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Using Dendrochronology to Reconstruct the History of Forest and Woodland Ecosystems

Kurt F. Kipfmueller and Thomas W. Swetnam

Tree rings are an important source of long-term proxy information that can be used in reconstructing and understanding the history of past cultures, landscapes, and environments. Dendrochronology—or tree-ring dating—relies on the practice of cross-dating, which is the assignment of exact calendar dates to each annual ring through the matching of patterns of growth and other tree-ring characteristics. The best-known applications of dendrochronology have been in the fields of archaeology and paleoclimatology (e.g., Stokes and Smiley 1968; Fritts 1976; Baillie 1995; Schweingruber 1996). The tree-ring dating of ancient cliff dwellings and pueblos of the southwestern United States, for example, is widely known and celebrated in both scientific and popular literature (Douglass 1929; Baillie 1995). Likewise, the unique insights derived from tree-ring reconstructions of past climatic variations are commonly referenced in assessments of climatic change and its implications at global scales (Oldfield 1998; USGCRP 1999).

A somewhat less well-known application of dendrochronology is in the field of historical ecology (or paleoecology). Although the potential of tree rings for ecological research was recognized by the founder of modern dendrochronology, A. E. Douglass (1920), it is only recently that the subdiscipline of dendroecology has received much attention by dendrochronologists or ecologists (e.g., Fritts and Swetnam 1989; Schweingruber 1996). In 1986, for example, an international conference on the ecological aspects of tree-ring research resulted in seventy-nine conference papers (Jacoby and Hornbeck 1987), and a recent tree-ring conference with the broad theme of "Environment and Humanity" (Dean, Meko, and Swetnam 1996) contained about thirty papers (out of a total of eighty-two) that directly addressed ecological topics. Moreover, the utility of tree rings in addressing important ecological questions is gaining recognition among the larger community of ecologists. This trend is exemplified by recent W. S. Cooper Awards (for "outstanding contributions in geobotany, physiographic ecology, or plant succession") presented by the Ecological Society of America to the authors of four papers that made extensive use of dendrochronological techniques (Hupp 1992; Fastie 1995; Arseneault and Payette 1997; Lloyd and Graumlich 1997).

A primary reason for this expanded interest in dendroecology is that both ecologists and natural resource managers have become increasingly aware of the fundamental importance of historical perspectives. This appreciation stems, in part, from recognition of the ubiquity of nonequilibrium dynamics arising from historical processes, such as climatic change and aperiodic disturbances (Sprugel 1991). To understand how ecosystems arrived at their current configurations, we must know about past events and trajectories of change (Brown 1995; Christensen et al. 1996). This interest in history is reflected in an increasing demand for reconstructions of past ecosystem processes and structures that would be useful in defining the "historical or natural range of variability" (Morgan et al. 1994; Kaufmann et al. 1994; Landres, Morgan, and Swanson 1999; Stephenson 1999; Swetnam, Allen, and Betancourt 1999).

Dendrochronology is particularly well suited to historical-ecological research because trees tend to be long-lived and the variations in characteristics of their annual rings can be used to reconstruct long and detailed histories of the surrounding environment. Another reason is that *cross-dating*—the most important principle and practice of dendrochronology —facilitates a multidisciplinary and multiple-lines-of-evidence approach that is very effective in historical reconstruction (Swetnam, Allen, and Betancourt 1999). Cross-dating is the matching of tree-ring characteristics within and among trees across a range of temporal and spatial scales for the purpose of exactly dating individual rings and the structures and elements contained within the rings. Cross-dating is most commonly due to regional climatic variations (e.g., drought and wet years) that cause synchronous changes in tree growth processes (Douglass 1941; Stokes and Smiley 1968; Fritts 1976). Hence, by carrying out tree-ring cross-dating, most dendrochronologists are at least indirectly involved in the study of climatic variability, even though their primary focus may be on the study of ecological and cultural events and processes (e.g., births and deaths o trees, wildfires, insect outbreaks, and construction of ancient dwelling and human demography).

The use of dendrochronological principles and techniques affords sev eral important advantages over other dating techniques. The primar advantage of dendrochronology is accuracy of dating. The use of dendrochronological principles ensures that the assignment of annual dates to a series of tree rings is exact. This accuracy in turn facilitates the establishment of connections between the temporal occurrence of events and the timing of other changes to the physical system. Without this level of accuracy, dendrochronologists cannot establish important relationships between tree growth and events in the surrounding environment.

Second, tree-ring data represent an extraordinary natural archive of ecological variation over long periods of time. Depending upon the physical environment and the rate of decay, tree rings can be used to reconstruct past events or changes in ecological systems spanning centuries and, in some cases, millennia. This is especially true when a large number of samples are cross-dated, as opposed to simple ring counting of a few samples. Simple ring counting is limited temporally by the longevity of the tree species being sampled. Though this may be very long in some species that attain great age, such as bristlecone pine (*Pinus longaeva*), the cross-dating of remnant material (i.e., samples from logs, stumps, and standing dead trees) can extend the record of change considerably. The bristlecone pine chronology developed by cross-dating currently exceeds nine thousand years, almost twice as long as the oldest currently living individual (the oldest living bristlecone pine that we know of is about forty-eight hundred years old). Remnant material has also been an integral part of development of fire histories in the Southwest (e.g., Baisan and Swetnam 1990) and of documentation of changes in forest communities (LaMarche 1973; Lloyd and Graumlich 1997; Donnegan and Rebertus 1999).

Another benefit of dendrochronology is that it can assist in identifying potential mechanisms of variability. For instance, tree-ring–based fire history reconstructions indicate that fires occurred in many mountain ranges of the southwestern United States during 1748 (Swetnam and Baisan 1996; Swetnam and Betancourt 1998) (figure 8.1). Study of historical documents and climate reconstructions from tree rings and corals indicate that the El Niño–Southern Oscillation was probably a climatic mechanism for those events (Swetnam and Betancourt 1990). An unusually strong El Niño event occurred in 1747 and may have led to an increase in fine-fuel abundance, leading to those widespread fires during the dry year of 1748. The regional climate signal is clearly evident in the growth characteristics of precipitation-sensitive conifers collected throughout the region, with a wide ring forming in 1747 followed by an extremely narrow ring during the dry year of 1748 (figure 8.1). Similar relationships between climate and natural disturbance exist in the case of insect-caused epidemics, as we will describe later.

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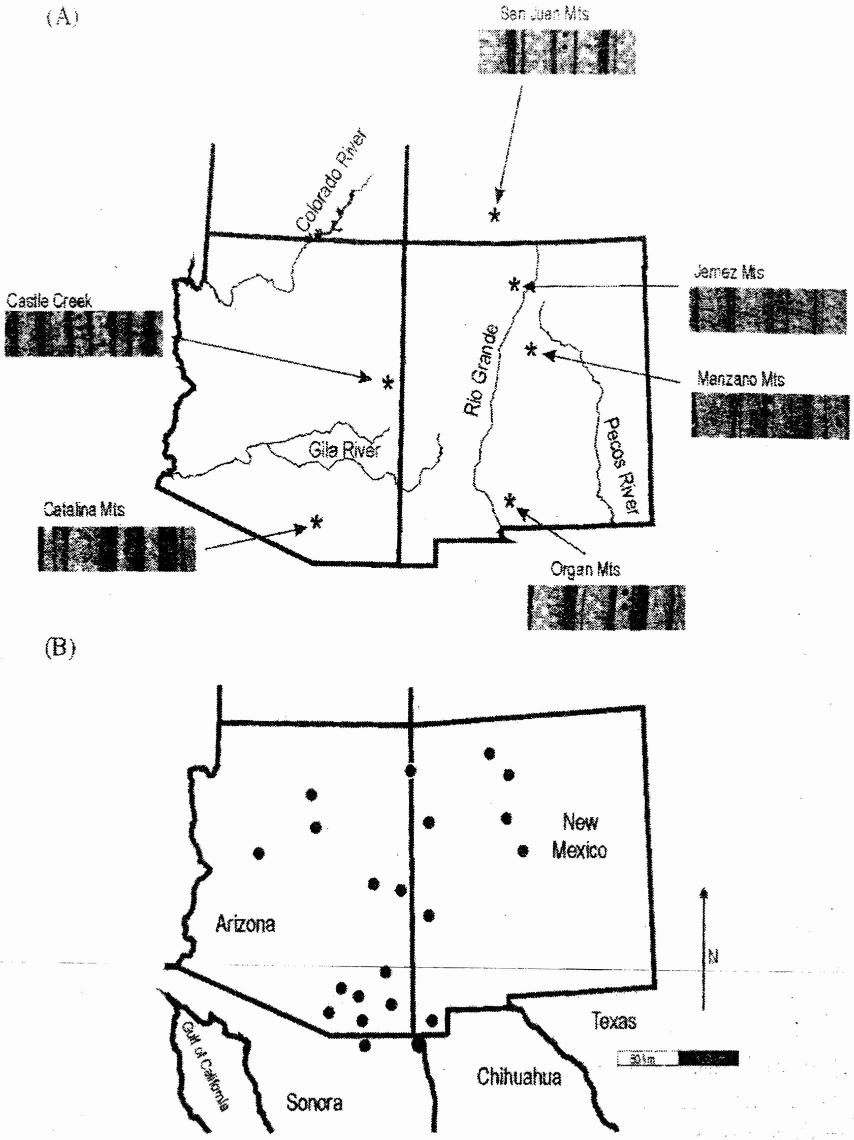

Figure 8.1. (A) The characteristic ring sequence that occurred across a broad region of the Southwest around 1750. Growth is from left to right. Double black dots indicate the 1750 ring. The rings of 1748 and 1752 are noticeably narrow; that of 1747 is wide in some series, likely due to higher amounts of winter-spring precipitation associated with a strong El Niño year. (B) The network of fire history sites that contain evidence of the 1748 fire year throughout the Southwest, indicating the regional nature of that event.

Cross-dated and measured tree-ring width chronologies are commonly incorporated into networks of chronologies for broad-scale climatic reconstruction (e.g., Fritts 1991; Cook et al. 1999). As spatial networks of climate and disturbance are built up for landscapes and regions, it becomes possible to directly compare independently derived time series of the key events and processes over long temporal and broad spatial scales. Examples include comparisons of climatic reconstructions with chronologies of fire events (Swetnam 1993; Veblen et al. 1999); tree births and deaths (Betancourt et al. 1993; Allen and Breshears 1998; Villalba and Veblen 1998); and human population changes (Dean et al. 1985). These multiple, independent lines of evidence can be particularly effective in disentangling natural from cultural causes of ecosystem variations (Allen, Betancourt, and Swetnam 1998; Swetnam and Betancourt 1998; Veblen et al. 1999).

Historical knowledge and understanding are often of central importance in the field of restoration ecology because "restoration" directly implies the return of degraded ecosystems to some desired condition or state that existed in the past. The identification of specific reference or desired conditions, however, is problematic in that a given condition at a particular time and place represents a "snapshot" of a system's structure and composition (Stephenson 1999). However, natural systems are dynamic, i.e., they fluctuate at a variety of spatial and temporal scales due to complex interactions among periodic natural disturbances, humans, atmospheric variability, and changes in species composition through successional processes (White and Walker 1997). Recognition of the dynamic, nonequilibrial nature of most ecosystems has led to the conceptualization of a "historical range of variability" as a framework for evaluating current ecosystem conditions relative to the range and variation of past conditions (Cissel 1994; Morgan et al. 1994). Deciding on specific goals or targets for restoration, however, is dependent on other considerations as well, such as costs and practicality. Even if historical conditions are not useful for identifying restoration goals, the knowledge of past conditions and changes is often important for understanding how current conditions developed.

In this chapter we review the guiding principles of dendrochronology as they relate to reconstruction of the ecological history of forests and woodlands. We also discuss some basic techniques and practices used to cross-date and ensure accurate dating of tree rings. Using "classic" and recent examples, we focus on the use of dendrochronology to understand the mechanisms of ecological change and variability across time and space, and on applications toward the restoration of ecosystems. Finally, we discuss some important limitations of dendrochronology as a tool for historical ecology.

The Principles of Dendrochronology

Refined over the last century, the principles that have served as the foundation of dendrochronological practice are still central to the science of dendrochronology. The following principles lead directly to cross-dating and are essential as guiding concepts and approaches to the analysis and interpretation of tree rings. The principles outlined here are discussed in greater detail elsewhere (e.g., Fritts 1976; Fritts and Swetnam 1989).

The Principle of Uniformity. Simply put, this principle states, "The present is the key to the past." This means that those processes operating at present are assumed to be reasonably similar to processes that operated in the past. Although processes may be similar, their rates or other aspects of the processes may vary through time. The principle of uniformity as applied to dendrochronology implies that the factors currently controlling tree growth are similar to those that affected tree growth in the past. This principle is the logical basis for quantitatively estimating (reconstructing) variations of past processes from tree rings.

The Principle of Limiting Factors. The rate and timing of tree growth can be affected by many different factors, such as moisture, temperature, animals, and others. Although different factors can affect tree-growth processes, growth is usually limited by the factor that is most critically in demand; that is the most limiting factor (Fritts 1976; Barbour, Burk, and Pitts 1987; Kozlowski, Kramer, and Pallardy 1991). For example, in arid climates, moisture is typically the factor most limiting to tree growth. During exceptionally dry periods, trees throughout a region will grow very slowly and produce a narrow annual ring. The factors limiting to growth in a particular setting in a particular sequence of years establishes the pattern of wide and narrow rings that is useful in cross-dating.

The Principle of Site Selection. Site selection is an important aspect of most dendrochronological investigations. Dendroclimatological investigations typically focus on sites that maximize tree-growth responses to the climate variable of interest. For example, if a climate reconstruction focuses on summer temperature, then sites are selected near the upper elevation or latitudinal limits of a species range where temperature is most limiting to growth. Site selection for investigations focusing on the reconstruction of ecological parameters, such as natural disturbance or successional processes, however, may be more often based on a need to obtain spatially representative information for particular landscapes or ecosystems. In the case of restoration, for example, the site to be restored is often predetermined, and therefore the selection of a particular site to maximize an environmental signal may not be warranted, but is driven by the objectives of the investigation.

The Principle of Ecological Range. The principle of ecological range refers to the range of habitats and abiotic conditions in which a given species can survive and reproduce (Fritts 1976). A given species can usually be found growing across a gradient or a range of habitats with differing physical characteristics. The differing physical characteristics of trees along such gradients have an important influence on the growth characteristics of annual rings and the data that are recorded (Fritts 1976). Generally, species most suitable for dendroclimatic investigations are found growing near the margins of their ecological range. Trees growing near these range limits often have greater responsiveness to limiting factors such as precipitation or low temperatures than species growing near the center of their ecological range (Fritts 1976).

The Principle of Replication. The reduction of "noise" in a tree-ring data set is typically achieved by increasing the number of samples collected both from an individual tree and from a site as a whole (Fritts 1976; Wigley, Jones, and Briffa 1987; Cook and Kairiukstis 1990). The climatic "signal" in tree-ring records refers to the information contained within a tree-ring record that can be directly attributed to environmental variability, as opposed to the "noise," or random or residual variation in tree growth, that cannot be related to environmental variations (Fritts 1976). The principle of replication, then, is the maximization of the climate signal through an increase in sample size and temporal depth. The collection of additional samples for any given year may amplify the signal of interest (up to a point) while helping to identify characteristics that may be restricted to one or a few trees.

The Principle of Cross-Dating. The most important principle (and technique) in dendrochronology is cross-dating (Fritts 1976). Cross-dating is a technique used to ensure the assignment of accurate calendar dates to individual growth rings. The technique of cross-dating involves the systematic comparison of annual ring-width patterns between radii from the same tree, from several trees from the same area, and from trees over regions (Douglass 1941, 1946; Ferguson 1970; Fritts 1976). The most common mechanism creating cross-dating is interannual climatic variability at a scale broader than a forest stand. This extrinsic environmental variability results in synchroneity of growth relationships in trees growing within a given area, thus yielding characteristic sequences of ring growth identifiable between trees (Stokes and Smiley 1968).

The annual ring of a tree is composed of both early wood and late

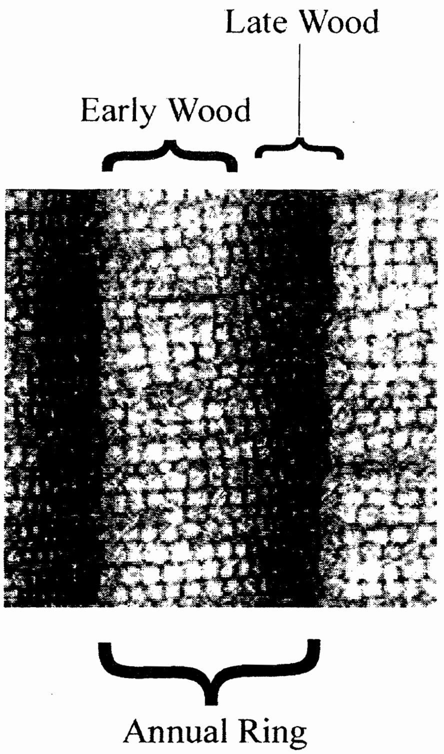

Figure 8.2. The annual ring structure of subalpine larch (*Larix lyallii* Parl.) from Montana. The lighter portion of the ring is the early wood, when tree growth is relatively rapid. Those cells are lighter because their walls are thinner than the cell walls of late wood, which is noticeably darker.

wood (figure 8.2). The early-wood portion of the annual growth ring is composed of cells with thinner cell walls than the cells forming the late wood. The thicker cell walls in the late wood result in that portion of the ring appearing darker. Cross-dating ensures that all rings in a given series are dated to annual precision by aiding the identification of locally absent and false rings (figures 8.3, 8.4d, and 8.4e) (Douglass 1946; Ferguson 1970; Fritts 1976; Swetnam, Thompson, and Sutherland 1985). In some tree-ring series, an annual ring may be missing from part or all of a tree stem due to extreme climatic conditions or an injury that limits growth in a given year.

False rings, or intra-annual growth bands, result from changes in cell structure within an annual ring, resulting in a band of cells that resembles true late wood. The occurrence of false rings, like the occurrence of locally absent rings, can often be attributed to changes in water availability or an injury during the growing season (Telewski and Lynch 1991).

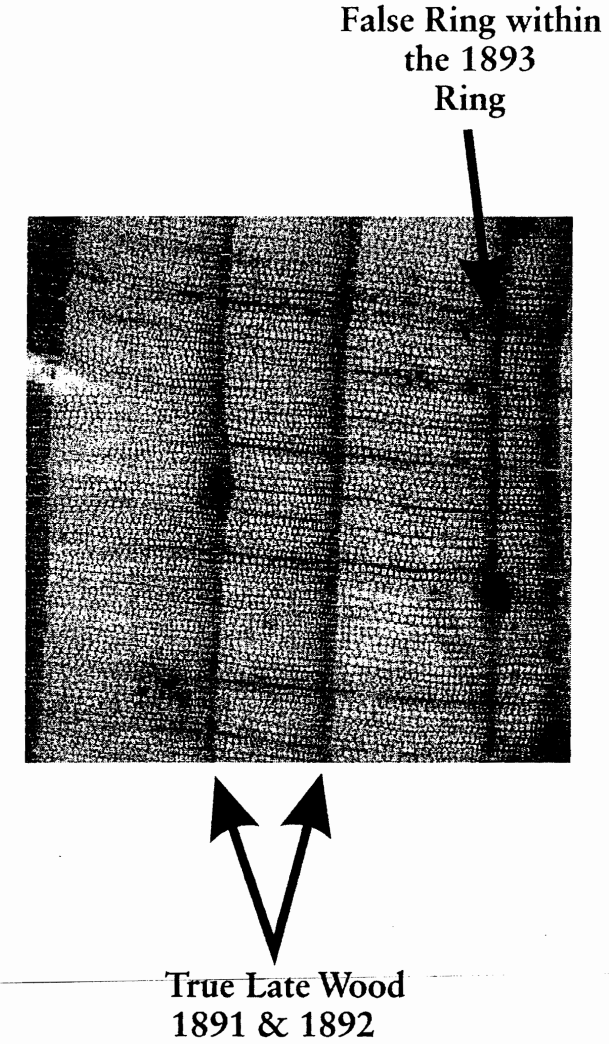

Figure 8.3. False ring from Rhyollite Canyon, Arizona. The rings 1891 and 1892 have noticeably thinner late wood. A false ring, interrupted by a resin duct, is evident in 1893. Historical evidence suggests that the summers of 1891 and 1892 were extremely dry, resulting in the death of numerous cattle in the southwestern United States. This is generally attributed to the failure of the summer monsoon (photo courtesy of C. H. Baisan).

False rings can be distinguished from true annual rings by their morphological appearance and by comparisons with other samples. False rings usually show a gradual transition from late-wood cells to early-wood cells, whereas true late-wood boundaries are very abrupt. Resin ducts are often useful in the identification of false rings because they interrupt the false

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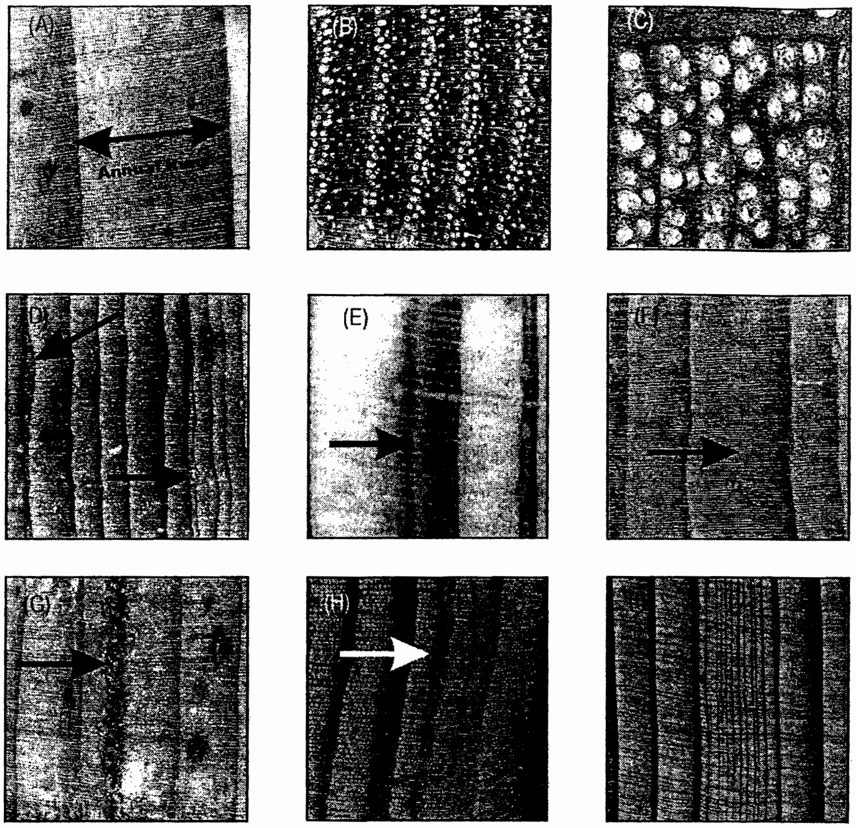

Figure 8.4. Tree-ring diagnostic features: (A) annual ring in an eastern white pine (*Pinus strobus*); (B) annual ring from ash (*Fraxinus* spp.), a ring-porous species showing clustered vessels in the early wood of the annual ring; (C) annual ring from an oak (*Quercus* spp.) collected in Arizona, showing diffuse porous-ring structure in which vessels are distributed throughout the annual ring; (D) locally absent rings of 1610 and 1616 found in a whitebark pine (*Pinus albicaulis*) collected in Idaho; (E) intra-annual growth band (false ring, in a conifer collected in the Southwest; common in areas experiencing an arid fore-summer followed by monsoonal rains) in a conifer collected in the Southwest; (F) thin late wood characteristic of the 1801 annual ring in whitebark pine growing at upper elevations of Idaho and Montana, is a useful cross-dating marker year; (G) frost ring showing disrupted cells in the late wood of the 1866 ring in whitebark pine; (H) catastrophic resin ducts in the 1993 ring of subalpine larch (*Larix lyallii*); (I) growth suppression in Douglas fir (*Pseudotsuga menziesii*) beginning in 1851 due to defoliation by western spruce budworm.

ring while the true late wood forms around resin ducts (figure 8.3). The occurrence of false rings or locally absent rings can be determined for certain only by using cross-dating techniques.

Dendrochronology in Practice

Tree-ring specimens require careful preparation to ensure that accurate measurements can be taken and the information contained within annual ring structures processed accordingly. A brief description of some of the techniques used to prepare suitable wood surfaces to carry out cross-dating is presented here, but more thorough treatments can be found in Stokes and Smiley (1968) and Swetnam, Thompson, and Sutherland (1985).

Upon selection of a study site, dendrochronologists usually collect tree-ring specimens using a drill-like tool called a Swedish increment borer. Increment borers are used to remove a very small, cylindrical sample of wood (commonly referred to as a tree core or increment core). Two or more increment cores are traditionally sampled from each tree to reduce the effects of intra-tree growth differences and aid in the identification of false or missing rings (Stokes and Smiley 1968). Increment core sampling of fire scars or other kinds of injuries is difficult, but it is possible when only a single injury needs to be dated along the sampled axis (Sheppard, Means, and Lassoie 1988; Barrett and Arno 1988). Dating of multiple scars on the same tree, or of scars in highly resinous or decayed trees, can be infeasible or impractical.

In the case of sampling fire scars or other types of cambial scars, full or partial cross sections are usually collected (Arno and Sneck 1977). The sampling of partial cross sections involves the removal of a small portion of wood, eliminating the need to fell trees completely. Partial cross sections can be taken with a chainsaw from the boles of trees, and if carefully done, the tree may not be significantly weakened. Although detailed follow-up studies have not yet been done, it appears that most fire-scarred trees will survive when relatively small partial sections (less than about one-third of the basal area) are taken from their boles (personal observation of the authors).

To protect partial and full cross sections for transportation to a laboratory, filament tape or plastic shrink wrap is often used to prevent damage and keep broken pieces with their respective samples. Increment cores can be stored and transported using paper or plastic drinking straws or core holders. If plastic drinking straws are used, increment cores should be removed from them as soon as possible, or slits should be cut in the straws to allow cores to dry and prevent molding.

In preparation for surfacing, increment cores are removed from the straws or carriers and secured into grooved wooden core mounts in such a way that the tracheid cells (the tube-like cells that form most of the wood tissue) are aligned in a vertical position. The vertical alignment of tracheid cells produces the cross-sectional surface that is required to identify ring boundaries. Preparation of full or partial cross sections involves gluing broken samples back together and, in some cases, mounting cross sections on pieces of plywood to prevent further damage during the surfacing process.

The development of highly polished surfaces on tree-ring samples is of the utmost importance in order to identify false, micro, or locally absent rings. Very fine surfaces are also needed for proper dating of scars. Surfaces should be of sufficient quality to distinguish individual tracheid cells under 20x to 30x magnification. This can be accomplished by sanding samples with successively finer grades of sandpaper. Sanding should progress through grades of 100, 220, 320, and 400 to ensure a high-quality surface. In the case of tree-ring samples with very narrow rings, sandpaper of 15 μm can be used to provide a very high polish that more clearly distinguishes annual rings.

Once the samples are prepared, the dendrochronologist can begin to analyze and record the data—a skill that comes only through practice and experience. This includes recognizing the pattern of wide and narrow rings and other features, such as light-colored or thin late wood or frost damage (figures 8.4f and 8.4g). One of the most common dating tools used by dendrochronologists is known as "skeleton plotting." It involves graphically representing the wide and narrow features of a tree-ring series on a strip of graph paper (figure 8.5). Beginning traditionally with trees that were living when sampled, plotting begins at the innermost ring and progresses outward. By convention, one dot is placed on every tenth ring, two on every fiftieth, and three on every hundredth ring. As additional samples are plotted and the dates verified by comparing plots with one another and making adjustments for false and missing rings, the common features between samples begin to emerge. They are summarized as a master skeleton plot or master dating chronology. Samples collected from dead material can also be plotted and the patterns compared to the master chronology, thereby extending the chronology further back in time as additional remnant wood is dated. This process is commonly referred to as chronology building (figure 8.6). With practice, and as familiarity with the ring-width patterns increases, these patterns are gradually committed to memory and cross-dating can sometimes be done directly on the wood without the use of skeleton plot aids.

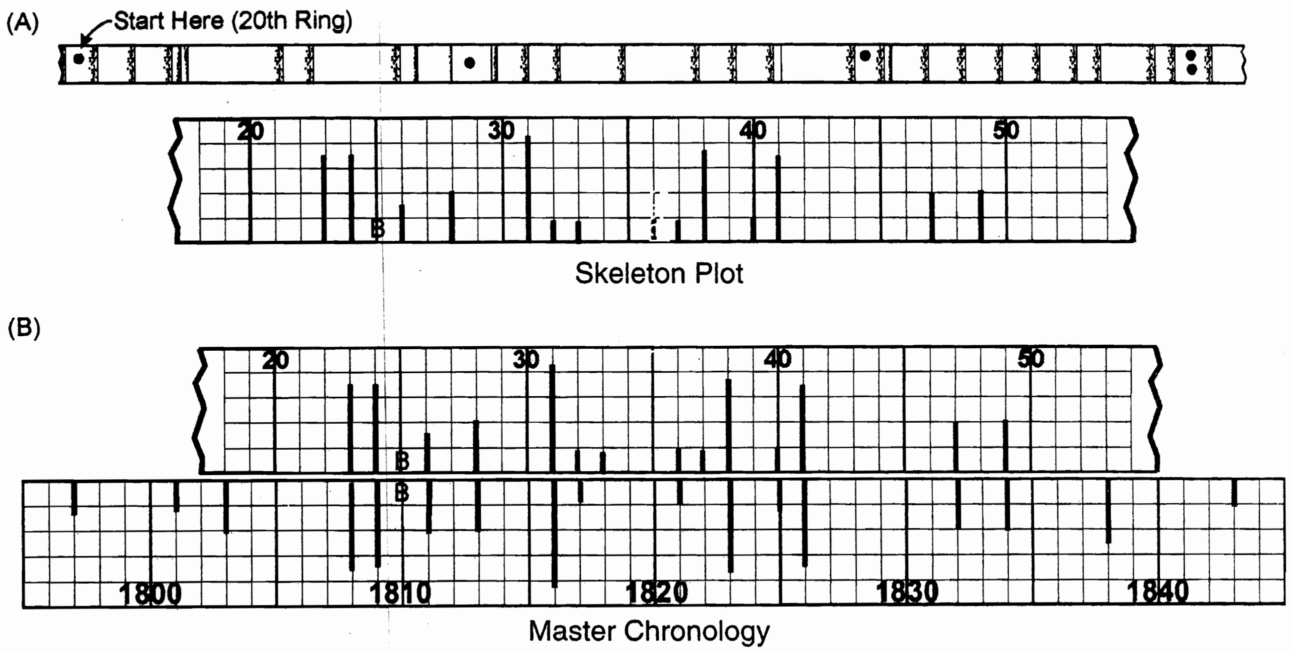

Figure 8.5. Skeleton plotting is a commonly used graphical cross-dating technique. (A) From the hypothetical increment core, longer lines are drawn for rings that are narrower than those around them. Single black dots denote decades, double black dots are used to mark fifty-year intervals. It is also sometimes useful to denote larger rings, or other anatomical features such as frost rings or resin ducts, with a "B." (B) The skeleton plot patterns can be matched to a master chronology to assign exact dates to each annual ring.

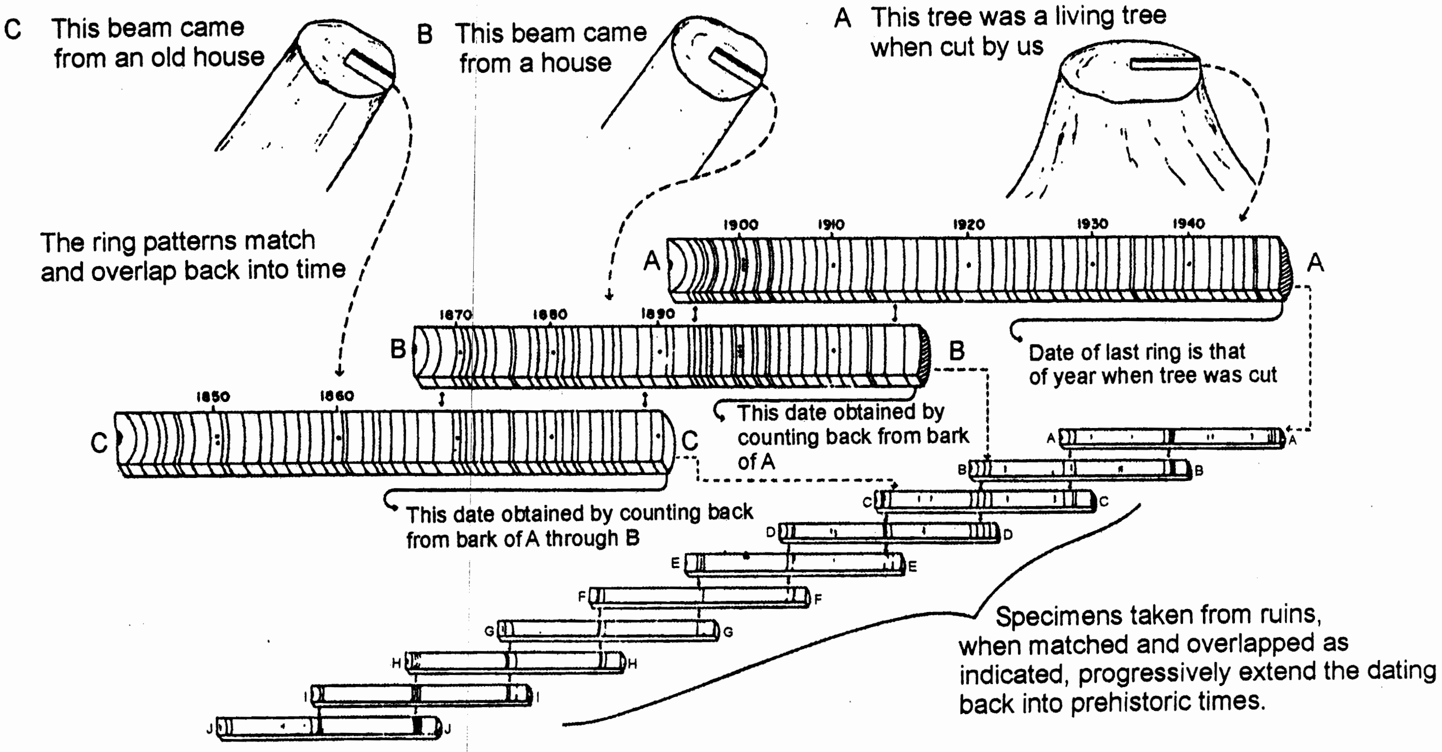

Figure 8.6. The overlapping of successive series (chronology building) is used to extend tree-ring chronologies back in time. Remnant materials (logs, stumps, and standing dead trees) or archaeological materials are especially useful for chronology extension (from

Dendrochronologists also use other methods of cross-dating. These methods are sometimes used in combination with skeleton or visual dating. Computer software programs, for example, can be used to statistically compare the dating among measured tree-ring series (Baillie and Pilcher 1973; Holmes 1983). If computer techniques are used to cross-date measured series, it is imperative that the dating also be verified by reexamining the actual specimens (and graphical plots of ring series) for common patterns and to ensure that the dating is correct. For example, if the computer output from a cross correlation of ring-width series suggests that an absent or false ring problem exists at a certain point in the measured time series, one should visually examine the wood specimen in question before inserting a zero value (for an absent ring) or deleting a ring value (for a suspected false ring). If a full or partial cross section (or multiple cores from the same tree) is available, a search around the circumference of the specimen (or of the paired core) often results in discovery of the locally absent ring as a "partial" ring, or verification that a ring is indeed false by its morphological characteristics at another position on the stem. In material with many false or missing rings, the best use of computerized programs is to verify the dating on tree-ring series after careful visual and graphical cross-dating techniques have been used.

The Application of Dendrochronology in Forest Ecosystem Restoration

Dendrochronology is a broad, interdisciplinary field of investigation, and new approaches and applications are constantly being developed. Although there are many applications of dendrochronology, they are linked by the use of cross-dating and are often pursued in a combined and comparative manner. For instance, it is common for dendroecological investigations to be conducted simultaneously with dendroclimatic reconstructions, such as in fire climatology investigations, insect outbreak studies, and climate studies.

Changes in forest ecosystems can be examined using dendrochronological techniques by determining the natality and mortality rates of forest species, the growth patterns preserved within annual rings, or the occurrence of cambial scars resulting from discrete events. Forest demography may be reconstructed from tree-ring dating the births and deaths of trees. Birth or "recruitment" processes may be estimated by obtaining and dating the tree rings near the pith at ground level (Villalba and Veblen 1998). Death processes can be evaluated by cross-dating the outermost rings, or the last formed ring beneath the bark of dead trees (Allen and Breshears 1998; Swetnam and Betancourt 1998; Mast et al. 1999).

Annual accuracy is not always possible in determining germination dates or the timing of events that caused changes in growth rates. Several years may be necessary for a tree to reach the height at which a sample is collected, which makes determination of the precise year of germination difficult. The loss of annual rings due to decay processes may also make determination of accurate death dates difficult (Lloyd and Graumlich 1997). In addition, dramatic reduction in the rate of growth or an increase in a tree's rate of growth lags somewhat following the event that caused the growth change (Lorimer 1985; Veblen et al. 1991). The use of cambial scarring (e.g., fire scarring) does not have this limitation, however, because the actual year or season in which the scarring event occurs is preserved with the annual ring (Dieterich and Swetnam 1984).

Historic Forest Structure and Change

The reconstruction of past forest structures is being used to assess changes during the twentieth century in forest conditions due to human land use, and to better understand the composition of old-growth forests in the past (Abrams, Orwig, and Demeo 1995; Foster, Orwig, and McLachlan 1996; Fulé, Covington, and Moore 1997). Researchers at Northern Arizona University, for example, have made extensive use of dendrochronological techniques and principles to evaluate changes in forested ecosystems since the time of EuroAmerican settlement, and have used this information in support of restoration plans (Covington and Moore 1994; Fulé, Covington, and Moore 1997; Mast et al. 1999; Moore, Covington, and Fulé 1999). They have collected information on the current structure and composition of forests and on fire history in northern Arizona and determined changes through time. They have also made use of remnant materials, such as logs and snags, to obtain a more complete reconstruction of presettlement forest structure. Their research indicates that relative to past forest structure and composition, the modern landscape has higher tree density and basal area. Their research also indicates that the mean diameter of ponderosa pine has diminished significantly compared with periods prior to settlement, suggesting an increase in the abundance of small-diameter ponderosa pines and a possible decline in the number of large trees that were likely present prior to EuroAmerican settlement.

The power of dendroecological approaches in historical ecology over the well-known "chronosequence" method of inference was elegantly demonstrated by Fastie (1995) in a reexamination of the classic successional studies in Glacier Bay, Alaska (Cooper 1923). Fastie examined ring-width releases and growth rates, and used remnant materials to reconstruct the chronological order of succession. He found that succession at

Glacier Bay had multiple trajectories, and that successional patterns previously inferred at Glacier Bay were not as orderly as had previously been thought. Citing the lack of ring-width characteristics of suppression-and-release patterns as evidence, Fastie showed that spruce (*Picea* spp.) and hemlock (*Tsuga* spp.) became established on oldest sites in the absence of an initial shrub layer. In contrast, spruce and hemlock collected from more recently deglaciated sites had reduced initial growth followed by a dramatic release. Fastie used experimental canopy gaps to show that more recently deglaciated sites were composed of a shrub layer, and that spruce and hemlock germinating on those sites had reduced growth until they were able to attain heights great enough to extend above the shrub layer.

Disturbance

Perhaps the most important application of dendroecology is the reconstruction of the history of disturbances in forests and woodlands. Dendrochronologists can reconstruct and investigate some of the most important characteristics of disturbance regimes—disturbance size, duration, intensity, seasonality, and frequency (Pickett and White 1985). Numerous disturbances can be examined using dendrochronology, including windthrow (Veblen et al. 1989), hydrological changes (Hupp 1992; Tardif and Bergeron 1997), volcanic eruptions (Lamarche and Hirschboeck 1984; D'Arrigo and Jacoby 1999), earthquakes (Van Arsdale et al. 1998), and snow avalanches (Veblen et al. 1994). We focus here on the application of dendrochronology to reconstruct the history of fire and insect epidemics.

Fire

Fire is a nearly ubiquitous disturbance of North American forests (Pyne 1982; Williams 1989; Agee 1993). Fire regimes range from frequent, low-intensity surface fires to relatively infrequent, catastrophic events that initiate new growth. Human land uses and activities, such as grazing, have reduced fire frequencies in some southwestern forests (Savage and Swetnam 1990; Swetnam, Allen, and Betancourt 1999), and the suppression of fires across much of North America has also reduced the frequency and extent of fires and resulted in current forest conditions, unlike those of past forest conditions (Covington and Moore 1994). Fire history investigations suggest that the effects of reduced fire activity have led to increased and possibly unnatural fuel accumulations that could lead to large catastrophic fires in areas historically dominated by smaller, patchy, nonlethal, surface fires. The restoration of landscapes through the reintroduction of fire, using prescribed burning or management policies that allow some natural fires to burn under certain conditions, is becoming more common across most federal land management agencies (Arno and Brown 1991; Agee 1993; Stephenson 1999). However, the proper prescriptions for restoration of landscapes with altered fire regimes require information concerning the natural occurrence of fire at long timescales. In addition, information concerning the factors that influence fire activity, such as climate or subsequent disturbance, is also necessary to ensure ecosystem sustainability for the long term (Christensen et al. 1996). Cross-dated fire histories are often essential for understanding how and why fire regimes have changed, relative to the modern record of fire.

The development of fire histories to better understand fire frequency at different timescales is generally approached using fire-scar analysis, stand-origin dating, or a combination of those two techniques (Johnson and Gutsell 1994). The dating of fire scars is the most commonly used technique, especially in areas where frequent, low-intensity fires occur.

A fire scar is a lesion formed when a fire is sufficiently intense to partially kill the cambium of a tree (figure 8.7; Gutsell and Johnson 1996). As a tree heals, new wood forms around the lesion and preserves the date of the fire event. Subsequent fires burning around the tree can result in the formation of an additional fire scar. In some instances, the seasonal

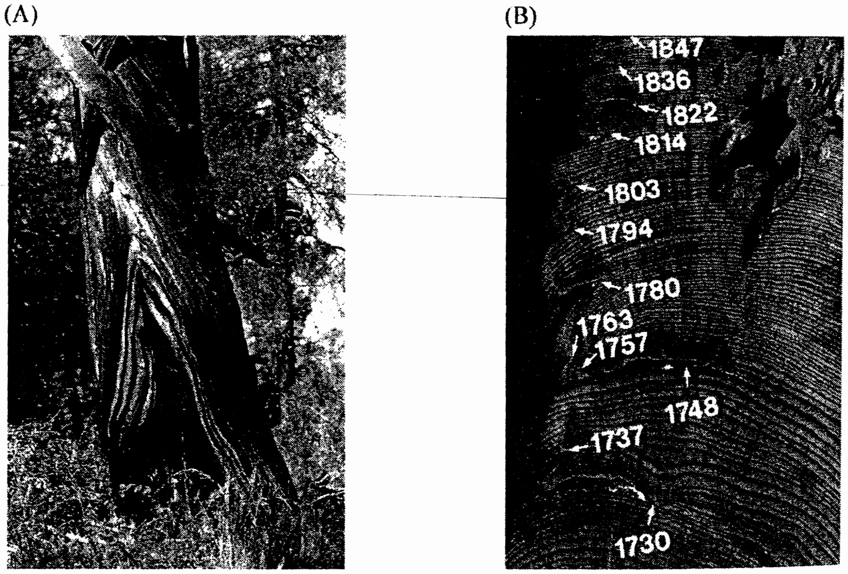

Figure 8.7. (A) A fire-scarred snag in the Rincon Mountains of southern Arizona; this tree recorded multiple fire events prior to its death. (B) A fire-scarred cross section showing the dates of the fire scars within the annual rings (photos courtesy of C. H. Baisan).

occurrence of fire can be determined based on the positioning of a fire-scar lesion within an annual ring (Baisan and Swetnam 1990). The dating of fire scars is the most precise method of assigning dates to the occurrence of fire, providing annual resolution. However, missing or false rings within a fire-scarred sample can lead to errors in the assignment of calendar dates to individual fires, so cross-dating should always be used to ensure annual precision (Madany, Swetnam, and West 1982; Johnson and Gutsell 1994). This may require additional time when compared to simple ring-counting procedures. In our experience, most time involved in accurately dating fire scars is spent securing good specimens and preparing them for visual assessment. This time is well spent, whether in ring-counting approaches or in cross-dating, as we have found poorly prepared surfaces are the most common source of error.

The dates of fires determined from fire-scar analysis can then be compiled into a single figure, and inferences concerning the spatial characteristics of fire events can be explored. For example, fire history studies conducted in twenty-seven mountain ranges of the southwestern United States indicate that some fires were widespread (figure 8.8). Other fire years were more localized. In addition, around 1900 there is a nearly synchronous reduction in fire occurrence throughout the Southwest due to the effects of fire suppression. Examination of fire events at multiple spatial scales can help elucidate some of the spatial characteristics of fire and determine potential factors that influence the occurrence and spread of fire.

In areas where relatively infrequent catastrophic crown fires destroy most or all living trees, the dating of fires is often done using stand-origin dating techniques (Arno, Reinhardt, and Scott 1993; Johnson and Gutsell 1994; Larsen 1997). Stand-origin dating involves the collection and dating of age data from trees that regenerate following a catastrophic fire event. Patches created by catastrophic fire events are first identified using aerial photography or remote-sensing methods. The patches are then visited, and the date of stand-origin is determined by collecting increment cores or cross sections from species likely to colonize a site shortly after a fire. However, stand-origin dating does not always provide precise dates of fire occurrence. The unknown time required for vegetation to become established following a catastrophic fire, or a difficulty in determining the number of years required for trees to reach the height at which age samples are collected can be potential sources of error. Moreover, the accuracy of a fire date is dependent in part upon the number of trees sampled to determine its occurrence (Kipfmueller and Baker 1998). To overcome these problems, fire-scar-dating techniques can be used in conjunction with stand-origin dating to improve the accuracy of fire date estimates. Fire scars can often be found along the boundaries of patches. Trees

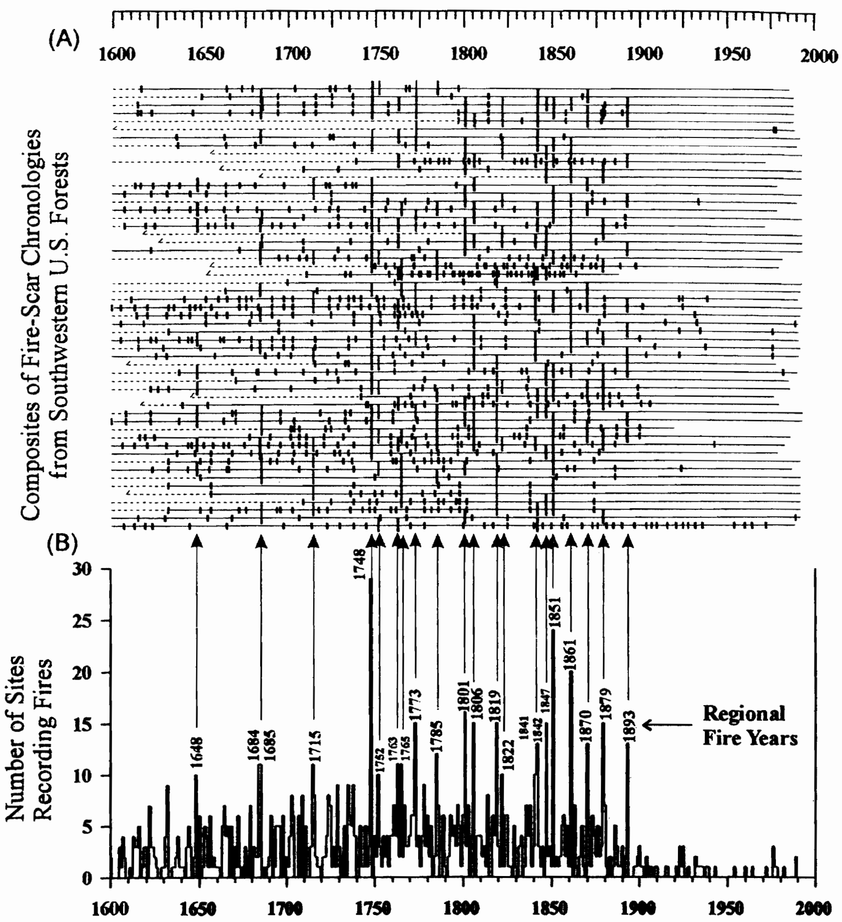

Figure 8.8. Composite fire-scar chronologies from fifty-five fire history sites located in Arizona, New Mexico, and northern Mexico. (A) In the upper chart, each horizontal line represents one fire history site, and the vertical tick marks represent the recording of a fire event using fire-scar dating. When fires are synchronous between adjacent sites, the tick marks form a continuous vertical line. (B) The bottom graph tracks the total number of sites recording a fire event each year. Years that have fire events recorded in at least ten sites across the network are labeled indicating regional fire years (reprinted from Allen, Betancourt, and Swetnam 1998).

within a patch may also survive a fire and record its occurrence as a fire scar (Kipfmueller and Baker 1998).

Several measurements can be used to identify the history of fire within an area and identify changes through time. The most commonly used measurements include fire frequency (the number of fires occurring within a given area through time) and mean fire interval (a measure of the average number of years between successive fires, measured either at a point on the landscape or for an area of known dimensions) (Arno and Petersen 1983; Agee 1993). Fire rotation (a measure of the number of years required to burn an area equal in size to the area under investigation) (Heinselman 1973; Agee 1993) is sometimes estimated. Fire rotation requires either mapped fire perimeters (e.g., fire atlases compiled by management agencies (McKelvey and Busse 1996) or the reconstruction of fire boundaries using other sources of information (Agee 1993). Statistical approaches have been developed for the description of fire regimes using stand-origin and time-since-fire data and are treated in detail by Johnson and Gutsell (1994).

The analysis of climate variability in conjunction with fire history investigations is a particularly important aspect of determining potential courses of action for the restoration of forests affected by fire suppression. Although twentieth-century changes in fire regimes are most often attributed to human activities and forest management practices, climate has undoubtedly been a major determinant of fire regime changes at long timescales. Increasingly, fire history studies are being conducted concurrently with reconstructions of climate. This enables comparisons of fire and climate variability to assess the relative roles of climate and human land uses on fire regimes. Short-term, interannual controls on fire frequency, for example, have been attributed to year-to-year changes in precipitation (Swetnam 1993; Veblen et al. 1999), which are often related to large-scale atmospheric anomalies, such as El Niño. Longer-term, multidecadal fluctuations in fire occurrence, for example, have been shown to be related to long-term temperature changes in giant sequoia forests in California (Swetnam 1993) and precipitation patterns in the Southwest (Grissino-Mayer and Swetnam 2000).

The restoration of fire in forested landscapes is not without difficulty. Because fire frequency can vary considerably through time, even in the absence of significant human impacts, it is difficult to determine which fire frequency characteristics should be used as baseline conditions (Stephenson, Parsons, and Swetnam 1991). In addition, spatial heterogeneity within past fire regimes can be difficult to reconstruct or restore. Fires are often patchy in nature, with some areas experiencing low-intensity fires and others more destructive fires. It is imperative that the design and implementation of fire restoration plans examine not only the frequency by which fire has occurred, but also the spatial variation inherent in fire occurrence.

Insects

The temporal occurrence of insect-caused epidemics has been examined using the dates of tree death (Perkins and Swetnam 1996) as well as changes in the growth patterns of both host and nonhost tree species (e.g., Swetnam, Thompson, and Sutherland 1985, Veblen et al. 1991; Hadley and Veblen 1993; Swetnam and Lynch 1993). The effects of climate can be removed, and suppressions due to insect defoliation enhanced, by comparing the growth between host and nonhost tree species (Swetnam, Thompson, and Sutherland 1985). A similar approach uses the growth patterns of trees that survive insect-caused epidemics, but rather than examining suppressions in the host species, the researcher identifies ring-width releases in surviving nonhost trees (Veblen et al. 1991; Fastie, Berg, and Swetnam, in review). Other approaches have also been used that rely simply on visual identification of suppressions and releases to assign dates to the outbreaks (Weber and Schweingruber 1995; Weber 1997).

Like fire, the patterns of insect outbreaks can be related to variability in climate and the impacts of human land use. Swetnam and Lynch (1989, 1993), for example, identified important relationships between western spruce budworm outbreaks in northern New Mexico and wetter than average conditions. In addition, they identified outbreak changes during the twentieth century that may have been due to fire suppression and past timber harvesting practices. Their results indicate that relative to earlier time periods, the twentieth century has experienced the longest intervals of reduced budworm activity, and that recent outbreaks have been among the most severe. Extensive logging of pine trees and severe fires reduced the density of trees in these forests. This was followed by a period of favorable climate and fire suppression that enabled host species (Douglas fir and true firs) to establish in these forests. In the decades following the logging and severe fires, these forests were less susceptible to disturbance by budworms, but as they reached maturity, host species became more homogenous across the landscape, leading to an abundance of susceptible host species over a large area. This resulted in more widespread and severe defoliation events in the late twentieth century than had occurred in previous centuries (Swetnam and Lynch 1989, 1993; Hadley and Veblen 1993; Weber and Schweingruber 1995).

The Limitations of Dendrochronology

Although there are important advantages to the use of dendrochronologic data, it is important to note its limitations. First, dendrochronology is limited to areas where trees form annual rings, so that variability can be used for cross-dating. Generally, these are areas where trees are sufficiently sensitive to climate (Fritts and Swetnam 1989). For example, tropical areas lack well-defined growing seasons, and, as a result, most tropical tree species lack clearly defined, annual growth rings. However, exploratory advances in tropical dendrochronology are being made using a variety of techniques to explore potential relationships with seasonal changes in environmental variability (Jacoby 1989). In contrast, some locations contain trees that may be too sensitive to variations in environmental conditions. For example, in some extremely arid regions, trees may be so sensitive to climate that a large number of annual rings are missing, making them difficult to date and utilize in dendrochronological investigations (Fritts and Swetnam 1989).

Tree rings, and other sources of paleoecological data, are subject to loss with increasing time before present. As tree-ring materials decay and are lost, the record and resolution of changes within the ecosystem diminishes. The resolution of the record may also be limited with respect to the sample depth during early portions of the record. This can be especially problematic in examinations of fire events but is a factor in all types of dendrochronological investigations.

Like most proxy records, tree rings record events through complicated physical and biological processes. Tree growth, therefore, acts as a filter through which environmental variability is recorded imperfectly. Our ability to accurately reconstruct the processes recorded by tree rings is directly related to our ability to understand and model this complicated filtering process, and therefore understand the signal recorded by tree rings (Swetnam, Allen, and Betancourt 1999).

Related to the problem of filtering complex environmental signals through biological processes is the concept of "no analogue." The "no-analogue" problem arises from processes or events that occur either during the modern period or in the past for which there is no related reference condition. This can lead to problems relating past or current growth characteristics with those for which there is no record. This may lead to complications in interpreting environmental variability from tree-ring data and may violate some aspects of the principle of uniformity.

Although tree rings can be applied to many aspects of historical ecology, it may not always be an appropriate approach to some questions of particular management concern or restoration. Care must be taken to determine if tree rings are appropriate recorders of a particular environmental variable, either through the matching of historical records with tree-ring data or through experiments that manipulate specific environmental conditions and monitor tree response.

Tree-ring analysis does have limits in its applicability to restoration ecology. Nevertheless, tree rings represent a useful, dynamic tool that can help capture the history of landscape change. Tree rings are a valuable source of long-term information that can be used to discover the range of environmental variability within forests and woodlands. The power of dendrochronology lies not only in the determination of events in time, but also in its ability to make inferences concerning the processes of environmental change. Information on the long-term fluctuations within the environment is crucial to the design and implementation of plans that seek to restore and maintain forests and woodlands within a range of their natural variation. New dendrochronological techniques and approaches aimed at understanding ecosystem variability will continue to evolve as resource managers and restorationists are faced with new problems and questions concerning our ever changing environment.

Resources for Dendrochronologists

There are a number of good references that can help those with little experience in dendrochronology. Guidelines for collecting, preparing, and cross-dating tree-ring samples can be found in M. A. Stokes and T. L. Smiley's book *An Introduction to Tree Ring Dating* (1968). Several texts focusing on the theoretical and practical aspects of dendrochronology have also been produced, including *Methods of Dendrochronology: Applications in the Environmental Sciences* (Cook and Kairiukstis 1990). A mainstay of the dendrochronology community is *Tree Rings and Climate* by H. C. Fritts, published in 1976. Unfortunately, it is out of print, but it can be found in most university libraries. A good resource for those interested in using tree rings to reconstruct insect-caused epidemics can be found in Swetnam, Thompson, and Sutherland, 1985.

In addition, the World Wide Web has become an important source of information on tree-ring research. The NOAA Paleoclimatology Program www.ngdc.noaa.gov/paleo/ archives includes more than one thousand tree-ring chronologies representing five continents. Those chronologies can be downloaded free of charge for a variety of uses. An additional online resource for those interested in pursuing dendrochronology is Henri Grissino-Mayer's Tree-Ring Web Pages web.utk.edu/~grissino. They include information on where to find commonly used dendrochronology supplies and useful links to tree-ring resources, as well as a searchable database of books and articles related to tree-ring research. An additional tool found on the World Wide Web is an interactive cross-dating tutorial developed by Dr. Paul Sheppard at the Laboratory of Tree-Ring Research tree.ltrr.arizona.edu/skeletonplot/introcross-date.htm. This tool allows users to apply skeleton-plotting techniques to date hypothetical tree-ring series.

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