Dendroecology: A Tool for Evaluating Variations in Past and Present Forest Environments

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I. INTRODUCTION

It is well known that yearly tree-ring width sequences, called chronologies, have been used to date structures, such as archaeological ruins, historic buildings and early Dutch paintings (Anon. 1977; Baillie, 1982; Trefil, 1985). A. E. Douglass, an astronomer working in Arizona, is credited with

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developing tree-ring dating (1919, 1928, 1936) and is considered the founder of the discipline of "dendrochronology" (Webb, 1983). *Dendro* refers to the Greek root word meaning tree and *chronology* to the study of time. The discipline is most appropriately characterized as the systematic use of tree-ring "cross-dating", a procedure that uses variability of ring characteristics to establish the exact year in which each ring was formed. Cross-dating was first used to date beams or charcoal fragments from archaeological and historical structures in the southwestern United States, and the technique provides archaeologists with the most precise time control ever devised spanning the last two thousand years (Douglass, 1935, 1937; Dean, 1986).

Similar tree-ring width sequences have also been used to reconstruct records of past climatic changes (Douglass, 1914; Schulman, 1947, 1951, 1956; Fritts, 1976; Hughes *et al.*, 1982) and to study past hydrologic history (Cook and Jacoby, 1983; Stockton *et al.*, 1985). The terms *dendroclimatology* and *dendrohydrology* are commonly used to refer to dendrochronological studies of climatic and hydrologic phenomena. Dendrochronology can also be used to study various ecological problems. The term, *dendroecology*, refers to applications of dendrochronological techniques to problems in ecology. The first conference devoted entirely to this subject was held in August, 1986 in Tarrytown, New York (Jacoby and Hornbeck, 1987).

There are four basic ways that dated tree-ring information can be applied to ecological studies: (1) specific ecological events can be dated by their association with dated ring structures or injuries; (2) past forest disturbances can be dated and their importance evaluated by distinctive changes in ring widths or other ring features; (3) climatic or hydrologic conditions can be calibrated and reconstructed by using the variations in ring structure; and (4) climatically related variations in animal populations and behavior can be identified and reconstructed.

In the first application, all associated tree-ring materials are carefully dated to place all growth rings in their correct time sequence (Douglass, 1941, 1946; Stokes and Smiley, 1968; Baillie, 1982; Holmes, 1983). Unusual ring features or evidence of injury are dated by their association with rings formed in a particular growing season. Thus, Sigafoos (1964) used the rings in flood-damaged trees to date scars and to deduce past flooding history. Shroder (1978, 1980), Alestalo (1971) and Giardino *et al.* (1984) dated the scars of trees growing on steep slopes to study rock slides and other types of geomorphic changes.

Dieterich (1980), Ahlstrand (1980) and Swetnam and Dieterich (1985) used tree-ring dated fire scars to reconstruct fire history. Unfortunately, many fire histories have been based upon simple ring counting techniques that can lead to large dating inaccuracies and uncertain conclusions. Madany *et al.* (1982) and Dieterich and Swetnam (1984) demonstrated that dendrochronological dating is considerably more reliable and can be used to establish the exact fire-history sequences. The high precision of dendrochronology also allows comparisons of fire histories among trees within study areas and between study areas (Swetnam and Dieterich, 1985) as well as between fire occurrence and variations in climate.

Dendrochronology can also be used to date fire scars in standing dead trees, logs or stumps, while this cannot be accomplished with simple counting of the rings. The use of tree-ring dating techniques in the study of tree death and dynamics of woody debris in forest ecosystems also has considerable potential (e.g. Gore *et al.*, 1985), but has been infrequently applied in this important and developing field of forest ecology (Harmon *et al.*, 1986; Franklin *et al.*, 1987).

The second general application of dendroecological analysis deals with past forest disturbances that may leave no scar but affect the ring character by influencing the tree's productivity and growth (Fritts, 1976; Lorimer, 1985). For example, Marchand (1984) dated rings and analyzed their characteristics to evaluate wood production efficiency in wave regenerated fir (*Abies balsamea* [L.] Mill.) forests. LaMarche (1966) identified periods of accelerated stream erosion by observing growth reduction effects in trees that have sustained a rapid uncovering of their roots. LaMarche (1968) dated exposed roots and used their age and depth to estimate the rate of slope degradation. Smiley (1958) and Yamaguchi (1983, 1985) dated eruptions of volcanoes by observing distinctive ring patterns of trees that had grown within the ash-fall zone. Brubaker and Greene (1979), Ferrel (1980) and Swetnam *et al.* (1985) have studied the effects of insect defoliation on tree growth by dendrochronological dating of the annual rings, and by comparing the differences in ring growth of host trees and non-host trees. Accurate dating is especially important in studies of insect defoliation and related forest disturbances, because many rings can be locally absent or missing in severely defoliated or suppressed trees (Keen, 1937; Evenden, 1940; Wagener, 1961), and this condition would be undetected by simple ring counting.

In the third general application of dated tree-ring information to ecological problems, the characteristics of the dated rings are used to reconstruct past variations in drought (Stockton and Meko, 1975, 1983; Cook and Jacoby, 1977), temperature and precipitation (Fritts *et al.*, 1979), stream flow (Phipps, 1972; Stockton and Jacoby, 1976; Holmes *et al.*, 1979; Cook and Jacoby, 1983) and water levels (Stockton and Fritts, 1973; Phipps *et al.*, 1979). Taylor (1981) and Graumlich and Brubaker, (1987) have also used dendrochronological methods in studies of forest productivity.

This third type of dendroecological application is usually needed because the existing climatological or hydrological records are too short to detect long-term climatic variability and changes (Hecht, 1985; Gates and Mintz, 1975), and because understanding and resolving the ecological problems at hand require this information. The tree-ring information on climate from the oldest trees is calibrated and verified with the existing records of climate and the tree-ring variations in the past are converted to estimates of past variations in climate (Fritts, 1976, Stockton *et al.*, 1985). Consider how tree-ring analysis of past hydrologic variability was used to help resolve the following environmental problem.

A newly constructed dam, which was completed in 1967, reduced the peak spring discharge of the Peace River, Canada that usually flooded the rich natural wildlife habitat of the 1·5 million-acre Peace–Athabasca delta. Measurements of levels in Lake Athabasca showed a marked decline after the gates in the dam had been closed. A public outcry, as early as 1972, expressed fears that this valuable natural habitat would be destroyed by these abnormal changes. It was argued by the proponents of the dam that the 33 years of water-level measurements made before dam construction were anomalous because of recent climatic changes, and the recent low water levels after dam closure were simply a return to natural conditions.

It was hypothesized that rings of white spruce (*Picea glauca* [Moench] Voss) growing along the flood plains and levees in the delta region might be influenced by unusually high or low water levels and that a dendroclimatological study might provide an objective basis for resolving this issue. Trees with 200 or more rings were found growing on the better-drained sites throughout the delta area. Visible differences in ring-width patterns in widely scattered trees suggested that some macro-scale environmental conditions had been growth limiting.

The rings were sampled by coring 10 or more replicate trees (two cores per tree) growing on six widely scattered sites over the delta system. The locations of these sites were largely determined by availability of old trees, but where possible they were chosen so as to reflect differences in the water levels within the inlets and outlets of the delta hydrologic system. The rings were dendrochronologically dated, the widths measured, and these data analyzed to obtain six different records of growth throughout the region (Stockton and Fritts, 1973).

While 61% of the ring-width variations were common to the six growth chronologies, there were differences that appeared to be associated with site drainage and soil–water relationships. Multivariate techniques were used to calibrate the variance in the six chronologies with the 1935–1967 record of water levels averaged for three 10-day periods (May 21–30, July 11–20, and September 21–30) for the year in which the rings were produced and for the year prior to that. The partial regression coefficients were applied to the tree-growth data to obtain reconstructions (statistical estimates) of average water levels for the six 10-day periods.

The 1810–1967 means of the reconstructions were 686·0, 688·7 and 685·5 ft above mean sea level which differed by only 0·6, 0·6 and −0·1 ft from the means for 1935–1967 gauged records. However, the reconstructed variances for the 1810–1967 time period were estimated to have been 5·62, 7·71 and 3·66, which are 309%, 179% and 89% of the variances for 1935–1967 calibration period. It was concluded that the variances of the May 21–30 and the July 11–20 gauge measurements were substantially below the variances for the longer record estimated from the tree-ring measurements, but the variance of the September 21–30 gauge measurements was substantially higher than for the longer estimates.

A few years were reconstructed when water levels were as low as they were early in the season after impoundment, but the reconstructed low levels were isolated cases with higher water levels in the years both before and after them. No low levels had been reconstructed to persist as long as was observed after impoundment. These results led to the conclusion that the low values after impoundment were extreme but within the range of the earlier estimates and hence within the range of natural variability. However, the persistence of these extremes was unprecedented in the earlier estimates.

These results led to the recommendation that the present-day Lake Athabasca levels might be managed to counteract the effect of the impoundment. The extremely low levels from impoundment could be interrupted frequently, raising water levels to match the higher levels associated with pre-impoundment conditions. For example, this might be accomplished by constructing temporary earthen dams across one or more of the outlets before the spring floods begin. This would temporarily impound the water in the Peace–Athabasca area for the early part of that year until the temporary dams washed out, helping to maintain the habitat conditions nearer to pre-impoundment levels.

The fourth type of dendroecological application involves one or more animal species that are so affected by climate that an aspect of their behavior or population can be related to the climatic information found in tree-ring width variations. For example, Clark *et al.* (1975) were interested in determining whether the large scale changes in the fisheries along the North Pacific coastal waters during the last four decades were unusual compared to earlier time periods. They studied the correlations between dated chronologies from arid-site trees of western North America and yearly "landings" of albacore tuna (*Thunnus alalunga*) which reflected population changes or migrations of tuna into or out of the coastal waters north of San Francisco. These changes were found to reflect variations in sea surface temperatures that were, in turn, related to the atmospheric conditions that influenced the growth of arid-site trees in the West. As in the previous example, a regression was obtained between the fish landing data and the variations in the tree-ring chronologies from 1938 through 1973. The regression was then applied to tree growth before 1938 to reconstruct yearly tuna landings, which were inferred to be surrogates of variations in the population of albacore tuna during the past. It was concluded that the past fluctuations in tuna population were as variable as in the 1938–1973 period, and such variations would be expected to continue in the future.

In other similar applications, Young (1979) studied factors influencing hunting success of mule deer (*Odocoileus hemionus*) in Arizona and used tree-ring widths as indicators of the availability of natural forage. Spencer (1964) used tree-ring chronologies as well as dated scars from trees grazed by porcupine (*Erethizon epixanthum*) to document past changes in porcupine populations at Mesa Verde, Colorado.

Today we are faced with a number of very important ecological problems for which dendroecological techniques are well suited. These include (1) widespread outbreaks of herbivorous insects in forests (Doane and McManus, 1981; Schmitt *et al.*, 1984; Brookes *et al.*, 1987), (2) tree decline that was first observed in forests of central and northern Europe and is now reported for some areas of the United States (Abrahamsen *et al.*, 1976; Binns and Redfern, 1983; Johnson and Siccama, 1983; Bormann, 1985; Hornbeck and Smith, 1985; Smith, 1985) and (3) potential environmental changes brought about by the rising concentration of atmospheric CO_2 and other gases (Lemon, 1983; Woodwell *et al.*, 1983; LaMarche *et al.*, 1984).

Because the relevant tree-ring analysis techniques needed for such research may be unfamiliar to some ecologists or are simply misunderstood, the following discussion will summarize the basic principles and practices of the field, describe some of the most relevant new developments, indicate some of the limitations and suggest how dendrochronology can help to illuminate some of the current day environmental issues. This work updates an earlier article on the subject (Fritts, 1971).

II. PARAMETERS REFLECTING TREE-RING VARIABILITY

A variety of structural characteristics of tree rings, such as width, wood density (Schweingruber, 1983; Schweingruber *et al.*, 1978a) and vessel size (Eckstein and Frisse, 1982), show variability from one ring to the next. The variations in ring width have been studied most often (Fritts, 1976; Baillie, 1982), because width can be observed and measured easily from a finely sanded or microtomed surface by using a hand lens or dissecting microscope.

Early in the 1960s, Polge (1963, 1966, and 1970) discovered that a thin section of wood can be X-rayed, and the image on exposed film scanned by an optical densitometer to obtain detailed ring density measurements. Parameters such as minimum density, maximum density, earlywood width and latewood width are now derived from these types of measurements

(Schweingruber, 1983). These can be correlated with climatic variations as well as various physical, chemical and biological features of the environment (Keller, 1968; Parker and Henoch, 1971; Fritts, 1976; Huber, 1976; Schweingruber *et al.*, 1978a, 1978b; Conkey, 1982a, 1982b, 1986; Cleaveland, 1986).

Stable and unstable isotopes of oxygen, hydrogen and carbon in tree rings, as well as accumulations of heavy metals, are other promising sources of information (Lepp, 1975; Jacoby, 1980; Long, 1982; Wigley, 1982; Brubaker and Cook, 1983; Guyette and McGinnes, 1987). While these new sources of tree-ring data may become viable alternatives to studies of ring width, they often require custom-made equipment, relatively complicated procedures and some of the methods are not fully worked out.

Densitometric analysis appears to offer considerable promise for environmental and climatic analysis of moderately moist forest habitats such as the central deciduous forest and southern boreal forest of North America, as well as in the forests of western Europe. Here the rings may be wide and the widths may exhibit much less variability than wood density characteristics. In areas of little width variation, dendroecology may be possible only because of the greater variability in density measurements.

The implementation of densitometry for studies in more extreme sites may not be practical, because the rings from many old trees growing on stressed sites are sometimes too small to be resolved by the densitometer and the additional information provided by densitometric measurements may not justify the high cost of measuring these variations. These problems may be partly circumvented with further development of image analysis techniques (Telewski *et al.*, 1983; Jagels and Telewski, in press), where digitized measurements of reflected light from surfaces of tree-ring specimens may provide estimates of wood density as well as other detailed information on structural variations within annual rings.

In the meantime, some collection teams sample and mount cores in a manner that allows for both ring-width and densitometric work (Holmes *et al.*, 1986). The ring widths are processed and when better equipment and more reliable densitometric procedures become available and financially supportable, these cores can be X-rayed and the film scanned for wood density analysis. With a few modifications, the principles and practices described for ring-width analysis also apply to densitometric analysis. The information that can be obtained from both types of measurements are complementary. Most laboratories are experimenting with densitometric analysis, and the procedures of the Radiodensitometric Laboratory at the Eidgenössische Anstalt für das forstliche Versuchswesen, Birmensdorf, Switzerland are most often emulated.

III. GENERAL PRINCIPLES AND PRACTICES OF DENDROECOLOGY

The "principles" referred to in the following text are essentially the fundamental framework of understanding including the operational procedures that are followed in the discipline of dendroecology. These "principles" are not laws or even necessarily rules of nature but are rather well-tested best inferences based upon known facts at a particular time. Principles are more or less stable over sustained time periods and are revised or overthrown only during periods of scientific revolutions (Kuhn, 1970). The general principles of one field, such as ecology, frequently apply to subfields, such as dendroecology, but they may be viewed and applied in unique ways. The following is a brief description of what we believe to be the most important principles and practices of dendroecology, particularly those that relate to dendrochronological applications.

A. Uniformitarianism

The principle of "uniformity in the order of nature" was first enunciated for geology by James Hutton in 1785. It is commonly stated as: "The present is the key to the past". Its dendroecological implications are (1) the physical and biological processes that link today's environment with today's variations in tree growth were also operating in the past, (2) tree-ring features in a given tree are related to the same environmental conditions in the present as in the past, and (3) environmental conditions associated with present day ring features may be inferred to have existed when that feature occurred in the past. This principle does not imply that environmental or tree growth conditions were all the same in the past as in the present, only that the relationships that govern them must have been the same.

However, a set of unusual conditions in the past could be missed if that set is completely absent from the modern record. This is referred to as the "no analog problem" because there may be no analog in the present to deduce a similar condition in the past. Similarly, there may be no analog in the past for present day conditions. For example, a new condition, such as pollution or a forest management practice, could create a "no analog condition" in that it does not occur anywhere in records of the past. The lack of an analog in the past could prohibit applying some dendroecological inferences to the past from information collected after that condition was introduced. Sometimes, there may be alternative strategies available that do not violate the uniformitarian principle, or will at least minimize the violation's effects.

For example, Bryson (1985) discusses the "no analog problem" applied to paleoclimatic inference and research. His analysis focuses on interpretations of spatial patterns in pollen assemblages and Holocene climate. He points out: "Climate is multidimensional (a vector), not a *single scalar datum.*" He suggests that there are so many independent variables in the climate system that probably no *perfect* analog could be found. Partial analogs (involving a large number of correlated as well as causal relationships) may be all that are necessary; and methods such as canonical analysis that consider a large number of variables may provide a good way to transfer proxy data records into estimates of climate. Increased availability of density as well as ring-width information may help to mitigate some "no analog problems". However, in the case of new environmental conditions created by pollution or other effects of man, the absence of a true analog remains a serious problem.

Since Hutton's day geologists and paleontologists have studied the spatial arrangement of Earth's strata with the perspective of modern processes that are now producing similar strata in order to reconstruct the "deep time" chronologies of Earth's history. This method of inference, utilizing layered records and uniformity of process, has been an extremely important tool for reconstructing past Earth history and thereby building our knowledge of this planet and its lifeforms.

The essential point here is that documentation of history, i.e., the correct ordering and placement of events in time, depends on the understanding of process, and *vice versa.* We believe that understanding and exploiting this duality of history and process (or "time's arrow" and "time's cycle", see Gould, 1987) will continue to be a fruitful approach in the study of the geosphere and biosphere. In this chapter we advocate the use of dendroecology techniques where possible for obtaining many new chronologies (histories) of disturbances, climatic change and other environmental changes in forest ecosystems of the world. We also recognize the need for more experimental studies of the ecophysiological linkages between trees as organisms and the environment. This effort will provide the necessary documentation of history that must go in hand with improved understanding of processes and mechanisms toward a clearer picture of our world.

B. Limiting Factors

The well known biological principle of "limiting factors" also leads to sampling procedures important to dendroecology. It is not our intent here to weigh the relative merits or weaknesses of the arguments concerning additive versus interactive effects or whether the concept of single factors acting in successive limitation is a profitable paradigm. We recognize that a variety of factors can influence the complex process involved in ring growth, and each factor may operate in a variety of ways and at different times. For example, the number of tracheid cells within annual rings, their size and wall thickness are often controlled by a variety of limiting factors. However, if one examines individual years in which growth is minimal or sites where a particular ring feature is evident, some kind of limiting condition can usually be found to dominate. For example, the narrowest rings in arid-site and low-elevation trees from southwestern North America can be attributed to climatic patterns in years when drought had been the most probable but not the only limiting condition. For years in which the rings are wider, drought-related conditions are less likely to have occurred and other factors were probably more limiting. The rings with the lowest maximum density are related to climate through the predominance of limiting (low) temperatures (Schweingruber *et al.*, 1978a; Conkey, 1986; Kienast and Schweingruber, 1986).

The relative importance of different limiting factors also varies over space and time owing to micro-environmental changes as well as changes in trees as they grow and occupy different positions in the forest. In spite of these complexities, simplification of the problem is possible. Ecological insights and field observations can be tested by sampling along particular ecological gradients and measuring any changes in ring characteristics. This assumes that there is adequate replication to minimize the confounding effects of factors not associated with the gradient that was sampled. It is also helpful to measure tree growth and other related factors throughout the year, or to manipulate, control or modify the environment to study these relationships. Once relationships are documented in this manner it is possible to make ecological inferences from tree-ring information (Fritts *et al.*, 1965b; Fritts, 1969, 1976; Norton, 1983; and Kienast and Schweingruber, 1986).

Fox *et al.* (1986) use this principle to study pollution effects on ring-width chronologies. They report an increase in mean width and an increase in variance for trees growing downwind from the point pollution source after emission controls had been installed. Presumably, growth increased as pollution levels became less limiting and became more variable as the variations in climatic conditions became more critical.

The specific growth response to environmental factors can vary markedly from one kind of habitat to another. For example, the ring widths of northern hemisphere trees growing at their species' northern or high altitude limit are likely to be affected adversely by unusually cold growing conditions which slow down the growth processes (LaMarche, 1974; Schweingruber *et al.*, 1979; Garfinkle and Brubaker, 1980; Jacoby *et al.*, 1985; Graumlich and Brubaker, 1986). The ring-width growth of such trees located at the southern or low-elevation limits of the species are more likely to be adversely affected by lack of moisture or unusually warm conditions in summer (LaMarche, 1974; Fritts, 1976). Temperature is most likely to become limiting through its effect on evapo-transpiration, tree water potential and water stress. Different species of trees, growing at widely different altitudes, may respond directly to temperature in spring and autumn if the individuals are equally close to the upper margin of their species' habitat range. In addition, one might also expect trees growing at increasing elevations to be decreasingly responsive to low moisture, because evapo-transpiration may become less limiting as the ambient temperature declines with the higher altitude (LaMarche, 1974, 1982; Fritts, 1976; Phipps, 1982). These relationships are by no means simple ones. The Kienast and Schweingruber (1986) paper is a landmark that documents the tremendous variability in growth that can be noted in both Europe and North America at different elevations and exposure associated with variations in macroclimate. More discussion of limiting factors is included under the topic Tree and Site Selection (p. 134).

C. Crossdating

Crossdating refers to both a principle and a practice. The principle refers to the general year-to-year agreement or synchrony between variations in ring characteristics of different trees. This synchrony can be shown to be the limiting effects of variations in climate on tree growth (Fritts, 1976). The practice involves detecting and correcting for any lack of synchrony in ring features when the patterns are out of sequence. This occurs when the ring for a particular year is missing from a sampled radius, when intra-annual latewood bands are indistinguishable from the true boundary of the annual ring, or when there are simply mistakes in counting or in growth-layer identification. Practiced correctly, crossdating assures that all ring features are placed properly in the correct time sequence.

All the various approaches to crossdating involve the following six basic steps:

(1) Visual and statistical comparisons are made of the ring sequence through time involving features such as total ring width, earlywood/latewood width, color, wood density or other differences in structure. It is sometimes useful to plot one or more features, or to use symbols to represent the varying ring characteristics.

(2) If one and only one ring is formed in a year, the chronology of these features is synchronous among trees as long as the count is begun with the same ring. If a ring is absent or two layers of latewood are formed in one year, the chronology from that tree will match the chronology in other trees up to the location of the discrepancy. Beyond that location the chronologies will appear to be one year out of phase. This pattern usually becomes complicated by shifts in the matching of patterns at a number of locations.

(3) Crossdating utilizes the presence and absence of synchrony from different cores and trees to identify the growth rings that may be misinterpreted.

(4) Knowledge of ring structure and chronology is used to correct the sequence by entering zero values for locally absent rings, combining the widths of double rings, and adjusting for miscounting or any other problem with the ring sequence.
(5) The comparison, checking and correcting are replicated many times using different trees. The time period spanned by the rings must be long enough to include some years when climate had been limiting to growth. Crossdating of samples is repeatedly checked, so any prior interpretations of the chronology are verified by the successful matching of all independent ring information from additional samples. Computer programs have been developed that analyze the statistical crossdating of tree-ring series (Baillie, 1982; Holmes, 1983). These programs are most useful for assisting in the dating of samples that have a relatively small number of errors, and they are also valuable as a check of dating accuracy and measurements. No computer program has been able to substitute for the thought processes and judgment required for successful crossdating.
(6) The final step in crossdating is checking the site dating sequence against the independent chronology sequences from trees in other more distant sites. This last step may not be absolutely necessary because of the internal consistency and rechecking that has already been built into the dating of trees within the sample. If enough trees including various age classes are properly crossdated, the likelihood of a mistaken date is so small that for all practical purposes it is zero. If step 6 is included, it serves as an additional confirmation that the chronology is accurate to the exact year. Step 6 should always be used if there is a likelihood that other chronologies have not been dated accurately.

The synchrony in ring features that is used in crossdating is relatively easy to observe in the ring-width patterns of certain conifers growing on arid sites. For example, in south-western United States, approximately 60 to 80% of the ring-width variation or variance is coincidental in most trees of a given species and region if they are growing on similar sites. Even in trees of different species there may be as much as 50 to 70% of the variance in common as long as the trees are subjected to aridity. The similarity in the ring-width pattern is correlated with seasonal variations in macroclimatic factors that are closely coupled with local environmental conditions controlling physiological processes important to ring growth. Thus, the synchrony used in crossdating is evidence that a factor like macroclimate, which varies from one year to the next throughout the region, has affected ring growth. In fact, one can infer how often climatic factors are more or less limiting to ring-width variation from the amount of crossdatable variance (Fritts, 1976).

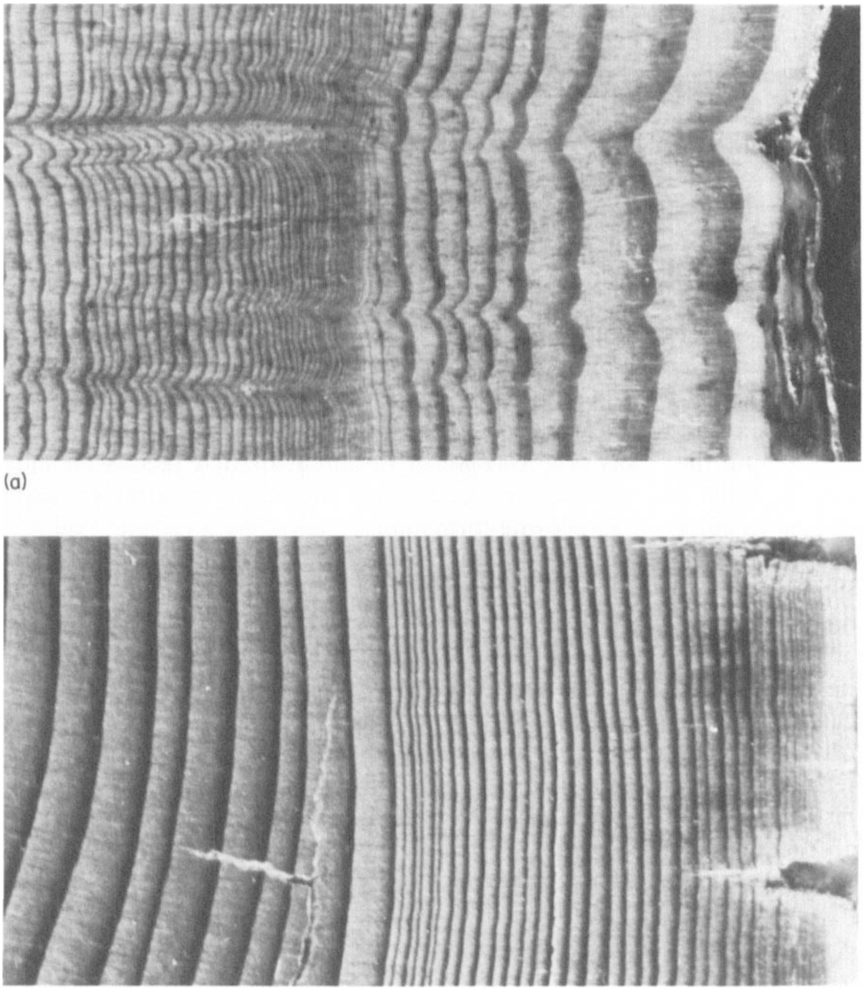
After the growth rings have been crossdated, the measurements for rings produced in each year can be standardized into chronology values (discussed in the next section), and averaged to show the yearly ring-width variations that are common to the trees of a stand. These measurements also can be related to the environmental or climatic conditions that had originally affected tree growth on the site.

Unusual conditions may sometimes produce characteristic ring features that may not be due exclusively to climate but will enhance the crossdating between trees or sites. Abnormalities of the ring structure caused by early or late frosts (Glock, 1951; Glock *et al.*, 1960) can be recognized and have been used as an independent test of the accuracy of crossdating (LaMarche, 1970; LaMarche and Harlan, 1973). Filion *et al.* (1986) demonstrated that "light rings", characterized by one or a few latewood cell layers, were an indication of shortened growing seasons in black spruce (*Picea mariana* [Mill.] BSP) at the tree-line in Quebec. They found that light rings were useful for crossdating because there was little ring-width variation for that species on those sites, and that low temperatures occurring at the end of the growing season seemed to initiate the light ring formation.

Sudden removal of the overstory will usually be reflected as a sudden increase in growth of all surviving trees (Fig. 1a), while a stand-wide disturbance such as a volcanic ash fall may result in the sudden decrease in growth of surviving trees (Fig. 1b). Such growth effects are usually distinguishable from the effects of climate by the sudden onset of the growth change, the persistence of the effect and the spatial variability in the response of trees. Some caution should be exercised in the use of disturbance events reflected in tree rings for crossdating, because the stressful effects of the disturbance on the tree increases the likelihood of ring anomalies such as ring absence.

Many cases of absent rings have been found in fire history studies (Craighead, 1927; Zackrisson, 1980; Dieterich and Swetnam, 1984). Madany *et al.* (1982) compared fire scar dates that were estimated only by ring counting and matching of fire scars between samples with fire scar dates determined by crossdating the rings of the same samples. Crossdating revealed numerous absent rings, and as a consequence, the dates estimated by ring counting were found to be accurate only 26% of the time.

Other dendroecology studies have clearly demonstrated the necessity of crossdating, especially when studying stressed trees. Marchand (1984) found many cases of absent rings in a study of wave-regenerated fir forests. Evenden (1940), O'Neill (1963) and Swetnam (1987) noted many rings were missing in trees that had been defoliated by insects. Athari (1981) emphasized that precise ring dating is essential in tree-ring/air pollution studies, especially where increment losses are to be calculated. He reported 1,879 missing rings in samples from 328 emission-damaged Norway spruce trees and 119 missing rings from 148 trees from undamaged check stands. There



(a)

(b)

Fig. 1a. A rapid increase in the ring widths in this ponderosa pine follows the removal of competing trees in a 1966 timber harvest (Dieterich and Swetnam, 1984).

Fig. 1b. A rapid decrease in the ring widths of this Douglas-fir specimen from a northern Arizona archaeological site appears to be the result of a volcanic eruption which may have damaged the crown or roots of the tree in 1064 or 1065 AD (Smiley, 1958).

was a maximum of 19 missing growth rings per radii in the damaged trees, while the undamaged trees had a maximum of 6 missing rings per radii.

D. Standardization

The growth potential of the seedling and its capacity to respond to climate change slowly as the seedling grows, matures and attains a dominant position in the canopy of the forest. These changes affect the character of the rings in young trees, creating the well-known ring-width sequences of Duff and Nolan (1953). Some of the techniques of Duff and Nolan were applied to older trees used for dendrochronology by comparing 20-year means of ring characteristics rather than comparing the yearly ring-width values (Fritts *et al.*, 1965a). They show that the rings are widest near the base and central portions of the stem. The ring width decreases with increasing age of the cambium, with increasing height in the young stem, and with decreasing amounts of apical growth. These changes produce a downward trend in ring width and variance that are due to intrinsic factors such as aging and changes in bole geometry. To study changes in the extrinsic environment of trees, the time series of these measurements must be transformed before applying most statistical analyses.

The procedure of standardization is designed to make this transformation. It usually involves the fitting of a curve or straight line to correspond to the average growth potential as it changes over time (Fritts *et al.*, 1969) (Fig. 2a). The curve is data dependent in that its values vary for each year, measured radius, tree, species and site. To correct the series for the intrinsically related decline in mean and variance the ring width is divided by the value of the curve to express width as an index or percent (× 100) of the potential average growth for that year (Fig. 2b). The mean or expected value of the index is 1·0, and the variance of the standardized index is generally stationary through time. With a stationary variance, the indices can be averaged with the indices from other cores and trees to obtain a chronology for the site (Figs. 2c,2d) and the data can be easily analyzed using techniques of time series analysis (Jenkins and Watts, 1968; Meko, 1981; Monserud, 1986).

The lowest possible index value is zero, when the ring is absent, but there is no upper limit. Even with this constraint, approximately 90% of the standardized chronologies from drought-subjected sites in western North America are normally distributed (Fritts, 1976). The normality of indexed chronologies from other types of sites and for other regions has not been examined extensively.

The standardization curve for ring widths is not a simple linear function of the volume growth and changing geometry of the growth layer throughout the tree. Models based exclusively on geometric considerations rarely

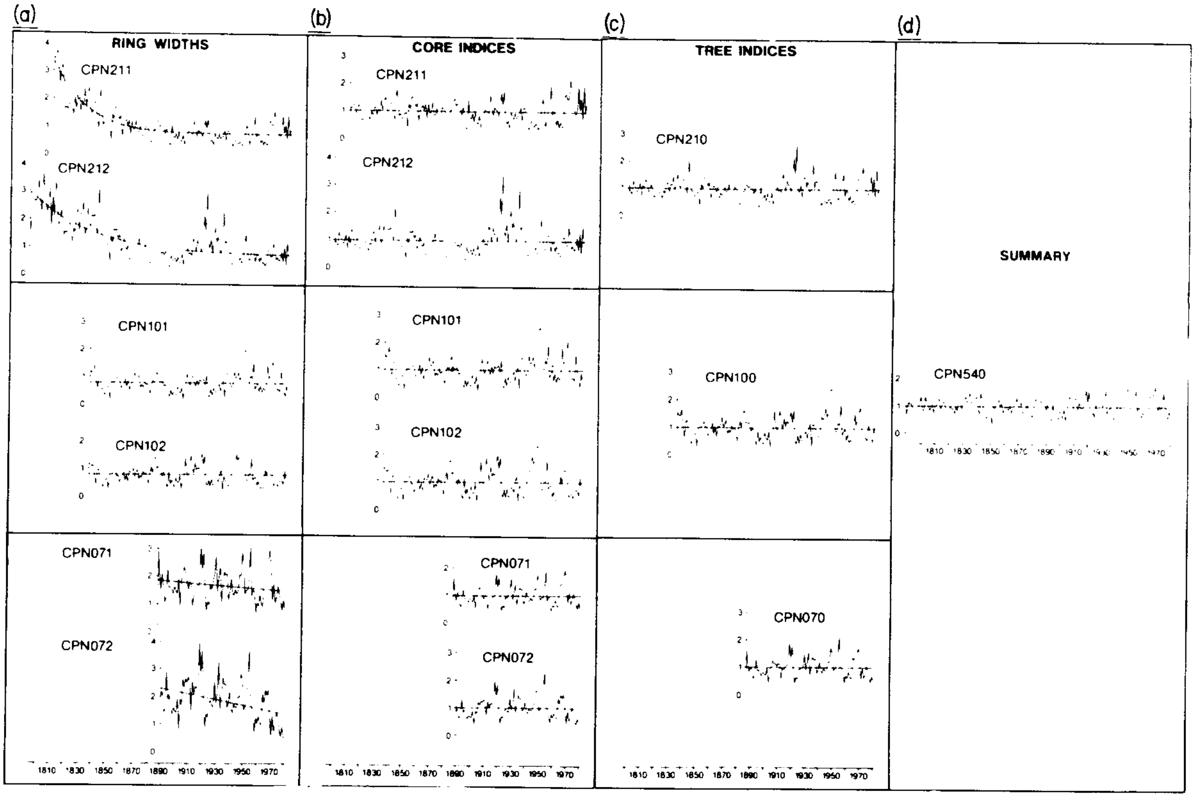


Fig. 2. The dated ring widths are transformed into a standardized chronology by: a. Fitting a curve or straight line to the ring widths from each core, b. Dividing by the values of the fitted curve to obtain the indices, c. Averaging the cores for each tree to obtain the tree indices, and d. Averaging the tree indices to obtain the summary or the site chronology.

linearize the observed changes in ring width over time (Fritts, 1976). In addition, a variety of intrinsic and extrinsic factors associated with increasing tree height, changes in the overstory, the varying proximity of neighbors and other within stand conditions are added to the geometric effects. Flexible empirical models, rather than inflexible physical models, appear to be needed to express these complex changes (Fritts, 1976; Graybill, 1979; Cook and Peters, 1981; Blasing *et al.*, 1983; Cook, 1985). Graybill (1982) and Cook (1987) have constructed what Cook calls a linear aggregate model that distinguishes between the major sources of ring-width variation by considering their inter-relationships and statistical differences. The model suggests several statistical approaches to the study of these sources of variation. A brief description of this model is presented in Section IV with a discussion of its implication in the study of "forest decline" and pollution.

In the past, dendrochronologists have been more interested in studying climatic factors than in studying age or stand-related changes in tree growth, so the changes in growth potential have been estimated primarily to remove them from the ring-width measurements. Only the indices are retained for further analysis. The dendroecologist, however, may have different objectives in mind. Standardization may still be advisable to remove age-related growth changes that contribute unwanted variance. However, other problems and questions may require measurement and assessment of some or all of this variation. In these cases standardization techniques may be modified or an alternative analysis used to preserve the age or growth variations related to stand dynamics for subsequent analysis.

E. Variance of the Mean and the Signal-to-Noise Ratio

After standardization, the indices for all trees from a site are averaged for the cores from each tree and then averaged for all trees in the site (Figs. 2c, 2d) to obtain the mean indices or yearly chronology values. The variance of these values is always less than the pooled population variance of the individual standardized indices making up each set.

The variance of the yearly chronology value can be considered the result of two kinds of influences: large-scale factors operating on the forest as a whole and small-scale factors that act on the individual trees or part of the tree. The first is represented by the variance in common among all trees on a site; the second is the error variance which can be associated with measurement error, growth differences from one side of the tree to the next and growth differences from tree to tree in the same site (Fritts, 1976; Cook, 1987).

Assuming that the ring series are relatively free of the effects of large-scale pollution and exogenous disturbances (see Section IV), the variance in common can be considered to represent the effects of macroclimate or the "climate signal" (s) because it seems to result primarily from large scale climatic variations that have been limiting either directly or indirectly to growth in all trees (Fritts, 1976). Using this same terminology, the remaining more-or-less random error can be considered as "noise" (n) which dilutes and perturbs the expression of the "signal" in the chronology for a given site. For example, conifers in semi-arid sites commonly have about 60% or more of the variance in common among trees. This leaves 40% of the variance as noise, so that an individual tree has a signal-to-noise ratio of 60/40 with a decimal value of 1·5.

The amount of variance attributed to the signal can be estimated from the components of standard analysis of variance (Fritts, 1976), but autocorrelation must be considered when estimating the degrees of freedom. Also, the variance of the signal can be approximated by calculating and averaging the correlation coefficients between all possible combinations of trees on the site, excluding the correlations between cores from the same tree (Wigley *et al.*, 1984). An adjustment for degrees of freedom is made by multiplying the average correlation by $(n-1)/n$, where n is equal to number of years in the analysis period. The percentage of signal variance is subtracted from 100 to estimate the average error variance (i.e., information that is not common among trees). An s/n ratio for a tree is converted to the s/n ratio of a chronology by multiplying by the number of trees included in the chronology. In the above example, a chronology made up 10 trees with a 1·5 s/n ratio would have a chronology s/n ratio of $1{\cdot}5 \times 10$ or 15:1. This is a typical s/n ratio for chronologies from western United States semi-arid sites.

For ring widths in the more moist deciduous forests of the eastern United States or western Europe, the percentage of signal in a single radius index series can be as low as 20 to 40%, although judicious sampling and standardization can be used to minimize some of the noise and to increase the percentage of variance in the signal. The s/n ratios for a single radius from the deciduous forest trees would then range from 20/80 to 40/60, which are decimal values of 0·25 and 0·67. However, if the indices from 10 trees are averaged the chronologies would have s/n ratios ranging from 2·5:1 to 6·67:1.

The s/n ratio in a standardized ring-width chronology is dependent in part upon how limiting climatic factors and any other stand-wide conditions have been to growth of the trees during the years that were sampled, and in part upon the number of cores and trees that were averaged to obtain the chronology for a site. Figure 3 illustrates how this relationship can vary in a chronology with changes in sample size over time (Holmes *et al.*, 1986). Four separate 10-year segments have been selected from a well-replicated ring-width chronology from a site named Hager Basin, California. The chronology plots over the four segments are enlarged and shading added to show the standard error around each chronology value. The signal is the variance of the 10 average index values shown in each 10-year segment. The error is calculated by squaring each standard error, multiplying by the sample size,

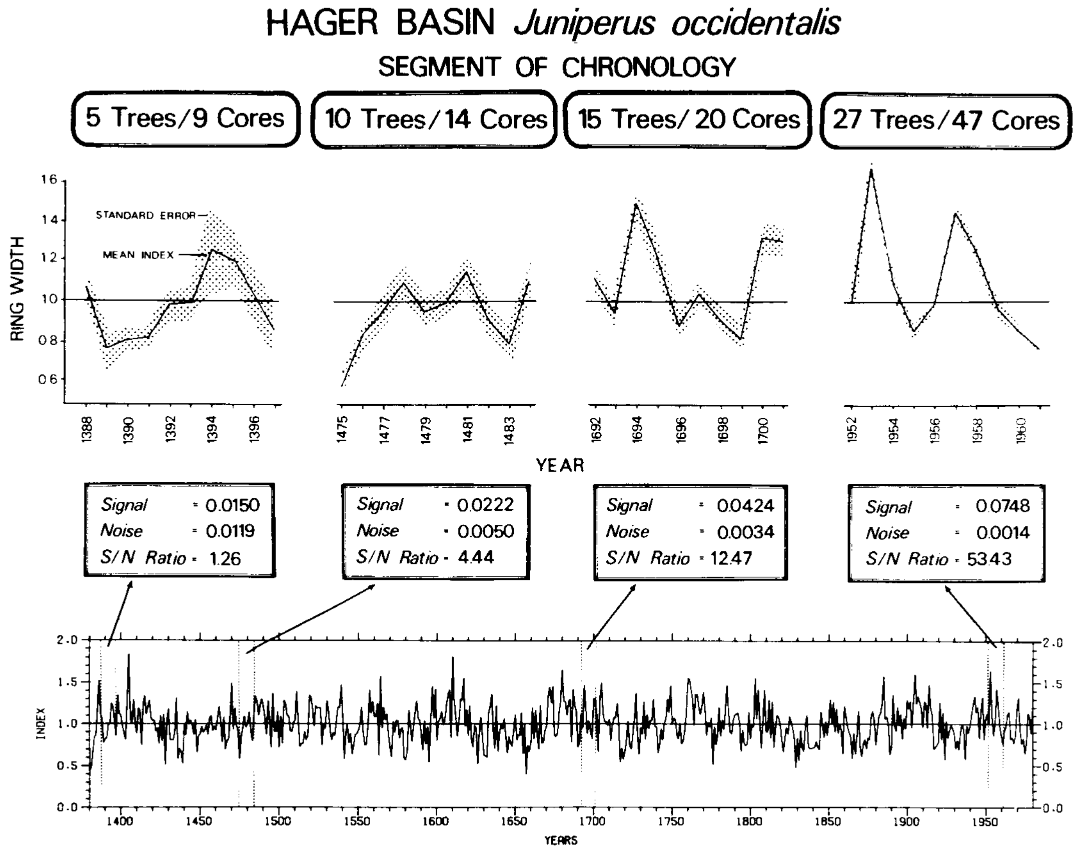


Fig. 3. Index plots for four 10-year segments of a dated and standardized chronology from western juniper in Hager Basin, California. The shading shows the standard error as a departure from each mean index value. The number of trees and cores available for each segment, and the signal, noise and *s/n* ratio are shown in boxes.

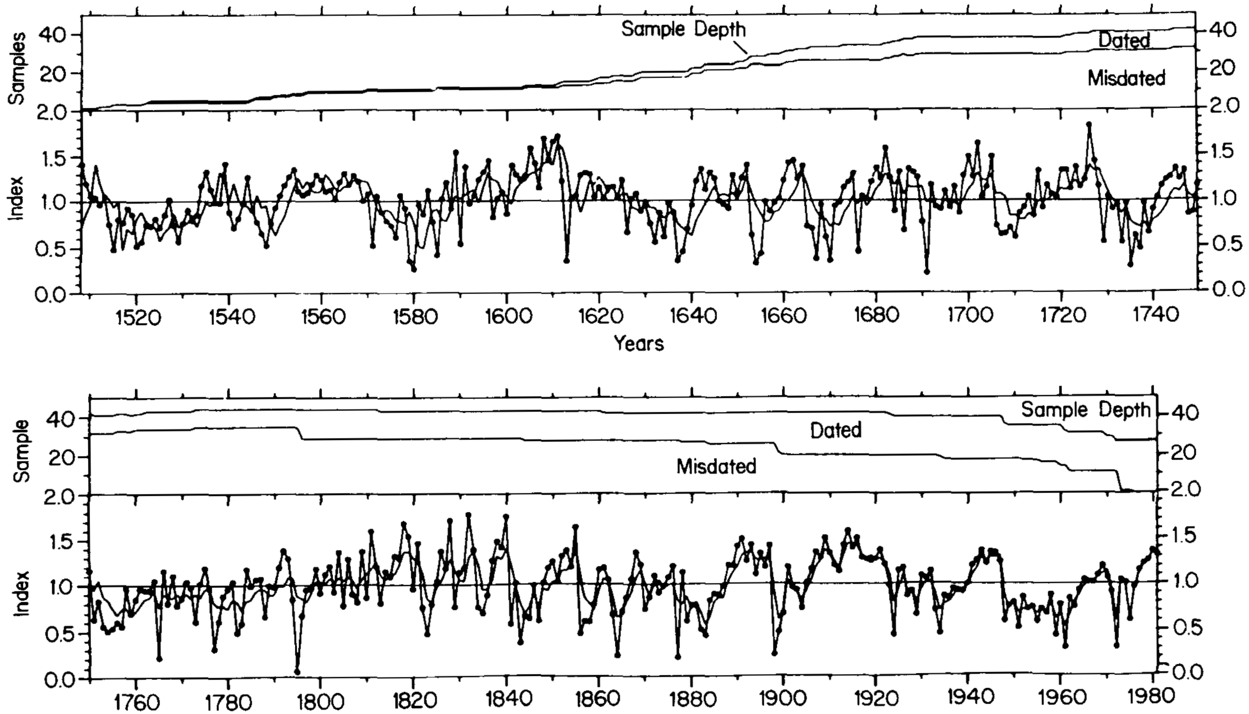
summing the results over the decade and dividing by 10, the number of years in each segment. The *s/n* ratios are calculated from these two values using the numbers of trees and cores shown above each segment. To simplify the calculation for the purpose of this illustration, the variance in common within trees is assumed to be identical to the variance in common between trees (Fritts, 1976; Cropper, 1982).

The first segment began in 1380, and measurements from nine cores were standardized and averaged to obtain the chronology. The *s/n* ratio, estimated in the above fashion, amounts to only 1·26. In the second segment which began in 1475, the indices from 14 different cores were averaged. The error, shown by shading, was reduced and the *s/n* ratio rose to 4·44. By the year 1692, the beginning of the third segment, 20 ring measurements were available for each chronology value. The error was reduced further with an *s/n* ratio of 12·47. The last segment began in 1952 and was the average of 47 different measurements. The error estimate is so small as to be barely visible and the *s/n* ratio is 53·43.

Techniques such as crossdating and standardization influence the *s/n* ratio, because they reduce the error resulting from incorrect dating and nonclimatic growth features of ring widths (Fritts, 1982). Figures 4a,b serve as an example. Figure 4a shows the standardized mean ring-width chronology for a group of dated cores sampled from trees growing in California. The dating indicated that about 1% of the rings were locally absent from the cores that were sampled. A chronology made up entirely of undated ring widths was simulated by simply deleting all zero values representing missing rings from the dated ring-width measurements and reassigning dates by counting from the outside to the inside rings. These data were restandardized and the indices pooled to simulate an "undated" chronology series.

The dated chronology (with points) and the "undated" series (without points) are superimposed and shown on the same scale in the lower plot of Figure 4a. The uppermost plot is the total number of samples. The next plot is the number of incorrectly dated samples, so the difference between the two is the number of correctly dated samples. The values from the correctly dated set are subtracted from the values of the incorrectly dated set and the differences are plotted in Figure 4b. The chronologies of the counted and dated sets from 1976 to 1980 were almost the same, because no ring absence (missing ring) was encountered over this time period. The small differences that do occur reflect the higher average values of the curves fitted to the incorrectly dated series.

However, the 1975 ring was missing in one out of 27 cases and the 1972 ring was missing in 11 out of 27 cases. The result of these discrepancies is a reduction of the deviations from the overall series average value of 1·00 and an increase in the magnitude of the differences between the two series. As one moves further back in time, more and more absences are encountered, the



(a)

Fig. 4a. A Jeffrey pine chronology from Sorrel Peak, California with ring widths correctly dated (with dots) and incorrectly dated using only ring counts (without dots). The total numbers of samples and the number of misdated samples in the counted set for each year are shown in the uppermost plots. The difference between these two values is the number correctly dated in the counted set.

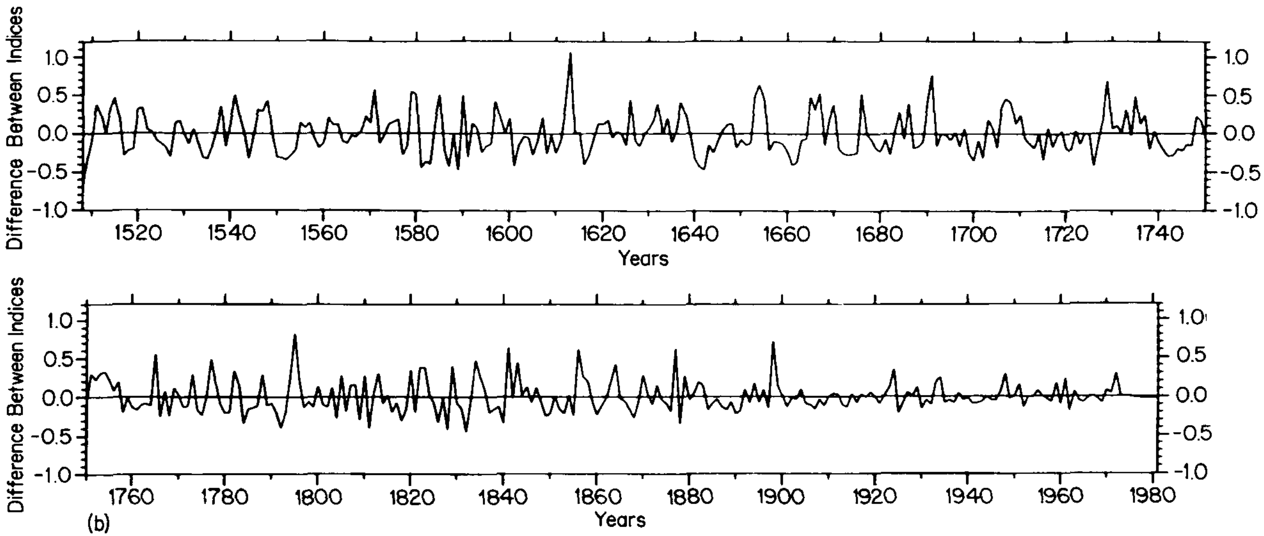


Fig. 4b. The chronology value of the counted set minus the chronology value of the dated set. This difference increases from right to left as the dates on more and more samples become incorrect.

differences become larger, and the ring index average values of the counted series include increasing numbers of rings formed in other years. The net effect is to reduce the magnitudes of chronology variations, especially the very low values where there were missing rings. The peaks and troughs of the undated chronology become displaced several years forward in time (to the right) of the series with the correct dating.

The percent variance in common to all trees after standardization is 57·8 in the dated set and only 27·6 in the counted set. The *s/n* ratio for a chronology from 10 trees was estimated to be 13·70 for the dated and 3·81 for the counted ring series. The dated set is not only more variable, but its variations are clearly better related to causal limiting conditions. The variance of the dated series is stable with the passing of time, and can be used to relate 20th-century conditions to those in earlier times (Fritts, 1976; Stockton and Jacoby, 1976; LaMarche, 1978; Hughes *et al.*, 1982; Cook and Jacoby, 1983). On the other hand, the variance characteristics of the counted set are unstable. The variance decreases and the first order autocorrelation increases as more and more rings become mismatched going backwards in time. With this instability comparisons from one time period to the next cannot be made.

F. Sample Replication

Sample replication and the law of large numbers are included here as their consequences in dendrochronological procedures are frequently overlooked. If a large number of trees and cores are crossdated and analyzed in each site so all years have been identified on all specimens (i.e. no rings are missing from the final dated series), it is highly likely that the chronology dating is correct. This is easily checked by comparing two independently dated chronologies from the same geographic area (LaMarche and Harlan, 1973).

The actual number of cores, trees and sites to be sampled for a particular investigation will depend in part upon the strength of the signal in the individual core samples and the strength of the *s/n* ratio desired in an analysis. The *s/n* ratio and other related statistics have been described in Section E. These statistics can be routinely calculated (Fritts, 1976; Wigley *et al.*, 1984) to help one decide on the adequacy of a particular sample.

Although it is difficult and probably unwise to argue that all studies must attain a given *s/n* ratio, this ratio can help one to evaluate data comparability and to decide upon future collection strategies. For example, in the early 1960s before the *s/n* statistics had been applied to dendrochronological work, the faculty of the Laboratory of Tree Ring Research launched a program to update and expand their arid-site conifer chronologies. They arbitrarily decided that a collection strategy of two cores from approximately 10 trees in a site appeared to provide adequate replication.

Later, when analysis of variance techniques were applied to the new collections, it was noted that chronologies made up of 10 trees often had a *s/n* of 15:1 or more (Fritts, 1976; DeWitt and Ames, 1978). When the same calculations were applied to chronologies from more mesic sites, such as in the eastern United States, it was noted that the signal in the final chronology was weaker. It was estimated that more than 30 or 40 trees would have to be collected and analyzed to obtain an *s/n* ratio as high as 15:1. Although they did not recommend that an *s/n* of 15:1 was necessary for all applications, the result suggests that the signal should be estimated at an early stage in an investigation, a decision made as to what *s/n* was desirable and a sampling strategy developed which would achieve the desired objective.

Cook (personal communications) suggests an alternative sampling strategy for dendroclimatic reconstruction that makes sense in the temperate forests of eastern North America. Instead of increasing the size of each sample to enhance the *s/n* ratio, he recommends keeping the same sample size but increasing the total number and density of the sites that were collected. He argues that in eastern North America the effects of local stand competition and other nonclimatic factors are more important than those in western sites. These factors are more likely to be retained as part of the signal in a given eastern North American site chronology, even if a large number of trees are sampled, because they arise from stand-wide disturbances. Assuming that these effects are more likely to be random between sites than within sites, an increase in the replication of sites, rather than trees within sites, would provide the best estimate of macroclimatic conditions. The same strategy seems reasonable for dendroecological studies. A certain amount of replication is needed not only for enhancing the signal of the chronology but also to provide an adequate number of specimens for crossdating.

G. Tree and Site Selection

Tree and site selection is an extension of the principles of limiting factors and sample replication. The choice of trees and sites for a dendroecological problem requires an understanding of the micro-environmental relationships affecting growth in the landscape being investigated in order to visualize and hypothesize how the rings may vary in response to changes in limiting factors (LaMarche, 1982). Then the effects of a particular control factor can be investigated by selecting trees from a number of "target sites" (LaMarche, 1982) along an environmental gradient upon which that control factor is thought to vary (Fritts *et al.*, 1965b; Fritts, 1969; LaMarche, 1974; Norton, 1979, 1983; Kienast and Schweingruber, 1986). However, the replicated trees within each target site must be sampled very carefully to minimize any differences in the ring patterns due to the control factor. An attempt should also be made to minimize the effects of as many other factors as possible by using within-site replicates from trees of the same species, age and stand history.

The selection and replication of trees and sites are simply a stratification of the sample to minimize the noise and maximize the common signal in the site chronology, so that subtle differences in the chronologies can be statistically tested. Based on these selection criteria, sampling can be considered essentially "random" within the bounds of the target population representing a specific set of environmental conditions (LaMarche, 1982).

Studies addressing different ecological issues may require different stratifications of sites and a more formal sampling design. However, if it is a dendroecological problem, attention must be given to the age of the trees, the importance of limiting conditions that provide crossdating and the homogeneity of forest stands that are to be sampled. A dendrochronologist working in semi-arid southwestern North America who is interested in climatic reconstruction, can recognize the oldest climate-stressed trees at a distance by the flat or spike-topped shape of the crown and the large size of the lateral branches, and he would sample the trees accordingly. A similar strategy may or may not be required in an ecological or climatological investigation elsewhere, depending upon the question to be investigated. The following studies provided new information and perspective on different ecological problems by examining trees along particular gradients using a variety of sampling strategies.

Morrow and LaMarche (1978) studied the effect of insect herbivory on ring-width and related phenomena. They stratified ring series from insect-infested trees before and after treatment with insecticides, and they also compared ring series of treated and untreated trees and examined the differences in ring growth.

Brubaker and Greene (1979), Ferrel (1980) and Swetnam *et al.* (1985) investigated the effects of insect infestation on forest growth. They sampled species that were susceptible and unsusceptible to the insect and looked for differences in ring character associated with periods of known insect outbreaks.

Fox *et al.* (1986) studied the effects of a point pollution source on ring widths by obtaining replicate samples of trees at increasing distances down wind from the pollution source. Several stands with no obvious pollution source were sampled for controls. The study also involved differences in the ring-width chronologies for years before pollution, after pollution and after pollution controls were installed.

Schweingruber *et al.* (1983) studied ring characteristics of trees growing at increasing distances from a pollution source. By studying a large number of trees and noting site characteristics and related conditions, they were able to evaluate differences in the pollution effect associated with tree age, with soil acidity and with elevation of the tree sites as well as with distance from the source.

Marchand (1984) compared replicated samples of older balsam fir stands (with an average age 74 years) to replicated samples of younger stands (with an average age 35 years) to determine whether wave-mortality (dieback) was age related.

Payette *et al.* (1985) compared the rings from living trees to those from trees that had died at some earlier time period. They inferred from differences in ring structure, as well as from differences in age distributions, that climate had been different in the earlier time period.

H. Calibration and Verification

If the s/n ratios in tree-ring chronologies are large enough, and the chronology values are linearly related and well correlated with one or more environmental factors, it is possible to derive a relatively simple equation using least-squares techniques that rescales the chronologies in terms of the correlated environmental factors (Lofgren and Hunt, 1982; Blasing and Duvick, 1984). The variations of past growth can be substituted in the equation to estimate statistically the variations in past environmental factors.

The statistical procedure of deriving the coefficients of the equation is called "calibration". Tree-ring data and climatic data are compared over an interval of time called the calibration period. The coefficients are unique to the data in the calibration period and independent of any observations not included in the period (Gordon, 1982). Therefore, it is possible that even a well-calibrated equation may produce unreliable reconstructions when it is applied to data independent of the calibration.

The reliability of a calibrated equation can be tested by withholding some of the observations on the variable to be reconstructed when making the calibration, and then using these independent observations to test whether the reconstructions for those particular years are correct. This procedure is called "verification". An array of verification statistics (Gordon and Leduc, 1981; Gordon, 1982; Fritts *et al.*, in the press) can be calculated to estimate the similarities between the independent estimates and the observations that were withheld from the calibration. These statistics are tested for significance to ascertain whether the independent reconstruction is better than would be expected solely by chance variations.

A simple correlation, however, is usually an inadequate model for calibration because the tree-ring chronologies are noisy records of a complex set of interacting climatic and environmental factors (Fritts, 1976). One solution is to calibrate a chronology using least-squares techniques in a multivariate regression model that statistically estimates the chronology value from a number of predictor climatic variables such as monthly precipitation and temperature. The sign, size and significance of the partial regression coefficients obtained in the calibration are examined and interpreted as a tree-ring response to the monthly climatic factors (Fritts *et al.*, 1971; Fritts, 1974; Guiot, 1986). This solution is called a response function.

Another solution is to use a number of chronologies in a multivariate regression model to predict statistically one or more climatic factors. In this solution the values of the chronologies are calibrated with the climatic factors, and the resulting equation is used to reconstruct past climatic variations from the variations in past tree growth (Fritts *et al.*, 1971; Blasing, 1978; Lofgren and Hunt, 1982). This solution is called a transfer function, which Bryson (1985) defines as "an empirically determined quantitative relationship between a proxy 'data vector' and a climatic 'data vector'". In the case of tree rings, the variance of the chronologies is transferred to statistical estimates of climatic variance.

Several attributes of tree-ring chronologies and climatic data complicate the form of the equation used in calibration. The predictor variables may be so colinear that the reliability of the coefficients may be underestimated. This and related problems with the response function can be partly resolved by using special types of multiple regression (Cropper 1985; Marquardt and Snee, 1985). ARMA modeling techniques (Jenkins and Watts, 1968; Meko, 1981; Richards, 1981; Monserud, 1986; Cook, 1985; Graumlich and Brubaker, 1986) also provide alternative procedures. Guiot (1986) and Fritts (in press) use both univariate and multivariate ARMA modeling along with canonical analysis to accomplish calibration (Fritts *et al.*, in the press).

Often a certain amount of tree-growth variance may be attributed to a lag in growth of one or more years behind the occurrence of climate because of autocorrelation and other types of persistence in the tree-ring chronologies. These effects can be modeled by (1) lagging the tree-ring series one or more years behind the climate occurrence in a transfer function (Fritts, 1976), (2) considering the size of the prior ring as well as climate as a predictor factor in the response function (Fritts *et al.*, 1979), (3) using variable transformations (Fritts and Gordon, 1982), and (4) using techniques of time series analysis (Meko, 1981; Jones, 1985; Guiot, 1986). The last techniques efficiently handle time-series properties and can be combined with various multivariate models to obtain reconstructions of both single points representing climatic stations or grid points and arrays of points portraying spatial surfaces (Briffa *et al.*, 1988b).

Calibration and verification procedures can be applied whenever tree-ring or climate relationships are important contributors to the tree-ring variance. They can be used to derive an equation for extending a relatively short record of instrumental climatic data, drought severity indices or hydrologic information, from a study area, backward in time (Fritts, 1976; Hughes *et al.*, 1982; Brubaker and Cook, 1983; Stockton *et al.*, 1985). Observations on environmental and other data, which may be correlated with the relationships related to ring growth, can also be correlated with and reconstructed from the chronology variations (Stockton and Fritts, 1973; Clark *et al.*, 1975). Separating and removing the effects of climatic factors on ring growth from the effects of other factors can also be done (Nash *et al.*, 1975; Swetnam *et al.*, 1985).

It is not possible to recommend a particular technique for all calibrations. Time series analysis is currently in vogue but its application to reconstructing large spatial grids has yet to be tested and evaluated. Simulation techniques like those of Cropper (1985) can be used to generate time series with a known signal of climate. The various calibration procedures can then be applied to these data to see how well they can recover the climatic information.

I. Modeling

As in other disciplines, it is helpful to construct models that depict hypothesized physical or physiological interrelationships. Models not only provide hypotheses to be tested; they can be used to make projections or calculations of conditions resulting from changes in the model inputs (Cooper *et al.*, 1974). Horton and Bicak (1987) add, "Models provide a framework for organizing knowledge as it is acquired. This framework is particularly convenient since, as knowledge expands, the number of attributes in a model can be increased without a change in the fundamental form."

Early attempts at dendrochronological modeling took the form of diagrams. Figure 5 includes examples that model some of the interacting relationships linking temperature and precipitation with ring-width variations (Fritts, 1976; Koerber and Wickman, 1970; Stockton, 1971; Young, 1979). Other models are more quantitative ranging from energy balance relationships within the tree (Brown, 1968; Gates, 1980) to simulations of the response function relationships (Cropper, 1982).

Modeling of cambial activity for conifers, which was introduced by Wilson (1964) and Wilson and Howard (1968), was adapted to dendroecology by Stevens (1975). The model simulates daily cell growth and differentiation in a single radial file of cells which ultimately forms a tree ring. The growth processes are controlled by 22 model parameters which are the only inputs to the program. Variations in limiting environmental factors must act on these inputs to affect ring structure. Fritts (in press) is attempting to model these linkages, and also has developed a stochastic model that generates a number of time series representing limiting conditions in different seasons. The tree-ring responses to these time-series are weighted averages, and random variance is added to simulate the error component. ARMA processes, the growth trend, and other features can then be introduced to simulate the ring response to various forest influences.

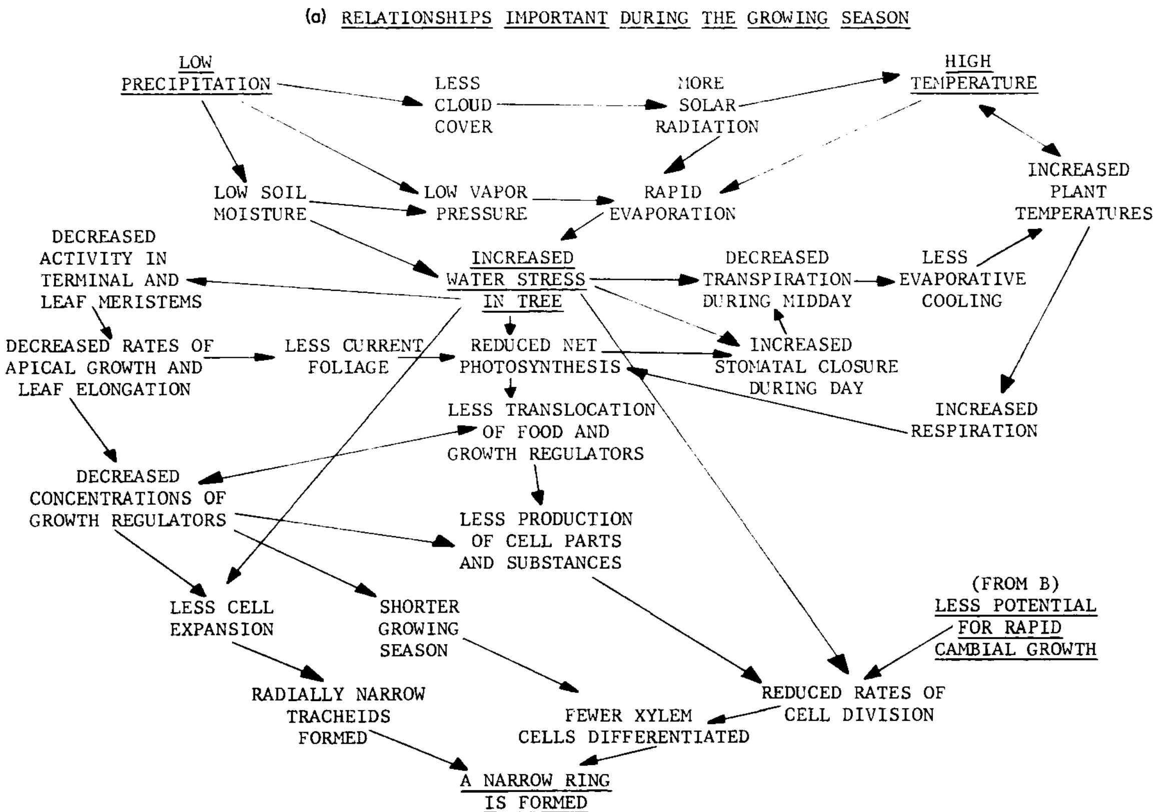


Fig. 5a. Model diagram representing some of the relationships that cause climatic factors of low precipitation and high temperature during the growing season to lead to the formation of a narrow ring in arid-site trees. Arrows indicate the net effects and include various processes and their interactions. It is implied that the effects of high precipitation and low temperature are the opposite; that is, ring width will increase (from Fritts, 1976).

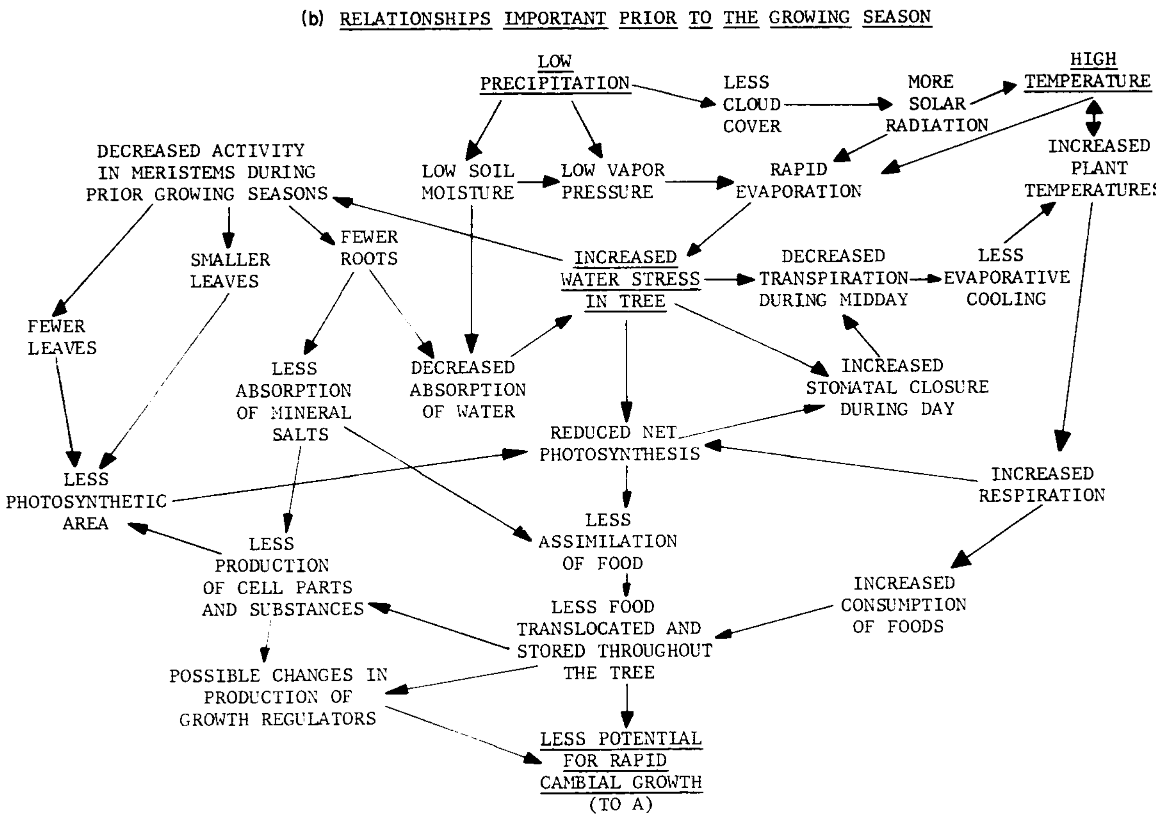


Fig. 5b. Model diagram representing some of the relationships that cause climatic factors of low precipitation and high temperature occurring prior to the growing season to lead to the formation of a narrow ring in arid-site trees (from Fritts, 1976).

(c) HIGH PRECIPITATION AND LOW TEMPERATURES MAY IN CERTAIN CIRCUMSTANCES LEAD TO LOW GROWTH

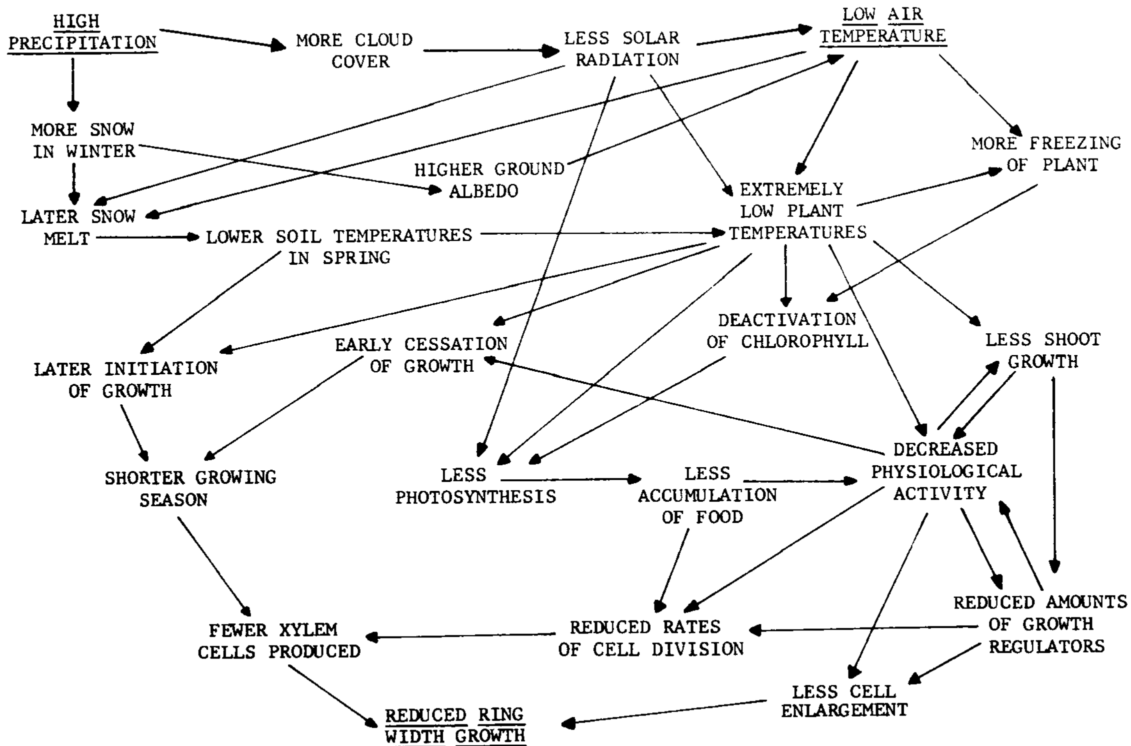


Fig. 5c. Model diagram representing some of the relationships that cause the climatic factors of high precipitation and low temperature to lead to the formation of a narrow ring (from Fritts, 1976).

Another model, developed by Zahner and Myers (1986a, 1986b), calculates the impact of soil water deficits on the radial growth of southern pines in the Piedmont region of the southeastern United States. Daily water deficits affect daily radial growth, and thus account for the major environmental stress acting on southern pine growth. The model adjusts annual ring widths upwards to the long-term mean during periods of severe water stress and downwards during years of mild water stress. Zahner and Myers (1987) applied this model to adjust ring widths measured on over 2000 increment cores and were able to use the adjustments to test whether there has been a significant decline in ring width over time independent of soil water deficits in the Piedmont region. They found a decline in ring width of approximately two-thirds of the annual growth increment for equivalent trees 36 years earlier that was associated with an undetermined stress factor.

A model with four different controls of ring-width growth was proposed by Graybill (1982). The controls include (1) a macroclimatic signal common to the trees on a site, (2) a biological growth curve of variable form, (3) tree disturbance signals including disturbance resulting in growth differences among the sampled trees as well as disturbance resulting in similar features of growth in all trees, and (4) a randomly varying component analogous to error. Section IV describes a modification of this model to include six controls (Cook, 1987) which was applied to the forest decline problem.

IV. A LINEAR AGGREGATE MODEL OF RING-WIDTH MEASUREMENT

The dependent variable in this model (R_t) represents a ring-width measurement in the radial direction along a cross-section of a tree stem. Each ring is assumed to have been accurately dated in year t. Ring width is expressed as an aggregate of 6 basic components of the equation:

$R_t = G_t + C_t + aD1_t + aD2_t + aP_t + E_t$ where

G = the age-related growth trend value in year t that is shared by that species growing on that type of site;

C = the climatically related growth variations common to a stand of trees in year t including the mean persistence of these variations due to physiological preconditioning and interaction of climate with site factors

$D1$ = the endogenous disturbance pulse originating from competition, changing tree stature and other forces acting on specific trees in year t

$D2$ = the exogenous disturbance pulse originating from forces outside the forest community such as that due to an ice storm, a late frost or an insect infestation in year t

P = the variance due to anthropogenic pollutants that have stand-wide impact on radial growth in year t

E = the series of more-or-less random variations representing growth influencing factors in year t unique to each tree or radius, including error in the ring-width measurement.

The a associated with $D1_t$, $D2_t$ and P_t is a binary indicator of the presence ($a = 1$) or absence ($a = 0$) of a subseries in R for some year or a group of years. There is an assumption of linearity and independence among variables that is not strictly true, as most environmental variables are highly interrelated. In spite of this oversimplification, the model does provide a useful framework for identifying and separating the different types of influences.

Component G_t corresponds to the slowly changing ring-width variations that are commonly modeled and removed by standardization. Cook (1987) states, "The growth trend, G_t, is a non-stationary process that arises, in part, from the geometric constraint of adding a volume of wood each year to a stem of increasing radius." For many open grown trees, where competition is a minor factor, the trend in radial growth associated with G_t can be adequately modeled and removed by deterministic mathematical models fitting a variety of curves (Fritts *et al.*, 1969; Fritts, 1976; Graybill, 1979, 1982). Cook continues, "Unfortunately, the growth trends of trees growing in closed-canopy forests are usually very complex and stochastic because of disturbances and competitive interactions within the forest. Therefore, G_t must be generalized to allow for a variety of linear and curvilinear growth trends of arbitrary slope and shape."

According to Cook (1987), the input that produces C_t reflects certain broad-scale meteorological variables that directly or indirectly limit the growth processes of trees in a stand. These variables are assumed to be uniformly important for all trees of a given species and on similar sites. "As a common signal in the ring widths of all trees, C_t could be mistakenly identified as a pollution signal if the recent behavior of C_t mimics the expected pollution effect on ring widths. Thus, the effects of climate on ring width must be carefully modeled and removed before a pollution effect can be inferred" (see Zahner and Myers, 1987).

Cook (1987) goes on to explain that $D1_t$, the endogenous disturbances,

> . . . are caused by factors related to characteristics of the vegetation that are independent of the environment (White, 1979). Such disturbances occur when dominant overstory trees senesce, die and topple as a natural consequence of competition, aging and stand succession. In the context of searching for a pollution signal in tree rings, endogenous disturbances can be expected to occur randomly in space and time in forest communities. Thus, the loss of a dominant tree in one section of a stand is not likely to be related temporally or spatially to similar losses at other locations in the stand. This property suggests that endogenous disturbance pulses in tree rings will rarely be synchronous among separated trees in a stand except by chance alone. Thus, the lack of synchrony

in ringwidth fluctuations between trees during a hypothesized pollution effect period may be used as evidence for rejecting the presence of a pollution signal.

Exogenous disturbances are caused by natural environmental forces that lie external to and are independent of the vegetation (White, 1979). Unlike endogenous disturbances, these disturbances can affect large areas of forest. Some of the important causal agents are fire, windstorms, ice storms, frost damage, disease and insect infestation. Since the areal extent of an exogenous disturbance can be great, the resultant disturbance pulse, $D2_t$, may occur contemporaneously in virtually all trees in a stand. This property presents obvious difficulties for differentiating a pollution-caused ringwidth decline from that caused by a natural exogenous disturbance. Historical documentation of exogenous disturbances in forests may be needed to determine the presence or absence of this confounding source of variance.

The pollution signal, P_t, is assumed to be common to all ringwidth series in the sampled trees of a stand. This assumption could be criticized for being too restrictive in requiring a pollution effect on all sampled trees. It could be argued, for example, that the crowns of canopy trees "scrub out" wet and dry atmospheric pollutants before they reach understory trees. If this were the case, then the understory trees might not show a pollution effect. This possibility indicates the need for the stratified sampling of trees based on *a priori* criteria such as crown class or canopy position.

Hopefully $D2_t$ and P_t can be distinguished from C_t because they have more persistence. If their time-series characteristics are similar to those for climate, it may be necessary to model and remove as many climatic effects as possible before study of these non-climatic factors. It is self-evident that methods of standardization that might remove some of the variance of $D2_t$ and P_t could not be used if these factors were the object of the investigation.

Component E_t is the random variance in the ring-width series due to such variables as localized responses to micro-environmental factors, variations around the circuit of a ring and measurement errors, and is assumed to be unrelated to the variance accounted for by the other components. In addition, it is assumed to be serially uncorrelated within each tree and spatially uncorrelated within the stand of trees. The usual way to reduce this random variance is through replicate sampling and averaging after standardization (Fritts, 1976).

The above model is only descriptive at present. It uses statistical characteristics of ring widths or standardized time series to identify the source of the variation and does not consider features other than ring-width variation. As our understanding of ring features including cell size, density of the wood and chemical composition improves, it may be possible to make the model more quantitative and to add features other than ring width, which should increase its capability of discriminating between sources of variation.

V. DENDROCHRONOLOGICAL APPLICATIONS TO SPECIFIC ENVIRONMENTAL ISSUES

We have described the field of dendroecology by listing the nine most important principles along with illustrations of various applications. The most distinctive feature of all dendrochronological studies is the requirement that the tree-ring sequences must be dendrochronologically crossdated. This is the only method by which the integrity of the dendrochronological time series can be assured because the procedure automatically validates the results whenever two time series that were independently dated are compared. Most dendroecological methods assume that the annual measurements are correctly identified as to the year in which they belong. Thus, dendroecology provides an exact time control as well as a historical perspective to ecological investigations.

Assuming the above, we will direct our attention to three environmental issues that have been given much public attention: insect infestations and forest growth; the forest decline problem; and ecological questions of climatic variability and change over periods of years to centuries.

A. Spruce Budworm Effects on Forest Growth

Spruce budworms (*Choristoneura* spp.) are considered to be the most destructive forest pests in North America (Sanders *et al.*, 1985). Forestry records indicate that outbreaks lasting 10 to 20 years have recurred several times in the last century in North American forests. Substantial losses to timber resources have stimulated intense research efforts in the last decade to understand better the ecology and impacts of these insects (Sanders *et al.*, 1985). Tree-ring studies have played an important role by providing a long-term historical perspective of this episodic phenomenon. In addition to documenting growth impacts, which are necessary for the formulation and justification of forestry management strategies, tree-ring reconstructions of budworm history have been useful for improving our understanding of the dynamics of insect populations and forest stands, including the interactions of climate and human activities. The following dendroecological investigation provides an example of one approach for reconstructing past budworm history and impacts and the ecological implications of such tree-ring derived disturbance chronologies.

Eleven recently defoliated mixed conifer stands in the southern Rocky Mountains were sampled along a north–south transect from northern Colorado to northern New Mexico (Swetnam, 1987). The working hypothesis was that a recognizable exogenous disturbance component in host trees (Douglas-fir, *Pseudotsuga menziesii* [Mirb.] Franco., and white fir, *Abies* *concolor* [Gord. and Glend.] Lindl.) could be used to infer past insect outbreaks. Response function analysis had shown that a large and similar climatic component can be found in Douglas-fir and ponderosa pine (*Pinus ponderosa* Laws.) growing on similar semi-arid sites (Fritts, 1976). Therefore, the standardized ring-width chronology in ponderosa pine, which is a non-host species, could show the variations in the climatic component without the variations due to spruce budworm infestation. If graphical and statistical comparisons of the host and non-host series, in conjunction with forestry records of budworm outbreaks, showed that the above hypothesis was reasonable, then variations in the difference between the host and non-host chronologies could be used as an index of budworm outbreaks.

The eleven stands were originally chosen by the United States Forest Service for monitoring budworm populations and impacts and were generally considered to be representative of areas currently defoliated by budworms. These stands included a fairly broad range of topographic positions, elevations (2400 to 3000 meters), soil moisture conditions, and mixtures of conifer tree species (Swetnam, 1987).

Cores were obtained from at least 15 randomly selected mature host trees in each of the eleven stands (more than 40 trees were sampled in five of the stands). Two replicate samples were extracted from each tree. Five to ten of the oldest host trees within the stands were also sampled to ensure that the collection included the maximum possible record length. An additional 15 to 20 non-host trees (ponderosa pine) were collected within and near the study plots for comparative purposes.

All of the Douglas-fir and ponderosa pine ring-width series were cross-dated. Crossdating revealed that absent rings were relatively common in the cores from host trees, with a maximum of 30% of the cores from a stand having one or more absent rings. In nearly all cases the absence of annual rings in host trees were observed to be associated with low growth during periods of known or inferred budworm outbreaks. Absent rings were also detected in non-host trees, but they were more evenly distributed throughout the ring series and were often associated with drought years.

The Douglas-fir and ponderosa pine chronologies from one of the 11 stands are shown together in Figure 6a. The general correspondence between the year-to-year values in the plot of the host chronology (line with triangles) and the non-host chronology (line without triangles) was characteristic of most samples.

The average correlation between the host and non-host chronologies was 0·65. Additional statistical comparisons of the host and non-host chronologies included climatic response function analysis and spectral analysis (LaMarche, 1974; Fritts, 1976). These analyses generally confirmed the working hypothesis that the chronologies from both species had similar climatic signals, especially in the higher frequencies.

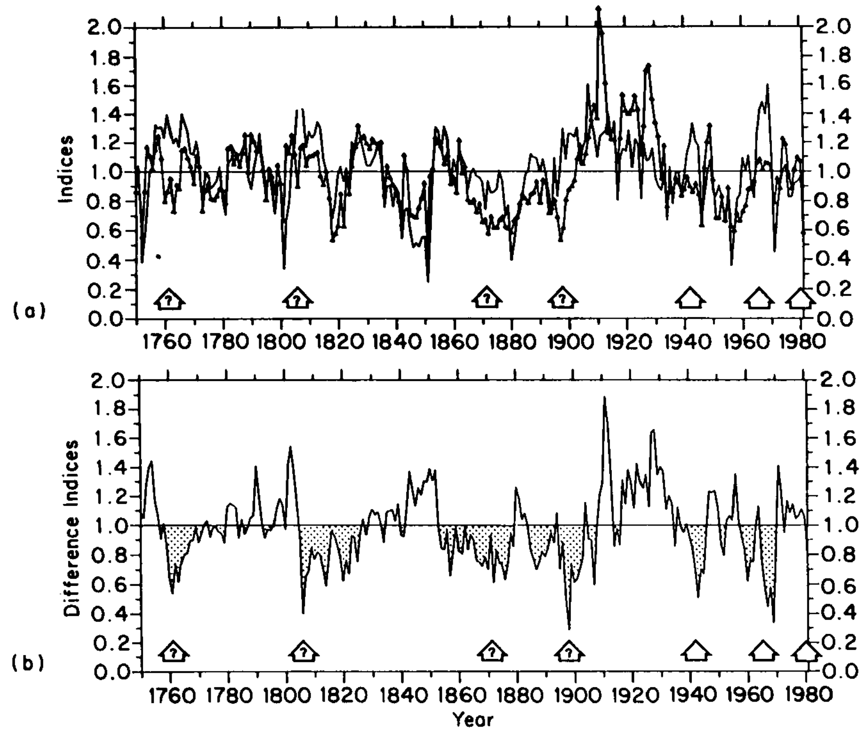


Fig. 6. Comparisons of ponderosa pine (lines without triangles) and Douglas-fir (lines with triangles) chronologies from a northern New Mexico spruce budworm study plot. (a) shows the standardized chronologies and (b) shows the difference series derived by rescaling the ponderosa pine chronology (non-host series) and subtracting it from the Douglas-fir chronology (host series). The arrows with question marks indicate periods of low growth in the Douglas-fir that are inferred to be records of past budworm outbreaks. The open arrows are known periods of budworm outbreak.

The climatic signal in the host chronology was then removed, or at least reduced, by computing the "difference" chronology (Figure 6b). This chronology was computed by subtracting a rescaled version of the non-host chronology from the host chronology (Nash *et al.*, 1975; Swetnam *et al.*, 1985). There are three periods of known budworm outbreak after the 1900s (shown by open arrows in Figure 6). The first two outbreaks are visible as low growth periods (difference indices less than 1·0) during the early 1940s and 1960s. The duration of these low growth periods, and the years of lowest growth, correspond very well with historic documentation of budworm defoliation in this area. During the most recent outbreak, defoliation of trees did not exceed 10% of current years foliage until 1980, and a growth reduction (index value less than 1·0) does not appear until 1981, the last year sampled.

The positive differences following several of the inferred outbreaks reflects an increased growth in the host trees that is not matched in the non-host trees. This phenomenon is probably due to opening of the stand through budworm induced mortality or thinning of crowns of competing trees. The non-host trees were sampled from a pure ponderosa pine stand growing nearby, so these trees would not have benefited from mortality or thinning of host trees. The positive differences may also be a result of other unidentified systematic differences in the growth response of the host and non-host trees. However, analysis of the ring-width series and age class data from this stand provides strong evidence that the inferred outbreak in the 1890s resulted in considerable mortality, followed by growth release of survivors (thus, the large positive differences in the 1910s and 1920s) and establishment of a younger age class of trees (Swetnam, 1987).

The results of this study indicate that as many as nine spruce budworm outbreaks have occurred within southern Rocky Mountain mixed conifer forests since 1700. The average duration of budworm induced low growth periods was about 13 years and the period between outbreaks (period between initial outbreak years) was about 35 years. Although no apparent change in the frequency of outbreaks was observed, the pattern of outbreaks was noticeably different in the twentieth century compared with earlier periods. When chronologies were compared among all sampled stands the timing of initial and maximum growth reduction years of outbreaks was relatively non-synchronous prior to 1900, but they were markedly more synchronous during the twentieth century. This evidence suggests that spatial and temporal pattern of pre-1900 budworm outbreaks was relatively patchy, while post-1900 outbreaks were more widespread or coincident in time among the stands.

One explanation for these results may be derived from the perspective of "patch dynamics" (Pickett and White, 1985) and the recognition that disturbance regimes, forest structure, and forest dynamics are intimately linked. For example, consider the following historical observations: the structure (age distribution, and species composition) of mixed conifer forests in many areas of the southern Rocky Mountains has been altered by human activities, especially through fire control and timber harvesting (Peet, 1981; Veblen and Lorenz, 1986). Elimination of periodic surface fires has led to increased stand density and multi-level canopies through establishment of tree seedlings that otherwise would have been killed by surface fires.

Timber harvesting has primarily involved removal of the non-host pine species, which has led to stands composed of a larger host component than was present in pre-1900 forests. Dense stands dominated by host species are known to be highly susceptible and vulnerable to budworm infestation. Thus, the general pattern of development of these forests has been toward greater homogeneity across the landscape. This is not to say that the age structure or species composition is necessarily less heterogeneous within stands, but that stands throughout the region are more similar in structure to each other than they were before the settlement era. Owing to widespread tree establishment, stands are now also more closed and continuous. In contrast, the structure and spatial distribution of pre-1900 forests was almost certainly more patchy. Indeed, the patchiness of these stands was created by, and interacted with, the natural disturbance regimes of these ecosystems, including fire and insects. The basic interpretation is that a patchy pre-1900 forest structure favored a patchy disturbance regime, and vice versa, but now forests are less patchy and less open with larger areas covered by contiguous, dense host stands and this has led to a less patchy disturbance regime (i.e. larger outbreaks).

There are many additional potential uses of disturbance chronologies derived by tree-ring analysis, such as the budworm history described above, which have not yet been explored in any depth. For example, studies of the interactions of climate, and disturbances (especially fire and insect outbreaks), and the influence of disturbances on the dynamics of forest populations could greatly benefit from the long historical perspective provided by dendroecology. Accurate long-term disturbance chronologies in combination with forest structure data will also be most useful in development and/or testing of forest dynamics models (e.g. Shugart, 1984, 1987).

B. Studies of Forest Decline

Dead and dying conifers have been observed in scattered high elevation locations in the eastern United States and in more widespread areas in northern and central Europe (Johnson and Siccama, 1983; Tomlinson, 1983; Bormann, 1985; Blank, 1985; Hornbeck and Smith, 1985; Zedaker *et al.*, 1987). This phenomenon has generated considerable concern among the general public, as well as forest managers and scientists. It has stimulated interest in research to determine the probable causes and consequences of the problem (Morrison, 1984; McLaughlin, 1985; Smith, 1985).

Acid deposition has been suggested to be a causal agent of the observed forest decline in some areas. The first tree-ring evidence suggesting that there may be a link was reported by Jonsson and Sundberg (1972) for areas in Sweden, but they were careful to state that their results were not conclusive. In a follow-up investigation Jonsson and Svenssen (1982) found that their tree-ring evidence linking acid deposition and forest decline was even more tenuous than originally thought. There was no indication of either positive or negative growth due to acid deposition; nevertheless, this work did focus world-wide attention on forest decline and tree-ring analysis.

Several other tree-ring studies have attempted to identify the timing, severity and causes of observed forest decline (Cogbill, 1977; Johnson *et al.*, 1981; Johnson and Siccama, 1983; McLaughlin, 1984), but the tree-ring evidence presented in these studies lacks the precision expected from dendroecological analysis and was therefore unconvincing or inconclusive. Some of the difficulties with these studies is due partly to the regional nature of forest decline, which poses the problem of finding adequate control tree-ring data to compare to the air pollution data set. It also appears that a number of the principles and practices of dendroecology were ignored or improperly applied. Often no mention is made of crossdating, and many of the illustrations show the inconsistent variations that would be expected to result from improperly dated samples (see Figure 4).

McLaughlin *et al.* (1983) acknowledge the importance of dendroecology in their review of the forest decline problem. However, they presented data consisting of averaged ring-width series uncorrected for age, competition and stand history variations, and it was not clearly stated that the rings were crossdated. Similarly, photographs of tree cores and cross sections showing growth increment reduction from the pith to the bark have been presented as suggestive evidence of declines in growth of pines in the southeastern United States (Knight 1987; Sheffield and Cost, 1987). Though some of these data may be based on large numbers of measurements, they can not be considered evidence of forest decline until the effects of tree age, past forest history and climatic variations on growth have been dealt with (Sheppard and Jacoby, 1987; also see Zahner and Myers, 1987 for one approach to this problem).

1. Point Source Pollution

Dendroecological investigations of point source pollution and its effects on tree rings usually have resulted in more definitive and statistically supportable results than the above mentioned studies. Significant declines in ring width that are unrelated to age and climatic factors have been associated with rising emission levels and the increasing proximity of smelters or factories (Fox, 1980; Heikkinen and Tikkanen, 1981; Fox *et al.*, 1986). One study on arid-site trees from Nevada reported an increase rather than decrease in growth associated with smelter emissions (Thompson, 1981). This could have been a fertilizing effect of acidic deposition through nutrient release in the alkaline desert soils of the region, but this possibility was not tested or confirmed by any follow-up investigation. Other studies have related ring density changes to emission levels (Keller, 1980; Kienast, 1982; Kienast *et al.*, 1981; Schweingruber *et al.*, 1983; Yokobori and Ohta, 1983).

A strategy employed in point source pollution studies involves the sampling of forest stands at varying distances from a known emission source but otherwise affected by similar site, stand-history, age and climatic variations. For example, Fox *et al.* (1986) sampled the ring-width variations in trees from five stands of western larch (*Larix occidentalis* Nutt.) chosen at different distances down wind from the lead/zinc smelter at Trail, BC, Canada. Three control stands outside the area of known pollution were also sampled and studied. Two cores were extracted from a number of trees in each stand.

All materials were crossdated, the ring widths were measured, and these values were standardized by dividing by the sample mean so that any information in the growth trends was not removed by standardization. The chronology values of the control trees, and two lagged values from them, were used in regression models to estimate and remove the climate component from the pollution effects. Separate analyses were performed for years before and after installation of two tall stacks, for drought and non-drought years and for years prior to initiation of smelting.

For the period after smelting began, but before stack installation, the growth variation in the affected trees explained by the pollution decreased with the increasing distance from the smelter. Concomitantly, the variation explained by the climatic controls increased with distance. As pollution levels became more and more limiting to ring growth with the increasing proximity of the smelter, there appeared to be less opportunity for climate to be limiting. After pollution abatement procedures were installed, this pattern was reversed, with the greatest recovery observed in the trees that were nearest the smelter. No other environmental changes or stand conditions could be found to explain the large and systematic growth changes that were measured.

It is often difficult to ascertain what portions of the trend in a tree-ring chronology can be attributed to stand history, aging of the tree, long-term climatic variation or atmospheric pollution. When this happens, some of the variance caused by pollution may be removed in the process of standardization.

Nash *et al.* (1975) developed a procedure that can identify the signal due largely to climatic variation, remove it from the variance due to other effects and then restore the original ring-width variations without the effects of climate. The procedure begins with the usual standardization, which fits a growth curve and divides the width by the growth curve estimate to obtain the index. The climatic signal is estimated from the average yearly value of a number of chronologies from trees of the same species, age, and site characteristics, but from sites outside and surrounding the area that had the pollution effect. The normalized values of the averaged chronology are subtracted from the normalized indexed series. This difference is then multiplied by the value of the growth curve that had been fitted in the original standardization to produce the original ring widths minus the effects of climatic variation.

2. *Regional Forest Decline in North America*

Peterson (1985) and Peterson *et al.* (1987) report dendroecological studies of

Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) in Sequoia and Kings Canyon National Parks, California, that were exposed to moderate concentrations of ambient ozone (mean hourly concentrations of 6 to 9 ppm, and maximum hourly concentrations of 15 ppm during the late afternoon). Ozone is usually regarded as a regional air pollution problem (Peterson *et al.*, 1987). Dated ring-width chronologies from exposed trees were compared to dated chronologies from control trees growing in more remote sites where ozone exposure had not been reported. No significant difference between the chronology values was noted before 1965. After that date, the ozone exposed chronology values were approximately 10% lower, and the difference was statistically significant. Even though the ozone damage is classified as a regional pollution problem (Peterson *et al.*, 1987) in that it occurs over large areas, mountain terrain and wind patterns appeared to protect some trees, which Peterson and his colleagues used as control chronologies for the ozone effect.

Ozone damage to conifers in southern California has been extensively studied (Miller, 1973; McBride *et al.*, 1975; Miller, 1985). However, dendroecological techniques have not been applied in that area with the exception of one study (Gemmill *et al.*, 1982) reporting on crossdated tree-ring chronologies from an ozone-stressed forest.

In the eastern United States and Europe it may be more difficult to find control sites for the study of forest decline than it was for the study of ozone effects in California. If the hypothesized air pollution effects are widespread, trees free of the effects that could serve as controls might simply be unavailable. In addition, few, if any, long-term records of emissions on such a large scale are available. This limits the possibility of comparing rings in affected and unaffected trees during the same time period, and it limits the use of calibration. Differences in species or individual tree tolerance to various emissions may offer a possibility, but such an approach has not been reported yet.

The species and habitats that are available from the forest decline areas in the eastern United States and Europe may have a number of less desirable dendroecological characteristics than those in the more arid North American West. Some of the problems that may be encountered: (1) the climatic signal in the ring-width variations may be weaker and the noise stronger (Cropper, 1982), which would make crossdating more difficult to detect and apply (wood density variations exhibit a stronger climatic signal (Schweingruber *et al.*, 1978a) and this is one reason why densitometric analysis is considered so important in these areas); (2) the stands are more densely stocked, with more possible interactions between stand dynamics, aging of trees and pollution; and (3) the growth response to the various controlling factors may involve lags lasting for several years, resulting in autoregression and possible nonlinear or synergistic influences.

The comparison of growth before and after the onset of pollution is one promising research strategy for the study of regional forest decline. However, the diminishing ring width associated with increasing age of a tree could resemble the hypothesized forest decline effect. In addition, the ring-width changes associated with increasing age may vary greatly from tree to tree and from one stand to the next in these dense forests (Cook, 1985, 1987). Flexible standardization curves using cubic splines may help to resolve some of this difficulty, but if too much flexibility is used, one runs the risk of removing the pollution signal along with the age-related effects.

Sample stratification to include only the oldest trees, even though they are widely scattered throughout the forest, might be preferable to using many younger individuals from the same local habitat (Ashby and Fritts, 1972). The age-related growth changes in old trees are more consistent, smaller and less likely to resemble the hypothesized growth decline.

The primary objective of dendroecological studies, in the eastern United States (Cook, 1987; Cook *et al.*, 1987), in Germany (Eckstein *et al.*, 1984; Greve *et al.*, 1986) and in Switzerland (Kienast, 1982) was to determine if an exogenous growth decline could be measured. Comparisons were made of the chronologies between what were thought to be pre- and post-decline periods.

The growth-climatic variations in the chronology were calibrated using the pre-decline chronology and climatic data for the corresponding period. Climatic information from the post-decline period was applied to the post-decline chronology to estimate what the chronology would have been if it was affected only by climate. If the chronology had been adequately replicated, dated and standardized, then a departure of this estimate from the actual chronology should not be the result of aging, stand changes or climatic variation. If there is no evidence that nonclimatic factors such as fire, insect infestation, cutting history or some other factor can explain the departure, then pollution damage can be inferred to be the probable cause of the effect. Also, if the growth–climate relationship is significantly stronger before the decline than after it, the reduced strength may be considered as evidence for an increasing influence of nonclimatic factors, such as pollution, on ring growth. Some of these studies are described in detail to illustrate this type of application.

Cook (1987) applied dendroecological techniques to the problem of forest decline in the Adirondack Mountains of northern New York State. He obtained a stratified sample from 20 dominant and co-dominant trees, two cores per tree, of red spruce (*Picea rubens* Sarg.) growing at an elevation of 1150 meters and only 27·5 km from Whiteface Mountain where symptoms of red spruce decline were reported by Scott *et al.* (1984), and Johnson and Siccama (1983). Three cores were eliminated as they had unusual growth distortions (reaction wood) due to changes in the direction of stem growth that were unique to those individuals. The remaining 37 cores were crossdated, the ring-widths measured, the measurements converted to standardized indices and the indices averaged to obtain a chronology.

Cook applied his linear aggregate model (Section IV) to this growth decline problem. He described experiments with different statistical techniques to estimate the growth curve and apply it to standardization (Cook, 1985). Two estimates of the chronology were obtained. One was equivalent to using standardization techniques described in Section IIIE. For the other estimate, time-series techniques (Box and Jenkins, 1976; Cook, 1985; Holmes *et al.*, 1986) were applied to the ring-width data to remove excessive low frequency variations and autoregressive relationships. The terminology of time-series modeling calls this procedure "prewhitening", i.e. unusually large amounts of long-wave variations ("red noise") are removed to produce a "white noise" time series with equal amounts of variations at all wave lengths. Therefore, Cook applies the terms "unwhitened" and "prewhitened" to the first and second estimates of the chronologies. Cook reported that the mean chronology for the period common to all trees, 1837–1964, had an s/n ratio of 21·7:1.

Calibration equations for predicting the yearly chronology values were then developed using monthly divisional climatic averages from the prepollution period of 1890–1950. These data were the 19 candidate predictor variables. They were the monthly mean temperature from March one year before the annual ring growing season through September at the end of the ring growing season. Stepwise multiple regression analysis was used to select a subset of significant monthly climate predictors of the ring-width chronology. The equations for the unwhitened and prewhitened chronologies accounted for 50·2% and 53·8% of the chronology variance, and the climatic predictors were consistent with other reports in that temperature during and prior to the growing season were associated with growth (Conkey, 1982a; Cook, 1982). The prewhitened calibration gave slightly better growth estimates (see plots in Fig. 7).

The equation was applied to the climate data for 1951–1976 to estimate the ring-width chronology. The 1951–1967 period had no apparent trends that may have been due to the pollution component, so these data provided an independent test of verification. The 1968–1976 interval provided a test for possible effects of pollution.

The results are shown as plots in Fig. 7. The statistical estimates of the two equations mimic the chronology variations in both the calibration and verification periods. The calibration was excellent for this kind of data, and the independent verification statistics were found to be more significant than would be expected by chance variations. However, the amounts of disagreement between the estimates and the chronology values increase from 1968 to 1976, the post-pollution period.

As would be expected from these results, there are certain years in the

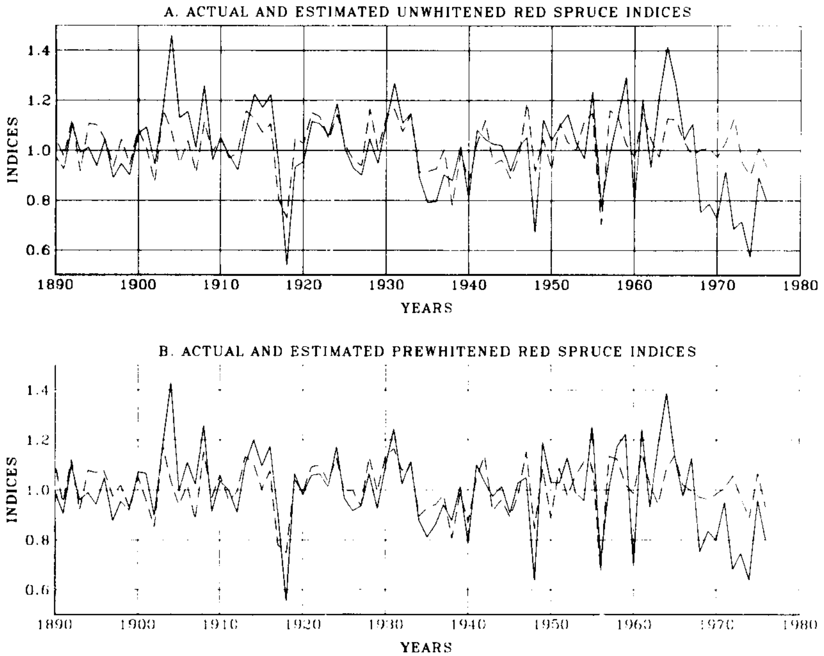


Fig. 7. Actual and estimated red spruce chronology values based on a temperature response model. The model was developed using the 1890–1950 data. Model predictions run from 1951 through 1976 (from Cook, 1987).

calibration period when estimates are substantially different from the chronology (e.g., 1904–1906, 1918, 1935–1936, 1948, 1959, 1963–1964). However, the residuals from the regression are more or less random until the 1960s. (A test of randomness was not reported.) After 1967 the chronology values are always lower than the estimates.

The estimates from a complex nonlinear equation with more variables might have approximated the actual biological relationships more closely. However, fewer degrees of freedom would have remained, thus reducing the reliability of the independent estimates.

The high calibrated variance, the significant independent statistics and the random variation of the residuals before but not after the 1960s, support the conclusion that factors other than the climatic variables that were calibrated, are responsible for the growth decline starting in the 1960s. While several alternative explanations are possible, acid deposition and other forms of pollution must be considered as possibilities. Pollution was also suggested by other investigations (Scott *et al.*, 1984; Johnson and Siccama, 1983).

Cook (1987) acknowledges: "These results indicate that the observed ring-width decline of red spruce in this stand cannot be explained by the verified climatic response models developed here. As a result, a change in the growth environment of these trees has probably occurred, which had a stand wide impact on the sampled trees." He goes on to emphasize, however, that climatic effects (representing variables other than the monthly climatic data used in the calibration) still cannot be excluded as possible causal agents in the observed ring-width decline. One hypothesis is that winter foliar damage might be involved (Friedland *et al.*, 1984). In this case it is possible that a climatic change may have led to a higher frequency of winter freeze damage events since 1967, or it is possible that red spruce have recently developed a heightened sensitivity to winter freeze damage that could be related to a predisposing stress such as acid deposition or nitrate fertilization (Friedland *et al.*, 1984). Cook (1987) suggests that a test of this hypothesis should involve both an examination of recent winter climate in relation to conditions necessary to cause freeze damage and studies of the long-term occurrence of this phenomenon.

Later, Cook *et al.* (1987) took this research one step further. They used ordinary least-squares for estimating climatic response models for forest decline studies in different stands of red spruce throughout the Appalachian Mountains. In northern Appalachian trees, the regression models were significant up to 1976, the last year with no observable pollution effects, but not over the 1968–1976 period when there was a marked growth decline and pollution. More importantly, a test for bias revealed there was a significant overestimation in the forecast of radial growth. This suggested there was a change in the relationship between red spruce tree rings and climate after 1967 which might have been the result of climatic change or a new form of stress, such as pollution.

Results from southern Appalachian trees supported the results from the northern trees, except that the climatic relationship with temperature was weaker, probably because important climatic variables such as precipitation had not been considered. The bias in the decline period was about half that found in the northern Appalachians.

The chronologies from 21 red spruce sites in New York and Vermont were examined very closely to determine whether the relationship between tree rings and climate during the most recent 20-year period examined was anomalous compared to earlier periods or whether the bias could be attributed to the standardization of the tree ring data (Cook *et al.*, 1987). They therefore removed all trends from the tree-ring data and compared these data to a regionally averaged temperature record that had been estimated back to 1820. The climate response model was calibrated using the data from the 1885–1940 time period, leaving ample data for two pre-decline verification periods, 1856–1884 and 1941–1960. The 1961–1981 interval was set aside as the decline period. Between 12 and 55% of the tree-ring variance was calibrated, and the most commonly selected predictors were July and

August temperatures of the previous growing season (negatively) and December and January temperatures prior to the growing season (positively). Verification statistics indicated that the climatic response models were, in general, quite time stable up to 1961 even though the variance calibrated was sometimes low. After that time little or no relationship with climatic data could be found.

They also considered possible effects of extreme temperatures in August and December by using all years when the standard normal deviates exceeded the 0·9 probability level and plotting them as indices of stress. The occurrence of stressful years was notable in the 1870s, the late 1930s and the late 1950s to early 1960s. There were also periods of abnormally high red spruce mortality. However, a period of noted high spruce mortality in the 1840s and 1850s does not correspond with their stress index results.

They believe that their results suggest that "abnormally high climatic stress may be acting as a predisposing factor or cause of red spruce decline, both past and present." They had not ruled out the possibility that some additional stress factor was present, such as air pollution. However, they caution that the question of survivorship bias in the analysis should be investigated. "It is possible that had the red spruce been sampled in 1880s, the relationship to climate would have broken down due to the inclusion of trees that eventually died from the mortality episode." Thus the role of anthropogenic pollution in causing or intensifying the present decline of red spruce remains uncertain. Nevertheless, it is clear that dendroecology has provided new insights and understanding of this problem, and like most seminal research, it has suggested new questions and areas of investigation.

3. Forest Decline in Europe

Extensive dendroecological investigations of regional forest decline problems have been conducted by dendrochronologists in West Germany (Eckstein *et al.*, 1984; Eckstein, 1985; Greve *et al.*, 1986). Their work has involved tree-ring sampling along suspected pollution gradients, study of sulfur and fluoride content in spruce needles as indicators of such gradients, and dendroclimatic analysis to determine if climatic changes such as drought could explain the observed growth reductions. Their findings have been similar to those of Cook and his colleagues in the eastern United States, in that growth reductions observed during modern portions of tree-ring chronologies (generally post-1940) cannot be explained by the climatic response models calibrated for earlier periods. Evidence of greater growth reductions in areas of West Germany with higher levels of suspected pollution than in areas with lower suspected levels seems to support, but does not prove, a cause and effect relationship between air pollution and tree growth reduction.

As an example we will describe dendroecological studies of forest decline in Switzerland. Kienast (1982) describes investigations of possible fluoride emission damage in the Rhône Valley in Switzerland. He used annual rings to ascertain in which years damage occurred and to estimate the radial growth loss. X-ray techniques were used to obtain a continuous wood density profile (Lenz *et al.*, 1976), and five parameters per ring, including width and density measurements, were derived for subsequent analysis. Instead of fitting the standardization age curves to the entire length of record, the age trends were estimated using the longest possible emission-free period (1874–1940). The trends in these curves were extrapolated through the period affected by pollution (1941–1979) (Pollanschütz, 1971). The indices were obtained and the standardized chronology calculated. The calibration between the chronology values and climate factors of temperature and precipitation used regression methods described by Kienast (1982) and response function techniques described earlier in this paper. The calibration was applied to the pre-pollution period and the equation was then applied to climatic data for the pollution period to estimate the expected growth for 1941–1979 due solely to climate. No mention was made of independent verification tests.

Comparisons among the densitometric measurements largely confirmed the visual dating and observations. On average, damage was most clearly established for latewood width, followed by total ring width, then by earlywood width and then maximum latewood density. The loss in growth over the pollution period was 20–30% of the ring width for the calibration period and 30–40% of the latewood width over the same period. No explanation was given for these differences.

Figure 8 includes two plots for maximum latewood density and the corresponding estimates obtained from climate. One plot is for an undamaged tree and the other for a damaged tree. The data were calibrated over the first period and the calibration applied in the extrapolation period to estimate density variations due solely to climate. The difference between the actual measurement and the estimated value is shaded to emphasize values indicating a probable pollution effect.

Kienast (1982) summarizes his results from the Rhône Valley as follows: "The pine forests of the Rhône Valley are severely damaged. Possible causative agents are fluoride and other harmful gases such as SO_2, HCl and NO_x in the emissions of nearby aluminum smelters and chemical plants. Droughts and aging may also have contributed to the damage ... Growth disturbances occurred most commonly during the droughts that began in 1938 when a new aluminum smelter was built in the main valley. It stood in the mainstream of the prevailing winds and was without precipitators until 1965. The harmful emissions of the late thirties may have damaged the trees to such an extent that they could no longer withstand natural stresses and finally died 30–40 years later. Although the fluoride emissions are not

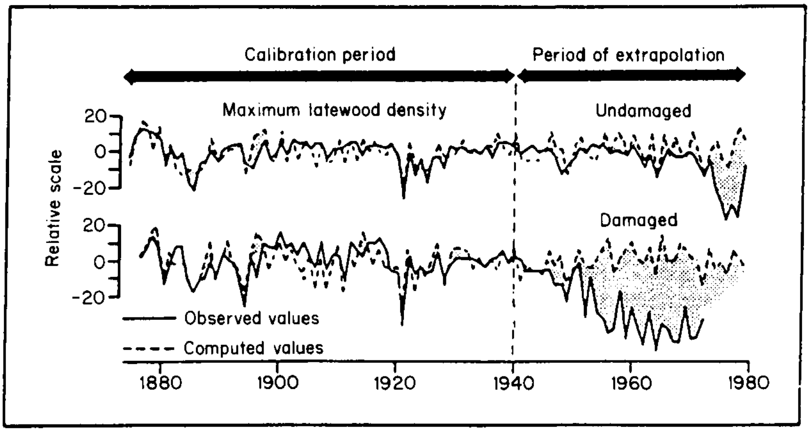


Fig. 8. Estimate of damage from indexed maximum density plots of two pine trees from Valais, Switzerland. The computed curves which are superimposed on the measured values were calculated from meteorological data and the difference which is shaded shows a possible pollution effect (from Kienast, 1985).

causally related to the forest damage, they provide a valid explanation of the results."

Kienast's study was an intensive analysis directed at point-source air pollution. It was a part of a larger effort concerned with a survey of possible regional decline in Swiss forests (Schweingruber *et al.*, 1983). This work is described below.

Dendroecological techniques were used to help answer the following questions. How has the vitality of tree growth changed from earlier times? Where and when did it occur? How extensive are the damaged areas? New rapid sampling and analysis techniques were needed to survey and map the ring changes over such a large area. They included a simple visual dating method that used the matching of "pointer" rings with narrow or reduced latewood bands that were known to occur in particular years. Cores were sampled and ring sequences dated in the field using the "pointer" rings for time control. Major changes in ring structure were visually identified from the dated series, and simple diagrams and other graphical techniques were used to record the information while at the collection sites.

The data from some 3800 cores and stem disks from firs and pines in northern Switzerland were recorded in this manner. From 75 to 86% of the materials were successfully dated by the "pointer" method. This is an acceptable margin for temperate forests in Europe. The "pointer" rings in subalpine trees often were associated with cold, moist and cloudy summers. For trees at lower elevations and dryer sites, the pointer rings were frequently associated with warm and dry summers. Only in the extremely dry years of 1921 and 1976 could pointer rings be identified in all stands that were sampled (Schweingruber *et al.*, 1983; Schweingruber, personal communications).

These well-dated materials established that disturbances increased markedly in the 1940s, especially in 1942, 1944 and 1947 (Kontic *et al.*, 1986). Mortality of trees in the study areas peaked several years later. They found that diseased trees exhibited an abrupt reduction in annual growth increments that was more than 50% in most cases. It was usually easy to recognize the first year in which the injury occurred.

The decline in ring-width or latewood density, however, begins at different times for different species and for different locations in Switzerland. It begins approximately at the turn of the century in the alpine region of central Valais with reduced growth of Scots pine (*Pinus sylvestris* L.) reflecting local pollution caused by industrialization. This general pattern is overlaid by the effects of climatic variation. More trees showed growth reductions apparently due to pollution in drought periods than in moist periods. The growth decline does not appear in silver fir (*Abies alba* Mill.) growing in the Central Plateau, until the 1940s (Schweingruber *et al.*, 1983). In the heavily populated areas north of the Alps, extensive damage was present in all the sites they investigated (Schweingruber, 1986). Firs that were examined in the southern Alps were undamaged (Schweingruber, personal communication).

In the Valais area of Switzerland, the decline in latewood density and ring width were observed from 3 to 6 years earlier than the appearance of unhealthy crowns (Kontic *et al.*, 1986). The possible causes of these differences are now being investigated. The initial changes in the crown may begin with increased shedding of the needles at the same time as the change in ring structure, but the crown may not appear unhealthy until several years later. These results suggest that changes in ring structure may be a more reliable indicator of the beginning of forest decline than the crown appearance (Schweingruber, personal communication).

The general forest decline as proposed by foresters could not be fully confirmed because the density of the crown does not always relate to abrupt growth changes. Schweingruber and his colleagues observed a combination of climatic effects and apparent disease, but they were uncertain as to whether pollution was the cause of abrupt growth changes, except in heavily polluted areas (Schweingruber, 1986).

C. Climatic Variability and Change

It was shown in Section I that a tree ring reconstruction of past hydrologic variability can provide a longer time perspective for viewing ecological problems than is generally available from short instrumental measurements.

In like manner, dendroclimatology also can provide a time perspective that generally focuses on environmental variations related to climatic variations from one year to the next. Thus, tree ring data provide paleoclimatic information over time scales representing years to centuries (Fritts, 1971). Most other paleoclimatic data can not resolve annual variations, and many respond to variations no shorter than a century.

In some situations and with some species such as high altitude *Pinus longaeva* Bailey and *P. flexilis* James, the tree-ring chronologies can span more than 1000 years, providing long records of yearly climatic variations (Ferguson, 1968; LaMarche, 1974, 1978; Graybill, 1987). A thorough discussion of dendroclimatology is beyond the scope of this chapter. However, we will cite some important reviews, comment on a few aspects relevant to dendroecological applications, and conclude with concerns about the adequacies of climatic models, including possible contributions of dendroclimatic studies in a systems approach to the problems of climatic change.

A general treatment of dendroclimatology can be found in Fritts (1976). Later developments and discussions on various methodologies are reported by Hughes *et al.* (1982). Schweingruber (1983) summarizes the field from the European point of view and describes new opportunities provided by wood density measurements. Brubaker and Cook (1983) and Stockton *et al.* (1985) summarize the field in a geological and meteorological context with considerable attention given to the world-wide distribution of climatically responsive tree-ring chronologies. Kairiukstis and Cook (in the press) have collected a series of papers which summarize some current methodologies. This could be a landmark volume, however, caution about the validity of some methods may be warranted. For example, some Soviet dendrochronologists apply Fourier analysis to existing tree-ring chronologies to forecast future variations but it is not clear from their papers whether such projections can be validated by independent verification.

Tree-ring chronologies from all continents except Antarctica are available for modern dendroclimatic analysis. ARMA modeling and both simple and multivariate regression techniques have been used for reconstructing past environmental variations (Fritts *et al.*, 1971, 1979; Fritts, unpublished; Stockton *et al.*, 1985; Guiot, 1986; Briffa *et al.*, 1983, 1986). Many involve the climate at one location or an average over a region (Briffa *et al.*, in the press a) and are based upon ring-width variations (Hughes *et al.*, 1982). However, analysts are beginning to deal with spatial variations in both tree-ring chronologies and climatic variables (Fritts *et al.*, 1971, 1979; Fritts, in press; Schweingruber *et al.*, 1978a; Briffa *et al.*, 1988a). Wood density is also being exploited for reconstructing past climatic variations (Briffa *et al.*, 1988b).

Sometimes dendroclimatological inferences based solely upon simple observation of marked anatomical features can lead to valuable insights about past ecological conditions. For example, LaMarche and Hirschboeck

(1984) note that frost injuries within annual rings of high altitude bristle cone pine in southwestern North America are significantly associated with years of major volcanic eruptions. They have now demonstrated that the rings with frost damage (called frost rings) represent new, independent proxy records of climatically important eruptions occurring during the past several thousand years. They report a notable occurrence of frost rings in 1626 BC which they attribute to the dust veil and the associated widespread cooling from the eruption of Santorini in the Aegean Sea (Lamb, 1977). This date was at first highly criticized by archeologists, who preferred the more conventional 1500–1450 BC date for the eruption based upon ceramic and artefact chronologies. However, LaMarche and Hirschboeck argued that their frost-ring date falls well within the error range of radiocarbon dating of organic artifacts and that the archaeological dates were more likely to be the problem. Hammer *et al.* (1987) recently announced an ice-core date of 1645 BC for the eruption; and this was followed by a review of the archeological evidence by Betancourt (1987) with the conclusion that the radiocarbon and associated tree-ring dates appeared to have been correct all along.

These arguments stimulated Baillie and Munro (1988) to examine more closely the crossdated ring-width data from bog oaks (*Quercus* sp.) growing under poorly drained conditions in Northern Ireland. They report that extremely narrow rings can be noted in these oak trees for the same dates suggested for major volcanic eruptions already demonstrated by other methods. They examined all of their data using an index of ring narrowness in bog oak chronologies from 5289–116 BC. A number of periods with narrow rings were identified, including a conspicuous interval with narrow rings in the 1620s BC coinciding with the frost ring date for Santorini. Baillie and Munro point out that the more precise tree-ring dates should take precedence over the ice-core date because the tree-ring dates can be shown to be internally more consistent.

Baillie and Munro conclude, "These results may have implications for interpreting the effects of volcanic dust veils. Even if volcanic ash clears from the stratosphere after two–three years, the Belfast tree-rings show effects which last much longer (*ca.* 10 years), suggesting than an initial trigger event (flooding?) caused severe long-term problems for trees growing on bogs. Other biological systems may show similarly extended responses. There are possible implications for the impact on human societies, which might suffer the effects of runs of bad harvests, poor pasturage and impeded communications."

Dendroclimatic reconstructions can be obtained for a single climatic record or for multiple records. Some of these multiple records can provide information on spatial variations in climate from spatial variations in tree-ring chronologies (Fritts, 1976; Hughes *et al.*, 1982; Stockton *et al.*, 1985).

Seasonal to century-long climatic variations can be reconstructed and mapped over both space and time using various dendroclimatic methods. Dendroclimatic reconstruction of these kinds can reveal synoptic scale climatic features and suggest certain ecological consequences of these variations (Fritts, in the press).

However, there is no simple solution to this complex ecological problem. Tree growth from a variety of sites representing different topographic localities, as well as from different species, must be related to a geographic array of climatic data. Fritts *et al.* (1979) and Fritts (unpublished) use stepwise canonical regression to deal with this problem. The tree-ring width variations from 65 arid-site chronologies throughout western North America are calibrated with 20th century temperature and precipitation records from the United States and southwestern Canada. A systematic analysis and elimination procedure was used to select the optimum calibration models from a variety of models of different structure. For example, the models differed as to whether or not ARMA modeling was applied to the tree-ring data before calibration. Different-sized grids of climatic data were calibrated to evaluate the effects of distance from the trees on the climatic reconstructions. Principal component analysis of tree-ring and climatic data was used to reduce the number of variables and to orthogonalize the variations; and different numbers of principal components were used to vary the size of the calibration equation. Different lags and different numbers of predicted principal components were entered into regression, a stepwise selection of variables was used to retain only the significant canonical variates, autocorrelation of the residuals was computed and used to adjust the degrees of freedom in the statistical analyses, and most important, verification statistics using all available independent climatic data from the 19th century were used to select the optimum model structure.

At each step in the analysis, only model structures that resulted in reconstructions with significant calibration and verification statistics were retained for the next step of the analysis. The choice depended first upon which models had the most significant statistics and second upon the ecological reasonableness of the model (Fritts *et al.*, 1979; Fritts, in the press) particularly regarding the lag of growth behind the climate input as opposed to preceding it. The simpler of two models with comparable statistics was selected. The results are available from the author on floppy disk.

The first calibrations used monthly, seasonal or annual climatic data to evaluate the response structure. Only seasonally averaged climatic data could be successfully calibrated. The annual climatic data appeared to contain too little meaningful information and the monthly intervals were too short a time span with too many predictors for the spatial analyses. Thus, the climate was calibrated one season at a time with the ring-width variance. At this stage in the analysis, unmodeled variance associated with the effects of climate in other seasons was simply carried along as part of the error variance.

Often several verified models of quite different structure produced seasonal reconstructions of comparable quality. This suggested that the reconstructions from several well verified models (Bates and Granger, 1969) might be combined to improve the statistical estimates. Thus the most promising combinations of two to three well-verified models were tested using the same calibration and verification climatic data used in the original analysis. Combinations of more than three models failed to show significant improvements in verification statistics. For each climatic variable, the combination of two to three models giving the best calibration and verification statistics were selected for the seasonal estimates. The annual values were obtained by summing or averaging the selected combined reconstructions for the four seasons. Calibration and verification statistics that were computed for these data using annually averaged climatic data were far superior to the statistics for the models that were directly calibrated with annual climatic data.

These results are consistent with the idea that the ring-width response of arid-site trees integrates the limiting conditions of climate over the four seasons. The importance of different variables in different seasons can change substantially from site to site and from one species to the next. In addition there were significant lags in growth of one year or more behind the occurrence of climate particularly for summer (July to August), which begins too late in the growing period for there to be a major effect of climate on total width of rings formed in that season.

The annual and seasonal reconstructed temperatures provided more reliable estimates of climate than precipitation. The independent temperature reconstructions span the interval 1602–1900 and extend the 20th century instrumental record for the United States and southwestern Canada to the beginning of the 17th century. This provided a unique opportunity to investigate the effects of volcanic dust-veils on the spatial variations in North American temperature (Lough and Fritts, 1987). Such a study was not possible before the reconstructions had become available because there were too few great eruptions coincident with the period of instrumental data to conduct a spatial analysis.

The beginning (key) dates of the 14 largest eruptions during 1602–1900 were subjected to superimposed epoch analysis to look for a climatic signal associated with the injection of aerosols into the stratosphere and subsequent cooling (Mass and Schneider, 1977; Taylor *et al.*, 1980; Self *et al.*, 1981; Kelly and Sear, 1984). Temperatures for the five years following the key dates were compared to the temperatures reconstructed for the five years prior to the key dates. The differences were calculated and then averaged for all the selected key dates. Monte Carlo techniques were used to assess the statistical significance of these averages. The differences for each data point were mapped to reveal any spatial patterns.

All 24 eruptions were analyzed without regard to the latitude of the eruption, and no significant pattern was noted. The volcanic events were then separated into seven high-latitude eruptions, eight mid-latitude eruptions, and eight low-latitude eruptions. Figure 9 shows the results from these analyses. After high-latitude eruptions there may have been some warming in the central northern United States and cooling in the southeast (Figure 9a), but only three grid-points were statistically significant. For the low-latitude events, the reconstructed warming was significant in the Pacific Northwest and southwestern Canada, and cooling was observed east of the Rocky Mountains to the Atlantic and Gulf coasts. Cooling was most pronounced and significant in the central and some eastern states (Figure 9c). It was concluded, that while annual temperatures decline over much of the United States following low-latitude eruption events, significant and marked warming occurs in many western states.

The pattern of anomalies varied among the seasons. The temperature anomalies reconstructed for winter, spring and summer are shown in Figure 10. Cooling was reconstructed in spring for the central United States (Figure 10b) with 38% of the stations significant. In summer, cooling was pronounced from the Rocky Mountains to the East Coast and significant warming was reconstructed primarily in the western coastal region and adjacent states (Figure 10c). Extensive warming was reconstructed in the West in winter (Figure 10a).

Lough and Fritts (1987) checked other tree-ring data and some climatic reconstructions including high-altitude sites where temperature was expected to be growth-limiting. They also examined some long temperature records and found general confirmation of cooling in the mid-continent and warming in the west, particularly in summer.

The strength of this analysis suggests that the reconstructions provide meaningful climatic information in these temperature reconstructions. They also confirm to some extent the work of LaMarche and Hirschboeck (1984) except that their work dealt with short-lived cold outbreaks at the end of the growing season that froze and injured the cells perhaps during one night. In contrast, Lough and Fritts (1987) reconstructed temperature conditions averaged over seasons to the entire year including a three-year lag after the eruption began.

All of these studies illustrate that the rings from many trees distributed over a wide spatial area can contain information on a variety of climatic variables. They also suggest that there is a detectable vegetational response in North America to low temperatures associated with dust veils from large low-latitude volcanic events. Cooling appears to occur over large areas in the

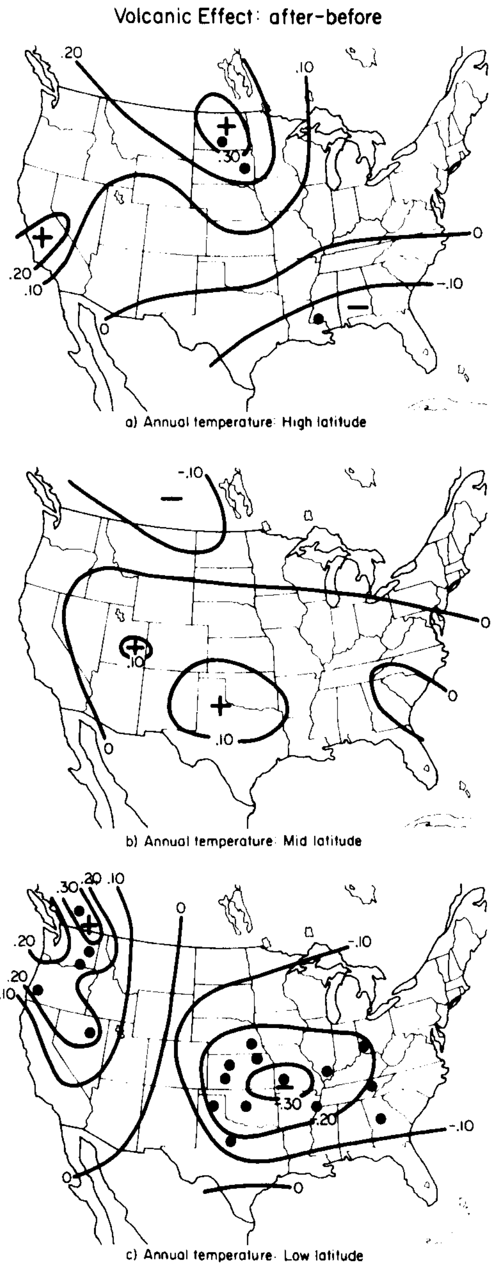


Fig. 9. Average reconstructed annual temperature differences (centigrade degrees) of the average of years 0 to 2 after key dates minus the average of years 1 to 5 prior to key dates for (*a*) high latitude, (*b*) mid latitude and (*c*) low latitude volcanic events. Heavy dots denote stations at which the temperature difference is significant at the 0·95 confidence level (from Lough and Fritts, 1987).

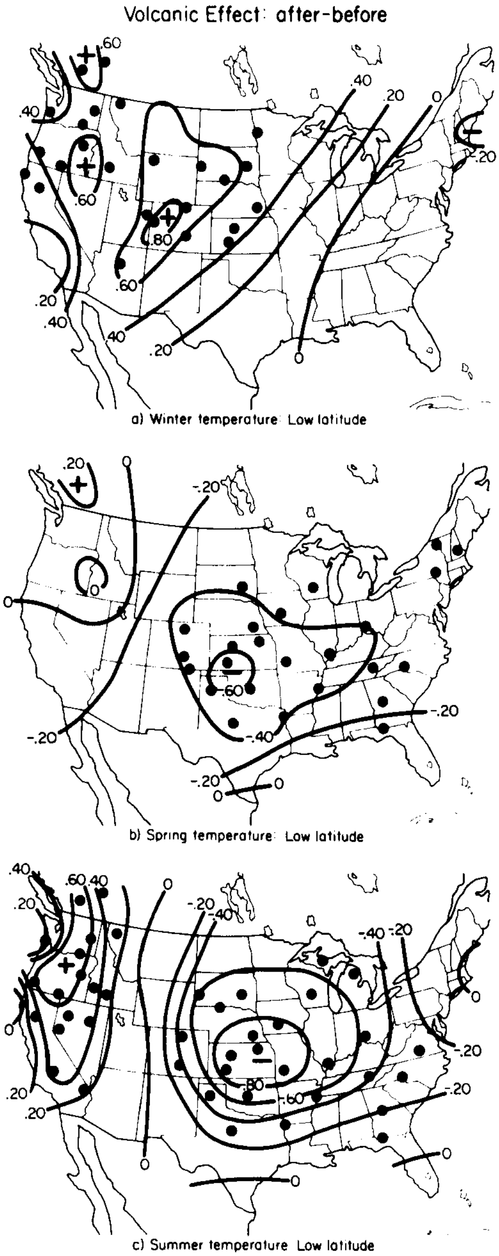


Fig. 10. Average reconstructed temperature differences (centigrade degrees) of the average of years 0 to 2 after key dates minus the average of year 1 to 5 prior to key dates for low-latitude eruptions for (*a*) winter, (*b*) spring and (*c*) summer. Bold dots denote stations at which the temperature difference is significant at the 0·95 confidence level (from Lough and Fritts, 1987).

United States in spring and summer for 0 to 2 years after a great eruption at low-latitudes. However, in winter, an equally marked warming appears to occur over large areas of the western United States, but the warming becomes more restricted in spring and summer including only areas along the Pacific coast and adjacent inland states. Volcanic eruptions at mid, and to some extent at high latitudes, do not appear to produce as marked a change in temperatures. This does not imply that there is no effect but rather that there is no unique response pattern detected through the verified climate–growth transfer functions developed for arid-site trees from western North America.

In previous sections we described the use of tree rings to detect pollution signals in the growth ring record. Now we turn to the problem of detecting possible changes in the amounts of atmospheric gases such as CO_2. LaMarche *et al.* (1984) report rising trends in the ring widths of trees growing at high elevations in the western United States that exceeded the increase in growth expected from known climatic trends in the same region. They proposed that rising levels of atmospheric CO_2 could be the causal factor. It was hypothesized that "subalpine vegetation generally, and upper treeline conifers in particular, could now be exhibiting enhanced growth due directly to rising levels of atmospheric CO_2."

Graybill (1987), who is a dendroclimatologist investigating this subject, explains: "One of the primary physiological bases for this hypothesis is that CO_2 becomes more limiting to photosynthesis as elevation increases because the concentration of CO_2 per unit volume is decreased from that nearer sea level. With substantially increasing CO_2 since the mid 1800s one might then expect to first see improved photosynthetic performance in trees growing under ambient conditions at relatively high elevations." (See also Gale, 1986; LaMarche *et al.*, 1986). These workers suggest that more effort should be directed to evaluating these growth changes at high altitudes, because of the ecological importance of these kinds of vegetational changes, if they have begun, as well as their implications for the global carbon budget.

Graybill (1987) extended the existing collections of very old high altitude *P. longaeva* and *P. flexilis* growing in the Great Basin and Rocky Mountain regions. He continues to find that trees at high altitudes (*ca.* 3400 m) near upper treeline show major and relatively continuous increases in annual growth rate since about 1850. He notes that in almost all cases the particular trees were growing on south exposures or on windswept crests where drought as well as temperature can be limiting. He suggests that water use efficiency of trees in these settings also may have increased with corresponding changes in CO_2, leading to more efficient utilization of site resources and growth enhancement.

Graybill used ARMA modeling techniques to examine the growth trends. He fitted an ARMA model to the 1380–1860 period and applied that model to the post-1859 period, but this failed to remove the trend in these data. Moreover, the mean of the post-1859 residual series was five times greater than the mean of the earlier values. He also examined temperature and precipitation records throughout the region and found that variation in the prewhitened ring-width indices could only be partially explained by those variables. However, he did not find a trend in either of these climatic variables that could account for the rising growth at high altitudes, and was unable to rule out CO_2 as an agent for the growth change.

He also developed several chronologies at the drier and lower limits of growth (*ca.* 2900 m) for Bristlecone pine in the Great Basin. In some cases these are from the same mountain ranges as the upper treeline chronologies. There is no overall upward trend in growth during the past 130 years, but instead these chronologies from lower elevations track the available moisture records of this century with reasonable fidelity (Graybill, personal communication, 1988).

In this section we have given only a few examples of dendroclimatic applications that can help to identify ecological problems and expand our knowledge of past environmental variations and changes. There are other major issues and problems dealing with climatic variation and changes to which dendroclimatology or dendroecology could make unique and significant contributions.

For example, Wood (1988) points out that the global climate system is immensely complex and that existing climate models make assumptions leading to important uncertainties in the model results. One important uncertainty involves how much of the hemispheric warming in the instrumental data analyzed by Jones *et al.* (1986) are really the effects of urban warming. He proposes that a variety of independent data, including the information from proxy records of past climate such as tree-ring measurements and alpine glacier changes (Wood, 1988), should be considered to validate this time series.

Wood also points out that "researchers have looked to the paleoclimatic record as an analogous indication of future climatic change (see Webb *et al.*, 1985; Kutzbach, 1985), especially with respect to the effects of increasing concentration of atmospheric trace gases. An important caveat is that current climatic conditions appear to be unprecedented, and therefore it is not clear whether and to what extent past climate behavior serves as a valid guide to the future."

Wood points out that (1) the atmospheric concentration of CO_2 appears to have already exceeded any level experienced over the last 160 thousand years; (2) that rate of increase in CO_2 concentration appears to be more than an order of magnitude faster than previously experienced; (3) several other trace gas concentrations are increasing almost as fast or faster than CO_2; (4) the present Interglacial is widely estimated to be about 10–11 thousand years old, and would be expected, on the average, to be in its late stages and to be characterized by long-term cooling; (5) the global forest cover has been reduced by a conservatively estimated 1·3 billion hectares since pre-agricultural times. The rate of global deforestation, especially in the tropics, appears to be at least an order of magnitude faster than that previously experienced due to natural causes, over at least the last 10 thousand years. "This suggests an unprecedented occurrence of an extremely rapid increase in trace gases and decreases in forestation during what would in geological terms be the late stage of an interglacial with its expected long-term cooling (Wood, 1988).

Because there are so many uncertainties in our understanding of the climate system and limitations of current climatic modeling efforts, Wood (1988) proposes that an intensive research effort be launched to deal with a wider range of inter-related relationships as a systems problem. An important first-order contribution that such systems research might make is the identification of key factors of climatic change and the integration of knowledge ranging across all of the disciplines that may be potentially relevant. Wood lists 21 relevant disciplines including botany, ecology, forestry and dendrochronology that could make meaningful contributions to such a systems analysis.

A third order contribution that he mentions is the identification of needs for climatic monitoring such as (1) the use of rural temperature networks, (2) a tropospheric temperature network, (3) monitoring alpine glacier trends, (4) permafrost thermal gradients, (5) lake levels and, possibly, lake freeze-up dates, (6) ocean plankton trends, and (7) tree-ring chronologies (as a climate-sensitive indicator of changes in terrestrial biomass, carbon flux, and albedo—perhaps under the auspices of the International Project in Dendroclimatology). This reference was to an organization of collaborating dendrochronologists who are attempting to assemble an international network of tree ring chronologies to check the instrumental record of past climatic variation and to extend that record back to the beginning of the 18th century or earlier where there is adequate dendrochronological coverage (Hughes, 1987).

Wood (1988) highlights various weaknesses of climatic models and stresses the importance of climatic and paleoclimatic information on time scales of years and decades to model improvement. Not only do precisely dated and well-replicated dendrochronological data sets allow us to extend knowledge about environmental variations backward in time; but if the unprecedented changes in the earth atmosphere system are truly induced by man's activities, trees already established around the world will be responding to that change. The ring record from these trees can be subjected to dendroecological analysis to assess the direction, magnitude and date of these changes whether or not sufficient instrumentation is in place to monitor these changes. Both dendroclimatology and dendroecology can provide quantitative and precise information on past environmental conditions associated with past tree-growth activity.

VI. LIMITATIONS OF DENDROECOLOGY

There are some areas of the world where dendroecology is not applicable because there are no suitable trees for the analysis. For example, the rings of many tree species, especially those growing in the tropics, may be indistinct, or bear no relationship with an annual growth cycle, or if they do, there are no visible patterns common between trees that can be used for crossdating (Eckstein *et al.*, 1981; Ogden, 1982). However, there are tropical forest sites with species that have crossdatable rings, which have provided useful chronologies (Ogden, 1982; Villalba *et al.*, 1985). It should also be kept in mind that very mesic and apparently favorable site conditions do not always mean that potentially useful species are not available for tree-ring studies (LaMarche 1982). For example, Stahle *et al.* (1985a,b) have found bald cypress (*Taxodium distichum* L. Rich) growing in swamps in the southeastern United States that are crossdatable, climatically sensitive, and exceeding 1000 years in age.

In other situations the growth of rings may generally follow an annual cycle, but there may be too little variability to distinguish a pattern for dating. In extremely arid regions or where a species is at the limit of its ecological range, so many rings may be missing from a sequence or so many intra-annual growth bands may be produced in any one year that the ring sequence cannot be dated (Glock *et al.*, 1960). Additionally, many trees may not attain sufficient age to be useful. Thus, dendroecology requires a tree species that (1) produces distinguishable rings for most years, (2) possesses ring features that can be dendrochronologically dated, and (3) attains sufficient age to provide the time control required for a particular investigation. Fortunately, there are many suitable species in the temperate forests of the Northern and Southern Hemisphere and crossdating has been observed in many of them (Hughes *et al.*, 1982; Stockton *et al.*, 1985). Many old trees with datable ring patterns can still be found in remote or protected areas of deciduous forests (Hughes *et al.*, 1982; Brubaker and Cook, 1983). Conifers have been investigated most extensively. Angiosperms have also been used, with oaks (*Quercus* spp.) being selected most often for ring-width analysis. The large vessels in oak, however, preclude densitometric analysis of oak species (Leggett *et al.*, 1978).

Even though the rings of many temperate forest species are potentially suitable for dendroecological investigation, the majority of trees, particularly in a second growth forest, may be undesirable for study. For example, youthful trees generally have too few annual rings to be of interest. Their ring patterns may be so dominated by competition between individual trees that no crossdatable pattern can be distinguished. Middle-aged under-story trees may grow so slowly that many rings are missing, or the rings become so compressed that they cannot be readily identified. Later, when these individuals penetrate the forest canopy, the growing conditions may become more favorable and the rings are much wider. Crossdatable ring-width patterns may become more evident, but in many second growth stands the ring-width variations due to nonclimatic factors often are much larger.

In second-growth stands, occasional large trees can be found that were inhabitants of the original forest. Frequently the ring record from these trees is incomplete because the heartwood is rotten or the trunk is hollow. Also, a tree may be large and still not be old. The rings from such large trees are not only wide but there is often insufficient ring-width variation for crossdating. However, density features of the rings from second-growth stands may be more datable (Schweingruber, 1980; Conkey, 1986). The greatest future contribution of densitometric techniques may be in the more productive temperate and boreal forests where there is little ring-width variation in common with other trees that can be used for dating.

The success of a project often depends upon how skilfully the sites and trees have been chosen. A well-trained dendroecologist often spends considerable time in the field examining the various habitats and species available before establishing a sampling strategy. For this reason, the responsibility for developing a strategy and selecting the sites cannot be delegated to technicians or to other professionals with little or no training in dendrochronology.

While it is desirable to remove the age-related trends from ring-width measurements for many applications, in practice it is difficult to be sure that this is all that is removed in the process of standardization. The statistical approaches and time-series analysis of Nash *et al.* (1975) and Cook (1985) are attempts to deal with this problem.

The relationship of indexed tree-ring chronologies to measurements of wood volume and biomass production have not been investigated adequately. Tree-ring indices may be useful proxy records of relative changes in forest growth, but these measurements are necessarily derived from samples of trees that have survived past disturbances. Thus, determination of wood volume lost, for example, due to a past insect outbreak, will not include the wood volume lost through mortality of trees that are no longer present in the stand. The tree-ring chronology does contain information that is useful in the estimation of forest productivity (Taylor, 1981; Graumlich and Brubaker, 1987), and it should be considered seriously as a possible forest mensuration tool.

The correlation statistic is only an empirical measurement of association between variables. It alone cannot prove that a cause and effect relationship exists, such as between acid deposition and forest decline. However, a correlation finding can be considered a conclusive result when the correlation is too high to have occurred solely by chance; it is verified using independent results; it is based upon a well-tested model of cause and effect; and alternative explanations have been examined and ruled out. Carefully conducted dendroecological studies offer a special contribution to the understanding and resolution of environmental problems because they provide a historical perspective and precise time sequence of environmental changes. Development and analysis of networks or grids of tree-ring chronologies may reveal spatial as well as temporal changes in forest decline.

VII. CONCLUSIONS

The basis for some of the fundamental techniques, principles and practices of dendroecology have been reviewed. Much of the evidence presented is drawn heavily from personal as well as cited references. The reference list, however, is far from exhaustive.

More attention should be given to dendroecological investigation of current forest ecology problems. The value of forest inventory collections could be enhanced greatly if crossdating and other dendroecological techniques were added to those procedures that have been adopted. Dendroecology is not in competition with standard forest mensuration approaches nor is it considered a substitute for stem analysis using the three-dimensional approach of Duff and Nolan (1953) (LeBlanc *et al.*, 1987). It provides different kinds of information and requires different kinds of analyses (Fritts *et al.*, 1965a; Swetnam *et al.*, 1985). Furthermore, standardized tree-ring chronologies can be used in combination with other growth projection systems to provide a more sensitive measure of relative changes in forest productivity through time than some of the standard mensurational approaches (Thammincha, 1981). Considering that the forestry values at risk are primarily economic, the measurement of growth reduction or non-reduction would be of considerable value if it could be expressed in terms of some type of timber volume measurement (Morrison, 1984; Peterson, 1985).

One alternative for obtaining such a measurement is to convert ring-width index chronologies, with or without adjustments for climatic effects, back to ring widths (e.g., Nash *et al.*, 1975; Greve *et al.*, 1986) and then these chronologies can be recomputed as basal area increments. Estimates of changes in volume growth from standardized ring-width chronologies would also require additional data on the growth potential of the site and height growth, but it should be possible to relate this index of growth in the lower stem to overall changes in volume growth.

Numerous computer simulation models have been developed to project forest growth and succession, and basic information on disturbance regimes and climatic relationships are often necessary inputs (Cooper *et al.*, 1974; Shugart, 1984, 1987). Computerized growth and yield models for forestry also depend on estimates of growth impacts of insects outbreaks in order to adjust forecasts (Wycoff *et al.*, 1982). We believe that dendroecology studies can provide much of the basic information that is required for calibrating or testing these types of computer models.

Dendroecology studies examining forest decline have a number of advantages over other types of tree-ring investigations. Site and tree selection strategies are designed to minimize sources of variation in the tree-ring series that may have little or no relation to the problem in question. Trees of similar species, age and stature are collected from similar sites, soil types, exposures and elevations. Accurate dating allows for replicate sampling and the averaging of results in a yearly sequence.

The variance due to large scale extrinsic growth controlling factors such as climate or to large scale stand disturbances remains in the stand chronology because the growth in all sampled trees was similarly affected by the same limiting conditions. The small scale variations unique to each tree or measured radius of a tree are minimized by both the sampling strategy and by the averaging process since these variations are approximately random over space and time. Sampling strategies can be designed to vary one factor at a time such as differences in suspected pollution damage (Schweingruber *et al.*, 1983) or differences in distance from a suspected source (Fox *et al.*, 1986; Greve *et al.*, in the press). These allow for a rigorous analysis of variance, regression or time-series analysis (Fritts, 1976; Cook, 1985, 1987).

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REFERENCES

Abrahamsen, G., Horntvedt, R. and Tveite, B. (1976). Impacts of acid precipitation on coniferous forest ecosystems. *General Technical Report* NE-23, US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Upper Darby, PA., pp. 991–1009.

Ahlstrand, G. M. (1980). Fire history of a mixed conifer forest in Guadalupe Mountains National Park. In *Proceedings of the Fire History Workshop*, Oct. 20–24, 1980, Tucson, Arizona. *General Technical Report* RM-81, US Department of Agriculture, Forest Service. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO., pp. 4–7.

Alestalo, J. (1971). Dendrochronological interpretation of geomorphic processes. *Societas Geographic Fenniae* **105**, 1–140.

Anonymous. 1977. Tales the tree-rings tell. *Mosaic* 8(5), National Science Foundation, Washington, DC, 10 pp.

Ashby, W. C. and Fritts H. C. (1972). Tree growth, air pollution, and climate near LaPorte, Indiana. *Bulletin of the American Meteorological Society* **53(3)**, 246–251.

Athari, Said (1981). Missing growth rings, an often disregarded problem in the studies of increment in emission-damaged and healthy Norway spruce stands. *Mitteilungen der forstlichen Bundes-Versuchanst.* (Wien) **139**, 7–25. In German, with English summary.

Baillie, M. G. L. (1982). *Tree-Ring Dating and Archaeology*. University of Chicago Press, Chicago.

Baillie, M. G. L. and Munro, M. A. R. (1988) Irish tree rings, Sanotini and volcanic dust veils. *Nature* **332**, 344–346.

Bates, J. M. and Granger C. W. J. (1969). The combination of forecasts. *Operational Research Quarterly* **20(4)**, 451–468.

Betancourt, P. P. (1987). Dating the Aegean Late Bronze Age with radiocarbon. *Archaeometry* **29**, 45–49.

Binns, W. O. and Redfern D. B. (1983). Acid rain and forest decline in West Germany. *Forestry Commission Research and Development Paper* 131. Edinburgh, Scotland.

Blank, L. W. (1985). A new type of forest decline in Germany. *Nature* **314**, 311–334.

Blasing, T. J. (1978). Time series and multivariate analysis in paleoclimatology. In *Time Series and Ecological Processes*, H. H. Shugart, Jr., ed., pp. 212–226. *SIAM-SIMS Conference Series*, No. 5. Society for Industrial and Applied Mathematics, Philadelphia.

Blasing, T. J. and Duvick, D. N. (1984). Reconstruction of precipitation history in North American corn belt using tree rings. *Nature* **307**, 143–145.

Blasing, T. J., Duvick, D. N. and Cook, E. R. (1983). Filtering the effects of competition from ring-width series. *Tree-Ring Bulletin* **43**, 19–30.

Bormann, F. H. (1985). Air pollution and forests: an ecosystem perspective. *Bioscience* **35**, 434–441.

Box, G. E. P. and Jenkins G. H. (1976). *Time Series Analysis, Forecasting and Control*. Holden-Day; San Francisco.

Briffa, K. R., Jones, P. D., Wigley, T. M. L., Pilcher, J. R. and Baillie, M. G. L. (1983). Climate reconstructions from tree rings: part 1. Basic methodology and preliminary results for England. *Journal of Climatology* **3**, 233–242.

Briffa, K. R., Jones, P. D. Wigley, T. M. L., Pilcher, J. R. and Baillie, M. G. L. (1986). Climate reconstructions from tree rings: part 2, spatial reconstructions of summer

mean sea-level pressure patterns over Great Britain. *Journal of Climatology* **6**, 1–15.
Briffa, K. R., Jones, P. D., Pilcher, J. R. and Hughes, M. K. (1988a) Reconstructing summer temperatures in Northern Fennoscandinavia back to 1700 A.D. using tree-ring data from Scots pine. *Arctic and Alpine Research* **20**, 385–394.
Briffa, K. R., Jones, P. D. and Schweingruber, F. H. (1988b) Summer temperature patterns over Europe: a reconstruction to 1750 A.D. based on maximum latewood density indices of conifers. *Quaternary Research* **30**, 34–52.
Brookes, M. H., Campbell, R. W., Colbert, J. J. Mitchell, R. G. and Stark, R. W. technical coordinators. (1987). Western spruce budworm. *Technical Bulletin* No. 1694, US Department of Agriculture, Forest Service, Washington, DC, 198 pp.
Brown, J. M. (1968). The photosynthetic regime of some Southern Arizona ponderosa pine. PhD dissertation, University of Arizona, Tucson.
Brubaker, L. B. and Cook, E. R. (1983). Tree-ring studies of Holocene environments. In *Late Quaternary Environments of the United States*, Vol. 2: *The Holocene*, H. E. Wright, Jr, ed., pp. 222–235, University of Minnesota Press, Minneapolis.
Brubaker, L. B. and Greene, S. K. (1979). Differential effects of Douglas-fir tussock moth and western spruce budworm defoliation on radial growth of grand fir and Douglas-fir. *Canadian Journal of Forest Research* **9**, 95–105.
Bryson, R. A. (1985). On climatic analogs in paleoclimatic reconstruction. *Quaternary Research* **23**, 275–86.
Clark, N., Blasing, T. J. and Fritts, H. C. (1975). Influence of interannual climatic fluctuations on biological systems. *Nature* **256**(5515): 302–304.
Cleaveland, M. K. (1986). Climatic response of densitometric properties in semiarid site tree rings. *Tree Ring Bulletin* **48**, 13–29.
Cogbill, C. V. (1977). The effect of acid precipitation on tree growth in eastern North America. *Water, Air, and Soil Pollution* **8**, 89–93.
Conkey, L. E. (1982a). Eastern US tree-ring widths and densities as indicators of past climate. PhD. dissertation, University of Arizona, Tucson, 204 pp.
Conkey, L. E. (1982b). Temperature reconstructions in the north-eastern United States. In *Climate from Tree Rings*, M. K. Hughes, P. M. Kelly, J. R. Pilcher and V. C. LaMarche, Jr., eds., pp. 165–168. Cambridge University Press, Cambridge.
Conkey, L. E. (1986). Red spruce tree-ring widths and densities in eastern North America as indicators of climate. *Quaternary Research* **26**, 232–243.
Cook, E. R. (1982). Eastern North America. In *Climate from Tree Rings*, M. K. Hughes, P. M. Kelly, J. R. Pilcher and V. C. LaMarche, Jr., eds., pp. 126–133. Cambridge University Press, Cambridge.
Cook, E. R. (1985). A time-series analysis approach to tree-ring standardization. PhD dissertation, University of Arizona, Tucson, 175 pp.
Cook, E. R. (1987). The use and limitations of dendrochronology in studying effects of air pollution on forests. In *Effects of Atmospheric Pollutants on Forests, Wetlands and Agricultural Ecosystems*, T. C. Hutchinson and K. M. Meema, eds. *NATO ASI Series*, Vol. G16. Springer-Verlag, Berlin and Heidelberg.
Cook, E. R. Personal communications. Tree-Ring Laboratory, Lamont-Doherty Geological Observatory of Columbia University, Palisades, New York.
Cook, E. R. and Jacoby, G. C. (1977). Tree-ring–drought relationships in the Hudson Valley, New York. *Science* **198**, 399–401.
Cook, E. R. and Jacoby, G. C. (1983). Potomac River streamflow since 1730 as reconstructed by tree rings. *Journal of Climate and Applied Meteorology* **22**, 1659–1674.
Cook, E. R. and Peters, K. (1981). The smoothing spline: a new approach to

standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-Ring Bulletin* **41**, 45–53.

Cook, E. R., Johnson, A. H. and Blasing, T. J. (1987). Forest decline: modeling the effect of climate in tree rings. *Tree Physiology* **3**, 27–40.

Cooper, C. F., Blasing, T. J. and Fritts, H. C. (1974). Simulation models of the effects of climatic change on natural eco-systems. In *Proceedings of the Third Conference on the Climatic Assessment Program (CIAP), February 26–March 1, 1974.* US Department of Transportation, Cambridge, MA.

Craighead, F. C. (1927). Abnormalities in annual rings resulting from forest fires. *Journal of Forestry* **25**, 840–842.

Cropper, J. P. (1982). Climate reconstructions from tree rings: comment. In *Climate from Tree Rings*, M. K. Hughes, P. M. Kelly, J. R. Pilcher and V. C. LaMarche, Jr, eds, pp. 65–67. Cambridge University Press, Cambridge.

Cropper, J. P. (1985). Tree-ring response functions. An evaluation by means of simulations. PhD. dissertation, Department of Geosciences, University of Arizona, Tucson, 132 pp.

Dean, J. S. (1986). Dendrochronology. In *Dating and Age Determination of Biological Materials*, M. R. Zimmerman and J. L. Angel, eds., pp. 126–165. Croom Helm, London.

DeWitt, E. and Ames, A. (eds) (1978). Tree-ring chronologies of eastern North America. *Chronology Series* VI, Vol. 1. Laboratory of Tree-Ring Research, University of Arizona, Tucson.

Dieterich, J. H. (1980). Chimney Spring forest fire history. *Research Paper* RM-220, US Department of Agriculture, Forest Service, Rocky Mountains Forest and Range Experiment Station, Fort Collins, CO.

Dieterich, J. H. and Swetnam T. W. (1984). Dendrochronology of a fire scarred ponderosa pine. *Forest Science* **30(1)**, 238–247.

Doane, C. C. and McManus, M. L. (eds) (1981). The gypsy moth: research toward integrated pest management. USDA Expanded Gypsy Moth Research Development Program, Forest Service, Science and Education Agency *Technical Bulletin* 1584.

Douglass, A. E. (1914). A method of estimating rainfall by the growth of trees. In *The Climatic Factor*, E. Huntington, ed., pp. 101–22. *Carnegie Institution of Washington Publication* No. 192.

Douglass, A. E. (1919). *Climatic Cycles and Tree Growth*, Vol. I. A Study of the Annual Rings of Trees in Relation to Climate and Solar Activity. *Carnegie Institution of Washington Publication* No. 289.

Douglass, A. E. (1928). *Climatic Cycles and Tree Growth*, Vol. II. A Study of the Annual Rings of Trees in Relation to Climate and Solar Activity. *Carnegie Institution of Washington, Publication* No. 289.

Douglass, A. E. (1935). Dating Pueblo Bonito and other ruins of the Southwest. *National Geographic Society Contribution Technical Paper, Pueblo Bonito Series* 1.

Douglass, A. E. (1936). *Climatic Cycles and Tree Growth*, Vol. III. A Study of Cycles. *Carnegie Institution of Washington Publication* No. 289.

Douglass, A. E. (1937). Tree rings and chronology. *University of Arizona Bulletin* **8**, Physical Science Series 1.

Douglass, A. E. (1941). Crossdating in dendrochronology. *Journal of Forestry* **39**, 825–831.

Douglass, A. E. (1946). Precision of ring dating in tree-ring chronologies. *University of Arizona Bulletin* **XVII**, No. 3.

Duff, G. H. and Nolan, N. J. (1953). Growth and morphogenesis in the Canadian forest species, I. The controls of cambial and apical activity in *Pinus resinosa* Ait. *Canadian Journal of Botany* **31**, 471–513.

Eckstein, D. (1985). On the application of dendrochronology for the evaluation of forest damage. In *Inventorying and Monitoring Endangered Forests. IUFRO Conference Zurich 1985*, pp. 287–290, Birmensdorf, Eidg. Anstalt fur das forstliche Versuchswesen.

Eckstein, D. and Frisse, E. (1982). The influence of temperature and precipitation on vessel area and ring width of oak and beech. In *Climate from Tree Rings*, M. K. Hughes, P. M. Kelly, J. R. Pilcher and V. C. LaMarche Jr (eds), p. 12. Cambridge University Press, Cambridge.

Eckstein, D., Ogden, J., Jacoby, G. C. and Ash, J. (1981). Age and growth rate determination in tropical trees: the application of dendrochronological methods. *School of Forestry and Environmental Studies Bulletin* No. 94, Yale University, pp. 83–106.

Eckstein, D., Richter, K., Aniol, R. W. and Quiehl, F. (1984). Dendroclimatological investigations of the beech decline in the southwestern part of the Vogelsberg (West Germany). In German, with English abstract. *Forstwissenschaftliches Centralblatt* **103**, 274–290.

Evenden, J. D. (1940). Effects of defoliation by the pine butterfly upon ponderosa pine. *Journal of Forestry* **38**, 949–955.

Ferguson, C. W. (1968). Bristlecone pine: science and esthetics. *Science* **159**(3817), 839–846.

Ferrel, G. T. (1980). Growth of white firs defoliated by Modoc budworm in northeastern California. *Research Paper* PSW-153, US Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkely, California.

Filion, L., Payette, S., Gauthier, L. and Boutin, Y. (1986). Light rings in subarctic conifers as a dendrochronological tool. *Quaternary Research* **26**, 272–279.

Fox, C. A. (1980). The effect of air pollution on western larch as detected by tree-ring analysis. PhD dissertation, Arizona State University, Tempe, 98 pp.

Fox, C. A., Kincaid, W. B., Nash III, T. H., Young, D. L. and Fritts, H. C. (1986). Tree-ring variation in western larch (*Larix occidentalis*) exposed to sulfur dioxide emissions. *Canadian Journal of Forest Research* **16**, 283–292.

Franklin, J. F., Shugart, H. H. and Harmon, M. E. (1987). Tree death as an ecological process. *Bioscience* **37**, 550–556.

Friedland, A. J., Gregory, R. A., Karenlampi, L., Johnson, A. H. (1984). Winter damage to foliage as a factor in red spruce decline. *Canadian Journal of Forest Research* **14**, 963–965.

Fritts, H. C. (1969). Bristlecone pine in the White Mountains of California: growth and ring-width characteristics. *Papers of the Laboratory of Tree-Ring Research* 4. University of Arizona Press, Tucson.

Fritts, H. C. (1971). Dendroclimatology and dendroecology. *Quarternary Research* **1**, 419–449.

Fritts, H. C. (1974). Relationships of ring widths in arid site conifers to variations in monthly temperature and precipitation. *Ecological Monograph* **44**, 411–440.

Fritts, H. C. (1976). *Tree Rings and Climate*. Academic Press, London, 567 pp. Reprinted in: *Methods of Dendrochronology* Vols. II and III, L. Kairiukstis, Z. Bednarz and E. Feliksik (ed). Proceedings of the Task Force Meeting on Methodology of Dendrochronology: East/West Approaches, 2–6 June, 1986, Krakow, Poland. IIASA, Laxenburg, Austria.

Fritts, H. C. (1982). An overview of dendroclimatic techniques, procedures, and prospects. In *Climate from Tree Rings*, M. K. Hughes, P. M. Kelly, J. R. Pilcher and V. C. LaMarche, Jr (eds), pp. 191–197. Cambridge University Press, Cambridge.

Fritts, H. C. Reconstructing large-scale climatic patterns from tree-ring data: a diagnostic analysis. University of Arizona Press, Tucson. (in press).

Fritts, H. C. and Gordon, G. A. (1982). Reconstructed annual precipitation for California. In *Climate from Tree Rings*, M. K. Hughes, P. M. Kelly, J. R. Pilcher and V. C. LaMarche, Jr., eds., pp. 185–191. Cambridge University Press, Cambridge.

Fritts, H. C., Smith, D. G., Budelsky, C. A. and Cardis, J. W. (1965a). The variability of ring characteristics within trees as shown by a reanalysis of four ponderosa pine. *Tree-Ring Bulletin* **27**, 3–18.

Fritts, H. C., Smith, D. G., Cardis, J. W. and Budelsky, C. A. (1965b). Tree-ring characteristics along a vegetation gradient in northern Arizona. *Ecology* **46**, 393–401.

Fritts, H. C., Mossiman, J. E. and Bottorf, C. P. (1969). A revised computer program for standardizing tree-ring indices. *Tree-Ring Bulletin* **29**, 15–20.

Fritts, H. C., Blasing, T. J., Hayden, B. P. and Kutzbach, J. E. (1971). Multivariate techniques for specifying tree-growth and climate relationships and for reconstructing anomalies in paleoclimate. *Journal of Applied Meteorology* **10**, 845–864.

Fritts, H. C., Lofgren, G. R. and Gordon, G. A. (1979). Variations in climate since 1602 as reconstructed from tree rings. *Quaternary Research* **12**, 18–46.

Fritts, H. C., Guiot, J. and Gordon, G. A. (in press). Methods for calibration, verification and reconstruction. In *Methods of Tree-Ring Analysis: Applications in the Environmental Sciences*, L. Kairiukstis and E. Cook, eds. Reidel Press, The Netherlands.

Gale, J. (1986). Carbon dioxide enhancement of tree growth at high elevations. *Science* **231**, 859.

Garfinkel, H. L. and Brubaker, L. B. (1980). Modern climate–tree-growth relationships and climatic reconstruction in subarctic Alaska. *Nature* **286**, 872–874.

Gates, D. M. (1980). *Biophysical Ecology*. Springer-Verlag, New York, 611 pp.

Gates, W. L. and Mintz, Y. (1975). *Understanding Climatic Change: A Program for Action*. Report of the Panel on Climatic Variation of the US Committee for GARP (Global Atmosphere Research Project), National Research Council, National Academy of Sciences, Washington, D.C.

Gemmill, B., McBride, J. R. and Laven, R. D. (1982). Development of tree-ring chronologies in an ozone air pollution-stressed forest in southern California. *Tree-Ring Bulletin* **42**, 23–31.

Giardino, J. R., Shroder, Jr., J. F. and Lawson, M. P. (1984). Tree-ring analysis of movement of a rock-glacier complex on Mount Mestas, Colorado, U.S.A. *Arctic and Alpine Research* **16**, 299–309.

Glock, W. S. (1951). Cambial frost injuries and multiple growth layers at Lubbock, Texas. *Ecology* **32**, 28–36.

Glock, W. S., Studhalter, R. A. and Agerter, S. R. (1960). Classification and Multiplicity of Growth Layers in the Branches of Trees at the Extreme Lower Forest Border. *Smithsonian Miscellaneous Collection* 140(1). *Smithsonian Institution Publication* 4421, Washington, DC.

Gordon, G. A. (1982). Verification of dendroclimatic reconstructions. In *Climate from Tree Rings*, M. K. Hughes, P. M. Kelly, J. R. Pilcher and V. C. LaMarche, Jr, (eds), pp. 58–61. Cambridge University Press, Cambridge.

Gordon, G. A. and Leduc, S. K. (1981). Verification statistics for regression models. *Seventh Conference on Probability and Statistics in Atmospheric Sciences*, Session 8.

Gore, A. P., Johnson, E. A. and Lo, H. P. (1985). Estimating the time a dead tree has been on the ground. *Ecology* **66**, 1981–1983.

Gould, S. J. (1987). *Time's Arrow, Time's Cycle*. Harvard University Press, Cambridge, Mass.

Graumlich, L. J. and Brubaker, L. B. (1986). Reconstruction of annual temperatures (1590–1979) for Longmire, Washington derived from tree rings. *Quaternary Research* **25**, 223–234.

Graumlich, L. J. and Brubaker, L. B. (1987). Increasing net primary productivity in Washington (USA) forests during the last 1000 years. In *Proceedings of the International Symposium on Ecological Aspects of Tree-Ring Analysis*, August 17–21, 1986, Marymount College, Tarrytown, New York, US Department of Energy CONF-8608144, pp. 59–69.

Graybill, D. A. (1979). Revised computer programs for tree-ring research. *Tree-Ring Bulletin* **39**, 77–82.

Graybill, D. A. (1982). Chronology development and analysis. In *Climate from Tree Rings*, M. K. Hughes, P. M. Kelly, J. R. Pilcher and V. C. LaMarche, Jr, (eds), pp. 21–28. Cambridge University Press, Cambridge.

Graybill, D. A. (1987). A network of high elevation conifers in the western US for detection of tree-ring growth response to increasing atmospheric carbon dioxide. *Proceedings of the International Symposium on Ecological Aspects of Tree-Ring Analysis*, August 17–21, 1986, Marymount College, Tarrytown, New York, US Department of Energy CONF-8608144, pp. 463–474.

Greve, U., Eckstein, D. Aniol, R. W. and Scholz, F. (1986). Dendroclimatological investigations on Norway spruce under different loads of air pollution. Allaemeine Forst- und Jagdzetund **157**, 174–179.

Guiot, J. (1986). ARMA techniques for modelling tree-ring response to climate and for reconstructing variations of paleoclimates. *Ecological Modelling* **33**, 149–171.

Guyette, R. and McGinnes, Jr, E. A. (1987). Potential in using elemental concentrations in radial increments of old growth eastern redcedar to examine the chemical history of the environment. *Proceedings of the International Symposium on Ecological Aspects of Tree-Ring Analysis*, August 17–21, 1986, Marymount College, Tarrytown, New York, US Department of Energy CONF-8608144, pp. 671–680.

Hammer, C. U., Clausen, H. B., Friedrich, W. L. and Tauber, H. (1987). The Minoan eruption of Santorini in Greece dated to 1645 B.C.? *Nature* **328**, 517–519.

Harmon, M. E., Franklin, J. F. Swanson, F. J. *et al.* (1986). Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* **15**, 133–302.

Hecht, A. D. (ed.) (1985). *Paleoclimate Analysis and Modelling*. Wiley, New York.

Heikkinen, O. and Tikkanen, M. (1981). The effect of air pollution on growth in conifers: an example from the surroundings of the Skoldvik oil refinery. *Terra* **39**, 134–144. In Finnish, with English summary.

Holmes, R. L. (1983). Computer-assisted quality control in tree-ring dating and measuring. *Tree-Ring Bulletin* **43**, 69–78.

Holmes, R. L., Stockton, C. W. and LaMarche, Jr, V. C. (1979). Extension of river flow records in Argentina from long tree-ring chronologies. *Water Resources Bulletin* **15**, 1081–1085.

Holmes, R. L., Adams, R. K. and Fritts, H. C. (1986). Tree-ring chronologies of western North America: California, eastern Oregon and northern Great Basin. *Chronology Series* VI, Laboratory of Tree-Ring Research, University of Arizona, Tucson.

Hornbeck, J. W. and Smith, R. B. (1985). Documentation of red spruce growth decline. *Canadian Journal of Forest Research* **15**, 119–1201.

Horton, J. C. and Bicak, C. J. (1987). Modeling for biologists. *Bioscience* **37**, 808–809.

Huber, F. (1976). Problemes d'interdatation chez le pin sylvestre et influence du climat sur la structure de ses accroissements annuels. *Annales des Sciences Forestieres* **33**, 61–86. In French.

Hughes, M. K. (1987). Requirements for spatial and temporal coverage. Introduction. In *Methods in dendrochronology: East/West Approches*, L. Kairiukstis, (ed.) IIASA. Polish Academy of Sciences.

Hughes, M. K., Kelly, P. M., Pilcher, J. R. and LaMarche, Jr, V. C. (eds). (1982). *Climate from Tree Rings*. Cambridge University Press, Cambridge. 223 pp.

Jacoby, G. C. (ed) (1980). *Proceedings of the International Meeting on Stable Isotopes in Tree-Ring Research*, New Paltz, New York. *Carbon Dioxide Effects Research and Assessment Program, Publication* No. 12, US Department of Energy, CONF-790518, UC-11, Washington, DC.

Jacoby, G. C. and Hornbeck, J. W. (compilers) (1987). *Proceedings of the International Symposium on Ecological Aspects of Tree-Ring Analysis*, August 17–21, 1986, Marymount College, Tarrytown, New York, US Department of Energy CONF-8608144, 726 pp.

Jacoby, G. C., Cook, E. R. and Ulan, L. D. (1985). Reconstructed summer degree days in central Alaska and northwestern Canada since 1524. *Quaternary Research* **23**, 18–26.

Jagels, R. and Telewski, F. W. (in the press.) Video image analysis in tree-ring research. In *Methods of Tree-Ring Analysis: Applications in the Environmental Sciences*, L. Kairuikstis, and E. Cook, eds. Reidel Press, The Netherlands.

Jenkins, G. M. and Watts, D. G. (1968). *Spectral Analysis and Its Applications*. Holden-Day, San Francisco.

Johnson, A. H. and Siccama, T. G. (1983). Acid deposition and forest decline. *Environmental Science and Technology* **17**, 294A–305A.

Johnson, A. H., Siccama, T. G., Wang, D., Turner, R. S. and Barringer, T. H. (1981). Recent changes in patterns of tree growth rate in the New Jersey pinelands: a possible effect of acid rain. *Journal of Environmental Quality* **10**, 427–430.

Jones, R. H. (1985). Time series analysis-time domain. In *Probability, Statistics, and Decision Making in the Atmospheric Sciences*, A. H. Murphy and R. W. Katz (eds), pp. 223–260. Westview Press, Boulder.

Jones, P. D., Wigley, T. M. L. and Wright, P. B. (1986). Global temperature variations, 1861–1984. *Nature* **322**, 430–434.

Jonsson, B. and Sundberg, R. (1972). Has the acidification by atmospheric pollution caused a growth reduction in Swedish forests? *Research Note* No. 20. Department of Forest Field Research, Royal College of Forestry, Stockholm.

Jonsson, B. and Svensson, L. G. (1982). A study of the effects of air pollution on forest yield. A follow-up of the report of Jonsson and Sundberg 1972 and a new study based on forest types. *Avdelningen för Skogsuppskattning och Skogsindelning, Sveriges Lantbruksuniversitet* No. 9, 61 pp.

Kairiukstis, L. and Cook, E. R. (eds) (in press.) *Methods of Tree-Ring Analysis: Applications in the Environmental Sciences*. Reidel Press, The Netherlands.

Keen, F. P. (1937). Climatic cycles in eastern Oregon as indicated by tree rings. *Monthly Weather Review* **65**, 175–181.

Keller, R. (1968). Des caractéristiques nouvelles pour l'étude des propriétés mécaniques des bois: les composantes de la densité. *Annales des Sciences Forestieres* **25**, 237–249. In French.

Keller, T. (1980). The effect of a continuous springtime fumigation with sulfur dioxide and carbon dioxide uptake and structure of the annual ring in spruce. *Canadian Journal of Forest Research* **10**, 1–6.

Kelly, P. M. and Sear, C. B. (1984). Climatic impact of explosive volcanic eruptions. *Nature* **311**, 740–743.

Kienast, F. (1982). Analytical investigations based on annual tree rings in damaged forest areas of the Valais (Rhone Valley) endangered by pollution. *Geographica Helvetica* **3**, 143–148. In German, with English summary.

Kienast, F. (1985). Tree-ring analysis, forest damage and air pollution in the Swiss Rhone valley. *Land Use Policy* **2**, 71–77.

Kienast, F. and Schweingruber, F. H. (1986). Dendroecological studies in the Front Range, Colorado, USA. *Arctic and Alpine Research* **18**, 277–288.

Kienast, F., Flühler, H. and Schweingruber, F. H. (1981). Jahrringanalysen an Föhren (*Pinus silvestris* L.) aus immissionsgefährdeten Waldbeständen des Millelwallis (Sacon, Schweiz). *Eidgenoessische Anstalt fuer das Forstliche Versuchswesen Mitteilungen* **57, 4**, 415–432.

Knight, H. A. (1987). The pine decline. *Journal of Forestry* **85**, 25–28.

Koerber, T. W. and Wickman, B. E. (1970). Use of tree-ring measurements to evaluate impact of insect defoliation. In *Tree-Ring Analysis with Special Reference to Northwest America*, J. H. G. Smith and J. Worrall, eds., *University of British Columbia Faculty of Forest Research Bulletin* 7, Vancouver, pp. 101–106.

Kontic, R., Niederer, M., Nippel, C. A., Winkler-Seifert, A. and A. (1986). Dendrochronological analysis on conifers for presentation and interpretation of forest damages (Vallis, Switzerland). Swiss Federal Institute of Forestry Research, Report No. 283, Birmensdorf.

Kuhn, T. S. (1970). *The Structure of Scientific Revolution. International Encyclopedia of Unified Science*, Vol. II, No. 2, University of Chicago Press, Chicago, IL., 210 pp.

Kutzbach, J. E. (1985). Modeling of paleoclimates. *Reviews of Geophysics* **28A**, 159–196.

LaMarche, V. C., Jr, (1966). An 800-year history of stream erosion as indicated by botanical evidence. In *US Geological Survey Professional Paper* 550-D, pp. 83–86, Washington, DC.

LaMarche, V. C., Jr (1968). Rates of slope degradation as determined from botanical evidence, White Mountains, California. Erosion and sedimentation in a semiarid environment. In *US Geological Survey Professional Paper* 325-I, pp. 341–377.

LaMarche, V. C., Jr (1970). Frost-damage rings in subalpine conifers and their application to tree-ring dating problems. In *Tree-Ring Analysis with Special Reference to Northwest America*, J. H. G. Smith and J. Worrall, eds., *University of British Columbia Faculty Forestry Bulletin* 7, Vancouver, pp. 99–100.

LaMarche, V. C., Jr, (1974). Frequency-dependent relationships between tree-ring series along an ecological gradient and some dendroclimatic implications. *Tree-Ring Bulletin* **34**, 1–20.

LaMarche, V. C., Jr (1978). Tree-ring evidence of past climatic variability. *Nature* **276**, 334–338.

LaMarche, V. C., Jr (1982). Sampling strategies. In *Climate from Tree Rings*, M. K. Hughes, P. M. Kelly, J. R. Pilcher and V. C. LaMarche, Jr., eds., pp. 2–6. Cambridge University Press, Cambridge.

LaMarche, V. C., Jr and Harlan, T. P. (1973). Accuracy of tree-ring dating of bristlecone pine for calibration of the radiocarbon time scale. *Journal of Geophysical Research* **78**, 8849–8858.

LaMarche, V. C., Jr and Hirschboeck, K. K. (1984). Frost rings in trees as records of major volcanic eruptions. *Nature* **307**, 121–126.

LaMarche, V. C., Jr, Graybill, D. A., Fritts, H. C. and Rose, M. R. (1984). Increasing atmospheric carbon dioxide: tree-ring evidence for growth enhancement in natural vegetation. *Science* **225**, 1019–1021.

LaMarche, V. C., Jr, Graybill, D. A., Fritts, H. C. and Rose, M. R. (1986). Carbon dioxide enhancement of tree growth at high elevations. In Technical Comments, *Science* **231**, 859–860.

Lamb, H. H. (1977). *Climate: Present, Past and Future, II. Climatic History and the Future*. Methuen, London. 835 pp.

LeBlanc, D. C., Raynal, D. J., White, E. H. and Ketchledge, E. H. (1987). Characterization of historical growth patterns in declining red spruce trees. In *Proceedings of the International Symposium on Ecological Aspects of Tree-Ring Analysis*, August 17–21, 1986, Marymount College, Tarrytown, New York, US Department of Energy CONF-8608144, pp. 360–371.

Leggett, P., Hughes, M. K. and Hibbert, F. A. (1978). A modern oak chronology from North Wales and its interpretation. In *Dendrochronology in Europe: Principles, Interpretation and Applications to Archaeology and History*, J. Fletcher, ed., pp. 187–194, *BAR International Series* 51, Oxford, England.

Lemon, E. R. (ed) (1983). *CO_2 and Plants*. American Association for the Advancement of Science Selected Symposium 84. Westview Press, Boulder, Colorado, 280 pp.

Lenz, O., Schar, E. and Schweingruber, F. H. (1976). Methodische probleme bei der radiographisch-densitometrischen bestimmung der dichte und der jahrringbreiten-von Holz. *Holzforschung* **30**, 114–123. In German.

Lepp, N. W. (1975). The potential of tree-ring analysis for monitoring heavy metal pollution patterns. *Environmental Pollution* **9**, 49–61.

Lofgren, G. R. and Hunt, J. H. (1982). Transfer functions. In *Climate from Tree Rings*, M. K. Hughes, P. M. Kelly, J. R. Pilcher and V. C. LaMarche, Jr., eds., pp. 50–56. Cambridge University Press, Cambridge.

Long, A. (1982). Stable isotopes in tree rings. In *Climate from Tree Rings*, M. K. Hughes, P. M. Kelly, J. R. Pilcher and V. C. LaMarche, Jr., eds., pp. 12–18. Cambridge University Press, Cambridge.

Lorimer, C. G. (1985). Methodological considerations in the analysis of forest disturbance history. *Canadian Journal of Forest Research* **15**, 200–213.

Lough, J. M. and Fritts, H. C. (1987). An assessment of the possible effects of volcanic eruptions on North American climate using tree-ring data, 1602 to 1900 A.D. *Climatic Change* **10**, 219–239.

Madany, M. H., Swetnam, T. W. and West, N. E. (1982). Comparison of two approaches for determining fire dates from tree scars. *Forest Science* **28**, 856–861.

Marchand, P. J. (1984). Dendrochronology of a fir wave. *Canadian Journal of Forest Research* **14**, 51–56.

Marquardt, D. W. and Snee, R. D. (1985). Developing empirical models with multiple regression biased estimation techniques. In *Probability, Statistics, and Decision Making in the Atmospheric Sciences*, A. H. Murphy and R. W. Katz, eds., pp. 45–100, Westview Press, Boulder.

Mass, C. and Schneider, S. H. (1977). Statistical evidence on the influence of sunspots and volcanic dust on long-term temperature records. *Journal of Atmospheric Science* **34**, 1995–2004.

McBride, J. R., Semion, V. and Miller, P. R. (1975). Impact of air pollution on growth of ponderosa pine. *California Agriculture* **29**, 8–10.

McLaughlin, S. B. (1984). FORAST: a regional scale study of forest responses to air pollutants. In *Proceedings of the Conference, Air Pollution and the Productivity of the Forest*. Izaak Walton League, D. Davis (ed.), pp. 241–253.

McLaughlin, S. B. (1985). Effects of air pollution on forests: a critical review. *Journal of the Air Pollution Control Association* **35**, 512–534.

McLaughlin, S. B., Blasing, T. J., Mann, L. K. and Duvick, D. N. (1983). Effects of acid rain and gaseous pollutants on forest productivity: a regional scale approach. *Journal of the Air Pollution Control Association* **33**, 1042–1049.

Meko, D. M. (1981). Applications of Box-Jenkins methods of time series analysis to the reconstruction of drought from tree rings. PhD dissertation, University of Arizona, Tucson, 149 pp.

Miller, P. R. (1973). Oxidant-induced community change in a mixed conifer forest. In *Air Pollution Damage to Vegetation. Advances in Chemistry Series* **122**, 101–117.

Miller, P. R. (1985). Ozone effects in the San Bernardino National Forest. In *Air Pollutant Effects on Forest Ecosystems*, May 8–9, 1985, St Paul, MN, pp. 161–196.

Monserud, R. A. (1986). Time-series analyses of tree-ring chronologies. *Forest Science* **32**, 349–372.

Morrison, I. K. (1984). Acid rain: a review of literature on acid deposition effects in forest ecosystems. *Forestry Abstracts* **45**, 483–506.

Morrow, P. A. and LaMarche, Jr, V. C. (1978). Tree-ring evidence for chronic insect suppression of productivity in subalpine *Eucalyptus*. *Science* **201**, 1244–1245.

Nash, T. H., Fritts, H. C. and Stokes, M. A. (1975). A technique for examining nonclimatic variation in widths of tree rings with special reference to air pollution. *Tree-Ring Bulletin* **35**, 15–24.

Norton, D. A. (1979). Phenological growth characteristics of *Nothofagus solandri* at three altitudes in the Craigieburn Range, New Zealand. *New Zealand Journal of Botany* **22**, 413–424.

Norton, D. A. (1983). A dendroclimatic analysis of three indigenous tree species, South Island, New Zealand. PhD dissertation, University of Canterbury, New Zealand, 439 pp.

Ogden, J. (1982). Australasia. In *Climate from Tree Rings*, M. K. Hughes, P. M. Kelly, J. R. Pilcher and V. C. LaMarche, Jr, (eds), pp. 90–103. Cambridge University Press, Cambridge.

O'Neil, L. C. (1963). The suppression of growth rings in jack pine in relation to defoliation by the Swaine jack-pine sawfly. *Canadian Journal of Botany* **41**, 227–235.

Parker, M. L. and Henoch W. E. S. (1971). The use of Engelmann spruce latewood density for dendrochronological purposes. *Canadian Journal of Forest Research* **1**, 90–98.

Payette, S., Filion, L., Gauthier, L. and Boutin, Y. (1985). Secular climate change in old-growth tree-line vegetation of northern Quebec. *Nature* **315**, 135–138.

Peet, R. K. (1981). Forest vegetation of the Colorado Front Range. *Vegetatio* **45**, 3–75.

Peterson, D. L. (1985). Evaluating the effects of air pollution and fire on tree growth by tree-ring analysis. In *Proceedings of the Eighth Conference on Fire and Forest Meteorology*, Detroit, Michigan, April 29 to May 2, 1985. Society of American Foresters, Bethesda, Maryland, pp. 124–131.

Peterson, D. L., Arbaugh, M. J., Wakefield, V. A. and Miller, P. R. (1987). Evidence of growth reduction in ozone-injured Jeffrey pine (*Pinus jeffreyi* [Grev. and Balf.]) in Sequoia and Kings Canyon National Parks. *Journal of the Air Pollution Control Association* **37**, 906–912.

Phipps, R. L. (1972). *Tree Rings, Stream Runoff and Precipitation in Central New York. US Geological Survey Professional Paper* 800–B, B259–264, Washington, DC.

Phipps, R. L. (1982). Comments on interpretation of climatic information from tree rings, eastern North America. *Tree Ring Bulletin* **42**, 11–22.

Phipps, R. L., Ierley, D. L. and Baker, C. P. (1979). Tree rings as indicators of hydrologic change in the Great Dismal Swamp, Virginia and North Carolina. *US Geological Survey Water Resources Investigations* 78–136, US Geological Survey, Washington, DC.

Pickett, S. T. A. and White, P. S. (eds). (1985). *The Ecology of Natural Disturbance and Patch Dynamics*, Academic Press, New York, 472 pp.

Polge, H. (1963). Une nouvelle methode de determination de la texture du bois: l'analyse densitometrique de cliches radiographiques. *Annales de l'ecole nat. eaux et forets et de la station de recherche et exper.* **20**, 531–581. In French.

Polge, H. (1966). Etablissement des courbes de variation de la densite du bois par l'exploration densitometrique de radiographies d'echantillons preleves a la tariere sur des arbres vivants. *Annales des sciences forestieres* **23**, 1–206. In French.

Polge, H. (1970). The use of x-ray densitometric methods in dendrochronology. *Tree-Ring Bulletin* **30**, 4–10.

Pollanschütz, J. (1971). Die ertragskundlichen Messmethoden zur Erkennung und Beurteilung von forstlichen Rauchschäden. In *Mitt. d. forstl. Bundes-Versuchanst (Wien)*. **92**, 153–206.

Richards, K. S. (1981). Stochastic processes in one-dimensional series: an introduction. In *Concepts and Techniques in Modern Geography*, Institute of British Geographers, London, 57 pp.

Sanders, C. J., Stark, R. W., Mullins, E. J. and Murphy, J. (1985). *Recent Advances in Spruce Budworms Research.* Proceedings of the CANUSA Spruce Budworms Research Symposium. Canadian Forestry Service, Ottawa.

Schmitt, D. M., Grimble, D. G. and Searcy, J. L. (1984). Managing the spruce budworm in eastern North America. *Agriculture Handbook* 620. US Department of Agriculture, Forest Service, Washington, DC, 192 pp.

Schulman, E. (1947). Tree-ring hydrology in southern Califormia. *Laboratory of Tree-Ring Research Series* No. 4, *University of Arizona Bulletin* **18(3)**.

Schulman, E. (1951). Tree-ring indices of rainfall, temperature, and river flow. In *Compendium of Meteorology*, American Meteorological Society, (eds), pp. 1024–1029. Boston, MA.

Schulman, E. (1956). *Dendroclimatic Changes in Semiarid America.* University of Arizona Press, Tucson, 142 pp.

Schweingruber, F. H. (1980). Density fluctuations in annual rings of conifers in relation to climatic-ecological factors, or the problem of the false annual ring. Swiss Federal Institute of Forestry Research, Report No. 213, Birmensdorf, 35 pp. In German, with English summary.

Schweingruber, F. H. (1983). *Der Jahrring: Standort, Methodik, Zeit und Klima in der Dendrochronologie.* Verlag Paul Haupt, Bern, 234 pp. In German.

Schweingruber, F. H. (1986). Abrupt growth changes in conifers. *IUFRO Report*, Lijubliana, Sept. 1986.

Schweingruber, F. H. (personal communications). Swiss Federal Institute of Forestry research (Eidgenössiche Anstalt fur das Forstliche Versuuchswessen), Birmensdorf, ZH Switzerland.

Schweingruber, F. H., Fritts, H. C., Braker, O. U., Drew, L. G. and Schar, E. (1978a).

The x-ray technique as applied to dendroclimatology. *Tree-Ring Bulletin* **38**, 61–91.

Schweingruber, F. H., Braker, O. U. and Schar, E. (1978b). Dendroclimatic studies in Great Britain and in the Alps. In *Evolution of Planetary Atmospheres and the Climatology of the Earth*, pp. 369–72. CERN, Paris.

Schweingruber, F. H., Braker, O. U. and Schar, E. (1979). Dendroclimatic studies on conifers from central Europe and Great Britain. *Boreas* **8**, 427–452.

Schweingruber, F. H., Kontic, R. and Winkler-Seifert, A. (1983). Application of annual ring analysis in investigations of conifer die-back in Switzerland. *Swiss Institute of Forestry Research, Report* No. 253, Aug. 1983, Birmensdorf, pp. 6–29. In German, with English abstract.

Scott, J. T., Siccama, T. G., Johnson, A. H. and Briesch, A. R. (1984). Decline of red spruce in the Adirondacks, New York. *Bulletin of the Torrey Botanical Club* **111**, 438–444.

Self, S., Rampino, M. R. and Barbera, J. J. (1981). The possible effects of large 19th and 20th century volcanic eruptions on zonal and hemispheric surface temperatures. *Journal of Volcanology and Geothermal Research* **11**, 41–60.

Sheffield, R. M. and Cost, N. D. (1987). Behind the decline. *Journal of Forestry* **85**, 29–33.

Sheppard, P. R. and Jacoby, G. C. (1987). Tree ring data. *Journal of Forestry* **85**, 50–51.

Shroder, J. F., Jr, (1978). Dendrogeomorphological analysis of mass movement on Table Cliffs Plateu, Utah. *Quaternary Research* **9**, 168–185.

Shroder, J. F. Jr (1980). Dendrogeomorphology: review and new techniques of tree-ring dating. *Progress in Physical Geography* **4**, 161–188.

Shugart, H. H. (1984). *A Theory of Forest Dynamics: The Ecological Implications of Forest Succession Models*. Springer-Verlag, New York, 278 pp.

Shugart, H. H. (1987). Dynamic ecosystem consequences of tree birth and death patterns. *Bioscience* **37**, 596–602.

Sigafoos, R. S. (1964). Botanical evidence of floods and flood-plain deposition. *US Geological Survey Professional Paper* 485-A, Washington, DC.

Smiley, T. L. (1958). The geology and dating of Sunset Crater, Flagstaff, Arizona. In *Guidebook of the Black Mesa Basin, Northeastern Arizona*, R. Y. Anderson and J. W. Harshberger, eds., New Mexico Geological Society, Socorro, pp. 186–190.

Smith, W. H. (1985). Forest quality and air quality. *Journal of Forestry* **83**, 82–92.

Spencer, D. A. (1964). Porcupine population fluctuations in past centuries revealed by dendrochronology. *Journal of Applied Ecology* **1**, 127–49.

Stahle, D. W., Cleaveland, M. K. and Hehr, J. G. (1985a). A 450-year drought reconstruction for Arkansas, United States. *Nature* **316**, 530–532.

Stahle, D. W., Cook, E. R. and White, J. W. C. (1985b). Tree-ring dating of baldcypress and the potential for millennia-long chronologies in the southeast. *American Antiquity* **50**, 796–802.

Stevens, D. (1975). A computer program for simulating cambium activity and ring growth. *Tree-Ring Bulletin* **35**, 49–56.

Stockton, C. W. (1971). Feasibility of augmenting hydrologic records using tree-ring data. PhD dissertation, University of Arizona, Tucson, 172 pp.

Stockton, C. W. and Fritts, H. C. (1973). Long-term reconstruction of water level changes for Lake Athabasca by analysis of tree rings. *Water Resources Bulletin* **9**, 1006–1027.

Stockton, C. W. and Jacoby, Jr, G. C. (1976). Long-term surfacewater supply and streamflow trends in the Upper Colorado River Basin based on tree-ring analysis.

Lake Powell Research Project Bulletin 18, University of California, Los Angeles Institute of Geophysics and Planetary Physics, 70 pp.

Stockton, C. W. and Meko, D. M. (1975). A long-term history of drought occurrence in western United States as inferred from tree rings. *Weatherwise* **28**, 244–249.

Stockton, C. W. and Meko, D. M. (1983). Drought recurrence in the Great Plains as reconstructed from long-term tree-ring records. *Journal of Climate and Applied Meteorology* **22**, 17–29.

Stockton, C. W., Boggess, W. R. and Meko, D. M. (1985). Climate and tree rings. *Paleoclimate Analysis and Modeling*, Alan D. Hecht (ed.), pp. 71–161., Wiley, New York.

Stokes, M. A. and Smiley, T. L. (1968). *An Introduction to Tree-Ring Dating*. University of Chicago Press, 73 pp.

Swetnam, T. W. (1987). A dendrochronological assessment of western spruce budworm, *Choristoneura occidentalis*, Freeman, in the Southern Rocky Mountains. PhD dissertation, University of Arizona, Tucson, 213 pp.

Swetnam, T. W. and Dieterich, J. H. (1985). Fire history of ponderosa pine forests in the Gila Wilderness, New Mexico. In *Proceedings-Symposium and Workshop on Wilderness Fire*; Nov. 15–18, 1983, Missoula, MT. *General Technical Report* INT-182, U. S. Department of Agriculture, Forest Service, Ogden, UT, pp. 390–397.

Swetnam, T. W., Thompson, M. A. and Sutherland, E. K. (1985). Using dendrochronology to measure radial growth of defoliated trees. *Agriculture Handbook* 639, US Department of Agriculture, Forest Service, Washington, DC, 39 pp.

Taylor, R. M. (1981). Tree-ring analysis in forest productivity studies: an investigation of growth-climate relationships in the New Forest, Hampshire. *Journal of Biogeography* **8**, 293–312.

Taylor, B. L., Tzin Gal-Chen and Schneider, S. H. (1980). Volcanic eruptions and long-term temperature records: an empirical search for cause and effect. *Quarterly Journal of the Royal Meteorological Society* **106**, 175–199.

Telewski, F. W., Wakefield, A. H. and Jaffe, M. J. (1983). Computer assisted image analysis of tissues of ethrel treated *Pinus taeda* seedlings. *Plant Physiology* **72**, 177–181.

Thammincha, S. (1981). Climatic variation in radial growth of Scots pine and Norway spruce and its importance in growth estimation. *Acta Forestalia Fennica* **171**, 57 pp.

Thompson, M. A. (1981). Tree rings and air pollution: a case study of *Pinus monophylla* growing in east-central Nevada. *Environmental Pollution* (Series A) **26**, 251–266.

Tomlinson, G. H. (1983). Air pollutants and forest decline. *Environmental Science and Technology* **17**, 246A–256A.

Trefil, J. S. (1985). Concentric clues from growth rings unlock the past. *Smithsonian* **16**, 47–55.

Veblen, T. T. and Lorenz, D. C. (1986). Anthropogenic disturbance and recovery patterns in montane forests, Colorado Front Range. *Physical Geography* **7**, 1–24.

Villalba, R., Boninsegna, J. A. and Holmes, R. L. (1985). *Cedrela angustifolia* and *Juglans australis*, two new tropical species useful in dendrochronology. *Tree-Ring Bulletin* **45**, 25–35.

Wagener, W. W. (1961). Past fire incidence in Sierra Nevada Forests. *Journal of Forestry* **59**, 739–748.

Webb, G. E. (1983). *Tree Rings and Telescopes: The Scientific Career of A. E. Douglass*. The University of Arizona Press, Tucson, 242 pp.

Webb, T., Kutzback, J. and Street-Perrott, F. A. (1985). 20,000 years of global

climatic change: paleoclimatic research plan. In *Global Change*, T. F. Malone and J. G. Roederer, eds. ICSU Press, New York, pp. 182–219.
White, P. S. (1979). Pattern, process, and natural disturbance in vegetation. *Botanical Review* **45**, 229–299.
Wigley, T. M. L. (1982). Oxygen-18, carbon-13 and carbon-14 in tree rings. In *Climate from Tree Rings*, M. K. Hughes, P. M. Kelly, J. R. Pilcher and V. C. LaMarche, Jr., eds., pp. 18–21. Cambridge University Press.
Wigley, T. M. L., Briffa, K. R. and Jones, P. D. (1984). On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Climate and Applied Meteorology* **23**, 201–213.
Wilson, B. F. (1964). A model for cell production by the cambium of conifers. In *The Formation of Wood in Forest Trees*, M. H. Zimmermann (ed), pp. 19–36. Academic Press, New York.
Wilson, B. F. and Howard, R. A. (1968). A computer model for cambial activity. *Forest Science* **14**, 77–90.
Wood, F. B. Jn. (1988) The need for systems Research on Global Climate Change *Systems Research* **5**, 225–240.
Woodwell, G. M., Hobbie, J. E., Houghton, R. A. *et al.* (1983). Global deforestation: contribution to atmospheric carbon dioxide. *Science* **222**, 1081–1085.
Wycoff, W. R., Crookston, N. L. and Stage, A. R. (1982). User's guide to the stand prognosis model. US Department of Agriculture, Forest Service *General Technical Report* INT-133, Intermountain Forest and Range Experiment Station, Ogden, UT, 112 pp.
Yamaguchi, D. K. (1983). New tree-ring dates for recent eruptions of Mount St. Helens. *Quarternary Research* **20**, 246–250.
Yamaguchi, D. K. (1985). Tree-ring evidence for a two-year interval between recent prehistoric explosive eruptions of Mount St. Helens. *Geology* **13**, 554–557.
Yokobori, M. and Ohta A. (1983). Combined air pollution and pine ring structure observed xylochronologically. *European Journal of Forest Pathology* **13**, 30–45.
Young, C. E. (1979). Tree rings and Kaibab North deer hunting success, 1925–1975. *Journal of Arizona Nevada Academy of Sciences* **14**, 61–65.
Zackrisson, O. (1980). Forest fire history: ecological significance and dating problems in the North Swedish Boreal Forest. In *Proceedings of the Fire History Workshop*, Oct. 20–24, Tucson, Arizona. *General Technical Report* RM-81. US Department of Agriculture, Forest Service. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, pp. 120–125.
Zahner, R. and Myers, R. K. (1986a). A computer simulation for estimating drought impacts on southern pine growth rates. *Proceedings, Tree Rings and Forest Mensuration*, ed. by NCASI, Laboratory of Tree-Ring Research, University of Arizona, Tucson. April 9–11, 1986.
Zahner, R. and Myers, R. K. (1986b). Assessing the impact of drought on forest health. In *Forests, the World, & the Profession*. Proceedings of the 1986 Society of American Foresters National Convention, Birmingham, AL, Oct. 5–8. Society of American Foresters, 5400 Grosvenor Lane, Bethesda, MD 29814.
Zahner, R. and Myers, R. K. (1987). Dendroecological analysis of loblolly pine tree-ring chronologies for the near-term survey. Progress Report to Southeastern Forest Experiment Station, USDA Forest Service, Ashville, NC. 20 pp.
Zedaker, S. M., Hyink, D. M. and Smith, D. W. (1987). Growth declines in red spruce. *Journal of Forestry* **85**, 34–36.