al. 2004 for an example where both fire and lake level data were compared with tree-ring climate reconstructions). In some cases regional ecological time series may be

less noisy and/or higher resolution indicators of climate variability that glacier and lake level fluctuations.

It is clear that dendroecological data, especially networks of such data, can be very useful for clarifying and identifying climatic variations and changes *that are important to ecosystems*. We refer to this as “ecologically effective climate change”, and we think this category of climatic variability deserves special attention by ecologists and other researchers. As climate change due to greenhouse gas-induced warming continues and perhaps accelerates, it will be increasingly important that climatologists, ecologists, managers, policy makers, and the public focus their attention on understanding and anticipating the impacts of climatic change on ecosystems. This will require more effective integration and comparative analyses of dendroclimatic and dendroecological studies. It may well be that the ecologically effective climatic changes that dendroecology can address will provide some of the most sensitive and insightful information about climate change impacts and the climate system. The great potential for ecological indicators is exemplified by time series of plant phenology, such as the timing of plant flowering (Cayan et al. 2001). These records (especially in networks) are now widely recognized and embraced as a key and valuable ecological indicator of climate change.

The final example we offer of the potential of using dendroecological responses to identify ecologically effective climate changes for guiding future research, and for applications, is the finding of the importance of wet/dry oscillations in fire occurrence in the western United States (e.g., Fig. 9.4). It was tree-ring analysis that first identified a strong statistical association between the wet/dry sequence of 1 to 3 wet years, followed by a dry year, and widespread fire occurrence during the dry year (Baisan and Swetnam 1990; Swetnam and Betancourt 1992; Swetnam and Baisan 1996). This finding has been replicated across the southwestern U.S. by numerous dendroecology studies, particularly in relatively dry, ponderosa pine ecosystems where grass and other fine fuel production was important for historical fire ignition and spread (e.g., Veblen et al. 2000; Donnegan et al. 2001; Brown et al. 2001; Stephens et al. 2003; Brown and Wu 2005). Subsequently, analysis of modern fire and climate records (i.e., 20th and 21st century data) confirmed that this pattern was important over large portions of the western US during recent times (Knapp 1995; Westerling et al. 2002, 2003; Crimmins and Comrie 2004). Now, this wet/dry pattern, in combination with ENSO-based climate forecasts (and ENSO-fire associations) are used to develop seasonal “outlook” (forecasting) products for fire managers (see Predictive Services at National Interagency Fire Center, Boise, Idaho: <http://www.nifc.gov/nicc/predictive/outlooks/outlooks.htm>).

In conclusion, we are optimistic that dendroecological contributions to dendroclimatological research, and vice versa, will greatly expand in coming years. The interest in ecological responses to climatic variability and change is already very large and will certainly increase as global warming continues and its impacts increase. The signs of this scientific interest are already evident in increasing numbers of dendroclimatic and dendroecological papers with a climate focus in leading forest science, ecology, and climatology journals. A challenge to dendroecologists is to work collaboratively and to promptly contribute data sets to publicly-accessible archives, in the same generous, ethical and forward-looking spirit as the hundreds of dendrochronologists around the world who have contributed ring-width and ring-density chronologies to the

International Tree-Ring Data Bank. A challenge to dendroclimatologists is to focus their studies on parameters and questions with relevance to ecologists, and in turn to utilize the climatically relevant findings and datasets that dendroecologists are developing to address new questions in historical climatology.

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9.6 References

- Abolt RA (1997) Fire histories of upper elevation forests in the Gila Wilderness, New Mexico via fire scar analysis and stand age structure analysis. M.S., University of Arizona, Tucson, AZ.
- Baisan CH, Swetnam TW (1990) Fire history on a desert mountain range: Rincon Mountain Wilderness, Arizona, U.S.A. *Canadian Journal of Forest Research* 20:1559-1569.
- Barton AM, Swetnam TW, Baisan CH (2001) Arizona pine (*Pinus arizonica*) stand dynamics: local and regional factors in a fire-prone Madrean gallery forest of Southeast, Arizona, USA. *Landscape Ecology* 16: 351-369.
- Baumgartner TR, Michaelsen J, Thompson LG, Shen GT, Soutar A, Casey RE (1989) The recording of interannual climatic change by high-resolution natural systems: tree-rings, coral bands, glacial ice layers, and marine varves. In: D.H. Peterson, ed., *Aspects of Climatic Variability in the Pacific and the Western Americas*. Geophysical Monograph 55: 1-14.
- Blackburn WH, Tueller PT (1970) Pinyon and juniper invasion in black sagebrush communities in east-central Nevada. *Ecology* 51: 841-848.
- Blais JR (1981) Recurrence of spruce budworm outbreaks for two hundred years in western Quebec. *Forestry Chronicle* 57: 273-275.
- Boyden S, Binkley D, Shepperd W (2005) Spatial and temporal patterns in structure, regeneration, and mortality of an old-growth ponderosa pine forest in the Colorado Front Range. *Forest Ecology and Management* 219: 43-55.
- Breshears DD, Cobb NS, Rich PM, Price KP, Allen CD, Balice RG, Romme WH, Floyd ML, Belnap J, Anderson JJ, Myers OB, Meyer CW (2005) Regional vegetation die-off in response to global-change-type drought. *Proceedings National Academy of Science* 102: 15144-15148.
- Briffa KR, Jones PD, Schweingruber FH (1994) Summer temperatures across northern North America: Regional reconstructions from 1760 using tree-ring densities. *Journal of Geophysical Research* 99: 25835-25844.
- Brown JH (1995) *Macroecology*. University of Chicago Press, Chicago, IL.
- Brown PM (2006) Climate effects on fire regimes and tree recruitment in Black Hills ponderosa pine forests. *Ecology* 87:2500–2510.

- Brown PM, Cook B (2006) Early settlement forest structure in Black Hills ponderosa pine forests. *Forest Ecology and Management* 223:284-290.
- Brown PM, Kaye MW, Huckaby LS, Baisan CH (2001) Fire history along environmental gradients in the Sacramento Mountains, New Mexico: influences of local and regional processes. *Ecoscience* 8:115-126.
- Brown PM, Shepperd WD (2001) Fire history and fire climatology along a 5° gradient in latitude in Colorado and Wyoming, USA. *The Palaeobotanist* 50: 133-140.
- Brown PM, Wu R (2005) Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. *Ecology* 86: 3030-3038.
- Cayan DR, Kammerdiener SA, Dettinger MD, Caprio JM, Peterson DH (2001) Changes in the onset of spring in the Western United States. *Bulletin of the American Meteorological Society* 82:399-415.
- Clark NE, Blasing TJ, Fritts HC (1975) Influence of interannual climatic fluctuations on biological systems. *Nature* 256(5515): 302-305.
- Cook ER (1990) A conceptual linear aggregate model for tree rings. In: E.R. Cook and L.A. Kairiukstis, eds., *Methods of Dendrochronology: Applications in the Environmental Sciences*. International Institute for Applied Systems Analysis, Kluwer Academic Publishers, Boston, MA: 98-104.
- Cook ER (2000) NINO3 index reconstruction. International Tree-Ring Data Bank. IGBP PAGES/World Data Center-A for Paleoclimatology Data Contr. Ser. #2000-052. NOAA/NGDC Paleoclimatology Program, Boulder Colorado, USA.
- Cook ER, Meko DM, Stahle DW, Cleaveland MK (1999) Drought reconstructions for the continental United States. *Journal of Climate* 12:1145-1162.
- Cook ER, Woodhouse CA, Eakin CM, Meko DM, Stahle DW (2004) Long-term aridity changes in the western United States. *Science* 306: 1015-1018.
- Cooper CF (1960) Changes in vegetation, structure, and growth of Southwestern pine forests since white settlement. *Ecological Monographs* 30: 129-164.
- Crimmins MA, Comrie AC (2004) Interactions between antecedent climate and wildfire variability across south-eastern Arizona. *International Journal of Wildland Fire* 13: 455-466.
- D'Arrigo R, Cook ER, Wilson RJ, Allan R, Mann ME (2005) On the variability of ENSO over the past six centuries. *Geophysical Research Letters* 32(3), doi:10.1029/2004GL022055: Art. No. L03711.
- D'Arrigo R, Villalba R, Wiles G (2001) Tree-ring estimates of Pacific decadal climate variability. *Climate Dynamics* 18: 219-224.
- Donnegan JA, Veblen TT, Sibold JS (2001) Climatic and human influences on fire history in Pike National Forest, central Colorado. *Canadian Journal of Forest Research* 31:1526-1539.
- Dunbar R, Wellington GM, Colgan MW, Glynn PW (1994) Eastern Pacific sea surface temperature since 1600 AD. The d18O record of climate variability in Galapagos corals. *Paleoceanography* 9, 291-316.
- Esper J, Buntgen U, Frank DC, Nievergelt D, Liebhold A (2007) 1200 years of regular outbreaks in alpine insects. *Proceedings of the Royal Society B* 274: 671-679 doi:10.1098/rspb.2006.0191

- Frelich LE, Graumlich LJ (1994) Age-class distribution and spatial patterns in an old-growth hemlock-hardwood forest. *Canadian Journal of Forest Research* 24: 1939-1947.
- Fritts HC (1976) *Tree Rings and Climate*. Academic Press, New York, 567 pp.
- Fritts HC (1991) *Reconstructing large-scale climatic patterns from tree-ring data*. Tucson: The University of Arizona Press. 286 pp.
- Fritts HC, Swetnam TW (1989) Dendroecology: A tool for evaluating variations in past and present forest environments. *Advances in Ecological Research* 19:111-189.
- Fule PZ, Covington WW, Moore MM, Heinlein TA, Waltz AEM (2002) Natural variability in forests of the Grand Canyon, USA. *Journal of Biogeography* 29: 31-47.
- Gray ST, Graumlich LJ, Betancourt JL, and Pederson GD (2004) A tree-ring based reconstruction of the Atlantic Multidecadal Oscillation since 1567 A.D. *Geophysical Research Letters* 31:L12205, doi:10.1029/2004GL019932.
- Grissino-Mayer HD (1996) A 2129-year reconstruction of precipitation for northwestern New Mexico, USA. In: J.S. Dean, D.M. Meko, and T.W. Swetnam, eds., *Tree Rings, Environment, and Humanity*. *Radiocarbon* 1996: 191-204.
- Grissino-Mayer HD, Swetnam TW (2000) Century-scale climate forcing of fire regimes in the American Southwest. *The Holocene* 10:213-220.
- Hadley KS, Veblen TT (1993) Stand response to western spruce budworm and Douglas-fir bark beetle outbreaks, Colorado Front Range. *Canadian Journal of Forest Research* 23: 479-491.
- Harper JL (1977) *Population Biology of Plants*. Academic Press, London. 892 pp.
- Hawkins BA, Holyoak M (1998) Transcontinental crashes of insect populations? *American Naturalist* 152(3): 480-484.
- Hessl AE, McKenzie D, Schellhaas R (2004) Drought and Pacific Decadal Oscillation linked to fire occurrence in the inland Pacific Northwest. *Ecological Applications* 14: 425-442.
- Henry JD, Swan JMA (1974) Reconstructing forest history from live and dead plant material - an approach to the study of forest succession in southwest New Hampshire. *Ecology* 55: 772-783.
- Heyerdahl EK, Brubaker LB, Agee JK (2002) Annual and decadal climate forcing of historical fire regimes in the interior Pacific Northwest, USA. *The Holocene* 12: 597-604.
- Jardon Y (2001) *Analyses temporelles et spatiales des épidémies de la tordeuse des bourgeons de l'épinette au Québec*. Ph.D. dissertation, Université du Québec, Montreal, QC, Montreal, QC. 157 pp.
- Johnson EA, Miyanishi K, Kleb H (1994) The hazards of interpretation of static age structures as shown by stand reconstructions in a *Pinus contorta*, *Picea engelmannii* forest. *Journal of Ecology* 82:923-931.
- Kitzberger T, Brown PM, Heyerdahl EK, Swetnam TW, Veblen TT (2007) Contingent Pacific-Atlantic Ocean influence on multicentury wildfire synchrony over western North America. *Proceedings of the National Academy of Sciences* 104(2):543-548.

- Kitzberger T, Veblen TT (1998) Influences of humans and ENSO on fire history of *Austrocedrus chilensis* woodlands in northern Patagonia, Argentina. *Ecoscience* 4:508-520.
- Kitzberger T, Veblen TT, Villalba R (1997) Climatic influences on fire regimes along a rain forest to xeric woodland gradient in northern Patagonia, Argentina. *Journal of Biogeography* 24: 35-47.
- Kitzberger T, Swetnam TW, Veblen TT (2001) Inter-hemispheric synchrony of forest fires and the El Niño-Southern Oscillation. *Global Ecology and Biogeography* 10:315-326.
- Knapp PA (1995) Intermountain west lightning-caused fires: climatic predictors of area burned. *Journal of Range management* 48:85-91.
- Kneeshaw DD, Bergeron Y (1998) Canopy gap characteristics and tree replacement in the southeastern boreal forest. *Ecology* 79: 783-794.
- Koenig WD, Knops JMH (1998) Scale of mast-seeding and tree-ring growth. *Nature* 396: 225-226.
- Krause C (1997) The use of dendrochronological material from buildings to get information about past spruce budworm outbreaks. *Canadian Journal of Forest Research* 27: 69-75.
- League K, Veblen TT (2006) Climatic variability and episodic *Pinus ponderosa* establishment along the forest-grassland ecotones of Colorado. *Forest Ecology and Management* 228:98-107.
- Levin SA (1992) The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology* 73:1943-1967.
- Logan JA, Régnière J, Powell JA (2003) Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and the Environment* 1: 130–137.
- Lorimer CG (1985) Methodological considerations in the analysis of forest disturbance history. *Canadian Journal of Forest Research* 15: 200-213.
- Mann ME, Bradley RS, Hughes MK (1998) Global-scale temperature patterns and climate forcing over the past six centuries. *Nature* 392:779-787.
- Mann ME, Bradley RS, Hughes MK (1999) Northern hemisphere temperatures during the past millennium: Inferences, uncertainties, and limitations. *Geophysical Research Letters* 26: 759-762.
- Margolis EQ, Swetnam TW, Allen CD (in review) A stand-replacing fire history in upper montane forests of the Southern Rocky Mountains. *Canadian Journal of Forest Research*.
- Martinat PJ (1987) The role of climatic variation and weather in forest insect outbreaks. In: Barbosa, P. and J. C. Schultz, eds. 1987. *Insect Outbreaks*, Academic Press, 241-268.
- Mattson WJ, Haack RA (1987) The role of drought in outbreaks of plant-eating insects. *BioScience* 37: 110-118.
- Mast JN, Fule PZ, Moore MM, Covington WW, Waltz AME (1999) Restoration of presettlement age structure of an Arizona ponderosa pine forest. *Ecological Applications* 9: 228-239.
- Mast JN, Wolf JJ (2004) Ecotonal changes and altered tree spatial patterns in lower mixed-conifer forests, Grand Canyon National Park, Arizona, USA. *Landscape Ecology* 19: 167-180.

- Michaelsen J, Thompson LG (1992) A comparison of proxy records of El Niño/Southern Oscillation. *El Niño: historical and paleoclimatic aspects of the Southern Oscillation* (ed. by H.F. Diaz and V. Markgraf), pp. 323–348. Cambridge University Press, Cambridge.
- Moran PAP (1953) The statistical analysis of the Canadian lynx cycle. *Australian Journal of Zoology* 1:291-298.
- Morin H, LaPrise D, Bergeron Y (1993) Chronology of spruce budworm outbreaks near Lake Duparquet, Abitibi region, Quebec. *Canadian Journal of Forest Research* 23: 1497-1506.
- Morneau C, Payette S (2000) Long-term fluctuations of a caribou population revealed by tree-ring data. *Canadian Journal of Zoology* 78: 1784-1790.
- Morrow PA, LaMarche Jr VC (1978) Tree ring evidence for chronic insect suppression of productivity in subalpine Eucalyptus. *Science* 201: 1244-1246.
- Myers JH 1998. Synchrony in outbreaks of forest Lepidoptera: A possible example of the Moran effect. *Ecology* 79: 1111-1117.
- Norman SP, Taylor AH (2003) Tropical and north Pacific teleconnections influence fire regimes in pine-dominated forests of north-eastern California, USA. *Journal of Biogeography* 30:1081–1092.
- Pearson GA (1950) Management of ponderosa pine in the Southwest, as developed by research and experimental practice. *Agriculture Monograph* 6, US Dept. of Agriculture, Forest Service, Washington, DC.
- Perkins D, Swetnam TW (1996) A dendroecological assessment of whitebark Pine (*Pinus albicaulis*) in the Sawtooth-Salmon River region of Idaho. *Canadian Journal of Forest Research* 26:2123-2133.
- Quinn WH, Neal VT (1992) The historical record of El Niño events. *Climate since AD 1500* (ed. by R.S. Bradley and P.D. Jones), pp. 623–646. Routledge, London.
- Ranta E, Kaitala V, Lindstrom J, Helle E (1997). The Moran effect and synchrony in population dynamics. *Oikos* 78:136-142.
- Ricklefs RE (1987) Community diversity: relative roles of local and regional processes. *Science* 235:167-171.
- Royama T (1984) Population dynamics of the spruce budworm *Choristoneura fumiferana*. *Ecological Monographs* 54: 429-462.
- Ryerson DE, Swetnam TW, Lynch AM (2003) A tree-ring reconstruction of western spruce budworm outbreaks in the San Juan Mountains, Colorado, USA. *Canadian Journal of Forest Research* 33: 1010-1028.
- Savage M (1991) Structural dynamics of a southwestern pine forest under chronic human influence. *Annals of the Association of American Geographers* 81: 271-289.
- Savage M, Brown PM, Feddema J (1996) The role of climate in a pine forest regeneration pulse in the southwestern United States. *Ecoscience* 3: 310-318.
- Schoennagel T, Veblen TT, Romme WH, Sibold JS, Cook ER (2005) ENSO and PDO variability affect drought-induced fire occurrence in Rocky Mountain Subalpine Forests. *Ecological Applications* 15(6):2000–2014.
- Schweingruber FH (1996) *Tree rings and environment dendroecology*. Paul Haupt, publisher, Berne, Switzerland.
- Schulman E (1956) *Dendroclimatic Changes in Semiarid America*. University of Arizona Press, Tucson, AZ, 142 pp.

- Sibold JS, Veblen TT (2006) Relationships of subalpine forest fires in the Colorado Front Range with interannual and multidecadal-scale climatic variation. *Journal of Biogeography* 33:833–842.
- Sinclair ARE, Gosline JM, Holdsworth G, Krebs CJ, Boutin S, Smith JNM, Boonstra R, Dale M (1993) Can the solar cycle and climate synchronize the snowshoe hare cycle in Canada? Evidence from tree rings and ice cores. *American Naturalist* 141: 173-xxx.
- Sinclair ARE, Gosline JM (1997) Solar activity and mammal cycles in the northern hemisphere. *American Naturalist* 149: 776-784.
- Speer JH, Swetnam TW, Wickman BE, Youngblood A (2001) Changes in pandora moth outbreak dynamics during the past 622 years. *Ecology* 82: 679-697.
- Spencer DA (1964) Porcupine population fluctuations in past centuries revealed by dendrochronology. *Journal of Applied Ecology* 1: 127-149.
- Stahle, DW, D'Arrigo RD, Krusic PJ, Cleaveland MK, Cook ER, Allan RJ, Cole JE, Dunbar RB, Therrell MD, Gay DA, Moore MD, Stokes MA, Burns BT, Villanueva-Diaz J, Thompson LG (1998) Experimental dendroclimatic reconstruction of the Southern Oscillation. *Bulletin of the American Meteorological Society* 79: 2137-2152.
- Stephens SL, Skinner CN, Gill SJ (2003) Dendrochronology-based fire history of Jeffrey pine - mixed conifer forests in the Sierra San Pedro Martir, Mexico. *Canadian Journal of Forest Research* 33: 1090-1101.
- Stokes MA, Smiley TL (1968) *An Introduction to Tree-Ring Dating*. University of Chicago Press, Chicago, IL, 73 pp.
- Swetnam, TW (1993) Fire history and climate change in giant sequoia groves. *Science* 262:885-889.
- Swetnam TW, Allen CD, Betancourt JL (1999) Applied historical ecology: Using the past to manage for the future. *Ecological Applications* 9:1189-1206.
- Swetnam TW, Baisan CH (1996) Fire effects in southwestern forests; proceedings of the second La Mesa fire symposium; Los Alamos, New Mexico March 29-31, 1994. USDA Forest Service General Technical Report RM-GTR-286.
- Swetnam TW, Baisan CH (2003) Tree-ring reconstructions of fire and climate history in the Sierra Nevada and Southwestern United States. *In Fire and Climatic Change in Temperate Ecosystems of the Western Americas*. Ecological Studies Vol. 160. Edited by T. T. Veblen, W. Baker, G. Montenegro, and T. W. Swetnam. Springer, New York. Pp 158-195.
- Swetnam TW, Betancourt JL (1990) Fire-southern oscillation relations in the southwestern United States. *Science* 249:1017-1020.
- Swetnam TW, Betancourt JL (1992) Temporal patterns of El Niño/Southern Oscillation - wildfire patterns in the southwestern United States. pages 259-270 In Diaz H. F. and V. M. Markgraf, eds., *El Niño: Historical and Paleoclimatic Aspects of the Southern Oscillation*, Cambridge University Press, Cambridge.
- Swetnam TW, Betancourt JL (1998) Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *Journal of Climate* 11:3128-3147.
- Swetnam TW, Dieterich JH (1985) Fire history of ponderosa pine forests in the Gila Wilderness, New Mexico. In: Lotan, J. E., Kilgore, B. M., Fischer, W. C., and

- Mutch, R. W., Tech. Coords., Proceedings-Symposium and Workshop on Wilderness Fire, November 15-18, 1983, Missoula, Montana. USDA Forest Service General Technical Report INT-182:390-397.
- Swetnam TW, Lynch AM (1993) Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecological Monographs* 63: 399-424.
- Swetnam TW, Thompson MA, Sutherland EK (1985) Using dendrochronology to measure radial growth of defoliated trees. *USDA Forest Service Agricultural Handbook* 639: 1-39.
- Swetnam TW, Wickman BE, Paul HG, Baisan CH (1995) Historical patterns of western spruce budworm and Douglas-fir tussock moth outbreaks in the Northern Blue Mountains, Oregon since A.D. 1700. *Research Paper PNW-RP-484*. Portland, OR: U. S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 27 p.
- Taylor AH, Beaty RM (2005) Climatic influences on fire regimes in the northern Sierra Nevada mountains, Lake Tahoe Basin, Nevada, USA. *Journal of Biogeography* 32: 425–438.
- Trotter RT, Cobb NS, Whitham TG (2002) Herbivory, plant resistance, and climate in the tree ring record: Interactions distort climate reconstructions. *Proceedings of the National Academy of Science U.S.A* 99: 10197-10202.
- Turner MG, Romme WH, Gardner RH, O'Neill RV, Kratz TK (1993) A revised concept of landscape equilibrium: Disturbance and stability on scaled landscapes. *Landscape Ecology* 8: 213–227.
- Veblen TT, Baker WL, Montenegro G, Swetnam TW, Editors (2003) *Fire and Climatic Change in Temperate Ecosystems of the Western Americas*. *Ecological Studies* Vol. 160. Springer, New York. 444 pp.
- Veblen TT, Kitzberger T (2002) Inter-hemispheric comparison of fire history: The Colorado Front Range, U.S.A., and the northern Patagonian Andes, Argentina. *Plant Ecology* 163: 187-207.
- Veblen TT, Kitzberger T, Villalba R, Donnegan J (1999) Fire history in northern Patagonia: The roles of humans and climatic variation. *Ecological Monographs* 69:47-67.
- Veblen TT, Kitzberger T, Donnegan J (2000) Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. *Ecological Applications* 10:1178-1195.
- Villalba R (1994) Tree-ring and glacial evidence for the Medieval Warm Epoch and the Little Ice Age in southern South America. *Climatic Change* 26: 183–197.
- Villalba R, Veblen TT (1997a) Regional patterns of tree population age structures in northern Patagonia: climatic and disturbance influences. *Journal of Ecology* 85: 113-124.
- Villalba R, Veblen TT (1997b) Improving estimates of total tree ages based on increment core samples. *Ecoscience* 4: 534-542.
- Weber UM (1997) Dendroecological reconstruction and interpretation of larch budmoth (*Zeiraphera diniana*) outbreaks in two central alpine valleys of Switzerland from 1470-1990. *Trees - Structure and Function* 11: 277–290.

- Westerling AL, Gershunov A, Brown TJ, Cayan DR, Dettinger MD (2003) Climate and wildfire in the western United States. *Bulletin of the American Meteorological Society*, May 2003, pp 595-604.
- Westerling AL, Gershunov A, Cayan DR, Barnett TP (2002) Long lead statistical forecasts of area burned in western U.S. wildfires by ecosystem province, *International Journal of Wildland Fire* 11:257-266.
- Westerling AL, Swetnam TW (2003) Interannual to decadal drought and wildfire in the Western US. *EOS*, *Transactions of the American Geophysical Union* 84(49):545-560.
- White TCR (1976) Weather, food and plagues of locusts. *Oecologia* 22:119-134.

Figures and Captions

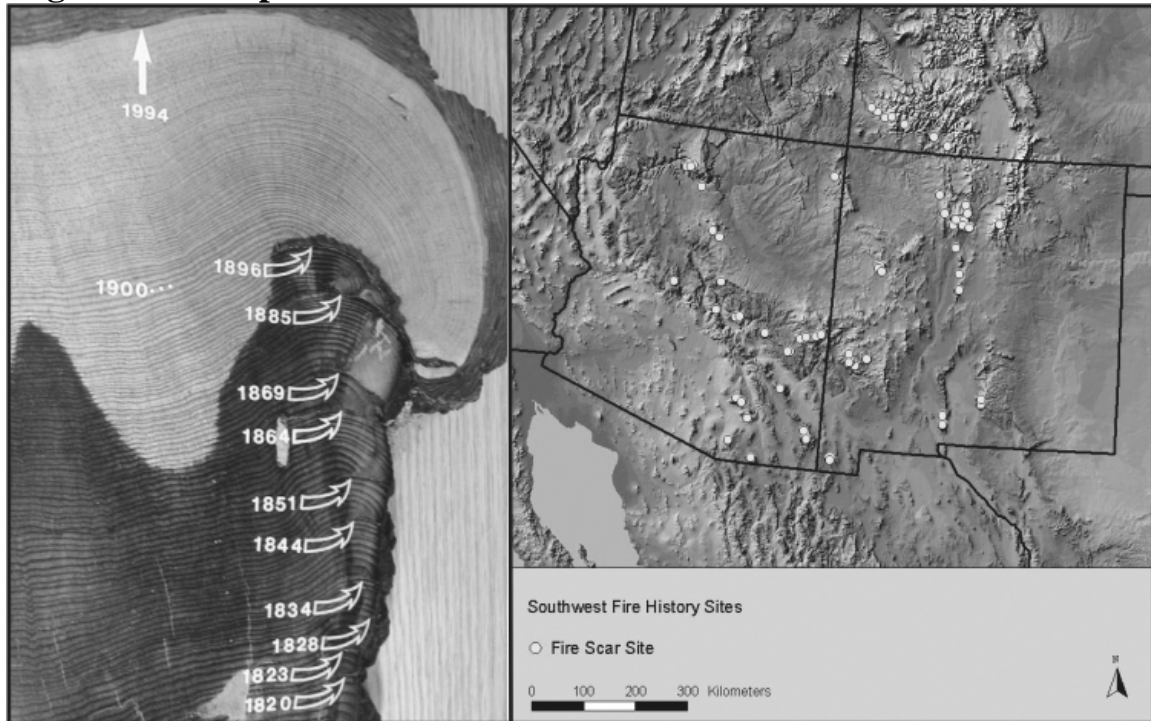


Figure 9.1. Photograph of a cross section of a fire-scarred ponderosa pine (left), and map of locations of 120 fire-scar collection sites in the Southwestern U.S (right). The arrows on the cross section point to fire scars created when surface fires burned near the base of this tree. After each fire left a scar, subsequent tree rings grew over the dead tissue. The last fire scar in 1896, and subsequent century of growth with no fire scars, reflects the effects of fire suppression and the exclusion of widespread surface fires.

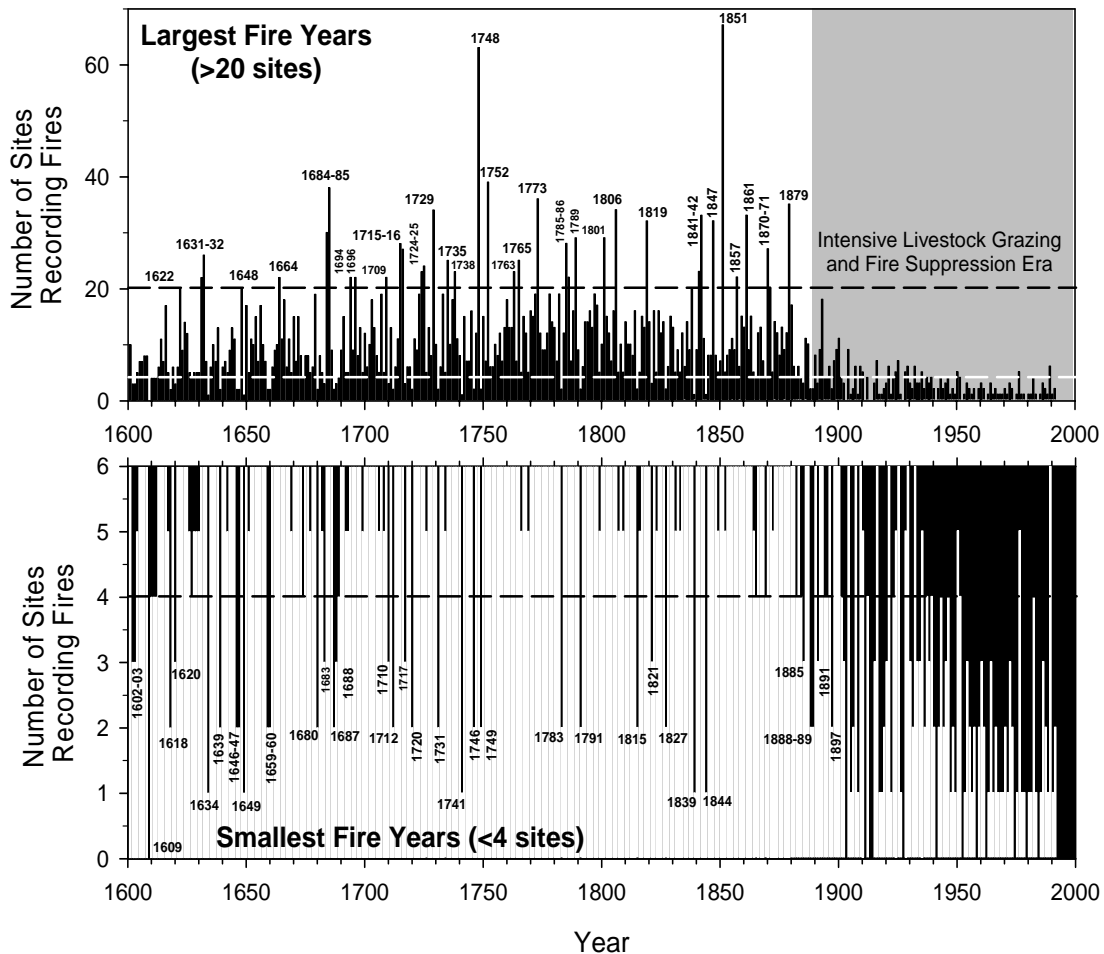


Figure 9.2. The number of sites recording fire scars in the Southwestern U.S. from 1600 to 2000. This chronology of regional fire occurrence is based on the 120 site network shown in Fig 1. The largest regional fires are labeled in the upper plot, and the dashed lines show the threshold of >20 sites and <4 sites used to identify “large” and “small” regional fire years, respectively. The lower plot shows the smallest fire years. Note that the values in the upper plot are shown as black vertical bars on a white background, and in the lower plot the values are white vertical bars on a black background. Because these were mainly surface fires burning through grass and herbaceous fuels, the widespread introduction of livestock grazing that accompanied Euro-American settlement in the late 1800s led to the decline of fires in virtually all sites.

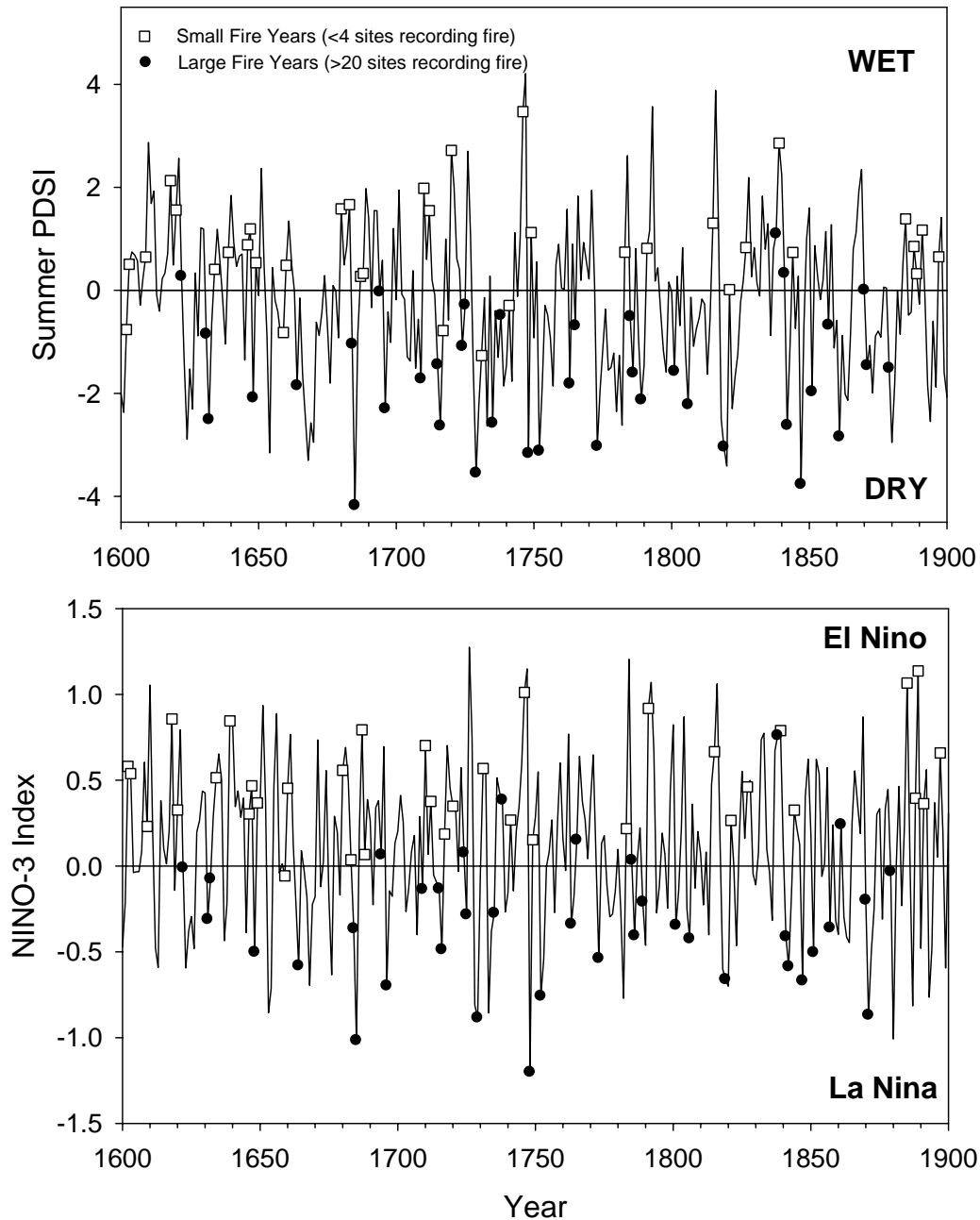


Figure 9.3. (Upper plot) Tree-ring reconstructed summer (July-August) Palmer Drought Severity Index (solid line) (from Cook et al. 2004), shown with the largest and smallest regional fire years identified from the 120-site fire-scar network from the Southwestern U.S. (Lower plot) Tree-ring reconstructed NINO3 index of sea surface temperatures (Cook 2000), shown with the same set of largest and smallest regional fire years.

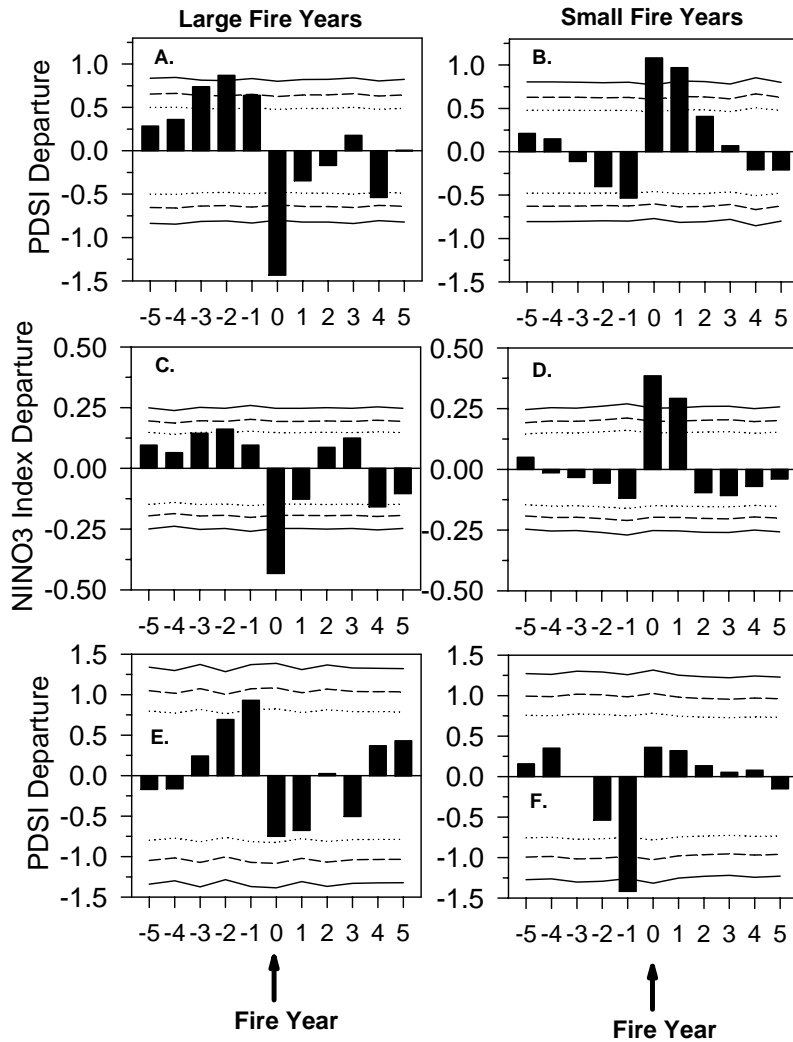


Figure 9.4. Superposed epoch analysis (SEA) of large and small regional fire years in relation to summer PDSI in the Southwestern U.S and NINO3 sea surface temperature. Plots A and B show results for largest (38) and smallest (36) fire years during the period 1600 to 1900, using tree-ring width reconstructions of Southwestern PDSI (Cook et al. 2004). Plots C and D show results from SEA using the same sets of fire years against a reconstruction of NINO3, and index of ENSO (Cook 2000). Plots E and F show SEA results using modern PDSI based on instrumental data and the largest (19) and smallest (23) fire years from area burned records from all federal, state and private lands in Arizona and New Mexico during the period 1905-2004. Lines in each plot represent the 0.05, 0.01, and 0.001 confidence intervals based on Monte Carlo simulations of random distributions of annual climate conditions for PDSI and NINO3.

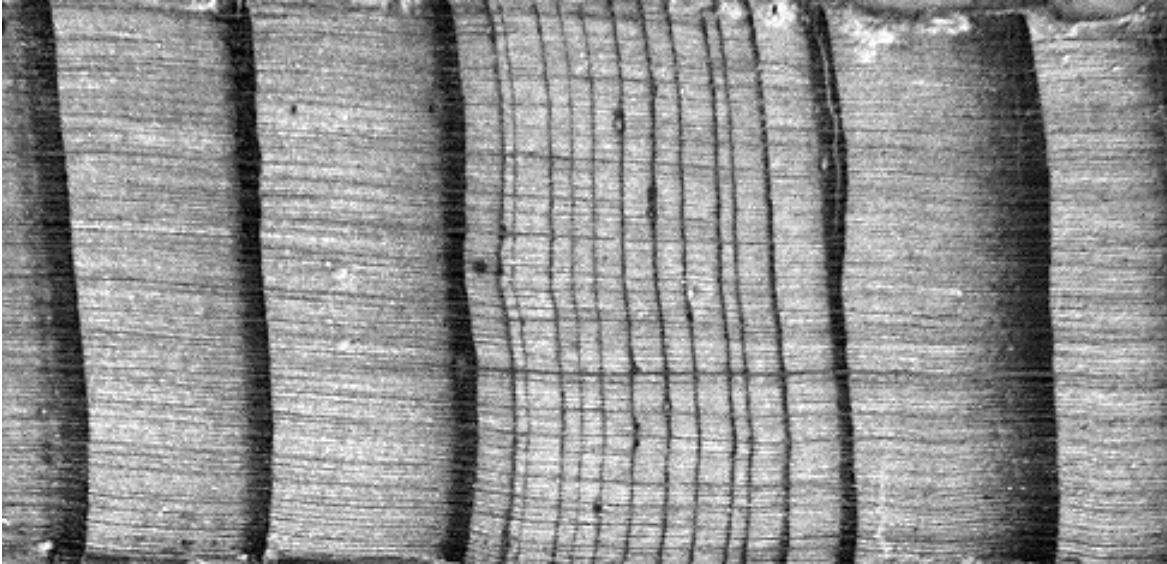


Figure 9.5. Photograph of reduced tree-ring growth in a Douglas-fir tree due to a defoliation event by western spruce budworm. This type of rapid and sustained growth reduction over a distinct period of time, often followed by a growth surge, is characteristic of defoliation events, and generally is not typical of drought responses.

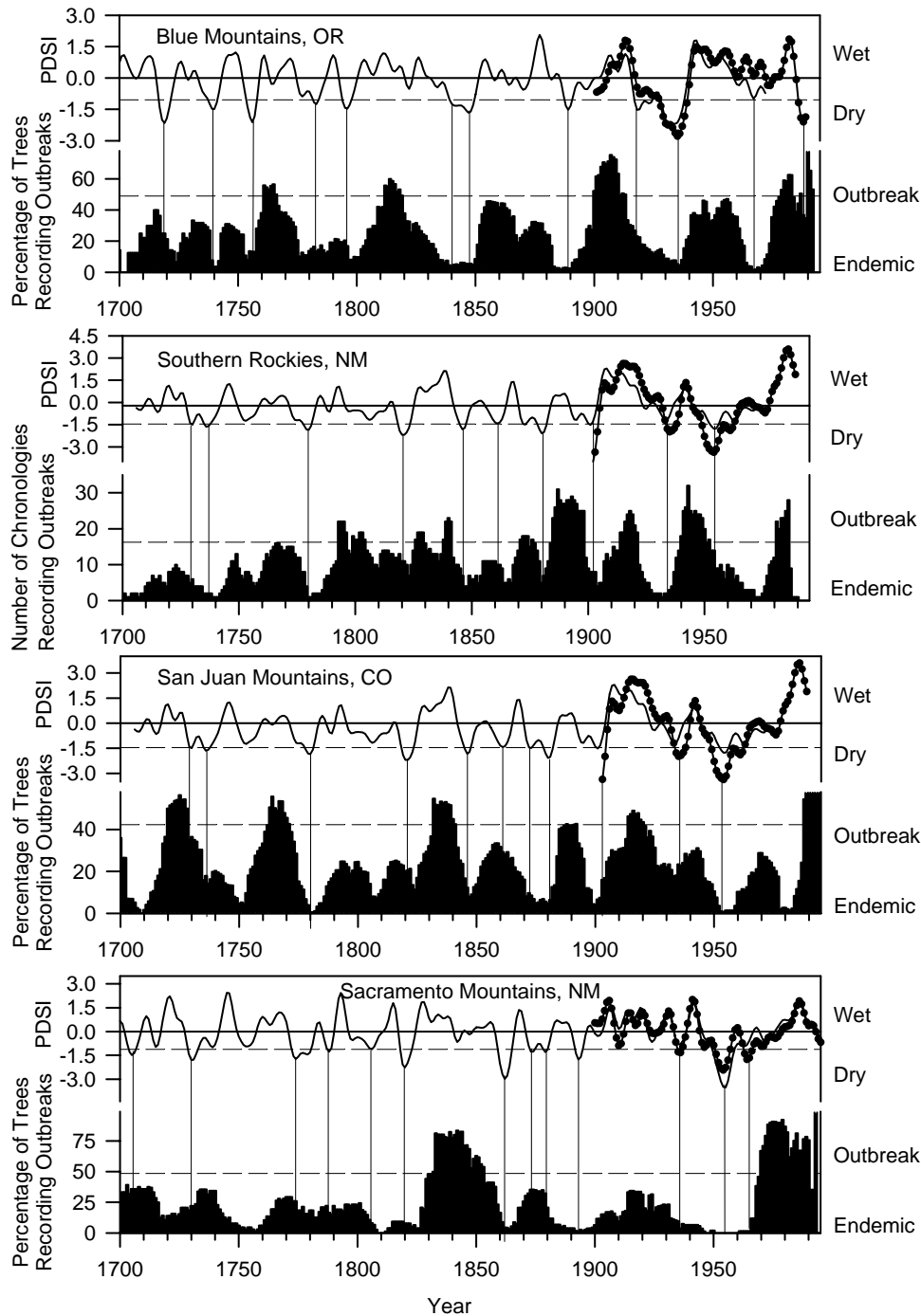


Figure 9.6. Composite western spruce budworm histories from four sub-regions in the western United States, compared with summer (July-August) Palmer Drought Severity Index reconstructions from independent tree-ring width chronologies (Cook et al. 1999). The Blue Mountains, Oregon, budworm data is partly described in Swetnam et al. 1995. The other budworm data sets are described in Swetnam and Lynch (1993; Southern Rockies, New Mexico), Ryerson et al. (2003; San Juan Mountains, Colorado), Swetnam, Archambault and Lynch, (unpublished; Sacramento Mountains, New Mexico).

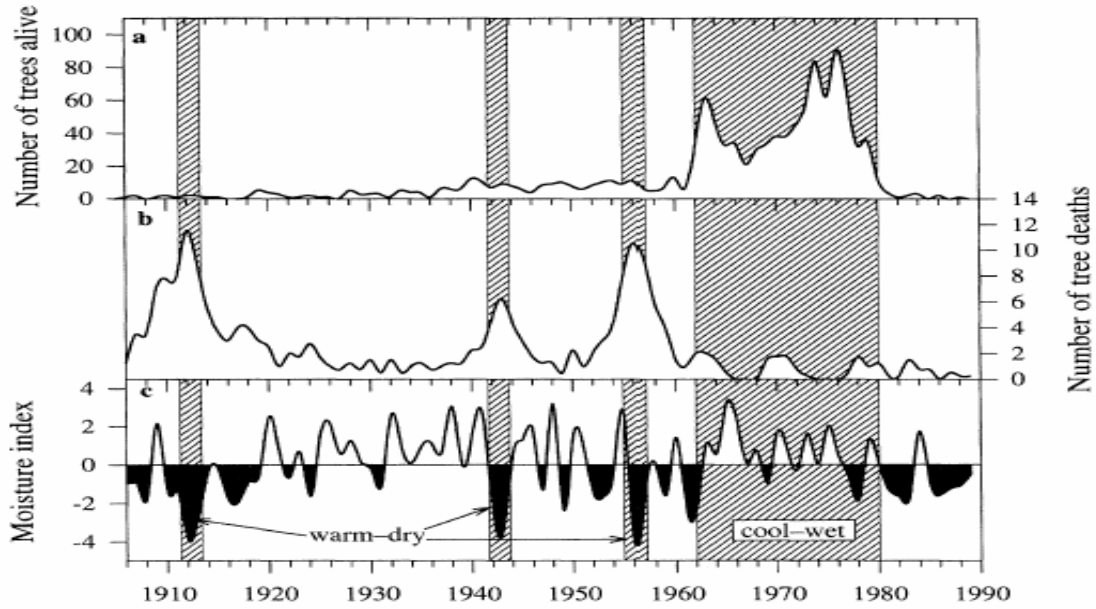


Figure 9.7. Tree establishment and mortality dates from *Austrocedrus chilensis* woodlands in northern Argentina driven by fluctuations in effective moisture (Villalba and Veblen 1997a). (Reprinted from Villalba & Veblen, [need permission from Journal of Ecology]).

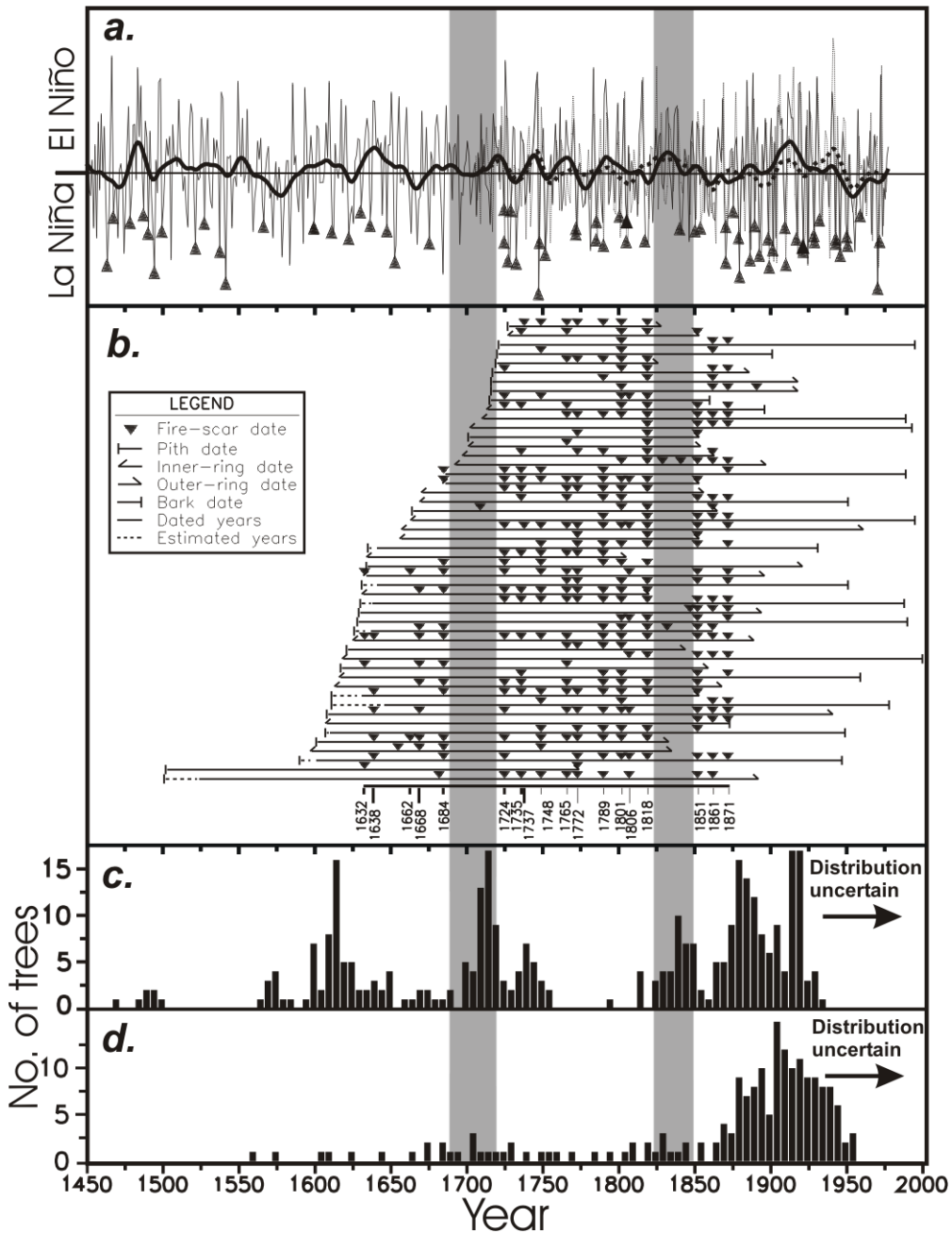


Figure 9.8. Fire history, age structure, and ENSO variations in a ponderosa pine forest in southwestern Colorado USA (Brown and Wu 2005). (a) ENSO time series (solid lines, NINO3 SST index [D'Arrigo et al. 2005]; dashed lines, SOI [Stahle et al. 1998]). SOI is reversed to be consistent with the NINO3 index. Heavy lines are annual series smoothed with 20-yr cubic smoothing splines. Years of significant triennial wet/dry oscillations identified by superposed epoch analyses are shown by arrows centered on the drought years. (b) Fire-year chronology for Archuleta Mesa. Horizontal lines mark time spans of individual trees, with fire scars designated by inverted triangles. Fire years at bottom are those recorded on >2 trees. (c) and (d) Tree recruitment dates by 5-yr periods for (c) ponderosa pine and (d) other tree species. The tree distributions are uncertain towards

the present since only larger (and hence, older) trees were sampled in the study. The gray bars mark fire-quiet periods when cohorts of ponderosa pine trees established and ENSO fluctuations were dampened. (Reprinted from Brown & Wu [need permission from Ecology])

1. Manitou Experimental Forest, CO, Boyden et al. 2005.

2. Turkey Springs, San Juan Mountains, CO, Romme unpublished

3. Archuleta Mesa, NM, Brown and Wu 2005.

4. Monument Canyon Research Natural Area, NM, Falk and Swetnam, unpublished.

5. Chuska Mountains, AZ, Savage 1991.

6. Powell Plateau, Grand Canyon National Park, AZ, Fule et al. 2002.

7. Walhalla Plateau, Grand Canyon National Park, AZ, Mast & Wolf 2004.

8. Gus Pearson Natural Area, AZ, Mast et al. 1999.

9. Maverick Fort Apache Reservation, AZ, Cooper 1960.

10. Malaygap, San Carlos Reservation, AZ, Cooper 1960.

11. Santa Catalina Mountains, Iniquez and Swetnam, unpublished.

12. Rhyolite Canyon, Chiricahua National Monument, AZ, Barton et al. 2001.

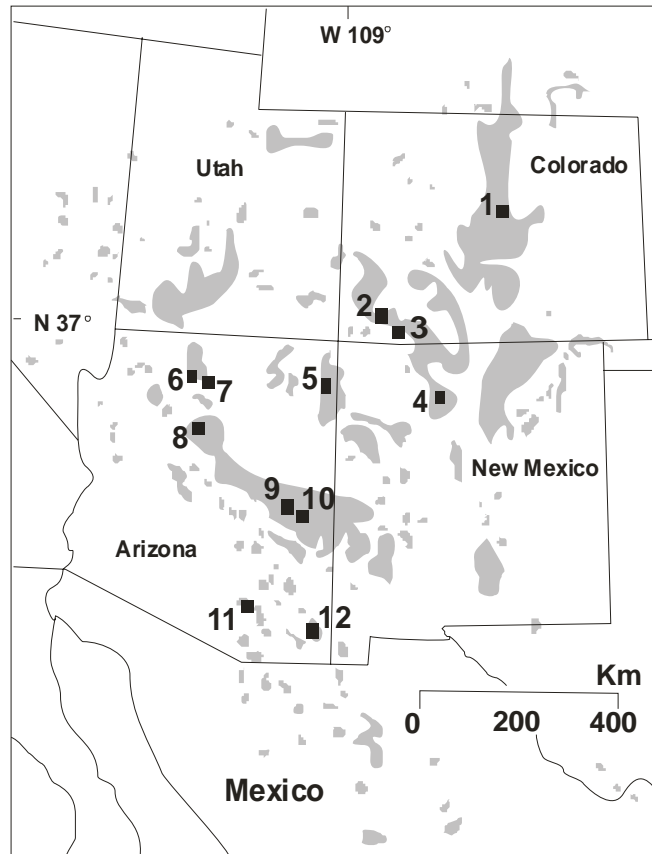


Figure 9.9. Map of the Southwest and Southern Rocky Mountains showing locations of the 12 sites where ponderosa pine age structure data have been collected and composited for analysis in this chapter. The gray shaded area is the approximate range of ponderosa pine in this region.

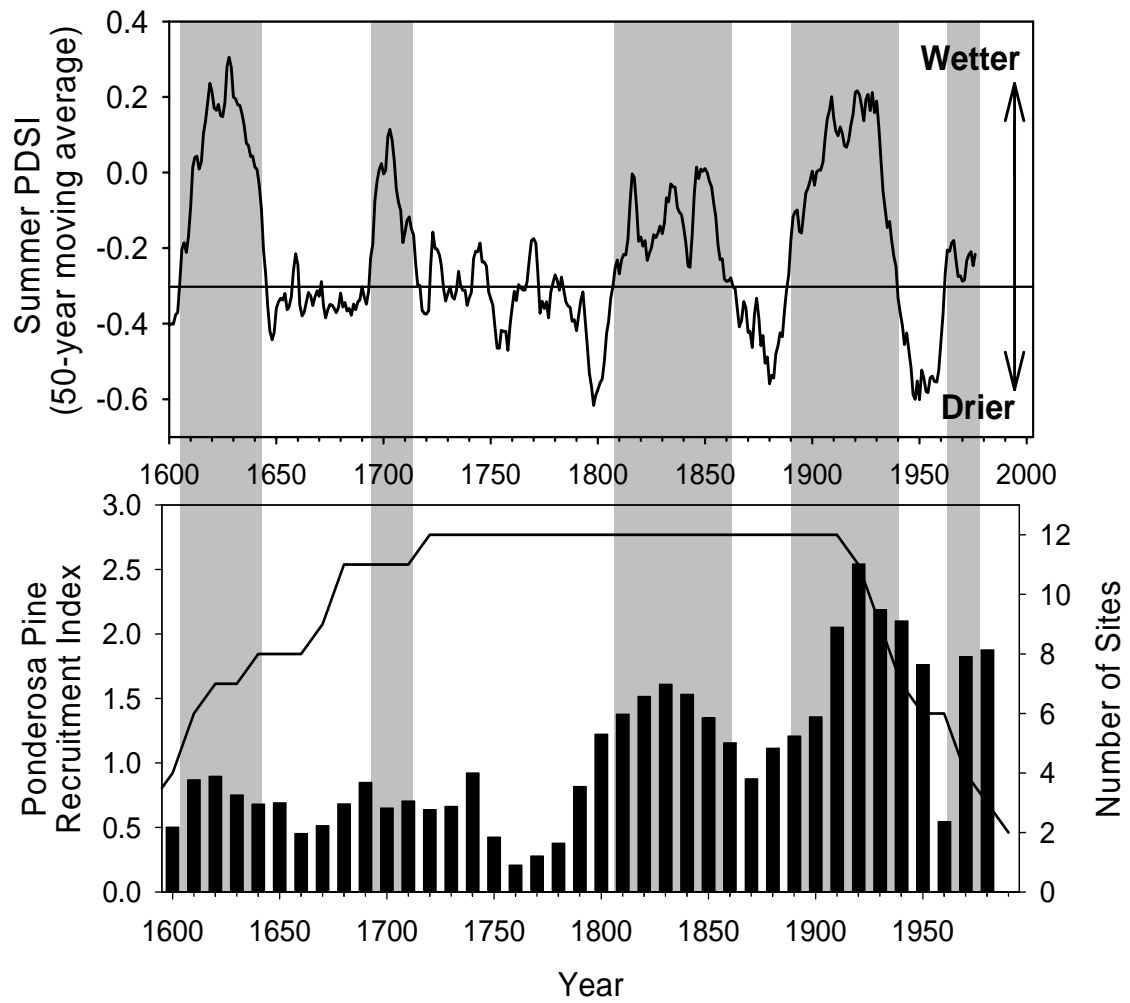


Figure 9.10. Composite age structure data from a network of 12 ponderosa pine stands and reconstructed summer Palmer Drought Severity Index (PDSI) from corresponding grid points in the Southwestern U.S. (Cook et al. 1999, 2004).

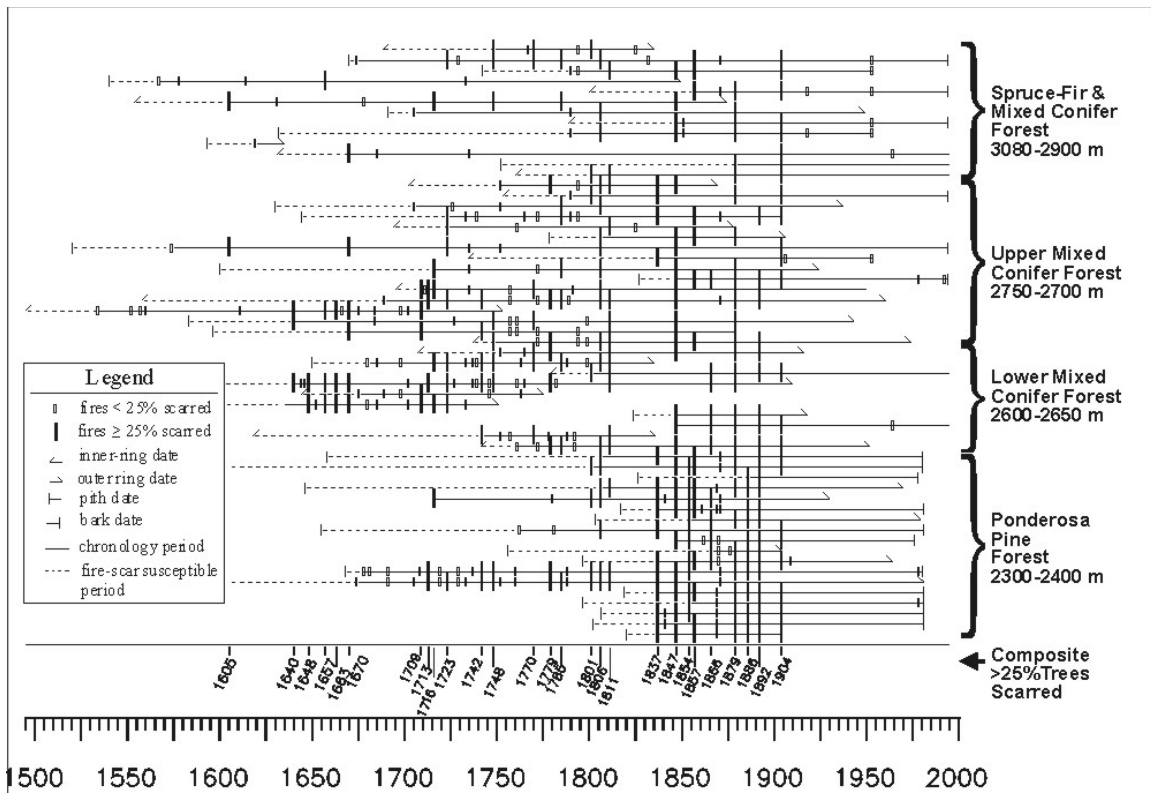
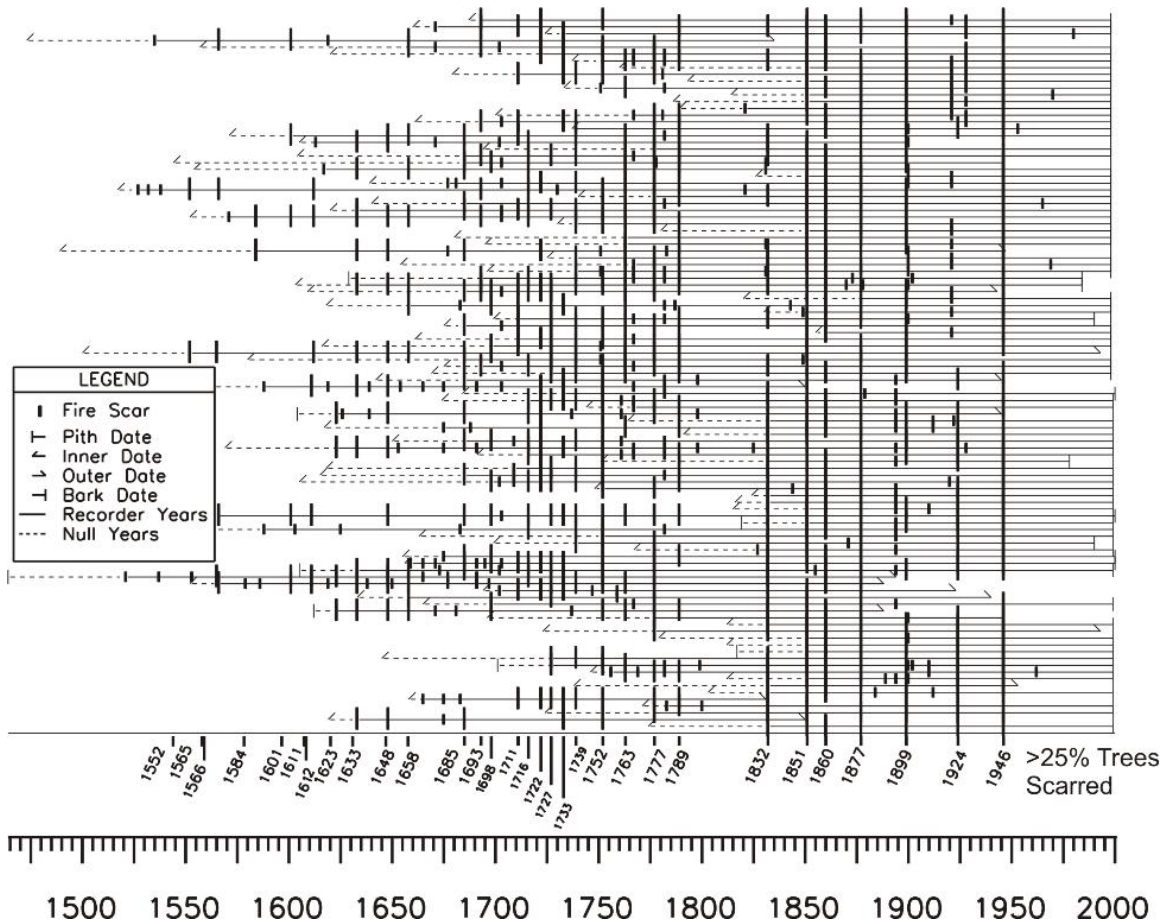


Figure 9.11. Fire scar chronologies from ponderosa pine and mixed-conifer forests in the Gila Wilderness, New Mexico (Swetnam and Dieterich 1985, Abolt 1997). Horizontal lines are tree-ring records from individual fire-scarred trees along an elevational gradient, and the vertical tick marks are the fire scar dates recorded on the trees. Note the “gap” in fire occurrence in the period 1811-1837. The lack of fire scars after 1904 was due to livestock grazing and fire exclusion by government fire fighters, and is a common feature to virtually all fire chronologies from forests around the western US.



1500 1550 1600 1650 1700 1750 1800 1850 1900 1950 2000
 Figure 9.12. Fire-scar chronology from Sierra San Pedro Martir, Baja California (Stephens et al. 2003). Note the gap in fire occurrence from about 1790 to 1830. Stephens et al. suggest the gap may be related to climate, or potentially land-use history (i.e., early livestock grazing by Spanish missionaries). Note that in contrast with the Gila Wilderness chronologies (Fig. 11), fires generally continue to burn in this area during the 20th century, probably indicating that livestock grazing and/or fire suppression were minimal in this area of northern Mexico until after about 1950. (Modified from Fig 1 in Stephens et al. 2003 [do we need permission? It is a modified version of the published figure?]).

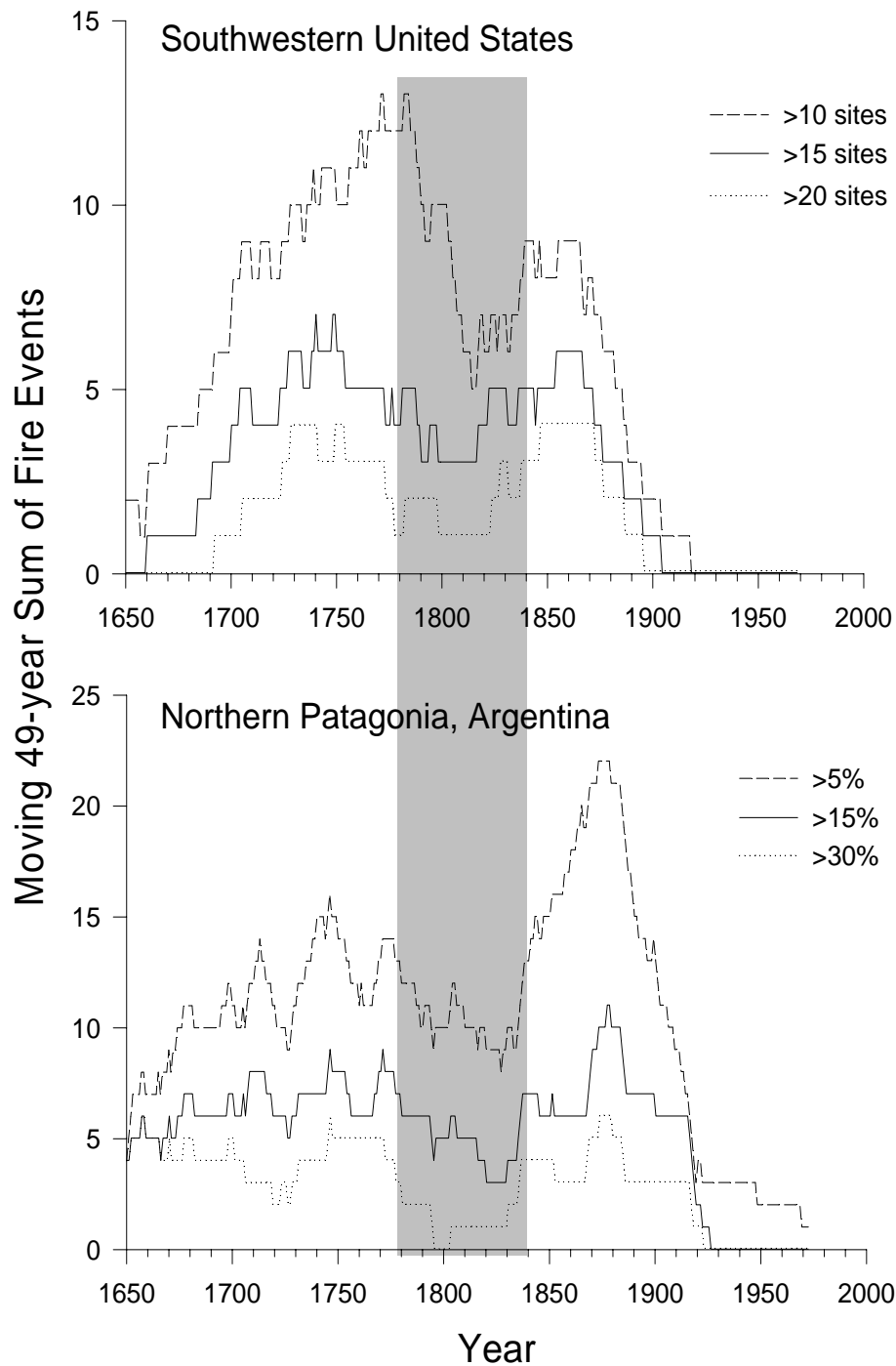


Figure 9.13. Fire frequency changes in Patagonia, Argentina and the Southwestern U.S. Both regional composites from fire-scar networks show reduced fire frequency during the 1780s-1840s period (shaded area) (Kitzberger et al. 2001). The dashed and solid lines show “moving” fire frequencies, computed as the sum of fire events that were synchronously recorded by the indicated numbers or percentage of sites within the networks during 49-year windows, plotted on the central (25th) year of the window (reprinted from Global Ecology & Biogeography [need permission]).

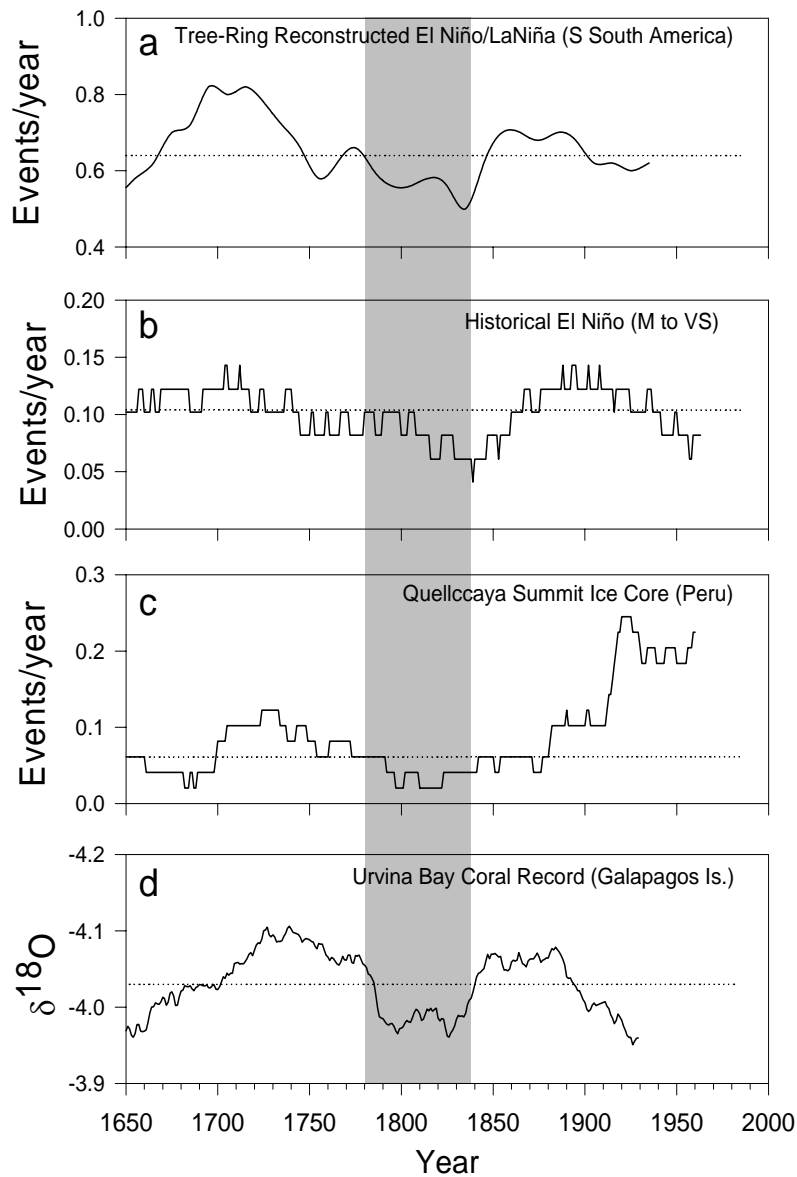


Figure 9.14. Multiple reconstructions of the El Niño-Southern Oscillation show a reduced occurrence or amplitude during the 1780s-1840s period (shaded area) (Kitzberger et al. 2001). (a) La Niña and El Niño events reconstructed from tree-ring chronologies in Patagonia and central Chile (Villalba 1994). (b) Recurrence of moderate to very strong El Niño events reconstructed from archival documents (Quinn and Neal 1992). (c) El Niño recurrence based on years when $\delta^{18}\text{O}$ was $> -16\text{‰}$ (i.e. warm events) in the Quelccaya summit ice core record (Michaelson and Thompson 1992). Plots are mean number of events per year based on moving 49-year sums of all indices. (d) Record of ENSO-related central Pacific upwelling based on $\delta^{18}\text{O}$ (‰) coral from Urvina Bay, Galapagos Islands (Dunbar et al., 1994; 49-year running mean). In all cases the horizontal solid line represents long-term mean values. (reprinted from *Global Ecology & Biogeography* [need permission]).