PROCEEDINGS

CALIFORNIA FOREST RESPONSE PROGRAM

PLANNING CONFERENCE

February 22-24, 1987
Pacific Grove, California

Edited by:

S. H. Bicknell
Forestry Department
Humboldt State University
Arcata, CA 95521

Sponsored by:

California Air Resources Board
Western Conifers Research Cooperative

PREFACE

The review papers and draft plan presented on the following pages are the culmination of an effort sponsored jointly by the California Air Resources Board and the Western Conifers Research Cooperative. As the contractor responsible for this project, I have seen the California Forest Response Program plan develop from embryonic stages to the fairly detailed document you will find here. This planning and review effort has been conducted independently of the government agencies which sponsored it. The completed plan has been submitted to the Air Resources Board and is currently under review and revision for consideration for adoption for California. Implementation for California is now up to the Air Resources Board.

The draft research plan presented here is for the purpose of discussion only. It does not imply a commitment of funds or personnel by the California Air Resources Board or by the Western Conifers Research Cooperative.

Comments on this document should be directed to Dr. John Holmes, Research Division, Air Resources Board, Post Office Box 2815, Sacramento, CA 95812. Additional copies of this document may be obtained from Humboldt State University Foundation, Arcata, CA 95521.

Susan H. Bicknell
Forestry Department
College of Natural Resources
Humboldt State University
Arcata, CA 95521

TABLE OF CONTENTS

CALIFORNIA FOREST RESPONSE PROGRAM DRAFT PLAN

THE PLANNING PROCESS

Susan H. Bicknell
Humboldt State University
Arcata, CA 95521

INTRODUCTION

In 1982, the California Legislature passed the Kapiloff Acid Deposition Act which set up a 5-year research and monitoring program to be implemented by the California Air Resources Board (CARB). This program was intended to "determine the present and potential environmental, public health and economic effects of continued acid deposition" in the State.

This mandate forms the rationale for the initiation of a California Forest Response Program (CFRP). An assessment of the effects or potential effects of acid deposition, alone or in combination with other air pollutants, on forest resources will be required as part of the final report of the Kapiloff program. This contract was the result of a request for proposals initiated by the Air Resources Board to meet the mandate of the Kapiloff Act.

The request for proposals called for a thorough literature review and a draft plan. The literature review was intended to supply a background in the effects of acid deposition and other air pollutants on forests. This background was necessary to ensure the development of a well-informed, well-considered, and state-of-the-art plan of research for the State of California. The objective of the plan was to evaluate the effects of acid deposition and associated pollutants on California forests and to determine the mechanisms of those effects.

The contractor's proposal argued that a conference of nationally respected scientists was the most efficient method of providing the wide range of expertise necessary to formulate an adequate plan for California. The Air

Resources Board agreed, and a conference of 44 experts was organized and convened February 22-24, 1987. Ten of these experts provided literature review papers. The literature review papers were supplied in draft form to all conference participants, were formally peer reviewed, and are included in this Conference Proceedings. The conference was also used for workshops, formal debate and formal peer review of the draft plan. The draft plan and appendices, including workshop summaries and biographies of the conference participants, are also included in this volume.

The development of the draft plan, and the conference were also supported by the Western Conifers Research Cooperative of the national Forest Response Program. The Western Conifers Research Cooperative (WCRC) is the research program charged with investigating the effects of acid deposition and associated pollutants on coniferous forests in the western United States (WA, OR, CA, NV, ID, UT, AZ, NM, MT, WY, CO). The Cooperative is administered by the Environmental Protection Agency at the Environmental Research Laboratory in Corvallis, OR.

The draft plan proposes that the initial year of the CFRP will be under the mandate of the Kapiloff Acid Deposition Program; subsequent years will continue as the responsibility of the California Air Resources Board and will additionally be supported by resources and expertise of the Western Conifers Research Cooperative. It is anticipated that other state and federal funds will also be used to support CFRP projects.

DRAFT PLAN DEVELOPMENT

Early in the conference planning it became obvious that if a conference/workshop effort were to successfully produce a workable plan for the Air Resources Board, that the conference participants needed a draft plan to serve as a starting point for debate and deliberations. The Contractor (Susan Bicknell), Kathy Tonnessen and William Walker of the Air Resources Board, and Richard Olson and John Duff Bailey of the Western Conifers Research Cooperative, provided the initial draft plan.

The assumptions we made in developing the plan were:

(1) Forest effects research under this plan will begin with the 1987 field season.

(2) The research will continue for a minimum of five years.

(3) The funding level will be approximately 3 million dollars for the five years.

(4) The California Air Resources Board and the Western Conifers Research Cooperative will share the cost of the research.

(5) The phrase "acid deposition" as used in the draft plan is defined as sulfur and nitrogen compounds and associated pollutants such as ozone, heavy metals and hydrocarbons.

(6) Forests are defined as all California forests and woodland vegetation dominated by trees, but not other woody vegetation such as shrub-dominated chaparral.

PLANNING CONFERENCE AND PEER REVIEW

The California Forest Response Program Draft Plan was subjected to careful technical review by experts in the various fields of forest response to atmospheric deposition. The conference participants wrote and submitted their formal peer reviews before attending the planning conference which was held February 22-24, 1987, at Asilomar Conference Center in Pacific Grove, California. Those written peer reviews are provided in Appendix IV of the attached Final Report.

Preparations for discussion of the plan were facilitated by the presentation of the ten literature review articles at the outset of the conference. Six workshops were then conducted, each concentrating on a section of the Draft Plan (Sections 4-9). Summaries of the workshops are presented in Appendix IV.

The draft plan presented in the following pages is the result of the rewriting effort by the workshop chairs in response to the peer reviews and discussions at the conference. The workshop chairs were Susan Bicknell, Kathy Tonnessen, William Walker, Richard Olson, John Duff Bailey, and John Watson. Their biographies are included in Appendix V.

SUMMARY OF THE DRAFT PLAN

The objective of the CFRP is to evaluate the effects of atmospheric pollution on California forests and to determine the mechanisms of these effects. The plan approaches this task simultaneously statewide, regionally and at intensive sites. The focus of effort of the CFRP plan is ponderosa pine. The plan is integrated by the biological linkages between the physiology of seedlings, growth responses of mature trees, dynamics of forest stands, and patterns in regional and statewide forests.

The approach proposed in the plan has four logical steps. First, the CFRP will establish correlations between deposition (or exposure) and forest condition. Second, the CFRP will conduct experimental studies to determine the mechanisms of effect. Third, the results of the correlative and mechanistic studies will be used in models of ponderosa pine growth, photosynthesis, respiration, and allocation to produce dose-response relationships. Finally, these models, which will be developed to predict single tree and stand response, will provide the framework for assessing the impact of acidic deposition and associated air pollutants on California forests.

This approach can not, however be conducted sequentially. There are six different areas of research activity which will be conducted simultaneously. These research activities include: regional and statewide assessment of forest condition; atmospheric monitoring; permanent forest research site location and development; experimentation and hypothesis testing; quality assurance, quality control and data base management; and synthesis and integration. Each of these areas is detailed in a section of the draft plan (Sections 4-9).

SIGNIFICANT RECOMMENDATIONS WHICH WERE INTRODUCED AT THE CONFERENCE

The conference revealed clear agreement among the experts that the major program focus for the CFRP should be a single species, ponderosa pine, and that the unifying product of the CFRP should be process oriented (growth, photosynthesis, respiration, and allocation) models of ponderosa pine response to air pollutant exposure. The participants agreed that the models should represent both the single mature tree response and the stand level response.

Although there was initial disagreement over some details of the plan, after debate, the consensus of the group was:

1) The CFRP should begin with an initial assessment of existing models of ponderosa pine growth and physiology (photosynthesis, respiration and allocation), and models of ponderosa pine stand dynamics. Early physiological work should concentrate on filling in the gaps to provide working models of normal ponderosa pine physiology and stand dynamics. Only after this step is taken can viable models of ponderosa pine response to air pollutant exposure be built.

2) A program of this nature should include field research.

This field research must be conducted at carefully chosen permanent forest research sites meeting the criteria outlined in the plan. The group did not come to agreement as to how many sites are necessary, nor as to what the most appropriate experimental design for arrangement and location of those sites should be.

3) The field research on forest response must be accompanied by air quality monitoring facilities at the permanent forest research sites.

4) In addition to the initial modeling effort, the group indicated that several other efforts ought to begin as soon as possible: a) analysis of the currently available data base on forest condition in California, b) completion of analysis of the data base on exposure and deposition of California forests, c) basic experimental studies of ponderosa pine physiology and growth to enhance model performance, and d) design and establishment of quality assurance/quality control and data base management systems, organization and procedures.

The disagreement about the experimental design for the location of permanent forest research sites stemmed from the lack of knowledge of exposure regimes in the forested regions of the State. The initial draft plan proposed to locate three permanent forest research sites along a hypothesized pollution gradient from south to north on the West Slope of the Sierra Nevada. Several of the conference participants pointed out that for ozone, the most obvious gradient was elevational, and not from south to north. Other participants suggested that for different air pollutants, the gradients were likely to have different distributions. Most participants agreed that it would be a good idea to design the locations of the permanent forest research sites along a pollution gradient. However, there was no agreement as to how this could be accomplished with our current knowledge.

With no answer to this dilemma immediately available, the conference struck a logical compromise. The initial efforts of the CFRP can all be accommodated at one primary permanent forest research site located on the northern West Slope of the Sierra Nevada. This site should be "clean" with respect to exposure and deposition of important air pollutants. The participants agreed that "clean" needs further clarification. The conference participants were also in favor of establishing secondary permanent forest research sites in "dirty" regions of the State which also meet the criteria of dominance by ponderosa pine and site similarity to the primary site. The participants agreed that these sites should be established in the third or fourth years of the CFRP, and that their location criteria should depend on the results of the initial efforts to characterize exposure and forest condition throughout the state, as well as the initial research efforts at the primary site.

One last point of agreement which colored the entire conference was that 3 million dollars for five years was a very small budget within which to accomplish the objectives set forth in the plan (Section 10 of plan). Many participants urged early efforts to enhance the budget with ARB augmentations, and contributions from other agencies in addition to the WCRC.

RECOMMENDATIONS

I have no reservations that the plan as presented here is the best possible plan for California now. I recommend that it be adopted by the California Air Resources Board and that funding be supplied through the Air Resources Board budget.

I do have reservations that all of the objectives of the CFRP can be met at the suggested level of funding. I recommend that the Air Resources Board begin efforts to increase the allocation to the CFRP. I also recommend that the Air Resources Board begin to actively seek collaborators for the CFRP. Representatives from many important agencies and organizations were present at the planning meeting. Because of their role there, they have a vested interest in the success of the CFRP. Now would be a good time to seek collaborative efforts from agencies and organizations such as NCASI, CDF, NPS, USFS, EPRI, and universities with access to federal Cooperative State Research funds such as the McIntire-Stennis Forestry Research Program.

The plan as it is currently proposed has at least one serious flaw, as has been pointed out by several of the peer reviewers. There is no solid link between the assessment for ponderosa pine and the assessment for all forests of California. As the plan now stands, a considerable amount of speculation will be necessary to make this leap. Experimental work, with a few other key species, patterned after the work with ponderosa pine would assist in making this leap. For this reason, I recommend that efforts to coordinate forest response research in California not be limited to ponderosa pine research, but that research with other key species be followed closely as well.

ATMOSPHERIC DEPOSITION: PROCESSES AND MEASUREMENT METHODS

Gary M. Lovett
Institute of Ecosystem Studies
The New York Botanical Garden
Mary Flagler Cary Arboretum
Box AB
Millbrook, New York 12545

INTRODUCTION

For many years, ecosystem-level ecological studies measured atmospheric deposition as that material which fell into a continuously open bucket or funnel/bottle apparatus. We now realize that this approach is inadequate and can give misleading results. Two types of atmospheric deposition are normally distinguished: wet deposition, involving substances dissolved or suspended in precipitating rain and snow; and dry deposition, involving particles and gases that are deposited directly to plant and soil surfaces from the ambient airstream. Deposition from fog and cloud water is a third type that does not fit neatly in either category, because the chemical substances are in solution but the droplets are not rapidly precipitating.

In this paper I will review the processes of atmospheric deposition and attempt a survey of measurement methods, pointing out strengths, weaknesses, and examples of each where appropriate. I will concentrate on dry deposition and cloud water deposition because they are at present the areas of greatest uncertainty. Finally, I will offer some recommendations on practical approaches to deposition measurement to complement studies of the effects of air pollutants on forest ecosystems.

WET DEPOSITION

Although the gravitational mechanisms that deliver raindrops and snowflakes to the surface are easily recognized, the physical and chemical processes that affect the "scavenging" of gases and particles by precipitation are much more complex. Several excellent reviews of these processes have been published (Fowler 1980, EPA 1983), and no attempt will be made to duplicate them here. However, a point regarding the "natural" or "normal" pH of precipitation is worth stressing. It is often assumed that unpolluted rain should have a pH of 5.6, which is the pH that results from the equilibrium of pure water with atmospheric CO_2. This assumes that CO_2 is the only natural atmospheric substance that can affect the pH of rain. In reality, natural sources of nitrogen and sulfur compounds, organic acids, and alkaline particles exist and could cause the pH of "natural" precipitation to vary in the range of about 5 to 7 (Charlson and Rodhe 1982, Galloway et al. 1982). Because of the spatial heterogeneity of these natural sources, no single value of "normal" rain pH is applicable to all areas.

The fact that raindrops fall by gravity makes them relatively easy to collect, and two basic types of collectors are commonly used (Galloway and Likens 1976). "Bulk" collectors are funnel-bottle arrangements that are left continuously open. They are sometimes fitted with anti-evaporation controls or plastic screens to keep out falling debris. They have the advantages of being inexpensive and easy to maintain and thus are widely used in forestry research. However, because they are continuously open, they collect gases and falling particles in addition to rainfall and are constantly exposed to contamination in the field. They measure wet deposition plus some unknown component of dry deposition, making the data difficult to interpret (Lindberg et al. 1986).

The other type of collector commonly used has its collection vessel sealed by a lid during dry periods. A precipitation sensor controls the lid position, exposing the vessel to rainfall and resealing it after the rain stops. These collectors eliminate contamination of the sample by dry deposition and other extraneous material, but they require AC or DC power and are subject to malfunction of the electronic and mechanical parts. This type of collector is used by the major atmospheric deposition monitoring networks, including the U.S. National Atmospheric Deposition Program (NADP) and the Canadian Network for Sampling Precipitation (CANSAP). Freedom from contamination by dry deposition makes this type of collector preferable where circumstances permit its use.

The time scales used in precipitation monitoring vary widely between different sampling programs. Annual element budgets for forest ecosystems can be compiled with precipitation averaged over weeks or longer, but physiological studies and some process-level biogeochemical studies require samples on the event or even sub-event time scale. Atmospheric studies relating precipitation chemistry to meteorological conditions or air mass trajectories also require event collections. For samples left in the field for extended periods, addition of a biocide is necessary to inhibit chemical transformations caused by microbes.

The national precipitation monitoring networks provide high-quality wet deposition data from which it is possible to discern spatial deposition patterns on continental and regional scales (e.g. NADP 1986). However, the sparseness of sampling locations obscures important spatial patterns that may occur on finer scales. Good examples are gradients in atmospheric deposition around major urban areas and within mountain ranges. To resolve these sorts of patterns, a more intensive sampling network must be used. This is very important for effects studies, because plant effects are usually manifested on a local, rather than regional, scale.

For sites with cold climates, collection of snowfall represents a problem because current designs of commonly-used automatic precipitation collectors are less reliable in sub-freezing conditions. Combined with the fact that many sites that receive frequent snow are relatively inaccessible, this means that snow samples are often bulk deposition samples that have been accumulated over weeks or months in the field, and as such are subject to contamination by dry deposition and falling debris.

DRY DEPOSITION

The physical processes that govern dry deposition are well understood theoretically. However, measurement of dry deposition is difficult and the data base from which to discern patterns is small. This section will review the relevant processes and discuss measurement methods.

Processes of deposition

Dry deposition involves both gases and particles. The gases that are likely to affect acid deposition are SO_2, NO, NO_2, HNO_3, NH_3, and HCl. Of these, HNO_3 and HCl are acids; SO_2, NO, and NO_2 are acidifying when oxidized (in the atmosphere or on a surface) to sulfuric and nitric acids; and ammonia (NH_3) is weakly alkaline. The particles of interest in acid deposition are sulfuric acid (H_2SO_4, usually occurring in small droplets) and soil dust and fly ash, containing minerals which may be alkaline. Particle-associated salts of NH_4^+, SO_4^{2-}, NO_3^-, trace metals (e.g., Pb and Cd) and the nutrient cations Ca, Mg, and K are also of concern to ecosystem ecologists although they are not acidifying.

The gaseous pollutants O_3 (ozone), PAN (peroxyacetyl nitrate), and the organic peroxides do not affect the S, N,

H^+ or nutrient cation budgets of ecosystems directly, yet are extremely phytotoxic and must be considered within the scope of the "acid deposition" problem. Because of their mode of action, these pollutants are generally considered on the basis of exposure (concentration in the air x time) rather than deposition, so determination of rates of deposition is less crucial than appropriate measures of peak and time-averaged atmospheric concentrations. Monitoring methods for these pollutants will not be discussed in this paper.

A diagrammatic summary of important dry deposition mechanisms is shown in Figure 1. The first stage of the deposition process involves transport of the particles and gases into the forest canopy. For small particles and gases, this occurs by entrainment in turbulent eddies of various sizes generated by the friction between moving air and the canopy surfaces. Larger particles (say, greater than 30 µm diameter) may fall through this turbulence, although their trajectory is unlikely to be straight downward if there is any significant air movement. At a forest edge, particles and gases can reach the lower layers of the canopy directly if the wind blows into the forest from an adjacent clearing.

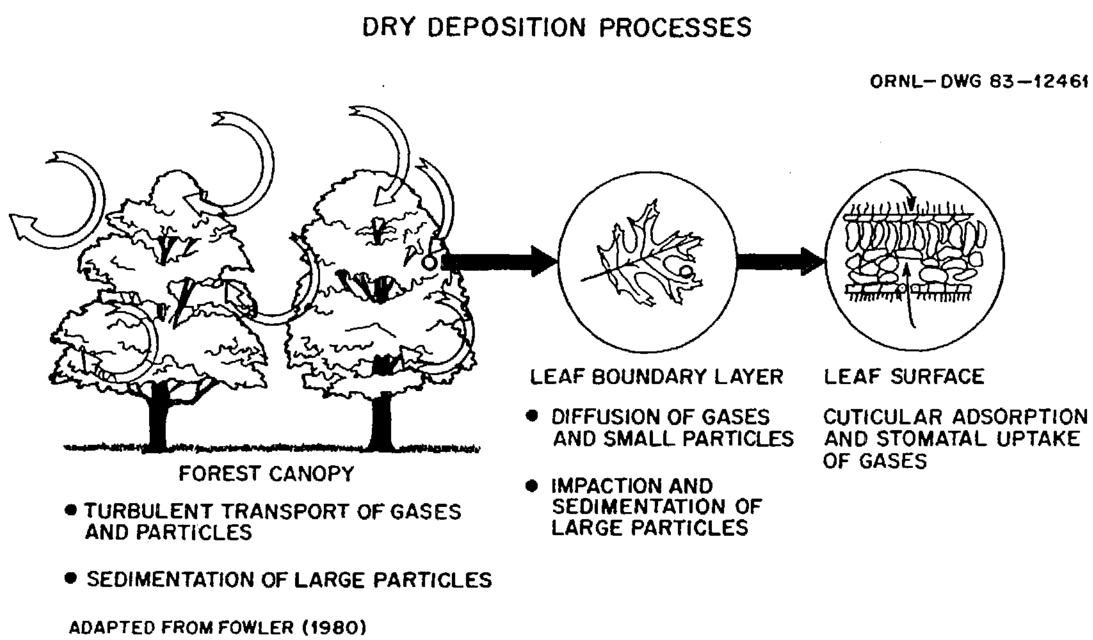

Figure 1. Processes involved in the dry deposition of particles and gases to forest canopies.

Once inside the canopy, the particle or gas must penetrate the boundary layer around canopy surfaces if it is to contact those surfaces. These boundary layers vary in thickness on the scale of a millimeter or less. Over smooth surfaces, such boundary layers would be laminar (indicating smooth flow parallel to the surface with little transfer to and from the surface), but the presence of microscopic protrusions on plant surfaces (leaf hairs, irregularity in waxy coatings, etc.) ensures that some turbulence must be present. In any event, the boundary layer presents a barrier to deposition of all but rapidly falling particles. Gases and very small particles (<0.1 µm diameter) can diffuse through this layer (albeit rather slowly), and particles larger than 2 or 3 µm diameter, if propelled by wind, may have enough inertia to penetrate the layer (this process is called impaction). Particles in the range of 0.1 to about 2 µm diam have no effective means of transport through the boundary layer, and this severely limits their rate of deposition to canopy surfaces (Davidson et al. 1982, Fowler 1980).

Figure 2 shows the mass distributions of several elements measured in airborne particles in central New Hampshire by Eaton et al. (1978). Note the dominance of submicrometer particle sizes for S and Pb, two important anthropogenic pollutants. Other studies (see EPA 1983) suggest similar size distributions for N and H^+, with most of the airborne mass in the particle size range of 0.1 to 1 µm. This is within the size range mentioned above as being inefficiently deposited by dry processes to natural surfaces. Note from Figure 2, however, that Ca and Al, two elements characteristic of soil dust, have mass distributions much more heavily weighted toward the supermicrometer particle sizes, which are more efficiently deposited by sedimentation and impaction. These observations lead to several important conclusions: 1) particle deposition of S, N, Pb and H^+ is likely to be small; 2) because they are readily deposited, S-, N-, Pb and H+-containing particles can be transported long distances before eventual deposition either in dry or wet form; and 3) particle deposition is potentially important for soil dust, which may be alkaline in nature and often contains Ca and Mg.

Gases which penetrate the boundary layer around a leaf must either adsorb chemically to the leaf surface or enter the interior of the leaf through the stomates (Figure 1). Which of these pathways is followed depends on the reactivity of the gas, the physical condition of the leaf surface, and whether the stomates are open or closed. Nitric acid vapor, for instance, may be sufficiently reactive to deposit effectively to all plant surfaces (Huebert and Robert 1985, EPA 1983). The deposition of sulfur dioxide, however, depends on the opening of the stomates (Fowler 1978), indicating that SO_2 is efficiently deposited in the moist substomatal space. Deposition of SO_2 has also been shown to increase with increasing relative humidity (McLaughlin and Taylor 1981). Stomates occupy only a small fraction of the leaf surface and are frequently closed, so they greatly impede the transport of gases to the interior of the leaves. The physiology of stomatal control is therefore of great importance in controlling deposition rates for some gases. Wetness on the leaf surface removes the leaf-surface barrier to deposition for water-soluble gases like SO_2. For this reason, the incidence of vegetation wetness by dew, fog, or rain can be very important in determining time-averaged dry deposition rates (Brimblecombe 1978, Mulawa et al. 1986).

Gaseous forms of S and N oxides are deposited more efficiently than their small-particle counterparts, at least in theory, and therefore the gases are expected to make a more significant contribution to S, N, and H^+ deposition in areas where the gaseous concentrations are significant (e.g., in areas close to pollution sources such as

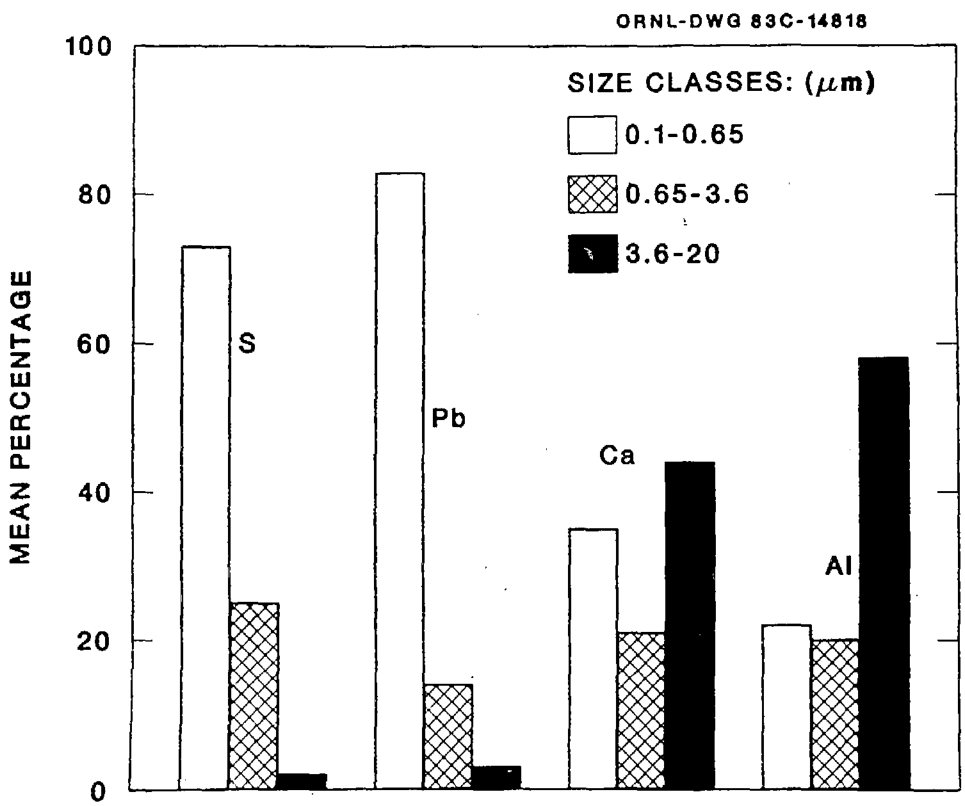

Figure 2. Percentage of the total aerosol mass of S, Pb, Ca, and Al present in three particle size classes at the Hubbard Brook Experimental Forest in central New Hampshire. Data from Eaton et al. (1978).

industrial or urban centers). However, this dichotomy of gas and particle deposition is somewhat confused by the fact that SO_2 and NO_x gases can adsorb to airborne particles of soot, sea salts, and soil dust in areas where both the particles and gases occur. These particles are characteristically quite large, and this gas adsorption phenomenon could have the effect of efficiently depositing S and N in particulate form. However, because the particles are large, deposition by sedimentation would tend to limit the dispersal beyond the point of adsorption. The importance of these gas-particle interactions to overall rates of S and N deposition is unknown.

Measurement methods

Unlike wet deposition, dry deposition is extremely difficult to measure. No reliable monitoring techniques are currently available, but this subject is being pursued actively by several research teams in North America and Europe. Field measurement methods fall into three broad categories representing different points of view: 1) micrometeorological techniques measure deposition as the depletion of the pollutant in the air above the canopy, and 2) surface accumulation methods measure the accumulation of the deposited material on natural or artificial surfaces, and 3) inferential techniques, which do not seek to measure dry deposition directly, but rather to calculate it using process-level models and measurement of relevant parameters. Each group of methods has distinct advantages and disadvantages; extensive analysis of this subject has been presented in several recent reviews (Hicks 1986, Hicks et al. 1987, Wesely and Hicks 1986), so only a brief synopsis will be attempted here.

The two most common micrometeorological techniques are eddy correlation and gradient analysis. In the former, one measures the pollutant fluxes associated with updrafts and downdrafts over a canopy; the difference is a measure of the pollutant "trapping" by the canopy. Shifts from up- to downdrafts occur very rapidly, thus computer-aided data acquisition and fast-response chemical sensors are needed. At this time, eddy correlation has been applied to SO_2 (Galbally et al. 1979), particulate S (Hicks et al. 1986), NO_2 (Wesely et al. 1982), ozone (Wesely et al. 1982), and total sulfur (Hicks and Wesely 1980). In gradient techniques a time-averaged vertical gradient of the pollutant is measured over the canopy, and this gradient is multiplied by a transfer coefficient to determine a flux to the surface. The gradients measured are usually quite small and therefore require very precise analytical techniques. The transfer coefficient is usually measured for some more convenient entity, such as heat or water vapor, and assumed identical to the coefficient for the pollutant of interest.

Fowler and Unsworth (1979), Huebert and Robert (1985), and Davidson and Elias (1982) provide examples of the use of this technique for SO_2, HNO_3 vapor, and particles, respectively.

Micrometeorological techniques are potentially very accurate and are currently the methods of choice among researchers in the field for determination of gaseous deposition to whole canopies in flat terrain. However, they require complex instrumentation (especially for eddy correlation) and highly trained personnel, and they impose many restrictions on the choice of measurement sites. They are in theory applicable only to homogeneous canopies in flat terrain, but their performance in more complex surface types has not been adequately tested. Because they require a meteorological tower and much instrumentation, spatial replication is very costly. In addition, they cannot measure the deposition of sedimenting particles (EPA 1983).

Surface accumulation methods have been applied to both natural and artificial surfaces. Artificial surfaces (sometimes called "surrogate" surfaces) have included buckets (Rensselaer Polytechnic Institute 1981), plastic or Teflon plates (Elias and Davidson 1980, Lindberg et al. 1982, Lindberg and Lovett 1985), artificial leaves (Tjepkema et al. 1981, Schlesinger and Reiners 1974), and various sorts of filters (e.g., Dasch 1983, Lovett and Lindberg 1986). Most of these surfaces collect only particles, although some filters can absorb gases as well. These surfaces are free from the chemical reactivity shown by plant surfaces, but the deposition measurements are difficult to interpret because the surfaces cannot precisely duplicate the aerodynamic or chemical characteristics of natural surfaces. Thus, extrapolation of deposition measurements from these surfaces must involve some sort of calibration against a natural surface (Lindberg and Lovett 1985).

Perhaps the best use of artificial surfaces is to estimate the deposition of large (>2 μm diameter) particles, which are deposited primarily by sedimentation and as such are less sensitive to the micro-scale characteristics of the deposition surface. In fact, the depositional flux of these particles may be easier to measure than their atmospheric concentration, because they are often collected inefficiently by standard air sampling equipment. These large particles may contribute substantially to the dry deposition flux of S, N, Pb and especially Ca, Mg, and K (Lindberg et al. 1986, Davidson et al. 1985). Lindberg and Lovett (1985) and Davidson and Elias (1982) discuss the use of artificial surfaces for particle deposition.

The natural surfaces used in deposition measurement have ranged in scale from individual leaves to whole watersheds. "Leaf washing" techniques measure the accumulation of dry-deposited substances during dry periods by rinsing the leaf at the end of the period and correcting for possible leaching of material from the leaves. For some leaves, leaching can be minimized by washing the leaves for only a very short time (Lindberg and Lovett 1985). Many samples are necessary to characterize deposition to whole canopies.

Measurement of stemflow and throughfall provides the same sort of measurement for whole canopies, but natural rainstorms do the washing. Stemflow and throughfall represent a combination of chemical fluxes resulting from incident wet deposition, accumulated dry deposition, and foliar leaching or uptake. Collections of stemflow and throughfall made after each dry period-rain event cycle can be analyzed statistically to isolate the dry deposition component of the flux. While not yet adequately tested, this technique provides a promising method for assessing dry deposition at the scale of the forest stand for substances and terrain inaccessible to micrometeorological techniques. An additional advantage is that the throughfall and stemflow measurements are likely to be useful for effects studies, thus affording further economy. Examples of the use of throughfall include papers by Lakhani and Miller (1980), Mayer and Ulrich (1978) and Lovett and Lindberg (1984).

Both leaf washing and throughfall methods measure only that portion of the total dry deposition removable in the subsequent washing. Presumably this includes all the water-soluble particulate material, but it is not known to what extent gaseous deposits can be washed off leaves and bark.

Whole-watershed nutrient balances can be used to estimate dry deposition if one has sufficient confidence in the other terms of the balance (Eaton et al. 1978). These terms usually include a wet deposition input, accumulation or loss by the vegetation and soils, and streamwater and gaseous outputs. The combined uncertainty in all these measurements renders the uncertainty in the dry deposition estimate quite high, but the technique has the advantage of naturally accommodating large temporal and spatial scales.

Dry deposition to snow is most often assessed by measuring accumulation of substances in the snow itself. This is usually done by sampling a snowpack immediately after it falls and again several days later, making certain that in the interim no melting has occurred which could remove solutes from the snow (Barrie and Walmsley 1978, Cadle et al. 1986).

The use of element isotopes promises to enhance the interpretation of surface accumulation studies in the future. Several reports in the literature suggest the potential of these tools. Bondietti et al. (1984) used natural radioactive isotopes of Pb and Be to trace submicron aerosol deposition to trees, and Garland and Branson (1977) used S-35 as a tracer of SO_2 deposition. Graustein and Turekian (1986) measured the ratio of Cs-137 to Pb-210 in soils and used this information to infer the relative amounts of dry and cloud water deposition averaged over long periods. Stable isotopes of Sr were used by Graustein and Armstrong (1983) to indicate the importance of airborne dust inputs to a mountain ecosystem in New Mexico.

Inferential methods, the third general class of techniques for estimating dry deposition, involve multiplying measured atmospheric concentrations by a deposition velocity to calculate a flux. Atmospheric concentrations can be monitored routinely for most chemical species of interest in acidic deposition. The deposition velocities are usually chosen from the literature to be appropriate to the depositing substance or are calculated using models parameterized with measurements of micrometeorological conditions and canopy structure (Hicks et al. 1985). Inferential techniques offer the ability to estimate dry deposition with a set of relatively simple measurements, and therefore are seeing quite wide acceptance for dry deposition monitoring. However, the models used should be calibrated against some other measurement technique to assess the accuracy of the deposition velocities. This brings up a major dilemma in dry deposition research: our ability to conceptualize and model the processes is more advanced than our ability to measure the fluxes, thus the models are impossible to "validate" in the traditional sense. The best one can hope for at present is that the model results fall within the range of measurements made by various methods.

Because dry deposition is strongly influenced by topography, canopy structure, micrometeorological conditions and species composition, it is expected to be extremely variable on small spatial scales. Moreover, the difficulty in measuring the flux leaves us unable to determine this variability from any existing data. Unfortunately, most dry deposition studies are confined to a single meteorological tower in a forest. High spatial variability and difficulty in measurement notwithstanding, several attempts to ascertain the magnitude of the dry deposition flux of N and S in the eastern U.S. suggest that it may be at least as important as wet deposition, and certainly cannot be ignored (Galloway and Whelpdale 1980, Lindberg et al. 1986).

The suspected importance of dry deposition combined with the lack of good measurement methods presents an awkward problem for those requiring information on total atmospheric deposition. Perhaps the best approach to this problem at present is to try several measurement techniques simultaneously and compare the results. With a knowledge of which component of the dry deposition flux is addressed by each method, reasonable upper and lower bounds for the estimate may be established. Examples of the use of multiple methods are reported by Lovett and Lindberg (1986) for a forest canopy and Cadle et al. (1986) for snow.

Because studies suggest the importance of S, N, trace metal and nutrient cation cycles as well as H^+ deposition per se in the effects of atmospheric deposition, it is important to take all these elements into account in deposition sampling. In particular, the nutrient cations K, Ca, and Mg are often ignored in sampling programs for dry "acid deposition". Some of the current hypotheses of forest decline in the U.S. and Europe involve depletion of these elements from foliage or soils. The only way to measure these depletions is by input-output budgets, and the dry deposition inputs can be extremely important (Johnson et al. 1985).

CLOUD WATER DEPOSITION

Cloud and fog droplets are on the order of 5-50 um in diameter and therefore behave much like very large aerosol particles. They are deposited primarily by sedimentation or, when significant winds are present, by impaction (Lovett 1984). Compared to dry deposition, droplet deposition is very efficient and can deliver large amounts of cloud water (and associated solutes) to vegetation when the canopies are immersed in cloud. This occurs most frequently on mountaintops and seacoasts, where these fogs are often associated with brisk winds, contributing to high deposition rates. Many good examples of this phenomenon can be found in the literature (e.g., Azevedo and Morgan 1974, Lovett et al. 1982, Waldman et al. 1985). For mountains that are frequently immersed in cloud, this can be the most important input of some nutrients and pollutants, and can increase deposition rates 3 to 4 fold over those in nearby lowlands (Lovett et al. 1982). The deposition can occur in sub-freezing conditions as rime ice, which is the accumulation of supercooled droplets that freeze on impact. Some lowland areas frequently develop nighttime radiation fogs, but these are formed in still air and deposition resulting from them is usually less important. For a given aerosol particle or gas molecule, incorporation into a cloud droplet can increase the rate of deposition by a factor of 10 or more (Lovett and Reiners 1983). However, the contribution of cloud water deposition to the total atmospheric deposition for an ecosystem depends on the proportion of time the vegetation is immersed in cloud, information which is rarely available.

Measurement of cloud water deposition is almost as difficult as measurement of other types of dry deposition. The variety of measurement methods reported include the gradient technique (Dollard and Unsworth 1983), artificial surfaces (Vogelmann 1968, Schlesinger and Reiners 1974), individual leaves (Waldman et al. 1985), throughfall (Olson et al. 1981, Lovett 1984) and inferential methods (Lovett et al. 1982). Cloud water has one convenient characteristic, however, not shared by particles and gases: if deposition amounts are sufficient to saturate canopy surfaces, the deposited water will drip to the forest floor as stemflow and throughfall, which is easily collected and measured. If the amount of water stored on the canopy is in steady state, then the deposition rate is equal to this drip rate after correction for evaporation from the canopy. The water deposition rate thus calculated can be multiplied by the chemical concentration of cloud water prior to interaction with canopy surfaces, the product being the chemical deposition rate. If the conditions are met, this provides an inexpensive and relatively accurate means of estimating cloud water deposition. In a comparison of methods for estimating cloud water deposition to a mountain in New Hampshire, Lovett (in press) concluded that this canopy water balance method provided the best hope for quantifying deposition at the spatial scale appropriate for effects studies.

CONCLUSIONS AND RECOMMENDATIONS

1) This survey of measurement methods has shown that, while measurement of deposition via rainfall is quite routine, snowfall is more difficult, and dry deposition and cloud water deposition pose formidable problems. The problems are difficult to ignore because particles, gases, and cloud droplets can contribute major fractions of the total atmospheric deposition in some areas.

2) Because of the nature of the atmosphere-canopy interaction, dry deposition and cloud water deposition may be quite variable from place to place on a local scale. Wet deposition will also vary locally around major source areas and in mountainous terrain. Consequently, rather dense sampling networks may be necessary to account for this expected variability.

3) In deploying an "acid deposition" sampling program, the trace metals, nutrient cations, and oxidant gases should not be ignored because they can be crucial for testing hypotheses of forest effects.

4) Applying multiple measurement methods offers the

best hope of generating confidence in dry deposition estimates. Inferential methods for both dry and cloud water deposition can be set up in a monitoring mode, and permit observation of any temporal trends in atmospheric concentrations, even if parallel trends on deposition are obscured by measurement uncertainty. Testing the calculated deposition velocities for SO_2, HNO_3 and O_3 against micrometeorological measurements can provide some validation for the model where the terrain is suitable. Careful collection of throughfall can provide reasonable alternative estimates for both cloud water and dry deposition, and permits evaluation of the deposition of a range of elements important in effects studies. Artificial surfaces can be useful for evaluating deposition of large particles.

5) An advantage of using multiple methods for estimating dry deposition is that the sampling scheme can vary between methods. For instance, an extensive throughfall sampling program could complement a more sparse network of air quality monitoring stations, which could serve as the basis for inferential estimates.

ACKNOWLEDGEMENTS

Financial support for the author was provided by the Electric Power Research Institute (Project RP-2621, through Oak Ridge National Laboratory) and the Mary Flagler Cary Charitable Trust. Portions of this paper were excerpted from a paper entitled "Atmospheric deposition to forests" presented by the author at the U.S.-Canadian Conference on Forest Responses to Acidic Deposition, Orono, Maine, 1983 (Proceedings of the conference available from the Land and Water Resources Center, University of Maine, Orono). This is a contribution to the program of the Institute of Ecosystem Studies of the New York Botanical Garden.

LITERATURE CITED

Azevedo, J., and D.L. Morgan. 1974. Fog precipitation in coastal California forests. Ecology 55:1135-1141.

Barrie, L.A., and J.L. Walmsley. 1978. A study of sulphur dioxide deposition velocities to snow in northern Canada. Atmos. Environ. 12:2321-2332.

Bondietti, E.A., F.O. Hoffman, and I.L. Larsen. 1984. Air-to-vegetation transfer rates of natural submicron aerosols. J. Envir. Radioactivity 1:5-27.

Brimblecombe, P. 1978. Dew as a sink for sulphur dioxide. Tellus 30:151-157.

Cadle, S.H., J.M. Dasch, and R. Van de Kopple. 1986.

Winter time wet and dry desposition in northern Michigan. Atmos. Environ. 20:1171-1178.

Charlson, R.J., and H. Rodhe. 1982. Factors controlling the acidity of natural rainwater. Nature 295:683-685.

Dasch, J.M. 1983. A comparison of surrogate surfaces for dry deposition collection. pp. 883-902 in Proceedings of the Fourth International Conference on Precipitation Scavenging, Dry Deposition, and Resuspension. H.R. Pruppacher, R.G. Semonin, and W.G.N. Slinn, eds. Elsevier, New York.

Davidson, C.I., and R.W. Elias. 1982. Dry deposition and resuspension of trace elements in the remote High Sierra. Geophys. Res. Lett. 9:91-93.

Davidson, C.I., J.M. Miller, and M.A. Pleskow. 1982. The influence of surface structure on predicted particle dry deposition to natural grass canopies. Water Air Soil Poll. 18:25-43.

Davidson, C.I., S.E. Lindberg, J.A. Schmidt, L.G. Cartwright, and L.R. Landis. 1985. Dry deposition of sulfate onto surrogate surfaces. J. Geophys. Res. 90(D1): 2123-2130.

Dollard, G.J., and M.H. Unsworth. 1983. Field measurement of wind-driven fog drops to a grass surface. Atmos. Environ. 17:775-780.

Eaton, J.S., G.E. Likens, and F.H. Bormann. 1978. The input of gaseous and particulate sulfur to a forest ecosystem. Tellus 30:546-551.

Elias, R.W., and C.I. Davidson. 1980. Mechanisms of trace element deposition to surfaces in a High Sierra canyon. Atmos. Environ. 14:1427-1432.

Environmental Protection Agency (EPA). 1983. The acidic deposition phenomenon and its effects: Critical assessment review papers, Volume I: Atmospheric sciences. EPA-600/8-83-016A. U.S. Environmental Protection Agency, Washington, D.C.

Fowler, D. 1978. Dry deposition of SO_2 on agricultural crops. Atmos. Environ. 12:369-373.

Fowler, D., and M.H. Unsworth. 1979. Turbulent transfer of sulphur dioxide to a wheat crop. Q.J.R. Meteorol. Soc. 105:767-784.

Fowler, D. 1980. Removal of sulphur and nitrogen compounds from the atmosphere in rain and by dry deposition. pp. 22-32 in Proceedings of the International Conference on the

Ecological Impact of Acid Precipitation, D. Drablos and A. Tollan, eds. SNSF Project, Oslo, Norway.

Galbally, I.E., J.A. Garland, and M.J.G. Wilson. 1979. Sulfur uptake from the atmosphere by forest and farmland. Nature 280:49-50.

Galloway, J.N. and G.E. Likens. 1976. Calibration of collection procedures for the determination of precipitation chemistry. Water, Air, Soil Poll. 6:241-258.

Galloway, J.N., and D.M. Whelpdale. 1980. An atmospheric sulfur budget for eastern North America. Atmos. Environ. 14:409-417.

Galloway, J.N., G.E. Likens, W.C. Keene, and J.M. Miller. 1982. The composition of precipitation in remote areas of the world. J. Geophys. Res. 11:8771-8786.

Garland, J.A. and J.R. Branson. 1977. The deposition of sulphur dioxode to a pine forest assessed by a radioactive tracer method. Tellus 29:445-454.

Graustein, W.C. and R.L. Armstrong. 1983. The use of Strontium-87/Strontium-86 ratios to measure atmospheric transport into forested watersheds. Science 219:289-292.

Graustein, W.C. and K.K. Turekian. 1986. 210-Pb and 137-Cs in air and soils measure the rate and vertical profile of aerosol scavenging. J. Geophys. Res. 91 (D-13):14355-14366.

Hicks, B.B., 1986. Measuring dry deposition: a re-assessment of the state of the art. Water Air Soil Poll. 30:75-90.

Hicks, B.B., D.D. Baldocchi, R.P. Hosker, Jr., B.A. Hutchison, D.R. Matt, R.T. McMillen, and L.C. Satterfield. 1985. On the use of monitored air concentrations to infer dry deposition. NOAA Technical Memorandum ERL ARL-141.

Hicks, B.B., M.L. Wesely, R.L. Coulter, R.L. Hart, J.L Durham, R. Speer, and D.H. Stedman. 1986. An experimental study of sulfur and NO_x fluxes over grassland. Boundary Layer Meteorol. 34:103-121.

Hicks, B.B., M.L. Wesely, S.E. Lindberg, and S.M. Bromberg. 1986. Proceedings of the Dry Deposition Workshop of the National Acid Precipitation Assessment Program. NOAA/ATDD, Oak Ridge, TN.

Huebert, B.J., and C.H. Robert. 1985. The dry deposition of nitric acid to grass. Journal of Geophysical Research 90:2085-2091.

Johnson, D.W., D.D. Richter, G.M. Lovett, and S.E. Lindberg. 1985. The effects of atmospheric deposition on potassium, calcium, and magnesium cycling in two deciduous forests. Can. J. For. Res. 15:773-782.

Lakhani, K.H., and H.G. Miller. 1980. Assessing the contribution of crown leaching to the element content of rainwater beneath trees. pp. 161-172 in Effects of Acid Precipitation on Terrestrial Ecosystems. T.C. Hutchinson and M. Havas, eds., Plenum Publ. Corp., New York. 666 pp.

Lindberg, S.E., R.C. Harriss, and R.R. Turner. 1982. Atmospheric deposition of metals to forest vegetation. Science 215:1609-1611.

Lindberg, S.E., and G.M. Lovett. 1985. Field measurements of dry deposition rates of particles to inert and foliar surfaces in a forest. Environmental Science and Technology 19:228-244.

Lindberg, S.E., G.M. Lovett, D.D. Richter, and D.W. Johnson. 1986. Atmospheric deposition and canopy interaction of major ions in a forest. Science 231:141-145.

Lovett, G.M., W.A. Reiners, and R.K. Olson. 1982. Cloud droplet deposition in subalpine balsam fir forests: Hydrological and chemical inputs. Science 218:1303-1304.

Lovett, G.M. 1984. Rates and mechanisms of cloud water deposition to a subalpine balsam fir forest. Atmos. Environ.18:361-371.

Lovett, G.M., and S.E. Lindberg. 1984. Dry deposition and canopy exchange in a mixed oak forest as determined by analysis of throughfall. Journal of Applied Ecology 21:1013-1028.

Lovett, G.M., and S.E. Lindberg. 1986. Dry deposition of nitrate to a deciduous forest. Biogeochemistry 2:137-148.

Lovett, G.M. A comparison of methods for estimating cloud water deposition to a New Hampshire (U.S.A.) subalpine forest. Proceedings: NATO Advanced Research Workshop on Acidic Deposition at High Elevation Sites, M.H. Unsworth, ed. Institute of Terrestrial Ecology, Edinburgh, Scotland, (in press).

Mayer, R., and B. Ulrich. 1978. Input of atmospheric sulphur by dry and wet deposition to two central European forest ecosystems. Atmos. Environ. 12:375-377.

McLaughlin, S.B., and G.E. Taylor. 1981. Relative humidity: An important modifier of pollutant uptake by plants. Science 211:167-169.

Mulawa, P.A., S.H. Cadle, F. Lipari, C.C. Ang, and R.T. Vandervenner. 1986. Urban dew: Its composition and influence on dry deposition rates. Atmos. Environ. 20:1389-1396.

National Atmospheric Deposition Program (NADP). 1986. NADP/NTN Annual Data Summary: Precipitation Chemistry in the United States (1984). NADP, Ft. Collins, CO.

Olson, R.K., W.A. Reiners, C.S. Cronan, and G.E. Lang. 1981. The chemistry and flux of throughfall and stemflow in subalpine balsam fir forests. Holarct. Ecol. 4:291-300.

Rensselaer Polytechnic Institute (RPI). 1981. Acidic precipitation in the Adirondack region. EPRI EA-1826. Electric Power Research Institute, Palo Alto, CA.

Schlesinger, W.H., and W.A. Reiners. 1974. Deposition of water and cations on artificial foliar collectors in fir krummholz of New England mountains. Ecology 55:378-386.

Tjepkema, J.D., R.J. Cartica, and H.F. Hemond. 1981. Atmospheric concentration of ammonia in Massachusetts and deposition on vegetation. Nature 294:445-446.

Vogelmann, H.W., T. Siccama, D. Leedy, and D.C. Ovitt. 1968. Precipitation from fog moisture in the Green Mountains of Vermont. Ecology 49:1205-1207.

Waldman, J.M., J.W. Munger, D.J. Jacob, R.C. Flagan, J.J. Morgan, and M.R. Hoffman. 1982. Chemical composition of acid fog. Science 218:677-680.

Waldman, J.M., J.W. Munger, D.J. Jacob, and M.R. Hoffman. 1985. Chemical characterization of stratus cloudwater and its role as a vector for pollutant deposition in a Los Angeles pine forest. Tellus 37:91-108.

Wesely, M.L., J.A. Eastman, D.H. Stedman, and E.D. Yalvac. 1982. An eddy-correlation measurement of NO_2 flux to vegetation and comparison with O_3 flux. Atmos. Environ. 16:815-820.

Wesely, M.L., and B.B. Hicks. 1986. Practical aspects of measuring dry deposition. Proceedings: Methods for Acidic Deposition Measurements EA-4663, EPRI, Palo Alto, CA.

FOREST AND WOODLAND VEGETATION OF CALIFORNIA: CHOICES FOR THE CALIFORNIA FOREST RESPONSE PROGRAM

Michael G. Barbour
Department of Botany
University of California
Davis, California

INTRODUCTION

The objective of this contribution is to provide some guidance in the selection of wooded vegetation to be studied regarding acid deposition. Woodlands and forests are defined by UNESCO (1973) as formations dominated by trees >5 m tall. Woodland has a tree canopy covering 25-60% of the ground, while forest canopy covers >60%. By these definitions, woodlands and forests occupy 40% of the state's 100 million acre area.

The vegetation off California has been reviewed by several ecologists within the past decade (Barbour 1987, Barbour and Major 1977, Barry 1985, Bolsinger 1980, Holland 1986, Latting 1976, Mooney and Chabot 1985, Plumb and Pillsbury 1987), but we are still at a rather superficial level of understanding. Our data remain largely uncentralized, unsummarized, unstandardized, incomplete, and anecdotal. Even major vegetation types are poorly known for stand dynamics, succession, response to disturbance and stress, nutrient cycling, biomass, and productivity. Such missing information, of course, would be valuable for assessing impacts of such recent and additional factors as acid deposition on vegetation. Even the relationship of vegetation boundaries to regional climate is open to estimation because our network of weather stations in upper montane regions is rather thin.

Within these overall limitations, however, some vegetation types are better known than others, and for a variety of reasons some may be more suitable for acid deposition study than others. Therefore, I propose to briefly survey the major forests and woodlands in the state. For the sake of simplicity and to fit the space limitations imposed on this contribution, we can divide these forests and woodlands into 10 major types: (1) riparian forest, (2) blue oak woodland, (3) southern oak woodland, (4) coastal and lower montane Douglas-fir forest, (5) mixed evergreen forest, (6) mid-montane conifer forest, (7) upper montane conifer forest, (8) mixed subalpine woodland, (9) desert-facing montane forest, and (10) pinion/juniper woodland. I shall not include such sparsely wooded types as desert riparian or wash communities. The frequency of literature citations may appear uneven, from type to type, and light overall. This is because more complete bibliographies can be found in the reviews cited earlier in this section, and my intent here is only to highlight certain types or subjects.

RIPARIAN FORESTS

These are the only extensive forests in California dominated by broadleaved, mesophytic, winter-deciduous taxa. Human activities have severely modified their extent and structure. Less than 10% of the statewide acreage present in 1800 still remains (Warner and Hendrix 1984), and little of this remnant has protected status. The most detailed description of the best remaining stands comes from the Sacramento Valley (Conard et al. 1977). Species composition significantly differs, in coastal and montane phases of riparian forest, from the central valley phase described below, but Fremont cottonwood (*Populus fremontii*) characterizes all phases below 1500 m elevation.

An elevational sequence of communities extend back from the river, progressing through a willow thicket, a cottonwood forest, and a valley oak forest. Cottonwood forest has a 25 m tall overstory dominated by Fremont cottonwood, associated with valley oak (*Quercus lobata*), white alder (*Alnus rhombifolia*), arroyo willow (*Salix lasiolepis*), and ash (*Fraxinus latifolia/velutina* complex). Subcanopy tree, shrub, vine, and herb canopies are also present. Relative canopy cover by cottonwood is >40%. Plant and animal species richness is possibly grater here than for any other California plant community.

Valley oak forest canopy reaches to 35 m, and it is close to being monospecific (75% relative cover by valley oak). Associated species include those listed above, and in addition California sycamore (*Platanus racemosa*). Both sycamore and valley oak are large trees; consequently, this forest is half as dense as the preceding one (only 125 trees per ha; 18 sq m per ha basal area). Subdominant tree, shrub, vine, and herb canopies are present, with herb canopies more extensive than in the cottonwood forest.

All riparian trees are phreatophytes, but cottonwood and alder seem more favored by shallower water tables than oak and sycamore. Valley oak exhibits maximum growth when the water table is ~10 m below the surface. Valley oak exhibits remarkably little variation in xylem pressure over the course of a year or between wet and dry years (Griffin 1973, MacDonald 1987).

Very little has been published on vegetation dynamics, productivity, and mineral cycling of California riparian forests. Short-term primary succession has been studied on a variety of substrates, but the course of long-term succession to forest is known only at an intuitive level. Although these forests lie close to potential sources of acid deposition, their limited acreage and already modified composition and structure make them a poor candidate for the forest response program.

BLUE OAK WOODLAND

This two-layered community forms a nearly continuous ring around the central valley, generally between 100 and 1200 m elevation. An overstory canopy, 5-15 m tall, is 30-80% closed, and blue oak (Quercus douglasii), with an importance value >67%, is dominant. Associated trees include coast live oak towards the coast (Q. agrifolia), interior live oak towards the interior (Q. wislizenii), Digger pine (Pinus sabiniana) and black oak (Q. kelloggii) at higher elevations, and valley oak at lower elevations on nearly level slopes.

Sapling and tree density combined is usually <200 per ha, but dense stands can reach 1000 per ha (Griffin 1977). Tree life span, except for valley oak, is <300 yr, and tree girth is modest, 20-30 cm dbh. Shrubs are regularly present, but cover is insignificant. The herbaceous ground stratum averages >80% cover. Oak woodland often occurs in a mosaic with grassland, savanna (<25% tree cover), and chaparral--a mosaic which reflects differences in slope, aspect, soil depth, and fire frequency more than differences in climate. Mean annual precipitation is 530 mm (range 280-1000). The upper elevational limit of blue oak woodland corresponds with changes in annual precipitation, mean annual temperature, annual amplitude of temperature, and soil content of C:N, Ca, P, and N (Axelrod 1965, Plumb 1980, Vankat 1982).

Studies in both the Coast Ranges (White 1966) and Sierra Nevada foothills (Vankat and Major 1978) indicate that successful establishment of blue oaks has been in decline since the 1870s. James Griffin (1980) concluded that major causes of oak seedling mortality are related to grazing animals. Evergreen oaks show a better record of recent establishment than deciduous oaks. Stand structure may also reflect disturbance from fires, but there has been surprisingly little research on the role of fire intensity and frequency on oak woodlands (McClaran 1986). All California oaks are capable of sprouting, following fire or cutting damage to above-ground parts. Woodland trees are also subject to local defoliation by western tent caterpillars on an 8-10 yr cycle, but I have seen no published information on the impact such herbivory must have on growth and survival.

It is clear, from Rundel's 1980 review of oak ecology, that we have insufficient data to define or compare photosynthetic rates, productivity, or patterns of biomass allocation among California oaks. We cannot yet assume that the generally held hypotheses of photosynthetic differences between evergreen and deciduous perennials apply to California oaks. These oaks would provide an excellent test for such hypotheses, and they even offer natural hybrids between evergreen and deciduous species (e.g., Q. morehus).

Oak woodland has potential as a study site for the forest response program. This type covers 8% of the state and lies close to potential sources of acid deposition. It is also going to be receiving research attention from foresters and ecologists throughout the 1980s and early 1990s because the California Department of Forestry and the University of California have placed a high research priority on it and have allocated budget funds for that research. Negative aspects include the unexplained phenomenon of poor regeneration throughout the 20th century and the relative paucity of ecophysiological data on the dominant species.

SOUTHERN OAK WOODLAND

This community occurs in the outer portion of the Central Coast Range, beginning near the northern border of San Luis Obispo County, and extending south into the Transverse and Peninsular Ranges and to the Sierra San Pedro Martir in Baja California. It occupies coast-facing slopes and interior valleys below 1200 m elevation, and has a stand architecture similar to that of blue oak woodland. In the Coast Range, coast live oak is dominant, but elsewhere it is associated with (and sometimes subordinant to) California walnut (Juglans californica) and mesa or Engelmann oak (Q. engelmannii). Southern oak woodland has the same mean annual precipitation and temperature as blue oak woodland (16 C), but seasonal fluctuations are dampened due to a maritime influence.

Very little stand data exist for southern woodlands. They occupy 2% of the state's area. According to surveys by Wieslander in the 1930s, most stands were dominated by coast live oak. Some mesa oak stands were savanna-like, with 27 trees per ha, but others were denser, with 50-150 trees per ha. Coast live oak seems to prefer steeper or moister slopes, and mesa oak prefers gentler, more arid slopes. The Nature Conservancy has put both mesa oak and walnut woodlands in the highest priority class for protection, because they are two of the state's 32 most endangered plant communities (Barbour 1987).

TEMPERATE NORTHWEST LOWLAND FORESTS

Forests which occupy a relatively narrow coastal strip, extending from the Oregon border south to Monterey County, are related to a temperate rainforest that dominates the very wet coastal lowlands of Oregon, Washington, and British Columbia. Douglas-fir (Pseudotsuga menziesii) is a characteristic member of that rainforest, and it continues to dominate the California extension, but is joined there by coast redwood (Sequoia sempervirens).

Redwood-Douglas fir forest is best developed on flats which are periodically flooded, but it extends up slopes to 1000 m and 100 km inland. Excavations of soil beneath pristine redwood stands in northern California show evidence of fire and flood disturbance every 25-600 yr, on average, for at least the past millenium (Jacobs et al. 1985, Viers 1980). Redwood is favored by low-intensity ground fires, in its possession of thick, fire-resistant bark; further, death of the trunk releases dormant buds on the crown which produce sucker shoots and (ultimately) a ring of daughter trees. Reproduction from seed is encouraged by fire, for the soil is cleared of litter and inhibiting decay products (Zinke 1977). Flood waters deposit a new layer of silt, which redwood is able to tolerate because it is capable of forming adventitious roots in the new silt above the older, suffocated roots.

Redwood apparently has narrower tolerance limits for moisture and temperature. Its distribution limits appear to parallel the inland limits of coastal fog, which contributes soil moisture in summer through fog drip (Azevedo and Morgan 1974) and dampens temperature oscillations. The optimum thermoperiod (difference between daytime high and nighttime low) for redwood seedling growth is zero (Hellmers 1966).

Lumbering practices over the past 130 yr have reduced the extent of old growth redwood forest to 10% of the original 800,000 ha. Initial reharvest is possible within 70 yr, but we do not have a long enough history of successive harvests to know whether such a short rotation cycle can be maintained into the future. k Redwood is among the fastest-growing conifers in the world, and it occupies areas with exceptionally high site quality. Stands have basal areas an order of magnitude higher than those for any other forest in California--several hundred square meters per ha. The overstory averages 70 m in height and 2.5 m dbh. Trees reach maturity in less than 300 yr; maximum age is about 2000 yr. Douglas-fir can be nearly as massive, though only half as long-lived.

Clearcut stands are often seeded with Douglas-fir, permitting redwood to return only vegetatively via stump sprouts. Dominance may shift, in such cases, away from redwood. Seral species, such as Ceanothus and tanbark oak, sometime become established and then slow the process of succession back to climax. It is not clear, from the forestry literature, that we yet understand what kinds of logging practices or site peculiarities favor the invasion of Ceanothus and tanbark oak.

Redwood and Douglas-fir forests offer some advantages as a study site for the forest response program. For economic and aesthetic reasons, their dominants have long been a focus of ecological research. Their response to many microclimatic factors, including disturbance and competition, are well known as are their growth rates and requirements for seedling establishment. Also, both are conifers. Conifers are easier to manipulate, age, and propagate than hardwoods; they also have faster growth rates and hence respond more dramatically to changes in the environment than hardwoods. However, their great disadvantage is that these forests lie in relatively unpolluted north coastal California, hence are unlikely to show symptoms of acid deposition stress.

MIXED EVERGREEN FORESTS

These forests are elevationally between oak woodland below and mid-montane conifer forest above. The floristic composition of the type and the distributional limits of its various phases are well known, but quantitative descriptions are few. The lack of stand data is surprising, given the type's wide distribution, covering 3-4% of California. Mixed evergreen forest extends in a broken ring, at 600-1200 m elevation, around the central valley, at similar elevations away from the valley in the Coast Ranges and Klamath Mountains, and at 1200-1800 m elevation in the Transverse and Peninsular Ranges. Mean annual temperature is 14^{o}C, and precipitation is 870 mm; thus, this forest is in a significantly cooler and wetter zone than oak woodland.

There are important variations in tree composition from north to south. A conifer overstory is usually present, but is scattered and 30-60 m tall. In the north, Douglas-fir and ponderosa pine are typical conifer elements. In the south, coulter pine (Pinus coulteri) and big-cone Douglas-fir (Pseudotsuga macrocarpa) are typical conifers. Beneath is a more completely closed canopy, 15-30 m tall, of broad-leaved evergreen trees with some scattered deciduous trees as well. Both tree canopies together may contribute 40-100% cover. Shrub, moss, and perennial herb cover may total 5-25%. In some hardwood forests, the community is made up mainly of trees: the ground is covered with a thick mat of undecomposed leaf litter, and shrubs and herbs are largely absent.

The most characteristic broadleaf evergreen tree is canyon live oak (Quercus chrysolepis). Others include tan-bark oak (Lithocarpus densiflora), madrone (Arbutus menziesii), bay (Umbellularia californica), and coast or interior live oaks. Deciduous trees include dogwood (Cornus nuttallii), hazelnut (Corylus cornuta), big leaf maple (Acer macrophyllum), and black oak.

"Mixed evergreen forest" implies a mixture of needle-leaf and broadleaf evergreen species. In the north, if conifers such as Douglas-fir predominate, then one has moved into either montane conifer forest or temperate lowland conifer forest; if broadleaf trees predominate, then one has moved into oak woodland. Harvest of Douglas-fir has often resulted in a dense stand of pole-size broadleaf hardwoods--because these can stump sprout following disturbance, whereas Douglas-fir must re-enter by seed.

Coulter pine is the most common conifer element in the southern phase of mixed evergreen forest. Its range extends from Mount Diablo through the Coast Ranges, then continues south through the Transverse and Peninsular Ranges. Vogl (1976) and Borchert (1985) have pointed out its spatial association with chaparral, as well as with mixed evergreen forest, and noted that it is a closed-cone species where it grows in frequently burned vegetation and that is an open-cone species where it grows in seldom burned vegetation. On steep, mesic, north-facing slopes and in ravines, big-cone Douglas-fir can be another conifer element (Minnich 1976, 1980). These stands appear to be more fire-free than mixed evergreen forest with Coulter pine. Coulter pine is being planted on disturbed sites because it has a relatively fast growth rate and its wood has economic value.

The mixed evergreen forest is probably not the best choice of study site for the forest response program. Although widespread and at low enough elevations to be near potential sources of acid deposition, the community ecology of the entire forest and the autecology of its dominants are very poorly understood. Furthermore, the dominants include many hardwood species. As discussed earlier, hardwoods are more difficult to manipulate and study in the field than conifers.

density, and a shift in species importance to white fir, have been attributed to a change in fire frequency (Biswell 1967, Komarek 1967, Kilgore and Taylor 1979, Kilgore 1973, Vogl 1973, Hartesveldt et al. 1975, Vankat and Major 1978, Harvey et al. 1980). Fire frequency prior to 1875 averaged about one fire every 8-16 yr. Many fires were the natural consequence of dry lightning strikes, but others were started by Indians, who used fire to manage food-gathering places. Whatever their cause, they were ground fires of low intensity.

A policy of fire suppression was instituted in California close to the turn of the century, with a result that ground fires are now rarer, and devastating crown fires more common, than prior to 1900. The large amounts of living and dead ground fuel which have resulted from 80 years of fire suppression now make it likely that ground fires will become crown fires; consequently, the US Forest Service, the National Park Service, the California Department of Forestry, and the State Department of Parks and Recreation have all begun programs of controlled burning and have modified their response to natural fires, permitting some to burn within limits. The specific ways in which several tree and shrub species require fire to complete their life cycles or to compete successfully with shade-tolerant species are relatively well known.

The effects of ozone on woody species of this forest are also well known. There is evidence that mixed conifer forests in the Transverse, Peninsular, and Sierra Nevada Ranges frequently experience ozone concentrations which exceed federal standards (Miller 1973, McBride et al. 1975). In a study of the San Bernardino Mountains, ponderosa pine was shown to be the most sensitive tree species to ozone chlorotic mottle disease (Kickert 1976, Taylor 1980). Similar symptoms were shown for mixed conifer forests of Sequoia-Kings Canyon National Park in the Sierra Nevada: 70-100% of all trees between 1300 and 1900 m elevation showed chlorosis (Williams et al. 1977, Williams 1983). Some evidence of chlorosis has been detected further north in Sequoia National Forest by Pronos and Vogler (1981) and downwind from Lake Tahoe near Luther Pass (California's Forest Resources 1979), but little attention has yet been paid to searching for ozone damage in the northern Sierra Nevada and Cascade Ranges.

Another important pollutant in this forest could be acid deposition. McColl (1981) has suggested that montane forests in California are very susceptible to acidification because they grow on shallow, granitic soils. Bradford et al. (1981), however, surveyed 170 Sierran lakes and found no statistical change in pH over a 15 yr period.

The mid-montane conifer forest may be the best choice

MID-MONTANE CONIFER FOREST

This vegetation type covers about 15% of the state's area. It is present in all northern mountain ranges which extend above 800 m elevation, and in all southern mountain ranges which extend above 1400 m. It is absent from the Central and Southern Coast Ranges and from the western part of the Transverse Ranges because their peak elevations lie below these limits. The lower elevational limit corresponds to a drop in mean annual temperature below 13^{o}C and a rise in annual precipitation above 850 mm. Well within the mid-montane zone, mean annual temperature is 11^{o}C and precipitation exceeds 1000 mm. About 33% of annual precipitation falls as snow (Major 1977).

The mid-montane zone extends from 800 to 2000 m elevation in northern California, and from 1400 to 2400 m in southern California. Within that zone are several variations (phases) of a central forest type, the mixed conifer forest.

The mixed conifer forest exhibits shared or shifting dominance by six conifers: ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*P. jeffreyi*), sugar pine (*P. lambertiana*), Douglas-fir, California white fir (*Abies concolor* var. *lowiana*), and incense-cedar (*Calocedrus decurrens*). Generally, ponderosa pine is the most abundant of the five on mountains to the west of the Sierra-Cascade crest, except on serpentine soils or at higher elevations where Jeffrey pine predominates. Jeffrey pine also predominates east of the crest--in southern California--in the most arid portions of this elevational belt.

Haller (1959), Thorne (1977), and Yeaton (1981) have hypothesized that Jeffrey pine is more tolerant of drought, low temperatures, poor soil conditions, and smog than ponderosa pine, but little experimental evidence exists to test this hypothesis. We need comparative data on water-use efficiency, photosynthetic rates, and carbon allocation patterns. Hybrids are regularly found, but hybrid frequency is kept relatively low by seasonal differences in date of pollen maturity, by reduced viability of hybrid seed, and by failure of hybrids to become established (Haller 1962). The zone of contact between the two species is most intense at 1900 m elevation in the north, 2100 m in the south.

There is abundant photographic evidence to show increasing tree density over the past century. The pristine mixed conifer forest was relatively open, with a mosaic of single-age tree clusters in miniature groves. Overstory conifer canopy cover was probably <60%. Rather open layers of subdominant deciduous trees, evergreen and deciduous shrubs, and perennial herbs lay below the overstory, probably contributing <20% cover altogether. The change in of study site for the forest response program, particularly if the low elevation portion--dominated by ponderosa pine--is selected. Forest ecologists have studied the growth, reproduction, and general autecology of ponderosa pine for nearly a century. Although the broad ecophysiology of the species is not well known (e.g., gas exchange, metabolism), at least such pertinent aspects as response to pollutant, drought, competition, and pathogen stresses have been studied.

This ponderosa pine fringe, however, has some drawbacks. It is an ecotone area, thus contains chaparral shrub elements from below and associated trees from above. One seldom finds the pure, open stands of ponderosa pine typical of the Rocky Mountains. The associated species can have varied effects on ponderosa pine, for they include nitrogen-fixing shrubs (*Ceanothus*), invasive shade-tolerant trees (white fir), and highly flammable and competitive ground covers which can suppress pine seedlings and saplings (mountain misery and several species of manzanita). Thus, study sites will need to be chosen carefully so as to minimize differences in associated species.

UPPER MONTANE CONIFER FORESTS

A thread of continuity which runs through the several upper montane forests of California is lodgepole pine (*Pinus contorta* var. *murrayana*). Although some southern California ecologists refer to lodgepole pine forests as subalpine, most would agree with MacMahon and Andersen (1982), who place them in the upper montane and reserve subalpine for open forests dominated by white bark and foxtail pines.

Upper montane forests cover about 3% of the state's area, and they extend from 1800-2400 m elevation in northern California to 2400-2800 m in southern California. Mean annual temperature is 5^{o}C, well below that of the mixed conifer forest. Mean annual precipitation may be as high as 1600 mm, in the north, but overall it may be insignificantly greater than precipitation in the mixed conifer forest. The major difference is the form of precipitation: snowfall accounts for 70-90% of all precipitation, leading to snowpack depths of 2.5-4 m and snow duration of close to 200 days (Smith 1978a and b).

The ecotone between mid-montane and upper montane forests is often narrow, spanning only about 150 m of elevation. It is an important separation point for several species pairs: ponderosa and jeffrey pines, sugar and western white pines, and white and red firs. There is speculation by myself and other ecologists that the ecotone is caused by winter--rather than growing season--conditions, but there have been no field or growth chamber experiments to test such speculation.

Two types of upper montane forest exist: the lodgepole pine forest and the red fir forest, the latter with lodgepole pine present but not dominant. Lodgepole pine forests are moderately dense, with 55-80% cover, and are of modest stature, the trees typically only 20 m tall and <70 cm dbh. Shrub and herb cover is generally insignificant. Lodgepole density is relatively high (500-1000 per ha), reflecting the small size of each tree but stand basal area is <65 sq m (Parker 1986). The bimodal habitat distribution of lodgepole pine in California is well known: it dominates on relatively arid, wind-swept, high elevation sites with shallow soils, and it dominates on relatively wet sites at the edge of meadows or lakes which also receive cold air drainage (Rundel et al. 1977). Although some of these wet sites appear to be successional, with fir saplings coming up underneath, others are climax (Parker 1986). In this respect, California lodgepole pine differs from Rocky Mountain lodgepole pine (P. contorta var. latifolia), which is serotinous and requires episodic disturbance to maintain dominance on most sites. Vankat and Major (1978) reviewed the evidence for lodgepole pine invasion of Sierran meadows. They concluded that the most recent wave began around 1900 and may have been stimulated by the elimination of sheep grazing, rather than by fire or climatic change. Much more is known of Rocky Mountain lodgepole stand structure, population dynamics, and autecology than of Sierran lodgepole pine.

The most mesic upper montane sites are dominated by red fir (Abies magnifica). Red fir is nearly endemic to California, but it is not genetically homogeneous within that range. It exists as the species, as Shasta red fir (A. m. var. shastensis), and as a series of hybrids in the southern Cascades between red and noble firs (A. procera). Barbour and Woodward (1985) recently reviewed stand data for 70 locations and showed that stand basal area averages 90 sq m per ha, tree density 570 per ha, tree canopy cover 60%, and importance value of red fir averages 82%. Commonly associated trees are lodgepole pine, Jeffrey pine, white fir, and western white pine (Pinus monticola). Their analysis of stand age structure indicated that red fir is a climatic climax type and does not depend upon disturbance to maintain site dominance. Thus, upper montane forests are not dependent upon fire and in this respect differ from mid-montane forests.

Relatively little has been published on red fir demography, stand dynamics, or autecology. Consequently, prescriptions for optimum recovery following harvests are not yet in hand. Ustin et al. (1984) and Selter et al. (1986) showed that seedling establishment was closely correlated with absence of high-intensity, high-frequency sun flecks. Once past the first decade of life, however, saplings appear to grow best where exposed to full sun. These findings suggest that natural re-establishment should be poor unless logging provides sufficient shade from slash, understory plants, or remaining overstory trees.

Within the upper montane zone, groves of trembling aspen (Populus tremuloides var. aurea) dominate local sites. This is the most widely distributed tree species in North America. Its California occurrences and biology have been monographed by Barry (1971). In northern California it occurs between 1500 and 3000 m elevation; it is nearly absent from southern California. Ecotones between aspen stands and adjacent dry meadow, wet meadow, and forest are often abrupt and may relate to soil moisture, soil temperature, and soil pH. Aspen stands are typically 1-10 ha in area and many--sometimes all--of the individuals represent ramets of the same clone. Genetic differences between clones can be detected by bole color, time of spring bud break, radial growth rate, fall leaf coloration pattern, and time of leaf drop.

Apart from Barry's study, I have found no published quantitative studies of Californian aspen stands for the past 60 yr (Aitro 1977). Overstory trees may attain 20 m in height and 65 sq cm dbh; canopy cover can reach 100%. White and red fir saplings can be common in the herbaceous understory, and it is possible that these stands are seral to conifer forest.

Although upper montane conifer forests have significant economic and ecological importance, they do not offer many advantages as a study site for the forest response program. Their distant, high location makes access difficult and the impact of acid deposition unlikely. Their short growing season and heavy winter snowpack also limit access. Weather stations at this elevation and above are almost nonexistent, so we have little information about the macroclimate and the factors which correlate with lower and upper limits to the forests.

They are simple forests, however; often a single overstory species and no significant cover underneath by any other species, woody or herbaceous. Simple vegetation offers the promise of being understood more quickly, especially with respect to quantifying response to some single stress.

MIXED SUBALPINE WOODLAND

This vegetation type covers about 2% of the state's area. It differs dramatically from the tall, rather dense red fir forest below. Although exceptional individuals reach 25 m in height, and some stands in locally mesic or protected sites approach the density of upper montane forests, typical subalpine woodland has a canopy height of 10-15 m and consists of clusters of otherwise widely spaced individuals which contribute only 5-15% cover. At the lower limits of the subalpine zone, trees are upright and with single trunks, but with increasing elevation they become dwarfed and multi-stemmed, finally reaching their upper limits as shrubs (Krummholz) <1 m tall. There is no evidence from North America that Krummholz forms are genetically different from tree forms of the same species.

Tree life spans are typically long, 500-1000+ years; but annual growth is small, so that trunks >1 m dbh are uncommon. Needle longevity may reach 30+ years. Photosynthetic rates of limber pine and bristlecone pine are modest, and the photosynthesis:respiration ratio is also low, below 2 (Lepper 1980, Mooney et al. 1964). The age structure of stands is generally very "flat," showing sporadic, rare periods of seedling establishment over long periods of time, but we have few autecological studies by which to conclude what the optimum conditions for establishment are. Stands in the southern Sierra Nevada have tree density and basal area values about half those for red fir forest in the zone immediately below.

Dominant conifers include western white pine, lodgepole pine, limber pine (*P. flexilis*), white bark pine (*P. albicaulis*), foxtail pine (*P. balfouriana* ssp. *austrina*), and mountain hemlock (*Tsuga mertensiana*). Western white pine and foxtail pine do not form Krummholz, but persist as upright trees right to timberline. Eyre (1980) applies the name "mixed subalpine" to this woodland because of a pattern of shared or shifting dominance exhibited by the six taxa. Patches of prostrate shrubs are characteristic, but their cover is of minor importance. Except where woodland encroaches on watercourses or wet meadows, herb cover and diversity are low (about 5% cover).

There are important north-south species shifts. Only lodgepole pine extends throughout California. A northern trio dominates as far south as 36°N, but not into southern California: white bark pine, western white pine, and mountain hemlock. Limber pine tends to dominate southern California stands, although it extends north to 38°N (central Sierra Nevada).

We have very little environmental data for this forest, and it may be dangerous to extrapolate from the few studies available. Mean annual temperature is 4°C (Lepper 1974, Major 1967, 1977). Precipitation on the west flank of the Sierra-Cascade axis and in northwestern California is 750-1400 mm, 95% of which falls as snow. Snow depth in late March may average 2 m. Precipitation on the east flank and in southern California is 350-750 mm. The growing season is 2 months long, but hard frost can occur at any time during that period. It is likely that the upper limit for tree growth corresponds to some minimum accumulation of degree-days during the growing season.

DESERT-FACING MONTANE FOREST

The eastern, desert-facing slopes of the Sierra Nevada and Cascade Ranges are physically quite different from the western slopes. Elevation changes precipitously, soils are more skeletal, and forest cover is less continuous than along the west face. In addition, the eastern escarpment is within a rain shadow. Major (1977) showed temperature and precipitation lapse rates to be significantly steeper on the east slope than on the west slope. Finally, forest zonation is less marked, so it is not inappropriate here for me to describe east slope forests as though they were part of one type, which occurs within the elevation belt 2000-2900 m elevation in the north and 2600-3400 m in the south.

Major associates include red fir, white fir, lodgepole pine, ponderosa pine, and Jeffrey pine. White fir and Jeffrey pine are most commonly the dominants. As the elevation drops, stands become open and park-like, with fewer than 200 trees per ha and tree canopy cover <65%. On the better sites, mature trees reach 40 m in height and 120 cm dbh. Understory deciduous trees are rare. Shrub cover is variable but may average 20%, and the list of common species includes a desert flavor (e.g., _Artemisia tridentata_, _Chyrsothamnus parryi_, _Haplopappus bloomeri_, _Purshia tridentata_). Herb cover may exceed 10% at its seasonal peak. We have relatively little stand data for eastside Sierran forests, and even less for eastside Cascadian forests.

Climatic analyses by Major (1967, 1977), Axelrod (1981), and McDonald (1982) indicate that this eastside forest receives 500-1000 mm precipitation per year and experiences a mean annual temperature of 5-8^{o}C; thus, it is a colder and drier habitat than that of westside montane forest.

PINION/JUNIPER WOODLANDS

As described by Vasek (1977), pinion pines and junipers tend to form separate woodlands in California, in contrast to the mixed pinion _and_ juniper woodlands which are so characteristic of the many Great Basin mountain ranges between the Rocky Mountains and the Sierra-Cascade axis. In northeastern California, a western juniper woodland occurs on open, rolling country through much of Lassen and Modoc

Counties at a mean elevation off 1500 m. Juniperus occidentalis ssp. occidentalis dominates, but common associates include ponderosa pine and mountain mahogany (Cercocarpus ledifolius). Desert shrubs (Artemisia, Purshia, Chyrsothamnus) contribute 30-50% cover. Sometimes ponderosa pine is the dominant. This woodland covers 2-3% of California's area.

The Sierran flank provides the westernmost extension of the one-leaf pinion (Pinus monophylla) and Utah juniper (Juniperus osteosperma) woodlands of the Great Basin. Pinion pine is typically an overwhelming dominant, except on the rockiest sites. Cold desert shrubs provide an understory similar to that in western juniper woodland. These two species continue to dominate woodlands southward into the Mojave Desert, but in some places California juniper (Juniperus californica) replaces Utah juniper and two-leaf pinion (P. edulis) or four-leaf pinion (P. quadrifolia) replaces one-leaf pinion. Representative stands in San Bernardino and Riverside Counties showed ~200 pinion and juniper trees per ha, contributing 20% canopy cover, associated with a mixture of desert and chaparral shrubs contributing another 20% cover. I believe that less is known about the autecology of pinion/juniper dominants than for any other woodland or forest type in California. I am unaware of any published data on photosynthesis, growth, productivity, water relations, or demography of pinions and junipers in California.

CONCLUSIONS

The major hardwood and conifer woodlands and forests of California, which cover 40% of the state's area, have briefly been described. Nine species serve as threads to characterize major community types: Populus fremontii for the riparian forests, Quercus douglasii and Q. agrifolia for the oak woodlands, Pseudotsuga menziesii for the temperate northwest lowland forests, Quercus chrysolepis for the mixed evergreen forests, Pinus ponderosa and P. jeffreyi for the mid-montane conifer forests, Pinus contorta var. murrayana for the upper montane conifer forests and the mixed subalpine woodland, Pinus monophylla and Juniperus occidentalis ssp. occidentalis for semiarid pinion/juniper woodlands.

Significant contributions to our ecological understanding of California's forests and woodlands can be made at all levels, from basic stand descriptions, to autecological studies of key species, to demographic studies of stand dynamics, and to the construction of predictive models. This review has emphasized the gaps in our knowledge. Community structure, dynamics, composition, and distribution are thought to be related to macroclimate, soil, and disturbance regimes--but few details based on experimental manipulation are known; consequently, management techniques are largely intuitive. Many of the 9 species are associated with spatial or temporal patterns of fire, flood, or herbivore disturbance; but their tolerances of, adaptations to, or even requirements for, such disturbances remain largely undocumented at the experimental level.

Among the best understood communities are: blue oak woodland, redwood/Douglas fir lowland forest, and mixed conifer forest. In each of those types we have some basic data on stand structure and the autecology of characteristic species, some understanding of historical changes, and some appreciation for how sensitive the dominant taxa are to environmental stress. Further, each of those three communities are relatively close to sources of the kinds of pollutants which contribute to acid deposition; therefore, they might exhibit responses to acid deposition well before, and more dramatically than, more distant communities.

The best choice for a study site in the forest response program, in my opinion, is the ponderosa pine fringe of the mid-montane (mixed conifer) forest. It offers an ecologically well-known type, accessibility, known sensitivity of dominants to pollutant stress, and an economically important and regionally widespread resource of California. Its usefulness is limited by its complex assortment of associated species and by its history of disturbance.

LITERATURE CITED

Aitro, V.P. 1977. Fifty years of forestry research, 1926-1975. USDA Forest Serv. Gen. Tech. Rep. PSW-23/1977, Berkeley, CA.

Axelrod, D.I. 1965. A method for determining the altitudes of Tertiary floras. Paleobotanist 14:144-171.

______. 1981. Holocene climatic changes in relation to vegetation disjunction and speciation. Amer. Nat. 117:847-870.

Azevedo, J. and D.L. Morgan. 1974. Fog precipitation in coastal California forests. Ecology 55:1135-1141.

Barbour, M.G. 1987. Californian upland forests and woodlands. In: M.G. Barbour and W.D. Billings (eds.), "Terrestrial Vegetation of North America," Chapter 5. Cambridge Univ. Press, New York (in press).

______ and J. Major (eds.). 1977. Terrestrial Vegetation of California. Wiley Interscience, New York.

_____ and R.A. Woodward. 1985. The Shasta red fir forest of California. Canadian J. For. Res.

Barry, W.J. 1971. The ecology of Populus tremuloides, a monographic approach. Ph.D. dissertation, Univ. Calif., Davis.

_____. 1985. A heirarchical vegetation classification system with emphasis on California plant communities. California Dept. Parks and Recreation, Sacramento, CA.

Biswell, H.H. 1967. Forest fire in perspective. In: Proceedings, California Fire Ecology Conference, Tall Timbers Research Station, Tallahassee, FL. pp. 43-63.

Bolsinger, C.L. 1980. California forests: trends, problems, and opportunities. USDA For. Serv. Res. Bull. PNW-89, Portland, OR.

Borchert, M. 1985. Serotiny and cone-habit variation in populations of Pinus coulteri (Pinaceae) in the Southern Coast Ranges of California. Madrono 32:29-48.

Bradford, G.G., A.L. Page, and I.R. Straughan. 1981. Are Sierra lakes becoming acid? Calif. Agr. 35(May-June):6-7.

California's Forest Resources. 1979. Calif. Dept. Forestry, Sacramento, CA.

Conard, S.G., R.L. MacDonald, and R.F. Holland. 1977. Riparian vegetation and flora of the Sacramento Valley. In: A. Sands (ed.), "Riparian Forests of California, their Ecology and Conservation,: pp. 47-55. Institute of Ecology, Pub. 15, Univ. Calif., Davis.

Eyre, F.H. (ed.). 1980. Forest cover types of the United States and Canada. Soc. Amer. Foresters, Washington, DC.

Griffin, J.R. 1973. Xylem sap tension in three woodland oaks of central California. Ecology 54:152-159.

_____. 1977. Oak woodland. In: M.G. Barbour and J. Major, eds., "Terrestrial Vegetation of California," p. 383-415. Wiley Interscience, New York.

_____. 1980. Sprouting in fire-damaged valley oaks, Chews Ridge, California. In: T.R. Plumb, ed., "Ecology, Management, and Utilization of California Oaks.", pp. 216-219. USDA Forest Serv. Gen. Tech. Rep. PSW-44, Berkeley, CA.

Haller, J.R. 1959. Factors affecting the distribution of ponderosa and Jeffrey pines in California. Madrono 15:65-71.

_____. 1962. Variation and hybridization in ponderosa and Jeffrey pines. Univ. Calif. Pub. Bot. 34:123-166.

Hartesveldt, R.J., H.T. Harvey, H.S. Shellhammer, and R.E. Sticker. 1975. The giant sequoia of the Sierra Nevada. USDI National Park Service, Washington, DC.

Harvey, H.T., H.S. Shellhammer, and R.E. Sticker. 1980. Giant sequoia ecology. USDI National Park Service, Sci. Mon. Series No. 12, Washington, DC.

Hellmers, H. 1966. Growth response of redwood seedlings to thermoperiodism. For. Sci. 12:276-283.

Holland, R.F. 1986. Preliminary descriptions of the terrestrial natural communities of California. California Resources Agency, Dept. Fish and Game, Sacramento, CA.

Jacobs, D.F., D.W. Cole, and J.R. McBride. 1985. Fire history and perpetuation of natural coast redwood ecosystems. J. For. 87:494-497.

Kickert, R.N. 1976. Photochemical air pollutant effects on mixed conifer ecosystems, a progress report. US EPA, Research and Development Office, Corvallis, OR, CERL-026.

Kilgore, B.M. 1973. The ecological role of fire in Sierran conifer forests: its application to national park management. Quart. Res. 3:496-513.

_____ and D. Taylor. 1979. Fire history of a sequoia-mixed conifer forest. Ecology 60:129-142.

Komarek, E.C. 1967. The nature of lightning fires. Proceedings, Tall Timbers Fire Ecology Conference 7:5-41.

Latting, J. (ed.). 1976. Plant communities of southern California. Special Pub. No. 2, Calif. Native Plant Soc., Berkeley.

Lepper, M.G. 1974. Pinus flexilis James and its environmental relationships. Ph.D. dissertation, Univ. California, Davis.

_____. 1980. Carbon dioxide exchange in Pinus flexilis and P. strobiformis (Pinaceae). Madrono 27:17-24.

MacDonald, R. 1987. Water relations of riparian, woodland, and chaparral vegetation in the Lake Berryessa region of California. Unfinished Ph.D. dissertation, Univ. California, Davis.

MacMahon, J.A. and D.C. Andersen. 1982. Subalpine forests, a world perspective with emphasis on western North America. Prog. Phys. Geog. 6:368-425.

Major, J. 1967. Potential evapotranspiration and plant distribution in western states with emphasis on California. In: R.H. Shaw, ed., "Ground Level Climatology," pp. 93-126. AAAS, Washington, DC.

_____. 1977. California climate in relation to vegetation. In: M.G. Barbour and J. Major, eds., "Terrestrial Vegetation of California," pp. 11-74. Wiley Interscience, New York.

McBride, J.R., V.P. Semion, and P.R. Miller. 1975. Impact of air pollution on the growth of ponderosa pine. Calif. Agr. 29(12):8-9.

McClaran, M.P. 1986. Age structure of Quercus douglasii in relation to livestock grazing and fire. Ph.D. dissertation, Univ. California, Berkeley.

McColl, J.G. 1981. Effects of acid rain on plants and soils in California, final report. Calif. Air Res. Bd., Contract A8-136-31, Sacramento.

McDonald, P.M. 1982. Climate, history, and vegetation of the eastside pine type in California. In: "Management of the Eastside Pine Type in Northeastern California," pp. 1-16. Proceedings of a symposium, Cooperative Extension, Univ. Calif., Berkeley.

Miller, P.L. 1973. Oxidant-induced community change in a mixed conifer forest. In: J. Naegle, ed., "Air Pollution Damage to Vegetation," pp. 101-117. Amer. Chem. Soc., Adv. Chem. Series 122, Washington, DC.

Minnich, R.A. 1976. Vegetation of the San Bernardino Mountains. In: J. Latting, ed., "Plant Communities of Southern California," Special Publ. No. 2, pp. 99-124. Calif. Native Plant Soc., Berkeley.

_____. 1980. Wildfire and the geographic relationships between canyon live oak, Coulter pine, and big-cone Douglas fir forests. In: T.R. Plumb, ed., "Ecology, Management, and utilization of California Oaks," pp. 55-61. USDA For. Serv., PSW-44, Berkeley.

Mooney, H.A. and B. Chabot (eds.). 1985. Physiological Ecology of North American Plant Communities. Chapman and Hall, New York.

_____, R.D. Wright, and B.R. Strain. 1964. Field measurements of the metabolic responses of bristlecone pine and big sagebrush in the White Mountains of California. Amer. Midl. Nat. 72:281-297.

Parker, A.J. 1986. Persistence of lodgepole pine forests in the central Sierra Nevada. Ecology 67:1560-1567.

Plumb, T.R. 1980. Response of oaks to fire. In: T.R. Plumb, ed., "Ecology, Management, and Utilization of California Oaks," pp. 202-215. USDA For. Serv., PSW-44, Berkeley.

_____ and N. Pillsbury. 1987. Management and utilization of California hardwoods. USDA For. Serv. Gen. Tech. Rep., PSW, Berkeley (in press).

Pronos, J. and D.R. Vogler. 1981. Assessment of ozone injury to pines in the southern Sierra Nevada, 1979/1980. USDA Forest Service, Forest and Pest Management Report No. 81-20, San Francisco.

Rundel, P.W. 1980. Adaptations of mediterranean-climate oaks to environmental stress. In: T.R. Plumb, ed., "Ecology, Management, and utilization of California Oaks," pp. 43-54. USDA For. Serv., PSW-44, Berkeley.

_____, D.J. Parsons, and D.T. Gordon. 1977. Montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges. In: M.G. Barbour and J. Major, eds., "Terrestrial Vegetation of California," pp. 559-599. Wiley Interscience, New York.

Selter, C.M., W.D. Pitts, and M.G. Barbour 1986. Site microenvironment characteristics and seedling survival of Shasta red fir (Abies magnifica var. shastensis). Amer. Midl. Nat. 115:288-300.

Smith, J.L. 1978a. Snowpack characteristics and the simulated effects of weather modification upon them. USDA For. Serv., Central Sierra Snow Laboratory, PSW, Berkeley.

_____. 1978b. Historical climatic regime and the projected impact of weather modification upon precipitation and temperature at the Central Sierra Snow Laboratory. USDA For. Serv., PSW, Berkeley.

Taylor, O.C. 1980. Photochemical oxidant air pollution effects on a mixed conifer forest ecosystem. US EPA, EPA-600/3-80-002. Corvallis, OR.

Thorne, R.F. 1977. Montane and subalpine forests of the Transverse and Peninsular Ranges. In: M.G. Barbour and J. Major, eds., "Terrestrial Vegetation of California," pp. 537-557. Wiley Interscience, New York.

UNESCO. 1973. International classification and mapping of vegetation. Paris. [See also D. Mueller-Dombois and H. Ellenberg, 1974, Aims and Methods of Vegetation Ecology, Wiley, NY.]

Ustin, S.L., R.A. Woodward, M.G. Barbour, and J.L. Hatfield. 1984. Relationships between sunfleck dynamics and red fir seedling distribution. Ecology 65:1420-1428.

Vankat, J.L. 1982. A gradient perspective on the vegetation of Sequoia National Park, California. Madrono 29:200-214.

_____ and J. Major. 1978. Vegetation changes in Sequoia National Park, California. J. Biogeogr. 5:377-402.

Vasek, F.C. 1977. Transmontane coniferous vegetation. In: M.G. Barbour and J. Major, eds., "Terrestrial Vegetation of California," pp. 797-832. Wiley Interscience, New York.

Veirs, S.D., Jr. 1980. The role of fire in northern coast redwood forest dynamics. In: "Proceedings of the Conference on Scientific Research in the National Parks, Vol. 10, Fire Ecology," pp. 190-209. National Park Service, Washington, DC.

Vogl, R.J. 1973. Ecology of knobcone pine in the Santa Ana Mountains, California. Ecol. Monogr. 43:125-143.

_____. 1976. An introduction to the plant communities of the Santa Ana and San Jacinto Mountains. In: J. Latting, ed., "Plant Communities of Southern California," Special Pub. No. 2, pp. 77-98. Calif. Native Plant Soc., Berkeley.

Warner, R.E. and K.M. Hendrix (eds.). 1984. California Riparian Systems. Univ. Calif. Press, Berkeley.

White, K.L. 1966. Structure and composition of foothill woodland in central coastal California. Ecology 47:229-237.

Williams, W.T. 1983. Tree growth and smog disease in the forests of California: case history, ponderosa pine in the southern Sierra Nevada. Environ. Poll. (Series A) 30:59-75.

_____, M. Brady, and S.C. Willison. 1977. Air pollution damage to the forests of the Sierra Nevada Mountains of California. J. Air Poll. Cont. Assoc. 27:230-234.

Yeaton, R.I. 1981. Seedling characteristics and elevational distributions of pine (Pinaceae) in the Sierra Nevada of central California, an hypothesis. Madrono 28:67-77.

Zinke, P.J. 1977. The redwood forest and associated north coast forests. In: M.G. Barbour and J. Major, eds., "Terrestrial Vegetation of California," pp. 679-698. Wiley Interscience, New York.

MONITORING TERRESTRIAL PROCESSES IN THE LONG-TERM ASSESSMENT OF FOREST EFFECTS: A MECHANISTIC APPROACH

Philip W. Rundel
Laboratory of Biomedical and Environmental Sciences
and Department of Biology
University of California
Los Angeles, California 90024

INTRODUCTION

Forest vigor, including components of most net primary production and reproductive outut, is strongly influenced by naturally occurring environmental stresses and/or limiting factors. For forest trees in California, such stresses include seasonal drought, nutrient availability, extreme high and low temperatures and shading. Anthropogenic air pollutants can similarly be considered as limiting stresses. The effects of sulfur dioxide (SO_2), ozone (O_3) and particulate sulfates and nitrates which originate from human activities are well known to have significant effects both direct and indirect on physiological functions in plants (see, for example, Winner et al. 1985, Guderian 1985, Smith 1981). The numerous detrimental effects of acid deposition and air pollution on vegetation have been described in reviews and symposia by Mudd and Kozlowski (1975), Hutchinson and Havas (1980), Miller (1980), Smith (1981), Ulrich and Pankrath (1983), Linthurst (1984), Winner et al. (1985), Gibson et al. (1986) and Zoettl (1987). The impacts of air pollution and acid deposition on forest growth is emerging as one of the most significant environmental issues of the decade.

Historically, the majority of studies of plant response to air pollutants could be described as either screening or dose-response studies. The research approach in such studies has been an attempt to rank species (or genotypes or cultivars) in order of their relative sensitivity to air pollutants and to develop quantitative relationships between pollutant level and plant response. This approach has led to our fundamental understanding of the potential of air pollutants to reduce plant productivity. There is a limitation, however, in how data from such studies can be extrapolated. Controlled experiments of this type inherently provide an experiment-specific or site-specific response relationship which may be very difficult to apply to different conditions.

In recent years there has developed a relatively new approach to studies of air pollution effects on plants. This approach is a mechanistic one which focuses on understanding the ways in which dynamic plant processes are affected by air pollutants. Mechanistic approaches of this type, based on a core of physiological process studies, offer the prospect for the development of a much more generic understanding of the impact of pollutant stress on plants. Mooney et al. (1986) suggest that a mechanistic approach to pollution research can:

1) Help establish cause-effect relationships between the presence of air pollutants and suspected damage to plants;

2) Help identify attributes of habitats and species which define their relative air pollution sensitivity;

3) Help indicate how the effects of air pollutants are modified by other environmental factors;

4) Help develop predictive models to be used by resource managers which will help them better estimate air pollution-caused losses in productivity.

Since much of the focus of this workshop is on forest monitoring studies which are site-specific in nature, I would like to focus in this paper on prospects for mechanistic studies which can be accomplished. This focus in no way is meant to minimize the significance of site-specific measurements. Rather, it is offered as a means of identifying prospects for exciting new developments in understanding the response of forest trees in California to atmospheric pollution.

Acid deposition in California differs from that in Europe and the Eastern United States. A larger proportion in California is deposited as dry deposition, and there is a higher ratio of NO_x to SO_x here. The ecological effects of acid deposition are not obvious in California, as in other areas. In southern California, ozone and other forms of air pollution have caused weakness and death of conifers (Miller 1980).

Potential problems of acid deposition and forest decline in California may well be strongly related to nitrogen oxides as a major component of air pollution. Increased rates of nitrogen uptake have been suggested as a mechanism involved in forest decline in both North America and Europe. One suggested mechanism for such an affect has been hypothesized to be the influence of late-season fertilization on winter-hardening in conifers (Friedland et al. 1984). An alternate hypothesis is that increased nitrogen uptake could result in increased rates of growth initially and thereby lead to deficiencies of other nutrients (Prinz et al. 1986, Zoettl 1987). Although these hypotheses are provocative, there are few data to directly support a connection between nitrogen nutrition and forest decline.

Since inputs of nitrogen from dry deposition may be a significant biogeochemical flux in forest regions of California today, it is important to be able to quantify these fluxes. Dry deposition monitoring stations now being planned may well be able to quantify regional levels of input under prescribed conditions; they will not provide any information on the significance of canopy interception of nitrogen species, as well as other potentially toxic aerosols and gases.

CLASSIFICATION AND EVALUATION OF EFFECTS

The effects of air pollution impact on forest trees can be considered at a variety of levels of biological organization. These can be seen, for example, in the effects of photochemical oxidants in natural plant communities (Table 1). At the cell level, effects may be initially expressed in changes in enzyme activity, altered rates of metabolism, and changes in cellular structure and organization (Guderian 1985). As the impact of such cellular changes are felt, tissue level changes in photosynthetic capacity, respiration rate and components of tissue water relations may occur. Altered rates of metabolic activity and allocation may lead to measurable effects on functional processes such as root growth, nitrogen fixation or mycorrhizal development. Degradation of chlorophylls can lead to chlorosis and/or necrosis. Such changes at the tissue level may or may not have effects at the whole plant level. It is important to keep in mind that significant reductions in net primary production may occur without visible damage, while visible chlorosis on foliage does not necessarily indicate reduced growth or yield. Finally, changes in growth and competitive ability of individuals or species in a plant community may lead to changes in stand structure and stability.

Recommendations

There are a variety of reasonably standard measurements which have been used in evaluations of the impact of air pollution on forest trees.

a) Analysis of visible injuries. Characteristic patterns of morphological and anatomical change in foliage are caused by specific types of air pollution. These should be quantified early and late in the growing season in relation to such variables as species, needle/leaf age and developmental stage, and habitat.

b) Foliage turnover. Longevity of needles or leaves and the seasonality and amount of litterfall can be important comparative patterns to monitor.

c) Photosynthetic pigments. Total amounts of individual photosynthetic pigments, and the ratios of such pigments, are often useful measures of plant vigor. Ratios of chlorophyll *a* and *b* to the total content of xanthophylls and carotenes, or total chlorophylls to phaeophytin are frequently used to indicate seasonal patterns of chlorophyll degradation.

d) Foliage nutrition. Foliar concentrations of important macronutrients such as nitrogen, phosphorus, potassium, magnesium and calcium provide a potential index of limiting nutrient availability. Similarly, high levels of potential toxic elements such as aluminum, manganese and trace metals could indicate pollutant imports of these materials. Ratios of elements may also be useful as, for example, with carbon and nitrogen. Again, variables of species, needle/leaf age and development stage and habitat must be considered.

e) Distribution of carbon allocation. A number of patterns of altered carbon allocation may be associated with pollution damage in trees.

Table 1.

Classification of photochemical oxidants effects on plants
(adapted from Guderian 1985)

Organizational level			
Cell	Tissue	Organism	Community
Increased membrane permeability	Changes in photosynthesis, respiration, and transpiration Alterations in the partitioning of metabolites	Changes in plant growth	Reduced plant growth and productivity Fluctuations in composition and reduction in species abundance
Altered enzyme activities	Alterations in growth and development of individual organs	Increased susceptibility to biotic and abiotic stresses	Changes in stand population structure
Increased stress ethylene production	Pigmentation, bleaching, and chlorosis	Disturbances in fruit production	Disruption of food chain Changes in plant succession Possible changes in nutrient cycling Risks to consumers and decomposers
Ultrastructural changes in organelles Changes in cellular metabolism	Necrosis	Reduced yield and quality	Impairment of ecosystem productivity, including its stability and capacity for self-regulation
Altered cellular structure	Reduction in rhizobium induced nodulation	Altered plant competitive ability	
Disrupted cellular functions	Disturbance of mycorrhizal development	Death of plants	
Cell death	Death or loss of plant organs	Reduced productivity	

These include a great decline in apical growth, "stork's nest" growth of lateral shoots, differential radial growth of trunks, and very heavy reproductive allocation. Below-ground allocation of photosynthates may also decline with pollution stress.

f) Susceptibility to herbivores and pathogens. Changes in susceptibility may indicate reduced tree vigor.

g) Seasonal water relations. Reduced allocation of carbon to below-ground tissues may manifest itself in lower water potentials. Such low water potentials may increase tree susceptibility to drought stress.

h) Net primary production. Allometric regressions for individual species may allow calculations of above-ground net primary production on an individual, or stand basis. Patterns of changes in levels of net primary production may be related to the integrated effects of air pollution. Below-ground net primary production is more difficult to quantify, but has important significance since pollution effects may be realized there first.

   NPP is an intrinsically variable parameter. Year to year climatic variation is perhaps the greatest single contributor to this inconsistency, but fluctuations in herbivore populations, fire, or other infrequent or random events could also exert considerable influence on NPP. A more subtle source of error is inherent in the way production measurements are usually made. When summing significant increments or decrements in biomass, the data retain a "memory" of any unusually high or low biomass values that occurred shortly before the study. One cannot be sure that memory has been "cleared" until the slope of the change in biomass changes direction. For these reasons, long term studies of NPP are much superior to short term studies. The more years of data, the more reliable the results and the better the quality of any management decisions based on those data.

i) Canopy density. Thinning in canopy structure over time could be an outcome of pollution effects. Fish-eye camera photographs provide a graphic means of quantifying year-to-year changes, but cannot of themselves establish a causality. Spectral measurements of red/far-red ratios in the forest understory may provide a measure of the leaf area index of the canopy.

In addition to these biological measurements, there are a variety of measurements of soil and atmospheric fluxes which can provide valuable data in an integrated study of pollutant effects on forest trees.

GENETIC CONTROL OF STRESS RESPONSE

Background

It has not been uncommon in the past to suggest a mean species tolerance for a particular pollutant. Genotypes within a single species, however, are well known to exhibit a wide range of stress tolerance. This is equally true for pollution stresses as it is for natural stresses. The basis for tolerance to an individual atmospheric pollutant, such as ozone or sulfur dioxide, is the genetic variance for this tolerance in the population. This means that experiments which are designed to investigate the nature of stress tolerance to pollutants must be performed at several stress levels and at different stages in plant maturity in order to understand the significance of the mean response of the test plants. Such an understanding is also critical in extrapolating experimental studies to community level predictions of change in productivity. Furthermore, the variance of a species response defines the potential for natural or artificial selection to alter mean stress resistance over time.

Recent studies suggesting associations between protein heterozyogosity, tree growth rates and developmental homeostasis (Mitton and Grant 1984, Mitton et al. 1981, Letig et al. 1983) have important implications for air pollution studies in forest trees. If increased heterozyogosity is associated with more rapid growth rates within a population under normal circumstances, then impacts of gaseous pollutants might well be expected to be most extreme on these trees which would have the highest mean stomatal conductances.

Recommendations

Genetic surveys utilizing patterns of isozymes can provide an important level of understanding of patterns of genotypic distribution among and beween populations of forest tree species. This type of study is particularly significant when related to dose-response investigations with full sib and half sib families of important forest species.

EFFECTS OF VEGETATION ON THE TRANSFER OF ATMOSPHERIC POLLUTANTS

Background

In a recent review, Hosker and Lindberg (1982) have clearly described the importance of vegetation canopies in influencing patterns of deposition of atmospheric pollutants. It is well known that vegetation is an important sink for airborne material originating from both natural and anthropogenic sources. The surface area of leaves and stems is commonly many times the ground surface area of a canopy, and this increased area provides large surfaces to react with atmospheric gases or aerosols. Gaseous pollutants may be absorbed rapidly through open stomata or diffuse slowly through outer cuticles. Plant surfaces may also initiate chemical changes to gaseous or aerosol pollutants through complexation, precipitation, oxidation, and/or reduction. Despite the importance of such interaction, very little is known about either the nature of pollutant interactions with plant surfaces or the consequences of such interactions with biotic processes. For nitrogen species in the atmosphere alone, there are a multiplicity of types of foliar interactions. Nitric acid adsorbs to or reacts with all surfaces, while gaseous NH_3 and NO_2 interact primarily inside leaf tissues. Finally, N_2O and NO exchange slowly with plant tissues, but may have potentially important interactions.

In addition to foliar surface area, biological variables of foliar surface structures and chemistry may strongly affect the interception of pollutants. Leaves may be smooth, pubescent, waxy, or resinous. These characteristics provide important microsites for the sorption and/or decomposition of gaseous and aerosol pollutants. Individual types of pollutants, of course, may behave very differently to different types of foliar surface characteristics.

For gaseous pollutants, a critical factor is typically the water solubility of the pollutant. The rate of uptake of gaseous pollutants is strongly correlated with their solubility. For aerosol pollutants, however, the most critical factors controlling effects on vegetation are the retention time of particle on leaves and the chemical reactivity of the pollutant. Rough-surfaced leaves, for example, may retain aerosol particles 10 times longer than on smooth leaves (Wedding et al. 1977). There are few quantitative data, however, on the effect of vegetation on the intermedia transport of pollutants and the reverse effect of pollutants on leaf chemistry and activity. Relevant studies are badly needed (Hosker and Lindberg 1982).

Recommendations

Studies should be initiated to investigate the effect of vegetation canopies on the capture and transfer of atmospheric pollutants. The basic experimental design should be to quantitatively assess the relative concentration, on a volume weighted basis, of precipitation collected in the open, that collected as throughfall under monospecific canopies, and the stem flow from the canopy capture of precipitation. This approach will be most straight forward with respect to trace metal pollutants and organic pollutants where potential leaching out of foliar tissues is not a problem. For nitrogen and major cations, however, controlled rainfall-simulation experiments will be necessary to quantify foliar leaching contributions.

TRANSFER RATES OF SUBMICRON AEROSOLS TO VEGETATION

Background

The removal of submicron aerosols from the atmosphere may occur as wet deposition from precipitation scavenging or as dry deposition by the direct capture of the aerosols by plant or soil surfaces. While impaction and gravitational settling are important processes in larger aerosol particulates, it is generally believed that diffusion processes control the deposition of aerosols <01 mm in diameter (Chamberlain and Little 1981). Since many atmospheric pollutants of significant ecological concern are transported as submicron aersols, it is important to develop techniques allowing estimates of their deposition velocities.

Indirect calculations of rates of deposition of aerosols to vegetation, particularly with regard to sulfur, have been made using micrometeorological methods (Garland 1978, Droppo 1980, Hicks and Wesley 1980, Sievering 1982) but there have been very few attempts at direct measurements. Russell *et al.* (1981) described the use of ambient ^{212}Pb to evaluate dry depositional fluxes of submicron aerosols to forest vegetation and suggested that ^{7}Be should also be useful in dry climates. Bondietti *et al.* (1984) further evaluated the use of ^{212}Pb and ^{7}Be, as well as ^{214}Pb and ^{210}Pb, as tracers of submicron aerosol transfer, and provided preliminay data on calculations of biomass-normalized deposition velocities. The assumption in these studies is that these short-lived, natural radionuclides, with a range of half-lives, could serve as tracers for submicron aerosols with which they are associated.

For ^{212}Pb ($t_{1/2}$ = 10.6 hr) and ^{214}Pb ($t_{1/2}$ = 26.8 min), the half-lives are shorter than the typical atmospheric residence time of one week or less for submicron aerosols (Bondietti et al. 1984). The opposite is true for ^{7}Be ($t_{1/2}$ = 53.3 days) and ^{210}Pb where decay half-lives are longer than the atmospheric residence times of the aerosols on which they reside and whose deposition behavior should be very similar. Bondietti et al. (1984) enumerate three advantages to the use of these natural tracers in air-to-vegetation transfer studies:

1) direct measuremenets of deposition to vegetation are possible;

2) The depositing aerosols and the rates of removal are natural, not biased by experimental designs; and

3) measurements can be made under a variety of conditions, at any time, and to complex canopies.

There is a decided advantage in utilizing ^{7}Be measurements in addressing an ecosystem focus on intermedia transport fluxes in the western United States. This results from the fact that ^{7}Be is a ubiquitous radionuclide whose atmospheric concentrations are relatively constant over broad geographical areas (Bondietti et al. 1984). This situation permits the measurement of geographic and climatic patterns of variation in transfer rates of submicron aerosols to the vegetation. Furthermore, the effects on depositional velocities of differing canopy architecture and leaf area index may also be investigated. For strongly seasonal climates, the use of ^{7}Be lends itself well to integrated measurements of depositional fluxes over relatively long periods without precipitation.

Recommendation

Since the presence of ^{7}Be on vegetation represents deposition from the atmosphere, the transfer fluxes of submicron aerosols to vegetation can be estimated by relating the concentrations on plant surfaces to their ambient air concentrations over the period of measurement. The same approach appears to be reasonable for the use of ^{214}Pb and ^{212}Pb (Bondietti et al. 1984). Since these radionuclides have a finite life, their presence on a plant surface represents a finite period of deposition. A biomass-normalized deposition velocity (V_D) can be calculated as follows:

$$V_D = \lambda_e \, CR_{va} \tag{1}$$

where λ_e is the effective loss rate from vegetation (d^{-1}) and CR_{va} is the vegetation/air concentration ratio derived from C_v, the concentration of the radionuclide on vegetation (pCi kg^{-1}) and from the C_a, air concentration (pCi m^{-3}). For studies with ^{7}Be, λ_e is defined as:

$$\lambda_e = \lambda_r + \lambda_w \tag{2}$$

where λ_r is the radionuclide decay constant and λ_w is the effective first order rate constant representing all other removal processes for ^{7}Be, including growth dilution, weathering, etc. The value of λ_r for ^{7}Be is 15×10^{-7} s^{-1}, but measurements of λ_e for Western climates have not been made. Bondietti et al. (1984) reported literature values of λ_e for crop plants ranging from 2.1 to 4.7 x 10^{-7} s^{-1}. For studies of the very short-lived lead isotopes, λ_w is considered to be zero. Values of V_D (m^3 kg^{-1} s^{-1}) represent the effective air volume being depleted of aerosols by 1 kg of vegetation each second.

Concentrations of ^7Be in plant tissues can be calculated from field collected samples. The preferential treatment is dry-ashing samples at 450°C for subsequent analysis using an intrinsic coaxial germanium photon detector and a computer-based multichannel analyzer system. The analyzer system is programmed to carry out a quantitative measurement of the count levels at appropriate peaks over the energy spectrum analyzed. Bondietti et al. (1984) used an atmospheric concentration of ^7Be of 0.087 pCi m^{-3} based on levels monitored at Livermore, California. Although these concentrations are thought to be relatively constant over broad areas, high volume samples with fiber glass filters may be used to collect site-specific concentration data.

The depositional velocity, V_d ($m\ s^{-1}$), can be calculated by multiplying the V_D by the biomass density (kg m^{-2} ground surface). The biomass density will, of course, vary greatly between species in a community. If the exposure time in ^7Be studies is sufficiently long to encompass a change in the biomass density of a canopy, then the mean biomass density must be considered:

$$V_d = CR_{va}\ \bar{Y}\ \lambda e\ (1^{-\lambda e}\ \bar{T}) \qquad (3)$$

where $\bar{Y}$ is the mean biomass density and $\bar{T}$ is the exposure time days (Bondietti et al., 1984).

The experimental design of such a study should be to calculate values of V_d and V_D for ^7Be deposition on a series of dominant forest tree species at field sites corresponding to the new CARB dry deposition network. Exposure times of 14-30 days or more without rain could be used as integrated periods of dry depositional flux.

If ^7Be concentrations on plant surfaces can be made subsampling all tissue types proportionally, it will be possible to scale vegetation removal processes to allow a complete estimation of submicron aerosol removal by the plant community on an ecosystem basis:

$$J_i = V_{di} \times C_i \qquad (4)$$

where J_i is the depositional flux for chemical species i is (ng cm^{-2} s^{-1}), V_{di} is the depositional velocity for species i (cm s^{-1}), and C_i is the air concentration of species i (ng cm^{-3}). Assuming that the depositional velocity determined for ^7Be is similar to that of other submicron aerosols of interest (and this is an important subject for study), then J_i can be readily calculated if C_i is measured.

GAS EXCHANGE MEASUREMENTS

Background

Steady-state gas-exchange systems allow a precise control of the micro-environment of photosynthetic tissues and a means to continuously monitor rates of gas exchanges between foliage and the environment for both CO_2 and water vapor. These systems provide an important tool to mechanistically describe the environmental and plant biochemical limitations of photosynthetic capacity. Gas exchange systems which allow the CO_2 concentration within the leaf to be varied allow a means of assessing dynamic changes in the relative importance of stomatal and/or mesophyll processes in limiting this capacity. With such CO_2-response curves, the effects of carboxylation efficiency (i.e. the availability of RUBISCO) can be separated from the effects of electron transport in limitation of photosynthetic capacity. Rate-limiting capacity of the light harvesting pigments and biochemical processes of the dark reactions, as well as resistances to CO_2 channels of diffusion into leaf cells, can be determined by cuvette measurements of photosynthetic response to variations in quantum flux.

Studies of pollution-induced changes in the photosynthetic capacity of plants can benefit greatly from the field measurements using steady state gas exchange systems. Careful studies, with appropriate controls, can provide an analysis of the specific aspects of the photosynthetic process which are impacted by physiological changes of the plant. Technological advances in instrumentation over the past few years has now made it possible to expand such pollutant studies from static measurements in the field to dynamic ones in which individual leaves within cuvettes may be fumigated with controlled levels of gas pollutants. Such a steady-state system is described by Atkinson et al. (1986) for use with SO_2. This system has the potential to clarify the ways by which biological and environmental factors influence plant responses to SO_2 under controlled cuvette conditions in the field.

Recommendations

Field portable gas-exchange systems should be used to establish baseline data on the nature of photosynthetic capacity in the dominant forest tree species in California. These data will be of critical importance in assessing the mechanisms of impact of pollutant-induced changes in such capacities which might occur in the future. Thus the impact of change in nitrogen availability, with possible effects on photosynthetic enzymes, could be separated from effects of gaseous pollutants or magnesium availability on light harvesting pigments and from changes in stomatal sensitivity. A field program of experimental studies manipulating fumigant levels of ozone, analagous to the design described by Atkinson et al. (1986), would be particularly valuable in providing a mechanistic understanding to how this oxidant pollutant might affect photosynthetic capacity. Physiological models based on such a study would provide the basis of projecting the possible effects of increasing pollution levels in forest vigor.

CHLOROPHYLL FLUORECENCE MEASUREMENTS

Background

It is well established that chlorophyll fluorescence serves as an intrinsic indicator of the photosynthetic reactions in the chloroplasts of green plant. The biochemical relationship beween chlorophyll fluorescence and the mechanisms of photosynthesis have been the subject of physiological research for more than half a century since Kautsky discovered that fluorescence intensity in green leaves displays characteristic changes upon illumination (Kautsky and Hirsch 1931). While past studies utilizing chlorophyll fluorescence have largely been oriented toward biophysical research on the primary pathways of the photosynthetic process, there are now obvious applications of the Kautsky effect to studies of whole plant stress physiology. Pollutant-induced problems of forest decline provide an important potential application of such techniques.

The thylakoid membranes of green plant chloroplasts contain three major types of protein comlexes. These are the light harvesting complex (LHC) or chlorophyll _a_/chlorophyll _b_ protein complex, the photosystem antenna complex I (PS I), and the photosystem II antenna complex (PS II). Proper functioning of the overall photosynthetic process requires balanced excitation of the two photosystems brought about by appropriate regulation of the LHC with the two photosystems (Bennett et al. 1980) Chlorophyll fluorescence originates from Chl _a_ II in photosystem II. Hence, changes in fluorescence yield primarily reflect properties of excitation and energy conversion at photosystem II. In comparison to the response of a control leaf or needle or standard conditions, stress-induced changes in the properties of the photosynthetic apparatus will be reflected in corresponding changes in the fluorescence induction kinetics (Schreiber and Bilger 1987, Krause and Weiss 1984). Analyses of such data can yield important data on the site and extent of stress-induced damage.

There are a wide range of practical applications for chlorophyll florescence measurements in field studies of stress physiology. The application of this methodology to field studies of tree vigor should provide a means to differentiate between the relative contributions of various stress factors which may be limiting photosynthetic capacity. In this regard, fluorescence studies are highly complementary to data collected by gas exchange systems. While the latter provides quantitative measurement of absolute rates of photosynthesis, fluorescence provides a quick means of comparing relative rates and provides information on specific steps limiting the overall process. In this way it may be possible to detect the difference between direct pollutant effects on the photosynthetic mechanisms and indirect stress effects induced by drought, heat stress, or photoinhibition. Fluorescence studies, furthermore, have demonstrated that stress-induced decreases in photochemical quenching and an increase in energy dependent quenching can be measured before there is any observable reduction in photosynthetic capacity, suggesting that Calvin cycle reactions (or possibly ATp-ase) are affected before any damage at the level of the primary reactions (Schreiber and Bilger 1987). Thus early conditions of "pre-stress" can be potentially measured before such effects become irreversible.

Field studies of chlorophyll fluorescence measurements have been pioneered by plant physiologists at the Botanisches Institut of the Universität Würzburg in Würzburg, West Germany. A new measuring system is now available which allows field monitoring of fluorescence in full sunlight under field conditions, and permits a simple analysis of the complex data contained in the fluorescence kinetics (Schreiber 1983, Renger and Schreiber 1986, Schreiber 1986). Extensive studies are now underway in West Germany by several research groups applying measurements of chlorophyll fluorescence to studies of forest decline.

Recommendations

Field measurements of chlorophyll fluorescence in foliage of the dominant forest trees in California could provide a significant component of physiological measurements of stress response. An appropriate design of season measurements could provide an important means to differentiate specific steps in the phtosynthetic process which might be limiting photosynthetic capacity. Since many of the hypothesized effects of atmospheric pollution on forest decline involve secondary effects which influence the tolerance of affected trees to natural stresses in their physical and biotic environments, field surveys using currently available fluorescence instrumentation could document spatial and temporal changes in these limiting factors. Interactions with German scientists working actively on this subject would be very useful.

STABLE ISOTOPE STUDIES

Nitrogen isotopes

As described in the beginning of this paper, there are reasons to believe that some effects of air pollution on forest trees may be a function of the consequences of nitrogen deposition. Unfortunately, there are few data to support hypotheses on the fate of nitrogen species deposited on the surfaces of foliage. Considerable amounts of nitrogen deposited on leaf surfaces by dry deposition (Lindberg et al. 1986) is likely washed off by ensuing rain. Plants, however, may absorb nitrogen directly through their foliar surfaces. While we have very little understanding of the magnitude of such fluxes, ^{15}N studies could provide an experimental approach to questions of foliar absorption of nitrogen. Winner et al. (1987) suggest four approaches to investigate possible pathways for such a flux:

a) <u>Absorption of gaseous nitrogen via stomata.</u> Potentially phytotoxic nitrogenous gases formed by water droplets on leaf surfaces could diffuse through stomata. This mechanism of uptake may be particularly important in conifers where dew or fog may collect on the smooth wax ridges along both sides of the stomatal fields. Solutions labeled with ^{15}N can be applied to leaves of differing stomatal aperature to quantify rates of gaseous uptake of nitrogen.

b) <u>Cuticular conductance of nitrogenous compounds.</u> Rates can be calculated by placement of labeled solutions with ^{15}N on leaves or needles with closed stomata.

c) <u>Role of solution pH on the cuticular conductance of nitrogen.</u> Interactive effects of acid deposition and foliar absorption of nitrogen can be examined by varying the pH of ^{15}N solutions used, as above. Reversibility of pH effects can be included in an experimental design.

d) Transport of absorbed nitrogen within a plant. Prolonged exposures of foliage to labelled nitrogen solutions should allow measurements to be made of patterns and magnitudes of nitrogen translocation. Such analyses, expanded to soils and litter, would help identify sinks for translocated nitrogen.

Sulfur isotopes

Stable isotope ratios of sulfur have been shown to be invaluable markers to quantify the emission of sulfur from anthropogenic sources, the distribution of such sulfur within ecosystems, and the uptake of such sulfur by vegetation (Krouse 1977, 1980, 1987, Winner et al. 1981). With limited problems of SO_2 pollution in California, I will not discuss these applications here.

Carbon Isotopes

Water use efficiency (WUE) is typically expressed as either the rate of net CO_2 uptake per unit transpiration (mol CO_2 mol H_2O^{-1}) or the ratio of dry matter accumulation to transpiration (gDM g H_2O^{-1}) measured at intervals from several days to several months. The former is an instantaneous measure derived from gas exchange measurements of photosynthetic tissue and the latter is a time-integrated measure that can be determined for plants in containers as well as in natural environments. As such, these two indexes of WUE represent a potential resource use efficiency in the case of instantaneous WUE and a realized resource use efficiency in the case of time-integrated whole plant WUE. Extrapolation from gas exchange measurements of WUE to WUE based on biomass accumulation must take into account the carbon content of the dry matter, respiratory losses in both photosynthetic and nonphotosynthetic tissue, and the possibility of nocturnal transpiration (Fischer and Turner 1978). The WUE ratio, in and of itself, does not provide enough information to judge plant performance or competitiveness. The pitfalls involved in using maximization of WUE as a criterion for plant performance become evident from the simple observation that, for most plants, maximization of WUE would require the stomata to remain nearly closed all of the time (Cowan 1977). An extreme example is that of plants with crassulacean acid metabolism, which have some of the highest WUE's measured, but have distinctly low competitive ability under conditions in which water becomes less limiting because their high WUE is achieved through a restriction of carbon gaining capacity. In C_4 plants, however, a system has evolved which enhances both carbon gaining capacity and WUE in comparison with C_3 plants.

Water use efficiency is in part controlled by stomatal movements and Cowan (1977) and Cowan and Farquhar (1977) have presented a theory describing optimization of gas exchange by stomata. According to the theory the optimal behavior criterion is the maximization of carbon gain for a given amount of transpiration. This would be accomplished by maintaining the ratio of the sensitivities of assimilation (A) and transpiration rate (E) to changes in stomatal conductance ($A/ g/ E/ g = A/ E$) constant during a specified time interval. The magnitude of this gain ratio is proposed to depend on the amount of water available to a plant (Cowan 1982). It should be noted that this criterion is quite different from maximization of WUE.

In view of the fact that WUE within growth form and photosynthetic pathway types tends to be similar (Fischer and Turner 1978, Larcher 1980), it would be informative to know its components, that is, whether a given WUE is achieved at the expense of carbon gain or by high photosynthetic capacity with accompanying high water use. This sort of detailed knowledge of WUE components is necessary for interpretation of WUE in relation to aspects of ecosystem function such as partitioning of resource use and competitive interaction. A potential disadvantage of tissue $\delta^{13}C$ values as indicators of time-integrated WUE is that only the ratio and not its components is measured, unlike more conventional methods such as gas exchange in which the ratio is calculated from its components. This disadvantage can be largely overcome through initial gas exchange calibration measurements for each species. These should result in the ability to estimate Adt from measurements of tissue $\delta^{13}C$ and nitrogen content. The latter value for most species is strongly correlated with photosynthetic capacity.

Preliminary studies by several research groups outside of California have established that carbon isotope measurements, in their reflection of elements of stomatal control, can be used to predict potential susceptibility to air pollution damage for individuals within a species. These data have profound implications for studies of pollution effects on California forest species.

Stable isotope studies are now offering exciting new possibilities for investigations of integrated physiological response in plants. This subject is the topic of chapter by Waring in this workshop where it will be discussed in greater detail. The examples described above are but a few of a great many possible avenues of productive research relevant to problems of forest vigor in California.

ACKNOWLEDGEMENTS

Background studies for this chapter were based on research supported by the California Air Resources Board, the Environmental Protection Agency through the National Center for Intermedia Transport Research at UCLA and the Ecological Research Division of the Office of Health and Environmental Research, U.S. Department of Energy.

LITERATURE CITED

Atkinson, C.J., W.E. Winner, and H.A. Mooney. 1986. A field portable gas-exchange system for measuring carbon dioxide and water vapor exchange rates of leaves during fumigation with SO_2. Plant Cell Envir. 9:711-719.

Bennett, J., K.E. Steinback, and C.J. Arntzen. 1980. Chloroplast phosphoproteins: regulation of excitation energy transfer by phosphorylation of the thylakoid membrane polypeptides. Proc. Nat. Acad. Sci. 77:5253-5257.

Bondietti, E.A., F.O. Hoffman, and I.L. Larsen. 1984. Air-to-vegetation transfer rates of natural submicron aerosols. J. Environ. Radioactivity 1:5-27.

Chamberlain, A.C. 1975. The movement of particles in plant communities. In: J.L. Monteith, ed., "Vegetation and the Atmosphere. Vol. 1. Principles," pp. 155-205. Academic Press, New York.

Chamberlain, A.C. and P. Little. 1981. Transport and capture of particles by vegetation. In: J. Grace, E.D. Ford and P.G. Jarvis, eds., "Plants and Their Atmospheric Environments," pp. 147-173. Blackwell Scientific Publications, Oxford.

Cowan, I.R. 1977. Stomatal behavior and environment. Adv. Bot. Res. 4:117-227.

Cowan, I.R. 1982. Regulation of water use in relation to carbon gain in higher plants. In: Lange, O.L., P.S. Nobel, C.B. Osmond and H. Ziegler, eds., "Encyclopedia of Plant Physiology, New Series, Vol. 12B," pp. 587-613. Springer-Verlag, New York.

Cowan, I.R. and G.D. Farquhar. 1977. Stomatal function in relation to leaf metabolism and environment. Symp. Soc. Exp. Biol. 31:471-505.

Droppo, J.G. 1980. Experimental techniques for dry-deposition measurements. In: D.S. Shriner, C.R. Richmond and S.E. Lindberg, eds., "Atmospheric Sulfur Deposition," pp. 153-162. Ann Arbor Press, Ann Arbor, Michigan.

Fischer, R.A. and N.C. Turner. 1978. Plant productivity in the arid and semiarid zones. Ann. Rev. Plant Physiol. 29:277-317.

Friedland, A.J., R.A. Gregory, L. Karenlampi and A.H. Johnson. 1984. Winter damage to foliage as a factor in red spruce decline. Can. J. For. Res. 14:963-965.

Garland, J.A. 1978. Dry and wet removal of sulfur from the atmosphere. Atmos. Environ. 12:349-362.

Gibson, J.H. et al. 1986. "Acid Deposition: Long Term Trends." National Academy Press, Washington, D.C.

Guderian, R. (ed.) 1985. "Air Pollution by Photochemical Oxidants: Formation, Transport, Control, and Effects on Plants." Springer-Verlag, Berlin.

Hicks, B.B. and M.L. Wesley. 1980. Turbulent transfer processes to a surface and interactions with vegetation. In: D.S. Shriner, C.R. Richmond and S.E. Lindberg, eds., "Atmospheric Sulfur Deposition," pp. 199-208. Ann Arbor Press, Ann Arbor, Michigan.

Hosker, R.P. and S.E. Lindberg. 1982. Review: Atmospheric deposition and plant assimilation of gases and particles. Atm. Envir. 16:988-920.

Hutchinson, T.C., and M. Havas. 1980. "Effects of Acid Precipitation on Terrestrial Ecosystems." pp. 363-374. Plenum Press, N.Y.

Jacobson, J.S. 1980. Experimental studies on the phytotoxicity of acidic precipitation: the United States experience. In: T.C. Hutchinson and M. Havas, eds, "Effects of Acid Precipitation on Terrestrial Ecosystems." pp. 151-160. Plenum Press, N.Y.

Kautsky, H. and A. Hirsch. 1931. Neue Versuche Zur Kohlenstoffassimilation. Naturwissenschaften 19:964.

Klein, R.M. 1985. Effect of acidity and metal ions on water movement through red spruce. In: Adams, D.D. and W.P. Page, eds, "Acid Deposition: Environmental, Economic and Policy Issues," pp. 303-322. Plenum Press, New York.

Krause, G.H., and E. Weiss. 1984. Chlorophyll fluorescence as a tool in plant physiology. II. Interpretation of fluorescence signals. Photosynthetic Research 5:139-157.

Krouse, H.R. 1977. Sulfur isotope abundances elucidate uptake of atmospheric sulfur emissions by vegetation. Nature 265:45-46.

Krouse, H.R. 1980. Sulfur isotopes in our environment. In: Fritz, P. and J.C. Fontes, eds, "Handbook of Environmental Isotope Geochemistry," pp. 435-471. Elsevier, New York.

Krouse, H.R. 1987. Sulfur isotope studies of the pedosphere and biosphere. In: Rundel, P.W., J.R. Ehleringer, and K.A. Nagy, eds, "Stable Isotopes in Ecological Research." Springer-Verlag, New York (in press).

Larcher, W. 1980. Physiological Plant Ecology. Springer-Verlag, New York, 2nd ed.

Letig, F.T., R.P. Guries, and B.A. Bonefield. 1983. The relation of growth to heterozygozity in pitch pine. Evolution 37:1227-1238.

Lindberg, S.E., G.M. Lovett, D.D. Richter, and D.W. Johnson. 1986. Atmospheric deposition and canopy interactions of major ions in a forest. Science 231:141-145.

Linthurst, R.A. (ed.). 1984. "Direct and Indirect Effects of Acidic Deposition on Vegetation." Butterworth, Boston.

Miller, P.R. (tech. coord.). 1980. "Proceedings of symposium on effects of air pollutants on mediterranean and temperate forest ecosystems." USDA Forest Service Gen. Tech. Report PSW-43. pp. 256.

Mitton, J.B., and M.C. Grant. 1984. Associations among protein heterozygozity, growth rate, and developmental homeostasis. Ann. Rev. Ecol. Syst. 15:479-499.

Mitton, J.B., P. Knowles, K.B. Sturgeon, Y.B. Linhart, and M. Davis. 1981. Associations between heterozygozity and growth rate variables in three western forest trees. In: M.T. Conkle, ed., "Proc. Symp. Isozymes North Am. For. Trees and Forest Insects." pp. 27-34. USDA Forest Service Gen. Tech. Rep. PSW-48.

Mooney, H.A., E.J. Pell, and W.E. Winner. 1986. Predicting plant response to multiple stresses. Unpublished research proposal.

Mudd, J.B., and T.T. Kozlowski. 1975. "Responses of Plants to Air Pollution." Academic Press, N.Y. 383 pp.

Prinz, B., G.H.M. Krause, and K.D. Jung. 1987. Responses of German forests in recent years: cause for concern elsewhere? In: "Effects of Acid Deposition and Air Pollutants." Springer-Verlag, Berlin (in press).

Reese, G.A., R.L. Bayn, and N.E. West. 1980. Evaluation of double-sampling estimates of subalpine herbage production. J. Range Management 33:300-306.

Renger, G. and U. Schreiber. 1986. Practical applications of fluorescence methods to algae and higher plant research. In: Govindjee, A.J. and D.C. Fork, eds., "Light Emission by Plants and Bacteria." Academic Press, New York.

Russell, I.J., C.E. Choquette, S. Fang, W.D. Dundulis, A.A. Pao, and A.P. Pszenny. 1981. Forest vegetation as a sink for atmospheric particulates: quantitative studies in rain and dry deposition. J. Geophys. Res. 86:5247-5363.

Schmel, G.D. 1980. Particle and gas dry deposition--a review. Atmos. Envir. 14:938-1011.

Schreiber, U. 1983. Chlorophyll fluorescence yield changes as a tool in plant physiology. I. The measuring system. Photosynthetic Research 4:361-373.

Schreiber, U. 1986. Detection of rapid induction kinetics with a new type of high frequency-modulated chlorophyll fluorometer. Photosynthetic Research (in press).

Schreiber, U. and W. Bilger. 1987. Rapid assessment of stress effects on plant leaves by chlorophyll fluorescence measurements. In: Tenhunen, J., F. Catarino, O.L. Lange and W.C. Oechel, eds., "Plant Response to Stress--functional Analysis in Mediterranean Ecosystems." Springer-Verlag, Berlin, (in press).

Sievering, H. 1982. Profile measurements of particle dry deposition velocity at an air/land interface. Atmos. Environ. 16:301-306.

Smith, W.H. 1981. "Air Pollution and Forests." Springer-Verlag, New York.

Ulrich, B., and J. Pankrath (eds.). 1983. "Effects of Accumulation of Air Pollutants in Forest Ecosystems." D. Reidel, Dodrecht, Holland.

Wedding, J.B., R.W. Carlson, J.S. Stukel, and F.A. Bazzaz. 1977. Aerosol deposition on plant leaves. Water, Air, Soil Pollut. 7:545-550.

Winner, W.E., V.S. Berg, and P.J. Langston-Unkefer. 1987. The use of stable sulfur and nitrogen isotopes in studies of plant responses to air pollution. In: Rundel, P.W., J.R. Ehleringer, and K.A. Nagy, eds., "Stable Isotopes in Ecological Research." Springer-Verlag, New York (in press).

Winner, W.E., H.A. Mooney, and R.A. Goldstein (eds.). 1986. "Sulfur Dioxide and Vegetation." Stanford University Press, Stanford.

Winner, W.E., C.L. Smith, G.W. Koch, H.A. Mooney, J.D. Bewley, and H.R. Krouse. 1981. Rates of emission of H_2S from plants and patterns of stable sulfur isotopes fractionation. Nature 289:672-673.

Zoettl, H.W. 1987. Hypothesis of forest decline. In: "Effects of Acid Deposition and Air Pollutants." Springer-Verlag, Berlin (in press).

ASSESSMENT OF THE INFLUENCE OF ATMOSPHERIC DEPOSITION ON FOREST ECOSYSTEMS: THE CHALLENGE OF DIFFERENTIAL EFFECTS OF LOCAL, REGIONAL AND GLOBAL SCALE POLLUTANTS

William H. Smith
Professor of Forest Biology
School of Forestry and Environmental Studies
Yale University
February, 1987

INTRODUCTION

One of the dictionary definitions of assessment, and the one relevant to the theme of this manuscript, is the "determination of the amount of damage." Analysis of the amount of damage currently imposed by the deposit of atmospheric chemicals onto trees and forest systems is a contemporary science topic and societal issue of great importance and visibility. These latter characteristics have led to much writing, debate, discussion and disagreement on specific effects of specific atmospheric deposits on specific forests!

There is, however, general agreement that forest trees generally follow the rules of toxicology and exhibit differential response in accordance with dose. This suggests that responses will be dose dependent but may be very different depending on the duration of exposure, pattern of exposure and concentration of the pollutant. As a result, no single assessment strategy will adequately inventory responses to all doses. Assessment is further complicated by the need to evaluate very different forest responses and the need to partition the relative importance of air pollution stress from other forest stresses also capable of causing similar responses. Consideration of effects caused by general dose categories is facilitated by examination of responses associated with the high, intermediate and low doses represented by local, regional and global scale pollutants. The objective of this paper will be to provide overview perspective on atmospheric deposition and forest systems at these different scales and to propose a strategy for extended term assessment.

Local, regional and global-scale air pollutants

Local

During the first two thirds of the twentieth century, research and regulatory efforts were focused on local air pollutants and acute vegetative effects. Pollutants of primary concern were sulfur dioxide, particulate and gaseous fluoride compounds and numerous heavy metals such as lead, copper, and zinc. Occasional interest was expressed in other inorganic gases including ammonia, hydrogen sulfide and chloride, and chlorine. The sources of these pollutants were and are typically discrete and stationary facilities for: energy production, for example, fossil-fuel electric generating plants, gas purification plants; metal related industries, for example, copper, nickel, lead, zinc or iron smelters, aluminum production plants; and diverse other industries, for example, cement plants, chemical and fertilizer plants and pulp mills.

It is appropriate for us to consider the above pollutants as local scale because forest areas directly affected by these facilities are typically confined to a zone of a few km immediately surrounding the plant and for a distance of several to tens of km downwind. The dimensions of the surrounding and downwind zones of influence are variable and primarily controlled by source strength of the effluent, local meteorology, regional topography and susceptibility of vegetation. In any case, acute forest influences have typically been confined to areas generally less than a thousand hectares.

Regional

During the past three decades we have become increasingly aware of regional-scale air pollutants. The regional designation is applied because these contaminants may affect forests tens, hundreds, or even thousands of kilometers from their site of origin. The regional air pollutants of greatest documented or potential influence for forests include: oxidants, most importantly ozone; trace metals, most importantly heavy metals - e.g. cadmium, iron, copper, lead, manganese, chromium, mercury, molybdenum, nickel, thallium, vanadium, zinc; and acid deposition, most importantly the wet and dry deposition of sulfuric and nitric acids. Ozone, sulfuric and nitric acids are termed secondary air pollutants because they are synthesized in the atmosphere rather than released directly into the atmosphere. Precursor chemicals, released directly into the atmosphere, which cause secondary pollutant formation, include hydrocarbons and nitrogen oxides in the case of ozone, and sulfur dioxide and nitrogen oxides in the case of sulfuric and nitric acid. The combustion of fossil fuels for energy production releases hydrocarbons and sulfur dioxide. The heat of combustion causes nitrogen and oxygen to react and form nitrogen oxides. Many combustion activities generate small particles (approximately 0.1

– 5 µm diameter). Those activities associated with energy combustion (particularly coal burning) can preferentially contaminate these small particles with trace metals. Because the formation of secondary air pollutants may occur over tens or hundreds of km from the site of precursor release, and because small particles may remain airborne for days or weeks, these pollutants may be transported 100 to more than 1000 km from their origin. Eventual wet and dry deposition of the pollutants onto lakes, fields, or forests occurs over large rather than small areas.

The U.S. Environmental Protection Agency and the U.S. Department of Agriculture, Forest Service established a network of air monitoring stations to measure ozone concentrations in remote areas of National Forests. Analysis of selected high ozone events during 1979 suggested that long-range transport of air masses contaminated by urban centers contributed to peak concentrations at remote sites (Evans et al. 1983). In a study of rural ozone episodes in the upper-midwest, Pratt et al. (1983) presented evidence that ozone and precursors were transported 275 km from Minneapolis-St. Paul. Studies of trace metal concentrations, in the atmosphere in remote northern and southern hemispheric sites revealed that the natural sources include the oceans and the weathering of the earth's crust, while the major anthropogenic source is particulate air pollution (USEPA 1983a). Murozumi et al. (1969) showed that long range transport of lead particles from automobiles significantly polluted polar glaciers. We estimated the annual lead deposition on a remote northern hardwood forest in New Hampshire to be as high as 266 g per hectare in 1978. This caused lead contamination of the forest floor 5-10 times greater than the estimated pre-industrial concentration (Smith and Siccama 1981).

Evidence is available; satellites, surface deposition of aerosol sulfate and reduced visibility (Chung 1978, Tong et al. 1976, Wolff et al. 1981), for long-range transport of acidifying pollutants from numerous sources. During the winter, approximately 20 percent of the emissions from tall power plant stacks in northeastern United States may remain elevated and relatively coherent for more than a day and 500 km (USEPA 1983b).

The long distance transport of regional pollutants means they may have interstate, international and even intercontinental significance. It means further that the forests subject to their deposition exceed tens of thousands of km^2.

Global

In the past 25 years, we have become concerned with a third scale of air pollution--global. Global pollutants affect the entire atmosphere of the earth. Two global air pollutants of special note include carbon dioxide and halocarbons.

Careful monitoring of carbon dioxide during the past two decades in Hawaii, Alaska, New York, Sweden, Austria and the South Pole has firmly established that carbon dioxide is steadily increasing in the global atmosphere. This increase is due to anthropogenic activities including fossil fuel combustion. It may also be caused by altered land use management, such as, forest destruction in the tropics. The atmospheric carbon dioxide concentration has been estimated to have been approximately 290 ppm (5.2×10^4 µg m^{-3}) in the middle of the nineteenth century. Today, the carbon dioxide concentration approximates 340 ppm (6.1×10^5 $\mu g\ m^{-3}$) and is increasing very approximately about one ppm ($1.8\mu \times 10^3$ $\mu g\ m^{-3}$) per year. In the year 2020, if the increasing rate continues, the carbon dioxide amount in the global atmosphere may be nearly two times the present value (Holdgate et al. 1982).

Naturally occurring stratospheric ozone is important because it screens the earth from biologically damaging ultraviolet radiation -- light with wavelengths between 290 and 320 nanometers -- released by the sun. Halocarbons released by humans can deplete the natural ozone layer surrounding the earth. In summary, halocarbon molecules, for example chlorofluoromethanes, released by various human activities, are slowly transported through the troposphere. They pass through the tropopause and lower stratosphere and are decomposed in the mid- to upper-atmosphere. Free chlorine, resulting from decomposition, causes a rapid, catalytic destruction of ozone. In 1979, the National Academy of Sciences estimated that release of halocarbons to the atmosphere, at rates inferred for 1977, would eventually deplete stratospheric ozone 5 to 28 percent, most probably 17 percent (NAS 1979). In 1982, the National Academy revised its previous estimate and suggested a depletion of from 5 to 9 percent (NAS 1982c).

AFFECT OF LOCAL-SCALE, REGIONAL-SCALE AND GLOBAL-SCALE AIR POLLUTION ON FOREST ECOSYSTEMS

Local

High deposition of local air pollutants has caused well documented forest destruction. High sulfur dioxide or fluoride doses, severely injure or kill forest trees. The ecosystems, of which the trees are a part, are simplified, lose nutrients, sustain soil erosion, have microclimates and hydrologic patterns altered and ultimately they are destroyed or converted to more resistant seral stages. Miller and McBride (1975) have reviewed the studies of forests destroyed by local air pollution. Early in this century, it was clearly documented in numerous locations throughout North America that sulfur dioxide and trace metal pollution destroyed forests surrounding metal smelting facilities. Smelting centered in Ducktown, Tennessee devastated the southern hardwood forest over 27 km^2 (10.5 mi^2) surrounding the plant, converted an additional 68 km^2 (17,000A) to grassland and created a 120 km^2 (30,000A) transition zone with altered species composition. Smelters in the Sudbury, Ontario, Canada area have caused simplification of the surrounding mixed boreal forest and have caused eastern white pine mortality in a 1865 km^2 (720 mi^2) zone to the northeast.

Aluminum reduction plants have also caused local forest destruction. In Montana, fluoride pollution killed or severely injured ponderosa pine and lodgepole pine on 8 km^2 (2000A) surrounding a plant. In Washington, ponderosa pine mortality and morbidity resulted over a 130 km^2 (50 mi^2) area in the vicinity of an aluminum plant.

Local pollution has caused extensive forest mortality throughout Europe. Examples are in Austria, Germany, Hungary, Norway, Poland and Sweden. Industrial operations along the northern border of Czechoslovakia have caused extensive forest destruction. In all of these cases, pollutant doses have been high and assessment largely based on visible symptom expression and inventory.

Regional

Deposition of regional pollutants subject forests to different perturbations thAn local pollutants because the doses are less. Rather than severe tree morbidity or mortality with dramatic symptoms, regional pollutants subtly change tree metabolism and ecosystem processes. Smith (1981) has provided a comprehensive review of subtle air pollution forest stress.

Regional air contaminants may influence reproductive processes, nutrient uptake or retention, metabolic rates (especially photosynthesis and respiration), and insect pest and pathogen interactions of individual trees. At the ecosystem level, regional air pollutants may influence nutrient cycling, population dynamics of arthropod or microbial species, succession, species composition, and biomass production. In the instance of high-dose local-scale pollution, the symptoms are typically acute, dramatic and obvious (severe disease, mortality, forest simplification). In the case of lower-dose regional-scale pollution, the symptoms are typically not visible (at least initially), undramatic and not easily measured. The integration of regional pollutant stresses is slower growth, altered competitive abilities and changed susceptibility to pests. Ecosystem symptoms may include altered rates of succession, changed species composition and biomass production. Symptom development is, of course, much slower at the regional scale. Visible symptom expression is not a useful assessment strategy. Evidence of the relative importance of regional pollutants is variable, caused in part by the length of time that has been devoted to the study of individual pollutants and in part by the subtleness and complexity of the pollutant interactions. The toxicity of trace metals has been studied for approximately 65 years, of ozone approximately 30 years and of acid deposition approximately 15 years.

Global

Increasing carbon dioxide concentration and decreasing stratospheric ozone concentration of the atmosphere may alter global radiation fluxes. Presumably a primary result of more carbon dioxide in the air will be warming. While incoming solar radiation is not absorbed by carbon dioxide, portions of infrared radiation from earth to space are. Over time, the earth would become warmer. While the forces controlling global temperature are varied and complex, the increase of 0.5°C since the mid-1800s is generally agreed to be at least partially caused by increased carbon dioxide. By 2000 it may increase an additional 0.5°C. Numerous models advanced to estimate the average global warming per doubling of carbon dioxide project 0.7 to 9.6°C. Natural impacts on climate, such as solar variability, remain important and of unclear relationship to anthropogenic causes. A mean global average surface warming, however, of 3 ± 1.5°C in the next century appears reasonable (National Academy of Sciences 1982 a, b).

The consequences of a warmer global climate, with even a very modest temperature increase, on the development of forest ecosystems, could be profound. Warming, with increased carbon dioxide in the atmosphere, might enhance forest growth. Manabe and Stouffer (1980) have estimated that a doubling of atmospheric carbon dioxide would cause a 3°C warming at the U.S.-Canadian border, while Kellogg (1977) has suggested that a rise of 1°C in mean summer temperature extends the growing season by approximately 10 days. Other changes associated with global warming, however, may restrict forest growth. Physiological processes of plants, especially photosynthesis, transpiration, respiration and reproduction are sensitive to temperature. With warming, respiration and decompositon may increase faster than photosynthesis. Transpiration and evaporation increases may enhance stress on drier sites. Reproduction may be altered by changes in dynamics of pollinating insects, changes in flower, fruit or seed set, or changes in seedling production and survival. The geographic or host ranges of exotic microbial pathogens or insect pests may expand. Previously innocuous endemic microbes or insects may be elevated to important pest status following climatic warming. Precipitation changes are associated with global warming, and certain areas will receive more and others less. Those areas receiving less precipitation will also experience increased evaporation and transpiration. Waggoner (1984) has estimated that the projected change in weather by the year 2000, caused by increased atmospheric carbon dioxide, will cause moderate decreases of 2-12 percent in yield of wheat, corn and soybeans in the American grain belt due to increased dryness. While agriculturists may be able to adopt new crop varieties to a drier climate, forests cannot be similarly manipulated. Increased drought stress over widespread forest areas would be expected to initiate new rounds of progressive tree deterioration termed dieback/decline disease. Drought is the most common and important initiator of general forest tree decline. Forest stresses caused by other air pollutants and other agents of stress must be evaluated against this background of forest change caused by climatic warming.

A serious consequence of anthropogenic release of halocarbons to the atmosphere is the depletion of naturally occurring stratospheric ozone. Some reduction in halocarbon release has been achieved in the United States and a few other countries. Immediate termination of all release worldwide, however, would still leave the world with important stratospheric ozone reductions during the next decade. Reduced upper-air ozone would increase ultraviolet radiation reaching the surface of the earth. Current understanding does not allow an inventory of the impacts of increased ultraviolet radiation on forests. Vegetation can acclimatize to changes in ultraviolet radiation. Higher plants also vary substantially in resistance to ultraviolet radiation. Because some plants are sensitive, however, reductions in biomass production and/or competitive strengths may be altered by changes in short-wave radiation flux at the surface of the earth (Caldwell 1981). Studies of more than 100 agricultural species showed that increased ultraviolet exposure reduces plant dry weight and changes the proportion of root, shoot and leaf tissue. Studies of more than 60 aquatic organisms showed that many were quite sensitive to current levels of ultraviolet radiation at the water surface (Maugh 1980). Chlorofluorocarbons can also contribute to global warming in a manner similar to carbon dioxide.

GLOBAL AND REGIONAL AIR POLLUTANTS ARE THE MOST IMPORTANT CONCERN.

The effects of local air contaminants on forests have stabilized in the vicinity of existing point-sources of air pollutants. In numerous cases improvements have been achieved. In the case of sulfur dioxide, increasing stack heights and use of scrubbers have reduced ground level concentrations of sulfur dioxide. New industries and electrical plants in the U.S. can employ the best available air quality technology.

Global- and regional-scale air pollutants exhibit both increasing trends and known and probable effects on forest ecosystems over large portions of the temperate region. The integration of stresses imposed by regional pollutants has the potential to cause growth reductions in some forest species and, ultimately, dieback/decline symptoms in susceptible tree species at ambient levels. At the ecosystem level this has or will cause changes in species composition and increases or decreases in biomass production depending on the specific ecosystem. Documentations of decreased tree growth and increased decline symptoms solely or primarily due to air quality in the field are very limited because the changes are subtle, not continuous but patchwork in character, and extremely difficult to separate from other factors that control tree growth (eg. age, stand structure, competition, moisture, temperature, nutrients, insects, pathogens) and that induce dieback/decline symptoms (eg. drought, other climatic stresses, insects, pathogens). In addition, species composition and patterns of forest succession are regulated by numerous determinants (eg. vegetative site alterations, plant species interactions, insect/pathogen activities, windstorms, fires and human cultural activities) and forest ecosystem production is influenced by several variables (system age, competition, species composition, moisture, temperature, nutrients, insects, pathogens).

A review of the current evidence available, to support the importance of air pollution induced forest change, has been provided by Fraser et al. (1985), Kozlowski and Constantinidou (1986), McLaughlin (1985) and Smith (1981). The comprehensive study of oxidant pollution in portions of the San Bernardino National Forest, California demonstrated air pollution effects on forest growth and succession (Miller et al. 1982). Additional evidence of reduced forest growth imposed by oxidant pollution in the west, mid-west and east has been provided (USEPA 1983a). For various forest ecosytems we are at, or near, the threshold of trace metal impact on nutrient cycling processes. Lead will continue to accumulate in forest floors as long as it is released into the atmosphere (USEPA 1983a). Although adverse effects on forest ecosystems from acid deposition have not been conclusively proven by existing field evidence, we cannot conclude that adverse effects are not occurring. Presently, tree mortality and tree morbidity and growth rate reductions in European and North American regions do occur where regional air pollution, including acid deposition, is generally high. Temporal and spatial correlations between wet acidic deposition and forest tree growth rates has been provided. Numerous hypotheses for adverse forest effects from acid deposition, worthy of testing, have been proposed (Linthurst 1984, SAF 1984). Under natural conditions, forest ecosystems are exposed to multiple air pollutants simultaneously or sequentially and interactive and accumulative influences are important. It is inappropriate to consider the effects of any regional pollutant on forests in isolation. The potential stresses imposed by regional-scale air pollutants must be viewed against the background of uncertainty associated with the changes in radiation balances associated with global scale air contaminants. The growth reductions and decline symptoms of the forests of the Federal Republic of Germany are dramatic and should warn all nations that the resiliency of forest ecosystems has limitations. Until the cause of this decline is more clearly understood, prudent natural resource science should not reject nor indict any single stress.

ASSESSMENT OF GLOBAL- AND REGIONAL- SCALE AIR POLLUTANT INFLUENCES ON FORESTS

Air pollution has been killing trees locally for centuries. We have been keenly aware of this in the United States for over 100 years. We now realize that in addition to mortality, global and regional air pollutants may be capable of causing alterations in species composition and growth-rate reductions in certain forest ecosystems over large areas and across national boundaries.

Assessment of these subtle influences cannot be based on visible symptom expression. It must be based on systematic monitoring of forest health and growth indices. Waring and Schlesinger (1985) have provided an excellent list of potentially useful forest ecosystem stress indicators (Table 1). Canopy leaf area and its duration of display is a very appropriate general index of forest ecosystem stress. Canopy quantity and quality is an indicator of productivity. Inventory techniques from the air (multispectral scanning, microwave transmission, radar, laser) and ground (correlations with stem diameter, sapwood cross-sectional area) for canopy leaf area are available. At a given site, detection of an increase in leaf area would suggest an improving environment, a decrease in leaf area would infer the system is under stress (Waring 1983). Baes and McLaughlin (1984) have proposed that trace metal analyses of tree rings can provide information on temporal changes in air pollutant deposition and tree health.

In addition to forest health assessment, systematic determinations must be made of the doses of air pollutants received by forests. This requires a rural air-quality monitoring network capable of measuring all important phytotoxic pollutants deposited by both wet and dry mechanisms.

Assessment of both forest health and atmospheric deposition would be most appropriately implimented by establishing a permanent plot network not unlike the Continuous Forest Inventory plots of the USDA Forest Service. Trends over time in both health and deposition would be regularly and continuously recorded.

A final component of the assessment program is research directed to understanding the mechanisms of low-dose influence on vegetative health imposed by air contaminants. This research program must be simultaneously conducted in managed environments (eg. laboratory and greenhouse chambers, open-top chambers, and other regulated environment facilities) and in natural environments (eg. field studies conducted in association with long-term ecosystem research areas, experimental forests of the USDA, national laboratory facilities or other sites presenting unique characteristics, ancillary data, security and long-term perspective).

Permanent assessment plots could be used to validate models developed in seedling/sapling studies. Stand-level models could be verified with permanent plot data.

CONCLUSIONS

Forests are variable in species, topography, elevation, soils and management. Air pollution deposition and influences are also variable and poorly documented in the field. Monitoring of species dynamics and productivity, necessary to detect effects of regional and global air pollutants, or any other environmental stress, are presently rarely available. Dendrochronological or other tree-ring analytical techniques are subject to enormous difficulty when they attempt to partition the relative importance of forces that may influence tree growth. Growth is regulated by precipitation, temperature, length of growing season, frost, drought, by developmental processes such as succession and competition, and by stochastic events such as

Table 1. Forest Ecosystem Stress Indicators

Indication	Examples
Canopy limitation	Maximum leaf area index
	Duration of leaf display
Production limitation	Diameter growth and cell division
	Growth efficiency per unit leaf area
Susceptibility to insect and disease attack	Starch content of twigs and large roots
	Tannin and terpene content of tissues
	Growth efficiency per unit leaf area
Moisture limitations	Predawn water stress
	Noon leaf turgor
	Sapwood relative water content
	Stomatal closure
Nutrient limitations	Foliar nutrient content
	Foliar nutrient ratios
	Nutrient retranslocations
	Mineralization indices
Physical stress	Sapwood/diameter index
	Bole taper
	Symmetry of wood growth
	Leaf-edge tatter

Source: Waring and Schlesinger 1985.

insect outbreaks, disease epidemics, fire, windstorms and anthropogenic activities such as thinning, fertilization, harvesting and finally air quality.

For a long time, dieback and decline of specific forest species, somewhere in the temperate zone, has been common (Smith 1987). Age, climate, or biotic stress factors have frequently been judged to be the principal causes for declines. Again, however, it is difficult to assign responsibility for specific cause and effect. Trees are large and long-lived and their health integrates all the stresses to which they are exposed over time.

The risks associated with regional and global air pollution stress and temperate zone forest ecosystem health are high. The evidence available to describe the total boundaries of the problem for all pollutants is incomplete. There is significant uncertainty about specific effects on forests of regional and global air pollutants.

Individual forest tree processes at greatest risk from wide area air pollutant stress include: carbon allocation; especially foliar metabolism (photosynthesis and respiration and root metabolismµ reproductive physiology, pest (arthropod and microbial) interactions and growth. At the ecosystem level, processes at greatest risk from wide area air pollutant deposition include; nutrient cycling (especially mineralization and nutrient uptake processes), biomass production, and population dynamics of insect and microbial pests. Major structural changes may be caused in impacted forests over the long term due to alteration of species composition and patterns of succession.

The primary needs to enable a more complete understanding and assessment of air quality and forest quality include the following:

1. Complete monitoring of gas and particulate, wet and dry pollutant deposition in forest ecosystems.

2. Systematic monitoring of forest growth and health parameters on permanent plots over extended time.

3. Coordinated field, controlled environment and laboratory studies directed toward tree and ecosystem processes identified at risk using single pollutant and pollutant mixtures in realistic (ambient) dose patterns. Dose studies should also include levels above and below ambient in order to evaluate the importance of changes in air quality.

4. Modelling and systems analysis studies to extend experimental conclusions to larger forest areas.

   Implimentation of wide-area forest monitoring of any nature involves two challenges. First, detection of stress does not suggest cause. We are keenly aware that tree and forest health are controlled by many factors in addition to air quality. We desperately need procedures to partition the relative importance of influencing variables for a given site. Fortunately we are making research progress toward this resolution (Fritts and Stokes 1975, Waring 1985). The second challenge is to convince natural resource managers that the time and cost of systematic forest health monitoring is justified. I feel it is not only justified, but essential for intelligent decisions regarding regulation of regional and global air pollutants.

Literature Cited

Baes and McLaughlin. 1984. Trace elements in tree rings: Evidence of recent and historical air pollution. Science 224: 494-497.

Caldwell, M.M. 1981. Plant response to solar ultraviolet radiation. Chap. 6. Encyclopedia of Plant Physiology, New Series, 12A: 169-197.

Chung, Y.S. 1978. The distribution of atmospheric sulfates in Canada and its relationship to long-range transport of pollutants. Atmos. Environ. 12:1471-1480.

Evans, G., P. Finkelstein, B. Martin, N. Possiel and M. Graves. 1983. Ozone measurements from a network of remote sites. Jour. Air Pollu. Cont. Assoc. 33:291-296.

Fraser, G.A., W.E. Phillips, G.W. Lamble, G.D. Hogan and A.G. Teskey. 1985. The Potential Impact of the Long Range Transport of Air Pollutants on Canadian Forests. Information Report No. E-X-36. Economics Branch, Canadian Forestry Service, Ottawa, Ontario, 43 pp.

Fritts, H.C. and M.A. Stokes. 1975. A technique for examining non-climatic variation in widths of annual tree rings with special reference to air pollution. Tree-Ring Bull. 35:15-24.

Holdgate, M.W., M. Kassas and G.F. White. 1982. World environmental trends between 1972 and 1982. Environ. Conserva. 9:11-29.

Kellogg, W.W. 1977. Effects of human activities on global climate. Technical Note No. 156. WHO-No. 486. World Meteorol. Org., Geneva.

Kozlowski, T.T. and H.A. Constantinidou. 1986. Responses of woody plants to environmental pollution. Forestry Abstracts 47: 5-132.

Linthurst, R.A. (ed.) 1984. Direct and Indirect Effects of Acidic Deposition on Vegetation. Vol. 5. Acid Precipitation Series. J.I. Teasley, ed. Butterworth Publishers, Boston, 117 pp.

Manabe, S. and R.J. Stouffer. 1980. Sensitivity of a global climate model to an increase of CO_2 concentration in the atmosphere. Jour. Geophys. Res. 85:5529-5554.

Maugh, T.H. 1980. Ozone depletion would have dire effects. Science 207:394-395.

McLaughlin, S.B. 1985. Effects of air pollution on forests. A Critical Review. Jour. Air Pollu Control Assoc. 35: 512-534.

Miller, P.R., O.C. Taylor and R.G. Wilhour. 1982. Oxidant Air Pollution Effects on a Western Coniferous Forest Ecosystem. U.S. Environmental

Protection Agency, Publica. No. EPA-600/D-82-276. Corvallis, OR, 10 pp.

Miller, P.R. and J.R. McBride. 1975. Effects of air pollutants on forests. In, J.B. Mudd and T.T. Kozlowski, eds., Responses of Plants to Air Pollution. Academic Press, N.Y., pp. 195-235.

Murozumi, M. T. Chow and C. Patterson. 1969. Chemical concentrations of pollutant lead aerosols, terrestrial dusts and sea salts in Greenland and Antarctic snow strata. Geochim. Cosmochim. Acta 33:1247-1294.

National Academy of Sciences. 1979. Stratospheric Ozone Depletion by Halocarbons. National Academy of Science, Washington, D.C., 249 pp.

National Academy of Sciences. 1982a. Solar Variability, Weather, and Climate (Studies in Geophysics). ISBN No. 0-309-03284-9. National Academy Press, Washington, D.C., 120 pp.

National Academy of Sciences. 1982b. Carbon Dioxide and Climate: A Second Assessment. ISBN No. 0-309-03285-7. National Academy Press, Washington, D.C., 92 pp.

National Academy of Sciences. 1982c. Stratospheric Ozone Depletion by Halocarbons. National Academy of Science, Washington, D.C., pp.

Pratt, G.C., R.C. Hendrickson, B.I. Chevone, D.A. Christopherson, M.V. O'Brien, and S.V. Krupa. 1983. Ozone and oxides of nitrogen in the rural upper-midwestern U.S.A. Atmos. Environ. 17:2013-2023.

Smith, W.H. 1981. Air Pollution and Forests. Springer-Verlag, N.Y., 379 pp.

Smith, W.H. 1987. Future of the hardwood forest: Some problems with declines and air quality. Proceedings 6th Central Hardwood Forest Conference. University of Tennesses, Knoxville, TN (in press).

Smith, W.H. and T.G. Siccama. 1981. The Hubbard Brook Ecosystem Study: Biogeochemistry of lead in the northern hardwood forest. Jour. Environ. Qual. 10:323-333.

Society of American Foresters. 1984. Acid Deposition and Forest Ecosystems. Task Force on the Effects of Acid Deposition on Forest Ecosystems. Report prepared for the Society of American Foresters, Bethesda, MD, 51 pp.

Tong, E.Y., G.M. Hidy, T.F. Lavery and F. Berlandi. 1976. Regional and local aspects of atmospheric sulfates in the northeastern quadrant of the U.S. Proceedings, Third Symposium on Turbulence, Diffusion and Air Quality. Amer. Meteor. Soc., Boston, MA.

U.S. Environmental Protection Agency. 1983a. Air Quality Criteria for Lead. Vol. I. Publica. No. 600/8-83-028A. U.S.E.P.A., Research Triangle Park, N.C. 169 pp.

U.S. Environmental Protection Agency. 1983b. The Acidic Deposition Phenomenon and Its Effects. Vol. I. Atmospheric Sciences. Publica. No. 600/8083-016A. U.S.E.P.A., Washington, D.C. p. 3-92.

Waggoner, P.E. 1984. Agriculture and carbon dioxide. Amer. Scient. 72:179-184.

Waring, R.H. 1983. Estimating forest growth and efficiency in relation to canopy leaf area index. Adv. Ecol. Res. 13: 327-354.

Waring, R.H. 1985. Imbalanced ecosystems - Assessments and consequences. For. Ecol. Manage. 12: 93-112.

Waring, R.H. and W.H. Schlesinger. 1985. Forest Ecosystems. Concepts and Management. Academic Press, N.Y., 340 pp.

Wolff, G.T., N.A. Kelly, M.A. Furman. 1981. On the sources of summertime haze in the eastern United States. Science 211:703-705.

INVESTIGATING THE EFFECTS OF ACID DEPOSITION AND GASEOUS AIR POLLUTANTS ON FOREST TREE PHYSIOLOGY

P. R. Miller, P. H. Dunn, D. L. Peterson, and M. A. Poth

Pacific Southwest Forest and Range Experiment Station
Forest Service, United States Department of Agriculture
Riverside, California

ABSTRACT

The role of mechanistic or process-driven models is considered as a framework for understanding the possible long-term effects of atmospheric deposition on California forests. An improvement in the predictive capability of mechanistic models of photosynthesis, carbon allocation, nutrient flux and water flux can provide an improved foundation for identifying imbalances induced by chronic, deposition of ozone and acidic compounds. Conceptual models can be used to great advantage as a guide for selecting new hypotheses for future study.

INTRODUCTION

In the past, air pollution effects investigations in forested regions usually centered around a particular pollutant source where visible symptoms of damage were easy to recognize. Damage could easily be shown to be the result of a single pollutant known to be emitted by the source. Zones of decreasing effect could be distinguished in vegetation at increasing distances from the source and were referred to as the denuded zone, the transition zone, the grass and shrub zone, the zone of dying trees, and the boundry zone of foliar effects (Haut van and Stratmann 1970). Smith (1981) has defined three classes of forest-pollutant interactions which include Class I interactions (forests are sources and sinks), Class II interactions (forests are influenced in a subtle manner), and Class III interactions (forests are influenced in a dramatic manner). The focus of concern today is on the more subtle effects of air pollutants on forest vegetation because we suspect that relatively low levels of both wet and dry deposited pollutants may now be inducing accumulative effects over wide regions.

Because of low pollutant levels and lack of visible impact it is very difficult to attribute unfavorable changes in tree or stand level function to air pollutants. Where there were cases of dramatic effects on forest vegetation in the past it was suitable to rely on statistical relationships between dose and foliage injury or growth changes but now additional tools are needed to investigate subtle effects of pollutants. Sharpe and Scheld (1986) propose that subtle levels of pollutants may shift the balance of physiological processes in chronically exposed trees, leading to new homeostatic levels of growth and development mechanisms. These new states may be characterized as a slow loss of tree vigor. No response is seen until a chain of relatively minor influences trigger a drastic response. These minor influences may include drought, pest outbreaks, fire scorch and wind damage. These are examples of the most common events, occurring independently at largely unpredictable intervals over the life span of the average tree or forest stand. Because trees have lower vigor many more may be killed by the event and some of the remaining trees have less ability to recover. The result is perceived as a sudden change or a catastrophic response. Sharpe and Scheld (1986) refer to advances in mathematical approaches to describing abrupt changes as "castrophe theory", and suggest the possibility of applying this approach in the study of multiple stress effects.

Significant support for this hypothesis of sudden change comes from observations of Waldsterben which began to attract serious attention during 1979 and 1980 (Schutt and Cowling 1985). At least 5 hypotheses have been advanced by separate research groups to explain Waldsterben. These include the acidification-aluminum toxicity hypothesis, the ozone hypothesis, the magnesium deficiency hypothesis, the general stress hypothesis, and the excess-nutrient or excess-nitrogen hypothesis (Schutt and Cowling 1985). Some of these hypotheses are more appropriate for particular regions, for example, the magnesium deficiency hypothesis is best supported by conditions in southern Germany. It is generally agreed that Waldsterben is a disease syndrome involving several predisposing and stress-inducing factors that are followed by numerous secondary effects of abiotic and biotic origin. Therefore the 5 hypotheses seem to be merging and overlapping as time advances. For example, injury to foliage by ozone disrupts membranes and enhances the effects of acidification by increasing nutrient loss (Prinz, et al. 1982).

Further support for the importance of multiple stresses is provided by the earliest investigations of ponderosa pine decline in the San Bernardino mountains (Parmeter et al. 1962). Between 1911 and 1960, the length of the available precipitation record, the years 1947 and 1953 were the driest ever recorded; and, the average deviation from the mean (41.24 in.) was always negative between 1946 and 1960. However, the 1941-1945 period had precipitation consistently above average. Air pollution (smog) damage to crops and ornamentals in the nearby basin had been recognized since 1953 (Middleton et al. 1956). Reliable data for ozone was not available for the 1940's and 1950's so it is impossible to determine the exact temporal relationship between the two stresses. The dramatic nature of the problem, as it progressed in the 1960's, was very likely due to the inability of drought stressed trees to recover under the chronic influence of ozone.

It is becoming more evident that new methods of investigation, must be attempted along with more traditional methods. A "Mature Tree Response Workshop", sponsored by the Southern Commercial Forest Research Cooperative, December 8-10, 1986, affirmed that studies on mature trees in forests should be guided by a process-driven model approach. The workshop also endorsed the need for "correlative" and "experimental" studies designed with the aid of and guided by mechanistic, process models. The emphasis on the application of mechanistic models is stressed because the response to be predicted is the result of subtle perturbations acting on complex interacting components of the tree or stand system over long periods of time. It is necessary to build conceptual models in which the mathematical functions are founded on an understanding of basic physiology.

The purpose of this review is to further define the role of mechanistic or process-driven models as a foundation for planning of future research and for understanding the possible long-term effects of atmospheric deposition on California forests. A set of null hypotheses are proposed to aid in the planning of the correlative and experimental studies which may be appropriately interfaced with the mechanistic modeling approach.

BACKGROUND ON USE OF MECHANISTIC MODELS FOR INVESTIGATING AIR POLLUTION EFFECTS

A comprehensive background on the use of models in ecology is available as a collection of benchmark papers (Shugart and O'Neill 1979). References directed toward the interpretation of SO_2 air pollution effects in a western coniferous forest ecosystem (Kercher and Axelrod 1981), and acidic deposition effects on tree physiology (McLaughlin, 1983), offer good examples of the conceptualization of multiple stresses in a modeling context. The study of photochemical oxidant effects on the mixed conifer forest of the San Bernardino National Forest provided a conceptual model of the effects on stand dynamics (Kickert and Gemmill 1980). In addition, Kercher and King (1985) discuss the essential attributes of process models for investigating pollutant effects, in particular, the variables to be studied. (Figure 1).

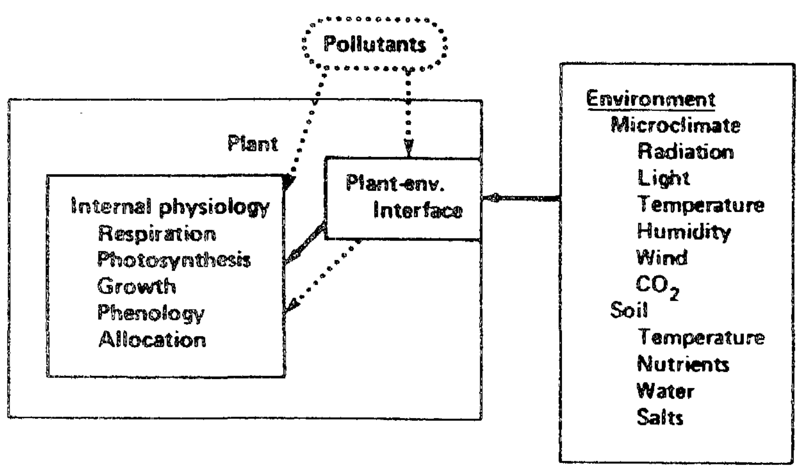

Figure 1. Conceptualization of plant response to environmental conditions and pollutants (Kercher and King 1985).

Sharpe and Scheld (1986) stress the need for balance and completeness in the inclusion of the component menchanisms of whole tree physiology. They contend, for example, that too much emphasis has been placed on photosynthesis and stomatal conductance and not enough on transport and allocation. Sharpe and Scheld (1986) propose their own list of components for a multiple stress hypothesis to be transformed in an additional step to a mathematical model construction (Table 1).

Table 1

Suggested Components of a Multiple Stress Hypothesis
(Sharpe and Sheld 1986)

Causes(s)	Interaction(s)	Mechanisms(s)	Effect(s)
1) Ozone	1) Cumulative	1) Increased membrane permeability	1) Leaf senescence
2) Acidic deposition	2) Catastrophic	2) Reduced photosynthesis	2) Canopy dieback
3) Drought		3) Increased respiration	3) Growth reduction
		4) Reduced translocation	4) Suscepti-bility to insects
		5) Root biomass reduction	5) Increased drought stress
		6) Reduced defensive chemical synthesis	6) Increased tree mortality
		7) Decreased water uptake	

The general recommendation was to develop conceptual models first so that appropriate data would be collected for the mechanistic models that would follow. Methods for organizing an interdisciplinary study of pollutant effects have been suggested based on experience in the San Bernardino

National Forest (Kickert and Miller 1979). Two methodological aspects were emphasized: 1) Before data collection begins develop a set of working hypotheses as computer simulation models; 2) Require new data collection to be guided by the results of sensitivity testing of computer simulation models. In the San Bernardino project the modeling work was done concurrently with new data collection by researchers, an obvious disadvantage. On the positive side, the modeling effort helped the project researchers view their own work as part of an integrated conceptual structure and it identified important new problems that led to research that might not otherwise have been done (Kickert and Gemmill 1980). A method of problem analysis and hypotheses building has been formalized under the name: "Adaptive Environmental Assessment and Management" (Holling 1978). A series of workshops are used to formulate simplified models that guide future data collection.

During the process of developing hypotheses it is necessary to recognize hierarchical levels in both time and space. The relationship between time and space are shown in Figure 2.

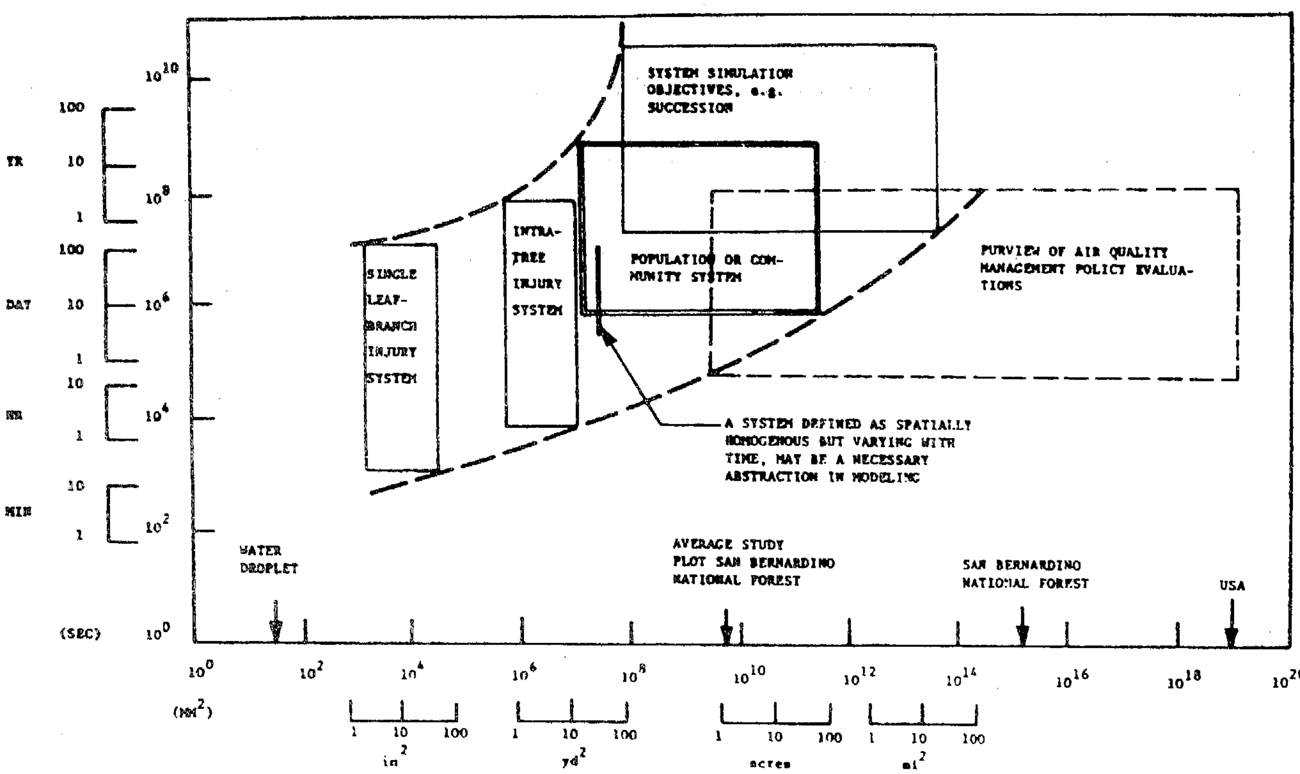

Figure 2. Time and space scales and their relationship to objectives in eclogical research. (Adapted from Ewing, et al. 1974 by Kickert and Miller, 1979).

A spatially lumped model, where changes do not occur heterogeneously in space, is diagrammed as a bold vertical line. A model that deals with spatial distributions is represented by a polygon; the location of it's sides indicate the time and space bounds of a model system. It is essential that the bounds of the model be determined based on the needs or goals of a research program, for example, the different cooperatives comprising the Forest Response Program, co-sponsored by the U.S. Environmental Protection Agency, the U.S. Forest Service and the forest industry. The task of linking different hierarchical levels in space (needle, tree, forest stand) and time (hours, days, years) remains a difficult task (Goldstein 1977) and it is very important to recognize this limitation.

Catastrophic events, referring to sudden perturbations occurring randomly during time spans of many years, may interact strongly with cumulative effects of pollutants. The recovery from individual catastrophic events, such as fire, windthrow and clear cutting, have been modeled by Bormann and Likens (1979) in an Eastern hardwood forest. They propose a shifting-mosaic, steady-state hypothesis, based on forest growth simulations with the JABOWA model (Botkin et al. 1972a,b) which describes events during a 500 year period after a major disturbance. The shifting-mosaic, steady-state is described as an array of irregular patches composed of vegetation of different ages. Patches pass from one age-state to another during four phases after disturbance: a) reorganization, b) aggradation, c) transition and d) steady state. Instead of a simple asymptotic model that assumes a gradual increase in biomass until steady-state is achieved, this model delineates four phases of biomass decline and recovery, with a sharp drop in the reorganization phase and maximum accumulation of biomass occurring prior to the steady state. These phases take place over a time span of several hundred years. This approach deserves further attention as a means of understanding the role of random, catastrophic events as factors which may incite or trigger forest deterioration.

A WORD OF CAUTION ABOUT ECOLOGICAL MODELING

It is fair to say that much has been promised in the name of ecosystem models but very little has been delivered. For example, the Biome studies, including the Coniferous Forest Biome Program, failed to produce valid ecosystem-level models (Gessel and Edmunds 1980). One of the problems was a lack of essential communication between modelers and researchers so that some data sets were not used for modeling because of inappropriate scales of resolution in certain cases. Communication was undoubtedly better within disiciplines because the Coniferous Forest Biome did have some success with selected process models including distinct models for carbon cycling (Coniferous Forest Biome Modeling Group 1977), nitrogen cycling (Riggan 1976), photosynthesis (Reed et al. 1976) and growth-succession (Reed and Clark 1979). The expressed need for a complex mechanistic model of multiple stresses (Sharpe and Scheld 1986) has merit, but it is easy to see how much difficulty may result from a poorly focused effort to achieve close collaboration among disciplines, and modelers.

RECOMMENDATIONS FOR MODELING ACTIVITIES

Three recommendations are proposed which may encourage the best use of modeling in the context of limited research funding and short project durations (less than 3-5 years). 1) Emphasize modeling as an up-front planning tool which can identify the context in which various processes will be studied. Furthermore, provide for constant interaction between models and researchers at all stages of the project. 2) Because large spatial scale and long time scale predictions depend entirely on the reliability of models of more fundamental processes, e.g., photosynthesis, nutrient flux, and water flux, it will be necessary to place the most new research emphasis on these and other processes at the leaf-tree-stand levels (Figure 3).

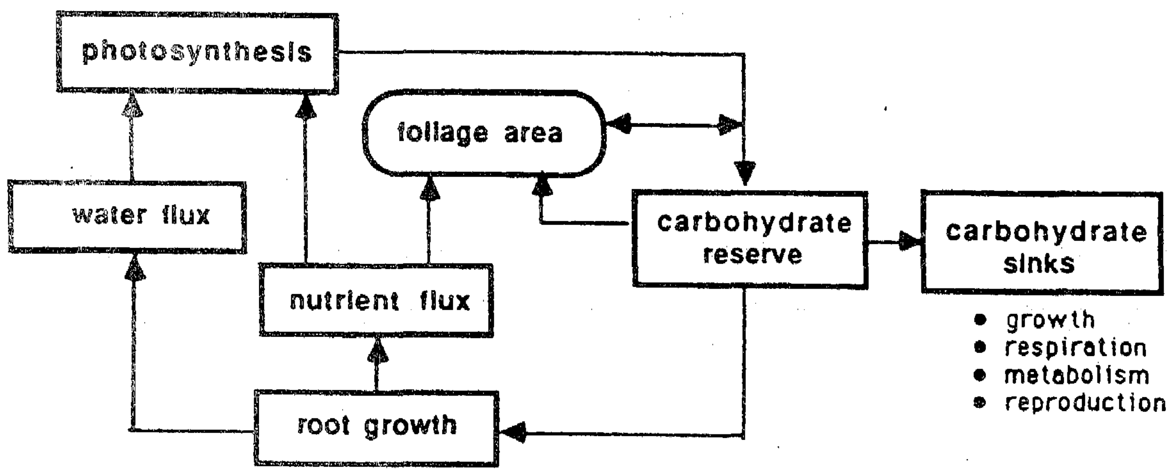

Figure 3. Inter-relationships of component physiological process models. (From Ford 1982).

The goal would be to balance the research effort among as many of the fundamental processes as were determined to be essential by the preliminary modeling effort. The purpose would be to encourage a better understanding of the response of 2 or 3 "controller" species (those species like ponderosa pine and white fir which are the dominants in the climax mixed conifer forest mixture). 3) Do not ignore the long time scale and, large spatial scale entirely. Invite the cadre of individuals (10-15) who worked in the preliminary model planning sessions to develop a model framework for these scales that will incorporate the results of process level work and introduce the problem of catastrophic, "trigger events". The core of this effort would be achieved through workshops and/or a single project.

GENERAL CONSIDERATIONS OF A MODEL-BASED RESEARCH PROGRAM FOR PREDICTING THE EFFECTS OF MULTIPLE STRESSES AT THE TREE AND STAND LEVELS

Two broad categories of research may be proposed. These could be typified by "controlled environment" studies using seedlings and saplings in open-top chambers located at forested sites and gradient studies focusing on the stand level using all ages of trees in forest plots. Such plots could be located along known gradients of pollutant concentration. "Controlled environment" studies should be done in a forest environment. It is necessary to establish long-term experiments in chambers at sites where climatic conditions are as similar as possible to the normal environment of the species being studied. For example, a Western component of the EPRI-sponsored ROPIS (Response of Plants to Integrated Stresses) program is being proposed for Whittaker Forest in the southern Sierra Nevada. The study will be done by University of California and Pacific Southwest Forest and Range Experiment Station researchers. This is proposed as an open-top chamber experiment with ponderosa pine, pre-selected for ozone sensitivity, which will be exposed to various treatments of ozone, acidic deposition (rain), and drought.

For California conditions ozone injury symptoms on conifer foliage serve to define the gradients of other dry-deposited pollutants. However, we do not know to what extent other dry-deposited pollutants may contribute to the leaf symptom (chlorotic mottle) which we know to be caused by ozone. The best examples of ozone gradients are in the San Gabriel, San Bernardino, and San Jacinto mountains of southern California, and to a lesser extent, the western slopes of the southern Sierra Nevada. The best opportunity for gradient studies is in the mountains of southern California, particularly because there is already a background data base to provide useful guidance for a variety of new studies (Taylor, 1980). The particular advantage of the San Bernardino mountains is that the summer ozone dose is usually high enough to induce severe levels of injury in the sensitive individuals, thus providing a good contrast between maximum and minimum effects on physiological processes.

Southern Sierra Nevada conifer forests exhibit injury levels that are mostly slight and occasionally moderate on the scale used to describe injury levels in the southern California mountains. For example, core samples collected from Jeffrey pines, with reduced needle retention (slight injury), at "ozone-exposed" sites in Sequoia and Kings Canyon National Parks were compared with cores samples from similar elevation, soils and direction of slope in the upper Kern River Canyon where incursions of ozone were judged to be minimal (Peterson et al. 1986 and 198_). Ring width indices showed consistent and significant departures below predicted growth at the "ozone exposed" sites but only for large diameter, open-grown trees. Trees at the remote sites did not show this trend. One spin-off from this study is a computerized data base for several climatic variables for the entire length of the record available.

It is assumed that the California mixed conifer forest type, comprised of ponderosa pine, Jeffrey pine, white fir, sugar pine, incense cedar and black oak, will be given top priority because it is presently facing the greatest risk from photochemical oxidants and associated wet- and dry-deposited acidic compounds. Alpine, subalpine, riparian, and chaparral vegetation should be given a lower priority.

New research should be balanced between the categories of "controlled environment" and "gradient studies". The planning process should result in an overlap of spatial scales (leaf, tree, stand) in some studies where it is essential to test whether results from young trees in controlled conditions can be extrapolated to mature trees.

SAMPLE HYPOTHESES TO GUIDE FUTURE RESEARCH ON INTEGRATED PROCESSES

It is proposed that Figures 1 and 3 be used for identifying hypotheses and for planning individual studies to be done in both "controlled environment" and "gradient" situations. The goal is that the relative importance of component physiological processes should be evaluated by preliminary sensitivity analyses so that resources can be allocated efficiently. Adherence to this standard during the planning phase may minimize the effect of inevitable compromises which could result from a less focused planning process.

The following null hypotheses are intended as suggestions for guiding the planning of an integrated research plan. This is not intended to be an exhaustive list. They are grouped under the headings of distinct processes (Figures 1 and 3).

Deposition

Mass transport of pollutants (air concentration X flow volume) varies widely with topography and stand density but does not influence accumulation rate of particulates on leaf surfaces or uptake of gaseous pollutants.

There is no relationship between phenology (stage of leaf development), and the components of the summer season ozone record (concentration, timing or length of episodes and respites) which maximizes effects on physiological processes leading to leaf injury.

Nocturnal ozone concentrations in mountain locations may remain high (0.10 ppm) but stomatal conductance of tree species comprising the mixed conifer forest type are too low at night to allow uptake of ozone or other pollutants.

Because of overall low physiological activity during winter the concentration of acid deposition in rime ice has no impact on tree physiology regardless of earlier ozone exposure.

Photosynthesis and Allocation of Carbon

Chronic ozone injury does not result in unfavorable allocation patterns of photosynthate among leaves, stems, and roots of conifer species.

Shifts of photosynthesis rate to lower homeostatic levels within and between seasons can not be confidently partitioned among the possible causal factors (ozone injury, nutrient imbalance and water deficits).

Patterns of enzyme response to free radicals in injured leaf tissue can not be used to predict changes in photosynthetic rate leading to imbalances of carbon and nutrient allocation.

Nutrient Flux

Cumulative atmospheric deposition of protons and nutrients, with or without injury to membranes by ozone, does not produce changes in nutrient balance or allocation in trees or stands as reflected in the present pool sizes or pool nutrient ratios.

Edaphic factors (soil parent material, depth, and water holding capacity) do not influence nutrient balance or uptake of non-nutrient ions following cumulative exposure to ozone and/or acidic deposition.

Nitrogen and proton deposition to trees and stands from fogs is not expected to have an effect on the foliar nutrient pool regardless of whether fogs occur in spring or autumn.

Nitrogen enrichment from atmospheric deposition can not alter foliage sensitivity to water stress or low temperature at present deposition rates.

Water Flux

Seasonal distribution of favorable soil moisture has a minor control on stomatal conductance, subsequent ozone uptake and development of leaf injury.

Morbidity and Mortality Processes

Chronic exposure to ozone and acidic substances resulting in reduced foliage surface area does not predispose root systems to infection and colonization by root decay fungi and other stresses, e.g. insects and drought.

CONCLUSIONS

Future planning of a balanced research program on the chronic effects of ozone and acidic compounds must emphasize the inter-relationship of basic physiological processes governing tree growth and stand development. An improvement in the predictive capability of mechanistic models of photosynthesis, carbon allocation, nutrient flux and water flux will provide the foundation of knowledge needed to identify whether imbalances are induced by chronic, low-level exposures. This approach can also provide a context for evaluating the role of catastrophic events, such as drought, that may trigger a more rapid phase of tree decline. The possible changes in the mechanisms of tree defense against insect pests and diseases must also be given thorough consideration.

REFERENCES CITED

Bormann, F. H. and G. E. Likens. 1979. Catastrophic disturbance and the steady state in northern hardwood forests. Amer. Scientist 67:660-669.

Botkin, D. B., J. F. Janak and J. R. Wallis. 1972a. Rationale, limitations and assumptions of a northeastern forest growth simulator. IBM J. Res. Devel. 16:101-116

Botkin, D. B., J. F. Janak and J. R. Wallis. 1972b. Some ecological consequences of a computer model of forest growth. J. Ecol. 60:849-872.

Coniferous Forest Biome Modeling Group. 1977. Conifer: A model of carbon and water flow through a coniferous forest. Documentation. Coniferous Forest Biome Bulletin No. 8, University of Washington, Seattle

Ewing, B., P. Rauch and J.F. Barbieri. 1974. Simulating the dynamics and structure of populations. Lawrence Livermore Laboratory, Livermore, CA. CONF-750101-1, 60 pp.

Ford, E. D. 1982. Catastrophe and disruption (by fire, wind, and pests) in forest ecosystems and their implications for plantation forestry. Scottish Forestry 36:9-24.

Gessel, S. P. and R. L. Edmunds. 1980. An overview of the successes and failures of ecosystem simulation studies. California Air Environment 7(3):4-9, Statewide Air Pollution Research Center, University of California, Riverside.

Goldstein, R. A. 1977. Realities of ecological modeling. EPRI Journal 2:49-52.

Haut, H. van and H. Strattman. 1970. Farbtafelatlas uber Schwefeldioxid-Wirkungen an Pflanzen. Girardet-Verlag. Essen, West Germany.

Holling, C. S. 1978. Adaptive Environmental Assessment and Management. John Wiley and Sons, New York 377 pp.

Kercher, J. R. and D. A. King. 1985. Modeling effects of SO_2 on forest productivity and growth of plants. p.357-372 In: Winner, W. E., H. A. Mooney, and R. A. Goldstein (Eds) Sulfur dioxide and vegetation. Stanford University Press, Stanford, CA 593 pp.

Kercher, J. R. and M. C. Axelrod. 1981. A model for forecasting the effects of SO_2 pollution on growth and succession in a Western coniferous forest. UCRL-53109. Livermore, California: Lawrence Livermore National Laboratory.

Kickert, R. N. and P. R. Miller. 1979. Responses of Ecological Systems. Chapter 14. In: Heck, et al. (Eds.) Handbook of Methodologies for the Assessment of Air Pollution Effects on Vegetation. Air Pollution Control Association, Pittsburgh, PA

Kickert, R. N. and B. Gemmill. 1980. Data-based ecological modeling of ozone air pollution effects in a southern California mixed conifer forest ecosystem. p. 181-186, In: Effects of air pollutants on Mediterranean and temperate forest ecosystems. Forest Service, USDA, Gen. Tech. Report PSW 43, 256 pp.

McLaughlin, S. B. 1983. Acid rain and tree physiology: An overview of some possible mechanisms of response. p. 67-76. In:Air pollution and the productivity of the forest. Davis, D. D., A. A. Millen, and L. Dochinger (Eds.) Izaak Walton League of America, Washington, D. C. 344 pp.

Middleton, J. T., A. S. Crafts, R. F. Brewer, and O. C. Taylor. 1956. Plant damage by air pollution. Calif. Agric. 10 (6):9-12.

Parmeter, J. R., R. V. Bega and T. Neff. 1962. A chlorotic decline of ponderosa pine in southern California. Plant Disease Reptr. 46:269-273.

Peterson, D. L., V. A. Wakefield, M. A. Arbaugh and P. R. Miller. 198_. Evidence of growth reduction in ozone-stressed Jeffrey pine (*Pinus jeffreyi* Grev. and Balf.) in Sequoia and Kings Canyon National Parks. (Accepted by JAPCA).

Peterson, D. L., V. A. Wakefield and M. J. Arbaugh. 1986. Detecting the effects of ozone air pollution on growth of Jeffrey pine in the Sierra Nevada, California. In: Proc. International Symp. on Ecological Aspects of Tree Ring Analysis. Lamont-Doherty Geological Observatory, Columbia Univ., Palisades, N. Y. (In Press).

Prinz, B., G.H.M. Krause and H. Stratmann. 1982. Forest damage in the Federal Republic of Germany. Landesanstsalt fur Immissionsschutz, Essen. LIS Report No. 28. 146 pp.

Reed, K. L., E. R. Hamerly, B. E. Dinger and P. G. Jarvis. 1976. An analytical model for field measurement of photosynthesis. J. Appl. Ecol. 13:925-942.

Reed, K. L. and S. G. Clark. 1979. SUCession SIMulator: A coniferous forest simulator. Model Documentation. Coniferous Forest Biome Bulletin No. 11. University of Washington, Seattle.

Riggan, P. 1976. Simulation of growth and nitrogen dynamics in a Douglas-fir forest ecosystem. pp. 146-157, In: Proc. Symp. on Terrestrial and Aquatic Studies of the Northwest Sci. Assoc., Eastern Washington State Coll. Press, Cheney, Washington.

Schutt, P. and E. B. Cowling. 1985. Waldsterben, a general decline of forests in central Europe: Symptoms, Development, and Possible Causes. Plant Disease 69:548-558.

Sharpe, P. J. H. and H. W. Scheld. 1986. Role of mechanistic modeling in estimating long-term pollution effects upon natural and man-influenced forest ecosystems. p. 76-82. In: Proceedings of workshop on controlled exposure techniques and evaluation of tree responses to airborne chemicals. NCASI Tech. Bullet. No 500. 82 pp.

Shugart, H. H. and R. V. O'Neill. 1979. Systems Ecology, Benchmark Papers in Ecology / 9. Dowden, Hutchinson and Ross. Stroudsburg, PA. 368 pp.

Smith, W. H. 1981. Air Pollution and Forests. Springer Verlag, New York 379 pp.

Taylor, O. C. 1980. Photochemical oxidant air pollution effects on a mixed conifer forest ecosystem. Final Report. U. S. Environmental Protection Agency, EPA-600/3-80-002, Corvallis Environmental Research Laboratory, 195pp.

DISTINGUISHING POLLUTION FROM CLIMATIC EFFECTS BY THE ANALYSIS OF STABLE ISOTOPE RATIOS IN THE CELLULOSE OF ANNUAL GROWTH RINGS

R.H. Waring
Visiting Professor
The Ecosystems Center
Woods Hole, MA 02543

ABSTRACT

The natural abundance of the stable isotopes ^{13}C and ^{12}C changes as CO_2 diffuses through leaf stomata and is incorporated enzymatically into simple 3-carbon sugars during photosynthesis. Recent studies show that the change in the ratio of $^{13}C/^{12}C$ reflects the relative constraint of CO_2 diffusion into the leaf vs. enzymatic activity within the leaf. A permanent record of seasonal and yearly change in the relative abundances of the stable carbon isotopes is incorporated in cellulose, a major component of cell walls in each annual growth ring.

Air pollutants that might induce stomata to partially close would decrease CO_2 diffusion and thereby enrich the ^{13}C composition of cellulose above normal; air pollutants that inhibited enzymatic reactions would, on the other hand, deplete the ^{13}C of cellulose below normal.

Soil drought or high evaporative demand can also decrease the diffusion of CO_2 through stomata and enrich cellulose in ^{13}C. Such climatically induced effects, however, can probably be isolated from those caused by pollution through analysis of hydrogen (^1H and ^2H) and oxygen (^{18}O and ^{16}O) isotopes in cellulose. The relative abundances of these isotopes mirror temperature and humidity conditions when the cellulose is laid down in each annual ring of a tree.

INTRODUCTION

The basic building blocks of wood cellulose are carbon, oxygen, and hydrogen. Each of these elements has a stable isotopic form with one or more extra neutrons. As these elements circulate in nature, however, various processes discriminate against the heavier or lighter isotopic form, causing the ratio of the heavier/lighter to change ever so slightly. Modern mass spectrometers can measure relative changes in isotopic abundance with great precision. Usually variation in isotopic abundance is expressed as a change (δ) in thousandths (‰) with respect to an internationally accepted standard:

$$\delta,‰ = \frac{\text{Ratio (sample)} - \text{Ratio (standard)}}{\text{Ratio (standard)}} * 1000 \qquad (1)$$

The standard for carbon is Pee Dee belemnite (PDB) carbonate from South Carolina. For hydrogen and oxygen the standard is mean ocean water (SMOW). Recent improvements in sample preparation and analytic techniques allow discrimination in the relative abundance of $^{13}C/^{12}C$ to 0.1‰ , of $^{18}O/^{16}O$ to 0.2‰ and D/H to 2‰ (Leavitt and Long 1986, Edwards et al. 1985).

In the last five years knowledge of how various isotope fractionations occur has increased sufficiently to suggest certain ecological interpretations. In this paper I will first summarize the major factors controlling the relative abundance of stable isotopes of C, H, and O in cellulose and then propose how variation in the relative isotopic abundance of these elements may help distinguish the effects of pollutants from climatic factors on photosynthesis and annual growth in forest trees.

CHANGES IN THE RELATIVE ABUNDANCE OF $^{13}C/^{12}C$

The internal concentration of CO_2 within the leaf (c_i) is dependent on the external concentration (c_a), the rate of diffusion into the leaf controlled by the conductance across the leaf boundary layer and through the stomatal pores (g), and the rate at which assimilation (A) depletes the available CO_2 to produce simple 3-carbon sugars. This can be described by the formula:

$$c_i = c_a - A/g \qquad (2)$$

What happens as the two stable isotopes of carbon diffuse from the atmosphere into the intercellular space within the leaf? The free atmospheric CO_2 level of $^{13}C/^{12}C$ in relation to the standard is depleted in ^{13}C by -7.8 ‰ . The diffusivity of $^{13}CO_2$ in air is 4.4‰ less than that of $^{12}CO_2$. Once CO_2 diffuses into the leaf $^{13}CO_2$ is further discriminated against by about 28 ‰ in C_3 plants by the carboxylating enzyme. Other processes such as photorespiration also discriminate slightly between the two isotopic forms but an adequate estimate of the observed $^{13}C/^{12}C$ (abbreviated $\delta\ ^{13}C$) in the photosynthate can be predicted by the formula:

$$\delta^{13}C\ (\text{photosyn.}) = \delta^{13}C\ (\text{air}) - a - (b-a)c_i/c_a \qquad (3)$$

where a and b are fractionation constants for diffusivity and the carboxylating enzyme respectively (Francey and Farquhar 1982). Substituting into the equation we get:

$\delta^{13}C$ (photosyn.) = $-7.8 -(4.4) - (28 -4.4)c_i/c_a$ (4)
which reduces to:

$$\delta^{13}C_p = -12.2 -23.6c_i/c_a \qquad (5)$$

With reference to equations 2 and 5, we can see that factors which reduce CO_2 assimilation rates through effects primarily on the enzymatic controls on photosynthesis (e.g., very low light intensities, and deficiencies in certain mineral nutrients) will increase c_i/c_a and reduce $\delta^{13}C_p$; factors which reduce CO_2 assimilation rates primarily through reduction of supply of CO_2 through by restricting diffusion through the stomata (e.g., large humidity deficits and soil drought) will decrease c_i and increase $\delta^{13}C_p$. Note that in some situations both A and g in equation 2 may be affected proportionately with subsequently no marked effect on c_i/c_a or $\delta^{13}C_p$. Such balanced adjustments in stomata conductance and enzymatic activity take time but are normal in unpolluted environments, accounting for the general stability observed in the $\delta^{13}C$ composition of cellulose (Freyer and Wiesberg 1974, Tans and Moob 1980, Yoshie 1986).

On the short-term, however, alterations in the climate usually cause stomata to respond faster than enzymes can be synthesized or degraded. In an experiment with spinach plants where water was differentially restricted by adding NaCl, the intercellular partial pressure of CO_2 (c_i) fell as diffusion limited photosynthesis (Fig. 1). This resulted in the first carbon products of photosynthesis becoming proportionately less negative, i.e. enriched in ^{13}C relative to ^{12}C.

One may ask how closely does the $\delta^{13}C$ in currently produced photosynthate correspond to that found in cellulose? During additional biochemical transformations from simple sugars to cellulose, the isotopic composition of carbon is further enriched in ^{13}C, but the enrichment is proportional so that cellulose carbon still reflects the isotopic composition of its origin (O'Leary 1981).

Cellulose in conifers is mainly produced from current photosynthate (Niziolek et al. 1969, Schier 1970). Changes in the isotopic composition of cellulose that may be measured across a single annual ring thus reflect environmental changes throughout the growing season (Farwell et al. 1987).

Cellulose is laid down in spirally arranged fibers so sampling must take account of this orientation or the wood sampled uniformly at the same height around the entire annual ring (Tans and Moob 1980). Some care must also be taken at what height wood samples are collected for the upper and lower crown are in different environments and produce cellulose with slightly differing isotopic composition (Leavitt and Long 1986). Sampling variation within a forest stand can be minimized by collecting wood from trees that have ceased growing in height and have established a relatively stable exposure to the sun. Before going into a more detailed analysis of how air pollutants might alter $^{13}C/^{12}C$ in wood cellulose, let's evaluate how hydrogen and oxygen isotopes are incorporated into cellulose.

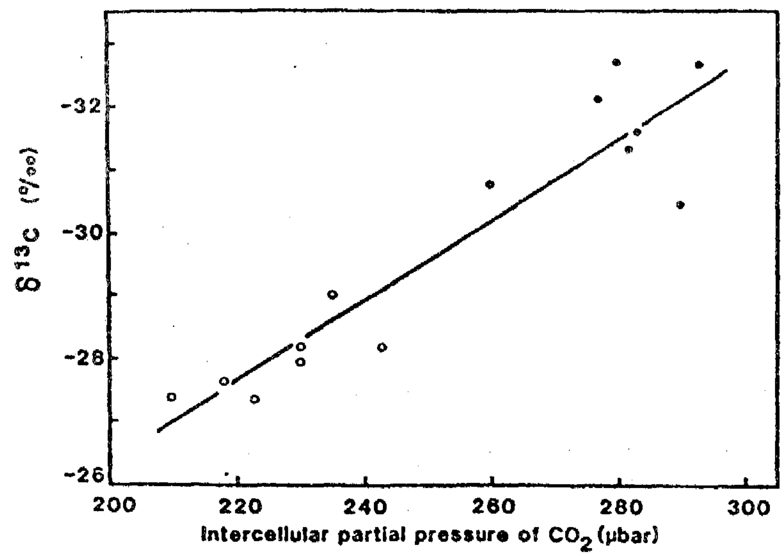

Fig. 1. Relationship of $\delta^{13}C$ in photosynthate to the intercellular CO_2 (c_i) for spinach plants grown with (O) and without (●) additions of NaCl. Irradiance and atmospheric CO_2 (c_a) were maintained essentially constant. After Downton et al. 1985).

CHANGES IN THE RELATIVE ABUNDANCE OF D/H AND $^{18}O/^{16}O$

About one-third of the oxygen and all of the hydrogen in cellulose comes from the splitting of water during the photosynthetic process. As water changes state from a liquid to a vapor or from a liquid to a solid, isotopic fractionation occurs. Under equilibrium conditions the amount of fractionation is basically a function of temperature. For oxygen and hydrogen at 25°C water vapor above water will be isotopically depleted in ^{18}O by 9.3‰ and D by 76‰ . As vapor is condensed the processes is reversed and enrichment occurs, taking into account that the vapor has previously been depleted in the heavier forms of the two elements.

Where precipitation comes from a single source, such as the ocean, and the temperature is fairly constant, the relative abundances of heavier and lighter forms of the two isotopes are easily predicted (Craig 1961, Dansgaard 1964). In such cases the mean $\delta^{18}O$ of the growing season precipitation is closely related to the mean daytime temperature. However, where seasonal temperatures vary, storms draw from different sources, or snow is a predominant form of precipitation, the isotopic composition of the actual source of water used by plant roots requires direct measurement.

From direct measurement of water in the sap of various Florida coastal plants, Sternberg and Swart (1987) were able to identify the source of water from a knowledge of isotopic abundances for δD and $\delta^{18}O$ in freshwater, ocean water, and various combinations in between (Fig. 2).

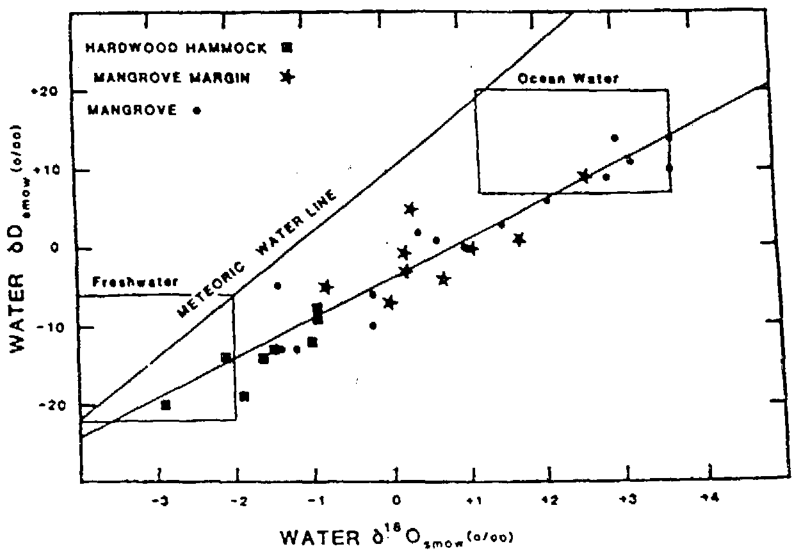

Fig. 2. The distribution of vegetation in magrove and hardwood hammock areas in costal Florida illustrates a gradient from fresh water to ocean water based on isotopic ratios of $\delta^{18}O$ and δD in cell sap (Sternberg and Swart 1987).

In New York State, White et al. (1985) discovered that the source water, as interpreted from the isotopic ratio of cell sap, was predominantly from the most recent storm for trees situated on ridges, a mixed source for trees able to tap ground water, and a stable source for those species situated in swamps or bogs that received nearly all of their water from runoff of snowmelt. This study and the previously cited one suggest that a reliable interpretations of stable isotope fractionation can only be derived by assuring that the sampled vegetation grows in a situation where the source of water is consistent throughout the growing season, i.e., exclusively from ground water or exclusively from current rainfall.

In cellulose, the source of oxygen is both water and dissolved carbon dioxide. Epstein et al. (1977) established that the fractionation of oxygen isotopes between the cellulose of aquatic plants and their source water is +27‰ for ^{18}O. They assumed the oxygen in cellulose is in balance, mole for mole, from water and from dissolved CO_2. Because there are two atoms of oxygen in each mole of CO_2, that source of oxygen is enriched by 41% (2/3 X 41 = 27). Cellulose synthesis in terrestrial plants is analogous to that in aquatic plants, with the added complication that isotopic enrichment of plant water occurs in the leaves through transpiration. The more intense the evaporative loss of water from the leaf, the more enriched will be the cellulose in ^{18}O and D.

Various formula have been derived to describe the relative enrichment of source water due to transpiration (Forstel 1978, Burk and Stuiver 1981, Yapp and Epstein 1982, Edwards et al. 1985). All of these empirical formula show that the relative humidity of the air is a major variable determining the extent to which hydrogen and oxygen bound in cellulose are enriched in heavier forms of their respective isotopes (Fig. 3).

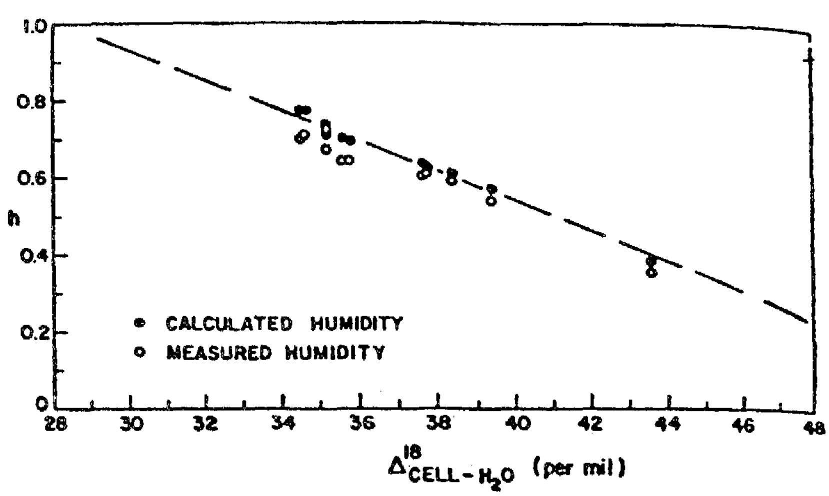

Fig. 3. The $\delta^{18}O$ in cellulose is proportionally enriched as the humidity (h) of the air around photosynthesizing leaves decreases. After Edwards et al. (1985).

From sampling trees with known sources of water, the natural abundance of ^{18}O and D bound in wood cellulose of annual growth rings should indicate whether significant changes in mean growing season humidity and temperatures occur year to year. This information alone can be helpful in analyzing growth patterns, independent of what happens with changes in the isotopic abundance of carbon.

EXPECTED IMPACT OF ATMOSPHERIC POLLUTANTS ON $\delta^{13}C$ IN CELLULOSE

The combination of pollutants that might affect the fractionation of carbon isotopes is very large, including such compounds as ozone, sulfur dioxide, nitrous oxides, heavy metals, and various hydrocarbons. In addition, leaching of the soil and foliage may lead to nutrient deficiencies and aluminum toxicity. Short-term exposures of any or all of these pollutants may well alter the expected value of $\delta^{13}C$ in cellulose (Fig. 4).

If plants were relatively resistant to sulfur dioxide, i.e., were able to reduce stomatal conductance following exposure (Winner and Mooney 1985), their cellulose should become more enriched in ^{13}C than normal. On the other hand, less resistant species or varieties of plants may allow pollutants to diffuse unrestrictedly into the intercellular spaces (Carlson 1979, Reich et a. 1986). If this happens, enzyme damage may result in reducing the ^{13}C of cellulose below normal.

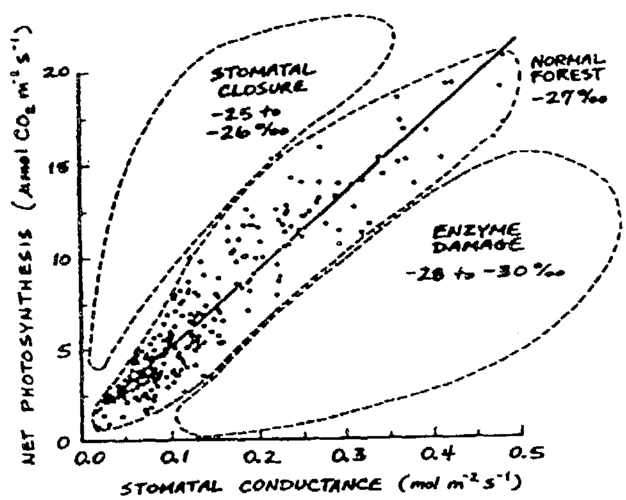

Fig. 4. Plants adapt to their environment by achieving a balance between photosynthetic capacity and stomatal conductance (data points from Yoshie 1986). Sudden alterations in the environment that force partial stomatal closure or cause degradation of enzymes alter the intercellular CO_2 and thus the $\delta^{13}C$ of cellulose.

These ideas need rigorous testing, first in the laboratory on small plants and then, if supported, on larger trees exposed to known levels of pollutants. Care should be taken that the selected trees have had an isotopically consistant source of water and have grown with their canopies uniformly exposed to the elements.

ACKNOWLEDGMENTS

I am indebted to Brian Fry from the Ecosystems Center at Woods Hole and James Ehleringer from the University of Utah in Salt Lake City for introducing me to some of the key references in the field of stable isotopes and for their helpful comments on earlier drafts of this paper.

LITERATURE CITED

Burk, R.L., and M. Stuiver. 1981. Oxygen isotope ratios in trees reflect mean annual temperature and humidity. Science 211:1417-1419.

Carlson, R.W. 1979. Reduction in the photosynthetic rate of *Acer*, *Quercus*, and *Fraxinus* species caused by sulphur dioxide and ozone. Environ. Pollut. 18:159-170.

Craig, H. 1961. Isotopic variations in meteoric waters. Science 133:1833-1834.

Dansgaard, W. 1964. Stable isotopes in precipitation. Tellus 16:436-438.

Downton, W.J.S., W.J.R. Grant, and S.P. Robinson. 1985. Photosynthetic and stomatal responses of spinach leaves to salt stress. Plant Physiol. 77:85-88.

Edwards, T.W.D., R.O. Aravena, P. Fritz, and A.V. Morgan. 1985. Interpreting paleoclimate from ^{18}O and ^{2}H in plant cellulose: comparison with evidence from fossil insects and relict permafrost in southwestern Ontario. Can. J. Earth Sci. 22:1720-1726.

Epstein, S., P. Thompson, and C.J. Yapp. 1977. Oxygen and hydrogen isotopic ratios in plant cellulose. Science 198:1209-1215.

Farwell, G.W., P.M. Grootes, D.D. Leach, F.H. Schmidt, and M. Stuiver. 1987. Rapid response of tree cellulose radiocarbon content to changes in atmospheric $^{14}CO_2$ concentration. Tellus. (in press).

Forstel, H. 1978. The enrichment of ^{18}O in leaf water under natural conditions. Radiation and Environ. Biophysics 15:323-344.

Francey, R.J., and G.D. Farquhar. 1982. An explanation of $^{13}C/^{12}C$ variation in tree rings. Nature 297:28-31.

Freyer, H.D., and L. Wiesberg. 1974. Dendrochronology and ^{13}C content in atmospheric CO_2. Nature 252:757-759.

Leavitt, S.W., and A. Long. 1986. Stable-carbon isotope variability in tree foliage and wood. Ecology 67:1002-1010.

Niziolek, S., J. Kaczkowski, and W. Zelawski. 1969. Incorporation of assimilated $^{14}CO_2$ into cellulose and lignin of Scots pine (*Pinus silvestris* L.) seedlings. Bull. Acad. Pol. Sciences 17:363-367.

O'Leary, M.H. 1981. Carbon isotope fractionation in plants. Phytochemistry 20:553-567.

Reich, P.B., A.W. Schoettle, and R.G. Amundson. 1986. Effects of O_3 and acidic rain on photosynthesis and growth in sugar maple and northern red oak seedlings. Environ. Pollut. 40:1-15.

Schier, G.A. 1970. Seasonal pathways of ^{14}C photosynthate in red pine labeled in May, July, and October. For. Sci. 16:2-13.

Sternberg, L.L., and P.K. Swart. 1987. Utilization of freshwater and ocean water by coastal plants of southern Florida. Ecology (in press).

White, J.W.C., E.R. Cook, J. R. Lawrence, and W.S. Broeker. 1985. The D/H ratios of sap in trees: implications for water sources and tree ring D/H ratios. Geochimica et Cosmachimica Acta 49:237-246.

Winner, W.E. and H.A. Mooney. 1985. Ecology of SO_2 resistance: V. Effects of volcanic SO_2 on native Hawaiian plants. Oecologia 86:387-393.

Yapp, C.J. and S. Epstein. 1982. A reexamination of cellulose carbon-bound D measurements and some factors affecting plant-water D/H relationships. Geochimica et Cosmachimica Acta 46:955-965.

Yoshie, F. 1986. Intercellular CO_2 concentration and water-use efficiency of temperate plants with different life-forms and from different microhabitats. Oecologia 68:370-374.

REVIEW OF THE STATE OF THE ART OF SURVEYING FOREST PRODUCTIVITY AND CONDITION OVER WIDE REGIONS FOR THE PURPOSE OF LONG TERM MONITORING OF FOREST HEALTH

JOSEPH E. BARNARD, Program Manager
National Vegetation Survey/Forest Response Program
USDA Forest Service, Forestry Sciences Laboratory
P.O. Box 12254
Research Triangle Park, NC 27709

INTRODUCTION

One-third of the land area of the United States is forest. In many regions of the country, forest is the major if not predominant land cover. When the continent was first discovered two-thirds or more of the land was in forest cover. Historically, we have always shown an interest in this vast forest resource. Let me begin with a brief overview, emphasizing just one aspect - resource information.

Descriptions of the forest resource began with the earliest explorations of the New World. Expeditions and colonization activities frequently included botanical teams specifically interested in identifying and describing the flora of the vast forested wilderness. As the growing Nation consumed more and more of its forest resource, concern about the future of that resource increased and the earliest cries of the conservationists were heard.

The forerunner of inventory, assessment, began in the late 1800s. Franklin B. Hough, the first forestry agent in the Department of Agriculture, prepared such a document in the 1870s. His assessment was the result of considerable personal observation plus the summary of available public and private records of forest harvest and land use activity. A landmark assessment of the timber situation was the "Capper Report" in 1920. These and other assessments did much to increase public awareness of the then rapidly depleting forests of the eastern United States. One major result was the passage of the Forestry Research (McSweeny-McNary) Act of 1928. Among other things, this act directed the Secretary of Agriculture to,"make and keep current a comprehensive inventory and analysis of the Nation's forest resources..."

The Forest Service of the US Department of Agriculture established Forest Survey units at the various Forestry Research Stations. Beginning on the west coast in 1930, these units have conducted periodic state-by-state inventories to determine the aerial extent of forest land along with the volume, growth, and condition of the trees occurring on these lands. In addition to the publication of state summaries of the inventory findings, there have been several national summaries with appropriate analyses and recommendations. The information provided has been used by industry, land managers, and public policymakers to direct and encourage various forestry related initiatives.

The 1960s and 1970s were decades of heightened concern over natural resources and the environment. The National Environmental Policy Act of 1970 laid out a policy relative to protecting the quality of environment. These concerns, in turn, produced a very active legislative period for forestry. The first major legislation was the Forest and Rangeland Renewable Resources Planning Act (RPA) of 1974. This law put major emphasis on long-range planning for forest and rangeland resources. In accomplishing this planning goal the Secretary of Agriculture was directed to, "make and keep current a comprehensive inventory and analysis of the present and prospective conditions of and requirements for the renewable resources of the forest and range lands of the United States..." In developing a program to accomplish the goals of the RPA, the Forest Survey expanded its data collection activities in order to provide information on the several resources occurring on forest and range lands --- forage, recreation, timber, water, wildlife habitat. A new term, multi-resource inventory, entered the vocabulary of the inventory specialist. Other legislation such as the Federal Land Policy and Management Act of 1976 and the Soil and Water Conservation Act of 1977 shares common themes with the RPA in providing specific direction to the Bureau of Land Management and the Soil Conservation Service.

Quite recently, the forestry community has been confronted with the issue of "acid rain" and the question of damage to forests. Existing inventory data and measurement procedures have served a broad and useful monitoring function by alerting us to changes in growth trends and other measures of forest condition. However, we are unable to fully address the concerns and to provide more specific responses because these inventories were not designed with monitoring and hypothesis testing concerns in mind. The needed forest resource information base is beyond the capability of the existing regional inventory. We have arrived at a new juncture. In the opinion of many experts, the concerns over regional forest health impacts by atmospheric deposition and other anthropogenic factors can only be addressed with information obtained by monitoring the forest. Public support for such an activity is growing and Congress has supported its development in the funding of the National Vegetation Survey of the Forest Response Program. The Program Charter of the National Vegetation Survey specifically calls for the development of a plan for the long term monitoring of the forest.

In this brief historical overview, I have noted the continuing interest in the significant forest resource of the United States. Specifically, I have show how the public appetite for resource information has progressed through four stages: (1) taxonomic curiosity, (2) observational assessment, (3) statistical inventory, and (4) resource monitoring.

Today, Americans are quick to react to any issue or problem that appears to threaten the forest. The injury and death of trees in the forest by a variety of vectors is part of the natural rhythm of the ecosystem. When injury or death occurs as an isolated incident, the natural resiliency of the system enables the forest to maintain an overall healthy state. However, when large numbers of trees or extensive areas of the forest are impacted, there is reason for concern. The need for factual information and correct interpretation of forest health and condition is essential. Public policy, land management, and individual ownership decisions with important social and economic impact must be made.

OVERVIEW - INVENTORY AND MONITORING

Let me begin this discussion by defining the two concepts-- inventory and monitoring, within a forestry context. Inventory is the enumeration of pertinent data such as area, species, diameter, volume, increment, mortality, etc., for the assessment of particular forest characteristics such as productivity, health, or damage at a particular point in time. Repeated continuous inventory implies the regular enumeration of particular characteristics in such a way as to provide a check on the changes taking place in that characteristic. Monitoring is the repeated recording or sampling of similar pertinent data for the comparison of that data to a reference system or identified baseline. It may include on-the-ground intelligence gathering and analysis of information from extraneous sources in addition to conventional, repetitive remotely-sensed data collection. Monitoring always involves the determination of changes over time and usually also involves interpretation with respect to the reference or baseline.

Monitoring can be divided into two broad categories of application having major differences in locational specificity, parametric detail, and time reference. The first category, descriptive monitoring, is directed at the provision of a regional basis of information for formulation of public policy and for signaling alarms relative to broad-scale environmental degradation. The second category, location-specific monitoring, is conducted for prescriptive purposes relative to implementation of management plans or impact assessment for particular tracts or habitats. In regional descriptive monitoring, aggregation of samples for purposes of estimation takes place over relatively extensive zones of political or ecological influence with low spatial densities of samples being sufficient to provide large sample sizes in the statistical sense.For regional descriptive purposes it may even suffice to be cognizant of trends rather than absolute levels, making it possible to track the behavior of composite environmental indexes in much the same manner as a physician tracks body temperature and blood pressure. For such cases, the focus of attention becomes formulation and interpretation of suitable indexes with comparison against a historical data base. In contrast, prescriptive monitoring to support local managerial action and impact assessment necessitates high spatial densities of samples to achieve even minimal sample sizes for stringent accuracy requirements pertaining to relatively small areas. In the latter case, production functions must be estimated in absolute terms and projected into the future.

A rather obvious point to note is that forest resource populations typically consist of large numbers of individual elements distributed over appreciable areas in such a manner that it is either logistically impossible or economically impractical to conduct a complete census. Forest resource inventory in the United States is based on statistical sampling methods. Sampling technology is an indispensable part of the process. Consequently, forest sampling for resource inventory relies on perhaps the largest body of technical estimation procedures among the natural resource disciplines.

Less obvious is the broad commonality among existing approaches to both the inventory and monitoring of forest resources. The conduct of either normally involves three fundamental components. The first component is an area classification or stratification portion in which relatively homogeneous environments are recognized. The second part is a direct measurement component in which selected readily observable characteristics are determined for a sample of population elements. The third part is an indirect measurement component in which less readily observable characteristics of the sampled elements are inferred through mathematical models of the resource developed in advance and driven by variables measured in the second phase. This third component may be absent in some cases, but such cases are becoming less frequent as ecological knowledge develops. Each of these phases may involve several subcomponents and alternative designs. Quite different types of technologies are involved in the respective components. Remote sensing and geographic information systems dominate the first component. Sampling theory, plot design, mensurational techniques and collection apparatus dominate the second component. Ecological theory, mathematical formulation, and algorithms dominate the third component.

APPROACHING THE PROCESS

A plethora of proceedings of scientific gatherings and other publications are available to enlighten one on the design and conduct of natural resource surveys (Ware and Cunia 1962; Loetsch and Haller 1964; Loetsch, Zohrer and Haller 1973; Cunia 1974; Frayer, Hartman and Bower 1974; Avery 1975; Lund, LaBau, Ffolliott and Robinson 1978; Anonymous 1978; Frayer 1979; Nishizawa 1981; Brann, House and Lund 1982; Bell and Atterbury 1983; Patil 1985; Schmid-Haas 1985). One message is clearly stated throughout all these, "begin by specifying the objectives."

From my years of experience with all aspects of forest resource inventory, I have identified four stages to the process: (1) Define, (2) Design, (3) Develop, (4) Display. **Define** the information needs by evaluating existing information on the topic, specifying the objectives and the analytical process, and identifying the constraints such as funding, time, etc. **Design** appropriate sampling solutions using the objectives expressed in statistical terms. Identify the data to be collected and the collection procedures to be used. **Develop** the data by the methods identified. **Display** the results by appropriate means taking advantage of information processing systems. Include appropriate analysis and interpretation of outputs. I believe this process is appropriate to follow in the design of specific forest monitoring programs.

Cunia (1982) proposes the following nine-step activity schedule:

1. Specify the objectives
2. Define the target population
3. Decide on data collection and measurement methods
4. Construct a frame for the population
5. Design the sampling method

6. Write down a set of general instructions
7. Train the field personnel
8. Do the field work
9. Data processing, analysis, and presentation of results.

Thomas and Wensel (in press) have developed a rigorous model for inventory (or monitoring) system development. They present distinctions in the design process that have not been well developed in the literature and demonstrate the application of the process in the context of several remote sensing-aided inventory experiments. Their model incorporates the ideas identified above with specifically identified opportunities for both new techniques development and performance evaluation.

The current methodologies for inventory or monitoring are workable. The continuing effective development of forest resource data by agencies of both the federal and state governments as well as many private companies and consultants is sufficient evidence of the fact. None-the-less there is room for improvement in all aspects through further research. Specific areas of high interest include: (1) the application and further development of remote sensing techniques, (2) increased use of geographic information systems, (3) further research on estimation methods and mensurational techniques, and (4) ecological studies to provide better understanding of ecosystem dynamics in order to improve the use of model-based indirect estimation procedures.

CURRENT APPLICATION OF MEASUREMENT SYSTEMS

A measurement system should provide the user with the capability to (1) identify and/or measure parameters of interest for individuals in the population (2) use this information in making inferences about the population (3) make a statement about the reliability of the population inferences (describe the error structure). With the possible exception of the Scandinavian region of Europe, the use of statistical sampling designs for forest resource measurements has only recently been recognized outside the United States. In some parts of the world there are still arguments going on for and against the use of statistical methods for forest resource enumeration (Cunia, 1974).

Four major categories of measurement systems have been identified by Cunia (1978): (1) complete enumeration techniques, (2) stand based techniques, (3) one occasion sampling techniques, and (4) successive occasion sampling techniques. The forest resource of the US is so vast that regional inventory and monitoring is dependent on sampling methodology. With this in mind, I will emphasize those methods in which sampling is paramount and give only minimal attention to the others.

As the name implies, the complete enumeration technique requires that every individual in the population of interest be visited in the field and measured. Since the entire population is sampled, there is no requirement for the development of statistical summaries to demonstrate the reliability of the data. The use of this technique for regional forest information needs in the United States is both logistically and economically infeasible.

Stand based techniques begin by subdividing the forest area into homogeneous stands of roughly the same age, species composition and site quality. Then, the stand is visited in the field, its general conditions or main parameters ocularly estimated and recorded. Finally, the parameters of interest within the stand are obtained from previously constructed tables or models according to the specific stand parameters and general description. Due to the subjective character of this method, no statistical statement can be made about the precision of the estimates. This technique is presently applied in the United States and Canada whenever the unit in the forest management system is the individual forest stand. This is the case, for example, in the southeastern United States where the volume and growth of the pine plantations is often estimated by yield tables or growth and yield functions. Another American system of stand based inventory is that of the Weyerhaeuser Company.

Sampling is based on the rules of probability (Avery 1975). In forest resource surveys, the basic objectives of the information gathering activity from a time perspective are to provide either one point in time information or continuing information at designated intervals. The measurement systems employed to gather the data are called one occasion sampling techniques and successive occasion sampling techniques. The principle difference between the two techniques is in the planned permanence of the basic sampling unit not in the statistical procedures used to select the sample and to expand the measurement data to population estimators.

The basic premise of the one occasion technique is that all data collection will be of a temporary nature. Individual samples and sampling units are not intended for use in recurring evaluations of the population. One may take another inventory periodically using any number of appropriate statistical procedures. However, since the inventories are independent of each other, the precision of each inventory's estimates of the change during the interval is very low. The reason for this can be easily demonstrated; the variance of the difference between two statistically independent estimates is equal to the sum of their variances (Cunia 1978).

Successive occasion techniques are intended to satisfy the need for a continuous flow of updated resource information. To accomplish this, data gathering needs to occur periodically at permanent sample locations. What seemed obvious to statisticians became intuitively obvious to some American Foresters some fifty years ago. A set of systematically selected and permanently established ground plots that could be measured at any desired point in time would provide a basic inventory system which preserved the same precision for current estimates (for equal number of plots) but increased tremendously the precision of the change component estimates. And this is how Continuous Forest Inventory or CFI came into being.

The classical CFI system makes use of systematically selected sample plots of fixed area. The main advantage of systematic sampling is the simplicity with which it can be applied in the field. In addition, it is generally more efficient than the simple random sampling, its most obvious alternative; because the sample units are much more evenly spread over the area of interest. The main disadvantage, however, is that one cannot derive statistically acceptable expressions for the precision of estimates. Empirical studies made in several countries have shown that treating the systematic sampling as random, results in an overestimation of the standard error (Cunia 1978). This problem can be solved by introducing random selection procedures. Double sampling in which the first phase stratifies the population allows for the efficient application of random selection procedures in the second phase.

Judging by the success of their application, several statistical concepts have provided major improvements in the execution of successive occasion sampling. Over twenty years ago it became obvious that the efficiency of the CFI system could be greatly improved if at remeasurement time, only a part of the permanent plots were remeasured with the remaining part replaced by a new set of sample plots; this is the basic concept of sampling with partial replacement or SPR (Ware and Cunia 1962). Sampling with partial replacement allows for the refreshment or replenishment of sample units at each successive measurement occasion. In addition, it incorporates the efficiency of regression techniques in the development of population information (Barnard 1974). More recently, the 3P Sampling concept (Lund 1975) and list sampling with probability proportional to size (Stage 1971) have been applied to the remeasurement of previously established plots.

As a generalization, today successive regional and state forest resource inventories are based on a double sampling for stratification procedure in which the first phase consists of the interpretation of remote sensing imagery to identify and stratify areas or points and the second phase is a subsample of ground plots at which a considerable amount of detailed data is collected. This low-intensity sample provides valid resource data only for relatively large areas. Three different approaches to resource data collection in the ground-plot phase are currently employed. The data are collected (a) on a fixed area, (b) by probability proportional to the area occupied by the stem, or (c) by probability proportional to prediction of some other selected attribute for individual trees occurring within a specified area or subarea (Poisson or 3P selection). In fixed-area sampling a designated area about a point is canvassed, and every plant stem having the indicated attributes is evaluated. This method samples vegetation proportional to its occurrence and often results in a minimal sample of candidates with the most desired attributes. It provides a constant area reference and is most satisfactory for repetitive measurements of the vegetation for change determination. With probability proportional to area occupied, plant stems are selected for evaluation when the cross-section at a set height exceeds a predetermined critical angle as viewed from plot center. The area represented by the individual sample candidate varies, however, according to candidate size. Collecting vegetation data using probability proportional to prediction is a technique that applies the efficiency of variable probability selection methods. The basic premise is that some estimate of the desired candidate is better than a mere count of the candidate and that these estimates may be corrected for bias by more fully sampling a smaller number of accurately measured candidates. The selection of candidates for accurate measurement is according to a probability rule with such probability proportional to the estimate made for the candidate. (Barnard et al. 1985)

The implementation of monitoring is similar in concept to that discussed above for inventory. The principal differences are in the degree and intensity of sampling and parametric detail, the frequency of sample collection, and instrumentation. None-the-less, monitoring adds considerable complexity to the inventory task. Since monitoring always implies the ability to determine change both in direction and magnitude, a system which anticipates future needs while maintaining continuity with the past is necessary. Probably the major problem confronting us in developing a monitoring capability is our limited understanding of the world in ecological terms. We have technical problems as well. A major one is the need for stable definitions and standards. Movement can only be described in relation to a fixed point and measured in terms of standards sensitive to change. We currently lack the ability to describe natural change and its variability in such a way that we can develop procedures and analytical techniques with significant sensitivity to identify the unnatural. (Wikstrom 1980)

CONCLUSION

Continuing interest in the significant forest resource of the nation has spawned the development and implementation of a variety of survey procedures. Current concern about the health of these forests with particular reference to anthropogenic factors has moved the forestry professional into the doorway of regional forest monitoring. Present systems for providing forest resource information are inventory efforts which depend on well developed statistical, mensurational, and remote sensing methodologies. While the distinction between inventory and monitoring is principally one of degree and timing, the implementation of regional monitoring awaits the development of an appropriate strategy and specific procedural detail.

REFERENCES CITED

Anonymous, editor. 1978. National Forest Inventory. 1978 June 18-26; Bucuresti, Romania.

Avery, T.E. 1975. Natural Resources Measurements. New York: McGraw-Hill, Inc. 331 p.

Barnard, J. 1974. Sampling with Partial Replacement Contrasted with Complete Remeasurement Inventory Designs: An Empirical Examination. pp. 384-390. In: Cunia, Tiberius, editor. Monitoring Forest Environment Through Successive Sampling. 1974 June 24-26; Syracuse, New York. State University of New York, College of Environmental Science and Forestry, Syracuse, New York.

Barnard, J., Myers, W., Pearce, J., Ramsey, F., Sissenwine, M., Smith, W. 1985. Surveys for Monitoring Changes and Trends in Renewable Resources: Forests and Marine Fisheries. American Statistician. 39 (4,Pt2) 363-373.

Bell, J.F., Atterbury, T., editor. 1983. Renewable Resource Inventories for Monitoring Changes and Trends. Proceedings, An International Conference; 1983 August 15-19; Corvallis, Oregon: College of Forestry, Oregon State University, Corvallis, OR 97331-5704.

Brann, T.B., House IV, L.O., Lund, H.G. editor. 1982. Proceedings of a National Workshop In-Place Resource Inventories: Principles & Practices; 1981 August 9-14; University of Maine, Orono, Maine. Society of American Foresters, Bethesda, Maryland.

Cunia, T., editor. 1974. Monitoring Forest Environment Through Successive Sampling. 1974 June 24-26; Syracuse, New York. State University of New York, College of Environmental Science and Forestry, Syracuse, New York.

Cunia, T. 1974. Forest Inventory Sampling Designs Used in Countries other than the United States and Canada. pp. 76-110. In: Frayer, W.E.; Hartman, George B.; Bower, David R., editor. Inventory Design & Analysis. 1974 July 23-25; Colorado State University, Fort Collins, Colorado. Inventory Working Group, Society of American Foresters, 1010 Sixteenth Street, N.W., Washington, D.C. 20036.

Cunia, T. 1978. A Short Survey of the Worldwide ForestInventory Methodology. pp. 114-120. In: Lund, H. Gyde; LaBau, Vernon J.; Ffolliott, Peter F.; Robinson, David W. tech. coord. Proceedings of the Workshop Integrated Inventories of Renewable Natural Resources: 1978 January 8-12; Tucson, Arizona. Gen. Tech. Rep. RM-55. Fort Collins,Colorado: U.S. Department of Agriculture, Rocky Mountain Forest and Range Experiment Station.

Cunia, T. 1982. The Needs and Basis of Sampling. pp 315-325.In: Brann, T.B, House IV, L.O., Lund, H.G., editor. Proceedings of a Natural Workshop In-Place Resource Inventories: Principles & Practices; 1981 August 9-14; University of Maine, Orono, Maine. Society of American Foresters, Bethesda, Maryland.

Frayer, W.E., editor. 1979. Workshop Proceedings ForestResource Inventories. (Vol. 1 & 2) 1979 July 23-26; Fort Collins, Colorado. Department of Forest and Wood Sciences, Colorado State University, Fort Collins, Colorado.

Frayer, W.E.; Hartman, G.B., Bower, D.R., editor. 1974.Inventory Design & Analysis. 1974 July 23-25; Colorado State University, Fort Collins, Colorado. Inventory Working Group, Society of American Foresters, 1010 Sixteenth Street, N.W., Washington, D.C. 20036.

Loetsch, F.; and Haller, K.E. 1964. Forest Inventory. Vol. I. BLV Verlagsgesellschaft, Munchen. 434 p.

Loetsch, F.; Zahrer, F.; Haller, K.E. 1973. Forest Inventory. Vol. II. BLV Verlagsgesellschaft, Munchen. 417 p.

Lund, H. G. 1975. 3 P sampling: annotated bibliography.USDA For. Northeast. Area, State and Private For., Upper Darby,PA.

Lund, H. G., LaBau, V.J., Ffolliott, P.F., Robinson, D.W., tech. coord. 1978. Proceedings of the Workshop Integrated Inventories of Renewable Natural Resources: 1978 January 8-12; Tucson, Arizona. Gen. Tech. Rep. RM-55. Fort Collins, Colorado: U.S. Department of Agriculture, Rocky Mountain Forest and Range Experiment Station.

Nishizawa, M., editor. 1981. Proceedings of Forest ResourceInventory, Growth Models, Management Planning, and Remote Sensing. 1981 Sept. 6-12; Kyoto Japan. Japan Association for Forestry Statistics, Niigata University, Faculty of Agriculture, Lab of Forest Mensuration, 2-8050 Ikarashi, Niigata 950-21, Japan.

Patil, G.P. 1985. Fishery and Forest Management. American Statistician. 39 (4,Pt2) 361.

Schmid-Haas, P. 1985. Inventorying and Monitoring EndangeredForests. IUFRO; 1985 August 19-24; Zurich. Birmensdorf, Switzerland: Swiss Federal Institutute of Forestry Research, CH-8903 Birmensdorf, Switzerland.

Thomas, R.W. and Wensel, L.C. 1986. A Model for Inventory System Development (In Press-Forest Science)

Stage, A.R. 1971. Sampling with probability proportional to size from a sorted list. USDA For. Serv. Res. Pap. INT-88.

Ware, K.D.; and Cunia, T. 1962 Continuous Forest Inventory with Partial Replacement of Samples. Washington: Society of American Foresters. 40 p.

Wikstrom, J.H. 1980. Monitoring Change in Forest and RangeLand and Associated Renewable Resources Use, Supply and Condition in the United States. pp. 253-261. In: Schmid-Haas, Paul and Johnson, Klaus, tech. coord. Growth of Single Trees and Development of Stands: Papers; 1979 September 10-14; Vienna. Birmensdorf, Switzerland: Swill FederalInstitute of Forestry Research, CH-8903 Birmensdorf, Switzerland.