David REED*, Susan MEDLARZ** and Reginald NOBLE***

INVESTIGATION OF EFFECTS OF FOREST STRESS FACTORS ALONG EXPOSURE GRADIENTS IN THE UNITED STATES

Abstract. In order to better predict future trends due to byproducts of human activity, long-term data on specific ecosystems are needed. When investigating the effects of an environmental stress factor on ecosystem processes, it would be ideal to have a controlled experiment in natural ecosystems where different levels of the factor under investigation could be applied to homogeneous experimental material. This is, of course, impossible to achieve in field experiments. One approach to field studies is to establish study sites in relatively homogeneous ecosystems which are subject to different levels of the environmental stress factor in question. By establishing study sites along a gradient with different levels of the stress factor, an approximation of a controlled experiment can be achieved. One of the most important decisions in the initial stage of site selection is the specification of the ecosystem of interest and the environmental factors which will ensure uniformity across a gradient. The gradient research in the U.S. includes study of mechanisms of pollutant response in plants, mechanisms of above-ground impact: soil mediated mechanisms, nutrient leaching from foliage, altered physiology and carbon allocation, winter injury, disruption of reproduction or regeneration, altered susceptibility to pests and pathogens.

A number of different gradient studies were initiated in the U.S. during the past decade. These studies were established to evaluate air pollution impact to forest ecosystems in different regions of the U.S. In Pennsylvania and Michigan, sample plots were established along gradients of sulfate deposition in mixed hardwood forests. Along the Appalachians, plots were established along an elevational gradient to assess the health of spruce and fir forests. In the West, in the Sierra Nevada Mountains, a gradient study was established to determine the impact of ozone to mixed conifer forests.

Key words: forest ecosystems, pollution, gradient.

Introduction

Byproducts of the activities of modern man have resulted in the creation of conditions that threaten to produce long-term deleterious effects on the earth's physical and biological environments. Acidic deposition, atmospheric oxidants, UVB and global climate change are but four phenomena where human activities have led to such conditions. The nature and degree of the impact of these conditions on natural ecosystems is, to a great degree, uncertain. This is in large part due to inadequate and unreliable historical data on ecological systems that would allow pre- and post-impact analysis.

In order to better predict future ecological trends due to byproducts of human activity, long-term data on specific ecosystems are needed. These data are essential for establishing a baseline against which future trends can be assessed and for validating predictions of future changes. Data of past decades, for the most part, are not detailed enough to permit us to distinguish man-induced changes from the inherent variability in natural systems. The fact that natural systems (especially forests) respond slowly to large-scale perturbation associated with regional or global change

^{*} School of Forestry, Michigan Technological University, Houghton, MI 49931, USA. ** SCFRC — US Forest Service, 1509 Varsity Drive, Raleigh, NC 27606, USA. *** Department of Biological Science, Bowling Green State University, Bowling Green, OH 43403, USA.

further amplifies the need for a comprehensive approach to the establishment of biological and physical baselines on a global basis. This is necessary if we are to ensure understanding of the current status of our ecosystems as well as establish a basis for understanding and forecasting future trends in these systems. The critically important ability to forecast long-term changes in earth's systems and to provide early warning of impending environmental problems requires long-term measurements that permit us to distinguish (and place in perspective) natural variability from changes brought about by modern civilization.

Rationale for Gradient Studies

When investigating the effects of an environmental stress factor on ecosystem processes, it would be ideal to have a controlled experiment in natural ecosystems where different levels of the factor under investigation could be applied to homogeneous experimental material. This is, of course, impossible to achieve in field experiments for several reasons. First, only a limited degree of homogeneity in experimental ecosystems can be achieved. Secondly, it is impossible to apply different levels of an environmental stress factor in a field setting on large plots in a realistic fashion. Timing and methods of application are inevitably artificial and can only mimic actual field conditions to a limited extent. In practice, it is necessary to conduct both field studies and controlled chamber experiments in order to fully investigate the effects of environmental stress factors on forest health and productivity.

One approach to field studies is to establish study sites in relatively homogeneous ecosystems which are subject to different levels of the environmental stress factor in question. By establishing study sites along a gradient with different levels of the stress factor, an approximation of a controlled experiment can be achieved. The objective is not so much to evaluate changes in the levels of an ecosystem process over a fixed time period at each study site, but to compare levels and rates of selected ecosystem processes at sites subjected to different levels of environmental stress. Field studies are often confounded by interacting stress factors, usually not considered in site selection. Therefore, it is often necessary to monitor external factors, such as annual temperature or moisture levels, which can affect the levels or rates of ecosystem processes in order to determine year to year and site to site differences that are not directly due to the environmental stress factor under study.

The variation of site characteristics is one of the biggest limitations of gradient studies. If the analysis of data reveals differences, it can not be attributed to any specific cause. Instead, it provides only correlative evidence. This correlative evidence can, however, be used as the basis for developing experiments to test the responses identified on gradient study plots.

Establishment Considerations

Site Selection. The problems associated with realistically applying an environmental stress factor in experimental situations can be addressed by establishing field study sites in areas subject to different levels of a specific stress factor. The degree of homogeneity in the study ecosystems can be controlled, to the extent possible given natural variation, through the careful selection of study sites along the environmental gradient of interest. Three facts must be recognized during the study site selection process:

1. No two sites have identical environmental conditions, even if they are contiguous.

2. The finer the resolution used in examining and characterizing two field systems, the more different they will appear.

3. In the end, the selection of study sites is a subjective decision based on the environmental factors it is deemed necessary to control and the degree of heterogeneity the investigators are willing to accept.

One of the most important decisions in the initial stage of site selection, following the identification of an existing gradient, is the definition of the ecosystem of interest and the environmental factors which will ensure uniformity across a gradient. This includes specification of community structure, ranges of soil physical and chemical properties, meteorological conditions and physiographic factors which may affect ecosystem response to environmental stress. Freedom from uncontrolled disturbance in the past, whether due to natural (insect, disease, and weather) or human (harvesting and recreation) causes, and the ability to protect the study sites from such disturbance in the future are important considerations. Other considerations, such as the availability of electrical power for some types of instrumentation and the logistics of conducting experimental manipulations on the study sites may also be important in selecting study sites.

Study Design

The design of large ecological studies presents a number of problems which must be considered in order to maximize the use of often scarce research resources. While some factors involved in installing a study over a great distance and at a number of different sites are common to all ecological investigations, there are factors which are unique to gradient studies.

Field Design. One of the greatest challenges in designing a large ecological field study is to develop a design which is sufficient to meet the scientific questions under study, yet, is flexible enough to be utilized to address unforeseen questions which may arise in the future. The expense and effort of installing a large field study should not be repeated for every scientific question which may arise. As documentation of the effects of pollution on forest health proceeds, there are natural questions concerning the mechanisms involved and the ecological processes which may be affected. A field study which is initially set up for monitoring and conducting correlative studies of levels of pollution and forest health can, if designed with forethought, be utilized for investigation of ecosystem processes which may involve the installation of additional instrumentation. Even though the types of questions which may arise in the future are difficult to foresee, the permanent installation of relatively large plots which are protected to the greatest extent possible from disturbance can provide a great degree of flexibility in the future. Plots on which forest growth, health, and vigor have been recorded for a number of years, and which have associated records of meteorological conditions and pollution levels, can be utilized to a great extent in designing and conducting process-oriented investigations. For example, the presence of relatively narrow (approximately 10 m) buffer zones surrounding each plot not only serves to protect the plots from disturbance but the buffer zone can also be used as a location for collecting materials for other studies. Understory vegetation or even seedlings of overstory species can be collected for use in chamber or laboratory experiments without disturbing the permanent plots. A field design which is flexible and which allows the addition of further studies in the future will greatly increase the value of a study beyond the immediate results.

Statistical Considerations. In the design of any field study, the scientific questions and statistical analysis of results should be established. Gradient studies may be utilized to provide correlative information as well as comparisons of levels or rates of ecosystem process as determined in an analysis of variance. In any case, an attempt to calculate the likelihood of detecting a difference, if one exists, should be made early in the design process to determine if the design has a good chance of providing meaningful results. Statistical power can be increased in several ways: increasing the number of replicates, increasing the precision with which field measurements are made, and by utilizing knowledge of associated factors which may affect response (covariates). Given budgetary limits, instrumentation limits, and natural variability in ecological systems, the utilization of covariates provides an attractive method for increasing statistical power of any given design. In most cases, the availability of covariates such as meteorological variables can greatly increase the ability to detect pollution effects without increasing the number of field plots. When installing replicate plots at a given level of deposition, it is important that they are not just multiple observations of one set of experimental conditions (pseudoreplication) but that they are true replicates. That is, they should not be just one large plot divided into smaller areas but there should be true replication of experimental conditions. This can be addressed, even in plots which are contiguous, by on-plot monitoring. If this is not feasible, the location of fewer measurement plots, for example, near different meteorological stations may be more efficient than the installation of a large number of subplots near one station. It is also important to give careful thought to the population of interest during the establishment of the criteria of site selection in order to maximize the generality of any results. Examples of different field designs and methods of addressing these statistical considerations are discussed in the descriptions of North American gradient studies which follow.

Sampling Variability. In order to evaluate statistical power or to address questions of sufficient replication, it is necessary to understand the level of natural variability in the different variables being measured. Data from meteorological and deposition monitoring networks, as well as existing information on forest inventory and health, can be utilized to obtain estimates of natural variability. After some data have been collected in the early stages of investigation - usually at the end of the first year of field work - the variability of each variable should be estimated. Given the study design, detection limits can be determined for any given probability level for each variable. Decisions should be made regarding the sufficiency of the existing levels of replication in addressing each scientific question of interest. It may be possible to reduce the level of effort and still achieve the desired scientific objectives. Conversely, it may be necessary to increase the level of effort in order to provide meaningful data. Given existing resources, it may even be better to postpone addressing some questions until increased resources are available. By evaluating sampling variability for information to be used in addressing each question, limited resources can be optimized to maximize the gain in scientific knowledge.

Data Collection Standards and Quality Assurance. Large ecological investigations are, of necessity, interdisciplinary and involve a number of scientists and technicians. They are also often designed to last many years

and may experience the turnover of key personnel involved with study design, data collection, and analysis. For these reasons, it is necessary to have complete documentation of field measurement methods, sample collection procedures, analytical procedures, and methods used to edit, verify, and archive data. Archiving multiple copies of data records is also desirable.

Due to the large scope of gradient studies and the fact that different field crews may be involved in taking measurements at different study sites, it is very important to insure that common field protocols and methods are used by all crews at all sites. Common training sessions, the use of common laboratory standards and sharing of laboratory samples are very valuable in insuring that the same procedures are used at all sites and that equal precision is obtained in all analyses. Verification of data through remeasurement of a small percentage of observations can be very useful in insuring that equal precision in measurement is achieved by all crews and that the same data collection standards are being used at all sites. Remeasurement of selected observations is also useful in defining the measurement error associated with the field and laboratory procedures; this is especially important if results of the ecological studies are to be part of the basis for developing environmental controls and pollution emission standards.

Review of Gradient Research in the U.S.

Mechanisms of Pollutant Response in Plants. Plant processes are subject to control by the genetic makeup of the plant and the environmental factors to which it is exposed. Pollutant deposition alters the plant's environment by changing the availability or utilization of carbon, water, and nutrients. Furthermore, it has the potential to change plant function. There are numerous ways in which plants respond to pollutants, and there are differences in the magnitude of the response and the mechanism of response.

Trees growing in a forest are impacted by many stresses. It is important to evaluate the relative role of pollutant stress because whether it is a primary or secondary stress, whether it leads to direct or indirect response patterns, and whether it causes acute or chronic damage is determined by the mechanism by which trees are injured. The goal of this section is to review the primary mechanisms by which plant processes are altered by air pollution stress.

Mechanisms of Impact. Mechanisms of impact to plant processes can be subdivided into three general categories: surface phenomena, biochemical phenomena, and physiological phenomena. Surface phenomena focus on the leaf cuticle which protects the photosynthetically active cells and retains leaf nutrients. Changes in stomata which regulate gas exchange are another potential location of surface impact from air pollutants. Biochemical phenomena include antioxidants, alterations in molecular and cellular structure, changes in nutrient and trace metal uptake, and changes in hormone regulation. Physiological phenomena which impact plant processes are primarily those which change carbon assimilation or allocation. This includes photosynthesis, respiration, alterations in root and/or shoot ratios and leaf biomass.

The prevalence of air pollutants in industrialized regions has led to many studies that have resulted in the formulation of numerous proposals for the mechanisms by which pollutants may injure plants. The various mechanisms are categorized as follows: Biochemical: soil mediated, winter injury, disruption of reproduction or regeneration, altered susceptibility to pests and pathogens.

Surface: nutrient leaching from foliage.

Physiological: altered physiology and carbon allocation.

Soil Mediated Mechanisms. In many soils, aluminum is normally present in an insoluble non-toxic form. Increased solution acidity may lead to increased weathering of clay minerals and thus increased concentrations of the soluble, toxic form. Heavy metals, especially lead, have been deposited on some forests where they accumulate in the litter and upper soil layer (Friedland, Johnson et al., 1984; Jackson et al., 1978). As with aluminum, increased solution acidity can cause increased concentrations of soluble metal ions in soil water. It is known that high concentrations of soluble metals are toxic to roots and mycorrhizae (Abrahamsen and Tveite, 1983; Foy, 1974; Schier, 1985; Ulrich, 1980; Wong, 1982) and can cause reduced growth (Shafer, 1985) and reduced photosynthesis (Rolfe and Bazzaz, 1975). Laboratory studies have demonstrated altered microbial activity resulting from increasing metal mobility with decreasing solution pH (Babich and Stotzky, 1979; Clark and Clark, 1981; Rühling and Tyler, 1973; Tyler, 1975). What remains unknown is whether acidic deposition sufficiently increases acidification of the soil solution beyond the natural acidification process to mobilize those metals to toxic concentrations. Soil microbial populations are indispensable mediators of nutrient cycles because of their role in decomposition and mineralization. Significant disruption of these populations would alter normal nutrient cycling and decrease nutrient availability to plants.

Although nitrogen plays a key role in maintaining the vigor of ectomycorrhizae, excess nitrogen may be harmful. Nitrogen toxicity can occur in the absence of acidification; it is the nitrogen itself that is of primary concern. The links between nitrogen deposition and mycorrhizal and plant response under field conditions, however, have not been ascertained.

Leaching of nutrient cations occurs as H^+ ions in the soil solution exchange with cations (K⁺, Ca²⁺, Mg²⁺, Na⁺, etc.) adsorbed to soil particles. Once in solution, the cations, along with mobile anions, are leached from the soil profile. Nutrient cation leaching has been demonstrated experimentally under both laboratory and field conditions (Abrahamsen, 1980a, b, c; Bjor and Teigen, 1980; Haman, 1977; Huete and McColl, 1984; Lee and Weber, 1982; Schier, 1984; Stuanes, 1980).

The applicability of this hypothesis to forest decline is dependent on demonstrating that acidic deposition increases the rate of soil acidification and that the increased rate of acidification and concomitant loss of nutrients have a negative effect on tree growth through a net increase in leaching. The major limitation to interpreting the role of cation leaching is that cation replacement (e.g., weathering) and recycling processes are not well understood. Weathering of minerals within the soil profile continually resupplies nutrients to exchange sites. Trees continually cycle and redistribute nutrients between soils and biomass. Atmospheric inputs of dry and wet deposition add base cations in addition to acidic cations and anions. The relationship between acidic deposition and these processes is not well known, even for intensively studied sites, and regional differences in the importance of these processes have not been quantified.

Nutrient Leaching From Foliage. Foliage leaching is also common in humid ecosystems and has been well documented (Johnson et al., 1982; Likens et al., 1977; Tukey, 1970). Leaching is a normal part of nutrient cycling and does not adversely affect the plant as long as the critical internal nutrient balance is maintained by plant uptake. Increased H⁺ loading by atmospheric deposition, however, may act to accelerate normal leaching rates. Several studies have demonstrated a correlation between precipitation pH and base cation removal (Hoffman et al., 1980; Scherbatskoy and Klein, 1983; Wood and Bormann, 1975). This hypothesized leaching response is also related to ozone toxicity in that leaching is increased after ozone caused injury to cell membranes (Prinz et al., 1982). A major unanswered question is whether an increased loss of cations from foliage results in a net nutrient imbalance and subsequent physiological impairment.

Altered Physiology and Carbon Allocation. Changes in allometric growth or internal photosynthate allocation can result in increased water or nutrient stress. Nitrogen inputs, for example, promote relatively more growth above ground than below ground and may ultimately lead to increased susceptibility to drought (Kramer and Kozlowski, 1979). More generally, however, any stress that reduces photosynthetic capacity below the level required for growth and development of above-ground tissues will result in reduced carbohydrate allocation to root systems (McLaughlin and Shriner, 1980). Ozone and other gaseous air pollutants have been demonstrated to interfere with photosynthate translocation to roots (McLaughlin and McConathy, 1983) and between growing and mature foliage.

Winter Injury. Plants develop resistance to winter freezing through a cold-hardening process involving metabolic changes that take place annually after the period of active growth. Nitrogen inputs may prolong active growth, delay cold hardening, and thus increase the risk of freezing in late autumn or early winter (Kramer and Kozlowski, 1979; Soikkeli and Kärenlampi, 1984; Tisdale and Nelson, 1975; Weetman and Fournier, 1984). Desiccation is another stress that can cause winter injury. Internal water status is particularly crucial in winter when soil water may be frozen and therefore unavailable to plants. Air pollutants may erode or retard the development of the leaf cuticle that restricts water loss (Fowler et al., 1980; Huttunen and Laine, 1983; Shriner, 1983). It has also been suggested that fertilization by atmospheric nitrogen may promote a break in dormancy during mid-winter warm periods that results in subsequent freezing damage. Friedland, Gregory et al. (1984) observed visible foliage damage on red spruce in Vermont that appeared to be caused by cold stress or winter desiccation.

Disruption of Reproduction or Regeneration. Reproduction and regeneration are fundamental processes of forest succession. Reduced pollen, seed, or seedling viability would have an important impact on community dynamics and successional patterns. Relatively little research has been done on the effects of air pollutants on the reproduction and regeneration of forest species and no specific physiological mechanisms have been proposed.

Altered Susceptibility to Pests and Pathogens. Pests and pathogens are normal components of forest ecosystems that trees are adapted to resist. Trees that are weakened from any kind of biotic or abiotic stress, however, may become more susceptible to attack by pests and pathogens. Air pollution induced stress is known to produce physiological changes and loss of vigor that are sometimes accompanied by pest and pathogen attack.

Examples of Gradient Research in the U.S.

A number of different gradient studies were initiated in the U.S. during the past decade. These studies were established to evaluate air pollution impact to forest ecosystems in different regions of the U.S. In Pennsylvania and Michigan, sample plots were established along gradients of sulfate deposition in mixed hardwood forests. Along the Appalachians, plots were established along an elevational gradient to assess health of spruce and fir forests. In the West, in the Sierra Nevada Mountains, a gradient study was established to determine the impact of ozone to mixed conifer forests. A short overview of these studies follows.



Fig. 1. a — average wet sulfate deposition levels 1980—84. b — average wet nitrate deposition levels 1980—84.

Michigan Sulfate Deposition Gradient. In 1986, a study investigating northern hardwood productivity and health was initiated in the Lake States across a sulfate deposition gradient (Fig. 1). Five study sites are located in mature, maple-dominated (*Acer-Betula*) forests across the gradient with deposition levels ranging from <10 to over 20 kg/ha/yr of SO₄. At each of the five study sites, there are three 30×30 m intensive study plots. The scientific hypotheses being investigated in the gradient study are given in Table 1; the data being collected to address each scientific question are given in Table 2.

Table 1

Scientific hypotheses being investigated in the Michigan sulfate deposition gradient

Hypothesis 1: The atmospheric pollution gradient is directly related to chemistry of throughfall and soil solutions, and to cations leaching from canopies and soils. Hypothesis 2: Atmospheric deposition of S, N, and acids alters foliage elemental ratios and litter decomposition. Growth efficiency (stemwood production/unit leaf area) of forest stands Hypothesis 3: declines as atmospheric pollution increases. Hypothesis 4: Inputs of atmospheric pollutants alter the pattern of allocation of carbon to leaves and fine roots. Rates of seedling mortality and recruitment into larger size classes decrease as atmospheric inputs increase. Hypothesis 5: Hypothesis 6: Species richness and diversity are negatively correlated to atmospheric inputs. Hypothesis 7: Genetic changes due to atmospheric pollution have already occurred over the gradient such that the existing populations of trees are more tolerant

to air pollutants at polluted sites than pristine sites.

2 Eesti TA Toimetised. Ö 1 1991

17

Data collected to accept or reject the scientific hypotheses

Hypothesis 1: Daily precipitation (amount and type); solution chemistry of precipitation throughfall and soils (SO2, NO3, NH4, base cations, pH, specific conductance).

Hypothesis 2: Chemistry of litter and fresh foliage (analysis of N, P, K, Ca, Mg, S). Hypotheses 3 & 4: Stemwood production (diameter and height change), leaf area (litterfall method), and fine root extension (via microvideo mini-

Hypotheses 5 & 6:

- rhizotron technology). Seedling growth (height, caliper shoot elongation), seedling mortality, and ground flora species identification, size, coverage,
- and frequency. Hypothesis 7: Chamber fumigation responses of two relatively sensitive tree species to air pollution (amount of visible leaf damage from SO2 and O3, shoot, root, and total tree biomass).



Fig. 2. Conceptual model for analyzing effects of deposition of atmospheric pollutants on nutrient cycles and productivity of overstory trees.

The study is designed to compare levels and rates of selected ecosystem processes in similar systems receiving different levels of anthropogenic sulfate, nitrate, and hydrogen ion deposition. A relatively simple five-compartment model (Fig. 2) provides the framework utilized for these comparisons. All of the components of the cycle are not known with equal precision. Some are measured directly and with high precision on the study plots, some are measured indirectly or with lower precision, and some are assumed from relationships given in the literature. At the initiation of the study, components of the cycles which were thought to be most susceptible to atmospheric deposition, and which were technologically feasible to measure with the resources available, were identified for detailed on-site determination. To date, information from the study plots suggests that deposition of sulfate and nitrate have altered the cycling of nutrients on the study sites; however, there is no conclusive evidence that productivity of the overstory species has been impacted by deposition.

Site and Stand Characteristics Associated With Potential Decline and Regeneration Success of Spruce-Fir Stands in the Appalachians. A gradient study has been established in the Appalachian Mountains to study spruce-fir stands. Permanent (400 m²) plots have been established on six geographically distinct areas: Mt. Rogers National Recreation Area (VA), the Black Mountains (NG), Great Smoky Mountains National Park (NC and TN), Whiteface Mt. (NY), Mt. Moosilauke (NH) and Howland (ME) (Fig. 3). The gradient here is an elevational gradient with the highest concentrations of ozone (total ppm hours), sulfate and nitrate occurring at the highest elevations.



Fig. 3. Six intensive research sites.

At each study area, stratification variables include elevation, exposure to prevailing winds, and slope position with three randomly located replicates per stratification combination. Vegetation data are taken in three structural classes: overstory (5 cm DBH), understory (<5 cm DBH and 1.37 m tall), and herb strata (<1.37 m tall). All trees on the plot are tagged, identified by species, measured for DBH, rated on a 4 point scale, and assessed for disturbance symptomatology. Ten randomly selected dominants and codominants are cored for age, and measured for total height, live crown ratio, and live crown width. Understory samples are taken in three 16 m² subplots and all woody stems are recorded by species, height, live crown ratio, and crown width. Herb and seedling strata samples are measured in two nested 1 m² sub-subplots for each understory subplot. All woody stems are counted by species and recorded in one of five age-size classes. Herbaceous vegetation is recorded for each species by percent cover. Seed traps are installed adjacent to the intensively measured area at a subsample of the plots for assessment of seed fall and viability by species.

Near the selected permanent plots, all overstory trees on a 10×10 m area are measured as on the 400 m² plot and then harvested. Stem analysis is conducted on 6 trees per plot by sectioning at two meter intervals and at breast height to determine historical growth data. The remaining trees are left to decay on site.

The objectives of this study are:

1. Characterize existing stand conditions in terms of spatial distribution, age, size, growth, biomass, species composition, and decline symptoms of the overstory and understory of spruce-fir stands.

2. Determine the relationship between stand attributes (composition, growth, decline symptoms) and site characteristics such as elevation, exposure, slope, latitude, and soil physical and chemical properties.

3. Characterize and determine regeneration success of spruce-fir type.

4. Monitor long-term changes in stand composition and growth.

Measurement of Forest Condition and Response Along the Pennsylvania Atmospheric Deposition Gradient. In 1987, a study investigating the effects of atmospheric deposition along a well-defined deposition gradient was initiated in the oak-hickory forests of north central Pennsylvania (Fig. 4). Along this 160 km gradient, sulfate (SO₄) deposition varies from approximately 20 kg/ha/yr in the eastern area (near Williamsport, PA) to over 40 kg/ha/yr in the western area (near Brookville, PA). Initial work focused on selecting and establishing study sites in 13 analogous stands across the deposition gradient. Stands were selected so as to minimize the variability associated with tree age, overstory species composition and stocking, soil physical characteristics, and natural or humancaused disturbances. The scientific hypotheses being investigated in this study are provided in Table 3, and the data being used to assess these questions are summarized in Table 4.

This study has four major components which include: 1) monitoring of wet deposition chemical composition at 11 sites across the gradient; 2) forest ecosystem studies focused on potential difference in soil chemical status, overstory and herbaceous biomass production, and red oak (Quercus rubra L.) growth in 13 analogous stands; 3) evaluation of overall stand health, and the incidence and severity of insects and pathogens with emphasis on crown condition; 4) ozone monitoring and evaluation of possible growth effects on four tree species at three opentop chamber sites. Each of these components addresses an attribute of ecosystem knowledge necessary to evaluate atmospheric deposition effects. The integration of these components will permit a comprehensive evaluation of deposition effects in this region of the oak-hickory forest. This report will summarize the approaches and findings of the second component: forest ecosystem studies.

Forest ecosystem studies are focused in the 13 analogous stands. Within each of these stands, 10 or 20 plots, depending on stand size, were randomly located for measurement of all trees 2.5 cm in a 12-m-radius plot. Plot centers also serve as reference points for herbaceous biomass sampling (1-m-radius quadrats) and soil and organic horizon sampling.



Fig. 4. Isopleth map of sulfate deposition (kg/ha) in Pennsylvania. The small squares are monitoring locations, and the dashed line is the approximate location of the gradient for the current study.

Table 3

Scientific hypotheses being investigated in the Pennsylvania atmospheric deposition gradient study

Hypothesis 1:	Forest productivity measures (e.g. overstory and herbaceous biomass, red oak basal area and height increments, species diversity, litter accumulation) are negatively related to the level of atmospheric inputs.
Hypothesis 2:	Atmospheric deposition inputs are reflected in soil chemical parameters and by leaching of nutrient cations.
Hypothesis 3:	Atmospheric deposition alters elemental ratios in woody plant foliage and herbaceous foliage.
Hypothesis 4:	Climatic sensitivity of red oak tree-ring chronologies is related to levels of estimated historical deposition inputs.
Hypothesis 5:	The severity and incidence of forest insect disorders and forest diseases are positively related to the level of atmospheric inputs.
Hypothesis 6:	The chemistry of red maple xylem sap is directly related to the chemistry of atmospheric inputs.
Hypothesis 7:	Productivity of four tree species is related to levels of ambient ozone.
	Table 4
	Data necessary to accept or reject the scientific hypotheses
Hypothesis 1:	Weekly precipitation (amount); solution chemistry of precipitation; stand stocking and density; amounts of herbaceous species; ring width measure- ments, height increment from stem analysis; litter amounts from a con- stant sample area
Hypothesis 2:	Weekly precipitation (amount) and solution chemistry; soil chemical characteristics of major horizons sampled in each stand; amounts of sulfate in each horizon
Hypothesis 3:	Chemistry of soils, foliage, and litter
Hypothesis 4:	Ring width measurements and chronologies; historical climatic records; estimated levels of historical deposition inputs based on 8 years of monitoring data
Hypothesis 5:	Survey data of insects and pathogens present in analogous stands with emphasis on crown condition; evaluation of stand health in all analogous stands; weekly precipitation amount and solution chemistry
Hypothesis 6:	Chemistry of red maple sap and soils: weekly deposition inputs
Hypothesis 7:	Height, diameter, total biomass, and amount of visible leaf injury on
	four tree species maintained in open-top chambers; amount of ambient ozone

Analysis of sulfate deposition effects on forest soils indicate accumulation of sulfate in B2 horizons. Preliminary analyses of the organic (O2) horizons sampled at all stands did not reveal substantial differences in total sulfur in this compartment. Other analysis investigating relationships between environmental factors, deposition inputs, A-horizon soil chemistry, and herbaceous biomass are in progress (Fig. 5). Tree-ring analysis of red oak chronologies developed from a minimum of 20 trees in each stand will be used with climatic modeling to detect any growth effects related to sulfate deposition (Fig. 6). A stem analysis project was initiated in 1989 to determine whether height increment of red oak is related to deposition inputs (Fig. 7). Integration of stand health data into analyses of growth effects will allow a detailed evaluation of factors affecting tree growth in these stands.

In 1988, a pilot lichen survey of communities present at 40 selected sites across the gradient revealed that lichen richness was comparatively greater on the low sulfate deposition portion of the gradient. Concentrations of Al, Fe, Cr, and Cu in *Hypogymnia physodes* were greater in the high deposition areas of the gradient. More detailed studies will be conducted in fall 1989.

Red maple (*Acer rubrum* L.) sap chemistry has been monitored for two years at seven sites (different sites from those used for ecosystem studies) along the gradient to determine the usefulness of sap chemistry as a biomonitor of soil and atmospheric deposition chemistry. Preliminary results indicate that elemental contents of red maple sap are valuable for indicating biological response to chronic atmospheric deposition, but may not be useful for detecting short-term effects of artificially added sulfate.



Fig. 5. Analytical methods and data necessary for investigating forest community responses to atmospheric inputs.



Fig. 6. Analytical methods and data necessary for evaluating red oak growth trends and climatic response to atmospheric inputs.



RED OAK HEIGHT GROWTH

Fig. 7. Analytical methods and data necessary for evaluating red oak height in response to atmospheric inputs.

Growth Trends in the Mixed Conifer Forest of Sierra Nevada. Mixed conifer stands were sampled in seven federal administrative units in California where symptoms of ozone injury had been previously recorded (Fig. 8). Four stands with oxidant injury (symptomatic) and four stands without injury (asymptomatic) were sampled in each forest or park. Symptomatic stands were located along the western edge of the Sierra, while asymptomatic stands were located in the interior. Twenty-four ponderosa pine were cored in each stand. Dbh, height, mistletoe infection, and level of oxidant injury (needle chlorosis and years of needles retained) were recorded for each tree.



Fig. 8. Ponderosa pine cores collected in 56 mixed conifer stands throughout the Sierra Nevada.

Cores were placed in wood blocks and sanded until individual tracheids were visible. Cores were initially crossdated and retained in the analysis only if they could be confidently crossdated. Ring widths were measured with an incremental measuring machine interfaced with a stereomicroscope, video camera and monitor, and Apple IIe microcomputer. Data were transferred to Data General MV15000 for subsequent analysis.

Ongoing studies of tree growth trends indicate that the use of traditional dendroclimatological techniques is inadvisable because "detrending" techniques used to remove age and bole diameter effects from the data also remove the nonstationary effects of exogenous disturbances. There is probably not a single "best" approach to the analysis of tree-ring data. A diversified analysis would incorporate the strengths of several techniques, and conclusions would be less dependent on the assumptions and constraints of a single methodology. Several techniques are currently being evaluated by researchers studying regional growth trends in the western United States. Our approach will emphasize use of the Kalman filter after appropriate curve-fitting. The major objectives of this study are:

1. Quantify growth trends and natural variability in growth for ponderosa pine in the mixed conifer forest of the Sierra Nevada:

(a) at the stand level,

(b) at the regional level.

2. Evaluate recent growth trends with respect to expected patterns: a) by comparing recent to previous growth with the use of multivariate generalized least squares analysis using Kalman filter and other appropriate statistical techniques,

(b) by comparing growth of trees with and without symptomatic oxidant injury.

3. Account for sources of variance in growth that can be attributed to injury level and environmental factors.

Acknowledgements. The authors would like to acknowledge the contributions of the following researchers: Dr. David Shriner for his assistance in developing the hypotheses section on air pollution effects on plants; Dr. Robert Long for his summary of the Pennsylvania atmospheric deposition gradient study; Dr. Shepherd Zedaker for summary information on the on-going study of spruce-fir stands in the Appalachians; and Dr. David Peterson for his summary of on-going studies on the mixed conifer forests in Sierra Nevada.

REFERENCES

- Abrahamsen, G. 1980a. Acid precipitation, plant nutrients, and forest growth. In: Eco-logical Impact of Acid Precipitation. D. Drablos and A. Tollan, eds. Proc. of an International Conference. Sandefjord, Norway. 58-63. SNSF Project. Oslo-As, Norway.
- Abrahamsen, G. 1980b. Effects of acid precipitation on soil and forest: Leaching of plant nutrients. In: Ecological Impact of Acid Precipitation. D. Drablos and A. Tollan, eds. Proc. of an International Conference. Sandefjord, Norway. 196. SNSF Project. Oslo-As, Norway. Abrahamsen, G. 1980c. Impact of atmospheric sulfur deposition on forest ecosystems. In:
- Atmospheric Sulfur: Environmental Impact and Health Effects. D. S. Shringer, C. R. Richmond, and S. E. Lindberg, eds. 397–416. Ann Arbor Science, Ann Arbor, Michigan.
- Abrahamsen, G., Tveite, B. 1983. In: Effects of Acid Precipitation on Terrestrial Eco-systems. T. C. Hutchinson and M. Havas, eds., 305-318. Plenum Press, New York.
- Babich, H., Stotzky, G. 1979. Abiotic factors affecting the toxicity of lead to fungi. Applied and Environ. Microbiol. 38, 3, 506—512.
- Bjor, K., Teigen, O. 1980. Effects of acid precipitation on soil and forest. 6. Lysimeter experiment in greenhouse. In: Ecological Impact of Acid Precipitation. D. Drablos and A. Tollan, eds. Proc. of an International Conference, Sandefjord, Norway. 200-201. SNSF Project. Oslo-As, Norway. Clark, R. K., Clark, S. C. 1981. Floristic diversity in relation to soil characteristics in a
- K. K. Churk, S. C. 1961. Honste diversity in relation to soft characteristics in a lead mining complex in the Pennines, England. New Phytol., 98, 799—815.
 Fowler, D., Cape, J. N., Nicholson, I. A., Kinnaird, J. W., Paterson, I. S. 1980. The influence of a polluted atmosphere on cuticle degradation on Scots pine (Pinus sylvestris). In: Ecological Impact of Acid Precipitation: Proceedings of an sylvestris). In: Ecological Impact of Acid Precipitation: Proceedings of an International Conference, Sandefjord, Norway, March 11-14, 1980. D. Drablos and A. Tollan, eds., 146, SNSF Project, Oslo, Norway.
 Foy, C. D. 1974. Effects of aluminum on plant growth. In: The Plant Root and Its Environment. E. W. Carson, ed., 601-642. University Press, Virginia.
 Friedland, A. J., Gregory, R. A., Kärenlampi, L., Johnson, A. H. 1984. Winter damage to foliage as a factor in red spruce decline. — Can. J. For. Res., 14, 963-965.
 Friedland, A. J., Johnson, A. H., Siccama, T. G. 1984. Trace metal content of the forest floor in the Green Mountains of Vermont: Spatial and temporal patterns. — Water, Air, and Soil Pollut. 21, 161-170.
 Haman, F. 1977. Effects of percolating water with graduated acidity upon the leaching

- Haman, F. 1977. Effects of percolating water with graduated acidity upon the leaching of nutrients and the changes in some chemical properties of mineral soils. -
- J. Sci. Agric. Society of Finland, 49(4), 250-257. Hoffman, W. A., Jr., Lindberg, S. E., Turner, R. R. 1980. Some observations of organic constituents in rain above and below a forest canopy. Environ. Sci. & Tech. 14, 8, 999-1002.

Huete, A. R., McColl, K. G. 1984. Soil cation leaching by "acid rain" with varying nitrate-to-sulfate ratios. — J. Environ. Qual. 13, 3, 366—371.
Huttunen, S., Laine, K. 1983. Effects of air-borne pollutants on the surface wax structure of Pinus sylvestris needles. — Ann. Bot. Fennici 20, 79—86.
Jackson, D. R., Selvidge, W. J., Ausmus, B. S. 1978. Behavior of heavy metals in forest microcosms: I. Transport and distribution among components. — Water, Air, Soil Pollut. 10, 3—11.

Johnson, D. W., Turner, J., Kelly, J. M. 1982. The effects of acid rain on forest nutrient status. — Water Resources Res. 18, 3, 449—461.

Kramer, P. J., Kozlowski, T. T. 1979. Physiology of Woody Plants. Academic Press, New York.

Lee, J. J., Weber, D. E. 1982. Effects of sulfuric acid rain on major cation and sulfate Likers, G. E., Bormann, F. H., Pierce, R. S., Eaton, J. S., Johnson, N. M. 1977. Biogeo-chemistry of a Forested Eco-System. Springer, New York.
McLaughlin, S. B., McConathy, R. K. 1983. Effects of SO₂ and O₃ on allocation of ¹⁴C-labelled photosynthate in Phaseolus vulgaris. — Plant Physiol. 73, 630—

635.

McLaughlin, S. B., Shriner, D. S. 1980. Allocation of resources to defence and repair. In: Plant Disease. J. G. Horsfall and E. B. Cowling, eds. Chap. 22. Academic Press, New York.

Press, New York.
Prinz, B., Krause, G. H. M., Stratman, H. 1982. Forest damage in the Federal Republic of Germany. LIS Report No. 28. Land Institute for Pollution Control, Landes-anstalt für Immissionsschutz des Landes Nordrhein-Westfalen. Essen. Wallneyer Strasse 6, Federal Republic of Germany. (C.E.G.B. Translation No. T14240).
Rolfe, G. L., Bazzaz, F. A. 1975. Effect of lead contamination on transpiration and photosynthesis of loblolly pine and autumn olive. — Forest Sci. 21, 1, 33—35.
Rühling, A., Tyler, G. 1973. Heavy metal pollution and decomposition of spruce needle litter. — Oikos 24, 3, 402—416.
Scherbatskoy, T., Klein, R. M. 1983. Response of spruce and birch foliage to leaching by acidic mists. — J. Environ. Qual. 12, 2, 189—195.
Schier, G. A. 1985. Response of red spruce and balsam fir seedlings to aluminium toxicity in nutrient solutions. — Can. J. For. Res. 15, 29—33.
Shafer, S. R. 1985. Effects of airborne chemicals on microorganisms. In: Proceedings:

Shafer, S. R. 1985. Effects of airborne chemicals on microorganisms. In: Proceedings: Air Pollutants Effects on Forest Ecosystems Symposium, May 8-9, 1985, St. Paul, MN. 285-296. The Acid Rain Foundation, St. Paul, MN.
Shriner, D. S. 1983. Air Pollution Impacts on Forest Trees: Acid Deposition: Effects on Terrestrial Ecosystems. Oak Ridge National Laboratory Publication No. 2062. Oak Ridge, TN.

Soikkeli, S., Kärenlampi, L. 1984. The effects of nitrogen fertilization on the ultrastructure of mesophyll cells of conifer needles in northern Finland. - Eur. J. For. Path. 14, 129-136.

Stuanes, A. O. 1980. Effects of acid precipitation on soil and forest, 5. Release and loss Stuanes, A. O. 1980. Effects of acid precipitation on soil and forest. 5. Release and loss of nutrients from a Norwegian forest soil due to artificial rain of varying acidity. In: Ecological Impact of Acid Precipitation: Proceedings of an International Conference, Sandefjord, Norway, March 11—14, 1980. D. Drablos and A. Tollan, eds., 198—199. SNSF Project, Oslo-As, Norway.
 Tisdale, S. L., Nelson, W. L. 1975. Soil Fertility and Fertilizers. MacMillan, New York. Tukey, H. B., Ir. 1970. The leaching of substances from plants. — Annual Rev. Plant Physiol. 21, 305—324.

Tyler, G. 1975. Heavy metal pollution and mineralization of nitrogen in forest soils. -

Intervention of intervention and inneralization of introgen in forest sons. — Nature, 255, 701—702.
 Ulrich, B. 1980. Production and consumption of hydrogen ions in the ecosphere. In: Effects of Acid Precipitation on Terrestrial Ecosystems. T. C. Hutchinson and M. Havas, eds., 255—281. Plenum Press, New York.
 Weetman, G. F., Fournier, R. M. 1984. Ten-year growth and nutrition effects of a straw treatment and of repeated fertilization on jack pine. — Can. J. For. Res., 14, 116. 402.

416-423.

Wong, M. H. 1982. Metal co-tolerance to copper, lead, and zinc in Festica rubra. -

Wood, T., Bormann, F. H. 1975. Increases in foliar leaching caused by acidification of an artificial mist. Ambio 4, 169–170.

Presented by J. Martin, D. Sc.,

Member of the Estonian Academy of Sciences

Received September 19, 1990