Reports

Aluminum-Induced Calcium Deficiency Syndrome in Declining Red Spruce

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Prolonged suppression of cambial growth has apparently caused a decline in radial growth in many mature red spruce, *Picea rubens*. Surveys indicate that this decline occurs in trees throughout the natural range of red spruce and is independent of elevation, tree size, and age class. In addition, crowns of mature red spruce at high elevations across the northeastern United States have been dying back. Understanding the physiological basis for the growth decline is essential for the judicious management of the red spruce resource. A sequence of events is inferred through which an imbalance of aluminum and calcium in the fine root environment reduces the rate of wood formation, decreases the amount of functional sapwood and live crown, and leaves large trees more vulnerable to extant secondary diseases and insect pests.

FOREST TREES HAVE BEEN DECLINING in growth rate and apparent vitality in Germany and the northeastern United States (Fig. 1) (*1*). Declining spruce and fir in Germany occur on soils of *p*H 3.0 to 4.5 in which aluminum (Al) is soluble (*2, 3*). Soluble Al in sufficient concentration is directly toxic to the roots of a wide range of agricultural and forest plants. However, healthy stands of trees occur on soils of similar acidity with similar concentrations of Al in both the soil and fine roots (*2, 3*). In addition to direct toxicity, aluminum interferes with the uptake of calcium (Ca) by fine roots when the soluble ions are in equimolar concentrations (*4*). We propose that impaired uptake of Ca, the fifth most abundant element in trees, causes decline in cambial growth and loss of crown of mature red spruce. Calcium is incorporated at a constant rate in the production of sapwood from cambial derivatives (*5–7*). Calcium, unlike nitrogen, phosphorus, and potassium, is not recovered as sapwood matures into a heartwood core (*8*). In that the demand for Ca per unit area of cambium surface is essentially constant and the surface area expands exponentially as mature trees add secondary xylem, restricted Ca uptake will suppress cambial growth and thus the widths of annual rings. Suppressed cambial growth reduces functioning sapwood as sapwood is continuously transformed into the heartwood core (Fig. 2). Both healthy and declining trees typically have the same number of sapwood rings, but, in healthy trees, the widths of the rings are greater (*9*). Leaf mass and area and associated crown density are positively correlated with the cross-sectional area of sapwood (*10*). As the cross-sectional area of sapwood decreases, crown density would also be expected to decrease.

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To test this notion we investigated mature canopy red spruce in eight stands across northern New England from Mount Abraham, Vermont (1000-m elevation), where more than half the canopy spruce are dead or dying, to Beddington, Maine (100-m elevation), where canopy spruce are uniformly healthy (Fig. 3). Two canopy red spruce from each of the eight locations were selected for destructive sampling. One member of the pair had a relatively full crown and the other had a relatively thin crown. Disks of wood were sawed from the trunks 140 cm above the ground. We sampled these disks to determine their major element chemistry and measured their yearly ring widths and sapwood areas (*11*). Samples of fine roots and accompanying humus and mineral soil layers were also collected for analysis from each location. The humus layer for all stands investigated had a *p*H of 3.2 to 4.6; the mineral subsoil was only slightly less acidic (*p*H 3.9 to 4.9). Similar *p*H conditions to these commonly occur in Germany in many areas where trees are seriously declining (*2, 3*). At Mount Abraham the molar Al to Ca ratio in fine roots of humus was greater than one (Fig. 3), a condition that is common in areas with severe tree damage in Germany (*12*). Equilibrium soil solution analysis confirmed that the Al to Ca ratio was significantly higher in humus from Mount Abraham than from Beddington (*12*). Taylor *et al.* (*13*) showed that Al to Ca ratios were also high in humus at Camels Hump, Vermont (25 km north of Mount Abraham), and low at Acadia National Park on the coast of Maine (60 km south of Beddington). Molar Al to Ca ratios greater than one have also been recorded in ground water in high-elevation spruce-fir stands on Mount Moosilauke in New Hampshire (*14*).

The molar Al to Ca ratio of the sparse population of fine roots in the mineral subsoil was greater than one at most locations (*3*). This high a ratio will almost certainly limit Ca supply to spruce trees in which mean cambial growth has been declining for two decades. The growth pattern in the eight pairs of sample trees from locations across northern New England was similar to the average pattern from 3001 red spruce trees from the same region (Fig. 1). The molar Ca concentration in the outer functional sapwood of the faster growing trees did not differ significantly from that of the slower growing trees, which indicates that Ca is incorporated at an essentially constant rate per unit volume of wood, independent of the growth rate (*5–7*). This relation between Ca concentration and growth rate was also found to be the case for spruce in Germany (*15*). Large trees require an increasing supply of Ca from the fine roots. A reduction of cambial growth is likely as fine roots become less able to take up Ca because of interference by increased amounts of Al.

An alternative scenario for the growth decline is that aging of the red spruce forest, as inferred from similarities of present growth patterns to historical patterns for red spruce, has caused the decline in growth (*16*). Irrespective of cause, a consequence of prolonged cambial growth suppression is a reduction in sapwood basal area. This means that less sapwood is available to conduct water, store food, and defend against infection (*17*). The shedding of part of the crown

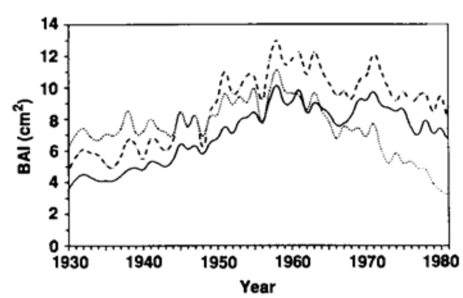

Fig. 1. Growth curves of canopy red spruce in the northeastern United States. The annual mean basal area increment (BAI) is plotted against calendar year. BAI was calculated from radial ring widths measured in transverse faces of stem disks that were obtained 140 cm above the ground (Fig. 3). There is general agreement among the growth trends for trees with full crowns (dashed line, $N = 8$), for trees with thinning crowns (dotted line, $N = 8$), and for site index trees (solid line, $N = 3001$) that were measured in another investigation (*1*).

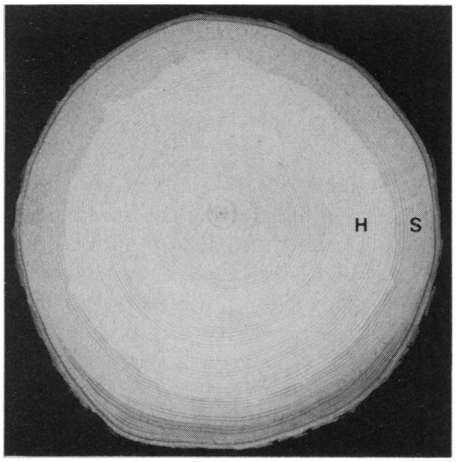

Fig. 2. Red spruce stem in transverse section. The sapwood (S) is visually distinguishable from the heartwood core (H) because the cut surface was sanded immediately after sectioning and photographed before the surface was allowed to dry. After drying, the distinction between S and H is not apparent.

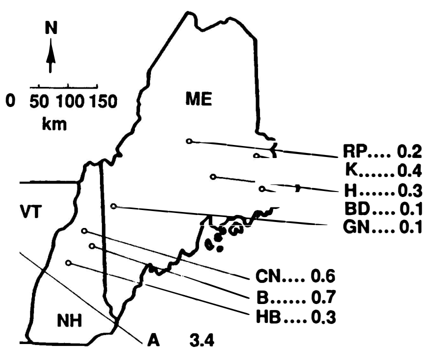

Fig. 3. Map of the red spruce study plots; A, Mount Abraham; CN, Crawford Notch; B, Bartlett; HB, Hubbard Brook; RP, Roach Pond; K, Kossuth; H, Howland; BD, Beddington; GN, Grafton Notch. Listed with the plots are the molar ratio values of Al:Ca in fine roots collected from the humus layer. The mean ratio for Mount Abraham was significantly different from that of all other locations ($P < 0.05$). Methods of analysis are given in (*2, 3*).

is a logical consequence of the progressive loss of sapwood basal area. The increased Ca demand of old trees and diminishing Ca supply may have hastened their decline; young trees are also declining in several areas (*1*). Once a tree has less than 25% sapwood in its cross-sectional area, it becomes highly vulnerable to death from secondary pathogens and insects (*11*). Trees at high elevation sites have apparently been most affected because the molar Al to Ca ratio is greater than one in both the humus (which contains the majority of absorbing fine roots) and the mineral subsoil (*3*).

Whether input of acids that are derived from sulfur and nitrogen emissions has caused the low soil *p*H conditions extant across the spruce-fir forests in the northeastern United States and Germany is moot. Continued input of strong anions of sulfur and nitrogen will increase amounts of Al in solution. This increase in Al concentration will reduce uptake of Ca through competition for binding sites in the cortical apoplast of fine roots. The problem is not one of Al toxicity (that is, an irreversible effect on the symplast), although this can happen with prolonged exposure to high Al concentrations, but rather a simple exchange phenomenon that can limit the rate of wood formation, decrease the amount of functional sapwood, and leave large trees more vulnerable to common diseases and insect pests. Similarly, any additional abiotic stress such as chronic air or soil pollution levels will also accelerate decline in trees that have already been weakened by the Ca deficiency syndrome.

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5. Newly formed red spruce sapwood contains 6.44 ± 0.71 μmol of Ca per cubic centimeter ($P < 0.05$) (*6*).
6. Calcium concentrations of spruce wood were determined by atomic absorption spectroscopy (*7*) and expressed as micromoles of dry tissue per cubic centimeter. No significant differences in molar Ca were evident for outer sapwood that formed 1.4 m above ground among locations. There was a small, but significant, increase in molar Ca concentration as sapwood was transformed into the dry heartwood core. Differences in mean values were determined by analysis of variance and tested at the $P = 0.05$ level of significance.
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10. Relation of red spruce foliage mass (y_1) and leaf area (y_2) to sapwood conducting area (x) from P. J. Marchand [*Can. J. For. Res.* **14**, 85 (1984)]:

$$y_1 = 0.072x - 0.410 \qquad (r^2 = 0.84)$$
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18. We are grateful for the technical expertise of K. R. Dudzik, P. J. Krusic, and G. P. Sredzienski.

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