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Soil Chemistry and Nutrition of North American Spruce-Fir Stands: Evidence for Recent Change

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ABSTRACT

One set of hypotheses offered to explain the decline of red spruce (*Picea rubens* Sarg.) in eastern North America focuses on the effect of acidic deposition on soil chemistry changes that may affect nutrient availability and root function. Long-term soils data suggest that soil acidification has occurred in some spruce stands over the past 50 yr, with plant uptake and cation leaching both contributing to the loss of cations. Studies of tree ring chemistry also have indicated changes in Ca/Al and Mg/Al ratios in red spruce wood, suggesting increases in the ionic strength of soil solution. Irrigation studies using strong acid inputs have demonstrated accelerated displacement of base cations from upper horizons. Spruce-fir (*Abies* spp.) nutrient budgets indicate that current net Ca and Mg leaching loss rates are of the same order of magnitude as losses to whole tree harvest removals, spread out over a 50-yr rotation. For most cations, red spruce foliar nutrient levels decline with elevation, but it is difficult to assess the contribution of the elevational gradient in atmospheric deposition to this pattern. Compared to northeastern sites, spruce-fir soil solutions in the southern Appalachians have higher nitrate levels and higher Al concentrations, which at times approach the Al toxicity threshold for red spruce seedlings and frequently are at levels known to interfere with cation uptake. There is little evidence that either nutrient deficiencies or Al toxicity are primary causes of red spruce decline in the Northeast, though both may play a role in the Southeast. Major factors that could affect soil chemistry in spruce-fir stands in the future are (i) changes in S and N deposition, (ii) climate changes affecting soil organic matter decomposition and nutrient uptake, and (iii) tree mortality and physical disturbances to soils resulting in soil nitrate release.

rubens Sarg.) in the eastern USA has prompted considerable speculation and debate as to the role that acidic deposition, interacting directly or indirectly with plant nutrition, may have played in this phenomenon (Johnson, 1983; McLaughlin, 1985; Hornbeck et al., 1987; Shriner et al., 1990). A number of hypotheses have been offered regarding the cause of the decline of red spruce, including changes in soil and soil solution chemistry resulting from acidic deposition, which in turn may have influenced nutrient availability, foliar nutrition, and/or root function (Shriner et al., 1990). The following review examines possible relationships between atmospheric deposition, changes in soil chemistry, and soil-mediated inhibition of forest growth by posing several questions:

1. Has the chemistry of North American red spruce-fir soils and soil solutions been altered in recent decades?
2. If so, what role have plant uptake and soil leaching (including leaching attributable to acidic deposition) played in this alteration?
3. Are there regional and/or elevational patterns in red spruce-fir soil chemistry, soil solution chemistry, and/or foliar nutrient concentrations?
4. What is the potential for future changes in chemistry of spruce-fir soils given predicted changes in atmospheric pollution?

The evidence relevant to the assertion that recent soil chemical changes have actually occurred in North American red spruce-fir stands in response to increases in acidic deposition falls into two categories: (i) long-term studies of soil change, including studies of tree ring chemistry as a record of soil solution chemistry; and (ii) experimental field studies. Leaching and plant uptake (coupled with harvest removal) are the two principle pathways by which base cations are removed from forest soils, resulting ultimately in soil acidification in most forest ecosystems. We will

THE co-occurrence of increases in acidic deposition and the unexplained decline of red spruce (*Picea*

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compare, for the base cations Ca, K, and Mg, current rates of plant uptake and of net ecosystem leaching loss, and we will attempt to place these cation transfers into a nutrient cycling perspective. We will also attempt to bracket the portion of gross leaching losses attributable to atmospheric deposition. Regional and elevational patterns in soil and soil solution chemistry, and in the foliar nutrition of red spruce and two associated fir species, balsam fir [*Abies balsamea* (L.) Mill.] and Fraser fir [*Abies fraseri* (Pursh) Poir.], will then be related to available information on nutrient deficiency levels and toxicity thresholds. Finally, we will evaluate the potential for future changes in spruce-fir soil chemistry in light of possible changes in global climate and in the atmospheric deposition regimes for S and N.

CHARACTERIZATION OF SPRUCE-FIR SOILS

This review focuses on ecosystems dominated by red spruce. For comparison purposes, we have divided red spruce stands into three geographic regions: (i) high elevations of the southeastern USA (spruce and spruce-fir stands are confined to elevations above 1300 m, which occur chiefly in Tennessee and North Carolina), (ii) high elevations of the northeastern USA (which occur in New York, Vermont, New Hampshire, and Maine), and (iii) low elevations of the northeastern USA (chiefly New York and the New England states) and eastern Canada (Nova Scotia, southern Quebec, and New Brunswick). Following Friedland et al. (1988), we have defined northeastern low elevation stands as those below 650 m. In low elevations of the Northeast, we will confine our review mainly to relatively pure red spruce stands, though data may be drawn from red spruce-deciduous or red spruce-black spruce [*Picea mariana* (Mill.) B.S.P.] mixtures on occasion. In high elevations, stands frequently are red spruce-Fraser fir (Southeast) or red spruce-balsam fir (Northeast) mixtures. More attention will be focused on high elevation red spruce, because red spruce decline has been more severe at the higher elevations. Studies from European Norway spruce stands will only be considered where they demonstrate processes or mechanisms applicable to North American spruce-fir stands.

Before we review the evidence relating to changes in soil chemistry, an overview of the chemical characteristics of red spruce-fir soils in eastern North America seems appropriate. Soils of red spruce-fir forests typically have thick organic horizons, ranging from 5 to 15 cm (McCracken et al., 1962; Wolfe, 1967; Arp and Manasc, 1988; Fernandez and Lawrence, 1989). In high elevation stands, depending on parent material and slope characteristics, these organic layers are commonly underlain by (i) shallow bedrock (usually Histosols), (ii) thick dark A horizons, rich in organic matter and formed in loamy or fine-textured soils (usually Inceptisols), or (iii) ashy gray sands over dark sandy loams (Spodosols) (Huntington and Ryan, 1988; Kelly and Mays, 1989). Low elevation red spruce stands generally occur either on well-developed Spodosols or on moderately well to poorly drained soils (usually Inceptisols). Regardless of soil classification, a high organic matter content is a nearly universal

characteristic. Observed pH values (0.01 M CaCl₂) exhibit modest variation among studies with most organic horizons falling into the 3.0 to 4.0 range and most mineral horizons in the 4.0 to 4.5 range (Table 3). Although the observed exchange capacities for many of these soils are moderately high, the percent base saturation is usually low, especially in the mineral soil.

Figure 1, adapted from Robarge and Smithson (1989), presents soil pH, base saturation, and C content as a function of depth for a red spruce-Fraser fir stand on Roan Mountain, NC. The patterns depicted in this figure are representative of those observed in both northeastern and southeastern spruce-fir soils (Wolfe, 1967; Fernandez and Struchtemeyer, 1985). The most acidic portion of a typical spruce-fir soil profile can be found in the organic horizon or in the vicinity of the organic-mineral soil interface. The pH minimum near this interface is probably the result of the combination of high cation exchange capacity (CEC), low base saturation, and high acid strength of the organic matter at this depth (Binkley and Sollins, 1990). Exchangeable Al concentrations also peak near this organic-mineral soil interface (Fig. 2).

A number of soil chemical properties are strongly influenced by organic matter content and decline with depth. Because there is a relatively small clay component in most spruce-dominated soils, organic matter plays a significant role in determining the CEC (McCracken et al., 1962; Losche et al., 1970; Lietzke and McGuire, 1987; Kelly and Mays, 1989); consequently, CEC, like organic matter content, is highest near the surface and declines with depth. The highest percentage base saturation is typically found in the upper portions of organic horizons and then declines abruptly to the mineral soil (Fig. 1) (Wolfe, 1967; Robarge and Smithson, 1989). Maximum concentrations of individual base cations similarly decline abruptly with depth below the O horizon (Fig. 2) (Fernandez and Struchtemeyer, 1985). In the work reported by Kelly and Mays (1989) and Huntington and Ryan (1988), soils classified as Histosols (i.e.,

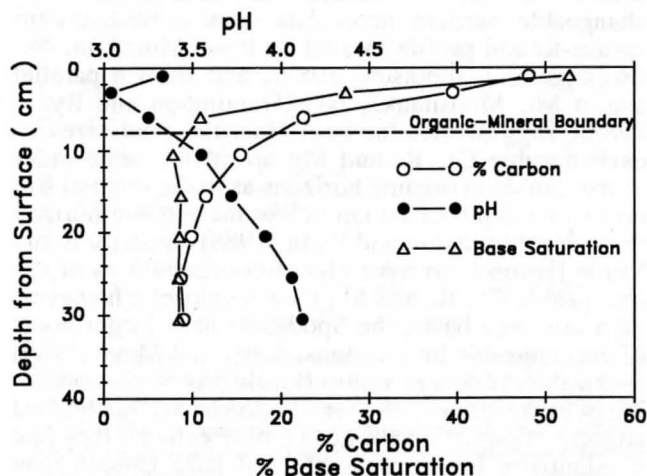


Fig. 1. Changes in soil pH (0.01 M CaCl₂), percent base saturation, and organic C content with increasing depth in a typical red spruce-fir soil profile. Data are from Robarge and Smithson (1989).

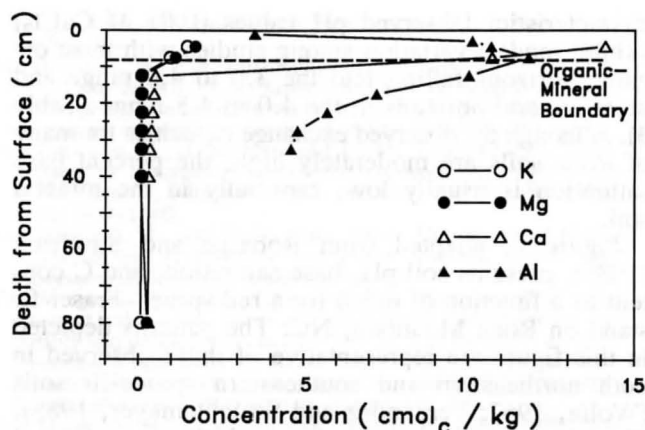


Fig. 2. Changes in the concentrations of exchangeable Ca, K, Mg, and Al with depth in a typical red spruce-fir soil profile. Base cation data from Fernandez and Struchtemeyer (1985) and Al data from Robarge and Smithson (1989). Some points have been interpolated to fill out curves.

soils composed primarily of organic material) had the highest concentrations of exchangeable bases of all the soils investigated in both studies. At some sites, there was a trend toward an increase in base saturation with depth in the C and CR portions of the soil profile (Fernandez and Struchtemeyer, 1985; Johnson et al., 1988b), due to differences with depth in the degree of weathering of soil materials. Nitrogen concentrations are also highest in the upper part of the soil profile, are strongly correlated with organic matter content, and decline with increasing soil depth (McCracken et al., 1962; Wolfe, 1967; Robarge and Smithson, 1989; Johnson et al., 1991).

The substantially lower exchangeable cation concentrations in mineral horizons does not necessarily result in their being a minor source of cations relative to organic horizons. Concentrations are expressed per unit of soil weight and organic horizons have much lower bulk densities and are usually thinner than mineral horizons. Consequently, mineral horizons may be as important as organic horizons when exchangeable cations are expressed in terms of "total pools." Exchangeable nutrient mass data from a southeastern spruce-fir soil profile located on Roan Mountain, NC (Robarge and Smithson, 1989), and from a parallel site at Mt. Moosilauke, NH (Huntington and Ryan, 1988), suggest that for both sites the pool sizes of exchangeable Ca, K, and Mg are of the same order of magnitude in organic horizons as in the mineral soil taken to a depth of 20 cm below the organic horizon (Fig. 3). Huntington and Ryan (1988) similarly found Lithic Histosols to have higher concentrations of exchangeable Ca, K, and Mg than Spodosols; however, on a unit area basis, the Spodosols have larger pools of exchangeable base cations. Kelly and Mays (1989) found that, although Lithic Borofolists (soils consisting of organic mats overlying bedrock) had the highest concentrations of exchangeable base cations, they had substantially lower pools of total base cations than deeper soils with mineral horizons.

Whereas the strong stratification of soil chemical and physical properties by depth is a dominant characteristic of most spruce-fir soils, many soils are con-

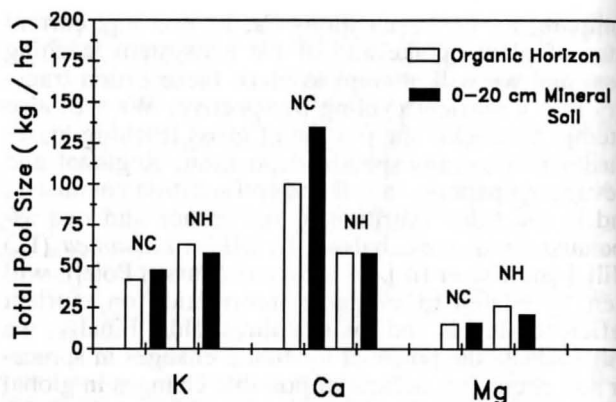


Fig. 3. Average sizes of pools of exchangeable cations (kg ha^{-1}) from organic horizons and the upper 20 cm of mineral soil for two locations, Roan Mountain, NC (Robarge and Smithson, 1989), and Mt. Moosilauke, NH (Huntington and Ryan, 1988).

tinually subjected to mixing as a result of windthrowing of trees and the downslope movement of colluvium. In fact, Kelly and Mays (1989) noted that even in the relatively ancient but steep landform of the southern Appalachian mountains, 77% of the soil profiles examined had little horizon differentiation and hence were classified Inceptisols. This continued mixing may play an important role in slowing the chemical stratification of the rooting zone as well as in providing fresh material for weathering and subsequent base release in southeastern spruce-fir stands. Slope stability considerations are less likely to be important in influencing the chemistry of soils across the lower elevation portions of the northern range of red spruce.

The preceding data summarization raises two significant points with respect to spruce-fir soils: (i) the importance of organic matter in influencing the vertical distribution of the concentrations of available nutrients and of soil chemical properties; (ii) the need to evaluate nutrient availability as a function of both pool size and concentration rather than on the basis of concentration alone. A number of soil characteristics— notably the size of exchangeable cation pools, CEC, percent base saturation, and organic matter content— influence the buffer capacity of forest soils (Federer and Hornbeck, 1985) and hence the sensitivity of these ecosystems to changes such as those induced by acidic deposition (McFee et al., 1977), to be discussed in the following sections.

EVIDENCE OF RECENT SOIL CHEMICAL CHANGES

Long-Term Studies of Soil Change

Forest floor characteristics and soil properties such as pH and exchangeable cation concentrations are more likely to be altered within decades than are other soil properties, especially soil physical properties (Alban, 1982). One approach that has been used to address both the occurrence and causes of soil change is the co-analysis of recent and historical soil samples combined with an analysis of cation uptake and changes in stand composition (Alban, 1982; Brand et al., 1986; Falkengren-Grerup, 1986; Hallbacken and Tamm,

1986; Tyler et al., 1987; Andersen, 1988; France et al., 1989; Binkley et al. 1989). Change in soil pH has been used most widely as the general indicator of change in soil acidity (De Vries and Breeuwsmma, 1987). Changes in soil pH over time have been attributed to alterations in cation pools as stands grow and mature, or as changes in species composition occur (Nilsson, 1983), as well as to acidic inputs from outside.

If base cations sequestered in the plant are removed from the site in a harvest, the result is a decrease in total base cation capital and a relative increase in H⁺ and Al saturation and hence system acidification. The net amount of acidification that actually occurs will depend on both the buffer capacity of that ecosystem and the rates of base cation replacement via deposition or weathering. Wiklander (1980) hypothesized that soils in the midrange of typical forest soil pH values (4.5–6) would be the most sensitive to pH change since more acidic soils would be buffered against further acidification by the relatively high levels of Al, and circumneutral soils would be buffered by a high degree of base saturation. Although the above-mentioned studies of soil change have dealt with a variety of forest cover types, they all have verified Wiklander's hypothesis that mid-pH range soils are much more subject to change.

One comparative study of great interest in the context of this analysis of spruce-fir systems, is the work of Hallbacken and Tamm (1986) on Norway spruce [*Picea abies* (L.) Karst] stands in Sweden. Figure 4 illustrates the average pH values by horizon across five spruce stands in 1927 and 1983, indicating a decline in soil pH in the intervening half-century. The data presented in Fig. 5, taken from the same study but ranked by stand age, illustrate an acidifying effect of forest development (i.e., stand age), depicted by the regression lines (solid). The data support the hypothesis of Alban (1982) that tree influence on soil is exercised primarily through litterfall and root activity and should hence decrease abruptly with depth. The Hallbacken and Tamm (1986) data (Fig. 4) certainly illustrate a near surface impact as might be expected, but they also suggest a continuing change with increasing depth.

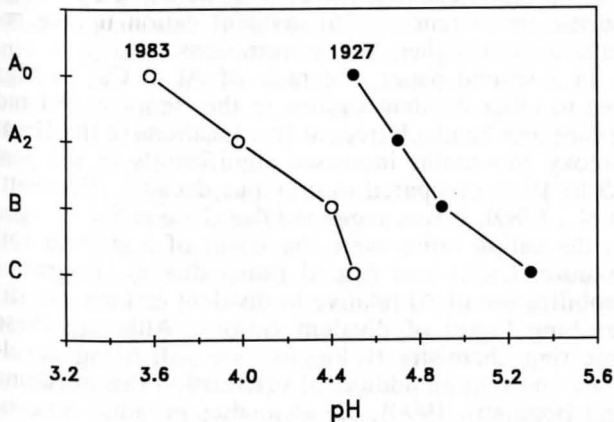


Fig. 4. Changes in mean soil pH (H₂O) with depth during the period 1927–1983 for five spruce stands in southwestern Sweden. Data are taken from Hallbacken and Tamm (1986).

This subsurface change suggests that factors in addition to forest development—such as atmospheric deposition—are affecting soil chemistry. Even stronger evidence of an additional acidifying agent is the fact that stand development alone cannot account for the rate of soil acidification. The total displacement of pH between 1927 and 1983 is depicted in Fig. 5 by dotted lines connecting remeasured plots; the slopes of these lines are much steeper than those of the forest development regression lines, suggesting an additional acidification source. When these data are further compared with observations on soil pH reductions in slow-growing oak forests with little or no wood removal over the same time period (Hallbacken and Tamm, 1986),

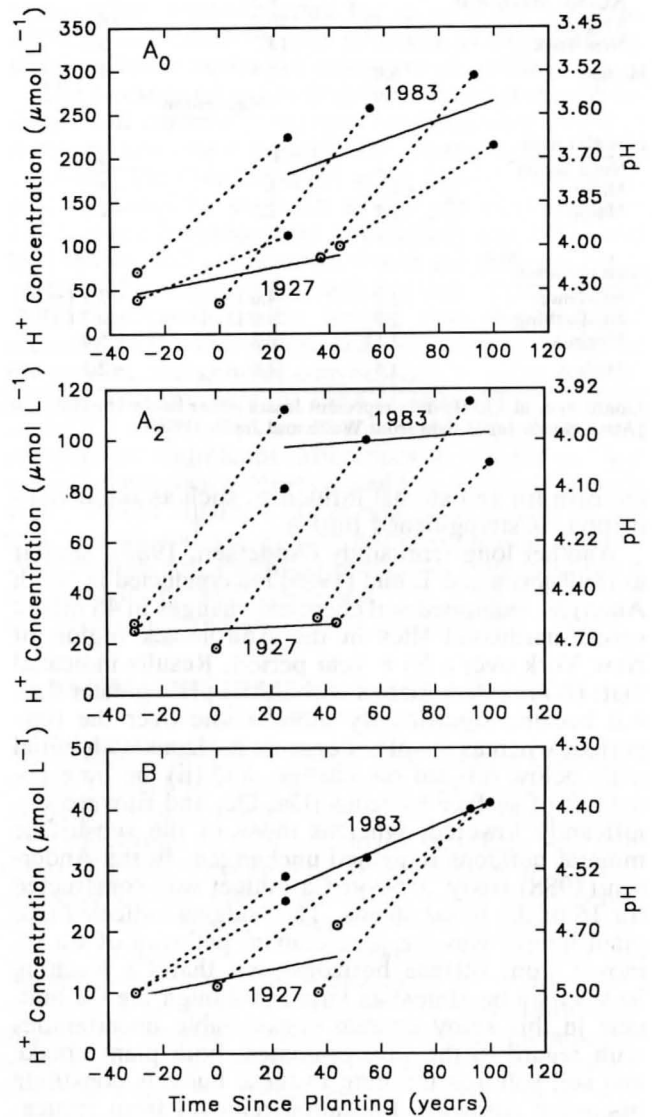


Fig. 5. Changes in soil H⁺ concentrations (from water suspension pH measurements) in samples from three soil horizons from five spruce stands in southwestern Sweden over a 56-yr period (1927–1983), as reported by Hallbacken and Tamm (1986). Stand ages varied but all sites were originally beech forests until planted to Norway spruce at "0 yr since planting." Solid regression lines depict the rate of acidification attributable to time under spruce forest. Dotted lines connect measurements of the same stand and therefore depict actual (measured) rates of soil acidification.

Table 1. Red spruce ecosystem atmospheric inputs and leaching outputs and net differences for major cations and nitrogen.

Location	Atmospheric inputs	Leaching outputs	Net	Atmospheric inputs	Leaching outputs	Net	Source
	kg ha ⁻¹ yr ⁻¹						
	Calcium			Potassium			
Low elevation							
Nova Scotia	-	-	-7	-	-	-0.6	Freedman et al. (1981)
Maine	1	16	-15	< 1	2	-2	Hornbeck et al. (1990)
New York	2.1	6.4	-4.3	-	-	-	Andersen (1988)
Maine	1.0	3.2	-2.2	1.0	3.0	-2.0	Lawrence & Fernandez (1991)
High elevation							
NC-Tower	16.0	11.6 (15) [†]	+4.4 (+1) [†]	6.6	4.7 (16.4)	+1.9 (-9.8)	Johnson et al. (1991)
NC-Becking	16.0	12.3 (17)	+3.7 (-1)	6.6	4.7(9.8)	+1.9 (-3.2)	Johnson et al. (1991).
NC-Mt. Mitchell I	-	12.3	-	-	10.0	-	Smithson et al. (1989)
NC-Mt. Mitchell II	-	8.2	-	-	7.4	-	Smithson et al. (1989)
Virginia	15.0 [‡]	25.2	-10.2	1.4 [‡]	21.8	20.4	Smithson et al. (1989)
New York	-	13	-5.8	-	-	-	Miller et al. (1987)
Median	8.0	12.3	-4.3	1.4	4.7	-1.3	
	Magnesium			Nitrogen			
Low elevation							
Nova Scotia	-	-	-2	-	-	+7	Freedman et al. (1981)
Maine	<1	5	-5	4	<1	+4	Hornbeck et al. (1990)
Maine	0.1	2.1	-2.0	4.5	0.2	+4.3	Lawrence & Fernandez (1991)
High elevation							
NC-Tower	2.3	4.6 (5.8) [†]	-2.3 (-3.5)	27	32	-5	Johnson et al. (1991)
NC-Becking	2.3	3.0 (5.0)	-0.7 (-3.7)	27	21	+6	Johnson et al. (1991).
Virginia	1.5 [‡]	6.5	-5.0	32 [‡]	47	-15	Smithson et al. (1989)
Median	1.5	4.6	-2.2	27	21	+4.2	

[†]Johnson et al. (1991) data represent losses either below the Bw2 horizon (no parentheses) or below the A horizon (parentheses).

[‡]Atmospheric input data from Wolfe and Joslin (1990).

the case for an external influence, such as acidic deposition, is strengthened further.

Another long-term study (Andersen, 1988), similar to Hallbacken and Tamm (1986) but conducted in North America, examined soil chemical changes in 48 mixed spruce-hardwood sites in the Adirondack region of New York over a 50+ year period. Results indicated that: (i) organic horizons with initial pH's greater than 4.0 became significantly more acidic over the time period, whereas the pH of organic horizons with initial pH's below 4.0 did not change, and (ii) the lime potentials of surface horizons (Oa, Oe, and E) were significantly lowered, whereas those of the subsurface mineral horizons remained unchanged. In the Andersen (1988) study, a 50-yr Ca budget was constructed for 15 of the forest stands. The budgets indicated that plant uptake was the predominant pathway of Ca removal from surface horizons, but that Ca leaching losses may be almost as large. Although the Ca budgets in this study contain considerable uncertainties with regard to the flux estimates, both plant uptake and soil solution leaching in these budgets constitute important pathways for cation removal from spruce-fir soils.

Bondiotti et al. (1989, 1990) have attempted to examine trends in cation concentrations in tree rings as an historical record of sap chemistry, and have interpreted these data also as an indirect record of soil solution chemistry. Although individual tree patterns appear to vary considerably with regard to the magnitude and timing of the changes, there is a general tendency for concentrations of divalent cations to increase in wood formed during the mid-1900s, fol-

lowed by a decrease in the latter part of this century. Bondiotti et al. (1990) interpreted changes in divalent cation concentrations to reflect changes in soil solution chemistry and came to the following two conclusions: (i) the inferred initial increases in sap divalent cations were the result of the accelerated release of divalent cations from soil exchange sites, caused by elevated anion concentrations in soil solution, which in turn resulted from rapid increases in the deposition of sulfate to eastern North America beginning around 1950; and (2) the subsequent decreases in divalent cation concentrations were the result of reduced availability of these cations caused by prior accelerated rooting zone leaching losses and, perhaps, by antagonistic interferences with divalent cation uptake resulting from higher Al concentrations.

In a related paper, the ratio of Al to Ca, to Mg, and to other divalent cations in the stemwood of red spruce and hemlock trees at five locations in the Great Smoky Mountains increased significantly in the past 15 to 40 yr compared to previous decades (Bondiotti et al., 1989). It was suggested that these radial changes in the cation ratios were the result of a shift in soil solution Ca/Al and Mg/Al ratios due to (i) greater mobilization of Al relative to divalent cations and (ii) leaching losses of divalent cations. Although these tree ring chemistry techniques are still being developed and require additional verification (Momoshima and Bondiotti, 1990), the anomalies in radial concentration trends of Ca and Mg in red spruce stemwood are difficult to explain by processes other than historical changes in sap chemistry. The authors have ignored the possible role that plant uptake may have

played in the particular stands studied, and have concentrated on soil leaching and soil ionic strength alterations as causal factors. Also, some of the proposed changes could be attributed to alterations in ionic strength and Al concentrations alone, without actual leaching losses of divalent cations having occurred.

Experimental Field Studies of Deposition Effects

There are only a few studies that have directly investigated the impact of increased strong acid inputs on forest soil properties under field conditions. Two major studies have been conducted in Europe in Norway spruce (Kreutzer, 1987; Kreutzer et al., 1989; Stuanes, 1980; Stuanes et al., 1988) and one in a low-elevation mixed conifer stand in Maine (Fernandez and Rustad, 1990). The common observation between these studies is that increased strong acid input to the soil can accelerate the displacement of base cations (particularly Ca and Mg) from the cation exchange complex, but that those changes are usually most prevalent in the upper part of the soil profile and associated with the most intensive strong acid applications (pH < 3).

Following 3 yr of acid irrigation to the forest floor, Kreutzer (1987; Kreutzer et al., 1989) observed a significant decline in exchangeable Ca and Mg from the organic O₁ and O₂ horizons associated with an increase in H⁺, and a significant decline in CEC due to protonation of the organic ligands. No change in the CEC and base saturation was observed in the O₃ and mineral horizons below. Acid irrigation did not significantly decrease the pH of soil solutions, an indication of strong buffering capacity of the soil attributed mainly to cation exchange in the organic horizons and dissolution of MnO₂ in the mineral horizons. The Ca and Mg solution concentrations of 20 and 40 cm started to increase considerably over control plot values in the third year of acid irrigation, presumably as a consequence of leaching from horizons above. Aluminum solution concentration exceeded 0.80 mmol L⁻¹ levels at 20-cm soil depth, but the increased Al concentration did not cause any visible injury to the trees, except for a decrease in the number of root tips (Kreutzer et al., 1989). A field experiment on a low elevation mixed conifer-spruce stand in Maine showed that strong acid irrigation significantly increased nitrate and/or sulfate solution concentrations, though nitrate increases were only observed in surface horizons (Fernandez and Rustad, 1990). Cation leaching increases were correlated with increases in sulfate concentrations, and Mg and Ca were the two base cations showing the largest increase.

The acid irrigation experiments at Nordmoen, Norway, have been conducted over the longest time period and have generated the most comprehensive data set on changes in soil chemistry, solution concentrations, and forest growth induced by increasing sulfuric acid inputs, as well as on the degree of recovery following the decline in acid input (Stuanes et al., 1992). An increase in sulfate input increased sulfate leaching output and concurrently increased the concentration of base cations in the soil solution collected below the rooting zone. An overall pH decline with time was observed in the upper mineral soil and forest floor of all treatment plots (including the control plots irrigated

with groundwater of pH 6), which reflected the acidifying influence of cation uptake by the trees. Superimposed on this natural acidification process was a decline in exchangeable bases and pH with acid treatment, which was most pronounced following the high acid inputs (pH < 3) and greatest in the upper soil horizons (Stuanes, 1980; Abrahamsen and Stuanes, 1986). The large changes in soil chemistry were reflected in a moderate decline in Ca and Mg foliar concentrations only in the most acid treatment (pH = 2.5), but none of the trees showed signs of nutrient deficiencies. No significant treatment effect on tree height and basal area increment was measured during the irrigation period. However, a growth decline gradually developed in the acid-treated plots after the treatments were stopped, lasted for about 5 yr, and were difficult to explain by tree nutrition as expressed by standard foliar analysis (Stuanes et al., 1988).

The Norway experiment demonstrated that acid-induced soil chemistry changes are reversible and that recovery can occur rapidly after strong acid input is curtailed. The O-horizon pH in the pH = 2.5 treatment plot increased by as much as 0.3 pH units between 1978 (when irrigation was terminated) and 1981, and by 1984 the soil pH associated with the different treatments had converged for each horizon. The base saturation followed similar trends, with the strongest recovery in the O horizon, smaller changes deeper in the profile, and general convergence between the different treatment plots by 1984 (Stuanes et al., 1988). In 1988, 10 yr after treatment application had been stopped, no significant differences in soil pH or base saturation between treatments could be detected (Stuanes et al., 1992). Again, a lag period between soil chemical changes and tree growth responses was observed: even though soil chemical properties improved most dramatically between 1978 and 1981, tree growth did not start to improve until 1983 (Stuanes et al., 1988).

ESTIMATING RATES OF SOIL CHEMICAL CHANGE

The objective of this section is to examine estimates of the current rates of change in soil exchangeable cation pools of spruce-fir forests, and to compare those rates of change to fluxes of major nutrients into and out of the forest ecosystem. A net decline in the exchangeable base cation pools can result from either plant uptake (with or without harvesting removal) or cation leaching, if not compensated for through increased weathering, mineralization, or atmospheric inputs of base cations. Atmospheric deposition can, through the introduction of mobile strong acid anions, lead to soil acidification via leaching of base cations from the exchange complex. A second form of acidification—soil solution acidification via Al mobilization—however, does not require any change in soil cation pools, but is simply associated with an increase in solution anion concentrations in acidic soils (Reuss, 1983; Reuss and Johnson, 1986).

Cation Leaching Losses

Table 1 summarizes ecosystem inputs, outputs, and net leaching losses for Ca, Mg, K, and N as estimated in a number of red spruce stands. Although there is

considerable uncertainty associated with the estimates of atmospheric deposition and leaching fluxes, available data indicate that red spruce stands in general are experiencing net losses from the rooting zone of the three major cations—Ca, Mg, and K. Data for Mg are the most consistent across stands indicating a fairly narrow range of net leaching losses; data for Ca and K are more variable. Estimated atmospheric inputs of Ca are especially variable and are the major reason that estimates of net Ca losses differ so much between studies. Studies at northeastern low elevation sites have ignored dry deposition inputs, which appear to be substantial in the Southeast for Ca and N (Johnson et al., 1991). Results from Johnson et al. (1991) differ from the other studies in that they indicate net ecosystem losses of Mg only. Results also vary with the depth of the soil profile considered, as illustrated by the data from Johnson et al. (1991) in Table 1, which includes estimates for losses from below both the A and the Bw2 horizons.

Several published studies have attempted to place leaching losses and/or whole-tree harvesting into a nutrient cycling perspective by comparing these losses to the size of exchangeable pools and/or to the size of total pools of a particular nutrient (Smith et al., 1986; Johnson et al. 1988c; Federer et al., 1989). The exchangeable pool measured at any point in time, however, is quite small compared with fluxes into and out of the ecosystem over several decades. In contrast, total cation pools are large compared to these fluxes and are dominated by mineral components that become available to plant roots slowly (fractions of a percent per year). Rather than showing these comparisons, we have compared leaching and harvesting losses to the size of the organic horizon pool for total contents of each element. The mineralization of these organic horizons is a major source of cations for plant uptake. Whereas mineral horizons also constitute an important source of cations, organic pools turn over much more rapidly than weatherable mineral pools. Table 2 presents projected cation leaching losses (assuming the median values from Table 1 continue at the present rate) over 50 yr and compares them to (i) soil losses that would result from 50 yr of gross plant uptake, (ii) losses from the removal of forest products via whole tree harvesting, assuming a 50-yr rotation, and (iii) the present amounts of these cations stored in the organic horizons.

Assuming the median values presented in Table 1 are accurate estimates of current leaching losses, Table 2 indicates that 50 yr of net Ca leaching losses are approximately half the amount of cation exports resulting from whole tree harvesting; Mg leaching losses, on the other hand, are two to three times the amount potentially removed by harvesting. For both cations over the same time interval, leaching losses are a considerably lower percentage of total gross plant uptake than of harvest removals. This lower percentage simply reflects the fact that gross plant uptake is two to three times as large as aboveground net biomass accumulation (which is removed by whole tree harvesting). Leaching losses over 50 yr also appear substantial for all three cations (Mg > Ca > K) when compared to the current amount stored in organic horizons. Fifty

years of cation leaching losses is approximately comparable, according to these data, to the loss of the current forest floor (organic horizon) pool of Ca, one to three times that pool of Mg, and a variable fraction (0.1–0.9) of the K pool.

These comparisons indicate that leaching losses, particularly of Mg, may constitute an important drain on the cation supplies of many red spruce stands, assuming replacements via weathering are minimal, as estimated by Federer et al. (1989) for northeastern forests. The problem for Ca and Mg appears greater for stands rooted almost entirely in organic horizons (as in Lithic Borofolists; see Kelly and Mays, 1989) or with restricted exploration of mineral horizons. Spruce stands with extensive rooting in mineral soil appear less at risk, but still may experience antagonism by Al toward the uptake of cations in these low base-saturated mineral horizons. Another factor that may also be important to cation availability is litter quality. The nutrient supplying capacity of organic matter depends on its nutrient concentrations and its decomposition rate, both of which are influenced by the type of litter inputs (e.g., foliage vs. wood) and the nutrient status of those inputs (Gorham et al., 1979). Nutrient deficiencies may become accentuated over time as nutrients become immobilized in increasingly recalcitrant organic matter, irrespective of uptake and leaching rates.

The Contribution of Acidic Deposition to Leaching Losses

To evaluate the role of acidic deposition in cation leaching losses, one must quantify the impact of anthropogenic emissions on natural cation leaching rates. The equivalent charge of cations and anions leaving an ecosystem in leachate must be equal because solutions must maintain electrical neutrality. Thus, one can evaluate the role of acidic deposition by focusing on the percentage of the anionic charge in leachate that is attributable to anthropogenic emissions. Because no data are available on preindustrial anionic levels of eastern North American spruce-fir soils, we can only assume that current levels of bicarbonate, chloride, and organic acids have remained relatively unchanged since preindustrial times.

Under relatively pristine conditions, cation leaching is generally dominated by bicarbonate in temperate forests and by organic acids in subalpine conifer forests (Johnson and Cole, 1980). In most forests of eastern North American, however, sulfate and nitrate currently comprise more than 75% of anion concentration sums (Johnson et al., 1988c); in high-elevation forests, the percentage is even greater (Johnson et al., 1988b, 1991; Smithson et al., 1989; Huntington et al., 1990a; Ross and Bartlett, 1990). Because N is often a limiting nutrient, nitrate solution concentrations are low in most eastern North American forests, including low-elevation red spruce stands, so that sulfate is the dominant anion with respect to cation leaching. Thus, in low-elevation red spruce stands, the contribution of anthropogenic emissions to cation leaching is related to the fraction of leachate anion concentration represented by sulfate, since most sulfate in forest soil solutions is of anthropogenic origin.

Table 2. Comparison of net cation losses due to 50 yr of leaching with (a) whole tree harvesting removal (50 yr rotation), (b) 50 yr of plant uptake (gross), and (c) current storage in organic horizon pools.†

Study	Location	(a)	(b)	(c)	Net leaching loss (50 yr)
		Whole tree harvesting	Gross plant uptake (50 yr)	Organic horizon pool	
kg ha ⁻¹					
Calcium					
Weetman & Webber, 1972	Quebec	413 (0.70)	1800 (0.16)	253 (1.15)	—
Hornbeck et al., 1990	Maine	494 (0.59)	—	237 (1.22)	—
Gordon, 1983	Ontario	563 (0.52)	2200 (0.13)	—	—
Johnson et al., 1991	Tennessee	—	500 (0.58)	384 (0.76)	—
From median value (Table 1)					215
Potassium					
Weetman & Webber, 1972	Quebec	159 (0.19)	750 (0.04)	1052 (0.03)	—
Hornbeck et al., 1990	Maine	224 (0.13)	—	105 (0.29)	—
Gordon, 1983	Ontario	352 (0.09)	800 (0.04)	—	—
Johnson et al., 1991	Tennessee	—	550 (0.05)	69 (0.43)	—
From median value (Table 1)					65
Magnesium					
Weetman & Webber, 1972	Quebec	36 (3.20)	135 (0.85)	154 (0.75)	—
Hornbeck et al., 1990	Maine	52 (2.20)	—	50 (0.75)	—
Gordon, 1983	Ontario	44 (2.60)	150 (0.77)	—	—
Johnson et al., 1991	Tennessee	—	95 (1.20)	37 (3.10)	—
From median value (Table 1)					110

†Numbers in parentheses are the ratio of the median net leaching loss (taken from Table 1) and the particular quantity (a, b, or c) at that site. Net cation leaching losses have been calculated by multiplying the median annual values in Table 1 by 50.

This fraction generally exceeds 50% (Johnson et al., 1988c; Lawrence and Fernandez, 1991).

However, in many of the high elevation spruce-fir soil solutions, particularly in the southern Appalachians, nitrate is of equal importance to, or more important than, sulfate. Depending on the particular stand and the particular year of measurement, nitrate may constitute from 5 to 70% of the total anion pool of the soil solution (Tables 6 and 7). In forests where nitrate is a major anionic component, determining the relative contributions of anthropogenic N and pre-existent soil N to soil solution nitrate is extremely difficult. Based on the data summarized in Table 1, N inputs and outputs are nearly balanced in most high-elevation stands, implying that most N deposited passes through the ecosystem in leachates. Although internal sources of N also contribute to nitrate leaching in two of the three high-elevation stands in Table 1, N inputs to high-elevation stands (most of which are of anthropogenic origin) appear to be the major cause of the elevation of soil solution nitrate concentrations. In these high-elevation stands, where nitrate is a major component, if we assume that 75% of the nitrate in current red spruce soil solutions is of anthropogenic origin, we can crudely bracket the current cation leaching losses in high-elevation red spruce stands in eastern Northern America to be between 50 and 90% the result of anthropogenic emissions. When applied solely to base cation leaching losses, this analysis is somewhat complicated by the fact that acidic cations—Al species and H⁺—occupy an increasingly larger fraction of total cations lost as soils become more acidic and/or soil solution ionic strength increases.

Aluminum Mobilization

Soil solution acidification (Reuss, 1983)—i.e., Al mobilization via increases in soil solution ionic

strength—may occur without decreases in soil pH or the loss of cations from the rooting zone. According to Reuss' model (Reuss, 1983; Reuss and Johnson, 1986), in acidic soils with low base saturation, solution acidification may occur without a measurable change in exchangeable cation pools, simply due to the preferential displacement of Al vs. base cations from the exchange complex. In soils with low base saturations, like those observed in the mineral horizons of most spruce forests (Table 3), a significant increase in soil solution sulfate and/or nitrate concentration (either from atmospheric deposition or from internal nitrification) will lead to the preferential mobilization of Al over base cations. This, in turn, may elevate soil solution Al concentrations above toxicity thresholds, or alter Ca/Al and Mg/Al solution ratios to a level where they negatively affect Ca and/or Mg uptake by trees. Such low base saturation soils, while offering little resistance to Al mobilization via increases in solution ionic strength, will not be very susceptible to accelerated base cation leaching. The next section on regional and elevational patterns discusses the evidence for elevated soil solution Al, its relationship to nitrate concentrations, and the possible impacts of such Al mobilization on spruce forest health.

REGIONAL AND ELEVATIONAL DIFFERENCES IN SOIL CHEMISTRY, SOIL SOLUTION CHEMISTRY, AND FOLIAR NUTRITION

Soil Chemistry

The limited soils data that are available allow only a general regional comparison of organic and mineral horizons in spruce-fir soils (Table 3). Organic horizons have much higher CEC's and higher exchangeable base cation concentrations, and much lower pH's, than their mineral horizon counterparts; however, values within each horizon type encompass a fairly nar-

Table 3. Regional comparison of soil chemistry of organic horizons and mineral soils of North American red spruce-fir forests.

Study	Location	pH [†]	CEC	BS	Exchangeable			Al
					K	Ca	Mg	
			cmol _c kg ⁻¹	%	cmol _c kg ⁻¹			
Organic horizons								
Northeast — low elevation								
Fernandez & Lawrence, 1989	Maine	2.8	31	47	1.4	9.7	2.9	5.7
Arp & Manasc, 1988	New Brunswick	3.9	—	—	1.3	7.5	2.0	0.7
Fernandez & Struchtemeyer, 1985	Maine	3.1	—	—	1.5	14.1	1.7	1.4
Federer & Hornbeck, 1985‡	Maine	3.7	19	68	1.0	9.4	2.3	0.8
Northeast — high elevation								
Johnson et al., 1988b	New York	—	18	75	1.3	10.4	1.6	4.5
Huntington & Ryan, 1988	New Hampshire	3.2	—	53	1.0	5.7	1.4	7.0
Southeast — high elevation								
Robarge & Smithson, 1989	North Carolina	3.2	27	27	0.9	5.8	1.3	8.5
Richter et al., 1989‡	North Carolina	—	—	—	—	—	—	—
Johnson et al., 1988b	North Carolina	—	16	33	0.9	4.0	1.2	10.1
Wolfe, 1967	North Carolina, Tennessee	4.0	—	—	1.8	7.9	2.7	8.0
Mineral soil								
Northeast — low elevation								
Fernandez & Lawrence, 1989	Maine	4.2	5	8	0.07	0.10	0.06	3.0
Arp & Manasc, 1988	New Brunswick	4.2	—	—	0.29	0.60	0.20	2.1
Fernandez & Struchtemeyer, 1985	Maine	4.6	9	8	0.08	0.31	0.10	3.3
Moore, 1987	Quebec	4.3	—	16	0.23	0.98	0.25	—
Federer & Hornbeck, 1985§	Maine	4.2	5	11	0.10	0.25	0.11	3.4
Northeast — high elevation								
Johnson et al., 1988a	New York	—	6	10	0.10	0.30	0.06	5.9
Huntington & Ryan, 1988	New Hampshire	3.9	—	10	0.11	0.34	0.16	5.9
Southeast — high elevation								
Robarge & Smithson, 1989	North Carolina	3.8	10	9	0.16	0.28	0.20	6.5
Richter, et al., 1989‡	North Carolina	4.7	6	7	0.05	0.09	0.06	—
Johnson et al., 1988a	North Carolina	4.0	8	6	0.13	0.10	0.14	6.7
Wolfe, 1967	North Carolina, Tennessee	4.5	14	3	0.06	0.12	0.16	4.5

†0.01 M CaCl₂.

‡Oa horizon.

§Means of separate values for E, Bhs, and Bs horizons.

¶20–40 cm depth = "mineral soil."

row range across regions and elevations. Although the data are limited, exchangeable Al values are generally lowest, and mineral horizon pH values are generally highest, at the low elevation northeastern sites. Mineral soil exchangeable Ca levels and base saturations are also generally lower at the southern high elevation sites. Data from southeastern (Robarge and Smithson, 1989; Richter et al., 1989), northeastern high-elevation (Huntington and Ryan, 1988), and northeastern low-elevation (Fernandez and Lawrence, 1989) sites suggest that for all three regions pool sizes of exchangeable K, Ca, and Mg in the various horizons are of the same order of magnitude (Fig. 3).

Total N pools suggest some distinct differences between the northeastern sites and the sites in the southern Appalachians. Based on data summarized in Table 4, the high-elevation spruce-fir systems in the Southeast generally have more N accumulated in the mineral soil and consistently lower C/N ratios compared to the northeastern sites. Based on soil C/N ratios, the

northeastern sites still appear to be at or above the transition point between net N immobilization and net N release (C/N = 20–30), whereas the southeastern sites (C/N < 20) should have little or no N immobilization and high N mineralization potential (Alexander, 1977). As total soil N content increases, competition for available N generally declines, and nitrification and nitrate leaching occur (Van Miegroet et al., 1992). The N storage capacity of the mineral soil, and consequently the availability of excess N that can be nitrified, is also influenced by the total soil C content which, in turn, is regulated by climatic conditions (Post et al., 1982, 1985). The combination of high soil N content and low C/N ratio that is characteristic for the southeastern spruce soils suggests high nitrification potential in those systems, which is substantiated by high solution nitrate levels.

Information on spruce soil N mineralization rates are summarized for high elevation spruce-fir forests in Table 5. The net N mineralization rates generally

Table 4. Regional comparison of soil N concentration, total N content, and C/N ratio of organic horizons and mineral soils of North American red spruce-fir forests.

Study	Location	Organic horizons			Mineral soil		
		N (conc.) g kg ⁻¹	C/N ratio	Total N (pool) kg ha ⁻¹	N (conc.) g kg ⁻¹	C/N ratio	Total N (pool) kg ha ⁻¹
Northeast — low elevation							
Smith et al., 1986	Maine	—	40	920	—	27	5 800
Van Miegroet et al., 1992	Maine	—	—	1 480	—	27	3 080
Fernandez (1990, unpublished data)	Maine	12.5	38	1 034	1.2	30	2 275
Northeast — high elevation							
Lang et al., 1981	New Hampshire	—	19	2 300	—	28	3 510
Southeast — high elevation							
Richter et al., 1989†	North Carolina	—	—	—	—	16	8 400
Wolfe, 1967	North Carolina, Tennessee	18.0	—	3 060	1.3–4.6‡	19	12 500
Johnson et al., 1991(1)	North Carolina	17.1	31	2 170	0.9–4.5‡	—	—
Johnson et al., 1991(2)	North Carolina	17.1	34	1 430	0.9–4.5‡	11	9 040
Johnson et al., 1991(3)	North Carolina	15.8	39	1 920	0.7–6.6‡	18	7 240
McCracken et al., 1962	North Carolina, Tennessee	14.4	28	—	0.6–4.6‡	9	5 360

†0 to 40-cm depth. ‡N conc. declines with depth.

exceed the reported N requirement and N uptake values for spruce and fir forests (Cole and Rapp, 1981; Van Miegroet et al., 1992), suggesting that excess N should be available for nitrification. In the southeastern sites a greater proportion of inorganic N is nitrified compared to the northeastern spruce-fir sites: nitrification accounts for 8 to 72% (an average of 31%) of N mineralization in the southeastern soil and forest floor vs. only 1 to 19% (average of 7%) in the northeastern high-elevation sites (Table 5). Thus, under current conditions, the spruce-fir ecosystems in the Southeast appear to have a greater nitrification and nitrate leaching potential than the northeastern high-elevation sites.

McNulty et al. (1990) compared mineralization and nitrification rates in the O_a and O_e layers of 11 spruce-fir sites (low and high elevation) across the Northeast. The highest nitrification rates were measured at Whiteface Mt., NY, whereas little or no nitrification was observed at the low elevation sites in Maine. Nitrification was not, however, significantly correlated with elevation. Nitrification generally declined from west to east and was positively correlated with estimated N deposition.

The latter finding underscores the indirect effect of atmospheric deposition on N dynamics, making the separation of anthropogenically caused and "natural" leaching processes even more difficult. It also sug-

Table 5. Estimated N mineralization rates and percent nitrification in high-elevation spruce-fir sites.

Study	Location	Substrate	Mineralization	Nitrification as percentage of mineralization
			kg ha ⁻¹ yr ⁻¹	%
Northeast — high elevation				
Sasser & Binkley, 1989	Whiteface Mt., NY	FF + soil	80–130	<5–19
Sprugel, 1984	Whiteface Mt., NY	Litter	40–76	—
Friedland et al., 1988	Whiteface Mt., NY	FF	19–56	1–3
Average — Northeast			73	7
Southeast — high elevation				
Strader et al., 1989	Clingman's Dome, NC	Soil (0–10 cm)	87–152	47–52
Strader et al., 1989	Mt. Mitchell, NC	Soil (0–10 cm)	82–134	8–29
Strader et al., 1989	Whitetop Mt., VA	Soil (0–10 cm)	73–93	39–51
Sasser & Binkley, 1989	Mt. LeConte, TN	FF + soil	35–100	18–32
Van Miegroet (1988, unpublished data)	Clingman's Dome, NC	Soil (0–10 cm)	290	16–17
		Forest floor	107	27–71
Average — Southeast				31

Table 6. Soil solution chemistry for organic horizons of high-elevation spruce-fir forests in eastern North America.

Location	Organic horizons								Source
	pH	Nitrate	Sulfate	N/S charge ratio	Ca	Total Al		Ca/Al ratio	
						Max	Mean		
— $\mu\text{mol L}^{-1}$ —		— $\mu\text{mol L}^{-1}$ —							
Northeast									
Low elevation									
Maine, Howland	3.8	4	49	0.04	29	—	11	2.64	Lawrence & Fernandez, 1991
High elevation									
Vermont, Camel's Hump†	3.8	261	95	1.38	—	28	25	—	Ross & Bartlett, 1990
(two sites)	3.6	126	89	0.69	—	31	28	—	Ross & Bartlett, 1990
New York, Whiteface- lysimetry‡	4.1	17	94	0.09	35	78	67	0.52	Johnson et al., 1988b
New York, Whiteface- syringe§	3.5	243	108	1.13	104	180	71	1.50	Huntington et al., 1990a
New Hampshire, Moosilauke¶	4.0	8	69	0.06	13	—	20	0.63	Cronan, 1980
Average—Northeast High elevation	3.7	131	91	0.67	51	79	42	0.88	
Southeast									
North Carolina, Mitchell (2 sites)	4.2	149	67	1.11	37	260	50	0.76	Smithson et al., 1989
Virginia, Whitetop	4.4	132	40	1.65	30	—	30	1.00	Smithson et al., 1989
North Carolina, GSM, Raven Fork	3.4	638	167	1.91	111	275	75	1.50	Smithson et al., 1989
North Carolina, GSM, Becking‡	3.9	90	130	0.35	—	—	43	—	Joslin et al., 1987
North Carolina, GSM, Tower‡	3.8	183	82	1.12	30	—	56	0.53	Johnson et al., 1991
North Carolina, GSM, Tower‡	3.7	284	82	1.73	25	100	80	0.31	Johnson et al., 1991
Average—Southeast	3.8	246	95	1.31	47	212	56	0.82	
Overall average— organic	3.7	194	93	1.02	49	136	50	0.84	

†Several extraction techniques—average.

‡Volume-weighted mean.

§Syringe extraction technique; total reactive Al reported.

¶Zero tension lysimetry—forest floor and A2 horizon percolate.

gests a possible synergistic relationship between internal N cycling and external N deposition, causing nitrate to become an increasingly important leaching agent as N deposition increases. This process, which Ulrich (1983) termed "initiation of humus disintegration by acid deposition," involves the accelerated breakdown of soil organic matter, caused by external acid input, and resulting in nitrate production exceeding tree uptake requirements and ultimately in an increase in soil acidification.

Soil Solution Chemistry

Data on soil solution chemistry in spruce-fir stands are summarized in Tables 6 and 7. In most studies, soil solutions were collected by low tension lysimetry from within or immediately below the O horizon and from at least one surface mineral horizon. Soil solutions from organic horizons are consistently more acidic and have slightly higher concentrations of nitrate, sulfate, and Ca. The southern Appalachian sites tend to have higher nitrate and Al levels than the northeastern high- or low-elevation sites, though between-site variability is high. Across all the high-elevation sites reported here, nitrate and sulfate on the average account for approximately equal portions of the anion charge total, though there is a wide range in the N/S charge ratio (Table 6). In these soils with low base saturation,

nitrate and sulfate both contribute to the mobilization of exchangeable Al and to the elevation of Ca/Al ratios through preferential displacement of higher valence cations ($\text{Al}^{3+} > \text{Ca}^{2+}$, $\text{Mg}^{2+} > \text{K}^+$, Na^+) from the exchange complex via solution ionic strength increases (Reuss, 1983). Aluminum concentrations, however, are more highly correlated with nitrate than sulfate, largely because of the larger spatial and temporal variability of nitrate (Joslin et al., 1987; Smithson et al., 1989; Van Miegroet et al., 1990). For the mineral horizon data summarized in Table 7, the correlation coefficient between mean nitrate concentration and mean Al concentrations is +0.93, whereas for sulfate and Al, $r = +0.75$. Correlations between Al and nitrate concentrations for individual weekly soil solution samples from Mt. Mitchell and Whitetop Mountain range from +0.80 to +0.86, depending on site and sample depth, whereas for sulfate and Al, r ranges from +0.26 to +0.33 (Smithson et al., 1989). Johnson et al. (1991) and Van Miegroet et al. (1990) reported similar temporal correspondence between nitrate and Al concentrations.

The soil solution Al concentrations summarized in Table 7 are of some concern especially in several of the southern Appalachian sites where peak values approach or exceed the Al toxicity threshold for red spruce (0.25 mmol L^{-1}) (Raynal et al., 1990). Calcium/Al ratios below 1.0 have also often been considered det-

Table 7. Soil solution chemistry for surface mineral horizons of North American spruce-fir forests.

Location	Surface mineral horizons								Source
	pH	Nitrate	Sulfate	N/S charge ratio	Ca	Total Al		Ca/Al ratio	
						Max	Mean		
— $\mu\text{mol L}^{-1}$ —		— $\mu\text{mol L}^{-1}$ —							
Northeast									
Low elevation									
Maine, Howland	5.0	<2	49	<0.02	13		4	3.25	Lawrence & Fernandez, 1991 Cronan et al., 1989
New York, Huntington Forest	4.7					64		1.60†	
New York, Big Moose Lake	4.7					102		0.76†	Cronan et al., 1989
High elevation									
Vermont, Camel's Hump (2 sites)	4.5	40	63	0.32	—	14	8		Ross & Bartlett, 1990
New York, Whiteface- lysometry	4.5	63	62	0.51	—	—	—		Ross & Bartlett, 1990
New York, Whiteface- syringe	4.5	13	88	0.07	30	59	42	0.71	Johnson et al., 1988b
Average—Northeast High elevation	3.6	414	75	2.76	98	140	81	1.21	Huntington et al., 1990a
Average—Northeast High elevation	4.1	133	75	0.92	48	71	52	0.96	
Southeast									
North Carolina, Mitchell (two sites)	4.6	24	58	0.21	17	90	25	0.68	Smithson et al., 1989
Virginia, Whitetop	4.7	63	33	0.95	14		21	0.67	Smithson et al., 1989
North Carolina, GSM, Raven Fork	3.8	568	125	2.27	67	320	176	0.39	Smithson et al., 1989
North Carolina, GSM, Becking	4.1	90	100	0.45	—		37	—	Joslin et al., 1987
North Carolina, GSM Tower	3.9	194	63	1.54	35		64	0.55	Johnson et al., 1991
North Carolina, GSM Tower	4.3	145	68	1.07	16	150	66	0.24	Johnson et al., 1991
Average—Southeast	4.1	182	75	1.08	30	187	60	0.50	
Average—Mineral	4.1	162	75	1.02	35	129	57	0.63	

†Ca/Al ratio based on solutions where Al was the maximum measured.

perimental to root growth and nutrient uptake (Clarkson and Sanderson, 1971; Rost-Siebert, 1983; Ulrich, 1983; Shortle and Smith, 1988), though supporting evidence for this threshold value is quite mixed (Thornton et al., 1987; Eldhuset et al., 1987; Joslin and Wolfe, 1989; Kreutzer et al., 1989; Raynal et al., 1990; Succoff et al., 1990; Cronan, 1991). By this Ca/Al ratio criterion, the surface mineral horizons in southern Appalachian sites do not provide favorable environments for root growth. In contrast, on Whiteface Mountain, Huntington et al. (1990a) found that fewer than 10% of the soil solution samples had Ca/labile Al ratios less than 1.0. The timing of Al peaks with regard to root elongation and nutrient uptake must also be considered. In sites where Al peaks are related to nitrate fluctuations, these commonly occur in late summer and early autumn (Smithson et al., 1989; Van Miegroet et al., 1990), when root elongation rates are normally the highest (Lyr and Hoffman, 1967; Rook and Hobbs, 1976; Teskey and Hinckley, 1981).

The role of Al is probably smaller in the organic horizons than in the surface mineral horizons, where a higher percentage of the Al is in inorganic forms. Organically chelated Al has generally been considered nontoxic (Bartlett and Riego, 1972; Rost-Siebert, 1983). Johnson et al. (1991) reported that 80 to 90% of the total soluble Al was in inorganic forms in the mineral soil solutions at their sites in the southern Appalachians. Joslin and Wolfe (1988) noted that when total Al exceeded 0.25 mmol L^{-1} , 92 to 97% of the Al was

in inorganic forms. In the high elevations of the Northeast, Huntington et al. (1990a) found that 59% of the total Al in organic horizon soil solution was "labile" Al (or "rapidly reactive" Al), whereas 70% of the total Al in surface mineral soil solution was "labile." Cronan et al. (1989) reported that 60 to 80% of total Al was inorganic monomeric Al in soil solutions from two low elevation red spruce-hardwood stands in New York.

Many of the Al concentrations presented in Tables 6 and 7 are also well within the range in which Al is antagonistic toward the uptake and transport of cations (Raynal et al., 1990; Cronan, 1991). Thornton et al. (1987) reported reductions of foliar Ca and Mg of 60 and 80%, respectively, in seedlings exposed to 0.25 mmol L^{-1} Al compared with controls. A mechanistic relationship, in which the relatively high soil solution Al concentrations act antagonistically toward divalent cation uptake and result in the low foliar Ca and Mg concentrations found at some high elevation spruce sites, is certainly plausible (Joslin et al., 1988; Cronan, 1991).

Little direct evidence has been found from North American sites that undeniably connects Al concentrations or Ca/Al ratios in solution with forest health. Huntington et al. (1990a) reported no relationship between soil solution Al concentrations or Ca/Al ratios and red spruce crown condition on Whiteface Mountain. On the other hand, Joslin et al. (1990b), in comparing fine root biomass distributions in two red spruce

Table 8. Red spruce foliar elemental concentrations, current year needles from "healthy" mature trees.

Location	N	P	K	Ca	Mg	Fe	Zn	Cu	Mn	Al	Source
	g kg ⁻¹					mg/kg ⁻¹					
Northeast (low elevation)											
Maine	10.3	1.3	7.6	3.5	0.81	34	—	—	750	52	Fernandez et al., 1990
Maine	11.1	2.3	8.2	2.7	0.7	52	26	5	1490	19	Safford & Young, 1968
Maine	11.4	1.8	8.8	2.7	0.7	47	31	4	1040	16	Safford & Young, 1968
Maine	11.4	1.9	7.7	2.6	0.7	67	36	7	860	24	Safford & Young, 1968
Vermont, New York	10.6	1.3	—	2.4	0.70	—	23	—	1040	50	Friedland et al., 1988
New York	—	1.0	—	2.5	0.65	—	—	—	—	29	Joslin et al., 1988
New York	—	1.1	—	2.6	0.72	—	—	—	—	28	Joslin et al., 1988
Mean—low elevation	11.0	1.5	8.1	2.7	0.71	50	29	5.3	1040	31	
Northeast (high elevation)											
Vermont, New Hampshire	10.9	1.3	4.6	2.8	0.7	31	21	3	390	44	Lord, 1982 (healthy)
Vermont, New York	11.1	1.2	—	1.5	0.44	—	18	—	1000	41	Friedland et al., 1988
New Hampshire	—	1.2	4.5	2.5	0.66	—	—	—	1090	31	Huntington et al., 1990b
New York	10.2	0.9	3.8	2.9	0.53	—	—	—	—	—	Johnson et al., 1988b
Mean—high elevation	10.7	1.2	4.3	2.4	0.58						
Southeast (high elevation)											
North Carolina	10.5	1.3	5.6	1.4	0.69	52	14	3.3	520	91	Robarge et al., 1989
North Carolina	10.0	1.3	6.9	1.2	0.56	—	—	—	—	—	Johnson et al., 1988b
North Carolina	10.0	1.1	7.8	1.3	0.57	—	—	—	—	—	Johnson et al., 1988b
Virginia	10.4	1.2	4.6	1.0	0.60	130	13	3.5	420	40	Joslin (1989, unpublished)
Virginia	10.0	1.3	5.4	0.9	0.58	130	13	3.8	430	37	Joslin (1989, unpublished)
Mean—southeast	10.2	1.2	6.1	1.2	0.60						
Mean—all high elevation	10.4	1.2	5.4	1.7	0.59	86	16	3.4	640	47	
Range of moderate deficiency											
Red spruce seedlings	11.0–13.0	1.0–1.4	1.9–3.0	0.5–0.8	0.4–0.6						Swan, 1971
Norway spruce seedlings	9.0–18.0	0.7–1.0	3.0–7.0	0.2–0.9	0.2–0.8						Ingestad, 1962/1963
Norway spruce	13.0	1.1	4.0	1.0	0.7		15–20		20		Huettl & Wisniewski, 1987
Normal range											
All spruce species						35–70+	13–117	3.6–10.8	45–5210		Stone, 1968

stands on Whitetop Mountain, VA, found that, in the surface mineral horizons of one stand where (i) soil solution Al concentrations were repeatedly observed to exceed the toxicity threshold and (ii) mean Al concentrations in mineral horizons were significantly higher than in the second stand, fine root biomass was only 30% of that in the mineral horizons of the second stand ($p < 0.05$).

Red Spruce and Fir Foliar Nutrition

Table 8 summarizes nutrient concentrations in current year foliage of apparently healthy mature red spruce from a number of studies. Data are grouped by region—southern Appalachians (all high-elevation sites) and northeastern North America subdivided into high elevation and low-elevation sites. With the exception of Ca, the data from the high-elevation sites of the two different regions are quite similar, whereas the high-elevation and low-elevation sites are consistently different. The average foliar concentrations of every element summarized, except Al and Fe, is greater at low-elevation sites. The relatively small Mg concentration difference between low and high elevation takes on more significance when one considers the low variability among sites within a given elevation grouping. Foliar Ca concentrations at the southeastern Appalachian sites are approximately half those of the northeastern low-elevation sites.

Determining whether these concentrations are "de-

ficient" or "sufficient" is difficult in light of the paucity of experimental data on red spruce nutritional response curves. The major source of information is a study by Swan (1971), which developed response curves for red spruce seedlings to N, P, K, Mg, and Ca under greenhouse conditions. Additional solution culture data are available for Norway spruce seedlings (Ingestad, 1962/1963). The range of "moderate deficiency" from these two studies is displayed in Table 8, along with "recommended" levels for Norway spruce from Huettl and Wisniewski (1987). These values must be taken as crude guidelines only, in that greenhouse-grown seedling foliage may be quite different morphologically and nutritionally from mature tree foliage in the field.

Based on these data, red spruce at high elevations is marginally deficient in N, P, and Mg, whereas foliar Ca and K levels are adequate. Low-elevation spruce, in contrast, would be marginally deficient only in N by these standards. The N deficiency suggested by these standards receives little substantiating evidence in the high-elevation stands. The fact that many of these high-elevation sites receive high atmospheric N inputs (Lovett et al., 1982; Mueller and Weatherford, 1988; Saxena and Lin, 1988) and have unusually high nitrate levels in their soil solutions, argues strongly against the limited availability of N in these high-elevation ecosystems. Robarge et al. (1989), citing Leaf et al. (1970), also pointed out that the absence

Table 9. Summary of foliar nutritional data for balsam fir and Fraser fir.

Location	Species	N	P	g kg ⁻¹			Source
				K	Ca	Mg	
<u>Average foliar concentrations</u>							
Northeast							
Low elevation	Balsam fir (11 sites)	13.2	1.7	4.8	5.2	1.1	Robarge et al., 1989
High elevation	Balsam fir (four sites)	18.8	1.8	4.7	3.2	0.8	Robarge et al., 1989
Southeast							
High elevation	Fraser fir (two sites)	15.4	1.8	5.3	3.4	0.89	Shelton, 1989, in Robarge et al., 1989
		-	-	7.7	2.7	0.89	Roberts, 1982
<u>Levels of sufficiency</u>							
	Balsam fir	14.4	1.9	4.9	4.3	1.0	Timmer & Stone, 1978; Salonius, 1981
<u>Recommended levels</u>							
	Fraser fir	17.5	2.0	6.0	6.0	1.2	Shelton, 1989, in Robarge et al., 1989

of declining N concentrations in older needle age classes of red spruce (Friedland et al., 1988; Robarge et al. 1989), a typical trend for mobile nutrients that are deficient, implies sufficiency with regard to N.

Although foliar Ca levels appear adequate by these standards, southern Appalachian levels are much lower than those reported in the Northeast (Robarge et al., 1989) and may reflect low soil Ca levels that could be influencing root growth (Matzner et al., 1986; Henderson and Krstansky, 1989) or cambial growth (Shortle and Smith, 1988). In the southern Appalachians, McLaughlin et al. (1990, 1991) noted a decrease in the photosynthesis:respiration (Ps/Rs) ratio in red spruce foliage that was associated with decreasing growth, increasing elevation, decreasing foliar Ca and Mg, and increasing foliar Al. The inverse relationship between Ps/Rs and foliar Ca was subsequently reproduced in greenhouse studies, and Ca fertilization improved Ps/Rs ratios (McLaughlin and Tjoelker, 1991). The hypothesis that these Mg and Ca concentrations are deficient is supported by Norway spruce studies which have reported either (i) poor crown condition (chlorotic needles, premature needle abscission, decreasing crown density, and depressed shoot growth) that is correlated with foliar Mg and Ca across similar concentration ranges (Rehfeuss et al., 1983; Zech and Popp, 1983) or (ii) growth responses to Mg fertilization of Norway spruce trees with initial foliar Mg concentrations below 0.6 g kg⁻¹ (Huettl and Wisniewski, 1987). Rehfeuss et al. (1983) found that "diseased" Norway spruce trees had Ca, Mg, and Zn mean foliar concentrations of 1.2, 0.51, and 13 g kg⁻¹, respectively, whereas healthy trees had concentrations of 1.7, 0.69, and 20 g kg⁻¹, respectively. Poor crown condition of "diseased" trees was attributed to "extreme Mg deficiency" and "very low" Ca levels.

A limited amount of data are available on micronutrient concentrations (Table 8). According to the ranges reported by Stone (1968), concentrations of Mn and Fe are sufficient at all locations, whereas Zn and Cu levels at high-elevation sites are near or below the "normal range" for spruce species. At the southeastern high-elevation sites, foliar Zn concentrations are just below recommended minimum levels for Norway spruce (15 g kg⁻¹, Huettl and Wisniewski, 1987).

The available data on the foliar nutrition of balsam fir in northeastern North America have been comprehensively reviewed by Robarge et al. (1989). Average concentrations for current year foliage from overstory trees at 11 low-elevation sites and four high elevation are presented in Table 9, along with foliar concentrations found "sufficient" in field fertilization trials (Timmer and Stone, 1978; Salonius, 1981). Foliage concentrations from high-elevation sites had noticeably higher N concentrations, similar P and K concentrations, and lower Ca and Mg concentrations than low-elevation sites. At high-elevation sites, only Ca and Mg appeared low relative to sufficiently levels. At one site (Lang et al., 1982), balsam fir foliar Ca (1.2 g kg⁻¹) and Mg (0.4 g kg⁻¹) were especially low. Limited data on Fraser fir in the southern Appalachians also indicate foliar levels of Ca and Mg considerably below "recommended" concentrations (Table 9).

There is little evidence linking the above-discussed trends in red spruce and fir foliar nutrition with patterns in soil chemistry. Soils data rarely were collected from the same locations that provided foliar nutritional data. On the other hand, the low exchangeable Ca levels in the southern high-elevation sites are consistent with the low foliar Ca concentrations there. Also, the higher exchangeable Al and lower mineral soil pH values at the higher-elevation sites may have some indirect effect on cation nutrition via antagonisms toward cation uptake.

Little evidence exists that connects foliar nutrient deficiencies directly with red spruce health either. Huntington et al. (1990b) found no correlations between red spruce crown conditions on Mt. Moosilauke and foliar Ca, Mg, K, Al, P, or Mn. Crown condition was, however, positively correlated with extractable soil P and exchangeable Ca and Mg in the forest floor and negatively correlated (weakly) with exchangeable Al in the surface mineral soil. In a related study, Huntington and Ryan (1988) noted that exchangeable Ca and Mg concentrations declined with elevation in all horizons, while exchangeable Al concentrations increased. These patterns were consistent with declining trends in foliar Ca and Mg with increases in elevation (Table 8). At 22 low-elevation sites in Maine, Fer-

nandez and Struchtenmeyer (1985) also found that exchangeable Ca and pH in the O horizon, and organic P in the B horizon, were significant factors in models predicting the productivity of these red spruce-balsam fir sites.

Some evidence suggests that in recent years red spruce decline in the high elevations of the Northeast is related to increased incidence of winter injury (Johnson et al. 1988a; Shriner et al., 1990). Increased susceptibility to winter injury in red spruce has recently been coupled with exposure to acidic cloudwater (Fowler et al., 1989; DeHayes et al., 1991). DeHayes et al. (1991) speculated that a relationship may exist between such increased susceptibility to winter injury and lower foliar concentrations of Ca and/or Mg, since seedlings exposed to cloudwater in their study had both reduced cold tolerance levels and significantly lower foliar Ca and Mg concentrations.

POTENTIAL FOR FUTURE CHANGES

Future rates of base cation leaching losses and/or Al mobilization in eastern North American spruce-fir forests will depend chiefly on the anion loading of soil solutions. These anion loads in turn will depend largely on sources and sinks for S and N. Retention in the soil of atmospherically deposited sulfate is largely dependent on the sulfate adsorption capacity of a given soil. Rochelle et al. (1987) noted that most Spodosols of the northeastern U.S. currently are retaining virtually none of the incoming sulfate deposited on them. Similarly, Fuller et al. (1985) found little sulfate retention at current solution concentrations in both hardwood and spruce-fir Spodosols at two locations in the Northeast, though they concluded that these soils were capable of adsorbing additional sulfate if concentrations were increased. Additions of highly concentrated sulfate (0.25 mmol L^{-1}) solutions to soils from spruce-fir sites in North Carolina, Maine, and New York indicated that most have some sulfate adsorption capability remaining (Harrison et al., 1989); however, the mean sulfate adsorption capacity of the five red spruce soil horizons included in this study ($0.50 \text{ mmol kg}^{-1}$) was considerably lower than the mean value ($1.63 \text{ mmol kg}^{-1}$) for the 32 other forest soils examined in the study. Other studies that have experimentally applied S to soils from spruce stands have found little retention of sulfate except at high solution concentrations (Fernandez and Kosian, 1986; David et al., 1989). Decreases in soil pH, however, do appear to increase sulfate adsorption capacity (Harrison et al., 1989; David et al., 1989).

Evidence reviewed above indicates that considerable N is available for nitrification in many red spruce stands. Regional differences in percent N nitrified (Table 5), soil C/N ratio (Table 4), and nitrate leaching patterns (Tables 6 and 7) suggest that spruce-fir ecosystems in the Southeast generally have a greater potential for nitrification and nitrate leaching than those in the Northeast. Dead and mature zones generally have shown higher N mineralization and nitrification rates, and higher rates of nitrate leaching, than the regenerating and juvenile phases of stand development, which are characterized by higher growth and N uptake rates (Sprugel, 1984; Sasser and Binkley, 1989; Joslin et

al., 1990a; Table 5). Physical disturbances to spruce-fir soils may also result in increases in N mineralization and nitrification whether during lysimeter installation (Johnson et al., 1991), sample collection (Ross et al., 1989; Ross and Bartlett, 1990; Huntington et al., 1990a), or forest harvesting operations (Weetman and Webber, 1972; Smith and Hornbeck, 1985; Hornbeck et al. 1987; Hornbeck et al., 1990). Although mechanical soil disturbance and reduced uptake have been cited as the major factors in these increases in nitrate release following harvesting, increases in soil temperature resulting from exposure of the forest floor to sunlight (Timmer and Weetman, 1968) may play an important role also (Stone, 1975; Covington, 1981). Predicted global temperature increases may have a similar impact on nitrate release in spruce-fir stands.

In these extremely acidic spruce-fir soils, any future increases in soil solution anion levels theoretically should be expressed largely as Al mobilization, whereas the displacement and leaching of exchangeable base cations should eventually decline and level off. Conservation of these cations by microbes and plant roots competing for limited supplies should further decrease leaching loss rates. However, irrespective of whether changes in anion loading result in base cation leaching or Al mobilization, either process could result in reduced plant uptake of base cations. A further increase in net cation leaching loss could lower the cation supply, whereas Al mobilization could act antagonistically toward the uptake of base cations, especially divalent cations. Reductions in base cation supplies may be partly or entirely counteracted by atmospheric inputs of base cations and/or by increased weathering of primary minerals as soil solutions become more acidic (Li et al., 1988; Federer et al., 1989).

On the other hand, if anion loadings in spruce-fir forests decrease in the near future, such decreases should immediately reduce Al levels and raise the pH of soil solutions, as demonstrated in the Norway field irrigation experiment (Stuanes et al., 1992). Rates of base cation leaching loss should also decline as anion levels drop. Soil solution sulfate concentrations should decline rather slowly with reductions in the atmospheric deposition of S, since the majority of sulfate adsorbed by most forest soils is water soluble and hence will desorb (Harrison et al., 1989). It is difficult to predict the immediate impact of reductions in N deposition on soil solution nitrate levels because these levels are mediated by internal N cycling mechanisms, which are numerous and complex. Nitrate itself is a very mobile anion and usually is quickly removed from system after it is produced; however, the large stores of mineralizable N currently available in high-elevation spruce stands may continue to act as a major nitrate source long after N deposition levels decline.

CONCLUSIONS

The preceding discussion of literature relating to possible changes occurring in the soil chemistry of eastern North American spruce and fir stands contain some evidence that suggests that the chemistries of Ca, Mg, and Al may be elements of concern, especially in high-elevation spruce stands. Decreases in soil pH and in soil lime potential have been docu-

mented in both Europe and North America at some sites. Losses of Ca and Mg from organic horizons in spruce stands have also been observed in experimental "acid rain" studies. Related changes in soil solution chemistry appear to be reflected in patterns of Ca and Mg concentrations in recent red spruce wood, as well as by recent decreases in Ca/Al and Mg/Al ratios in that wood. Both plant uptake and soil leaching appear to be important processes of base cation removal from soil pools. Estimates of current rates of net leaching losses of Ca and Mg are substantial when compared with whole tree harvesting removals, exchangeable soil pools, or organic horizon contents. Although our estimates are crude, acidic deposition probably accounts for more than half of current leaching losses in eastern North American red spruce stands.

Attempts to establish linkages of soil and foliar nutritional pattern with each other and with red spruce decline symptomatology have been inconclusive to date. Red spruce and balsam fir foliar concentrations of Ca, Mg, and Zn are higher at low-elevation sites than at high-elevation sites, and appear marginally deficient at some high elevation locations. Soil solution Al concentrations and Ca/Al ratios at some sites, especially those in the southern Appalachians, have been reported at levels demonstrated to be detrimental to cation uptake and/or red spruce root growth in controlled seeding studies. Mechanisms have been demonstrated, which would suggest a role for acidic deposition in creating or exacerbating these potential sources of stress. However, there is little evidence directly linking soil or plant nutritional status with the decline of red spruce.

Future rates of base cation leaching losses and/or Al mobilization in eastern North American spruce-fir forests will depend chiefly upon (i) rates of N and S deposition, (ii) the degree of saturation of sulfate adsorption sites in soils, and (iii) various factors controlling the internal cycling of N. The latter will be influenced by (i) the current N mineralization and nitrification potentials of the soils, (iii) rates of plant N uptake, (iii) physical disturbances to forest stands, especially the forest floor, and (iv) projected climate changes and their influence on soil moisture and temperature regimes and plant uptake.

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TECHNICAL REPORTS

Water Quality

The Transport of Bioavailable Phosphorus in Agricultural Runoff

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ABSTRACT

Bioavailable P (BAP) in agricultural runoff represents P potentially available for algal uptake and consists of soluble P (SP) and a variable portion of particulate P (PP). Evaluation of the impact of agricultural management on BAP in runoff will aid assessment of the resultant biological productivity of receiving water bodies. Soluble P, PP, and bioavailable PP (BPP) (estimated by NaOH extraction) were determined over a 5-yr period in runoff from 20 unfertilized and fertilized, grassed, and cropped watersheds in the Southern Plains. Soluble P, BPP, and BAP loss in runoff was reduced by practices minimizing erosion and runoff, with respective mean annual amounts ranging from 237 to 122, 1559 to 54, and 1796 to 176 g P ha⁻¹ yr⁻¹ (for peanut-sorghum [*Arachis hypogaea* L.-*Sorghum bicolor* (L.) Moench] and native grass watersheds, respectively). However, as vegetative cover improved, BAP (SP plus BPP) comprised a larger portion of total P (TP) loss (29% for peanut-sorghum and 88% for native grass). This results from an increasing contribution to BAP of SP (13% for peanut-sorghum and 69% for native grass watersheds) and BPP to PP (26% for peanut-sorghum and 69% for native grass watersheds). Clearly,

P bioavailability is a dynamic function of physiochemical processes controlling erosion, particle size enrichment, P desorption-dissolution reactions, and plant residue breakdown, in addition to soil and fertilizer P management. Hence, the change in trophic state of a water body may not be adequately reflected by TP inputs only. To more reliably evaluate the biological response of a water body to agricultural P inputs, particularly from conservation tillage practices, it may be necessary to determine BAP in runoff.

THE TRANSPORT of soluble and particulate P in runoff can result in accelerated eutrophication of a receiving water body (Schindler, 1977). Soluble P is for the most part immediately available for algal uptake (i.e., bioavailable) (Peters, 1981; Vollenweider, 1968; Walton and Lee, 1972). In contrast, PP associated with sediment and organic material in runoff, may constitute a variable but long-term source of potentially bioavailable P in lakes.

Passage of Section 319 of the 1990 Water Quality Act requires implementation of preventive and remedial measures to minimize P transport in agricultural runoff. Management strategies, which include practices to reduce erosion and accumulation of surface soil P, have been evaluated by criteria based on the transport of TP and to a lesser extent SP in runoff

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Abbreviations: BAP, bioavailable P; SP, soluble P; PP, particulate P; BPP, bioavailable particulate P; TP, total P.