CONF-9409307--1

Effects of Acid deposition on Calcium Nutrition and Health of Southern Appalachian Spruce Fir Forests

S. B. McLaughlin[1], J. D. Joslin[2], A. Stone[3], R. Wimmer[4], and S. Wullschleger[1]

[1]Environmental Sciences Division
Oak Ridge National Laboratory
Oak Ridge, TN

[2]TVA/ORNL Cooperative Studies Program
Tennessee Valley Authority

[3]Graduate Program in Ecology
University of Tennessee
Knoxville, TN

[4]Austrian Agricultural University
Vienna, Austria

"The submitted manuscript has been authored by a contractor of the U.S. Government under contract No. DE-AC05-84OR21400. Accordingly, the U.S. Government retains a nonexclusive, royalty-free license to publish or reproduce the published form of this contribution, or allow others to do so, for U.S. Government purposes."

DISCLAIMER

Portions of this document may be illegible in electronic image products. Images are produced from the best available original document.

This research was sponsored by the U.S. Environmental Protection Agency and the U.S. Forest Service under interagency agreements with the US Department of Energy (DOE). Oak Ridge National Laboratory is managed by Martin Marietta Energy Systems, Inc., under contract DE-AC05-840R21400 with the U.S. Department of Energy.

ABSTRACT

The role of acid deposition in the health of spruce fir forests in the Southern Appalachian Mountains has been investigated by a wide variety of experimental approaches during the past 10 years. These studies have proceeded from initial dendroecological documentation of altered growth patterns of mature trees to increasingly more focused ecophysiological research on the causes and characteristics of changes in system function associated with increased acidic deposition. Field studies across gradients in deposition and soil chemistry have been located on four mountains spanning 85 km of latitude within the Southern Appalachians. The conclusion that calcium nutrition is an important component regulating health of red spruce in the Southern Appalachians and that acid deposition significantly reduces calcium availability in several ways has emerged as a consistent result from multiple lines or research. These have included analysis of trends in wood chemistry, soil solution chemistry, foliar nutrition, gas exchange physiology, root histochemistry, and controlled laboratory and field studies in which acid deposition and/or calcium nutrition has been manipulated and growth and nutritional status of saplings or mature red spruce trees measured. This earlier research has led us to investigate the broader implications and consequences of calcium deficiency for changing resistance of spruce-fir forests to natural stresses. Current research is exploring possible relationships between altered calcium nutrition and shifts in response of Fraser fir to insect attack by the balsam wooly adelgid. In addition, changes in wood ultrastructural properties in relation to altered wood chemistry is being examined to evaluate its possible role in canopy deterioration under wind and ice stresses typical of high elevation forests.

INTRODUCTION

A multidisciplinary research team that investigated the symptoms and causes of decline in health of red spruce throughout much of its range in the United States has recently summarized those findings (Eagar and Adams, 1992). A principal conclusion of that research was that acid deposition operating in concert with natural stresses was a significant contributor to the loss in vigor of these forests over the past three decades (Johnson et al., 1992). This conclusion was based on the timing and spatial distribution of changes in tree growth rates, canopy condition, or mortality in relationship to spatial and temporal patterns of acid deposition; the existence of close relationships between acid deposition and changes in soil chemistry; and the existence of changes in tree physiology and/or growth that could be linked to increased exposure to acidic deposition either across natural gradients in acidic deposition in the field or in controlled exposures in the laboratory (McLaughlin and Kohut, 1992).

Throughout the history of the Forest Response Program of which the research discussed above was a part, the major research emphasis has been on the red spruce forests of Northern Appalachia. Northern forests contain over 90% of the extant distribution of this species in the United States. Extremely high mortality rates in northern red spruce generated much of the early concern about possible anthropogenic causes and solutions. By contrast, the southern red spruce forest is smaller in geographical distribution, but contains most of the existing old growth red spruce in the United States (White and Cogbill, 1992).

Red spruce in the Southern Appalachians is confined to approximately 30,500 ha in the cooler and more moist high elevations, above approximately 1200 m. Over 75% of that forest type occurs in the Great Smoky Mountains in Tennessee and North Carolinas (Dull et al., 1988). These forests have historically been less disturbed by logging, and to date red spruce mortality has been low compared to rates at high elevations in the Northern Appalachians (Peart et al., 1992). By contrast mortality of a companion species, Fraser fir has been extremely high, and over 90% of the Fraser fir > 5" in diameter was found to be dead in the Smoky Mountains in a 1988 survey (Dull et al., 1988). Mortality is commonly ascribed to the Balsam woolly adelgid (adelges picea), an introduced insect pathogen which has been active in the Southern Appalachians since around 1956.

The Southern Appalachian red spruce forest, because it has been less disturbed in the past and now is undergoing perhaps the first stages of a more serious decline offers very interesting opportunities to gain additional understanding of the mechanisms underlying forest responses to combinations of natural and anthropogenic stresses. There has now been an active research program in the South for 10 years, which has provided many valuable insights into both the patterns of responses of large trees as well as the processes by which those patterns have been altered (McLaughlin and Kohut, 1992). We will review that research briefly here as a basis of (1) contrasting responses of the northern and southern components of the spruce/fir forest, and (2) providing a framework for testing new hypotheses about the role of changing calcium nutrition on forest responses to natural stresses.

A SUMMARY OF RECENT RESEARCH FINDINGS

The linkages between observed spatial and temporal patterns of forest system response and biological and chemical processes have played an important role in analyses of the health of southern Appalachian forests. Several of these patterns are highlighted in Figure 1 which describes changes in tree growth in relationship to regional atmospheric emissions and wood chemistry of high elevation red spruce.

Mature tree growth patterns - A slowdown in radial growth of red spruce trees has been a significant early indicator of alterations in forest health in both the Northern and Southern Appalachians. Cook and Zedaker (1992) provided a comprehensive review of dendorecological studies and the issues involved in evaluating the relative roles of climate, competition, and atmospheric pollution in observed growth declines. These conclusions as well as those of McLaughlin et al. (1987) reached in an earlier study indicate that the decline began in the late 1950s to early 1960s in the North and was delayed 5-10 years in the South.

Neither unusual climate nor stand competition appear to have played a major role in initiating the stress though interacting roles, particularly for climate cannot be excluded (McLaughlin et al., 1987). An important differentiating feature of the Southern growth decline relative to patterns observed in the North is its confinement to higher elevations and the absence of alarmingly high levels of spruce mortality, which have typically occurred in Northern spruce-fir forests. Deterioration of canopies of red spruce was observed to have increased markedly over a 1984-88 study interval in the Southern Appalachians (Nicholas and Zedaker, 1989). An apparent increased sensitivity of northern forest to damage by low winter temperatures has been an important early visual symptom of the decreasing health of northern spruce forests (Johnson et al., 1988). Increased sensitivity to low temperatures has now been tied to exposure of branches to acidity in ambient mist exposures (Vann et al., 1992). A much less severe, but cumulative, winter discoloration of needles has been found in Southern red spruce (Andersen et al, 1991).

<u>Soil solution chemistry</u> - The soils of the southern spruce fir forest are naturally acidic, poorly buffered, high in aluminum, and currently nitrogen saturated (Johnson et al., 1991; Joslin et al., 1992). Under these conditions the addition of strong anions SO_4 and NO_3 in acidic deposition provide the stimulus to mobilize aluminum in soil solutions (Reuss and Johnson, 1986). Soil solution monitoring in the Great Smoky Mountain National Park (GSMNP) has documented the close relationship between strong anion inputs and peaks in soil solution aluminum (Johnson et al., 1991). Aluminum levels in soil solution periodically reach levels known to be directly toxic to roots (Joslin et al., 1992). However, the greater significance of the high aluminum levels in these soils is their interference with uptake of calcium. Ca:Al levels in soil solutions at high elevations are frequently in the range at

which uptake of calcium and alteration of root function occurs (Johnson et al., 1991; Joslin et al., 1992).

Atmospheric deposition - Atmospheric deposition of SO_4 and NO_3 at a high elevation Smoky Mountain site was found to be the highest of 13 interregional sites examined in the recently completed Integrated Forest Study (Johnson and Lindberg, 1992). Deposition of S (36 kg/ha/y) and N (31 kg/ha/y) within the region is highest at high elevation sites and is heavily influenced by the frequent exposure of these forests to acidic clouds (Lindberg and Lovett, 1992). At nearby Mt. Mitchell exposure of spruce canopies to acidic fogs was found to occur on approximately 70% of the days and 35% of the time (Saxena and Lin, 1990). Over 50% of the exposures were at pH < =3.5, and in two successive years cloud events with pH values < 3.0 occurred 5 and 30% of the time. The minimum recorded pH was 2.7 (Saxena and Lin, 1990).

Temporal changes in emissions and tree chemistry - In the absence of long term records of atmospheric deposition, two indicators have been used to evaluate temporal changes in exposure of southern Appalachian forests to acidic deposition: historical changes in emissions and shifts in tree ring chemistry. Historical changes in emission density of the S and N precursors of acidic deposition upwind of the Smoky Mountains are shown in Figure 1. The source area includes emission density in the predominant upwind quadrants (SE and SW) within a 900 km radius, an index that described regional wet deposition of SO_4 and NO_3 well in earlier analyses (McLaughlin et al., 1984). The emissions density pattern of S and N shows the strong upswing in regional emission patterns in the late fifties and early 1960s.

Tree ring chemistry patterns provide a means of describing changes in the chemical environment experienced by the tree as a function of shifts in soil solution chemistry (Bondietti and McLaughlin, 1992). Analysis of shifting patterns of Al:Ca in red spruce wood from high sites in the GSMNP (Fig. 1) have shown that increases in availability of aluminum relative to calcium occurred in the late 1950s in parallel with changes in regional emission density of the strong anions known to mobilize aluminum (Bondietti et al., 1989, 1990).

Alterations in physiology of saplings and trees - McLaughlin and Kohut (1992) have reviewed a series of published field and laboratory studies that have demonstrated that sapling trees growing at high elevation sites in the GSMNP have increased levels of foliar aluminum, decreased levels of foliar calcium, and shifts in carbon metabolism associated with increasing exposure to acid deposition, and reduced soil Ca:Al levels. The altered carbon metabolism was mostly a function of increased dark respiration rates and was significantly increased by decreasing foliar Ca and high soil Al (McLaughlin et al., 1991). Foliar Ca has also been shown to be decreased through leaching by the acidity in ambient cloud exposures (Joslin et al., 1988; Thornton et al., in press)

The decreased ratio of photosynthesis to dark respiration (P:R ratio) observed in foliage would be expected to lead to reduced carbohydrate availability and reduced growth rates of trees growing at high elevation sites. Confirmation of the role of acidic deposition in reducing P:R ratios, reducing growth, and altering root distribution of red spruce seedlings was provided in controlled greenhouse studies using ambient range mist/rain chemistry and exposure frequency and native soil from the red spruce zone of the GSMNP (McLaughlin et al., 1993). Reduced growth of fine roots in deeper soil horizons was also noted in the across an increasing gradient in exposure to acidic fogs at Whitetop Mtn. in Virginia (Joslin et al., 1992).

Additional confirmation of the role of calcium in reducing growth and altering P:R ratios of sapling trees in the field has been provided by calcium fertilization studies (Van Miegroet et al., 1993; Wullschleger et al., in preparation). Large trees have now also been shown to respond to calcium fertilization with increased foliar Ca and increased growth of shoots in the canopy (Joslin and Wolfe, 1994).

CONCLUSIONS FROM STUDIES WITH RED SPRUCE

The series of studies briefly described above provides a strong argument for the significance of acidic deposition in altering nutrient availability, physiological function, and growth of red spruce in the Southern Appalachian Mountains. In this capacity, acid deposition appears to act as a significant modifier of natural stresses including naturally high acidity, high aluminum levels in soil, and high hydrologic fluxes. A primary mechanism by which the system is altered appears to be a disruption of the availability and uptake of calcium by atmospheric input of strong anions (McLaughlin and Kohut, 1992).

Calcium is an extremely important plant nutrient because it is required for formation and function of membranes and cell walls, serves as a enzyme cofactor, and regulates many physiological functions at the cell and plant level (Bangerth, 1979). The fact that calcium is not stored in the plant but must be supplied form the soil uptake when it is needed places calcium in a position to be limiting to growth under conditions where plant supply may be altered by chemical interference in soil or by foliar leaching.

NEW RESEARCH ON THE IMPLICATIONS OF CALCIUM DEFICIENCY FOR THE SPRUCE FIR ECOSYSTEM

The fact that low calcium availability is limiting growth and physiological function in red spruce has led us to explore additional implications of ecosystem level shifts in nutrient cycles for the spruce-fir ecosystem. Two primary areas of emphasis have evolved: potential changes in canopy integrity related to structural integrity of wood and branches, and altered susceptibility of Fraser fir to lethal attack by the balsam wooly adelgid. A brief description of the rationale for these lines of research and some preliminary findings are detailed below.

Wood structural changes - Increasing levels of canopy thinning and deterioration have been the most obvious visual sign of reduced vigor in the southern appalachian red spruce forest (Peart et al., 1992). While damage from ice storms has played an obvious role in some of the canopy loss occurring in the Black Mountains of North Carolina (Nicholas et al., 1989), thinning has also occurred in the GSMNP without an obvious increase in such episodes, which are a natural part of the high elevation climatology. One possible explanation for increasing canopy deterioration is enhanced sensitivity of branches to winter ice damage and wind because of structural weakening of wood. The rational for such an hypothesis is that calcium is known to play an important role in wood formation. Calcium is an important crosslinking molecule in the chemical bonding associated with lignin formation (Westermark, 1982; Eklund, 1991). It is also important in formation of non-cellulosic cell wall polysaccharides such as pectins (Eklund and Eliasson, 1990). Since soil aluminum has played a role in low foliar Ca levels, we anticipate that similar decreases may have occurred in the fine branches of the upper canopy.

Investigations into possible structural changes in wood are proceeding by using a combination of techniques to examine Ca and lignin distribution and structural attributes in wood (Wimmer and McLaughlin, 1994). Energy dispersive X-ray spectroscopy, coupled with transmission electron microscopy, has been used to measure Ca and lignin distribution at various locations in earlywood and latewood of spruce tracheids. These measurements have been combined with microtechniques used for testing material hardness. Results indicate that such techniques can be applied to tissues removed from increment cores to evaluate properties such as lignin content, wood hardness and plasticity (Wimmer and McLaughlin, 1994). Initial exploratory analyses suggest that lignin in red spruce stem wood may decrease with increasing elevation and that lignin levels have decreased in more recent years. An inventory of red spruce and Fraser fir cores collected from elevations ranging from 1200 to 2000 m on two mountains in GSMNP is being examined to focus measurements across an appropriate range of conditions to efficiently test the hypothesis that acid deposition has structurally weakened the forest by reducing calcium availability.

<u>Fraser fir ecophysiology and adelgid damage</u> - The damage to mature Fraser fir in the Southern Appalachians by the wooly adelgid has been extensive over the past 15 years. A 1988

survey reported that 91% of the adult Fraser fir over 12 cm DBH were dead (Dull et al., 1988). While heavy infestation noted on many dying trees is unquestionable evidence that the adelgid plays a major role in killing these trees, it is also important to consider the role of predisposing factors in susceptibility of stressed forests to pathogens (Manion, 1981).

Several bits of evidence warrant examination in evaluating factors influencing resistance or susceptibility of Fraser fir to adelgid induced mortality. First is the fact that some fir trees have a resistance to this introduced pathogen and can survive attack. Within the Southern Appalachians the most resistant population has been at Mt. Rogers, in southwestern Virginia where mortality has been very light and evidence of resistance pockets in the bark indicates that resistant mechanisms do exist (Eagar, 1984). As the northernmost extension of the range of Fraser fir, the apparent resistance at Mt. Rogers could be due to genetic differentiation within the Fraser fir population. However, there is now increasing evidence of attack at low elevation sites at Mt. Rogers (Dull et.al., 1988) suggesting that site related factors may influence sensitivity.

Significant temporal and spatial variability in susceptibility of the closely related Balsam fir (Abies balsameri) has been evidenced across its eastern range since the adelgid was introduced around 1900 (Timmel, 1986). Mortality of this species has been significant in the Canadian maritime provinces, particularly in the mid 1980s. Tree vigor, bark characteristics, and the formation of compression wood are apparently related to resistance to the adelgid (Eagar, 1984; Timmel, 1986).

Several seemingly converging lines of inference have led us to examine the role of acid deposition on calcium supply as an additional resistance factor. First, there is dendroecological evidence that Fraser fir in GSMNP began a growth decline around 1960 in parallel to that experienced by red spruce (McLaughlin et al., 1984). Second, recent physiological measurements on Fraser fir indicate a decline in P:R ratio with increasing elevation (and acid deposition exposure) parallel to that documented for red spruce (Stone et al., in preparation). Third, preliminary contrasts between Mt. Rogers and Clingmans Dome (GSMNP) indicate much higher foliar and soil calcium and lower aluminum levels at the high elevation Mt. Rogers site than found for more sensitive populations at Mt. Rogers low elevation or either high or low elevation GSMNP sites. There was also no significant P:R gradient with increasing elevation at Mt. Rogers (Stone, in preparation). Finally, the known role of calcium in disease resistance, including wound repair (Bangerth, 1979) and formation of lignin, which is a major constituent of compression wood, make calcium a likely modifier of resistance of Fraser fir to fatal adelgid infestation.

Our current investigations of Fraser fir ecophysiology in the Southern Appalachians include contrasts in deposition, soil solution chemistry and tree growth among sites differing in levels of acid deposition and/or cation nutrient status; fertilizer studies to examine the role of nutrition on physiology and growth; and wood structural analysis to explore the relationships among wood chemistry and structural properties that may provide defense against adelgid attack or stress from wind and ice.

SUMMARY

Collectively our results suggest that calcium is an important modifier of the physiology, growth, and function of high elevation ecosystems. Inferential lines of evidence point to but have not yet established a much broader role for calcium in regulating the resistance of spruce and fir to a wide range of stresses in the naturally stressful high elevation environment. Understanding the nature of these interactions will likely play an important role in our capacity to understand and perhaps manage the future health of these systems in a changing environment.

REFERENCES

Adams, H.S., McLaughlin, S.B., Blasing, T.J., and Duvick, D.N. 1990. A survey of radial growth trends in spruce in Great Smoky Mountains National Park as influenced by topography, age, and stand development. ORNL/TM-11424. 62 p.

Anderson, C.P., McLaughlin, S.B., and Roy, W.K. 1991. Foliar injury symptoms and pigment concentrations in red spruce saplings in the southern Appalachians. Can. J. For. Res. 21:1119-1123.

Bangerth, F. 1979. Calcium related disorders in plants. Annu. Rev. Phytopathol. 17:97-122.

Bondietti, E.A., Baes, C.F., III, and McLaughlin, S.B. 1989. Radial trends in cation ratios in tree rings as indicators of the impacts of atmospheric deposition on forests. Can. J. For. Res. 19:586-594.

Bondietti, E.A., and McLaughlin, S.B. 1992. Evidence of historical influences of acidic deposition on wood and soil chemistry. In Johnson, D. W., and S. E. Lindberg, (eds.), Atmospheric Deposition and Forest Nutrient Cycling. Springer-Verlag, New York. Pp. 358-377.

Bondietti, E.A., Momoshima, N., Shortle, W.C., and Smith, K.T. 1990. A historical perspective on changes in divalent cation availability to red spruce in relationship to acidic deposition. Can. J. For. Res. 20:1850-1858.

Cook, E.R., and Zedaker, S.M. 1992. The dendroecology of red spruce decline. Chap. 8. Edited by C. Eagar and B. Adams. Ecology and decline of red spruce in the eastern United States. Springer-Verlag, New York. Pp. 192-234.

Dull, C.W., Ward, J.E., Brown, H.D., Ryan, G.W., Clerke, W.H., and Uhler, R.J. 1988. Evaluation of spruce and fir mortality in the southern Appalachian mountains. USDA, Forest Service, Protection Report R8-PR 13, Atlanta, GA.

Eagar, C. 1984. Review of the biology and ecology of the balsam woolly aphid in southern Appalachian spruce-fir forests. In White, P.S. (ed.), The Southern Appalachian Spruce-Fir Ecosystem: Its Biology and Threats. USDI, National Park Service, Southeast Regional Office, Research/Resource Management Report SER-71, Atlanta, GA. Pp. 36-50.

Eagar, C., and Adams, B. 1992. Ecology and decline of red spruce in the eastern United States. Springer-Verlag, New York.

Eklund, L. 1991. Regulation of cell wall formation in Norway spruce (Picea abies). Doctoral dissertation at Department of Botany, Stockholm University. 75 p.

Eklund, L., and Eliasson, L. 1990. Effects of calcium ion concentration on cell wall synthesis. J. Exp. Bot. 41:863-867.

Johnson, D. W., and Lindberg, S.E. 1992. Atmospheric Deposition and Forest Nutrient Cycling. Springer-Verlag, NY. 707 p.

Johnson, D.W., Van Miegroet, H., Lindberg, S.E., Todd, D.E., and Harrison, R.B. 1991. Nutrient cycling in red spruce forests of the Great Smoky Mountains. Can. J. For. Res. 21:769-787.

Johnson, A.H., Cook, E.R., and Siccama, T.G. 1988. Climate and red spruce growth and decline in the northern Appalachians. Proc. Natl. Acad. Sci. USA 85:5369-5373.

Johnson, A. H., McLaughlin, S.B., M. B. Adams, M.B., Cook, E.R., DeHayes, D.H., Eagar, C., Joslin, J.D., Kelly, J.M., and Van Miegroet, H. 1992. Soil chemistry and nutrition of North American spruce-fir stands: Evidence for recent change. J. Envir. Qual. 21.

Joslin, J.D., Kelly, J.M., Wolfe, M.H., and Rustad, L.E. 1988. Elemental patterns in roots and foliage of mature spruce across a gradient of soil aluminum. Water Air Soil Pollut. 40:375-390.

Joslin, J.D., Kelly, J.M., and Van Miegroet, H. 1992. Soil chemistry and nutrition of North American spruce-fir stands: Evidence for recent change. J. Environ. Qual. 21:12-30.

Joslin, J.D., McDuffie, C.M., and Brewer, P.F. 1988. Acidic cloudwater and cation loss from red spruce foliage. Water Air Soil Pollut. 39:355-363.

Joslin, J.D., and Wolfe, M.H. 1992. Red spruce soil solution chemistry and root distribution across a cloudwater deposition gradient. Can. J. For. Res. 22:893-904.

Joslin, J.D., and Wolfe, M.H. 1994. Foliar deficiencies of mature southern Appalachian red spruce determined from fertilizer trials. J. Soil Sci. Soc. Am. 58:(in press).

Lindberg, S.E., and Lovett, G.M. 1992. Deposition and forest canopy interactions of airborne sulfur: results from the Integrated Forest Study. Atmos. Environ. 26:1477-1492.

Manion, P.D. 1981. Tree Disease Concepts. Prentice-Hall, Englewood Cliffs, NJ.

McLaughlin, S.B., Downing, D.J., Blasing, T.J., Cook, E.R., and Adams, H.S. 1987. An analysis of climate and competition as contributors to decline of red spruce in high elevation Appalachian forests of the eastern United States. Oecologia 72:487-501.

McLaughlin, S.B., Andersen, C.P., Hanson, P.J., Tjoelker, M.G., and Roy, W.K. 1991. Increased dark respiration and calcium deficiency of red spruce in relation to acidic deposition at high-elevation southern Appalachian Mountain sites. Can. J. For. Res. 21:1234-1244.

McLaughlin, S.B., and Kohut, R. 1992. The effects of atmospheric deposition on carbon allocation and associated physiological processes in red spruce. Chap. 8. Edited by C. Eagar and B. Adams. Ecology and decline of red spruce in the eastern United States. Springer-Verlag, New York. Pp. 338-384.

McLaughlin, S.B., Tjoelker, M.G., and Roy, W.K. 1993. Acid deposition alters red spruce physiology: laboratory studies support field observations. Can. J. For. Res. 23:380-386.

McLaughlin, S.B., Blasing, T.J., and Duvick, D.N. 1984. Summary of a two year study of forest responses to anthropogenic stress. Draft synthesis report (FORAST). Oak Ridge National Laboratory. 300 p.

Nicholas, N.S., and Zedaker, S.M. 1989. Ice damage in spruce-fir forests of the Black Mountains, North Carolina. Can. J. For. Res. 19:1487-1491.

Peart, D.R., Nicholas, N.S., Zedaker, S.M., Miller-Weeks, M.M., and Siccama, T.G. 1992. Condition and recent trends in high-elevation red spruce populations. In C. Eagar and B. Adams. Ecology and decline of red spruce in the eastern United States. Springer-Verlag, New York.

Reuss, J.O., and Johnson, D.W. 1986. Acid Deposition and the Acidification of Streams and Waters. Springer-Verlag, New York.

Saxena, V.K., and Lin, N.H. 1990. Cloud chemistry measurements and estimates of acidic deposition on an above cloudbase coniferous forest. Atmospheric Environ 24A(2):329-352.

Stone, A.S., McLaughlin, S.B., and Wullschleger, S.D. Effects of elevation and nutrition on growth and physiology of Fraser fir at southern Appalachian mountain sites. Manuscript in preparation.

Thornton, F.C., Joslin, J.D., Pier, P.A., Neufeld, H., Seiler, J.R., and Hutcherson, J.D. Cloudwater and O_3 effects upon high elevation red spruce: A summary of study results from Whitetop Mt., VA. J. Envir. Qual.

Timmel, T.E. 1986. Compression wood induced in firs by balsam wolly aphid (Adelges picea). Pp. 1907-1969 in Compression Wood, Vol. 3. Springer, Berlin.

Van Miegroet, H., Johnson, D.W., and Todd, D.E. 1993. Foliar response of red spruce saplings to fertilization with calcium and magnesium in the Great Smoky Mountains National Park. Can. J. For. Res. 23:89-95.

Vann, D.R., Strimback, G.R., and Johnson, A.H. 1992. Effects of air borne chemicals on freezing resistance of red spruce foliage. For. Ecol. Manag. 51(1-3):69-80.

Westermark, U. 1982. Calcium promoted phenolic groups by superoxide radical - a possible lignification reaction in wood. Wood Science and Technology 16:71-78.

White, P.S., and Cogbill, C.V. 1992. Spruce-fir forests of eastern North America. Chap. 8. Edited by C. Eagar and B. Adams. Ecology and decline of red spruce in the eastern United States. Springer-Verlag, New York. Pp. 3-39.

Wimmer, R., and McLaughlin, S.B. 1994 (submitted). Evaluating effects of reduced calcium and lignin on mechanical properties of red spruce tree rings. Radiocarbon (submitted proceedings manuscript).

Wullschleger, S.D., McLaughlin, S.B., and Stone, A. Growth and physiology of high-elevation red spruce (Picea rubens Sarg.) as influenced by calcium fertilization (in preparation).

FIGURES

Figure 1. Composite chronology of red spruce growth, tissue chemistry and atmospheric emissions: southern Appalachians. Data and sources are as follows reading top (1) to bottom (5) on left, then top to bottom (8) on the right. (1) mean ring-width chronology of 15 canopy dominant trees near summit (Adams et al. 1990); (2-3) high- and low-elevation ring width chronologies, 15 trees each (McLaughlin et al. 1987); (4-5) ring-width chronologies from two midelevation 40-year-old Norway spruce stands collected within 10 km of Mt. LeConte, NC, samples (Adams et al. 1990); (6) aluminum/base cation ratios (Bondietti et al. 1989); (7) wood chemistry: cation trend (Bondietti et al. 1990); (8) SW of eastern Tennessee (McLaughlin, unpublished data). Dashed vertical line on each graph indicates the year 1960 as a common reference point. After Johnson et al. (1992).