Accurately predicting multi-decadal interactions between increasing atmospheric CO_2 and forest ecosystems is critical for setting carbon management policy (Comins 1997). Given that wood has high C:N ratios (up to 500) and long turnover times (100+ years) (Townsend et al. 1996), changes in wood productivity can greatly affect whether forests store carbon and slow the increase of atmospheric CO_2 or release carbon and exacerbate it (Rastetter et al. 1991). Ability to predict carbon sequestration by forests hinges on understanding of the role of increased nitrogen deposition on tree growth (GCTE 1999). A solid understanding of the role of nitrogen on tree growth should include the effects of changing nitrogen deposition on productivity levels of ecosystem components (Curtis et al. 1994). However, current understanding of multi-decadal effects of nitrogen deposition on wood productivity needs strengthening (Magill et al. 1997).

The goals of the research proposed herein are to improve understanding of the multi-decadal role of increased nitrogen deposition on tree growth and then apply that knowledge in modeling carbon sequestration by forests. The key features of this research include (1) study of mature, natural forest ecosystems along a steep gradient of nitrogen deposition, (2) fine-scaled spatial analyses of relative soil nitrogen availability for each sampled tree, (3) dendrochronological analyses of trends in relative ring width, nitrogen concentration, and C:N ratios through past time, and (4) explicit statistical linking of variation in temporal trends of tree growth to spatial trends in nitrogen availability. The specific tasks of this proposed research are as follows:

1. Measure and compare ring width and soil nitrogen availability at the tree scale within subalpine forests along a steep gradient of nitrogen deposition. Initially, sites downwind of Los Angeles with heavy nitrogen deposition will be compared to one in Baja California that putatively has ambient nitrogen deposition. Trends in relative ring width of trees spanning all microsite conditions will be modeled with the relative nitrogen availability for those trees. Such modeling at the tree scale will help identify the soil/microsite conditions that mediate nutrient availability as well as the areal extent of the forest that is truly affected by increased nitrogen deposition. This approach will identify primary effects of changing nitrogen availability on relative tree growth of recent decades.
2. Measure nitrogen within tree rings to interpret temporal variation of nitrogen assimilation by trees as proxy for nitrogen availability. Given that ring nitrogen variation is independent of ring widths, a combined analysis of width and nitrogen will isolate the role of nitrogen deposition in tree productivity. This task will require the following basic research:
   A. Refine analytical protocols for unambiguously measuring nitrogen in tree rings. For this, rings without temporal variation in nitrogen concentration will be tested using various wood pre-treatment and measurement strategies to obtain time series with no temporal variation in nitrogen concentration. Such rings will be from periods prior to anthropogenic impacts (e.g., from centuries ago) and without severe disturbance (e.g., no fire scars). Additionally, rings of trees with a labeled ^{15}N fertilization treatment will be measured to track cross-ring mobility of nitrogen.

   B. Calibrate the nitrogen and C:N responses in tree rings to known changes in nitrogen availability. For this, trees from controlled fertilization experiments will be tested.
3. Incorporate improved understanding of the role of the nitrogen on tree growth into existing models of changing nutrient levels and CO_2 on forest productivity. This incorporation will be in the form of improved parameterization for linking responses of tree growth to changing environmental conditions so that models predict future scenarios realistically.

PRESENT STATE OF KNOWLEDGE

Increased Atmospheric CO_2 and Nitrogen Deposition

Atmospheric concentration of CO_2 has been steadily increasing for several decades, especially during the most recent few decades (Hanson et al. 1998). Atmospheric CO_2 has increased from ~300 ppm to ~360 ppm since the end of the last century, primarily as a result of emissions from fossil fuel combustion and wide-scale deforestation (Tans et al. 1990). As a radiatively active greenhouse gas, increased CO_2 affects Earth's climate (Rind and Overpeck 1993), especially temperature, which has also been rising recently (Hulme and Jones 1994). While the role of increasing CO_2 on the current global warming trend is a leading ecological issue at present (Idso 1988; Tol and de Vos 1993), accurately accounting for all components of the global carbon cycling is critical and terrestrial plants are one possible sink for this increased atmospheric carbon (Tans et al. 1990; Kheshgi et al. 1996).

Carbon is an essential macronutrient for plant growth, and as CO_2 is a reactant in the photosynthesis equation (Kramer and Kozlowski 1979), its increasing availability should favor photosynthesis and increase plant growth. Accordingly, observed increases in relative tree growth of some dendrochronological studies has been ascribed tentatively to increasing atmospheric CO_2 as a direct stimulation effect (LaMarche et al. 1984; Jacoby 1986). An important implication of such an interpretation is that global plant biota may ameliorate the anthropogenic increase in atmospheric CO_2, as well as its effects on climate, merely by increased productivity.

However, the potential role of plant biota in ameliorating the anthropogenic increase in atmospheric CO_2, and more generally the global carbon budget, is not clear (Rastetter et al. 1991; Galloway et al. 1995; Townsend et al. 1996). Plant growth response to elevated CO_2 may depend upon the availability of other resources, namely macronutrients that are otherwise typically limiting, especially nitrogen (Johnson and Ball 1990/91; Vitousek and Howarth 1991). Low soil nitrogen availability may severely limit positive growth responses of vegetation to increased CO_2 (Curtis et al. 1994) while greater nitrogen availability may increase the capacity of forests to respond to increased atmospheric CO_2 (Sinclair 1992). Thus, changes in nitrogen availability can alter the global cycle of carbon by regulating plant growth and affecting both the rate of increase of atmospheric CO_2 and the response of ecosystems to that increase (Vitousek et al. 1997).

The most fundamental human-caused change in the global nitrogen cycle is the recent doubling of the transfer from the vast and unreactive atmospheric pool to biologically available forms on land (Vitousek et al. 1997). The increasing deposition of nitrogen onto terrestrial ecosystems in recent decades is a byproduct of internal combustion, fertilizer production, and cultivation of nitrogen-fixing plants (Galloway et al. 1995). This anthropogenic nitrogen deposition has been recorded in ice layers of Greenland as a phenomenon of at least the Northern Hemisphere (Mayewski et al. 1986, 1990, Figure 1). The added nitrogen is deposited unevenly in the Northern Hemisphere, with temperate zones being profoundly altered (Vitousek et al. 1997).

Therefore, it is possible that increases in both nitrogen availability and atmospheric CO_2 may be causing observed increased tree growth as a complex interactive environmental phenomenon (Haettenschwiler et al. 1996). Indeed, another conjecture about observed increased tree growth in some natural forests of North America (LaMarche et al. 1984) and Europe (Spiecker et al. 1996) is that it may be caused by the higher nitrogen availability as an effect of low-grade but persistent nitrogen deposition (Johnson and Ball 1990/91).

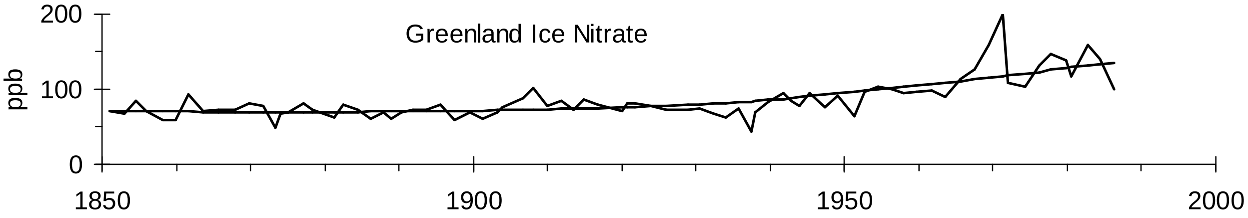

Figure 1. Time series of nitrate deposition in Greenland ice (Mayewski et al. 1986, 1990).

On the other hand, increased nitrogen deposition may play only a minor role in carbon sequestration, in part because nitrogen itself is a minor component of woody tissue (Nadelhoffer et al. 1999a, b) and because experimental nitrogen applications have not always resulted in increased wood production (Aber et al. 1993b, Magill et al. 1997). Given that wood C:N ratios are very high (up to 500), even subtle changes in wood productivity can greatly affect whether terrestrial ecosystems store carbon and slow the increase of atmospheric CO_2 or release carbon and exacerbate the increase of atmospheric CO_2 (Rastetter et al. 1991). Consequently, improved understanding of the role of increased nitrogen deposition on tree growth will be critical for understanding carbon cycling (Magill et al. 1997; Kiefer and Fenn 1997).

At a minimum, a better understanding of the web of interactions of multi-decadal changes in CO_2 and nutrient levels, as well as in temperature and moisture, is desirable (Johnson and Ball 1990/91; Norby 1998). This objective is part of the core project of Global Change and Terrestrial Ecosystems Program of the International Geosphere-Biosphere Program (GCTE 1999): To determine through case studies how these different anthropogenic stresses affect ecosystem productivity and processes, and to determine why ecosystems respond differently. Studies should focus on mature forest ecosystems, particularly with undisturbed soils (GCTE 1999), and they should assess long-term responses of forest ecosystems to nitrogen deposition (Aber et al. 1993b). While much past research on this topic has employed intensive site-level controlled experimentation (Aber et al. 1993b; Kahl et al. 1993; McNulty and Aber 1993; McNulty et al. 1996; Currie et al. 1996; Magill et al. 1996, 1997; Nadelhoffer et al. 1999a,b), less research has been done analyzing past tree growth along a space-for-time nitrogen deposition gradient (the strategy proposed herein), and a combination of both approaches would be ideal (Aber et al. 1998). Indeed, retrospective information in this regard would help establish "normal" processes of the past against which to assess current "abnormal" departures (Arbaugh et al. 1999b; Biondi 1999).

General Research Objective and Strategy: The goals of the research proposed herein are to improve understanding of the multi-decadal role of increased nitrogen deposition on tree growth and then apply that knowledge to modeling of carbon sequestration by forests. The key features of this research include (1) study of mature, natural forest ecosystems along a steep gradient of nitrogen deposition, (2) fine-scaled spatial analyses of relative nitrogen soil availability and tree growth , (3) dendrochronological analyses of relative trends in ring width and nitrogen concentration through past time, and (4) explicit statistical linking of variation in temporal trends of tree growth to spatial trends in nitrogen availability.

Effects of Increased Nitrogen Deposition on Tree Growth

By itself, this extra nitrogen deposition can impact plant growth in various ways. Nitrogen is an essential macronutrient for plant growth, one that is limited in ionic forms in terrestrial ecosystems (Pritchett and Fisher 1987). More generally, accumulation rates of biomass in terrestrial ecosystems are typically limited by nitrogen supply (Vitousek et al. 1997) and can increase with nitrogen fertilization (McNulty and Aber 1993). Most temperate forest ecosystems have a significant capacity to assimilate and retain additional nitrogen (Aber 1992), and therefore a likely initial response to increased nitrogen inputs is increased tree growth (Johnson and Ball 1990/91; Aber 1992). Indeed, many direct nitrogen fertilization experiments have shown increased tree growth in controlled situations (Kenk and Fisher 1988; Johnson 1992).

On the other hand, excessive nitrogen deposition may harm forest ecosystems (Bytnerowicz and Fenn 1996). Nitrogen saturation may be defined as the availability of ammonium and nitrate in excess of total combined plant and microbial demand over a long period of time (Ågren and Bosatta 1988; Aber et al. 1989). Among other deleterious effects, nitrogen saturation may cause soil deficiencies of cationic macronutrients, toxic nitrate loads in hydrological outflow, and increased emissions of greenhouse gas oxides of nitrogen (Skeffington 1990; Vitousek et al. 1997; Miller et al. 1998). The forest floor plays a key role in the nitrogen saturation status of a forest ecosystem (Currie et al. 1996), and evidence of nitrogen saturation does not necessarily imply that forest health is impacted (Skeffington 1990; Fenn et al. 1996). Indeed, there is a little evidence for nitrogen saturation from atmospheric deposition causing nutrient deficiencies and forest decline in North America (Johnson and Ball 1990/91), though it may be occurring in selected conifer forests of the Northeast (Aber et al. 1995) as well as in various areas of Europe (van Breeman and van Dijk 1988).

Furthermore, hemisphere-scale nitrogen deposition represents a continuous addition to background nitrogen availability to natural forests, which is quite different from one-time only applications of nitrogen as a fertilizer to intensively managed forests (Skeffington and Wilson 1988; Aber et al. 1989; Johnson and Ball 1990/91; Johnson 1992). In the endeavor to better understand current role of nitrogen deposition on tree growth and carbon sequestration, it would be helpful to compare the current anthropogenically affected nitrogen cycling with that of prior to extensive human alterations. However, as with many global changes, determining the background state of the nitrogen cycle is difficult, and our understanding of nitrogen cycle prior to the extensive human effects is still poor (Vitousek et al. 1997). To rectify this, studies of the long-term effects of nitrogen deposition and availability on plant community composition and health are needed (Bytnerowicz and Fenn 1996).

Specific Research Objective and Strategy: The first objective of the research proposed herein is to isolate and assess the effects of increasing nitrogen deposition on multi-decadal tree growth in mature, natural forests. This will be done initially with dendrochronological sampling of tree growth of high-elevation sites chosen along a steep gradient of nitrogen deposition and with quantitative analyses that factor out climate-tree growth relationships (Jacoby 1986; Cook 1987a). Such sites exist in southern and Baja California, where this proposed research will take place.

Soil Nutrient Availability: Linking Nitrogen Deposition to Tree Growth

Hemisphere-scale deposition of nitrogen over large regions is one thing, but nitrogen availability for individual tree uptake is another (Tamm 1989; Fenn and Bytnerowicz 1993). Nitrogen deposition can either harm or benefit soil nutrient availability depending upon inherent soil nutrient status (Johnson and Ball 1990/91), and soils play a key role in whether or not ecosystems become nitrogen saturated (Ågren and Bosatta 1988). For example, microorganisms in the soil and forest floor can immobilize nutrients (Johnson 1992), and even nitrogen-limited ecosystems can lose high levels of nitrate if soils are highly porous (Fenn et al. 1998). While plants can absorb some deposited nitrogen directly through foliage (Lovett and Lindberg 1993), most nitrogen enters forest ecosystems through the soil (Miller et al. 1979; Norby 1998). Thus, to truly understand the relationship between nitrogen deposition and tree growth, the link of soil nitrogen availability must be measured and understood.

Soil properties that regulate nutrient availability can vary dramatically across just a few meters (George et al. 1997; Poth and Wohlgemuth 1999) such that neighboring trees might be growing in soils of substantially different quality (Curtis et al. 1994). Trends in tree growth can also vary across neighboring trees, and it is ecologically intuitive that spatial variation in tree growth is causally related to some degree with that of soil quality such that relationships between tree growth and nutrient availability can be quantified within sites (Fritts 1976). The strength of these relationships across different sites with different levels of nitrogen deposition can be exploited to isolate the separate effects of nitrogen deposition on tree growth from those of other environmental influences. If nitrogen deposition were affecting tree growth, then recent trends in tree growth would correlate strongly with relative nitrogen availability within sites, especially within a site with heavy nitrogen deposition. Such an effect would be noticeably weaker at a site with ambient nitrogen deposition. If tree growth-nitrogen availability relationships were similar across such different sites, then perhaps the role of nitrogen deposition on tree growth is weak.

Specific Research Objective and Strategy: The second objective of the research proposed herein is to model relative soil nutrient availability and ring-width trends at the tree scale within sites along the gradient of nitrogen deposition of southern and Baja California. Differences in tree growth-nutrient relationships between and within sites will be exploited to isolate the separate effects of nitrogen deposition and availability on tree growth and just how soils mediate the availability of the nitrogen deposition. I have already performed this kind of investigation on a small (0.2 ha) subalpine site, where significant relationships existed between recent tree growth and current nitrogen availability (Sheppard et al., in review; see also Results from Prior NSF Support).

Measuring and Interpreting Nitrogen in Tree Rings

According to the core project of Global Change and Terrestrial Ecosystems program of the International Geosphere-Biosphere Program, chemical analysis of plant tissues should complement field research on effects of nitrogen deposition on plant growth (GCTE 1999). Such data would confirm if or when increased nitrogen deposition began affecting tree growth in a particular forest, stand, or tree. For this, it would be ideal to be able to interpret nitrogen concentration in dated tree rings themselves to complete the link of nitrogen deposition-availability-uptake-assimilation from time periods prior to anthropogenic increases in nitrogen deposition (Lewis 1995). Additionally, assessing trends in wood C:N ratio would be important because that variable represents the carbon storage capability of forests (Comins 1997).

One difficulty in achieving this ideal is that uncertainty exists around what to expect in nitrogen concentration in tree rings as a result of changes in nitrogen availability and uptake. One scenario is that a low but constant rate of nitrogen deposition will not lead to detectable increases in ring nitrogen concentration, but rather it may cause a gradual increase in tissue biomass with a constant nitrogen concentration (Aber et al. 1989). An alternative scenario is that greater nitrogen availability may lead to higher nitrogen levels in plant tissues (Fenn 1991). Yet another scenario is that increased nitrogen uptake may precede increased tree growth, possibly resulting in a ring-nitrogen response that is temporally independent of a ring-width response (Miller and Miller 1988).

Another difficulty in achieving the ideal of interpreting nitrogen concentration in tree rings is that nitrogen is notoriously mobile across plant tissues, rendering questionable its interpretability in tree rings as temporal indicators of environmental availability at the time of ring formation (Poulson et al. 1995). Nonetheless, there may be a measurable component of nitrogen that is immobile in tree rings as proteins within cell walls (Merrill and Cowling 1966), and such an immobile component may be interpretable as environmental availability of nitrogen through time (Sheppard and Thompson, in final prep.). Overcoming these two difficulties is a critical basic research need that must be met to accurately measure and unequivocally interpret nitrogen concentration in tree rings as indicators of past nitrogen availability-uptake-assimilation (Smith and Shortle 1996).

Specific Research Objective and Strategy: The third objective of the research proposed herein is (1) to refine protocols for accurately measuring nitrogen in tree rings and accounting for possible translocation of nitrogen across rings, and then (2) to calibrate the response of nitrogen concentration in tree rings to known changes in nitrogen availability. Measurement protocols will be refined by measuring nitrogen in rings that should have little temporal variation (e.g., rings formed hundreds of years ago in trees without evidence of severe disturbance. Responses of nitrogen content and C:N ratio in rings to known changes in availability will be identified by measuring rings from trees of controlled, long-term nitrogen fertilization experiments will be measured.

With these two basic research needs met, the dendrochemistry component of this proposed research will be merged with the southern and Baja California field components into a comprehensive analysis of the effects of regional deposition, site availability, and tree uptake and assimilation of nitrogen on tree growth. Given that nitrogen content in tree rings is legitimately interpretable for environmental nitrogen availability at the time of ring formation, I will measure nitrogen concentration and C:N ratio in rings from tree samples from field sites of heavy versus ambient nitrogen deposition. This will complete the link of deposition-availability-uptake-assimilation of nitrogen for determining its effects on tree growth in mature, natural ecosystems.

Applying Improved Understanding to Models of Deposition-Nutrient Cycling-Tree Growth

The practical utility of biogeochemical research often manifests itself in empirical models with which to test different environmental scenarios (inputs) to suggest various future responses (outcomes). Models play the important role of linking site-level data to regional-scale interpretations and then serve as a way of assessing policy strategies such as changes in the Clean Air Act (Aber et al. 1993a). Such models require quantified parameters such as those that relate nitrogen deposition to soil availability and to tree growth, and thus the primary results of this proposed research should be useful in larger modeling contexts. For example, the Nutrient Cycling Model (NuCM) and the Century Model have been run using data from forests of southern California to model effects of atmospheric deposition on soil processes and tree growth (Miller et al.

1998; Arbaugh et al. 1999a). Among their many input parameters are site physiography, soil chemistry, and vegetation growth, and their output results include plant growth versus time.

Recent research with these models has concluded that further refinement of parameters would be valuable in the study of long-term effects of nitrogen deposition on tree growth (McBride and Miller 1999). In general, for such models to maintain their utility as tools of understanding current and future interactions between forests and their changing environments, their parameters will always need updating when particular processes are better understood (Rastetter et al. 1991). In particular, the key features of study in this proposed research, i.e., links between changes in deposition-availability-assimilation of nitrogen and in multi-decadal tree growth along steep gradients of both nitrogen deposition and availability, should prove useful either for fine-tuning existing parameters of NuCM and Century or for adding in new parameters.

Specific Research Objective and Strategy: The fourth objective of this proposed research is to apply the understanding from this research in comprehensive models of the complex interactions of regional deposition, site availability, and tree uptake and assimilation of nitrogen on tree growth. This application will be in the form of either an improved quantification of existing model parameters for linking responses of trees and forests to changing environmental conditions and/or the addition of yet new parameters so that model outcomes match current reality more closely and predict future scenarios more realistically and with better confidence. The data from this research can also serve for validation testing of existing models.

RESULTS FROM PRIOR NSF SUPPORT

As part of my NSF-NATO Postdoctoral Fellowship (DGE-9633840, The Role of Soil Variation in Dendrochronology, ~$40,000 for 12 months [September 1996 through August 1997] at the University of Barcelona, Spain), I have done a preliminary study of relationships between relative ring-width growth and soil nutrient availability at the tree scale in a subalpine pine site. My postdoctoral research showed substantial spatial variation in nutrient availability, as measured using ion-exchange resins, across distances of only several meters within a small (0.2 ha) and apparently homogeneous tree-ring site (Sheppard et al., in review). Ion-exchange resins proved to be an excellent method for obtaining information on soil nutrient availability because they function similarly to tree roots with respect to nutrient absorption or uptake and therefore reflect reasonably well the availability of nutrients to trees (Skogley and Dobermann 1996; Dobermann et al. 1997). The current spatial pattern of variation of nutrient availability was assumed to reflect that of at least the last few decades (Billett et al. 1990). At least part of the spatial pattern of nutrient availability was related to geomorphic hillslope positions (e.g., summit, footslope, toeslope), which is thought to affect soil moisture and nutrient availability (Hall and Olson, 1991; Hammer et al. 1991). This phenomenon needs further investigation across more sites of different forest types. If it were true that geomorphic hillslope position correlated strongly with nutrient availability, then it would become important to add hillslope data to other physiographic variables that are normally recorded in dendrochronological field studies.

My postdoctoral research also showed significant correlations between recent trends in tree growth and current nutrient availability, especially nitrogen in the form of nitrate (Sheppard et al., in review). Consequently, measuring and analyzing soil nutrient availability at the tree level substantially enhanced the environmental interpretability of those dendrochronological data. Specifically, subgroups of trees within the tree-ring site were distinguished by nitrate availability and the subchronologies showed significantly different growth trends at the decadal scale. Trees

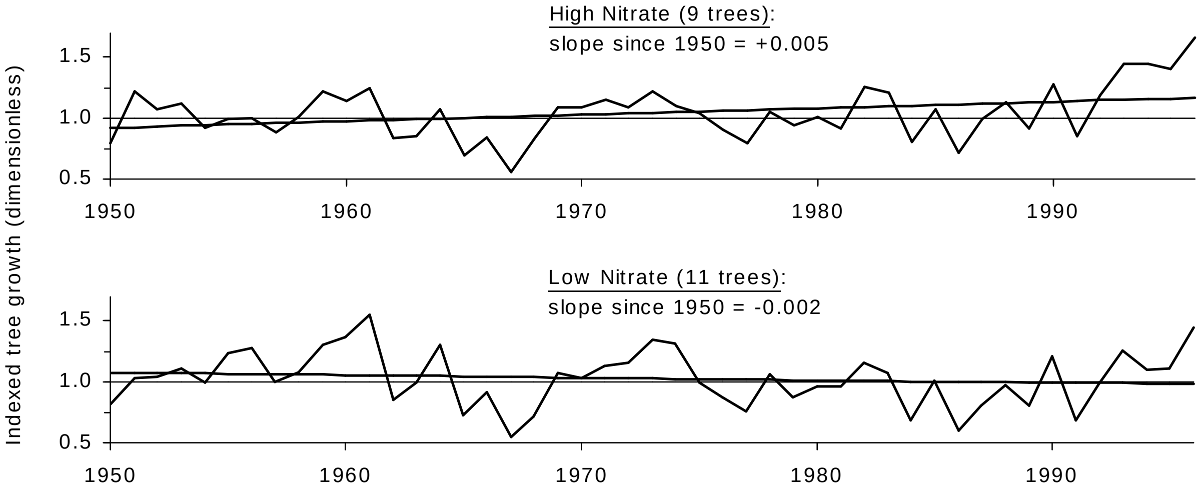

Figure 2. Results from NSF-NATO Postdoctoral research. Recent tree-ring growth within a site after accounting for variation soil nitrate availability (Sheppard et al., in review).

with high nitrate availability now have been growing better than expected since 1950 (Figure 2, top), while trees with low nitrate availability now have been growing merely as expected since 1950 (Figure 2, bottom). This research was then applied to modeling by adding a new parameter–current, relative soil nutrient availability–to the linear aggregate model of dendrochronology (Cook 1987b) to improve its function of isolating environmental signals in tree-ring data and better explaining total variance within dendrochronologies.

OTHER PERTINENT WORK IN PROGRESS

Field Study: Southern California Case Study

From prior work in the subalpine forest of Mt. San Jacinto of southern California (Figure 3), a dendrochronology of lodgepole pine shows a ramp of increasing growth since ~1950 (Figure 4, top). This ramp of increasing growth was originally interpreted as possible evidence of direct growth enhancement by increasing atmospheric CO_2 (Jacoby 1986). However, dendrochronological data collected since then from limber pines that are growing at essentially the same subalpine site as the lodgepole pines do not show similar growth trends since 1950 (Figure 4, bottom). Given that the trees of both chronologies exist within the same atmosphere and should experience equally its increasing CO_2, the interpretation that CO_2 is enhancing lodgepole pine growth–but not that of limber pine–is probably too simplistic.

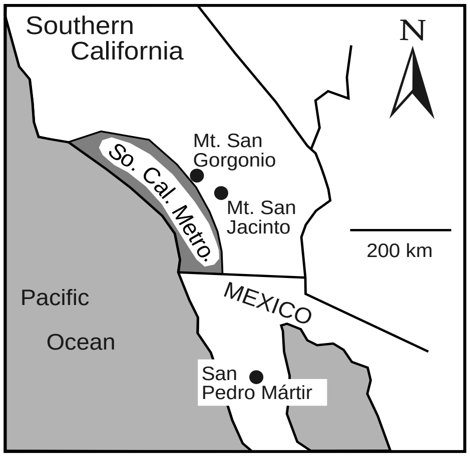

Figure 3. Map of field sites of southern and Baja California.

The difference in low-frequency trends since 1950 in the two San Jacinto chronologies (Figure 4) resembles that of the two subchronologies from my NSF-NATO postdoctoral research (Figure 2, Results From Prior NSF Support). While the different growth patterns at San Jacinto may depend in part on species, they probably also depend to at least some degree on different

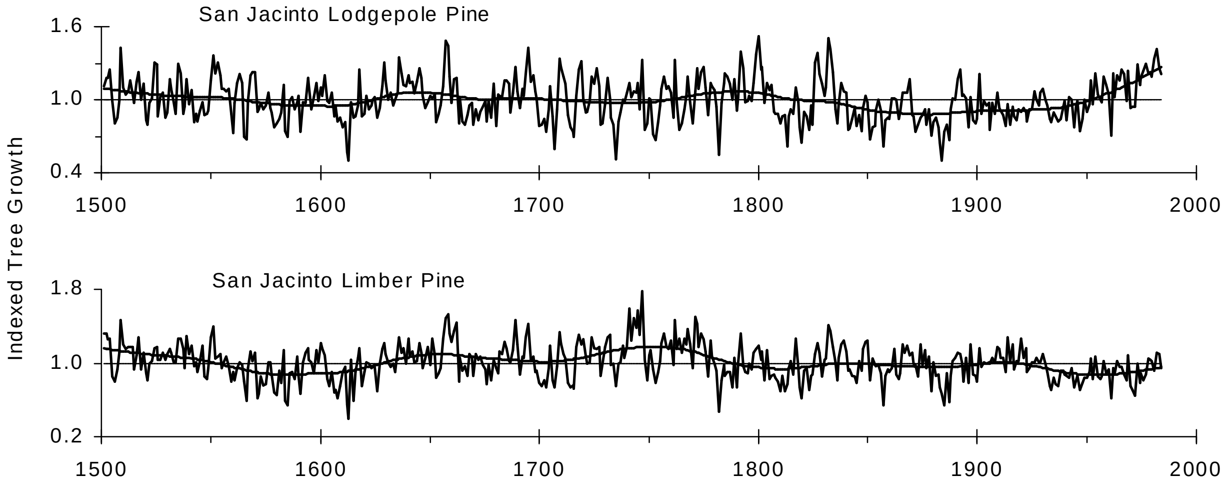

Figure 4. Tree growth of high-elevation pines of Mt. San Jacinto. Lodgepole pine is growing better than expected since 1950 (top, Jacoby 1986), but limber pine is growing about as expected since 1950 (bottom, Sheppard, unpublished data).

microsite qualities, especially those that affect soil quality and nutrient availability. Lodgepole pine of San Jacinto preferentially grows on flat sites with reasonably well developed soil while limber pine preferentially grows on steep slopes with relatively poor soils (Hamilton 1983). Furthermore, San Jacinto, which is located just downwind of the southern California metropolitan area (Figure 3), has been receiving deposition of nitrogen during recent decades (Takemoto et al. 1995). Thus, a reasonable alternative cause of the difference in growth trends since 1950 in the two San Jacinto chronologies (Figure 4) is that different soil qualities mediate different levels of nitrogen availability from its regional deposition (Kiefer and Fenn 1997). This suggests the obvious strategy of employing ion-exchange resins to actually quantify soil nutrient availability for dendrochronologically sampled trees of the San Jacinto site.

Dendrochemistry: Measuring Nitrogen in Tree Rings

Past dendrochemistry research has concluded that variation in nitrogen concentration of tree rings cannot provide information on past conditions of the environmental availability of nitrogen (Poulson et al. 1995). This conclusion stemmed from the general characteristic that nitrogen is highly mobile in xylem (Cutter and Guyette 1993) as well as from specific work that showed temporal variation of nitrogen concentration in tree rings to be related to effects of heartwood versus sapwood as well as the last rings formed (Merrill and Cowling 1966). However, various wood extraction and digestion pre-treatments have been tested to remove mobile forms of nitrogen from the rings prior to measuring nitrogen (Merrill and Cowling 1966), and such pre-treatment strategies might reduce the extraneous effects of heartwood versus sapwood and radial translocation that affect dendrochemistry in general (DeWalle et al. 1995). Accordingly, I have tested extraction pre-treatments of wood to remove mobile nitrogen and thereby enhance the environmental interpretability of nitrogen in tree rings (Sheppard and Thompson, in final prep.).

Extraction of wood prior to Kjeldahl measurement significantly reduced temporal variation of nitrogen concentration, much of which was probably biogenic, i.e., due to translocation of nitrogenous substances across rings (Figure 5). More specifically, extraction eliminated most of

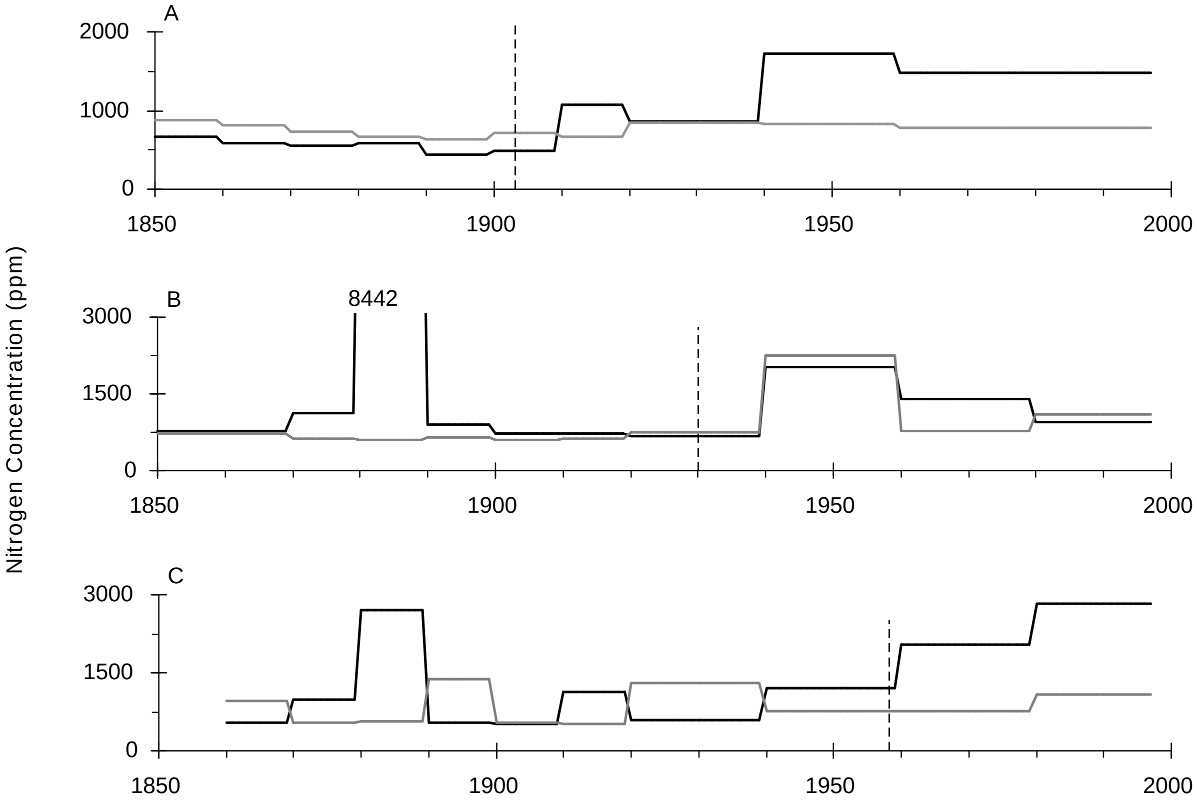

Figure 5. Nitrogen concentration in rings of three Douglas-firs (A, B, and C). Dark lines represent untreated wood, light lines represent extracted wood. Vertical dashed lines represent heartwood-sapwood boundary. Sheppard and Thompson (in final prep).

the variation in nitrogen concentration that could be attributed to the most-recently formed rings. The nitrogen removed by extraction from the wood was presumably soluble in the tree sap and therefore mobile across rings. By contrast, the non-extractable nitrogen was less soluble in tree sap and therefore less mobile across rings, and as such it is potentially interpretable as a relative measure of environmental nitrogen availability at the time of ring formation. Thus, pre-treating wood by extraction substantially reduced the ambiguities of interpreting nitrogen concentration in tree rings as relative indicators of environmental availability at the time of ring formation.

Overcoming these problems of interpreting nitrogen in rings is a prerequisite for integrative research of tree-growth responses to controlled levels of nutrient availability and/or anthropogenic increases in nitrogen deposition. Further research on this topic should investigate other pre-treatment strategies. For this it will be necessary to step back one level and pre-treat and measure wood that should have no substantial temporal variation in nitrogen content. Additionally, further research is need to calibrate the response of nitrogen in rings of trees with known changes in nitrogen availability, such as those in long-term nitrogen fertilization experiments.

GENERAL PLAN OF WORK

Proposed Research Field Sites

The proposed strategy for assessing the effects of increased nitrogen deposition on tree growth is to analyze tree growth in a comparative study (Tamm 1989) of different remote high-elevation old-growth sites that are similar ecologically but exist along a steep gradient of different loadings of nitrogen deposition (Kiefer and Fenn 1997). Extreme environmental cases are particularly useful for demonstrating processes and effects and therefore are of special importance in ecological research (Lang et al. 1982). Changes in nutrient cycling of high-elevation ecosystems may serve as early warning indicators for disruption of nutrient cycling in other forested ecosystems (Williams et al. 1996), and old-growth forests are particularly appropriate for evaluating links between atmospheric deposition and ecosystem response (Hedin et al. 1995). Exploiting a strong gradient in nitrogen deposition, including a site of ambient deposition, can be quite helpful in testing its separate effects (Riggan et al. 1994; GCTE 1999). Additionally, remote sites, including official wilderness areas, have experienced minimal human land-use disturbances that can play a substantial role in nitrogen cycling (Vitousek and Melillo 1979) and in how forest ecosystems respond to nitrogen deposition (Aber et al. 1998).

Across the western United States, nitrogen deposition is substantially elevated primarily downwind of isolated urban centers (Fenn et al. 1998). The potential for high nitrogen exposures and extensive distribution of nitrogen pollutants is strongly dependent on widespread use of vehicles in large urban centers with poor public transportation systems (Bytnerowicz and Fenn 1996). In particular, dry deposition of oxidized nitrogen (Russell et al. 1985) in the southern California air basin is among the heaviest in North America (Solomon et al. 1992), with a west-to-east gradient of decreasing deposition (Bytnerowicz et al. 1999). Consequently, the Transverse and Peninsular Ranges of southern California, which are downwind of one of the largest metropolitan centers in the world, have forests that are receiving heavy nitrogen deposition.

An active research program of the USDA Forest Service Pacific Southwest Research Station has been focusing on the effects of air pollution and climatic impacts on western forest ecosystems, including and especially those of southern California (Miller and McBride 1999). Consequently, an outstanding infrastructure is in place there for investigating environmental effects of nitrogen deposition on tree growth, and I propose to collaborate with researchers within that effort. The Pacific Southwest Station research has focused mostly on mid-elevation forests and would benefit from the addition of other sites to observe forest-level responses to air pollution. See Supplementary Documentation for a letter of support from that research program.

I am personally familiar with subalpine forests of southern California from previous investigations there (Sheppard et al. 1988; Sheppard and Lassoie 1998; see Other Pertinent Work–Southern California Case Study). I propose to initiate this research in the subalpine forests of Mt. San Gorgonio and Mt. San Jacinto (Fig. 3), with which I am especially familiar from past forest ecology research (Lassoie, Hamilton, and Sheppard 1988; Graumlich and Sheppard 1988; Sheppard and Lassoie 1998). In particular, San Gorgonio and San Jacinto have high-elevation (3,000+ m elevation) old-growth forests of lodgepole and limber pines (Thorne 1988), including those that formed the chronologies of Figure 4. These sites have very old trees and fire regimes of infrequent, low-intensity fires (Sheppard and Lassoie 1998; Minnich 1999). Soils are generally described as young, thin, coarse, and low in productivity (Cohn and Retelas, n.d.; Poth and Wohlgemuth 1999). Based on nitrate loadings in drainage streams, San Gorgonio is clearly receiving nitrogen deposition and is possibly nitrogen saturated (Fenn and Poth 1999b). Because of the gradient of decreasing air pollution from west to east across southern California (Fenn and Poth 1999a), San Jacinto presumably receives lighter deposition than San Gorgonio, thus providing this proposed research with a gradient of nitrogen deposition. These sites appear to be ideal for this research on long-term nitrogen deposition (Minnich 1999).

Studying a site with essentially ambient deposition will be important for providing a reference point of natural ecosystem processes against which the sites with heavier deposition can be compared (Hedin et al. 1995). For the ambient deposition endpoint site of this proposed research, the main stretch of the Peninsular Range in Baja California is downwind of primarily the Pacific Ocean and receives as little as one-third the nitrogen deposition of southern California (Galloway et al. 1994). More precisely, just west of Los Angeles (i.e., not downwind), a coastal island receives only a tenth of the nitrogen deposition of monitoring sites east of Los Angeles (Solomon et al. 1992) and probably approximates well the nitrogen deposition levels of Baja California.

In particular, the Sierra San Pedro Mártir of northern Baja California (Fig. 3) has subalpine forests of the Sierra variety lodgepole pine (Minnich 1987; Lotan and Critchfield 1990) and is otherwise similar to San Gorgonio and San Jacinto in geology (granite batholiths), soils (poorly developed, course-textured, and thin with slow nutrient cycling), climate (Mediterranean with cool wet winters and hot dry summers) and physiography (steep slopes and peaks up to 3100 m elevation) (Delgadillo 1992). Indeed, existing dendrochronologies from various conifer species of San Pedro Mártir correlate well with chronologies of southern California (Biondi et al. 1999). Again, in all respects, San Pedro Mártir appears to be ideal for this research as the site with ambient nitrogen deposition. Although I do not yet have a firm collaboration with forest ecologists in Baja California, I expect to develop one by the time this proposed research would begin.

Field Experimental Methods and Procedures

Approximately 40 mature lodgepole pines of full-bark growth forms will be selected for dendrochronological sampling within each site along a systemic grid pattern of sufficient density to account for a wide range of aspects, slope angles, and geomorphic hillslope positions, all of which may affect nitrogen movement through soils (Dise and Wright 1995). For each selected tree, two increment cores will be collected to represent radial growth through time. Also for each tree, two units of ion-exchange resins will be buried within root zones and left there over the next year to absorb ions that flow near them in the soil solution. Relative nitrogen deposition will be measured with two additional ion-exchange resin units placed at the ground surface of each sampled tree. The average nitrogen absorption by the surface resin units for all trees within sites will indicate relative deposition loads across sites. The differences between trees within sites will quantify relative differences in nitrogen deposition at the tree scale, which is known to be spatially highly variable in high-elevation sites (Lovett and Kinsman 1990). The following growing season, the resin units will be retrieved for chemical analysis to measure the quantity of nutrient deposition and soil nutrient availability throughout the year. New resin units will also be placed for Year 2 to measure interannual variation in nutrient deposition and availability, which should help quantify climatic control of nutrient cycling.

Laboratory Analysis

All tree cores will be processed and archived following standard dendrochronological protocols (Phipps 1985). Cores will be set into protective sticks and surfaced with steel razor blades to expose a cross-sectional view of the rings. All growth rings of will be crossdated by matching patterns of relatively wide and narrow rings as well as other ring features to account for the possibility of ring-growth anomalies such as missing or false rings (Douglass 1941). Year dates of formation will then be assigned to all rings back in time beginning with the known year of sampling for the outermost ring.

Ring width of all dated rings will be measured to ±0.01 mm and checked for dating and measurement errors using cross-correlation testing at multiple time lags (Program COFECHA, Holmes 1983). For each tree, measured values for years held in common by both cores will be averaged into a single time series. To remove age- and/or size-related growth trends from these time series, measured values will be divided by curve fit values for each tree series. A cubic-smoothing spline fit will be calculated for this step, in particular the spline that leaves variation at the 100-year period in the resultant index series (Cook and Peters 1981). This strategy will allow for specifically analyzing growth trends of up to 50 years in length.

All deposited nutrients and soil nutrients absorbed by the ion-exchange resins will be extracted from the resins in three steps using 20 ml of 2 M HCl agitated for a total of one hour (Dobermann et al. 1997; Skogley et al. 1997). The solutions from the soil resins will then measured for ammonium and nitrate, phosphate, and potassium, while those from the surface resins will be measured for just ammonium and nitrate. This step will quantify current relative nutrient availability for each tree sampled within each site. The wet chemical analysis will be done at the Riverside ChemLab, which is associated with the Pacific Southwest Research Station and which is well equipped and staffed and conforms to standards of the US Environmental Protection Agency.

Quantitative Analysis

Quantitative relationships between (1) current relative soil nutrient availability and (2) trends of indexed tree growth will be determined using correlation and multiple regression tests as well as time-series and bivariate plots. Trends since 1950 in growth indices for each tree will be emphasized because other sources indicate that anthropogenic nitrogen deposition began in earnest at that time (Mayewski et al. 1986, 1990 [Fig. 1]; Arbaugh et al. 1999a, b). Thus, recent trends in relative tree growth will be statistically associated with current patterns in relative soil nutrient availability (Sheppard et al., in review). This approach rests on the assumption that spatial variation in relative soil nutrient availability has remained the same over the last few decades, i.e., the Principal of Uniformitarianism applies in this case. This is probably true based on other long-term soil chemistry data showing the same spatial variability across several different soil pits over the last 50 years (Billett et al. 1990).

The strength of the statistical associations between tree growth and soil nutrient availability will be further analyzed across different physiographic and hillslope positions within sites as well as between sites. Results from this analysis will serve as the basis for identifying microsite characteristics that should be recorded in future dendrochronology research and also be used in modeling tree-growth responses to nitrogen deposition. Differences in the statistical associations between tree growth and nitrogen availability between sites of different deposition loadings will help isolate the direct role of nitrogen pollution on tree growth.

Dendrochemistry: Measuring and Interpreting Nitrogen in Tree Rings

Measuring Rings Without Temporal Nitrogen Variation: Tree rings with putatively little to no variation in nitrogen concentration will be measured to refine analytical techniques until obtaining time series with no temporal variation. For this, rings from the old lodgepole pines of San Jacinto (Lassoie, Hamilton, and Sheppard 1988) will be used to provide wood dating to several hundred years ago, which clearly will avoid impacts of modern anthropogenic changes in nitrogen fixation. Given that fire has the effect of redistributing and changing availability of nutrient elements in the soil (Raison 1979; Riggan et al. 1994), only trees with no external fire scars will be chosen for this study. Fires have been especially infrequent in the highest parts of the subalpine forest of San Jacinto (Sheppard and Lassoie 1998). Methods of wood pre-treatment such as extraction (Park et al. 1992) and bleaching (Leavitt and Danzer 1993) and of nitrogen measurement such as Kjeldahl and chromatography (Artiola 1990) will be tested using this wood. This research will determine which wood extraction pre-treatments are effective for eliminating ambiguities in nitrogen concentration related to translocation across rings, and it will identify feasible and appropriate methods for measuring nitrogen in tree rings. Measurements will be done by the Riverside ChemLab, which has capabilities for both Kjeldahl and chromatographic measurement of carbon and nitrogen in plant tissues.

Additionally, wood from trees with a fertilization treatment using ^{15}N will be measured to test for the cross-ring mobility of the tracer nitrogen (Rolfe 1974). For this, rings will be measured from pines of the North Carolina State Forest Nutrition Cooperative, which has an ^{15}N treatment scheduled for the growing season of 2000. This research will confirm if wood extraction pre-treatments are effective for overcoming the issue of nitrogen translocation across rings. I have initiated contact with the Cooperative for possible official collaboration on this topic. Measurement of ^{15}N will be done by the Cooperative, which has equipment for such measurements.

Measuring Rings With Known Temporal Nitrogen Variation: Rings from trees that have been fertilized with various known concentrations of nitrogen will be measured to identify and calibrate the response of ring nitrogen to known changes in availability. This step will require trees from controlled fertilization-growth response experiments that are typical of production forestry science. A wide range of situations would qualify for this step, though none exists in southern California that I know of. For this, rings will be measured from pines of the Sierra Nevada of northern California where fertilization treatments have been done for several years. This research will calibrate the ring-nitrogen and C:N responses to changes in nitrogen availability. Hopefully those responses will be independent of ring-width and therefore represent additional environmental information. I have initiated contact with Dr. Robert Powers of the Pacific Southwest Research Station in Redding, California, for possible official collaboration on this topic. Again, measurements will be done by the Riverside ChemLab.

Measuring Rings From Southern and Baja California: Given that the first two steps of the proposed dendrochemistry research are successful, then core samples from the field study part of this proposed research will be measured and interpreted for nitrogen concentration. This step will link nitrogen deposition-availability-uptake-assimilation by quantifying the amounts of nitrogen that are retained in woody tissue and the temporal patterns of changes in nitrogen assimilation and wood production by trees. Ring carbon will also be measured in order to have time series of wood C:N to assess changes in potential carbon sequestration by forests.

I have been actively researching the measurement and environmental interpretation of nitrogen in tree rings, often in collaboration with other technical experts of wood chemistry and techniques of analytical chemistry (Sheppard and Thompson, in final prep.; see Other Pertinent Work–Dendrochemistry). I have gained valuable experience in this research and know which lines of research to pursue for wood pre-treatment and measurement techniques.

Model Validation/Parameterization

Results from this proposed research will serve as the basis for quantifying parameters that link atmospheric deposition and nutrient availability to tree growth in ecosystem-level models. In collaboration with mathematical ecologists who have written or are modifying comprehensive ecosystem-scale nutrient cycle models, results of this research will be incorporated as changes in or additions of key parameters that describe ecosystem processes or link major inputs and outputs relating nitrogen deposition with tree growth.

While I do not have personal experience creating or modifying comprehensive models linking nutrient cycling with tree growth, it should be easy to collaborate with those who do by providing them the primary results of this proposed research to make necessary adjustments in the pertinent code. Indeed, the Pacific Southwest Research Station has been adjusting parameters of the NuCM and Century models to analyze effects of air pollution on tree growth of southern California, and it should be routine to continue collaborating with the modeling experts there to effectively apply the results of this research in a useful modeling exercise.

TIMETABLE FOR RESEARCH

Year 1 (May 2000 through April 2001)

Summer: Fieldwork in Mt. San Gorgonio, Mt. San Jacinto, and Sierra San Pedro Mártir, sites representing a nitrogen deposition gradient, to collect tree cores and install ion-exchange resin units in soil and on ground surface for each tree.

Fall and winter: Begin dendrochronological analysis of ring-width growth of tree cores from the mature, natural forests.

Fall and winter: Test dendrochemistry protocols on San Jacinto lodgepole pine growth rings from centuries ago, well before any possible anthropogenic changes of the environment.

Spring: Continue applications of nitrogen fertilization of trees in long-term controlled experiments, but add tracer ^{15}N to help evaluate cross-ring translocation of nitrogen within trees.

Year 2 (May 2001 through April 2002)

Summer: Follow-up fieldwork to replace ion-exchange resin units of Year 1.

Fall: Finish dendrochronological analysis of ring-width growth of tree cores from the mature, natural forests of Mt. San Gorgonio, Mt. San Jacinto, and Sierra San Pedro Mártir.

Fall and winter: Chemically measure ion-exchange resin units of Year 1 for relative nutrient availability and atmospheric deposition.

Fall and winter: Dendrochemically measure rings from controlled nitrogen fertilization experiments, paying attention to the temporal variation of ^{15}N within trees. Submit for peer review a manuscript on pre-treatment of wood for dendrochemical measurement of ring nitrogen.

Winter and spring: Begin statistical analysis to model tree growth with relative soil nutrient availability data and geomorphic hillslope positions.

Year 3 (May 2002 through April 2003)

Summer: Fieldwork to collect ion-exchange resin units of Year 2.

Fall and winter: Chemically measure ion-exchange resin units of Year 2 for relative nutrient availability and atmospheric deposition.

Fall and winter: Finish statistical analysis to model relative tree growth with relative nutrient availability and geomorphic hillslope attributes, incorporating differences in nutrient availability and climate between Years 1 and 2.

Winter and spring: Dendrochemically measure rings since 1850 from Mt. San Gorgonio, Mt. San Jacinto, and Sierra San Pedro Mártir according to protocols identified in the dendrochemical studies of this proposed research.

Spring: Finish analyses and submit for peer review manuscripts on environmental interpretation of ring nitrogen and on tree-growth responses to nitrogen deposition. Begin collaborations with tree growth-nutrient modelers to improve parameterization of roles of nitrogen deposition and soil and forest productivity.

SAMPLE AND DATA DISPENSATION

Because the dendrochemistry measurements of this proposed research will involve destructive measurement of the wood itself, there will not likely be much tree-ring material to archive. Whatever tree-ring material remains after completing all measurements and analyses will be archived in the collections of the Laboratory of Tree-Ring Research of The University of Arizona. All tree-ring data, including widths as well as elemental concentrations, will be submitted to the International Tree-Ring Data Bank of the NOAA World Data Center A in Boulder, Colorado (Grissino-Mayer and Fritts 1997). Consequently, these data will not only be securely archived, but they will also be fully available to other scientists for continued analytical research.

LONG-TERM GOALS

An important part of ecological model building and testing is validating models with extensive collections of data sets from sites that are chosen throughout a homogeneous region (Aber et al. 1993a). With respect to nitrogen deposition, much of the Sierra Nevada falls within the end points of San Gorgonio versus San Pedro Mártir. Subalpine zones of the Sierra Nevada have sparse but extensive forests of lodgepole pine and similar species (Rundel et al. 1988), and they also are otherwise similar geologically, pedologically, and climatically to the Transverse and Peninsular Mountain sites further south. Thus, to have a full continuum along a gradient of nitrogen deposition, sites of the Sierra Nevada will be considered in the next phase of this research.

BROAD IMPACTS OF PROPOSED RESEARCH

A broad objective of this proposed research is to continue merging detailed analysis of soil quality with dendrochronological study of tree growth. This was also an objective of my NSF-NATO Postdoctoral Fellowship research (see Results From Prior NSF Support). Generally speaking, dendrochronologists have focused only rarely on the soils that their sampled trees grow in, in spite of the fact that soil is obviously a key environmental factor for plant growth. When dendrochronologists have mentioned soils data in publications, it has been mostly as a single site-level description, which is better than nothing but still can not account for variation at the tree scale. The successful completion of this proposed research will include descriptions of field and laboratory protocols that dendrochronologists can reasonably do to better understand soil variation at the tree scale within their sites. This should lead to improved environmental interpretability of dendrochronologies (Sheppard et al., in review) as well as improved cross-disciplinary interactions between dendrochronologists and soil scientists.

RIVERSIDE FOREST FIRE RESEACH LABORATORY,
USDA - FOREST SERVICE

June 15, 1999

Paul R. Sheppard
Laboratory of Tree-Ring Research
The University of Arizona
Tucson, AZ 85721

Dear Paul:

The Atmospheric Deposition Effects on Montane Forests in the Western United States Project is excited to cooperate with your NSF proposal "Effects of Nitrogen Deposition on Tree Growth…". Several scientists in our project are currently working on this important issue for western forest growth and development, and can provide important technical and theoretical assistance to your work.

The effects of N deposition on high elevation forests is an area we have not previously considered in our project, largely because we spend our time understanding the effects of single and multiple air pollutants on highly impacted montane forests. It is an area of great interest however, and one that has not been examined previously in forests of the Sierra Nevada and Transverse Ranges of California. This work is particularly important for understanding the possible present and future effects of N deposition to unique natural resource areas such as Sequoia-Kings Canyon and Yosemite National Parks, both of which receive significant amounts of air pollution from the San Joachin Valley.

As such, I see your work being an important contribution to scientific knowledge, benefiting both our present program at RFL, and providing direction for future programs of air pollution effects on high elevation forests of North America.

Thank you for including us in this project, and we look forward to an exciting and productive collaboration.

Sincerely,

Michael J. Arbaugh	Andrzej Bytnerowicz	Mark E. Fenn	Nancy L. Grulke	Mark Poth
Systems Ecologist	Ecologist	Plant Pathologist	Plant Physiologist	Soil Scientist

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A. Professional and Academic Essentials

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Education

Ph.D. (1995) The Univ. of Arizona, Geosciences; major: Paleoenvironmental-Quaternary Studies with an emphasis in Dendrochronology; minor: Soil and Water Sciences.
M.S. (1984) Cornell Univ., Natural Resources; major: Forest Science; minor: Statistics.
B.S. (1982) Humboldt State Univ., CA, Forestry Resources Management (magna cum laude).
A.S. (1980) Long Beach City College, CA, lower division general science.

Recent Employment

Research Specialist Senior, Lab. of Tree-Ring Res., Univ. of Arizona (since Sep. 1997). Developing web-based teaching modules for dendrochronology, assisting research on assessment of climate of the Southwest, continuing personal dendrochronological-environmental research.
NSF-NATO Postdoctoral Fellow, Dept. d'Ecologia, Univ. de Barcelona, España (Sep. 1996 to Aug. 1997). With Dr. Emilia Gutiérrez, researched effects of soil microsite conditions on tree growth, and collaborating with other dendrochronologists of NATO-member countries.
Visiting Assistant Professor, Lab. of Tree-Ring Res., Univ. of Arizona (Sep. 1995 to Aug. 1996). Taught Introduction Survey, Advanced Workshop, and Graduate Seminar courses in Dendrochronology, advised students, and researched environmental science projects.

B. Five Publications Related to Proposed Research

Sheppard, P.R. and T.L. Thompson. In final prep. Measurement and interpretation of nitrogen in tree rings. **Chemical Geology (Isotope Geoscience Section)**.
Sheppard, P.R., P. Casals, and E, Gutiérrez. In review. Relationships between soil nutrient availability at the tree scale with dendrochronological tree growth. **Proceedings of the 9th North American Forest Soils Conference** (Lake Tahoe, CA).
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C. Five Other Significant Publications

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