FOREST DECLINES: SOME PERSPECTIVES ON LINKING PROCESSES AND PATTERNS*

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ABSTRACT

The regional decline in vigor of some species of forest trees has become an important component in the ecological, aesthetic, and economic criteria by which the costs of anthropogenic pollution are weighed. Because declines are often complex and virtually never without significant natural environmental modifiers, determining the role of specific anthropogenic stresses in initiating or enhancing the rate and direction of change in forest condition represents a significant research challenge. Separation of primary mechanisms that point to principal causes from secondary responses that result from internal feedbacks and the milieu of modifying agents is a critical issue in diagnosing forest decline. Air pollutant stress may have its most significant effects on forest processes by accelerating or amplifying natural stresses. Studies of changes in forest metabolic processes have played an important role in evaluating the role of air pollution in four regional forest declines that are the focus of this paper. The decline of ponderosa pine in the San Bernardino Mountains of California, Norway spruce and silver fir in Europe, loblolly and shortleaf pine in the Southeastern United States, and red spruce in the Eastern Appalachian Mountains provide case studies in which physiological responses to air pollutants under field and laboratory conditions have provided important analytical tools for assessing likely causes. These tools are most effective when both mechanistic explanations and larger scale patterns of response are evaluated in an iterative feedback loop that examines plausible mechanisms and patterns of response at levels ranging from cell membranes to plant populations.

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INTRODUCTION

During the past decade, forest declines have become an important component of the valuation system by which society has weighed the costs of regional scale environmental pollution. The deterioration of health of some forest species across widespread geographical areas has occurred concurrently with significant increases in atmospheric pollution in both the U.S.A. (McLaughlin, 1985) and in Europe (Prinz, 1987). These trends have led to intensive research programs

aimed at determining both the specific causes and consequences of forest declines. While there are still many unanswered questions about the roles that gaseous pollutants and acidic deposition play in influencing forest health, a substantial amount has also been learned during the past decade about the processes and mechanisms by which these pollutants impact forest processes in North America (Shriner et al., 1991) and in Europe (Schulze and Freer-Smith, 1991; Landmann, 1991).

The results of these studies have been derived from research teams that have employed multidisciplinary approaches to address an innately complex problem: evaluating the role of specific components among a complex of factors that ultimately control the rate and direction of forest decline. The conceptual framework used by Manion (1981) to describe the progression and interaction of stresses involved in forest decline provides a good demonstration of the complexity of interactions among the predisposing, inciting, and contributing factors that can sequentially carry a tree form the chronically weakened initial condition through successive stages that accelerate the decline process and can ultimately lead to tree death. That complexity raises the important issue of documenting primary causes and the interrelationships among initial causes and secondary effects. That issue is the topic of this article. How do we study forest declines in a scientifically efficient way so that the chances of correctly linking the processes involved to the patterns observed are maximized?

Forest decline research can obviously be approached at many organizational levels ranging from the cytological and biological changes that are the "primary events" of pollutant impacts to the larger scale changes in forest condition that have provided clear visible evidence of deteriorating health. In Figure 1, the array of growth related forest processes that have been shown to be affected by

air pollutants at levels of increasing integration and complexity is shown. In addition, the expression of a measurable response at the organ or whole tree level will often be the result of linked combinations of primary and secondary reactions that are integrated over time and strongly influenced by natural environmental stress (see Figure 2). The question of where to focus research is an intriguing one because emphasis on either end of the organizational spectrum can fail to provide the appropriate level of understanding between the larger response patterns that tell us that a significant response has occurred and the mechanistic processes that identify the primary causes.

There are four significant case studies by which we can examine the interplay between processes and patterns and, in parallel, some of the significant findings and common themes from forest decline research. These are: The San Bernadino Mountain Study (SBMS) involving ponderosa and jeffrey pines in Southern California (Miller, 1983), the regional decline in southern pine growth in natural stands (Sheffield and Cost, 1987), the decline of Norway Spruce and other species in central Europe (Schulze, 1989; Prinz, 1987), and finally the decline in red spruce in the Appalachian Mountains of the U.S. (Eagar and Adams, 1992; Johnson et al., 1992, and McLaughlin and Kohut, 1992). In each case, the role of pattern identification in directing and interpreting a variety of process level studies is discussed.

DIAGNOSIS OF FOUR CASE STUDIES

I. The San Bernardino Mountain Study - The occurrence of foliar symptoms of ozone damage on foliage of sensitive tree species in the San Bernardino Mountains of Southern California out to a distance of 120 km from Los Angeles led to a benchmark study by the US Forest Service entitled the San Bernardino Mountain

Study (SBMS, Miller, 1983). The SBMS has provided the forest community with perhaps its most complete case study of ecosystem level effects from atmospheric pollutants. This study is somewhat unique in that very clear signs of ozone injury were detectable on foliage throughout the study region leading to an early focus on ozone as the principal causative factor. Exposure of these forests to elevated levels of photochemical oxidants had been recognized for approximately 20 years (Miller, 1983) at the time this multidisciplinary study was begun in 1972. The initial focus of this project on ecosystem level processes by a well coordinated research team assured a high degree of integration in the ensuing studies. The patterns of forest response observed and the principal physiological changes detected are summarized in Table 1.

Collectively, the findings clearly supported the conclusion that ozone was a significant factor in the damage occurring in these forests. The primary mechanism appeared to be a reduction in carbon assimilation due to both loss of photosynthetic capacity of foliage and a lower retention of photosynthetic area. Though not specifically examined, it can be assumed that these forests have also experienced a loss of root vigor due to reduced translocation of carbon belowground as commonly occurs with ozone effects on carbon allocation (McLaughlin, 1988 and Cooley and Manning, 1987). The combined effects of reduced carbohydrate supply in these forests provided a logical framework for the increased susceptibility of these forests to both above and belowground pathogens (bark beetles and root diseases, respectively). Increased attack by bark beetles was noted on ponderosa pine trees visibly damaged by ozone (Stark et al., 1968) and subsequent studies revealed reduced quantity and quality of resin production of ozone damaged trees (Miller et al., 1968).

In summary, the response patterns observed and the associated processes affected indicated that significant changes in species composition were a possible outcome of the combined influences of ozone on carbon, water, and nutrient allocation of the San Bernardino Mountain forests (Miller, 1983). An interesting followup to this prognosis was provided by a 1974-1988 resurvey of the SBM (Miller et al., 1989). Significant improvement in air quality (approximate 40 ppb reduction in annual average ozone) through emissions reductions had been accompanied by improved canopy condition and basal area growth of all plots but those which had been most severely affected in 1974.

II. Southeastern Pine Decline - An interesting parallel to the SBNS project but without either well-defined foliar symptoms or a strong ozone gradient, has been the regional decline of pine growth in the Southeast initially reported by Sheffield and Knight (1983). Analysis of data from continuous forest inventory (CFI) plots across a wide diversity of sites within the region showed that diameter growth of natural stands of southern pines had dropped by 30-50% below expectations across the region during the past three decades (Sheffield and Cost, 1987). Questions regarding the extent to which these trends were unexpected based on natural stand dynamics and of the validity of using the CFI data for diagnosing the growth trends observed have been the subject of considerable controversy within the forest mensuration community. Changing stand structure and/or rainfall patterns have each been hypothesized as the principal causative factor in the reported declines. Although the CFI plots were not originally designed for analysis of causation of observed trends in tree growth, these plots are widely enough distributed across the region that the data can be stratified for the purpose of examining the extent to which trends can be explained by such natural stresses as climate and competition (Schreuder and Thomas, 1991).

Two separate studies have examined stratified data sets to evaluate the role of natural factors in the observed trends and both have reached the same conclusion. Zahner et al. (1990) developed a tree ring model to analyze the growth trends across 131 even aged natural, well-stocked stands in the Southeast. After adjusting for stand age, stand competition, and historical climate changes they found that a decline in radial increment of about 1% per year since 1950 and that a significant portion of the decline could not be explained by natural responses to climate and stand competition. More recently, Bechtold et al. (1991) evaluated the role of stand competition on regional reductions in growth of natural pine stands in Georgia. After adjusting for differences in stand basal area, site index, and hardwood competition, basal area growth was found to have declined in naturally regenerated loblolly pine (19%), shortleaf (28%), and slash pine (28%) during the ten year interval between 1972 and 1982. While neither of the two studies prove that air pollution has contributed to the observed growth decline, they considerably strengthen the argument that air pollutants should be considered logical contributors to those patterns.

Several lines of evidence suggest that ozone should be examined as a causative factor in the observed growth patterns. They include the results of the San Bernardino Mountain studies, the clear documentation of the adverse effects of ambient ozone on regional crop yields (Heck et al., 1984), ozone responses of many species of tree seedlings in controlled studies (Pye, 1988), and the relatively high levels of ozone in the Southeast (Taylor and Norby, 1985). A network of five controlled exposure field studies with open top chambers was initiated in the Southeast in 1986 as a part of a U.S. National Forest Response Program (Hertel and McKinney-McNeal, 1991). These studies were specifically designed to examine the extent to which ozone and acidic deposition might have

contributed to observed growth trends in southern pines. They included open top field chamber sites at five regional sites to study physiological and growth responses of the three primary species of commercial importance to southeastern forests, loblolly, shortleaf, and slash pines. An analysis of the pattern and process linkages for those studies are presented in Table 2 for ozone and Table 3 for acid deposition.

Collectively the controlled studies support the hypothesis that ambient levels of ozone have contributed to the decline of southern pine species. These studies indicate that primary effects on seedlings and saplings result through changes in availability and allocation of carbohydrates. Reduced photosynthetic rate and ultimately reduced photosynthetic area and increased dark respiration can be considered the primary responses leading to reduced growth, reduced translocation to roots, and reduced ectomycorrhizal activity.

While the open top chamber studies represent the best currently available approach for evaluating ozone effects on whole trees, they support, but cannot prove that similar effects are occurring on larger trees. From the standpoint of carbohydrate dynamics one might expect larger trees, with their higher respiratory demand relative to photosynthetic production capacity, to be more sensitive to reductions in carbohydrate supply (McLaughlin and Shriner, 1980). Measurements in branch chambers on larger trees to date suggest that ambient air also reduces photosynthetic rates of larger trees (Teskey and Daugherty, 1991).

Current experimental evidence does not strongly support an adverse effect of acidic deposition on growth of southern pines. Responses of most physiological and growth parameters indicate positive rather than negative growth effects at near ambient acidity levels. However, it should be noted that acid deposition appears to influence forests primarily through its cumulative effects on nutrient

cycles, and short term seedling studies may not be adequate to detect these effects. Positive growth effects, such as have been found in numerous short term studies should be expected where acid rain is applied in the presence of adequate nutrition. Edwards et al. (1992) found evidence of a cumulative effect of acid deposition on LLP growth that, in contrast to ozone effects, was not apparent until the third year of chamber studies.

The fact that growth stimulation and reduction have been reported documents the capacity of acid deposition to influence pine growth. It should be expected that such effects, if they occur with natural forests, will vary widely depending on soil nutrient status and the presence of other stresses. Binkley et al. (1988) suggest that from 10 to 15% of the southeastern commercial pine forests may be limited by cation supply and hence would likely be sensitive to further acceleration of cation losses. Short term studies do not support synergistic effects of acid deposition and ozone (McLaughlin et al., 1988), however the capacity of ozone to reduce root mass and function represents a point of logical longer term interaction with any limitations in soil cation availability.

III. <u>European Forest Decline</u> - The appearance and spread of symptoms of forest damage to silver fir and Norway spruce across extensive areas of Europe beginning in the late 1970's has been the subject of much controversy and generated many hypotheses to explain the diverse symptoms observed (Schutt and Cowling, 1985; Prinz, 1987; Rheufeuss, 1991). The widespread association of the visual foliar symptoms of decline with nutrient deficiencies, particularly Ca and Mg (Cape et al., 1990 and Simmleit et. al., 1991) strongly supports a role for acid deposition as a contributing factor to declines observed in many, but not all (Rheufeuss, 1991) areas. Perhaps the strongest evidence of linkages between atmospheric deposition and observed symptoms comes from the integrated studies

performed in the mountains of Northeast Bavaria and reviewed by Schulze (1989). This research provides an excellent example of an integrated physiological approach focused on changes in performance of many key components of this stressed forest.

The visual discrimination of healthy and declining trees in these forests based on yellowing of older foliage has been an asset in evaluating other distinguishing physiological features of decline. A principal feature of the yellowing of foliage associated with decline on acidic soils in Europe has been the role of Mg deficiency. Magnesium deficiency appears initially in older needles and is related to a greater relative demand for nutrients in newly developing needles. This results in translocation of Mg from older needles to relatively stronger sinks in developing foliage. Both the fact that bud removal can protect older needles from yellowing (Lange et al., 1987) in the presence of ambient gaseous pollutant levels, and the lack of an age (dose) dependency of photosynthetic suppression associated with this yellowing (Zimmerman et al., 1988), indicate that other factors affecting nutrient supply are relatively more important in symptom development than exposure to gaseous pollutants (Schulze, 1989).

Studies of productivity levels associated with yellowing and thinning of crowns have found reduced wood production per unit leaf area indicative of a reduced efficiency of production processes (Oren et al., 1988). Differences in production capacity were not directly proportional to reductions in photosynthetic capacity, which was not substantially reduced until very low (< 0.05 ppm) Mg levels developed (Zimmerman et al., 1988). Oren et al. (1988) interpreted reduced mobilization and depletion of reserve carbohydrates as indicative of a weakened overall carbohydrate economy for declining trees.

Magnesium deficiency in the Bavarian forest is clearly related to reduced supply of nutrients from soil. Evidence for the importance of belowground processes included lower sap concentrations of nutrients in declining trees (Osunibi et al., 1988) and reduced root tip and mycorrhizal development associated with lower Ca:Al ratios in soil extracts (Meyer et al., 1988). In support of these results from field research have been laboratory studies of uptake of Mg and Ca by Norway spruce seedlings, demonstrating that both Al and Fe inhibit uptake of Ca and Mg by fine roots (Steinen and Bauch, 1988). Both decreasing solution pH and increasing Al also reduced binding of Ca in cell walls of fine roots (Schroeder et al., 1988). Subsequent controlled exposure studies in open top chambers have shown that rainfall acidified to pH 4.0, particularly in interaction with O_3 and SO_2, strongly reduced mycorrhizal development of Norway spruce saplings in open top chamber experiments (Blaschke, 1990). Lab studies suggest that mycorrhizae do not prevent Al from penetrating fine roots and displacing Ca from cell walls (Jentscke et al., 1991).

Schulze (1989) concluded from the collective results of many studies that the alterations in the nutrient utilization patterns, linked to changes in atmospheric and soil chemistry, are dominant features of forest decline in Europe and are influenced by deposition of sulfur, nitrate, and ammonia. Changes in nitrogen metabolism were seen as an important part of this syndrome. Preferential uptake of ammonium from soil as well as foliar absorption of atmospheric sources of nitrogen resulted in reduced uptake of nitrate from soil solutions. Resultant higher concentrations of nitrate in soil solutions further enhanced leaching losses from soil and reduced Ca:Al and Mg:Al ratios. Additional leaching losses of cations, suggested to occur primarily through the bark of twigs (Katz et al., 1989), further aggravate cation imbalance.

Under limitations in supply of base cations any stimulation of growth or shift to increased growth in the canopy at the expense of root growth would further exacerbate nutrient deficiency. Foliar deposition of nitrogen directly to canopies represents one route for canopy processes to be stimulated at the expense of root production. Estimates of canopy uptake of nitrogen from atmospheric sources ranged from 8% of annual demand for healthy trees to 20% for a declining site (Shulze, 1989). Thus, the imbalance between nitrogen and cation supply was hypothesized as a central component in development of nutrient deficiency symptoms, not only on acidic soils where Mg was limiting, but also on limestone, where K deficiency develops, and on dolomite, where Mn and Fe deficiency occur (Schulze, 1989).

Weather and many other natural factors are important contributors to the diverse symptoms noted in many areas of Europe; however, nutrient deficiencies induced or amplified by acid deposition have also been important contributors to forest decline in the most seriously affected mountain ranges (Rehfuess, 1991). Forest condition has improved in some areas of Europe in recent years under less stressful weather conditions; however, high elevation forests have continued to decline (Schulze and Freer-Smith, 1991). It is clear that nutrient deficiency, induced or amplified by acid deposition has been an important factor in the destabilization of those forests. In this regard, there are some distinct similarities to the patterns of red spruce decline noted in the Eastern United States.

IV. <u>Red Spruce Decline in the Eastern Appalachian Mountains</u> - The decline in vigor of red spruce detected initially in the mountainous areas of the Northeastern United States (Siccama et al., 1982; Johnson and Siccama, 1983), and subsequently in the southern Appalachians (Adams et al., 1985; McLaughlin et al.,

1987; Bruck et al., 1988), is the most obvious example of regional growth decline in North America. The decline of red spruce in the Northeast is the only example of regional increases in mortality with a strong linkage to air pollution. The results of intensive studies on the nature and causes for red spruce decline have recently been summarized by Eagar and Adams (1992). As a component of that effort, McLaughlin and Kohut (1992) have reviewed the relationships between observed patterns of forest response and physiological studies designed to evaluate possible causes. Their findings are summarized in Table 4.

The decline of red spruce in the northern and southern Appalachian mountains provides some interesting contrasts and comparisons of the interplay of climate, geology, and anthropogenic emissions on observed response patterns. In the northern Appalachians a decline in radial growth and vigor of trees in many size classes across a wide range of sites with widely varying stand histories began in the late 1950's and early 1960's (Johnson and McLaughlin, 1976). Mortality has typically been greatest at high elevations, and both the mortality and accompanying severe loss of foliage appear to be closely tied to an increased incidence of winter injury beginning in the early 1960's (Johnson et.al., 1988). That injury occurred at winter temperatures which apparently did not produce similar levels of injury in earlier years, indicating that trees had apparently become more sensitive to freezing damage.

The decline in radial growth of red spruce at predominantly low elevation second growth sites in the Northeast, which occurred at the same time as that at high elevation sites (Cook, 1992), has been suggested to be attributable principally to stand dynamics (Hornbeck et al., 1985). The potential for competition to contribute significantly to observed growth patterns of fully stocked younger stands with an even age distribution must certainly be

recognized; however, the regional synchronization of that growth decline across trees and stands of widely varying ages and past growth dynamics within a five state area does not fit the conceptual model of a competition driven stress response since observed growth preceding the approximate 1960 growth decline reflect quite variable growth rates and dynamics of change.

In comparison, red spruce in high elevation southern Appalachian stands began a similar pattern of radial growth decline that typically lagged behind that in the North by about 5-10 years, but was similarly not predicted by past relationships to climate or stand competition (McLaughlin et al., 1987). In contrast to the North, abrupt declines in radial growth in the South have typically been limited to elevations above 1500 m (Adams et al., 1990). An additional contrast to the northern decline has been the lack of severe mortality of red spruce in southern stands to date (Nicholas and Zedaker, 1989). However, deterioration of canopy condition of red spruce in the South has accelerated rapidly during the past five years both in the Black Mountains, where severe ice damage has occurred (Nicholas and Zedaker, 1989), as well as in the Great Smoky Mountains, where ice damage was much less severe, but where crown condition is worse. In addition, there has been very significant mortality to Fraser fir in southern stands with 70% or higher mortality in approximately 24% of the spruce-fir forest (Dull et al., 1988). The balsam wooly adelgid (Adelgis picea) first discovered in the Southern Appalachians in 1956, has played the major role in killing these trees, imposing significant changes in stand structure at the highest elevations.

Winter temperatures are not as severe in the southern Appalachians, and winter defoliation of shoots is atypical, although winter flecking of foliage (Anderson et al., 1991) and an increase in sensitivity to winter damage of chambered

seedlings grown in ambient mist (DeHayes et al., 1992) have been reported. Based on foliar nutrient surveys by Friedland et al. (1988) and Robarge et al. (1989), deficiencies in foliar nutrients, most notably Ca and Mg appear likely across high elevation southern sites just as in the North.

In both the North and the South, a combination of field and laboratory tests have confirmed the capacity of acid deposition, in concert with natural factors, to disrupt normal patterns of carbohydrate production (McLaughlin and Kohut, 1992). In the North, the principal mechanism appears to be a loss of foliage damaged by low winter temperatures. Field chamber studies with mature trees (Vann et al., 1992) and laboratory studies with red spruce seedlings (Fowler et al., 1989) have confirmed the capacity of acidic mist to reduce the frost hardiness of red spruce foliage. Most controlled exposure studies with red spruce suggest that this species is relatively insensitive to ozone at ambient levels. However, when exposures (Amundson et al., 1991) were extended to multiple growing seasons in open top chambers results indicate that chronic exposure to ozone may reduce red spruce biomass increment and alter foliar carbohydrate and pigment levels with exposure to ozone over multiple seasons (Amundson et al., 1991). Field and laboratory studies suggest that antioxidants may be involved in responses of red spruce to ozone, but their role as primary or secondary responses and their significance is unclear at present (Madamanchi et al., 1991).

In the South, physiological studies along elevational gradients in the Smoky Mountains have shown that carbon allocation patterns are altered at high elevations and that an increase in dark respiration (McLaughlin et al., 1990), linked to changing allocation of photosynthate (Andersen et al., 1991), is a primary component of that response. Increases in dark respiration were well

correlated with low levels of foliar Ca, which were, in turn, related to high levels of soil Al (McLaughlin et al., 1991). Both the low Ca uptake on high Al soils, and the low Ca:Al levels found consistently in soils sampled at high elevation sites, support the importance of Al as an inhibitor of Ca uptake. Very low soil solution Ca:Al levels and high soil nitrate levels (Johnson et al., 1991; Joslin and Wolfe, 1992) and evidence of direct canopy utilization of foliar N (Norby et al., 1989) provide further parallels to the findings with Norway spruce in Europe (Schulze, 1989). Furthermore, studies of foliar leaching in the field (Joslin et al., 1988) confirm the role that acid mists play in leaching Ca and other nutrients from shoots. Collectively the physiological gradient studies indicate that current levels of Ca at high elevation eastern mountain sites are in the growth limiting range, and that factors like acid deposition, which limit the uptake and retention of calcium, will reduce growth under these conditions.

The stimulus for reduced availability of cations is the high level of input of the strong acid anions, SO_4 and NO_3, which mobilize Al. Deposition levels of these strong acid anions are highest at high elevation sites, where cloud exposure is frequent, and are currently higher in the Southern Appalachian mountains than at any of the northern mountain sites sampled by the Integrated Forest Study (Lindberg and Lovett, 1992). Controlled greenhouse studies have now documented that acid mist and rain, approximating the chemistry of that occurring at high elevation sites, can reduce red spruce growth, reduce foliar Ca, and cause shifts in gas exchange physiology which closely parallel those observed in the field (McLaughlin and Tjoelker, 1992).

In summary, the research on red spruce to date indicates that acid deposition is disrupting the carbon economy of this species across a wide range of sites. This has occurred through both reductions in foliage area, as noted in the North,

and reductions in the efficiency of carbon metabolism, as documented in the South. Disruption of the integrity of root systems appears to be closely tied to increased deterioration of canopy function (Wargo et al., 1992) and there is evidence from both root chemistry studies in the North (Shortle and Smith, 1989) and wood chemistry (Bondietti et al., 1989) and foliar chemistry (McLaughlin et al., 1991; Joslin and Wolfe, 1992) studies in the South that competitive inhibition of Ca uptake by Al may be an important factor in observed symptoms. Aluminum appears to play more of a role on the Southern Appalachians where soil Al levels are relatively higher than in the North (Joslin et al., 1992). Nutrient deficiency, particularly low levels of foliar calcium, is a common denominator in many of the physiological changes observed in these studies. The importance of Ca to a wide range of cellular functions (Marschner, 1974 and Bangerth, 1979) including membrane stability, cell wall growth, and adaptation of cells to chilling injury (Minorsky, 1985), coupled with its limited mobility in plants and susceptibility to leaching by acid deposition, has led to the hypothesis that Ca deficiency may be an important feature of many of the physiological responses induced by acid deposition (McLaughlin and Kohut, 1992).

SUMMARY AND CONCLUSIONS

As one looks across the four case studies discussed above, it is clear that both the description of larger scale patterns of response in the field as well as integrated physiological studies have played an important role in evaluating causes and potential longer term significance of forest decline. A wide variety of physiological and/or ecosystem processes have now been linked to exposure of forests to pollutant levels that occur at regional scales. In general, these may be grouped into two major categories of primary response which are obviously

linked at the whole plant level to a variety of secondary responses. The primary responses are (1) changes in root function and nutrient availability associated with chronic effects of acid deposition on soils and (2) changes in the availability and distribution of carbohydrates available for growth, defense, and repair occurring in response to the effects of ozone on production and/or utilization of photosynthate.

While there is still much that we do not know about both the primary mechanisms of response and the longer term consequences of these responses for forest ecosystems, the implications of what is known are clearly significant. On a mechanistic basis, it is apparent that ultimate responses lie at the membrane level, where a loss of membrane integrity will change a wide range of biochemical and physiological responses required for adjustment to natural environmental stresses (Heath and Costillo, 1987). At the whole plant level, changes in the flow of nutrients and carbon can have far reaching consequences for growth, competition, and selection processes (Sinclair, 1969; McLaughlin and Norby, 1992). As one evaluates the spectrum of responses of forests to air pollutants, it is apparent that a wide diversity of approaches are necessary to further advance our understanding of both causes and implications of forest declines. Air pollutants clearly can cause a wide variety of very significant physiological changes at current ambient levels. The way in which these changes are expressed at the whole plant level will vary widely in the field, including significant amplification of sensitivity to some natural stresses, particularly drought, insects, disease, and poor nutrient status. Potential changes in global climate will likely further amplify the importance of physiological resilience in tree response to more pronounced climatic fluctuations. We should expect pollution derived stresses to often be subtle, chronic, and difficult to detect

in short term experiments. Near term responses to acid deposition should be expected to be positive in situations where soil nutrients are adequate for growth but become increasingly negative as available pools of some nutrients are depleted (Abrahamson, 1980). Both increased nitrogen deposition and mobilization of available cations by acid deposition (Bondietti et al., 1991) may produce such near term responses. Improved growth has been reported in recent years in some low elevation European forests (Schulze and Freer-Smith, 1991; Landmann, 1991).

Because a mosaic of responses driven by natural variability across the landscape is expected, it is useful to focus research both on indicator sites, where hypotheses of response can most effectively be tested, and on indicator processes, which allow us to evaluate how these responses are controlled at the physiological, biochemical, and soil chemical levels. Natural variability can be used to experimental advantage by including hypotheses that encompass gradients in stress interactions. Only through iterative feedback between process studies which define the physiological and chemical basis of responses to air pollution, and studies of plant system changes at tree, stand and regional levels, can we hope to define both the causes of change and the significance of that change to future forest function and forest health.

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DISCLAIMER

TABLE 1

Forest response patterns and associated physiological responses examined in the San Bernardino Mountain Study [see Miller (1983) for references unless otherwise indicated].

Patterns Observed

Increasing visible foliar injury, decreased needle retention, cone production, and stem growth, and increasing susceptibility to insects and mortality spatially associated with an increasing ozone gradient.

Processes Examined

Photosynthesis - reduced PS capacity with increasing total ozone dose (to 10% of maximum rate after 450 pphm/hrs for sensitive trees)

Stomatal Conductance - reduced, but less reduction than for photosynthesis, indicating an increase in mesophyll resistance

Transpiration - reduced per unit foliage based on stomatal conductance and per tree based on foliage loss.

Carbon metabolism - Reduced quantity and altered composition of resin production (Miller et al., 1968).

Growth - increased in sapling trees by charcoal filtering air.

Disease susceptibility - decreased in saplings in charcoal filtered air.

Foliar nutrition - Increased levels of N, P, K, Ca, and Mg in foliage with increasing foliar injury and reduced retranslocation of nutrients and carbon (2 tree sample). Increased nutrient loss in throughfall.

Litter nutrients - Increased N,P, and K, and decreased Ca in fresh litter. Increased decomposition rate with increasing foliar injury, but reduced release of N and Ca in decomposing litter of ponderosa pine.

TABLE 2

Forest patterns associated with growth reductions of southeastern pine species and related growth and physiological responses observed in controlled studies with ozone.

Patterns observed

Radial growth decline - An approximate 30-50% concurrent decline in mean radial growth of southern pines in natural stands distributed across a wide array of stand ages, stocking levels, and composition (Sheffield and Cost, 1987; Bechtold et al.,1991)

Processes affected

These refer to measured responses at an approximate ambient dose of pphm*h during a 6 month growing season or to artificially increased ozone exposure at indicated levels.

Reduced photosynthesis - 25% after 3 mo. and 788 pphm*h (Hanson et al., 1988). Reduced photosynthesis, reduced foliar chlorophyll, and a carry over suppression on subsequent year photosynthetic capacity at 144-193 pphm*h (Sasek et al., 1991).

Reduced foliage area - Reduced needle retention and decreased foliage area associated with premature loss of the older age classes of foliage (Stow et al.,1992) at ambient and above ambient O_3 concentrations.

Reduced spectral reflectance - increased reflectance at ambient and above ozone levels that was dependent on genetic and seasonal variables (Carter et al., 1992)

Increased respiratory losses - Decreased retention of photoassimilated C-14 for foliage of seedlings (Adams et.al., 1988) exposed to twice ambient O_3.

Altered carbohydrate metabolism - A linear reduction in foliar and whole plant starch levels with increasing ozone (Meir et al. 1990).

Reduced root growth and activity - responses include reduced root mass (Meir et al, 1990; Edwards et al. 1992; Adams and O'Neill, (1992) and Adams et.al. (1988)), and decreased root respiration (Edwards, 1991)

Reduced mycorrhizal colonization of roots - 25% reduction in mycorrhizal colonization at 788 pphm*h (Adams and O'Neill, 1992) and a linear reduction in ectomycorhizzal development (Meir et al, 1990) with increasing ozone dose.

Reduced height and diameter growth - For both seedlings (McLaughlin et al., 1988 and Edwards et.al.1992) and saplings (Schaefer et al, 1987) in ambient air and Shelburn et.al.(1991) at 2.5 X ambient.

Reduced foliar nutrients - Lower levels of N, and K and reduced Al at 788 pphm*h (McLaughlin et al., 1988).

TABLE 3

Larger scale patterns of soil nutrient status and some results of controlled studies to evaluate the potential influence of acidic deposition in growth responses of southeastern pines.

Patterns Observed

Low soil buffering capacity - Based on an evaluation of the regional distribution of forest soils, their parent materials and their buffering capacity, Binkley et al. 1988) estimated that growth of natural pine stands would be limited over approximately 10-15% of their range by current supplies of base cations.

Growth declines - as noted in Table 2.

Processes Affected by Acid Deposition

Growth responses - Growth responses of seedlings in controlled studies have typically been bimodal with stimulation of height and diameter growth at intermediate acidity levels (pH 3.8 to 4.3). Both growth reduction (McLaughlin et al. 1988, Edwards et al. 1992) and growth stimulation (Wright et al.; 1991 and Shelburn et al., 1991) being reported in the range of pH 3.3.

Carbohydrate metabolism - Acid rain has been found to stimulate reducing sugars in shortleaf pine foliage at both ambient (near pH 4.3) above ambient (pH 3.3) acidity levels (Paynter et al., 1991.).

Foliar nutrition - Increased foliar nitrogen associated with increased growth has been reported in loblolly pine seedlings in response to both near ambient (pH 4.3) and high acidity (pH 3.3) rainfall treatments (Wright et al., 1991.)

Photosynthesis - Photosynthesis does not appear to be sensitive to suppression from acidic deposition with either no effects (Sasek et al., 1991) or stimulation (Hanson et al., 1988) being reported in experiments with seedlings.

Aluminum toxicity - Loblolly pine seedlings has been reported to be intermediate among species tested in sensitivity to the toxic effects of aluminum in soil solution on seeding growth (Raynal et al., 1990). Root regeneration studies in sand culture suggest that aluminum may be very toxic to regeneration and elongation of new roots in soils with very low buffering capacity (Paganelli et al., 1987).

Leaf spectral reflectance - Carter et al. (1992) have reported decreased visible and infrared spectral reflectance of loblolly pine in response to acid deposition. Responses were opposite those induced by ozone, where increased reflectance was indicative of physiological damage to pigment systems.

TABLE 4

Summary of some dominant patterns of response of red spruce in the Appalachian Mountains and linkages to those responses derived from physiological studies (summarized from McLaughlin and Kohut, 1992).

Patterns Observed

<u>Decline in forest condition</u> - increased mortality and canopy deterioration which is more advanced at high elevations and in the northeast and accompanied by loss in stand basal area.

<u>Changing wood chemistry</u> - a shift to higher aluminum and lower calcium levels in wood and accompanied by low Al:Ca in fine roots.

<u>Foliar chemistry</u> - Relatively low levels of foliar Ca and Mg, more pronounced at high elevation sites

<u>Increased sensitivity to winter injury</u> - increased frequency of needle damage noted primarily at high elevation northern sites and accompanied by loss of younger foliage.

<u>Decreased radial growth</u> - Regionwide decrease in radial growth at high elevation sites across the region not predicted by climate or competition. Also apparent at low elevations in the Northeast, but not in the Southern Appalachians.

Physiological Processes Linked to Acid Deposition

<u>Decreased carbohydrate availability</u> - Reduced photosynthesis, increased dark respiration, reduced foliar carbohydrates, and altered patterns of carbon allocation.

<u>Decreased foliar nutrients</u> - Increased loss rates of foliar Ca and Mg detected in field and laboratory experiments and linked to rainfall acidity

<u>Increased sensitivity to winter injury</u> - found in field chamber studies at both Northern and Southern Appalachian sites under ambient conditions.

<u>Decreased membrane integrity</u> - increased leakiness of cellular electrolytes before and after freezing in foliage exposed to ambient levels of acid deposition.

<u>Decreased growth</u> - reduced growth of tree seedlings and reduced deep rooting.
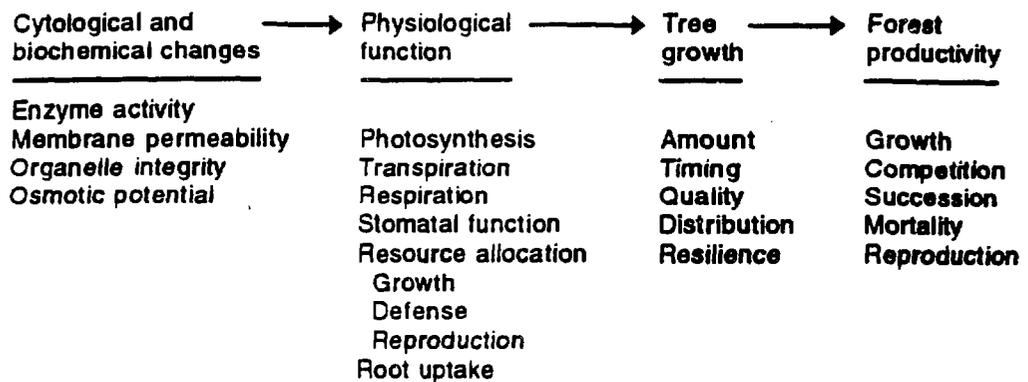
Increasing Integration Of Processes and Complexity

Cytological and biochemical changes ⟶	Physiological function ⟶	Tree growth ⟶	Forest productivity
Enzyme activity			
Membrane permeability	Photosynthesis	Amount	Growth
Organelle integrity	Transpiration	Timing	Competition
Osmotic potential	Respiration	Quality	Succession
	Stomatal function	Distribution	Mortality
	Resource allocation	Resilience	Reproduction
	Growth		
	Defense		
	Reproduction		
	Root uptake		

Fig. 1. Forest processes have been shown to be affected by air pollutants at many oganizational levels (after McLaughlin, 1985).

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Response Sequences

Pollutant Exposure

Process Affected

Level of Response
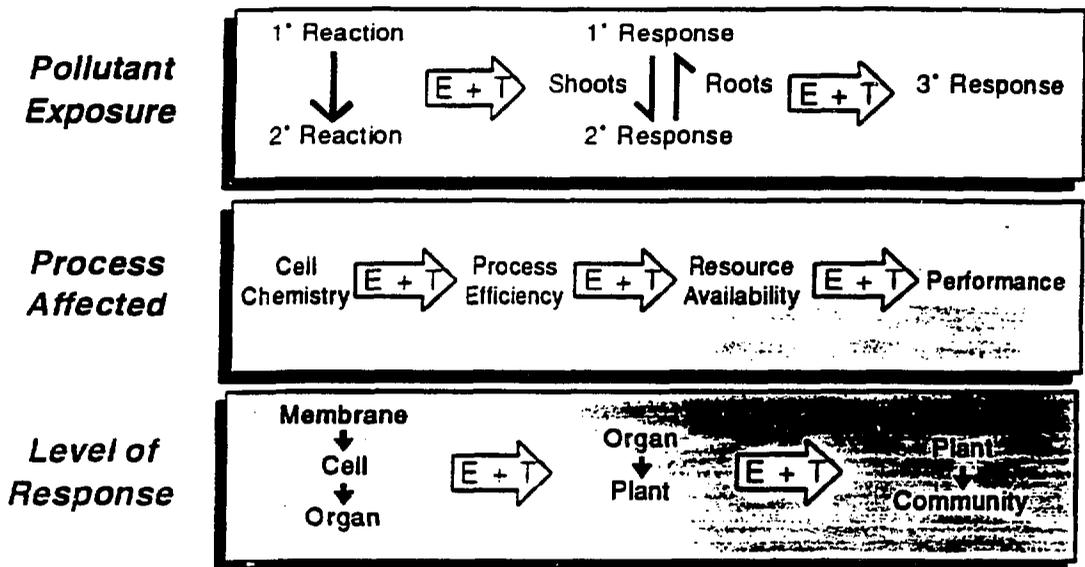
E = Environment   T = Time

Fig. 2. The expansion of a measurable response in forest function will typically be the result of linked combinations of primary and secondary responses that develop over time under the influences of natural environmental amplifiers.