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DENDROCHRONOLOGIA

Dendroecological applications in air pollution and environmental chemistry: research needs

Samuel B. McLaughlin,[1] Walter C. Shortle,[2] and Kevin T. Smith[3]

[1] Oak Ridge National Laboratory, Oak Ridge, TN, USA
[2] USDA Forest Service, Northeastern Research Station, Durham, NH, USA
[3] USDA Forest Service, Northeastern Research Station, Durham, NH, USA

Summary

During the past two decades, dendrochronology has evolved in new dimensions that have helped address both the extent and causes of impacts of regional scale environmental pollution on the productivity and function of forest ecosystems. Initial focus on the magnitude and timing of alterations of baseline growth levels of individual forest trees has now broadened to include characterization of the geographic extent of effects, their distribution among species, and their relationship to soils and biogeochemical cycles. Increasingly dendrochronology has benefitted from and contributed to improved understanding of the physiological and biogeochemical basis of air pollution effects on forest ecological processes. In addition, the need to consider levels and types of remedial action has raised concerns about the relative roles of anthropogenic and natural causative factors. The subdisciplines of dendroecology and dendrochemistry have evolved in response to those needs. Such applications have extended the field from its initial primary focus on historical growth and climatic reconstruction to an emerging role as an exploratory research tool with the potential to address basic questions about the roles of air pollution in modifying relationships between the amount, timing, distribution, and quality of tree growth and biogeochemical and atmospheric processes. In this paper we focus on two regional scale air quality issues, acidic deposition and tropospheric ozone, as stressors. We evaluate past success, current limitations, and future potential of dendrochronology as an investigative tool for both quantifying and understanding the effects of these stressors on forests. Important issues related to the use of dendrochemistry to evaluate effects of acidic deposition include the role of natural vs anthropogenic processes in cation mobilization in soils; biological and geochemical significance of increases in potentially phytotoxic metals and depletion of essential base cations in stem wood; and quantitative vs qualitative interpretation of patterns of element changes in wood related to metal mobility and species differ-

Address for correspondence:
Samuel B. McLaughlin, Oak Ridge National Laboratory,
P. O. Box 2008, Oak Ridge, TN 37831–6422, USA
Tel.: 1-8 65-5 74-73 58, Fax: 8 65-5 76-99 39
un4@ornl.gov

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ences in accumulation. Shifts in root growth, function, and distribution and increased sensitivity of tree growth to temperature stress are important indicators that cation depletion can alter forest function and the dendroclimatic signal. Critical challenges in evaluating forest responses to ozone, include defining the relative roles of episodic and chronic exposures in seasonal and annual growth cycles, and the quantifying impacts of ozone on the water relations of trees and stands. Here high-resolution measures of diurnal growth and water use patterns have the potential to identify critical features of both pollutant exposure and plant response. These insights should enhance our analytical capabilities in examining annual-scale measures of growth and provide needed understanding of changes in relationships of growth to climate. We conclude that dendrochronology, when coupled with mechanistic understanding of underlying ecological processes influencing growth, has been, and will continue to be, a valuable monitoring and investigative tool for exploring relationships between trees and their growing environment. We expect this role to become even more important in the future as better ways are sought to evaluate and predict forest growth and function in a changing global environment.

Keywords: Growth, forest decline, stress, acidic deposition, ozone, climate, growth – climate relationships

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Introduction

"For 70 years dendrochronology belonged to the purely academic sciences; today certain aspects have become accepted in the sphere of applied sciences" – Schweingruber 1986.

The evolution of dendrochronology as a research tool over the past 30 years has been a function of both improved measurement and analytical technology and improved understanding of the mechanisms of pollution effects on forests. This evolution has represented a natural response to the societal need for information on past and expected future response of forests to environmental change. The development of improved computational and statistical power initially provided the basis for deriving more refined and more powerful descriptors of relationships between tree growth and climate (Fritts et al. 1971). Such capabilities have become valuable both for the traditional reconstruction of past climatic patterns, and for examining the timing and characteristics of changes in the relationship of tree growth to chemical and physical climate over time.

Dendrochronology meets one of the basic research needs that confronted scientists initially trying to evaluate the nature and extent of forest responses to increases in regional air pollutants: to define changes in biological responses over time. Such changes may reflect either unique combinations of climatic factors or shifts in tree physiology or site quality that have altered tree growth potential. Consequently, technical advances that have broadened the capabilities of monitoring and characterizing changes in relationships between wood production and climatic variables have been important. These include techniques to measure tree-ring structure, chemical elemental concentrations, and isotopic ratios that reflect changes in both internal biological and external ecophysiological processes (Tessier et al. 1997).

As these capabilities have developed, dendrochronology has been able to contribute significantly to integrative studies of the magnitude and rate of changes, the strength of causal relationships, and ecological implications of the underlying responses of forests to air pollution stress. We define the application of dendrochronology to analysis of the ecological issues that necessarily involve tree biology, forest ecology, and soil biogeochemistry as dendroecology. Dendrochemistry represents a special application of dendroecology that addresses the relationship of wood chemistry to atmospheric, soil, and internal biological processes that influence element uptake and incorporation into annual growth rings.

The development of dendroecology as a tool in air pollution research has required a shift in emphasis and analytical techniques to address differences in both mechanisms and time scales of air pollution stress from those traditionally considered in dendroclimatic analyses (Cook, Kairiukstis 1990). The statistical and mathematical methods that have been developed have been designed to differentiate the trends or patterns of interest in the tree-ring record (the "signal") from the variation not attributable to the component of interest ("noise"). What constitutes signal and noise in the tree-ring series depends on the research question being investigated. Dendroclimatic reconstruction and the use of tree rings as a proxy record for climate depends on a stable, or at least definable, relationship of growth to climate. The signals of interest with air pollution effects have both similarities and differences from those in dendroclimatic analyses. On the one hand, the primary stresses from air pollutants may induce short term physiological changes that are similar to or interactive with climatic stresses (McLaughlin, Percy 1999) and like climate stress, they may vary strongly on annual or shorter time scales. For example, changes in root mass or rooting depth, and increased energy consumption in dark respiration may amplify tree responses to high temperature and drought. On the other hand, the fact that pollution may gradually alter the productivity of the site as well as the physiology of trees affected contributes to the greater relative emphasis on the slower or lagged responses associated with air pollution effects on forests.

The chemical signature from air pollution may change rapidly due to point source initiation, amelioration, or closure, however of greater current concern are the gradual changes that have occurred over decades, such as the buildup of regional emission burdens from diverse fossil-fuel sources. Associated biological effects at the tree and ecosystem level will reflect the temporal integration of physiological processes, which may include direct effects on carbohydrate production or allocation originating primarily in the canopy. Such changes due to lowered unit foliar rates and or reduced foliage production/retention under air pollution stress may affect growth over multiple seasons through reduction in carbohydrate reserves and result in reduced physiological resilience (McLaughlin et al. 1982). Alternatively responses may derive primarily from altered nutrient supply capacity, where altered root function or soil biogeochemical cycles are involved. A useful analogy for characterizing pollution effects on forest function and growth is that used in describing the types of effects of soil acidification on nutrient flow from forest soils (Robarge, Johnson 1992). It differentiates between changes in *intensity factors* related to short term alteration of processes and changes in *capacity factors* that influence the slower responding reservoirs of nutrients or energy. Both of these factors are important to understanding and measuring air pollution effects on forests and both should be considered capable of altering the influence of climatic stress on tree growth patterns (McLaughlin, Percy 1999). These interactions also call for diverse approaches to understanding the extent, nature, and implications of such effects on forest growth patterns.

McLaughlin and Braeker (1985) listed three levels of approach that can help focus dendroecological analyses of air pollution effects on forests. They included:

1. Definition of temporal and spatial patterns of change. This can help differentiate among candidate stresses based on correspondence of temporal or spatial patterns. Such patterns can help focus subsequent analyses by strengthening the case for some types of stresses and weakening the case for others.
2. Statistical analyses to define changes in relationships among tree growth or wood chemistry and changes in physical or chemical climate. These analyses may implicate potential mechanistic causative factors such as changes in overall carbohydrate economy, supply patterns of base cations, or shifts in the balance between roots and shoots.
3. Mechanistic studies that help define the underlying physiological mechanisms by which tree biology is altered by air pollution to influence the amount, timing, or chemistry of wood formed in

the annual growth cycle. These can be an important component of multidisciplinary investigative studies, which seek to understand the mechanistic basis of observed responses as well as identifying their magnitude and timing.

Figs. 1, 2, and 3 represent a sequence of responses that can be used to represent likely stages in alteration of tree growth by air pollution. They include alterations in the normal relationship of growth to climate, leading to increased statistical residuals in growth models (Fig. 1 after Grissino-Mayer, Butler 1993); reduced maximum latewood density reflective of reduced current-year carbohydrate reserves (Fig. 2, after Schweingruber et al. 1979); and, finally, reduced physiological resilience reflective of more severe limitations on carbohydrate reserves (Fig. 3 after McLaughlin et al. 1982). Although not inarguably linked to environmental change and air pollution, recent changes in the relationship between tree rings and climate have now been detected over a broad area of the northern hemisphere (Briffa et al. 1998) and specifically such changes are apparent for red spruce (*Picea rubens*) and silver fir (*Abies alba*) (Smith et al. 1999), two early responders to acidic deposition.

The occurrence of synoptic changes in the relationship of tree growth to climate has important implications for the use of dendroclimatolgy as a predictive tool and signals the need to better understand the role of contemporary stresses, including regional scale air pollution in those signals. Much has already been learned about the primary mechanisms of air pollution effects on tree growth, and, as interdisciplinary teams have explored the causes and implications of forest responses to regional air pollution (Schulze 1989, Eagar, Adams 1992, Fox, Mickler 1995, Miller, McBride 1998), we have gained increased understanding of the primary mechanisms underlying the patterns of observed changes in forest health. With that understanding has come the development of sequentially more refined hypotheses of causes and the need to test the robustness of these hypotheses in diverse forest settings. This has brought dendroecology to a level where it can function as an integral part of the exploratory process of successively testing and refining mechanistic hypotheses. We trace here some recent research findings and approaches that demonstrate the power and potential of dendroecology as a research tool for addressing the issues of regional

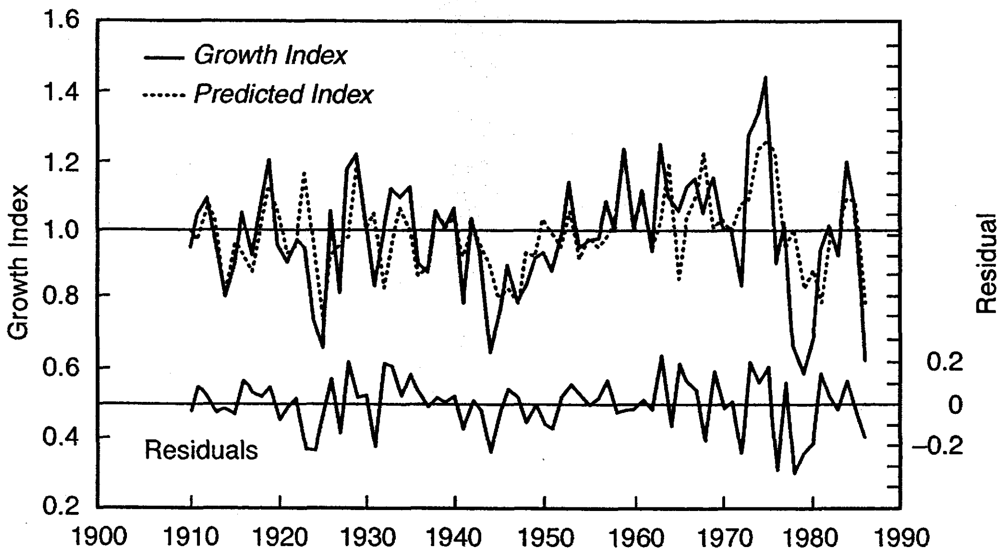


Figure 1. A sharp increase in residuals from a climate-growth model for shortleaf pine in the Southeastern U.S. occurred around 1960 and it was not explained by climatic variables or anomalous climatic events (after Grissino-Mayer, Butler, 1993). Retroactive examination of ozone exposure data for the region detected a statistically significant ($p < 0.05$) relationship between high annual ozone concentrations and higher negative residuals in this series (observations by SM).

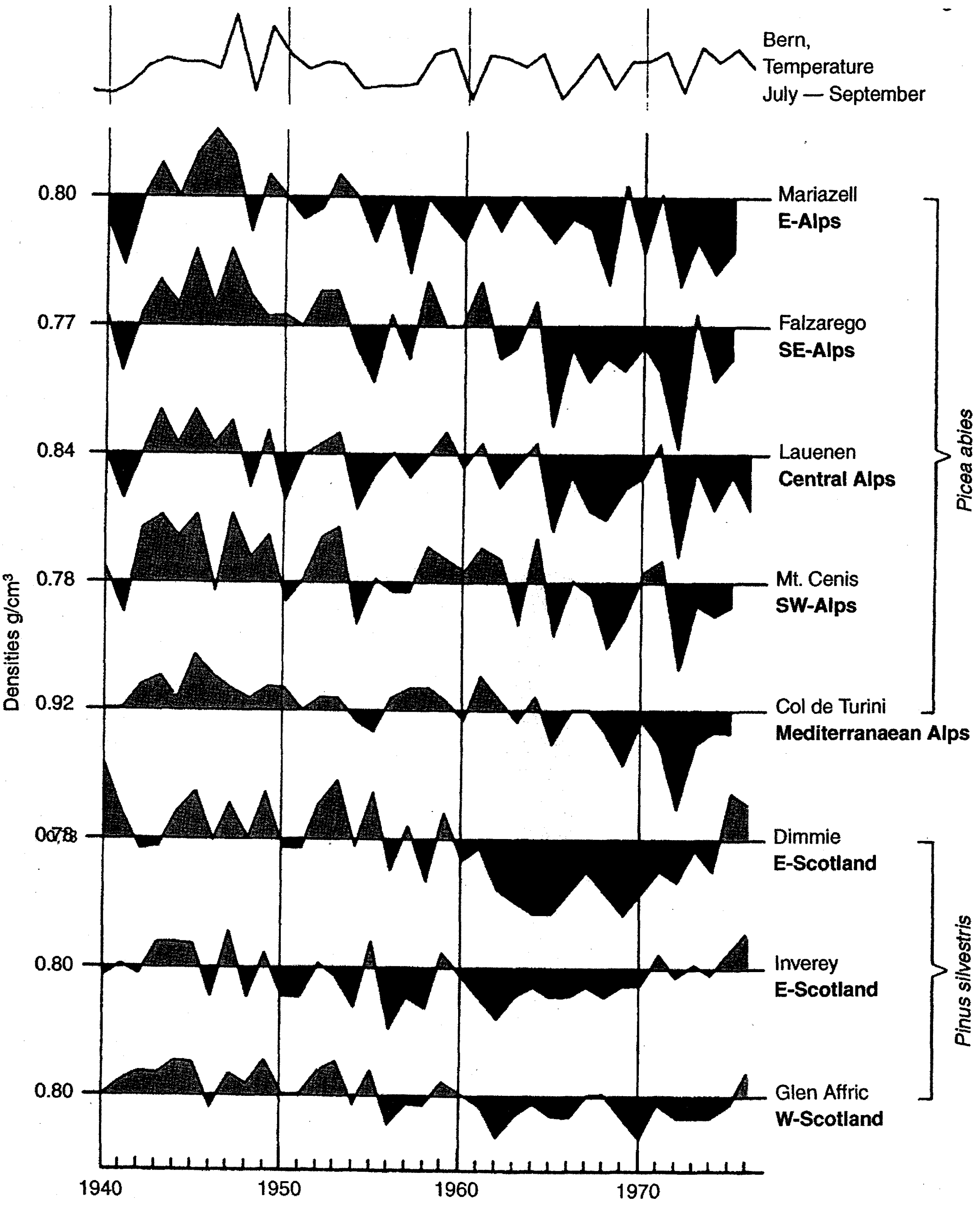


Figure 2. A consistent pattern of reduced latewood density of conifers was noted across a network of 115 study sites in Europe by Schweingruber et al. (1979). Reduced density was not associated with abnormal temperature patterns and suggests a possible reduction in late-season carbohydrate reserves.

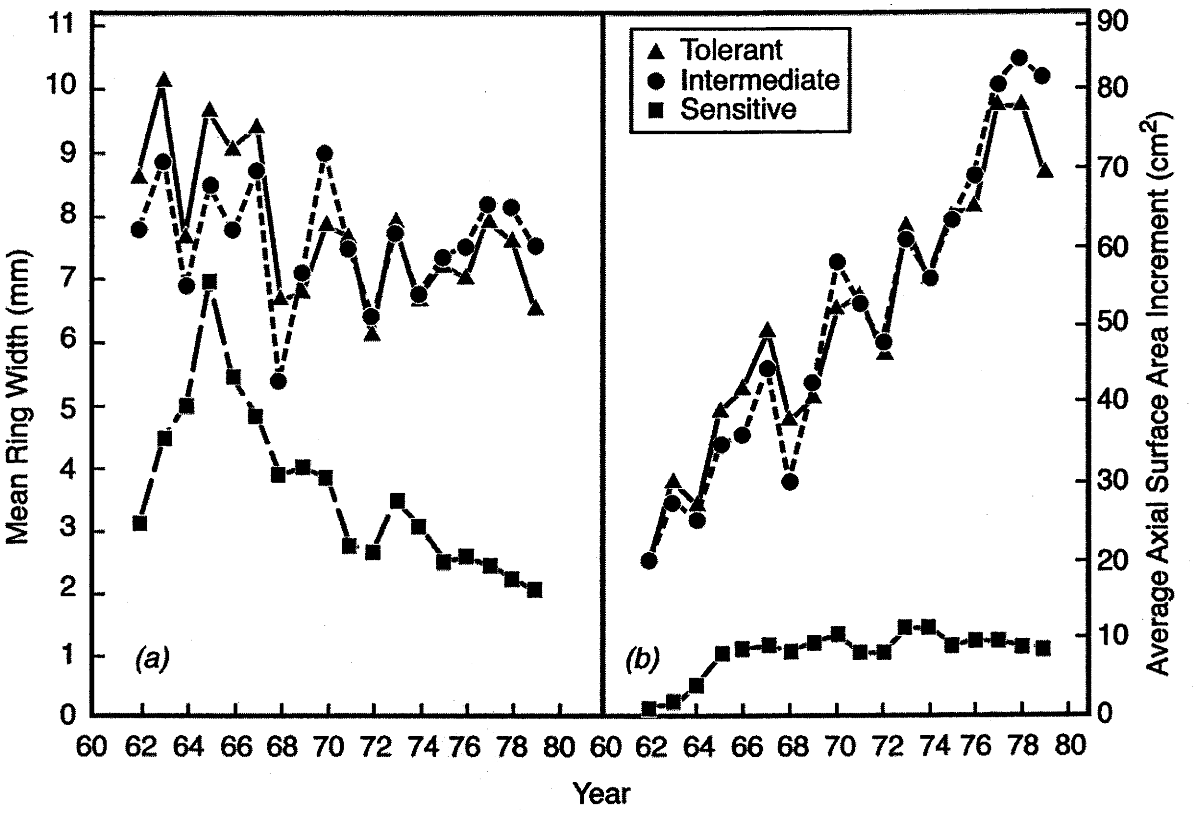


Figure 3. Physiological studies indicated that ozone-sensitive white pine trees transported less carbohydrates from needles that were both shorter in length and reduced in longevity. Reduced growth rates of sensitive trees were considered to reflect the accumulative effects of ozone and other climatic stresses and were associated with an apparent reduction of physiological resilience. This was evidenced by reduced capacity of these trees to recover from episodic climatic stress (after McLaughlin et al. 1982).

forest responses to air pollution. We use recent studies on the effects of acidic deposition and ozone as vehicles for this discussion and for the identification of future research needs.

Acidic deposition, tree ring chemistry, and forest growth

The effects of acidic deposition on forest health are closely related to changes in forest biogeochemical cycles and associated alterations in nutrient supply patterns. These linkages have led to interest in evaluating changing patterns of wood chemistry both as an indicator of changes in availability of soil nutrients, such as base cations, and as a record of temporal patterns of soil acidification *per se*. The chronosequence of changes in regional emissions of strong acid anions (SO_X and NO_X), the baseline status and changes in forest soil chemistry, and historical patterns of change in wood chemistry are all important considerations in dendrochemical analyses that have developed in response to those needs.

The strong regional increases (2X-5X) in atmospheric emission of sulfur and nitrogen oxides in industrialized countries during the 20th century (OECD 1977, Husar, Holloway 1983) have resulted in the sequential appearance of altered global biogeochemical signatures at diverse scales. Increased deposition of excess sulfate and nitrate in Greenland ice occurred in the first and seventh decade of this period (Mayewski et al. 1986). Changes in stem growth and wood chemistry of some sensitive forest species began in the fifth and sixth decades (Bondietti et al. 1989). In the seventh decade the acidity of lakes began to increase (Charles 1984) and some fish populations began to decline. By the eighth decade of the

20th Century, research on "acid rain" was well underway in aquatic ecosystems, and findings of long-term intensive studies at monitored watersheds have recently been reviewed (Driscoll et al. 2001).

In the eighth decade, concern about regional declines in forest health accelerated as spruce and fir on acid-sensitive sites were dying in central Europe and in the northeastern United States (Prinz 1987, Schutt, Cowling 1985, McLaughlin 1985). Research on dendrochronolgy and dendrochemistry coupled with work on soil of the rooting zone and biochemical markers of foliage was initiated at this time to learn about the timing and impact of acidic deposition on forest soil status and tree growth. Results of this work have also recently been reviewed (Shortle et al. 2000; Lawrence et al. 2000). Fundamental to the current understanding of both the changes that acidic deposition causes in forest soils and to the interpretation of chemical and biological signals recorded in tree rings as a consequence of those changes is recognition of the types and sources of soil acidity in forest ecosystems.

Forest growth is itself an acidifying process resulting from exchange of the acids and reducing power generated in photosynthesis as base cations required for growth are accumulated from the soil (Ulrich 1984). Natural acidification is a slow process that can take an initially base-rich soil through well recognized buffering stages to a strongly acid condition. There are important differences in this slow natural acidification, which is effected by internal biological activity, and the much-accelerated acidification produced by anthropogenic inputs of acidic deposition. Biological acidification occurs at the root surfaces and in the organic soil horizon in response to temperature and seasonal biological cycles. Base cations, Ca, Mg, K, Na, bound to organic matter are readily available for root uptake and exchange is facilitated through the production of biological acidity around the absorbing fine root tips. Thus mobilization and uptake are linked in biological acidification.

Increasing the input of inorganic acidity (sulfuric and nitric acids derived from atmospheric emission of sulfur and nitrogen oxides) increases the mobilization of ionically bound cations on the cation exchange system of forest soils. In contrast to biological acidification, this non-biological acidity mobilizes cations, not just around absorbing roots, but throughout the soil. In addition, mobilization occurs not just during periods of maximum biological demand, but in stochastic patterns linked to rainfall events throughout the year. It is controlled by the cation exchange capacity (CEC) of the soil, base saturation of CEC, soil pH, and inputs of strong anions (SO_4 and NO_X; Robarge, Johnson 1992). The mobilization of cations within forest soils includes both the base cations Ca, Mg, and K, which are important plant nutrients, as well as acidic cations Al, H, Mn, and Fe which compete with base cations, both on soil exchange sites and in cell walls within absorptive roots. Both Al and Fe have increased markedly in recent decades in stem wood of trees at some poorly-buffered or highly-leached sites and these elements appear to provide a time-stable signal of soil acidification (McClenahen et al. 1989). Increasing Al in wood of several species has been well correlated with decreasing radial growth (Baes, McLaughlin 1984, Bondietti et al. 1989, Jordan et al. 1990, Mohamed et al. 1997) and appears to provide a good indicator of soil acidification effects on growth. Long-term dendrochemical records indicate that increases in iron and aluminum in the wood of shortleaf pine (*Pinus echinata*) were good indicators of acidification produced by both 19th century emissions from a regional smelter and twentieth century acidic deposition from diverse regional sources (Fig. 4).

Uptake patterns of acidic cations as reflected in stemwood concentration profiles can provide important information about changes in soil acidity and cation exchange capacity. In spruce forests the cation exchange capacity is strongly linked to organic matter in the forest floor and the upper mineral soil. Under conditions of low soil pH combined with low base saturation of soil exchange sites, strong anions (SO_4 and NO_3) deposited in acidic deposition increasingly mobilize acidic cations. Mobile cations near absorbing roots are available for uptake, however at lower pH, acidic cations such as Al and Fe predominate in the soil solution and can block uptake and retention of base cations by fine roots (Schroder et al. 1988). The exchange reactions invol-

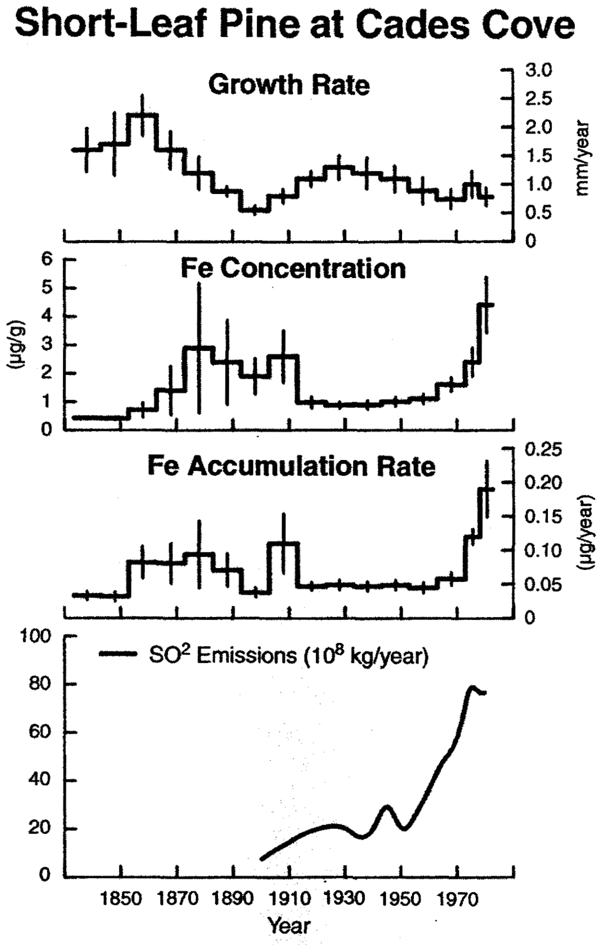


Figure 4. Increases in the acidic cations Al and Fe in shortleaf pine stem wood were detected in Tennessee in response to historical start-up and remediation (1910) of an iron smelter 88 km away. A subsequent increase in these elements was associated with more recent increases in emissions of sulfur and nitrogen from multiple sources within the region (after Baes, McLaughlin 1984).

ving cations in soil solutions follow an energy/size based hierarchy in which binding strength influences the balance between retention and release on cell walls and binding strength is in order of Al > H > Fe > Mn > Mg > Ca (Stienen, Bauch 1988). As cations absorbed by the roots move upward in the transpiration stream they participate in cation exchange with sites on and within the cell walls (Momoshima, Bondietti 1990). The signal retained in these walls is a function of both plant and soil chemistry and thereby provides the analytical basis for dendrochemistry.

Because cation uptake and deposition in woody tissues is both element specific and subject to internal biological regulation (Smith, Shortle 1996) there is substantial variability in the utility of wood chemical signals as indicators of environmental change. A review of the use of dendrochemical analyses in environmental monitoring (Watmough 1998) indicates that, while there is strong evidence linking metal uptake and metal deposition around point sources, there are still substantial gaps in our understanding of the processes that control uptake and behavior of metals at lower levels in the regional environment. Among the most promising applications for regional-scale analyses have been linkages between patterns of change of base cations and aluminum and hypothesized changes in soil acidification. We focus here on calcium because it has a rate-limiting role in many critical aspects of plant growth and health (McLaughlin, Wimmer 1999) and because it is a useful indicator of both physiological and soil chemical changes experimentally linked to soil acidification (McLaughlin, Kohut 1992).

Calcium is the most abundant metal element in trees and on the cation exchange sites of the forest floor. Its limited mobility in plants makes Ca supply rates important to many plant functions, including cell wall growth, membrane function, regulation of water and carbohydrate movement, and defense against diseases and repair of cellular injury (McLaughlin, Wimmer 1999). Its mobilization by acidic deposition and increased uptake by tree roots form the basis of using changes in calcium concentration of dated tree rings as a marker of calcium depletion in soil. An empirically derived model of cation binding in red spruce wood (Momoshima, Bondietti 1990, Bondietti et al. 1990, Shortle, Bondietti 1992) indicates that the binding capacity of spruce wood decreases from pith to bark. Therefore, if sap concentration and pH are constant over time (homeostasis), the calcium concentration is expected to decrease from one decade to the next. A steady decreases in calcium over time in tree rings is the expected pattern with age due to reduced Ca binding potential in the younger rings of older trees and may not indicate that Ca availability at the site has declined. Rather it is the normal pattern based on changes in wood anatomy and chemistry as trees grow older and larger. On the contrary, calcium depletion of soil would initially be seen as an enrichment in wood as calcium is transferred from the soil cation exchange system to the wood cell wall cation exchange complex. Increased calcium availability should be recorded in the tree-ring record as a "bump", indicating a brief period of enrichment before a return to homeostatic conditions in the sapstream (Fig. 5). This period of enhancement will not be recorded in a single ring, but in all rings of sapwood conducting sap, which might be 10 rings in a smaller, younger, fast-growing tree, or 30 rings in a larger, older, slower growing tree. The youngest rings closest to the cambium typically conduct more sap than older rings approaching the sapwood/heartwood boundary. Thus, annual-scale availability of Ca will influence cation exchange in the cross section of active rings during the year of occurrence. An individual ring will record an historical average of availability during the time when it was functional in water transport and cation exchange and the influence of subsequent transport will be roughly inversely proportional to the time since it was formed.

The pattern of enrichment of spruce sapwood by ^{90}Sr (Sr is an analog of calcium) is consistent with this view. When the atmosphere was enriched with this isotope of Sr due to open air testing of thermonuclear devices and Sr was deposited on forests, the enriched area covered 20–30 tree rings with the most enriched area being the newest sapwood at the time of deposition. Sr activity decreased in older rings toward the sapwood heartwood boundary (Bondietti et al. 1990, Momoshima, Bondietti 1990). Research to date on red spruce has shown that interpretation of patterns of cations in dated tree-ring tissue requires a thorough understanding of tree biology and its linkage to organic geochemical cycling in the forest environment (Smith, Shortle 1996). Trees are not passive recorders of environmental change, but strongly regulate the inward passage of matter from the external environment, a process which is highly variable in space and time. Internal biological processes that could potentially alter a record of calcium enrichment are sapwood aging, heartwood formation, infection of wood exposed by injury, and tree response to wall off the spread of infection, a process called compartmentalization (Smith, Shortle 1996). Calcium is actively excluded from the sym-

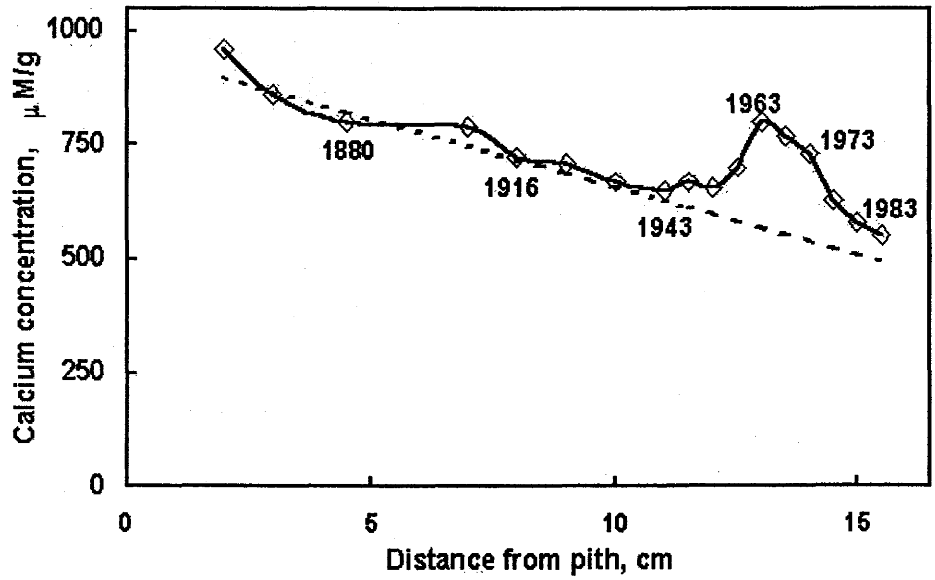


Figure 5. Increases in calcium concentration in stem wood have been an early response to increased acidic depostion and increased mobilization and loss of calcium from soils (after Bondietti et. al. 1992).

plast of living cells in the sapwood so it is relatively independent of changes in cell physiology that occur as sapwood ages and becomes heartwood. As long as no major change in acidity occurs at the sapwood/heartwood boundary in trees, the calcium enrichment signal brought about by a strong pulse of acidity acting in the root zone should be time-stable unless altered by wood infections and sapwood defense against the spread of infections, a consequence of the participation of Ca in woody defense mechanisms. In some tree species, e. g. black cherry (*Prunus serotina*), a marked decrease in pH at the sapwood/heartwood boundary is associated with marked decreases in Ca concentration; thus, potentially eliminating any signal of change in sapwood. In spruce, wood maturation is not accompanied by internal acidification. Consequently, the concentration of calcium in spruce wood is not affected by the transformation of sapwood into heartwood. Infection and responses to infection that can cause large changes in concentrations of calcium and other metals can generally be detected by careful visual inspection to identify color changes in wood and the altered wood can be eliminated from the sample.

After consideration of many of the physical, chemical, and biological factors that could affect the pat-

Table 1. Methods and markers of environmental change related to acidic deposition in the northeastern U.S.

Method:	**Environmental Monitoring**		**Glacial chemistry**		**Sediment biology**	**Dendrochemistry**			**Dendrochronology**		
Marker:	**Atmospheric emissions[1]**		**Ice incorporation[2]**		**Lake pH[3]**	**Increased calcium Tree age class[4]**			**Increased growth Tree age class[5]**		
Decade	**S**	**N**	**S**	**N**		**1871**	**1901**	**1931**	**1871**	**1901**	**1931**
1871–1880	x[6]	x	0	–	5.5–6.0	0	x	x	++	x	x
1881–1890	x	x	0	–	5.5–6.0	0	x	x	++	x	x
1891–1900	x	x	0	–	5.5–6.0	0	x	x	0	x	x
1901–1910	+	+	+	+	5.5–6.0	0	0	x	0	+	x
1911–1920	+	+	0	0	5.5–6.0	+	0	x	0	0	x
1921–1930	0	+	0	0	5.5–6.0	+	+	x	+	++	x
1931–1940	–	0	0	0	5.5–6.0	0	+	0	0	++	++
1941–1950	+	+	+	0	5.5–6.0	+	+	0	+	+	++
1951–1960	0	+	0	+	5.5–6.0	+	+	+	++	++	++
1961–1970	+	+	+	+	5.0–5.5	++	++	++	0	0	0
1971–1980	–	+	0	+	4.5–5.0	0	0	+	0	0	0
1981–1990	–	0	x	x	x	0	0	0	0	0	0
1991–2000	–	0	x	x	x	x	x	x	x	x	x

[1] Derived from National Acid Precipitation Program 1993. Total decadal emissions of sulfur and nitrogen that remained constant or decreased from the previous decade were marked "0". Total decadal emissions that increased relative to the previous decade were marked with a "+".

[2] Derived from Mayewski et al. 1986. Total decadal incorporation of sulfur and nitrogen that remained constant or decreased from the previous decade were marked "0". Total decadal incorporation that increased relative to the previous decade were marked with a "+".

[3] Derived from Charles 1984.

[4] Age classes were based on the earliest availability of wood for dendrochemical analysis. Age classes are named based on the starting year for decadal analysis. Within each age class, each decade of wood was scored for the percent frequency of trees with increased (> 5 %) calcium concentration. Scores were marked as "0" for < 10 %, "+" for 10–20 %, and "++" for > 20 % frequency of increased calcium concentration.

[5] Within each age class, each decade of ring widths was scored for the percent frequency of trees with increased annualized mean ring width (> 50 %) compared to the previous decade. Scores were marked as "0" for < 10 %, "+" for 10–20 %, and "++" for > 20 % frequency of increased growth.

tern of calcium in tree rings, and after development of a fast, safe, and reliable method for extraction of major inorganic cations from small quantities of wood (Minocha, Shortle 1993), a study was made of canopy red spruce standards growing on forest more exposed to decades of acidic deposition across a region from western New York to eastern Maine (Shortle et al. 2000). Tree-ring records of the frequency of calcium enrichment (an increase of 5 % or more relative to the prior decade) and the frequency of growth enhancement (an increase of 50 % or more in mean annual increment relative to the previous decade) were determined for 142 trees divided into three age classes. The resulting patterns were compared to records of changing atmospheric emissions, ice depositions, and lake pH derived from sediment records (Tab. 1).

Comparison of ring growth and dendrochemistry with other natural recording systems supports the linkage of air pollution and tree response that can be assessed using dendroecology. Twice in the 20th Century, S and N increased in air and ice, 1901–1910 and 1961–1970. During the first period, no effect was discernable in forests or lakes; but during the second, a strong enrichment signal occurs in wood and lake water became more acidic. Growth enhancement which had been strong across all age classes in 1951–1960, when N, but not S increased in air and ice, ceased when S increased strongly in 1961–1970 and has not been observed since. Enrichment of wood did appear to increase more often over the decades after 1901–1910, compared to earlier decades in the oldest trees, but patterns in younger trees indicate that a tree must be several decades old for the signal to appear. This most likely has to do with root development and a greater tendency of larger, older trees with higher calcium demand to be affected by changes in the lower forest floor and upper mineral soil. These are the sites first and most significantly altered by acidic deposition. Forest floor samples taken at these sites in the early 1990s indicated that Ca uptake is no longer related to exchangeable H concentration as would be the case if biological acidity were governing Ca availability (Shortle et al. 1997). Exchangeable Al now appears to be regulating the Ca availability as would be the case if non-biological acidity were mobilizing, Al as well as Ca. The tree-ring record of Ca enrichment coupled with a mechanistic understanding of processes regulating Ca availability indicate that the growth rates of some high elevation forests in the eastern United States, which have experienced thinning by high mortality and are currently exposed to high levels of nitrogen deposition, are more likely limited by reduced calcium and magnesium availability from acidified soils than by either nitrogen supply or carbon fixation in photosynthesis.

However, neither the critical levels of Ca in wood, nor how they relate to the residual wood chemistry signature, nor critical features of Ca supply patterns are presently well understood.

Acidic deposition, tree physiology, and shifts in growth-climate relationships

Investigation into the decline in health of red spruce, which first became apparent in the Northeastern United States in the early 1960s (Johnson, Siccama 1983), represents a classic case of dendroecology being used as one of a suite of approaches in multidisciplinary, multi-institutional efforts to test multiple hypotheses of causation (Eagar, Adams 1992 and Fig. 6). Early dendroecological studies (Johnson, Siccama 1983, McLaughlin et al. 1987) described a region-wide growth decline in red spruce. The decline was most severe at high elevation northern locations, where it was accompanied by severe mortality (≥ 50 % loss in many stands), and broadly synchronous (1955–1965) across the wide ranging Appalachian mountains. In Tennessee and North Carolina, it was restricted to high elevations, not initially accompanied by severe mortality and delayed approximately 5 years compared to northern sites (McLaughlin et al. 1987). Observed growth declines were not attributable to competition or tree aging (Cook, Zedaker 1992), but growth did exhibit evidence of negative departures from levels predicted by climate-based models derived from a 1900–1940 calibration interval (McLaughlin et al. 1987). In addition enhanced sensitivity to warmer late-summer temperatures was noted in this and following stud-

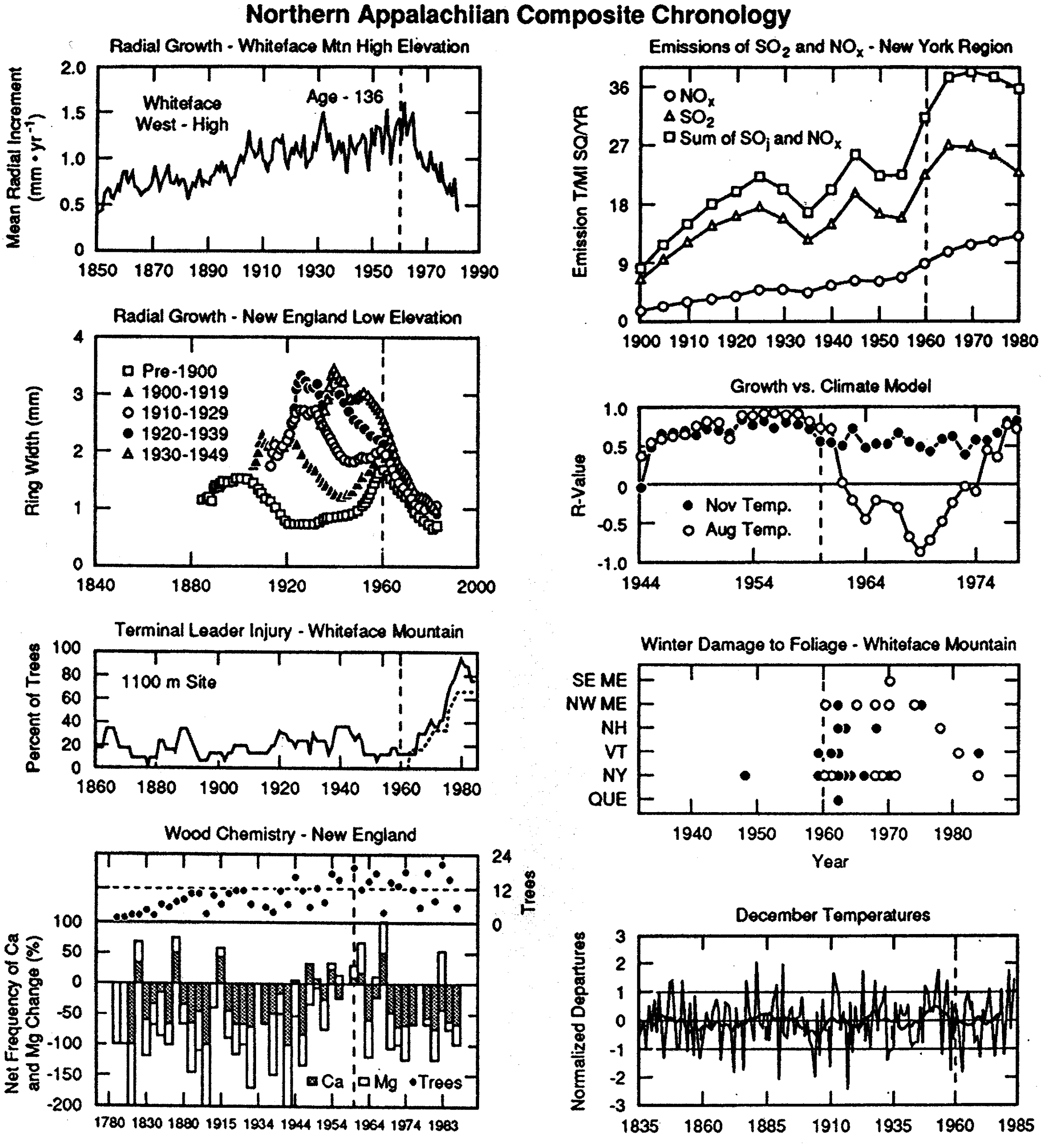
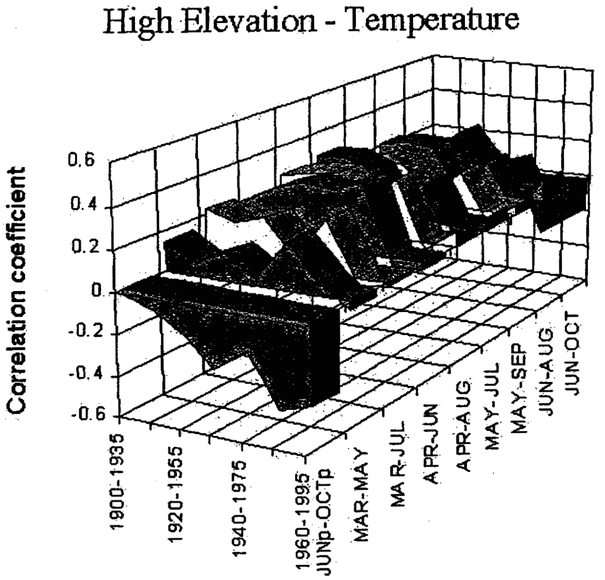


Figure 6. Dendroecological studies played an important role in defining growth patterns and supporting mechanistic interpretations of the role of acidic deposition in decline of red spruce at widespread locations in the eastern United States (after Johnson et al. 1992). Viewing from top to bottom and left to right, these included defining the timing and magnitude of growth reductions in large trees at high elevations across the region; eliminating age and competiton as major causal factors in decreases in growth also noted at lower elevations; identifying an increase in terminal leader injury associated with freezing injury; and defining an increase in base cation uptake into wood. A period of rapid increase in emissions of S and N around 1960 (upper right) is marked as a reference across plots) and was associated with a change in the growth-climate relationship. Dendroclimatic analyses identified an increasingly negative response to current August temperature. This and an increased frequence of winter cold injury to needles occurred in the absence of anomalous summer or winter temperatures.

ies (Cook, Zedaker 1992). Physiological studies reviewed by McLaughlin and Kohut (1992) recorded changes in carbohydrate economy (including reduced photosynthesis and increased respiration), and reduced growth associated with increasing exposure to acid mists and reduced calcium supply typical of high elevation sites. Both foliar and soil exposures to acidic deposition were involved in these responses. In addition acid deposition reduced deeper rooting in experimental exposures, a response that was reduced by calcium addition to soils (McLaughlin et al. 1993).

An apparent increase in the sensitivity of red spruce to winter injury associated with increased exposure of foliage to acid mists was detected in initial field studies (DeHayes et al. 1991, Vann et al. 1992). These results have been followed by more recent cytological studies identifying reduction of membrane-associated calcium as contributory factor to loss of cold hardiness (DeHayes et al. 1997). These physiological studies supported by dendroecological analyses of LeBlanc and Raynal (1990) and Cook and Zedaker (1992) have firmed the evidence that red spruce at sites most exposed to acidic deposition has become more sensitive to climate in recent decades.

In the Southern Appalachians where winter injury is much less severe, dendroecological analyses have highlighted the negative association of annual red spruce growth in recent decades with warmer temperatures and higher annual rainfall levels (McLaughlin et al. 1997 and Fig. 7). This explanation is compatible with the expected tree responses in a carbohydrate-limited system in which calcium deficiency induced by acidic deposition amplifies increased respiratory losses under warmer temperatures and is amplified by rain-induced mobilization of aluminum and accelerated leaching of calcium in these naturally acidic soils. Thus, both dendroecological and physiological approaches have played important, interactive, and reinforcing roles in contributing to the conclusion that acid deposition played an important role in the declining health of red spruce in the Eastern US in recent decades (Johnson et al. 1992).



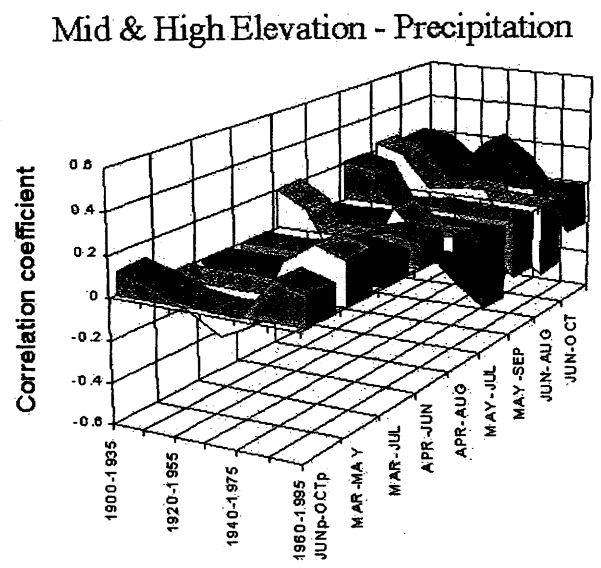


Figure 7. Changes in sensitivity of growth of mature red spruce trees to both temperature (a) and precipitation (b) on Mt. LeConte are compatible with physiological studies that indicated that reduced growth and increased respiratory costs were associated with Ca supply limitations in this acidic, high-elevation environment (after McLaughlin et al. 1997).

Ozone, tree physiology, and shifts in growth climate relationships

Perhaps the strongest evidence of the occurrence regional atmospheric pollution at levels sufficient to alter forest growth has come from numerous studies on thresholds of phytotoxicity and mechanisms of action of ozone. The threshold for plant damage from ozone (around 40 parts per billion (80 µg/l) is currently exceeded on a regular basis over large agroindustrial areas of the world and conditions in many of these areas are expected to worsen in the decades ahead (Chameides et al. 1994). Yet, despite decades of research predominantly on responses to ozone of crop plants and tree seedlings under controlled conditions and despite the occurrence of widespread visible injury of foliage of forest trees by ozone, there have been relatively few studies that have attempted to evaluate effects of ambient ozone pollution on growth of mature forest trees.

Based on controlled exposure studies conducted principally in laboratory or field chambers, the basic mechanisms of ozone effects have been identified (Reich 1987, NAS 1977). These include primarily reduced photosynthesis, increased dark respiration, changes in leaf conductance, and altered patterns of carbon allocation, including reduced allocation of carbon to root systems. Collectively these processes are important to dendroclimatology, since they provide a mechanistic basis for alterations of the relationship of growth to climate under increasing air pollution stress (McLaughlin, Percy 1999). Such effects may be expressed as a decrease in predictive capabilities of models based solely on physical climate (Grissino-Mayer, Butler 1993 and Fig. 1) or increased importance of climatic variables caused by increasing pollutant stress.

Effects of ozone on forest species have most frequently been expressed as reduced growth, and reviews are in general agreement in estimating losses at 0–10 % per year at ambient levels under controlled exposures (Chappelka, Samuelson 1998, Broadmeadow 1997). However, these results are based predominantly on studies with saplings and seedlings. When estimates for larger trees under field conditions are included, annual losses are similarly highly variable from year to year and have been estimated to range from 0–40 % in individual years (McLaughlin, Percy 1999). Differences in responses to ozone between those noted in controlled exposure studies with saplings and larger forest trees can be partially explained based on measurements of differences in leaf conductances related to size classes, leafing habit, and rooting environment between seedlings and saplings and larger forest trees (Samuelson, Kelly 2001). Other important differences relate to large differences in patterns of allocation of carbon to maintenance, defense, and repair between mature trees and seedlings or saplings (McLaughlin, Shriner 1980).

Interest in obtaining regional estimates of effects of ozone on forest growth has led to modeling relationships among ozone exposure, ozone uptake, and growth for multiple species and large regions (Hogsett et al. 1993, Ollinger et al.1997, Weinstein et al. 2000). From such efforts it has become increasingly apparent that mechanistic approaches based on data derived from controlled studies with tree seedlings and saplings, while useful in providing general estimates, may have many shortcomings when applied to mature forest trees (Samuelson, Kelly 2001). These differences relate to canopy architecture and exposure, and differences in rooting volume and water relations between containerized seedlings and naturally rooted forest trees. They also relate to previously mentioned differences in leaf conductance and carbon allocation demands between small and mature trees. Such differences suggest that the "top-down" approach offered by dendroecology should play a pivotal role in characterizing end point effects on growth and perhaps providing a basis for improved understanding and characterization of the mechanistic basis for such effects (McLaughlin, Downing 1997).

Several dendroecological studies now support the concept that mature trees may be more sensitive to growth inhibition by ambient ozone and may be affected differently than tree seedlings. A major issue appears to be potential differences in responses of mature trees to moisture stress. In controlled studies with smaller or containerized plants, stomatal closure can be an important response to increasing ozone exposure and can protect plants from further ozone uptake and associated foliar damage (Tingey, Hogsett 1985). However, such generalizations have not held up upon further scrutiny as, for example, Pearson and Mansfield (1993) found that ozone promoted stomatal closure in well-watered birch saplings and impeded closure in saplings previously stressed by drought.

The situation may also be very different in a forest environment where rooting is deeper and adaptations to modest drought are more typical. Dendroecological analyses in the US with southern pines (Zahner et al. 1989; McLaughlin, Downing 1996, 1997), with big-cone Douglas fir in California (Peterson et al. 1995) and with silver fir in the Jura Mountains of Europe (Bert 1993) suggest that drought and air pollution may interact to enhance growth reduction of mature forest trees. Potential mechanisms for such effects include both reduced root mass and fine root turnover as well as reduced control over stomatal regulation of transpiration (McLaughlin, Percy 1999). Differentiation among these processes is an important research need.

Numerous studies document reduced root biomass in response to increasing ozone (Cooley, Manning 1987). In addition root biomass reductions may be enhanced by combinations of ozone and nitrogen deposition (Gruelke et al. 1998), both of which reduce carbon allocation below ground. A wide range of mechanistic studies with tree seedlings or branches of mature trees now support the concept of ozone-induced reductions in stomatal control of transpiration. Mechanisms include increased conductance associated with enhanced opening or reduced stomatal closure at night, which can lead to increased transpiration and increased water stress in trees (Lee et al. 1990; Wallin, Skärby 1992; Maier-Maercker, Koch 1992; Maier-Maercker 1998). The implications of increased water use by mature forest trees under ambient ozone levels are significant, not only in terms of the potential for direct limitation of growth, but also in terms of changes in competitive status among overstory and understory strata and changes in forest hydrology. The potential for ozone to alter tree responses to a warmer and episodically drier climate has important implications for forest growth responses to projected increases in global warming (McLaughlin, Percy 1999).

From a dendroecological perspective the identification of shifts in the statistical strength of the tree growth x climate relationships over time in a traditional dendroclimatic approach (Grissino-Mayer, Butler 1993) as well as the inclusion of ozone as an additional climatic variable (Bartholomay et al. 1997) suggest that ozone exposure may be an increasingly important component of regional climate. Bartholomay et al. (1997) in fact found that ozone exposure, notably shorter term exposure episodes, reduced tree ring indices of white pine and was a stronger influence on growth than any of the climatic variables examined.

The need to understand the interplay of shorter term ozone exposure episodes and seasonal growth dynamics has led to a high resolution form of dendroecology that we have designated dendrophysiology. It represents an effort to relate shorter term (interannual and diurnal) patterns of stem expansion of individual trees in response to climatic variables, including ozone, to short to mid term growth rates. The rationale for such an approach is conceptually analogous to the use of short term physiological indicators of leaf function such as photosynthesis or transpiration to estimate forest growth potential. The difference is that organ-specific measures of physiological processes must be linked to whole tree performance by models, while whole tree measures such as stem growth patterns measure the ultimate end-point response (growth) that must be understood in the light of underlying physiological processes. McLaughlin and Downing (1996, 1997) have used the dendrophysiological approach to identify both a biologically significant threshold level for ozone exposure (exposures at or above 40 ppb) and amplification of drought stress by ambient ozone levels in mature loblolly pine trees. Such studies, based on serial manual measurements at daily or longer scales can identify important interactions, but not responsible mechanisms, which are important for developing improved understanding and predictive capacity. This approach may also provide important insights into the critical components of exposure dose that comprise the longer term critical loads associated with cumulative plant dysfunction.

Newer techniques which couple very high frequency automated measurements of daily stem expansion and contraction cycles (Herzog, Häsler 1995, Downes et al. 1999) provide an important new tool for exploring relationships of tree growth to physical and chemical climate. The diurnal stem expansion pattern noted in Fig. 8 describes several features that reflect the physiological integration of stem growth with water uptake and loss of an individual tree over a daily cycle. The inflection points for stem expansion and contraction provide a measure of the balance between water supply, water demand, and net stem dimensional gain that are physiological indicators of a trees responses to its external envir-

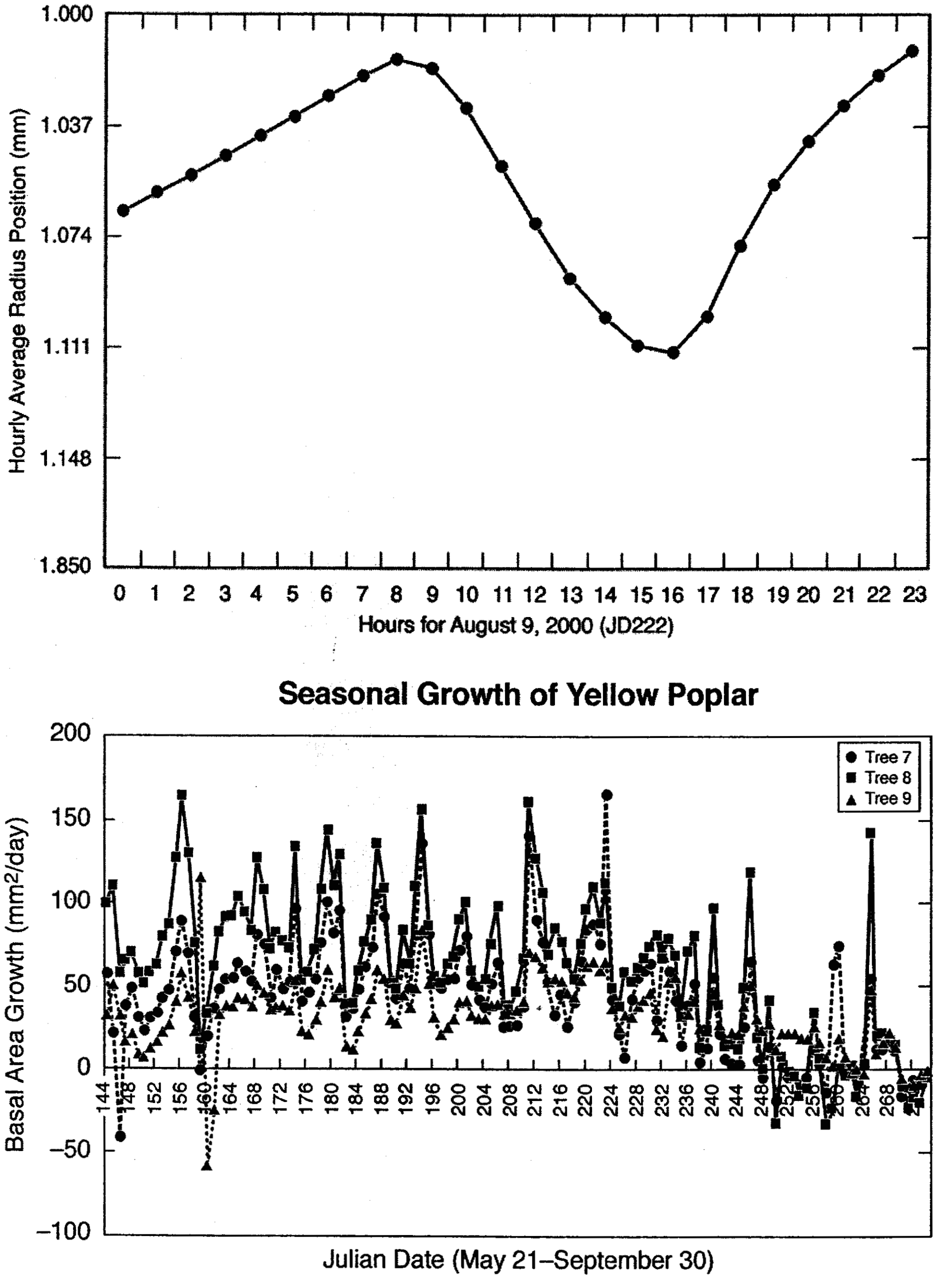


Figure 8. Seasonal growth patterns in growth of yellow poplar in East Tennessee display both diurnal (a) and seasonal (b) variations in stem expansion that reflect the influence of water supply, water demand, and carbon allocation on stem growth (unpublished data of McLaughlin).

onment. The magnitude of daily stem contractions has been found to relate well to the rate of sap flow (Herzog, Häsler 1995) and day to day depletion levels related well to changes in both water potential and growth (Lassoie 1979). Thus daily stem expansion patterns are a good measure of growth potential and of factors which influence that potential. Current efforts to couple measures of diurnal patterns of stem expansion with parallel measures of sap flow, soil moisture levels, and physical and chemical climate have been underway for the past two years at Oak Ridge National Laboratory (McLaughlin et al., unpublished data). The objective of these studies has been to provide a more mechanistic understanding of ozone impacts on water use and water stress in mature forest trees. The analytical techniques being used will include many similarities to the traditional dendroclimatic approaches to analyzing the influence of physical climate on growth at annual scales. Such analyses should provide new insights into the interactions of physical and chemical climate and a more mechanistic understanding of the processes by which these interactions occur.

Emerging research needs in dendroclimatology

The preceding examples of applications of dendrochronology to research issues in the areas of acidic deposition and ozone effects research have focused on its role in quantifying both growth changes and emerging understanding of the mechanistic basis for such changes in forest systems. In each case dendroclimatic analyses have been combined with other analytical techniques to help understand the physiological and/or biogeochemical basis for observed responses. There are a number of other examples related to both these and other issues of regional environmental pollution where further development of dendroclimatology and its subdisciplines can help address important research issues. In some cases the research needs relate to improved mechanistic understanding that can enhance interpretation or application of dendroclimatic signals, while in others there are opportunities for altered focus of existing analytical capabilities. We highlight these below as indications of potentially useful directions for further development and application of dendroclimatology.

Wood chemistry and wood structure – Among the changes in wood chemistry observed in response to regional increases in acidic deposition, alterations in calcium content are of particular interest because calcium is not only an indicator of changes in cation supply from soil, it is also an important structural component of wood. A review of studies with calcium as well as other elements, such as manganese, iron, and zinc that may be useful indicators of changes in environmental chemistry can be found in Watmough (1998). We focus primarily on calcium here because it is unique among plant macronutrients in that it is not readily translocated between tissues and hence growth is linked more closely to Ca supply rate than to total content (Bangerth 1979). A number of controlled studies with seedlings reviewed by McLaughlin and Wimmer (1999) indicate that calcium deficiency can cause substantial changes in the properties of wood including reduced strength per unit mass under tension, reduced resistance to rupture, and reduced elasticity. All of these changes could weaken wood in response to mechanical stress. While evidences of changes in patterns of Ca supply are evident in the dendrochemical analyses discussed in earlier sections, the degree to which these patterns may reflect a change in biological function versus merely an indication of changes soil supply capacity is not clear. The shift from predominantly biologically controlled Ca cation mobilization and uptake from soils to mobilization that is not tied to biological demand may have altered the biological significance of Ca signals in wood over time. It is likely that Ca supply during the active growth phase may be the critical component that most influences the amount and structural integrity of wood formed.

Additional research in two areas is needed to better apply and interpret the biological significance of changes in Ca supply signals in wood. These include: (1) determining the functionally active and critical levels of Ca in xylem cell walls as related to potential influences on the structural integrity of wood; and (2) determining whether indications of reduced Ca availability at breast height in stems signal changes in wood properties in both these tissues and in upper canopy woody tissues of large and older trees. Upper canopy tissues may be more susceptible to changing Ca supply as a consequence of increased hydraulic resistance to water movement associated with the geometric complexity of larger, taller canopies (Yoder et al. 1994). Thus, closer linkages between soil chemistry, wood chemistry, and wood structure are needed in dendrochemical analyses of the effects of soil acidification on forest function. The development of advanced techniques for evaluating changes in cell wall properties such molecular beam mass spectroscopy and computer-assisted x-ray tomography should assist in evaluating both the occurrence and potential functional significance of wood ultrastructural changes in dendrochemical studies (Tuskan et al. 2001).

Forest stand responses and relative sensitivity of component species – Dendroclimatology has traditionally focused on canopy-dominant trees to minimize the effects of stand competition and other factors not directly related to the influences of climate on growth. Future studies designed to understand how forest stands are responding to changes in physical and chemical climate, will need to consider changes in growth relationships among species and between overstory and understory component of the forest. For example, Heisey (1995) found that growth of overstory sugar maple was positively correlated with soil and foliar Ca levels across a wide range of growth rates, including both strong increases and strong decreases in growth over the most recent decade. Growth trends of understory trees were consistently negative across sites regardless of overstory growth trends and were more strongly related to soil base cation levels than to N, P, or K. The dependency of Ca supply patterns on transpiration rate would suggest that subcanopy trees should be relatively more susceptible to Ca supply limitations imposed by soil acidification. Evaluation of relative changes in Ca or ratios of Ca to other elements in tree rings would be a logical approach to evaluating relative changes among size classes over time. Such an approach could provide a better perspective on both observed growth response and expected impacts on forest structure over time.

In addition it is apparent that species differ in their relative sensitivities to many stresses including both climate and air pollution and focusing on only dominant trees or species or only averaged responses may obscure valuable information that can be derived from more responsive forest components (Tessier et al. 1997). For example differences in responses of species, site, and canopy strata to drought stress have been noted (Orwig, Abrams 1997) and such differences could provide important insights into potential changes in forest composition associated with changes in physical or chemical environment. Differences among species in growth response to the same external stressors over time can also provide useful insights about the nature of the effect and the potential for shifts in competitive status to occur among species. Liming experiments in the Northeastern US (Long et al. 1997) resulted in significant increases in basal area growth and canopy vigor of sugar maple (*Acer saccharum*), but neither black cherry nor American beech (*Fagus grandifolia*) showed similar responses. Comparative studies of the relationships among growth and the uptake and incorporation of Ca in wood and foliage of different species under different Ca supply levels would be expected to highlight species differences in coping with Ca – limiting environments.

Dendrophysiology and forest responses to global increases in CO_2 – An important component and driver of global warming is the approximately 50 % increase in global atmospheric CO_2 that has occurred since preindustrial times (IPCC 1998). The issue of how forests will respond to these and projected future increases is important both from the perspective of evaluating the capacity of forests to remediate the rate of rise in CO_2 as well as from the perspective of quantifying enhanced growth potential under CO_2 enrichment as influenced by species type and life stages. A wide variety of controlled studies now indicate that increasing CO_2 will result in significant increases in leaf photosynthetic rates and increased net primary productivity of forest trees (Norby et al. 1999). Although very limited data are available for mature trees, responses of smaller trees to date have appeared to be robust in terms of resistance to limitations in supply of other resources (Wullschleger et al. 1997). This would suggest that larger trees will also be positively affected by CO_2 enrichment. However, detection of growth signals reflecting CO_2 enrichment effects on large trees in the field has proven difficult (Kienast, Luxmoore 1988). One explanation is that CO_2 – induced growth effects are transitory and that larger trees in the field compensate physiologically for increased CO_2 or are limited from responding by nutrient supply limitations. This possibility is supported by early experimental results from field studies (Norby et al. 2001, Oren et al. 2001).

The implications of increased carbon flow into forests from increasing CO_2 levels include possible alterations in competition between species, growth stages, and responses to external stresses such as drought. A call for improved understanding of the physiological basis of these responses for larger trees in the field has been voiced (Saxe et al. 1998). An opportunity currently exists to explore the implications of CO_2 enrichment on shorter term growth rates and physiology of larger trees in the field at FACE (Free Air Carbon dioxide Enrichment) sites. A wide variety of these sites now exist in the US and Europe where trees are exposed in the field to ambient and enriched CO_2 in companion plots (Norby et al. 2001). We are currently into a second year of dendrophysiological analysis of responses of 12 m tall, sweetgum *(Liquidambar styraciflua)* to an approximate doubling of preindustrial CO_2 levels. Efforts to date to define differences in seasonal growth patterns, differences in responses among size classes, and possible reduced sensitivity of trees to moisture stress under CO_2 enrichment appear encouraging (McLaughlin et al., unpublished data). Results of dendrophysiological analyses have been mechanistically compatible with both leaf level studies that indicate that increased water use efficiency occurs under CO_2 enrichment (Gunderson et al. 1993) and studies of root dynamics that indicate that both fine root mass and fine root turnover are increased with CO_2 enrichment in this environment (O'Neill, personal communication). Thus, the FACE sites appear to offer unique opportunities to evaluate hypotheses of action of CO_2 enrichment in the field and similar studies at other sites are encouraged to examine the extent to which responses can be generalized across species and environments.

Wood formation, wood chemistry and disease resistance – The potential enhancement of susceptibility of forest trees to insects and disease by air pollutants is well supported by the multiple stress hypothesis of Manion (1981). Manion describes the interplay between predisposing, inciting, and accelerating stresses of both biotic and abiotic origin that can push forest trees from an initial weakened condition to increased susceptibility to a variety of secondary stresses and, if unabated, to death. Despite circumstantial association of increased disease occurrence with increases in air pollutants (Witkowski et al. 1987, Hain, Arthur 1985, McLaughlin 1985, Rehfuess 1991) there is little direct evidence of direct single-factor cause and effect relationships. Such associations, are difficult to prove, or even imagine in the regional environment because of the many interacting factors involved in plant sensitivity to stress. However in a warmer, drier future climate for which increased sensitivity of forests to disease is predicted (IPCC 1998), physiological stresses from regional air pollutants may be increasingly important.

There is a strong mechanistic basis for enhanced sensitivity of trees to disease resulting from physiological changes associated with air pollutants (McLaughlin, Percy 1999). A classic example has been the mechanistic evidence of increased sensitivity of ponderosa pine to bark beetle attack in the in the oxidant-stressed San Bernardino Mountains of the California (Miller, McBride 1998). In fact, the occurrence of growth reductions in association with air pollution or any other stress is evidence of a weakened, potentially more disease- sensitive host. Reduced allocation of resources to defense chemicals is recognized as an important response to stress in plants (Waring 1987) and an expected corollary of reduced growth. In addition depletion of base cations from forest soils may enhance susceptibility of forest trees to diseases through multiple pathways. Calcium is an important defense chemical, and can act as an intraorganismal signal to initiate chemical and physical defenses once a host is attacked or injured (McLaughlin, Wimmer 1999). One of the calcium-induced defense mechanisms is the formation of lignin and/or callose in cell walls. These compounds can serve to reinforce the existing cell walls and preventing further incursions by invading pests. Heavy lignin formation (compression wood) has been noted in the boles of balsam fir in response to attack by adelgid (Timmel 1986).

Dendroecology has the potential to provide several types of evidence that can help in assessing the likelihood of predisposition of forest trees to stress, including insects and disease. These can be broadly grouped into changes in growth efficiency or qualitative changes in wood properties. Among the former are reduced annual growth, reduced latewood density, increased sensitivity to climate, and changes in growth efficiency. In a functional sense these are indicators, respectively, of changes in carbohydrate supply capacity, changes in current-year carbohydrate "excess", changes in physiological resilience associated with altered energy supply or demand, and changes in the efficiency of wood production per unit of canopy area. The latter has been used to assess sensitivity of balsam fir to spruce budworm attack and involves reconstructing growth in relationship to sapwood area (an index of canopy area) over time (Coyea, Margolis 1995).

Among the potentially useful indicators of qualitative changes are evidence of increased limitations in calcium supply during wood formation and altered lignin content of cell walls. Both these and the indicators listed above represent areas of potential value in future dendroecological analyses, but as with many of the other analyses, to be most efficiently employed, they require improved understanding of tree physiology, the dynamics of wood chemistry, and both the etiology of diseases and their relationship to tree biology. With additional research these indicators may provide sensitive tools for early detection of enhanced sensitivity of forests to biotic as well as abiotic stress.

Statistical detection and differentiation among growth signals

New time series or other analytical techniques for differentiating among short and longer term components of the growth signal are needed to strengthen dendroecology as a tool in air pollution studies. The linear aggregate model (LAM) developed by Cook (1990) provides a useful framework for addressing these issues. Although conceptual in intent and not designed to be parameterized or to be quantitatively predictive, the LAM is a useful tool to partition the variance in observed ring widths. It partitions the variance in ring width (R) within an individual tree at a given year (t) as follows:

$$R_t = A_t + C_t + \_D1_t + \_D2_t + E_t$$

The model attributes variance to the age/size trend (A_t), climate (C_t), disturbance pulses that vary in timing across the stand, $D1_t$ ("endogenous disturbance" in the sense of Cook and Kairiukstis 1990) and disturbance that affects all trees in the stand at the same time, $D2_t$ ("exogenous disturbance"). The "stand" refers to the trees included in a common analysis. The D1 and D2 terms are accompanied by a binary (1 or 0) coefficient (_). A term is also included for otherwise unaccounted variation (E_t).

Each of the conceptual terms in this model is likely to have multiple components as the trees and stand respond to combinations of environmental stresses. Sampling design and dendroclimatic modeling focus on minimizing the effects of A, D1, D2, and E in order to define and strengthen the relationship of R to C. Dendroclimatic reconstruction and the use of tree rings as a proxy record for climate depends on a stable, or at least definable, relationship of R and C.

As previously discussed, air pollution signals, which may include both endogenous and exogenous disturbances, can occur as highly variable annual scale pulses or reflect gradual weakening of the tree or deterioration of the site. The timing of abrupt changes in radial growth can be identified using intervention detection and related to known or suspected changes in the environment (Downing, McLaughlin 1990).

In addition to abrupt changes, variation in ring width often contains periodic or cyclic components. Identification and preservation of low frequency variance that is common among trees in a stand and then combining this with high frequency components represents one way of considering both the intensity and capacity factors in the growth series (Cook, Zedaker 1992). The development and creative application of spectral analysis is needed to identify periodicity in growth across all time scales. Recent identification of pest outbreaks in long tree-ring chronologies using spectral analysis (Speer et al. 2001) provides a means to characterize the epidemiology of the insect as well as to identify relevant sources of variation that otherwise might be considered as "noise". Spectral analysis would also increase understanding of high frequency variation in diurnal cycles of growth and hydration, both of which affect the growth record contained in tree rings. Combining an empirical understanding of the periodicity of growth with the mechanisms of cambial mitosis and differentiation (Fritts, Shashkin 1995) would provide a powerful tool to determine biologically significant stress thresholds, including episodic stress from air pollutants. Intensive monitoring of individual trees could detect varying sensitivity over time and across species. Responses of the more sensitive individuals would be especially useful in developing a mechanistic understanding of pollution effects.

Conclusions

Dendroclimatology and its sub-disciplines of dendroecology and dendrochemistry have played vital roles in defining both observed growth signals associated with regional scale air pollution stress and enhancing our current understanding of the mechanisms involved in those responses. In the case of red spruce decline in the eastern US, early definition of the magnitude of growth declines, their relationship to elevation, climate, exposure, tree age and competitive status, their timing across the region, and their relationship to canopy deterioration and tree mortality were significant contributions to the search for plausible mechanisms. Dendroecological analyses contributed to early delineation of plausible hypothesis of action that led to subsequent more focused studies of tree physiology, soil chemistry, and wood chemistry and have highlighted the role of acidic deposition as an important contributor to regional decline in health of red spruce.

There is strong evidence that ambient levels of pollutants in some industrialized regions are presently above the threshold for physiological damage to forest trees and biogeochemical alteration of forest soils. Reductions in emissions of sulfur in some countries in the past two decades are having measurable positive effects on air quality and, if they continue, would be expected to reduce these stresses. However at present pollution levels, the types of physiological responses anticipated, while subtle, would be expected to enhance the level of stresses imposed by other abiotic factors. The evidence of increased sensitivity of mature forest trees to climate and evidence that factors other than climate are significantly influencing growth supports this concept. These interactions and/or distinctions are seen as likely to be increasingly important as research on the levels and mechanisms of future forest responses to global climate change continues.

Dendroclimatology is not a stand-alone science, but is most useful when combined with mechanistic studies that help define both appropriate sampling strategies and analytical sequences that are based on sound biology. Improvements in characterizing the health of forests are being made at scales ranging from remotely sensed evaluations of canopy spectral reflectance signatures (Martin, Aber 1997) to the chemistry and ultrastructure of wood fibers (Tuskan et al. 2001). These advances should aid and be aided by dendroclimatology as linkages between forest form and function are sought. They should also help keep dendroclimatology at the forefront in future assessments of forest health. Such measurements will hopefully also ultimately document improving trends in forest condition that reflect societal recognition that the linkages between forest health and human health are relevant and important.

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