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Methods for evaluating and predicting forest growth responses to air pollution*

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Summary. The challenges of quantifying and characterizing recent broad-scale changes in forest growth are substantial and exciting. The implications of these declines to the future growth and stability of forests in both Europe and the United States are significant. While the role of anthropogenic pollutants in initiating or exacerbating observed changes in growth and mortality is not clearly established, the possible implications of erroneous decisions with respect to pollution abatement are enormous and call for concerted, imaginative, and multidisciplinary research to provide much needed answers in the shortest possible time frame. Proof of cause and effect in complex natural ecosystems will not be absolute; however, diverse approaches can lead cumulatively to strong inferential evidence that substantially reduces the uncertainities of such decisions.

Key words. Forest decay; forest growth response quantification; air pollution; anthropogenic pollutants.

Introduction

The documentation of widespread dieback and decline of forest trees in western Europe[5] and the northeastern United States[9] during the past decade has generated great concern that such changes are of anthropogenic origin and that they may intensify unless atmospheric pollution is reduced. While there are many current hypotheses about the possible causes of these changes, there is currently no proof that any single factor has been the predominant causal agent. Atmospheric pollutants associated with accelerated combustion of fossil fuels during the past three decades, including the gaseous pollutants, SO_2 and ozone, acid rain, and trace metals, have all been implicated as possible causative factors.

The occurrence of forest declines and their recent intensification in areas currently receiving high levels of deposition of anthropogenic pollutants provides only circumstantial evidence of a cause-and-effect relationship. While many possible physiological mechanisms of response of forest trees have been discussed[16,30], clear demonstration of the role of these mechanisms in reported declines has yet to be documented in the field. The present lack of scientific proof of a cause-and-effect relationship between atmospheric pollutants and these extensive forest declines must be considered from the perspective of two alternative hypotheses: 1) the declines may be of natural origin and totally unrelated to pollution stress, or 2) we have not yet adequately characterized and quantified the changes to a point where pollution effects can be separated from the myriad stresses and modifiers that normally control forest growth and development. In either case, broad-scale, imaginative, multidisciplinary research that focuses on multiple hypotheses is required to quantify the changes and identify the responsible mechanisms. The paper focuses on both conceptual and experimental approaches that may prove valuable in defining, quantifying, and understanding the basis of recent deterioration of some forested ecosystems.

A conceptual basis for addressing the problem

Addressing the problem of defining causality in regional forest declines can be reduced conceptually to three basic tasks: 1) quantifying and characterizing spatial and temporal dimensions, 2) correlating changes in forest response with spatial gradients or temporal changes in a variety of potential causative agents, and 3) focusing mechanistic field and laboratory studies on testable hypotheses of specific cause-and-effect relationships based on field observations. Each task should address specific questions which successively narrow the range of uncertainties about the nature of the observed responses and more clearly delimit and define hypotheses to explain observed effects. Some appropriate questions for each of these tasks are detailed below:

1) Documenting and characterizing patterns of forest dieback, and decline. It is important that spatial and temporal patterns of forest decline be determined initially to quantify the extent, rate, and direction of change. This information serves to identify systematic patterns of occurrence which may suggest or eliminate specific causes. Important questions that should be addressed are: When did changes in forest growth begin to occur? Are there historical precedents for such changes? What were the earliest symptoms of change? Did changes begin in all affected regions at the same time? Are all species and age classes affected equally? Where are effects most severe or absent?

2) Correlating forest response to causative factors. Important insights into factors responsible for forest declines should become evident as the magnitude and timing of decline is examined across the broad array of environmental gradients spanning the affected regions. An essential component of this approach is identification of factors that show a consistent relationship to observed declines. Principal questions to be addressed in this context are: Are the effects most severe in areas of highest atmospheric pollution? Did effects begin to occur at a time when emissions patterns underwent substantial changes? Is there a consistent pattern of year-to-year variability in growth suppression which is clearly associated with periods of high pollution or changes in climatic factors such as temperature or rainfall? Is sustained drought consistently associated with initiation of the declines? How does variation in soil type, topographic features, competition, and tree age influence the severity of effects?

3) Focusing field and laboratory studies on mechanistic hypotheses. This research should both identify specific physiological responses associated with declining trees and demonstrate mechanistic linkages between such responses and primary causal agents. Specific questions to be addressed are: Do effects originate from initial responses in roots or shoots? What are the primary physiological changes consistently associated with declining vigor of affected trees? What are the concentration thresholds for physiological responses to acid rain, ozone, and trace elements? Do these stresses act interactively, and are they exacerbated or ameliorated by abiotic factors such as climate? Are relationships between host plants and symbionts or pathogens altered by these stresses?

The task of documenting anthropogenic influences on forest regions is extremely complex and satisfactory completion of this task will require patient and focused research. Yet, significant progress has already been made and can be predicted to continue at an increased pace as new methodologies are directed toward the problem. The primary purpose of this paper is to highlight some of the methodologies utilized in studying forest decline in Europe and the United States and some of the progress made in addressing the conceptual problems defined above.

Regional forest surveys

Regional surveys of forest damages are essential to provide early characterization of the scope of the damage. They may be based on several criteria including visual foliar damage[5], mortality[9], long-term growth changes[10,11,18,29] and changes in wood density[26].

Surveys based on visual damage, while easiest to perform, generally provide the least information because no indication of the timing of changes in growth that generally precede visual symptom development can be provided and the rate of change must be determined by repeated surveys. Yet, much information can still be gleaned from such surveys if they encompass a broad enough range of conditions. From the survey of forest damages in West Germany[5] the total areal extent of the damage (500,000 ha) was determined and factors *not* plausible as primary causes were identified. The identity of these factors and the basis of their exclusion emphasize the strength of examining changes across environmental gradients. Soil moisture, frost, stand structure, soil acidity, and pathogens did not appear to be primary factors, based on a lack of consistency in association of these factors with the intensity or distribution of observed effects. While atmospheric pollutants could not be proven as primary causants, evidence was considered to support a major role in the observed damage[5].

In the United States a survey of damage to high-elevation forest stands in the Appalachian Mountains at sites extending from Vermont to North Carolina has recently been completed[9]. The survey consisted of establishing 32 plots for assessing mortality of red spruce on both north-south and elevational gradients. Increment cores were removed from red spruce, balsam fir, and white birch to determine obvious shifts in growth patterns by quick visual inspection and longer-term changes in growth rate by dendroecological techniques. Extensive mortality of red spruce was found, with highest levels (40–50%) occurring in northern high elevation forests. Both virgin and regenerating stands were affected. Increased mortality was reported to be associated with a systematic growth reduction on remaining trees which began about 20–25 years ago.

In examining possible causal factors, Johnson and Siccama[9] used correlation analysis to relate stand mortality to a number of site factors including stand basal area, geologic and soil characteristics, elevation, and aspect. Increased mortality was significantly correlated only with elevation. An examination of aluminium levels in roots of healthy and diseased trees failed to show consistent relationship between tissue aluminium levels and the extent of decline. Foliar levels of sulfur increased with elevation and were 10% higher in visually declining trees. While soil lead levels, precipitation acidity, and exposure to very acid cloud moisture also increase with elevation, the authors pointed out that a variety of other abiotic stresses including wind, low temperature, and low soil-moisture-holding capacity are also more pronounced at higher elevations. An examination of regional weather records lead to the suggestion that a severe drought in the early 1960s may have acted to trigger the widespread declines. Acid rain was regarded as possibly one of several stresses acting in concert to weaken trees and predispose them to decline.

A second closely related but more extensive forest growth survey was begun in 1982 to document historical changes in growth of a broader variety of species in the geographical area of the eastern United States currently receiving the highest exposure to atmospheric pollution. The project entitled FORAST (Forest Responses to Anthropogenic Stress) was designed to provide a common experimental protocol for dendroecological sampling and analysis by 12 collaborating research sites[17]. Because this project focuses on development and application of regional-scale methodologies for separating the influence of anthropogenic stresses from other biotic and abiotic site factors, we will briefly describe some of these approaches as having broader scale applicability.

As a part of this experiment, over 70 forest stands, 6000 trees, and a total of 34 tree species have been sampled to date. The sampling protocol, which is described in more detail elsewhere[17], established a network of paired plots located on soils of differing acidity and nutrient levels within each subregion (fig. 1). 15 codominant trees (≥ 50 years old) of each of six species were sampled on each plot. Site and regional data collected for each plot include: stand biomass, soil fertility, average monthly temperature, total monthly precipitation, and generalized indices of historical exposure to atmospheric pollutants, which will be discussed in more detail later. In the still continuing analyses of these data, growth rate of sampled trees is being determined from analysis of two increment cores from each of the 90 trees per plot.

The principal advantage of dendroecological techniques, such as employed in this study, lies in their capacity for documenting growth responses of individual trees over their entire life span, thereby providing a record of tree response to the changing influence of a variety of internal and external variables. It should be noted that obtaining very accurate measurements of growth of forest trees over long time periods is only the starting point for the recently evolving discipline of dendroecology. Its major emphasis is on relating these growth patterns to patterns of change in the trees' chemical, physical, or biological environment. The principal tasks of dendroecology are: 1) obtaining accurate measurements of the width of annual rings for the desired period of record; 2) cross-dating those rings among cores taken from several trees of a particular species to ensure that each year's growth is accurately dated; 3) statistically analyzing the annual ring-width series to remove effects of tree age, changes in competitive status, and climate; and 4) analyzing relationships between both residual growth patterns and additional potentially significant biotic and abiotic variables that may influence the residual growth patterns either directly or through interaction with other parameters.

In practice, growth patterns evident in tree cores may be analyzed in several ways, including detailed examination of statistical changes in relationships of annual growth rate to climatic variables or levels of air pollutants, quantification of longer-term shifts in average growth rate[17], or tabulation of the frequency distribution of trees

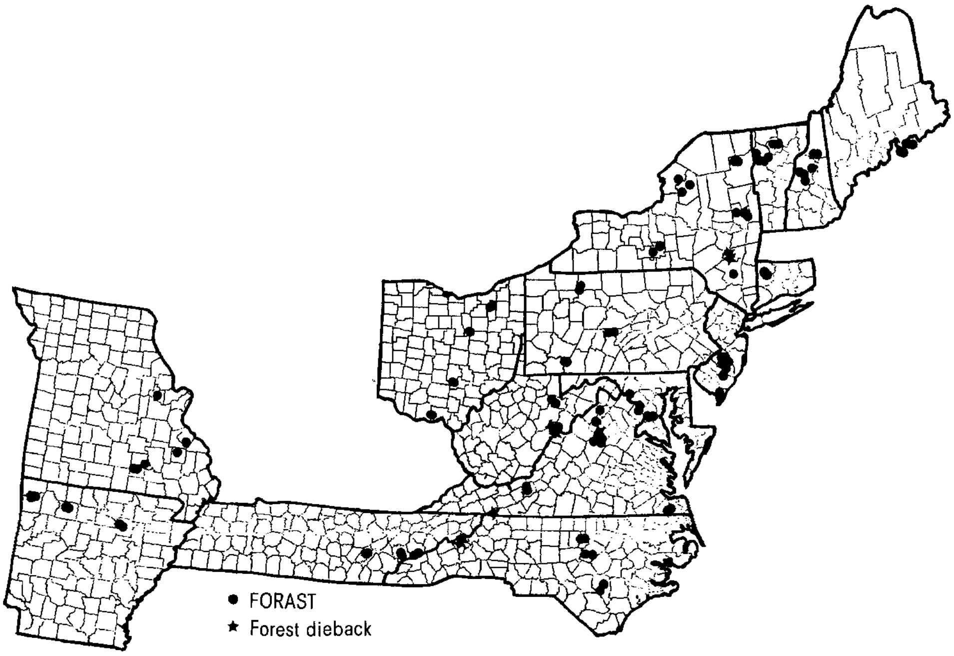

Figure 1. Distribution of forest stands in the FORAST tree-ring project and in the survey of red spruce dieback and decline in the northeastern United States. Some dieback sites in New Hampshire and Vermont are coincident with FORAST stands and are not identified separately.

showing abrupt shifts to a different pattern of growth[9,25]. Considerable insight into the nature of growth declines can also be provided by examining the raw ring-width series themselves as shown in figure 2. Here a comparison of mean growth rates of red spruce in New Hampshire in the northeastern United States and red spruce and Fraser fir at upper elevations and shortleaf pine at lower elevations in the Smoky Mountains of Tennessee documents the systematic nature of declining growth within this extensive region. Furthermore, an examination of the timing of growth declines for spruce within this region does not appear to be consistently related to drought, as shown by McLaughlin et al.[17]. An examination of a ring-width series for red spruce (fig. 3) from the Smoky Mountains in relationship to annual values of the Palmer Drought Severity Index[20] shows an obvious growth depression during the drought of the early 1950s, and a subsequent recovery before a sustained growth decline began around 1961 and continued during 20 years of generally more than adequate soil moisture.

While the rate of radial growth of trees is known to decline with age as a function of tree geometry, physiological aging of the tree, and developmental aging of the forest stand, the synchronized growth declines in the eastern United States do not appear to be caused principally by these processes. A separation of growth responses of the 10 youngest and 10 oldest red spruce trees from the Mount Washington, New Hampshire, collection of Johnson and Siccama[9] shows synchronous growth declines during the past 20 to 25 years for trees differing in age by more than 100 years (fig. 4). However, the knowledge of aging effects as components of undisturbed forest growth patterns is fundamental in estimating dendroecological effects or calculating the fraction of overall growth declines that may be attributed to pollution influences. Physiological aging not only affects average growth levels but also yearly growth variations that must be considered when calculating residual variability in tree-ring time series. Various methods proposed by different authors to estimate age trends, including linear trends, negative exponential curves, or Hugershoff functions[4], consider only low frequency changes associated closely with physiological aging processes. On the other hand, moving averages[21], binomial or Gaussian filters, polynomial or spline functions, or Box-Jenkins models may also contain and eliminate higher frequency information. These techniques normally are applied to single core series. To keep the information of low frequency growth decline within the residuals, it is necessary to calibrate the age trend only in a undisturbed time period, counting at least more than 30 years[22]. For short periods, these trends might be extrapolated but confidence decreases quickly with length of extrapolation period (15 years). Forest yield tables for similar sites and stand conditions as well as forest growth simulation models[28] may be used to calculate normal aging trends.

Densitometric studies

Additional important insights into interactions between tree growth and climate have been gained by combining

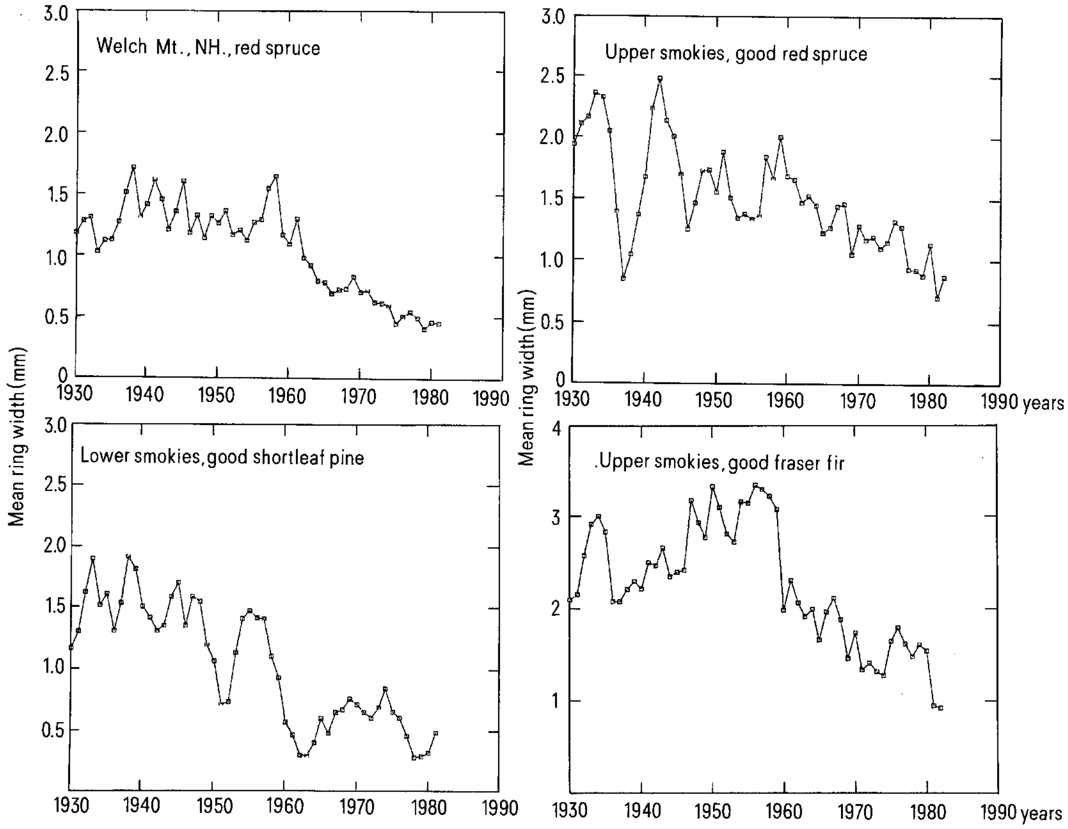

Figure 2. Comparisons of ring-width series from 30 cores each of red spruce, Fraser fir, and shortleaf pine in the northeastern United States. Note concurrent growth rate declines during the past 25 years.

measurements of annual variations in wood density with those of changing ring width[26]. A network of 115 study sites for analyzing density and growth patterns of living conifers in Europe was established in 1976 by the Swiss Institute of Forestry Research (fig. 5). The sites chosen were restricted to subalpine sites where the open stand form reduces competition from adjoining trees, where timber management influences were minimal, and where climatic stresses were considered to be well defined. In addition to the reconstruction of the past 300 years of climate from the cores by standard dendroclimatological techniques[6], measurements of both annual density and earlywood-latewood are being done by the techniques of Lenz et al.[15].

Analyses of growth responses at these sites have shown that ring-width and earlywood width in cool, temperate, and humid regions is related to carry-over and storage effects of the previous year mixed with many other synergistic or compensating effects during the actual growing season. In contrast, density patterns, especially latewood density and also latewood width, show precise additional information with clear relations to a short period during summer or fall, thus enhancing the ring-width information. Short-term climatic reconstructions with density, based on annual variations in maximum latewood, show 10 to 30% more variance in common with summer temperatures than do ring-width series. The combination of both types of measurements, densities, and widths, therefore, is a promising tool for climatic reconstructions[26].

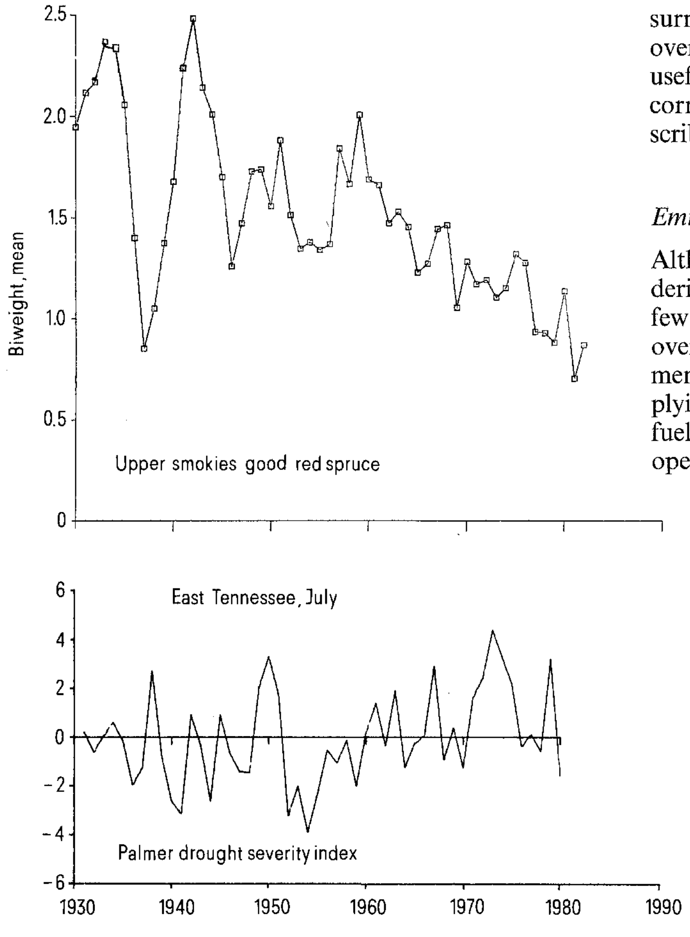

Figure 3. Growth rate of red spruce in the Smoky Mountains of Tennessee shows a clear response to dry years (negative values of the Palmer Drought Severity Index during 1953–1954), recovery during succeeding years, and then a decline during the past 20 years during periods of generally good moisture availability.

A survey of the European network shows generally remarkable decline of growth and density within the most recent time which cannot be explained by climate, age trend, or site difference only. The widespread distribution of this decline is an important documentation and first step for correlating decline pattern with additional stress factors as pollution effects or other ecological shifts (fig. 6). Although the network samples were taken mostly in subalpine regions within sites strictly defined by plant associations and only of dominant trees, the collected material is highly valuable for detection of dendroecological effects other than climate, objectives which were planned for future research and have grown in relevance today (site differences, pollution, stand competition).

Correlating growth declines with causal factors

While documenting the spatial and temporal dimensions of forest declines is an essential first step, subsequent determination of the association of these declines with hypothesized causal factors is essential to establishing defensible cause-and-effect linkages. Examples of natural stresses shown by survey techniques not to be consistently related to reported declines were discussed above. The more difficult task is determining associations of forest changes with anthropogenic pollution because none of the pollutants to which forest declines have been attributed have been monitored long enough or over an extensive enough area to cover the period of transition to slower growth which, in general, began two to three decades ago. Unter these conditions a variety of surrogate indices of relative changes in pollution levels over time must be sought. Some examples of potentially useful indicators of historical pollution trends utilized for correlation analysis in the FORAST project are described below.

Emissions

Although accurate records of emissions of pollutants derived from fossil fuels are available for only the past few years, data on changes in relative levels of emissions over much longer time spans can be provided by documenting total fuel use over corresponding times and applying temporally consistent methodologies to convert fuel use to emissions. Geschwantner et al.[7] recently developed such a data base in the United States, providing

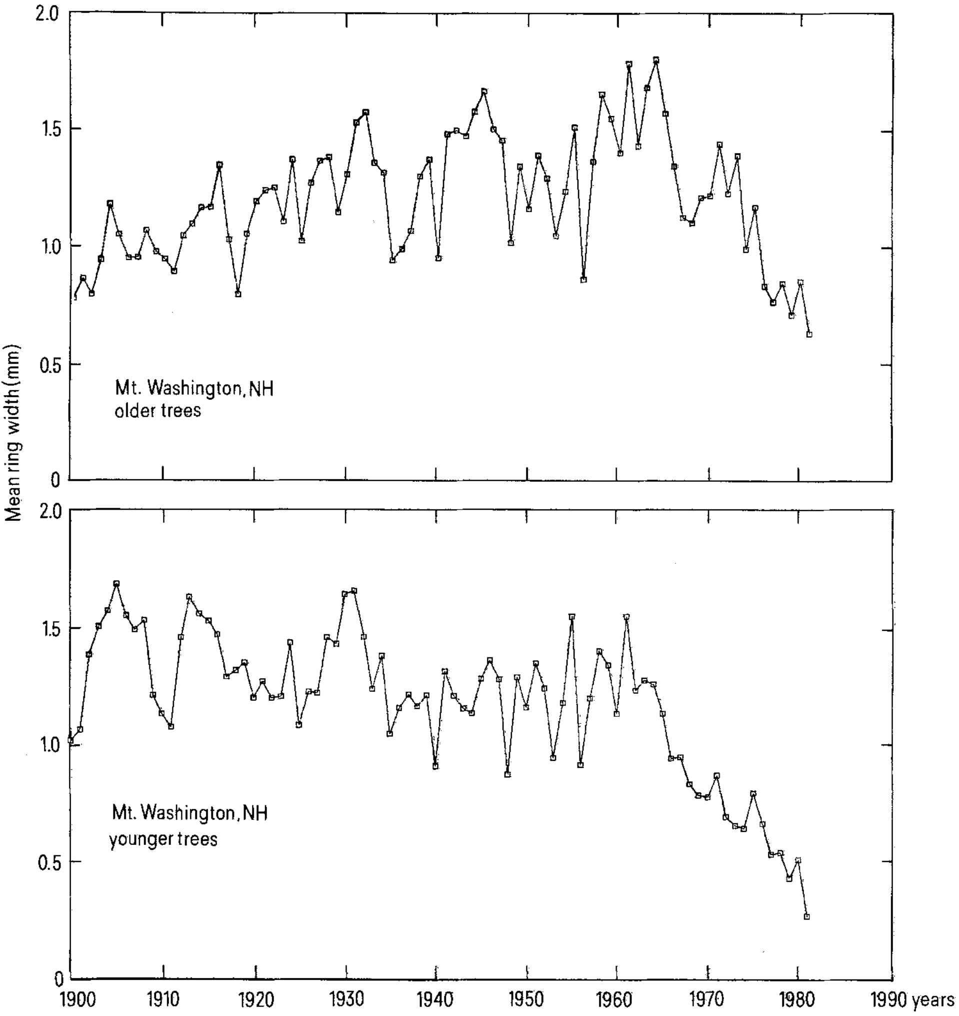

Figure 4. Growth rate comparisons between the 10 youngest and the 10 oldest (average ages are 84 and 226 years, respectively) red spruce trees at Mount Washington, New Hampshire, showing simultaneous growth declines.

Figure 5. Distribution of sites included in the European densitometric chronology network analyzed by the Swiss Federal Institute of Forestry Research.

state-level estimates of emissions of SO_2 and NO_x at five-year intervals over the time period 1900–1980. Such data may be used in two basic ways: 1) to establish points of significant change in exposure of regions to pollutants, or 2) to estimate specific levels of pollution loading at specific receptor sites. In either case some knowledge of relationships between emissions and deposition is needed.

While the link between emissions of pollutants and their deposition is intuitive, quantitative linkages between emissions in specific regions and deposition in adjacent regions have not been established to date. In examining SO_2 emissions data for use in the FORAST project, McLaughlin et al.[17] noted that both trends and levels of emissions could vary sharply between adjoining states, but useful empirical relationships could be detected between emissions in upwind areas and rainfall chemistry at a network of monitoring stations maintained by the National Atmospheric Deposition Monitoring Program. Subsequently, more extensive analyses of these data for 18 monitoring stations in the eastern United States have shown very good quantitative relationships between emissions of SO_2 at distances $\leq$ 900 km and deposition of SO_4 ($R^2 = 0.70$) and H^+ ($R^2 = 0.65$) in precipitation. This simplistic empirical approach indicates that deposition can be usefully correlated with short- to intermediate-range emissions, thereby providing a basis for using historical emissions data bases to quantify relative levels of changes in exposure of forests to wet-deposited pollutants.

Meteorological data bases

While emissions may provide a useful indicator of relative inputs of wet deposition of acidity, exposure of forests to gaseous pollutants, particularly secondary pollutants such as ozone, will be influenced strongly by patterns of atmospheric stagnation that lead to local and regional buildup of pollutants. In the United States the frequency of air stagnation episodes has been shown to vary widely from region to region[8]. Furthermore, the frequency of these events may vary dramatically from year to year at a single location. Korschover and Angell[14] documented the frequency of air stagnation events of $\geq$ 4-d duration for the eastern United States during the past 45 years, thereby providing a year-to-year record of

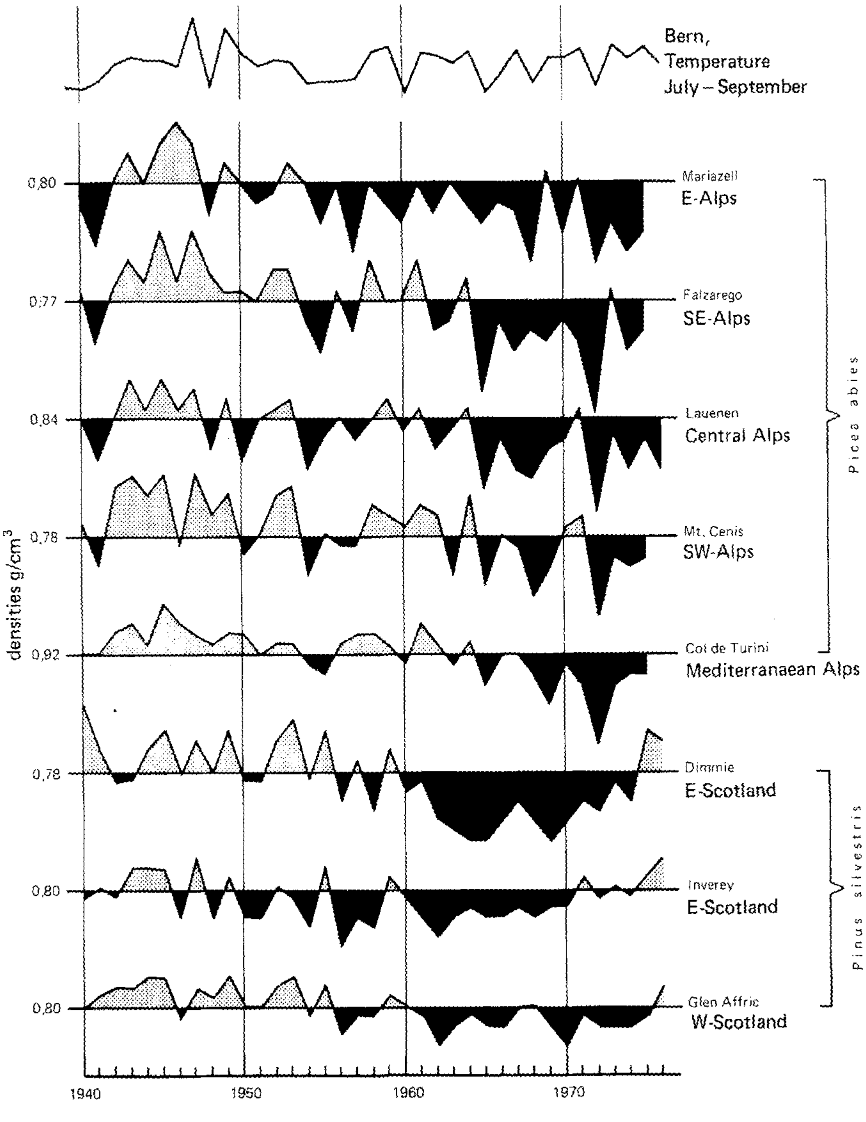

Figure 6. Mean monthly temperature of Bern, Switzerland, and maximum density chronologies of spruce and pine from various alpine and Scottish locations since 1940. Source: Schweingruber et al.[26].

conditions favoring pollution buildup – when pollutants were present.

Examination of long-term records of visibility recorded at airports can provide an extensive data base on changes in general atmospheric pollution levels including both gaseous and particulate types. These data may be examined with respect to either the frequency of hazy days (visibility less than 8 km) or in terms of specific changes in visibility occurring diurnally during air stagnation episodes. As a part of the FORAST study, for example, the number of days per growing season when visibility during stagnation episodes decreased between 1000 and 1300 h has been tabulated. It was reasoned that such changes would reflect anthropogenic buildup of pollutants, thereby separating out the days where high humidity would have been a major influence on visibility. A comparison of these data with air quality monitoring data in the vicinity of Knoxville, Tennessee, showed the highest number of such days occurred during 1977, a year when the frequency of high concentration of ozone was the greatest in recent years (T.J. Blasing, Oak Ridge National Laboratory, 1984, personal communication).

Elemental analysis of tree rings

Elemental analysis of tree rings offers another possible mechanism for determining when trees in a particular region began to be exposed to regionally elevated levels of pollutants from combustion of fossil fuels. A variety of mechanisms for such increases have been suggested, including both altered acidity of soil solutions and increased deposition to and uptake through foliar surfaces[16]. On a more local scale the content of lead, cadmium, and other metals in tree rings was used to document changes in atmospheric pollution from a variety of sources including smelters[24,31] and historical traffic patterns[2,12]. More recently, Baes et al.[1] examined radial changes in concentrations of aluminum, titanium, cadmium, copper, iron, manganese, and zinc in growth rings of shortleaf pine growing under conditions of both local and regional pollution. They found both a growth slowdown and increases in iron and titanium in wood formed between 1860 and 1910 at a 'remote' site which closely paralleled the period of uncontrolled releases of SO_2 and other pollutants from iron and copper-smelting operations 88 km upwind. Increases in iron, titanium, aluminum, cadmium, copper, and manganese were found during the past two to three decades corresponding to a period of increased regional combustion of fossil fuels and associated release of SO_2[1]. The patterns of accumulation of both iron and titanium during smelter operation and shutdown indicate that these elements are not significantly translocated after deposition in the xylem[1], and suggest that levels of these elements in annual growth rings may provide a useful indication of historical atmospheric pollution from regional combustion of fossil fuels. Further trace element analysis of selected sites throughout the FORAST network is planned during the coming year to document regional differences in accumulation rates.

Collectively, the techniques described above provide possibilities for establishing multiple lines of evidence for documenting the timing and rate of responses of forests to atmospheric pollution. The combined examination of annual tree-growth rate of red spruce, upwind emissions of SO_2, numbers of hazy days, and numbers of days with visibility changes indicative of diurnal pollution buildup for eastern Tennessee in the United States (fig. 7) illustrates the temporal linkages between several indicators of pollution and timing of growth changes. The power of these techniques is best realized, however, when these comparisons are made across several sites encompassing gradients in pollution levels.

Mechanistic studies

Obviously, research to determine mechanistic linkages between regional pollution stress and forest responses need not await and has not awaited the results of field surveys to move productively forward. The conceptualization and listing of hypothesized mechanisms of action is an iterative process which should lead to improved understanding at a variety of organizational levels. In reviewing the physiological evidence for various modes of action of acid deposition on forest growth, McLaughlin[16] lists several mechanisms that currently appear plausible. These include increased susceptibility to moisture stress based on changes in plant water balance (changes in stomatal function cuticular integrity, and water recharge rate from roots), reduced availability of nutrients (changes in foliar retention, root absorptive capacity, and soil supply), altered carbohydrate balance (increased foliar retention of carbohydrates, decreased photosynthetic production and increased turnover rates of fine roots), and direct effects on growth processes (accumulation of toxic levels of trace elements in active growing zones).

In addressing these mechanisms several important concepts should be recognized: 1) multiple pollutant stresses must be considered because acid rain, gaseous pollutants, and trace element loading have increased over the same approximate time span and in the same geographical regions as has industrialization during recent decades; 2) both direct effects of pollutants on plant organs and

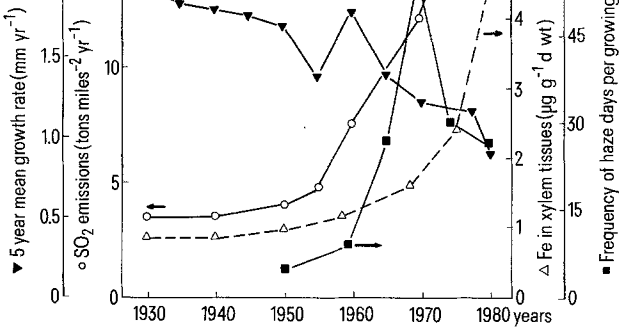

Figure 7. Changes in average radial growth of red spruce, iron content of tree rings, emissions of SO_2, and numbers of hazy days per growing season in the Great Smoky Mountains National Park in East Tennessee, USA.

indirect effects resulting from changes in soil chemistry must be considered; 3) the balance of resource supply and demand between shoots and roots must form a basis for explaining and differentiating primary and secondary responses; 4) chronic exposure to atmospheric pollutants may predispose trees to a variety of secondary stresses such as disease, drought, or competition from more vigorous neighbors; and 5) beneficial effects to forest growth from additions of nitrogen or sulfur in acid rain may occur in some situations where these elements are limiting for growth.

Determining the extent to which forest declines are induced by specific causal agents will require both field and laboratory studies that consider a large variety of biotic and abiotic modifiers. Thus, the relative influence of wet vs dry deposition, rain vs mist, gaseous pollutants vs acid rain, acidity vs other aspects of rain chemistry, direct vs indirect effects in the environment, and primary vs secondary responses in the trees in an important consideration in designing these studies.

Documenting mechanisms of action in the field will be difficult; however, characterizing which processes are affected and in what sequence may suggest more definitive, manipulative experiments. As examples, the documentation of low levels of calcium and magnesium in fir foliage by Rehfuss[23] and low levels of calcium in cell walls of the root cortex by Bauch[3] suggests that detailed studies of nutrient leaching and nutrient uptake are needed. The discovery of trace element accumulation at high levels in the cambium/phloem area of shortleaf pine[1] indicates a critical need for controlled studies of modes of uptake and levels of toxicity of the individual and combined trace elements that appear to have increased in availability in recent decades.

Sophisticated instrumentation including PIXE (Photon-Induced X-Ray Emission Spectrophotometry), ICP (Inductively Coupled Plasma Emission Spectroscopy), and laser spectrophotometry are currently available for examining site-specific nutritional and toxic element imbalances in plant tissues. Portable computer-based systems for collecting physiological data on in situ foliage of stressed and nonstressed trees in the field or laboratory were recently made available. Radioisotopes also offer many opportunities for examining sites of accumulation as well as turnover rates of both organic and inorganic chemical species. Collectively, these and other techniques, particularly when combined with inferential evidence from field surveys, offer both great challenges and opportunities for developing a mechanistic basis for examining forest declines.

Predicting the effects of forest declines on future forest development

Evaluating the significance of changes in forest growth on future growth and development of tree species and forest stands is an important process which can be initiated even while the causes of the declines are still poorly understood. This process can be approached either by modeling statistical relationships of growth of a species to environmental stress or by introducing various levels of stress into mathematical models of normal forest growth and development.

An example of the first approach is the analysis of density-climate relations for Scots pine at Saxon, Switzerland[13]. A comparison of trees with or without visual symptoms of decline (fig. 8) shows that the multivariate model of relationships of maximum latewood density developed during a 60-year calibration period predicted growth of the undamaged trees rather well from 1940 to 1975, while growth of damaged trees departed significantly from the predicted growth trend of that tree. Thus, the multivariate model in predicting normal density values provided a basis for estimating the magnitude of change induced by environmental stress.

Forest growth modeling has provided a variety of useful research tools for exploring the dynamics of air pollution effects on forest growth and development[28]. One application of these models is the determination of stand-level sensitivity to changes in growth rate of component species[19, 32]. In an application to determine the influence of varying levels of inhibition of growth and development of eastern deciduous forests, West et al.[32] assigned growth rate reductions to each of 33 tree species placed in one of three sensitivity classes, based on a generalized index of sensitivity to SO_2 obtained from the literature. Experiments simulating stand- and tree-level responses to imposed stress regimes were implemented by varying the level of stress, the stand age at which it was introduced, and the length of the stress periods. Results showed that stand competition could be an important modifier of both the rate and direction of change induced by a given level of external stress. Such simulations will attain additional significance in the future as actual growth rate declines are used to parameterize these models, thereby permitting the potential significance of these changes to future forest growth and development to be evaluated.

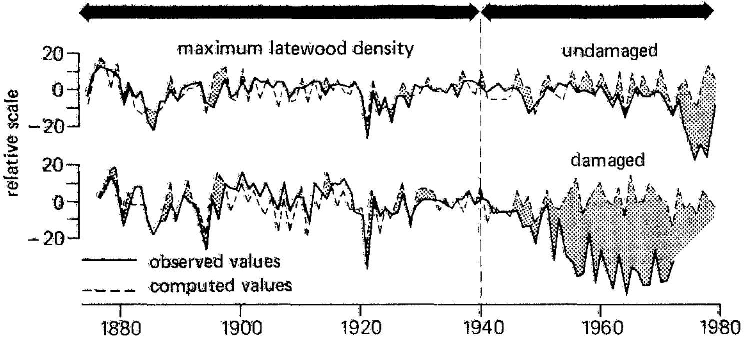

Figure 8. Two sets of maximum density series of *Pinus sylvestris* L. at the research field in Saxon, Switzerland. The solid lines show the indexed values of observed maximum densities; indices are calculated by a Hugershoff function fit to the raw values (parameter estimation of function only in calibration period). The broken lines show estimated indices by an applied multiple regression model using climatic data (model parameter estimation only in calibration period). Source: Kienast[13].

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