ES&T FEATURES

Acid deposition and forest decline

Available evidence does not show a clear cause and effect relationship between acid deposition and forest decline and dieback in the U.S. This article is the second of two on the subject

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Over the past 15–20 y, red spruce (*Picea rubens* Sarg.) in the high-elevation forests of New York, Vermont, and New Hampshire has shown marked dieback and a very large reduction in basal area and density. A number of studies have been conducted, but none have revealed any obvious causes for the widespread mortality. The decline of red spruce has characteristics of a stress-related disease (*1*). These characteristics include the lack of an obvious cause, dieback (loss of foliage beginning in the crown and branch tips and progressing downward and inward over time), and subsequent invasion by secondary organisms that normally do not cause substantial damage to vigorous trees.

In forests of West Germany, Norway spruce (*Picea abies* Karst.) and fir (*Abies alba* Mill.) currently exhibit dieback and mortality over large areas. In both West Germany and the U.S., the affected forests are located in areas that receive large atmospheric inputs of acidic substances and other pollutants. Because interest in the effects of acid rain on terrestrial ecosystems is accelerating, considerable attention has been given to the possibility that acid deposition is a cause of the mortality.

Forests are subject to many stresses including chronic and subtle pressures as well as short-term catastrophic events. Thus, the problem of conifer dieback should be viewed in light of the various factors that have been responsible for large-scale disturbances in forests in the past. The key question to be resolved is: Does the forest dieback represent an early phase of pollution-induced ecosystem destabilization that will lead to essentially permanent changes (for example, changes in species composition or reduced productivity), or is the dieback a relatively short-term periodic phenomenon that occurs naturally in ecosystems that are stable when viewed over longer time spans? Of particular concern is the possibility that acid deposition could have caused or may eventually cause soil changes detrimental to forest vegetation, either by stripping nutrients from the soil or by mobilizing phytotoxic elements. Such changes would constitute a problem that could be extremely expensive to correct. In this paper we present data on the decline of red spruce in the U.S., summarize hypotheses regarding spruce and fir dieback in Central Europe, and, in light of the available information, evaluate the hypotheses concerning cause.

Character of declining spruce stands

Red spruce is a long-lived (300+ y), shade-tolerant species that is a major component of the high-elevation forests of the northern and southern Appalachians. To date, most U.S. research has centered on the high-elevation (or montane) boreal forests of the northern Appalachians. These forests occupy the middle and upper slopes of the Adirondack, Green, and White Mountains. Soils are for the most part thin and rocky. The extensive areas of low-elevation, spruce–fir forests of northern Vermont, northern New Hampshire, and Maine, which are of economic importance, have been studied little with respect to dieback and decline.

The canopies of northern montane boreal forests are characterized by red spruce, balsam fir [*Abies balsamea* (L.) Mill.], and white birch [*Betula papyrifera*, var. *cordifolia* (Marsh) Regel] and differ slightly floristically from their counterparts in the southern Appalachians. The lowest elevation to which the montane boreal vegetation extends ranges from 750 to 800 m in New Hampshire and Vermont, to 900–1000 m in the Adirondack and Catskill Mountains of New York, to 1500 m in North Carolina and Tennessee (*2*, *3*). Because coniferous forest occupies the often-cloud-capped upper slopes and hardwoods occupy the lower slopes, the presence of high-elevation spruce–fir vegetation is believed to be related to the incidence of cloud moisture (*3*, *5*). In Vermont, New Hampshire, and New York, the northern hardwood forest of the low elevations is dominated by sugar maple (*Acer saccharum* Marsh.), beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britt.). Between the boreal and hardwood forests is a narrow transition zone where neither set of species dominates. Red spruce is a major component of the transition forest and a minor component of the hardwood forest.

The soils that support declining red spruce vary considerably in morphol-

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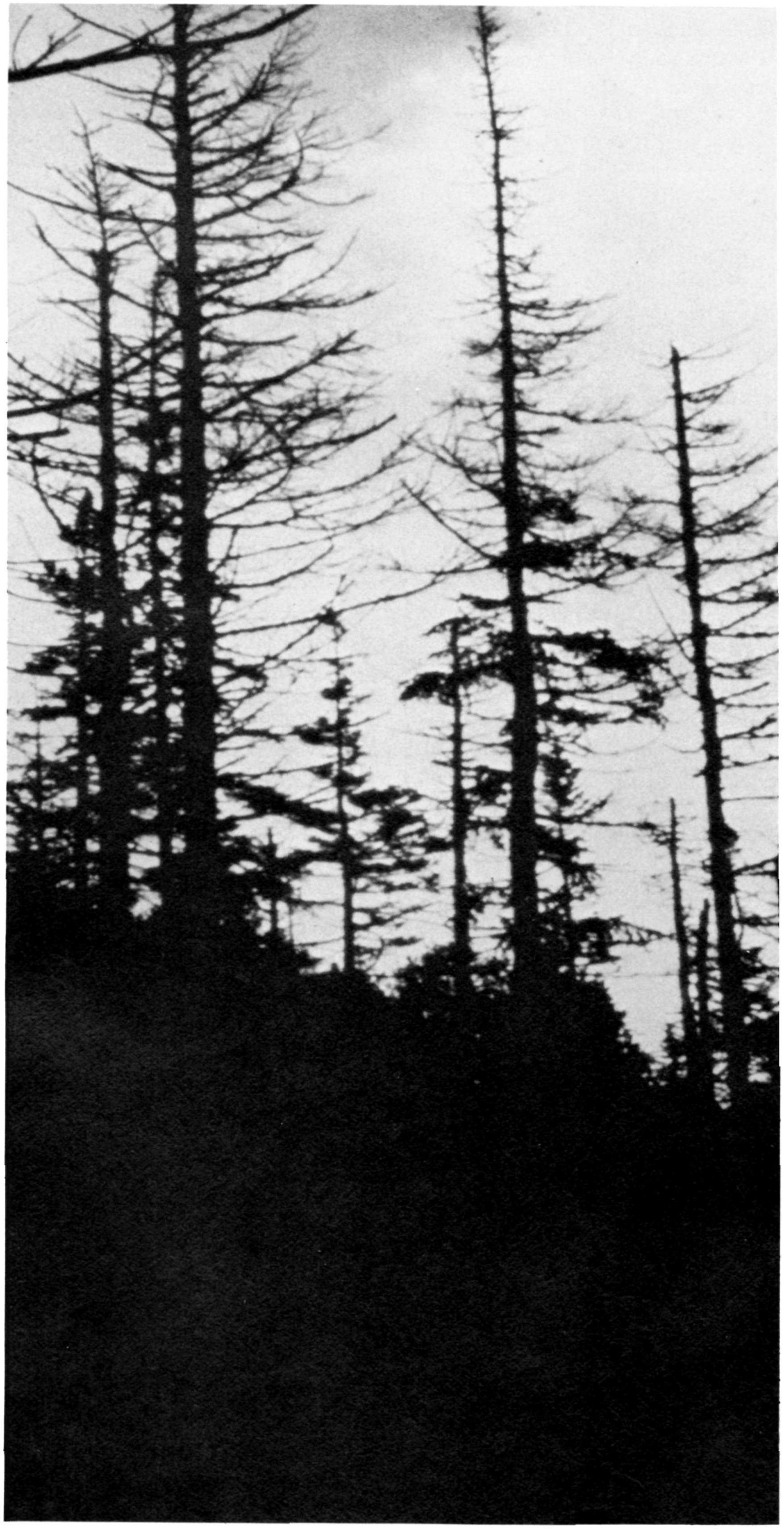


***Tree dieback.** This photo and the cover photo were taken at the same site. However, the cover photo was taken in 1964 and this photo was taken in 1981. Can acid deposition account for the difference?*

ogy and chemical characteristics. In the northern Appalachians at elevations above ~750 m, the soils are typically very acid (pH in water 3.5–4.5) Orthods, Humods, or Folists, with low base status, whereas below 750 m, Orthods or less acid (pH 4.0–5.5) Ochrepts with higher base status dominate (*3*, *6*). In the southern Appalachians, the dominant high-elevation soils are Ochrepts, Umbrepts, Udults, and Spodosols (*6*). By one set of current standards, the soils of the northern sites are considered nonsensitive or only slightly sensitive to nutrient loss due to acid deposition, whereas the soils of the southern sites are thought to be somewhat more sensitive (*7*). Another set of standards developed by Cowell et al. classifies soils with a pH of 4.5 or less as highly sensitive to acid deposition (*8*). Under these criteria, the northern Appalachian soils would be slightly more sensitive than the southern Appalachian soils.

Although the mountain summits in the Northeast are remote from large point sources of sulfur and nitrogen oxides, they receive extraordinarily high rates of acid deposition from high precipitation rates and from the effective interception of very acid cloud moisture by the coniferous vegetation. Using the data of Lovett et al. (*9*), we estimate that the middle to upper slopes where red spruce is a dominant species receive 2–3 keq H^+/ha·y. This is approximately 3–4 times the deposition rate measured at low elevations in the Northeast (*10*).

Few data have been collected that can be used to estimate H^+ deposition in the high-elevation forests of the southern Appalachians. But since the pH of the ambient precipitation is similar to that in the North (*10*), and since the interactions between clouds and vegetation are expected to be comparable to those at the northern sites, we expect that H^+ deposition does not differ markedly from the 2–3 keq/ha·y estimate noted above.

In addition to receiving high rates of acid deposition from rainfall, the montane boreal forest vegetation receives high inputs of acid deposition from clouds. Clouds are low enough to cover this vegetation for considerable portions of the year. Siccama estimates that in the northern Green Mountains, the spruce–fir forests are immersed in cloud moisture for 800–2000 h/y, or up to one-fourth of each year (*3*). Because cloud moisture is particularly acid [with average pH ~ 3.5 (*9*, *11*)], the potential for direct effects on the vegetative surfaces appears to be high.

FIGURE 1
Sites in the northern and southern Appalachians where forest damage has been studied[a]

[a]Multiple stands were surveyed in the Green, White, and Catskill Mountains, and at Whiteface Mt., N.Y.

As well as very large acid inputs, the high-elevation forests are accumulating heavy metals at a rapid rate, particularly lead (Pb), from atmospheric deposition. Friedland et al. (*12*) and Johnson et al. (*13*) showed a marked gradient of soil Pb, increasing with elevation. They also demonstrated that Pb concentrations in the organic horizons of Green Mountain forest soils have increased dramatically over the past 17 y and that current Pb concentrations lie in the range observed for polluted urban mineral soils. The measured increases in Pb levels are consistent with the amount deposited from the atmosphere and probably result almost entirely from that source. Thus, the montane boreal forests of the eastern U.S. are subject to particularly high inputs of airborne pollutants.

Extent of dieback and mortality

Quantitative vegetation surveys carried out in the northern Appalachians in the mid-1960s and early 1970s were repeated in the late 1970s and early 1980s. These surveys provide evidence that the basal area and density of red spruce and associated species have changed (Table 1). Details of the sampling designs and procedures are given in other publications (*3, 14–17*). Further quantitative evidence of spruce decline is provided by a 1982 survey of spruce stands throughout the Appalachians. The sampling sites are shown in Figure 1.

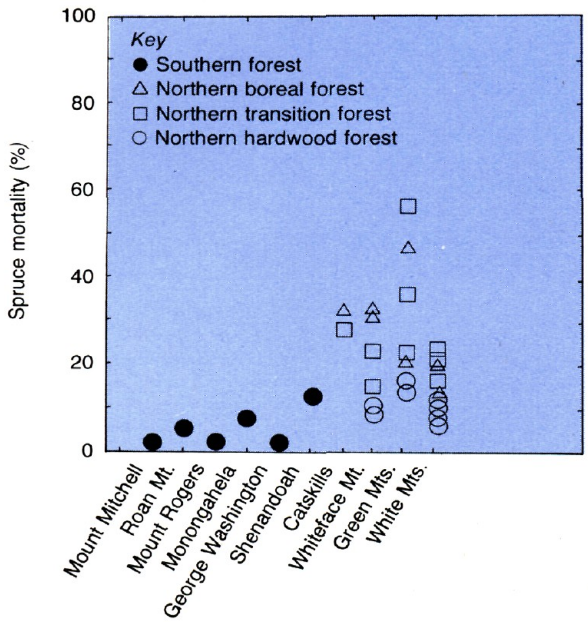
The data indicate that a wide variety of forests covering a broad area have experienced substantial losses of spruce. The extent of dieback and

TABLE 1
Changes in the composition of spruce stands in the Green Mountains, White Mountains, and at Whiteface Mountain during the past two decades [a]

				Red spruce			Balsam fir			White birch		
				Diameter at breast height (cm)								
Site	Stand type	No. of plots	Interval	>10	2–10	<2	>10	2–10	<2	>10	2–10	<2
				Percent change								
Camels Hump (Vt.)	Boreal	25	1965–79	−44	−42	−32	−12	+19		−22	+433	
	Transition	20	1965–79	−40	−84	−71	+17	−32		+263	−28	
	Hardwoods	40	1965–79	−42	−80	−50				+306		
Jay Peak, Mt. Abraham, Bolton Mt. (Vt.) (pooled)	Boreal	32	1965–79	+2	−69		−10	+2		−7	−46	
	Transition	24		−87	−90		−24	−74		−73	+33	
Hubbard Brook (N.H.)	Hardwoods	208	1965–82	+29	−83		+60	−73		+176	−65	
Whiteface Mt. (N.Y.)	Boreal	21	1964, 66–82	−72	−16	−79	−34	+52	+8	−33	+239	+6
	Transition and hardwoods	12	1964, 66–82	−43		+12			+42			+252

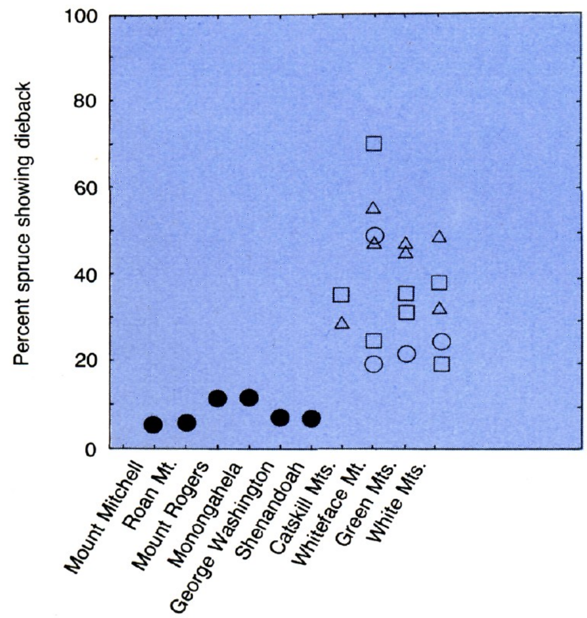
[a] Changes in basal area are given for the two larger size classes, and changes in density or frequency are reported for the class that has a <2-cm diameter at breast height. Data and methods are given in References 3, 14–16.

FIGURE 2
Northern sampling sites generally had a higher percentage of dead spruce than southern sites[a]



[a]Percentages were determined from prism counts of standing trees and stubs that were at least breast height. Sampling strategies and methods are given by Zanes (*17*). The survey included approximately 2300 spruce.

FIGURE 3
The percent of live spruce showing dieback was usually significantly higher at the northern sampling sites[a]



[a]Methods are given by Zanes (*17*).

mortality across the range of high-elevation spruce forests is shown in Figures 2 and 3. Spruce mortality has occurred rather evenly across small and large size classes, in a variety of stand compositions, and on a variety of soils. On some plots, balsam fir or birch show reductions in basal area and density, but generally to a lesser degree. Red spruce in the southern Appalachians appear to be unaffected, while from the Catskill Mountains of southern New York northward, considerable dieback and mortality are noted. In many stands, the percentage of standing, dead spruce and spruce showing dieback far exceeds the proportion of vigorous individuals. Considerable recent spruce and fir mortality has been observed in Maine and attributed to spruce budworm infestation (*18*). Because of the known problems associated with that insect pest, we confined the survey to areas known to be free of budworm infestation and did not sample in Maine.

Assessing possible causes

Major episodes of mortality in forests have been related to a wide variety of causes, both anthropogenic and natural. Accordingly, we reviewed the available information related to the following possibilities: long-term climatic changes, natural stand dynamics, pest infestation, disease, gaseous pollutants, drought, direct and indirect effects of acid deposition, and indirect effects of trace-metal accumulation in forest soils. The available data relevant to each are discussed.

Particular attention has been given to the possibility that aluminum (Al), a phytotoxic element mobilized in acidic forest soils by acid deposition, has induced effects on forest species (*19*, *20*). Such effects would constitute a serious threat to the stability of forest ecosystems on acidic soil, both those that already show signs of decline and those that are still healthy. Based on long-term, detailed ecosystem-level studies in the Solling region of West Germany, Ulrich and co-workers have offered a scenario by which aluminum mobilization could affect forest species (*20–23*). Using that framework, we present our evaluation of the likelihood that Al mobilization contributes to the observed red spruce mortality in North America.

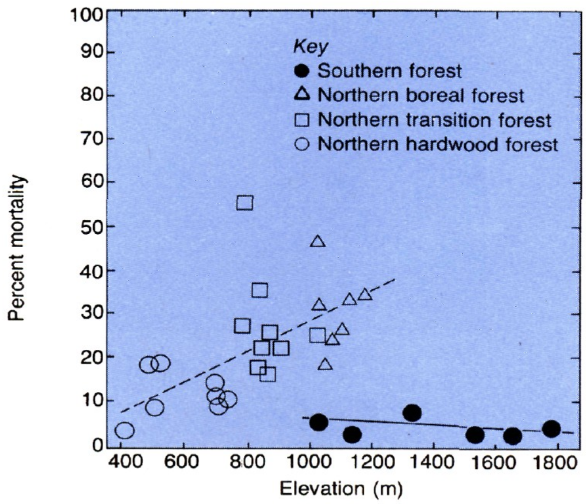
Possible natural causes

The high-elevation boreal forests in New York State and New England are similar to the low-elevation forests at higher latitudes in eastern North America. Since the declining stands represent the southern extension of the forest type, a long-term warming trend should not be ignored as a possible stressful influence. Owing to the difficulties of establishing long-term temperature, cloud cover, and precipitation trends for the sites in question, no definitive data can be marshalled to support or refute this possibility. However, because the mortality is largely confined to the northern Appalachians, we consider climatic change an unlikely possibility.

Roman and Raynal tested the relationship of increment size to climatic parameters and concluded that the observed decline in growth rate was not related to climatic changes (*24*). Long-term (200+ y) tree ring records from old spruce in the Green and White Mountains (Johnson and Siccama, unpublished data) show large variations in annual growth, but do not show any consistent pattern of declining growth between 1780 and 1965.

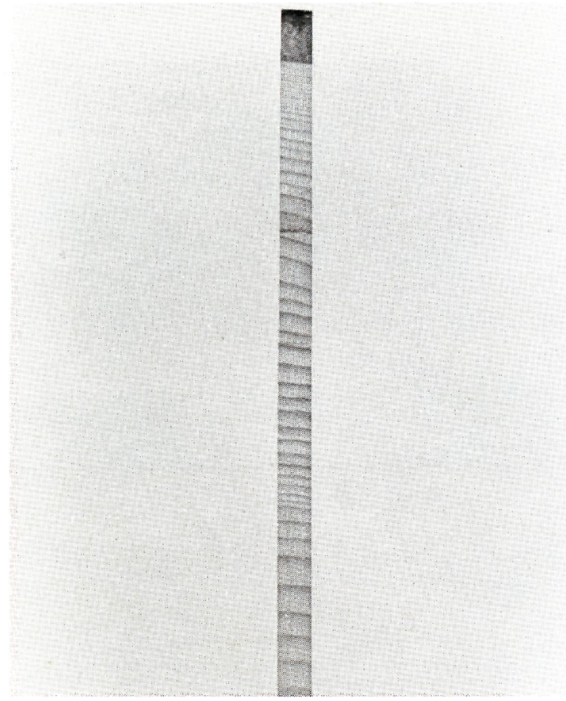
Synchronized mortality in the case of balsam fir in relatively pure stands is well-known from studies of wave regeneration in the subalpine forests of the northern Appalachians (*25*, *26*).

FIGURE 4
Mortality correlates with elevation in the northern forests[a]



[a]The sampling sites are the same as those in Figure 1. For sites in New York, Vermont, and New Hampshire, r = 0.553 and P <0.01.

FIGURE 5
An example of a spruce tree core that shows a rapid shift to abnormally narrow increments with no recovery



This phenomenon is characterized by mortality of extensive bands of old (80–120 y) fir and is visible from a great distance. Such extensive mortality is characteristic of stable ecosystems. But as spruce have died in all age classes, the mortality of bands of old fir cannot be considered analogous to the present mortality and decline of spruce.

Current models of forest development suggest that substantial numbers of trees normally die as aggrading forests (forests that are accumulating biomass) mature and as biomass approaches a steady state (*27*). Since spruce mortality in the U.S. occurred in both regenerating and virgin stands in all size classes (*14*, *16*, *17*), and since the mortality and dieback are so extensive, it is unlikely that a combination of natural thinning and breakup of old stands accounts for the observed mortality.

In the 1950s and 1960s, substantial areas of red spruce dieback were noted in Vermont and New Hampshire. These areas were studied to determine if primary pathogens or insect infestation was present. Approximately 400 trees were dissected and the only pathogenic organisms found were fungal pathogens including *Polyporous borealis*, *Fomes pini*, and *Armillaria mellea* (*28*, *29*). These fungi are normally present but inconsequential in vigorous stands. Moreover, their invasion is triggered by stress in dieback–decline diseases. Recent field investigations in southern Vermont indicate that red spruce in declining stands at low to moderate elevations are heavily infected with *Armillaria* (P. Wargo, U.S. Forest Service, personal communication). In northern Vermont, laboratory and field studies indicate that no root rot fungi are present and that no discernible damage has been caused by primary fungal pathogens, with *Fomes pinicola* the only secondary fungus observed (T. Chase, University of Vermont, personal communication).

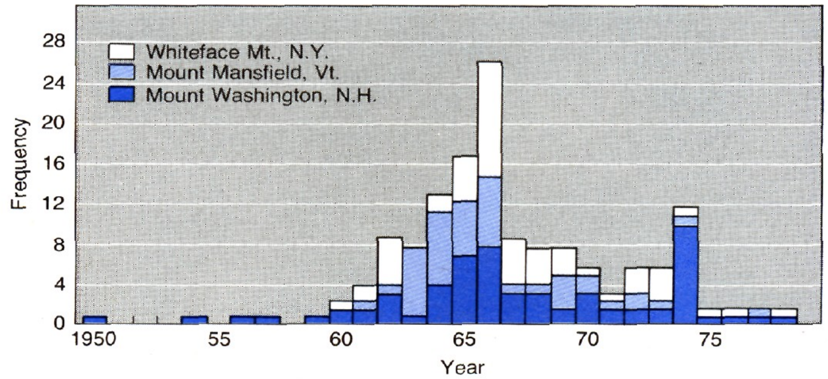
Given the lack of other causal agents and the characteristics of the observed dieback, it appears that the mortality is probably related to some environmental stress or combination of stresses. The conceptual framework for dieback–decline diseases developed by Manion (*1*) suggests that adverse site conditions may present a stress that predisposes trees to dieback–decline diseases. We used correlation analysis to relate stand mortality to a number of parameters including: stand basal area, the pH of regional precipitation, average ozone concentration and the frequency of ozone episodes, selected geologic and soil characteristics, elevation, and aspect. Mortality, which was more prominent in the transition and boreal forest than in the hardwood forest, correlated significantly only with elevation (Figure 4). Several stress factors are related to elevation; it is not currently possible to determine which factors are relevant. Wind speed, exposure to cloud moisture, H^+ deposition, and the heavy-metal content of the soil increase with elevation, whereas soil moisture-holding capacity, soil pH, base status, and soil and air temperature decrease with elevation (*3*, *13*).

Drought stress in combination with predisposing factors related to site conditions has triggered forest declines in the past (*1*, *30*). Increment cores were taken from approximately 700 red spruce in the northern and southern Appalachians at the sites shown in Figure 1. The tree ring records obtained from the cores indicate that drought was a possible triggering stress in the dieback and decline of red spruce. At the northern sites, a dramatic decrease in increment size began in the mid-1960s and continues to the present. Forty percent of the cores from the northern stands showed a rather abrupt shift to abnormally narrow increments in the early to mid-1960s with no subsequent recovery (Figure 5); 20% of the cores showed a few narrow increments in the 1960s with recovery to normal-sized increments after a few years. In the remainder of the cores, neither of these two distinctive patterns is present. Figure 6 shows that the initial abnormal ring appears in different years, even at the same site. The same pattern of tree rings was reported by Johnson et al. for pines in southern New Jersey (Figure 7) (*31*).

This very rapid shift to abnormally small annual rings is widespread, substantial, and sustained and appears to have important implications. The data in Figures 6 and 7 can be interpreted in several ways. We believe that the growth patterns shown in these figures resulted from a period of intense stress that triggered a lasting loss of vigor. We suggest that the growth reductions in red spruce during the mid-1960s represent the initiation of dieback and decline in these trees.

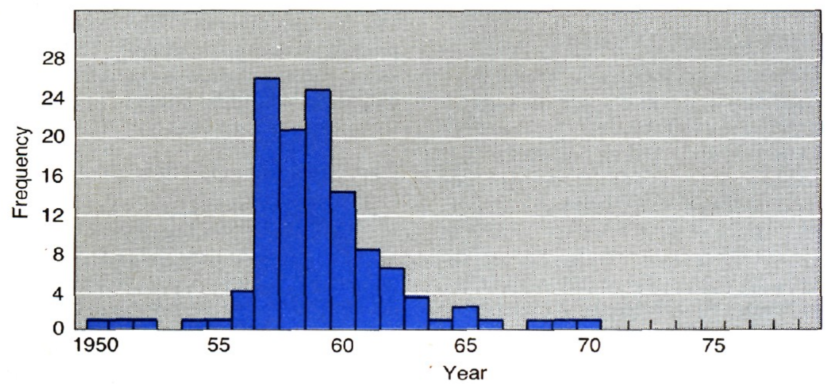
The early and mid-1960s were a period of drought in the Northeast. Figure 8 shows the minimum Palmer Drought Index for the growing season in Vermont. Several other indicators that may be more appropriate to drought at high elevations have been examined including high-elevation precipitation records from Mt. Mansfield, Vt., and Mt. Washington, N.H., and modeled soil moisture conditions in New Hampshire (*32*). These data confirm that during the late 1950s and early 1960s high- and low-elevation stands of the northern Appalachians experienced several relatively dry growing seasons. For the pines of southern New Jersey, the relationship between loss of vigor and drought is clear. As indicated in Figure 9, 1957 had the driest growing season on record, and 1954 and 1955 were also unusually dry. We believe that the 1957 drought was severe enough to have had important physiological consequences. Dendrometers (bands that measure changes in tree girth) on hardwoods in the Hutcheson Memorial Forest in New Jersey showed that in August 1957 the stems shrank abruptly and substantially in response to drought (*33*). The delayed response indicated in Figures 6 and 7 is not due to missing rings or false rings; that is, it is not an artifact of analyzing the cores. Delayed response to drought stress is well-known (*30*). The prolonged nature of the diminished growth is,

FIGURE 6
Frequency of appearance of the first abnormally narrow annual increment in spruce[a]



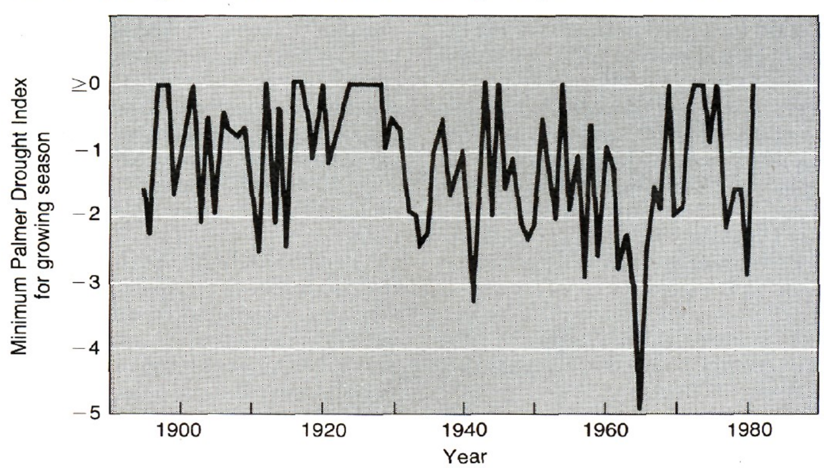
[a] Spruce shifted rapidly from "normal" to abnormally slow growth and did not recover as of 1982. On the three mountains listed, 148 of the 345 spruce cored had such a ring pattern.

FIGURE 7
Frequency of appearance of the first short annual ring in pitch and shortleaf pine sampled in southern New Jersey[a]



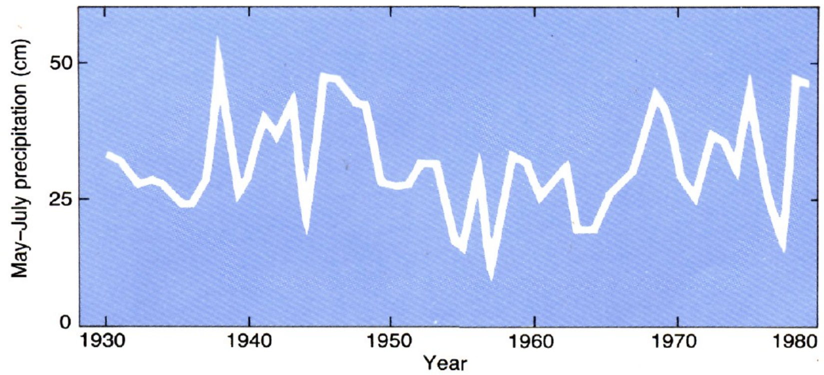
[a] Pitch and shortleaf pine in southern New Jersey shifted rapidly to abnormally slow growth and did not recover as of 1982. This type of response was observed in 118 of the 350 pines cored.

FIGURE 8
Palmer Drought Index for Vermont during the period 1895–1981[a]



[a] This is based on average weather data. The minimum value for the growing season (May–August) is shown. In this index, 0 represents an average year, and negative numbers indicate that precipitation is less than normal.
Source: T. J. Blasing, Oak Ridge National Laboratory, Oak Ridge, Tenn.

FIGURE 9
Precipitation during the growing season at Pemberton, N.J.[a]



[a]This shows that dry years occurred in the late 1950s and the late 1970s.
Source: P. Marucci, Rutgers University

however, difficult to account for. It suggests permanent alterations in physiology or, perhaps, continuing stress.

Possible effects of O_3 and SO_2

Gaseous air pollutants have well-known detrimental effects on vegetation, but the available information does not suggest that either sulfur dioxide or ozone plays a major role in the spruce decline. At Hubbard Brook, N.H., the average level of ambient SO_2 was determined to be 2.5 $\mu g/m^3$ (*34*). This is an order of magnitude less than levels thought to cause observable foliar symptoms through chronic exposure (*35*). We do not know how sensitive red spruce is to SO_2, but our field observations and tree core data from red pine (*Pinus resinosa* Ait.) growing on exposed ridges of the Green Mountains do not indicate any abnormal growth or mortality. Because red pine is very sensitive to SO_2, it should be a good indicator of the effects of SO_2 pollution (*35*). Although chronic exposure to SO_2 at low levels could enhance susceptibility to pathogens, particularly *A. mellea* (*35*), no current evidence suggests that SO_2 has been an important stress. In a review of the possible causes of the West German forest dieback, Binns and Redfern discuss several hypotheses regarding the possible involvement of SO_2, but conclude that definitive evidence is lacking. In Germany, SO_2 levels are relatively high, averaging 20–30 $\mu g/m^3$ (*36*).

As indicated by McLaughlin et al. (*37*) atmospheric conditions conducive to high ozone levels are far more frequent in the southern than in the northern Appalachians. Average ozone concentrations are higher at the southern stands (*38*), and preliminary experiments show red spruce to be relatively tolerant of ozone (B. Chevone, Virginia Polytechnic Institute and State University, Blacksburg, Va., personal communication). Therefore, since the mortality is centered in the North, it would be surprising if ozone were the leading cause of decline.

Possible acid deposition effects

From intensive ecosystem-level studies in the Solling forest of West Germany spanning nearly two decades, B. Ulrich suggested that acid deposition has caused or contributed to changes in H^+ generation and consumption; this in turn has caused soil acidification, mobilization of Al, mortality of fine roots, and ultimately dieback of spruce and beech (*Fagus sylvatica* L.) (*20–23*). His contention is based primarily on careful documentation of changes in the equilibrium soil solution chemistry; a nearly parallel decrease in fine root biomass and an increase in soil solution Al concentrations during the growing season; and nutrient solution studies indicating that the ratio of uncomplexed calcium (Ca) to Al found in the soil solution is in a range that can cause abnormal root growth and development.

Ulrich's findings certainly suggest the possibility of Al toxicity, but other German research on declining conifers indicates other possibilities. From observations of declining spruce and fir populations, Bauch determined that the roots of declining trees are Ca deficient relative to healthy roots (*39*); but healthy and declining trees contained similar concentrations of Al. Rehfuess observed declining silver fir stands on calcareous soils (*40*). His findings seem to preclude Al toxicity or Ca deficiency for these stands. Rehfuess showed that the parallel decrease in fine root biomass and the increase in the level of Al in the soil solution noted by Ulrich were not synchronized. He found that the fine root biomass decreased markedly before the concentration of Al in the soil solution increased (*40*). He pointed out that seasonal fluctuations in the fine root abundance can occur naturally and concluded that the depression noted by Ulrich could be the result of natural processes. Several studies of fine root dynamics in conifers support that contention (*40–43*). Rehfuess proposed that a series of dry summers interfered with root regeneration and led to inefficient water uptake. Thus, he concluded that drought is a possible cause of the dieback of European conifers. It is important to note that both Ulrich and Bauch (*39*) clearly established that dry summers are related to loss of vigor. Thus, in both the North American and European cases, dry summers may figure prominently in the observed forest dieback.

Studies of tissue chemistry in declining and healthy spruce stands in Vermont and New Hampshire suggest that Ulrich's Al toxicity hypothesis is not applicable to the red spruce decline in the U.S. Data collected by Johnson et al. (*44*) and Lord (*45*) indicate that declining spruce could have low (<500 ppm) Al concentrations in the fine roots and that healthy spruce roots could have high Al concentrations (>2000 ppm). The Al:Ca ratios showed a similar pattern. On the other hand, Vogelmann cites evidence of increasing Al concentrations in annual increments of red spruce after 1950 (*46*). This finding would be of considerable interest if documented for spruce growing at all elevations and if those findings contrasted with the Al levels in the annual increments of healthy stands in the southern Appalachians. In long-term Norwegian field studies. Norway spruce were irrigated with acidic water. Only unrealistically high concentrations of acid caused increased Al uptake, and elevated Al assimilation seemed to produce no apparent effects on growth or vigor (*47, 48*).

At Camels Hump, Vt., spruce are declining at low elevations where the soil pH is 4.5–5.4 and available Ca is approximately 5 meq/100 g (*3*) and also at high elevations where soils are essentially organic mats (Borofolists and Cryofolists) overlying bedrock or felsenmeer (literally, "sea of rocks"). Here, the soil pH values are 3.3–3.7, and available Ca is less than 1 meq/100 g (*3*, *44*). The Al contents of the foliage and fine root tissue are closely correlated with elevation, declining with increasing elevation (Figure 10). This can probably be attributed to the fact that Al binds to the abundant organic matter in high-elevation soils, rendering it unavailable to plants. The Ca:Al ratio increases with altitude because Ca availability decreases less rapidly than Al availability. Since mortality increases with altitude, it does not appear likely that Ca:Al imbalances are the primary cause of the spruce decline.

It should be noted, however, that Ulrich developed his theory of Al toxicity for roots in mineral soil. In this type of soil, Al toxicity is not likely to be masked at low pH by complexation with other chemical species. Given current chemical models of the behavior of Al in soils, it is conceivable that in organic soils, acid deposition could enhance the mobilization of Al in monomeric form. Experiments with organic soils have shown that Al levels in the soil solution can be increased by adding acid simulant (*49*), but it is not clear whether plant uptake of toxic forms increases as a result of acid deposition. To verify the possibility of Al inhibition of root development, it is necessary to demonstrate that root development is reduced in an organic soil matrix by acid additions.

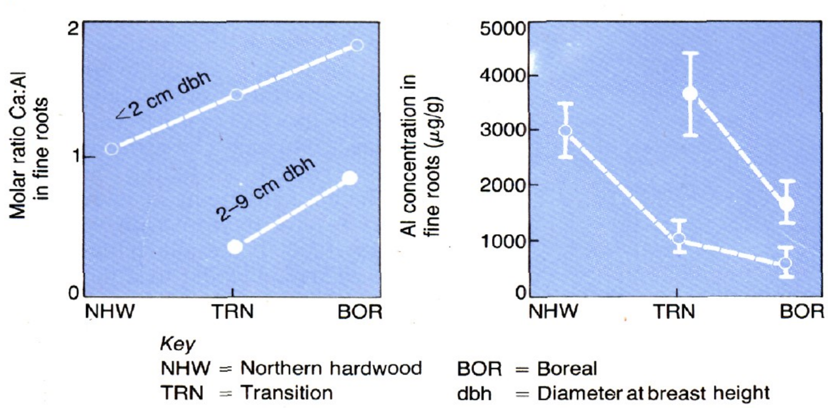
In short, the current data relevant to the Al toxicity hypothesis are inconclusive. In our opinion they do not support the contention that acid-deposition-induced effects have caused Al toxicity in roots, resulting in the red spruce mortality. On the other hand, since we do not have experimental evidence regarding Al uptake or root formation in soils subjected to high acid inputs, we cannot rule out the possibility entirely. If root Al levels were elevated during the dry period of the 1960s, the effect of drought stress could have been exacerbated (*50*). Similarly it would be of interest to determine if any changes in soil solution chemistry resulting from acid deposition inhibit water uptake or transport in tree roots. That type of interference could also increase the level of stress when moisture is limited.

Furthermore, it is also possible that the prolonged exposure of foliage to acid cloud moisture could contribute to drought stress. Shriner observed that artificial acid rain at pH 3.2 was associated with accelerated erosion of, or decreased production of, leaf surface waxes (*51*), and the data of Fowler et al. suggest that the resulting potential for water loss through leaf surfaces could be an important factor when moisture is limited (*52*). At present, there are no definitive data concerning the effects of cloud moisture on spruce foliage.

Other possible soil effects

Johnson et al. reviewed the possible effects that acid deposition could have on forest nutrient status (*53*). They pointed out a variety of ways acid deposition could alter cycling rates and pool sizes of nitrogen, sulfur, and essential nutrient cations. But very few data applicable to spruce decline are available.

FIGURE 10
In fine root tissue sampled at Camels Hump, Vt., the molar ratio Ca:Al increases with elevation, and the aluminum concentration decreases with elevation[a]



[a] Two size classes of trees were sampled. Methods of sampling, processing, and analysis are given by Lord (*45*).

Lord compared spruce tissue analyses from the literature (*45*). She found that analyses for declining and healthy red spruce in Vermont and New Hampshire do not differ substantially from values for healthy spruce in Maine and Canada. She noted, though, that root Ca levels were somewhat low in declining stands at Camels Hump compared to values in the literature, a finding that merits further investigation. It does not seem likely to us, however, that nutrient deficiencies are a primary cause of spruce decline, principally because spruce are declining in soils that have a moderate base status (such as at Camels Hump where low-elevation soils have a sum of bases >5 meq/100 g) as well as in soils in which the sum of bases is ≪1 meq/100 g (*3*).

As reviewed by Johnson et al., accelerated leaching of elements from foliage has often been observed in controlled experiments (*53*). Data on the foliar chemistry of Green Mountain spruce are consistent with the possibility that increased precipitation and fog frequency at higher elevations cause enhanced leaching of potassium from foliage (*45*). The data are not sufficient, however, to link acid deposition with the observed trends nor is there any evidence suggesting that foliar leaching constitutes an important stress to high-elevation forest species.

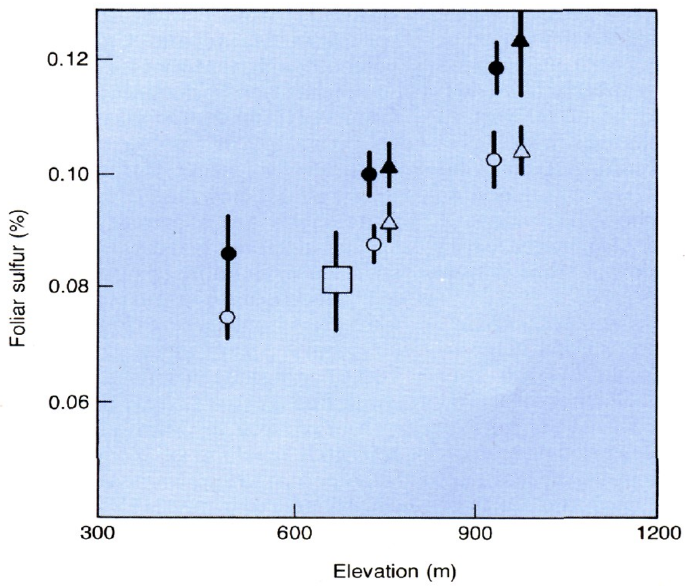
Adverse effects of acid deposition on mycorrhizae merit consideration, but in the absence of quantitative data, speculation about the potential for such effects has little meaning. High levels of trace metals, particularly Pb, have been observed in the organic horizons of the forest floor in the high-elevation forests of New England and have been reported in the Solling forest of Germany (*12*, *13*, *23*). Trace metals alone or in combination with acid deposition could have adverse effects on litter decomposition and nutrient cycling. We return to this possibility in a following section on the prospects for ecosystem stability.

U.S.–European parallels

It is probably significant that forest dieback and decline are occurring simultaneously on both continents and that there are few, if any, records of prior conifer declines of similar magnitude. There are several clear parallels in the way the North American and European diseases are expressed. The following similarities can be seen in the scientific literature:

- Conifer mortality has been observed over an extensive geographic

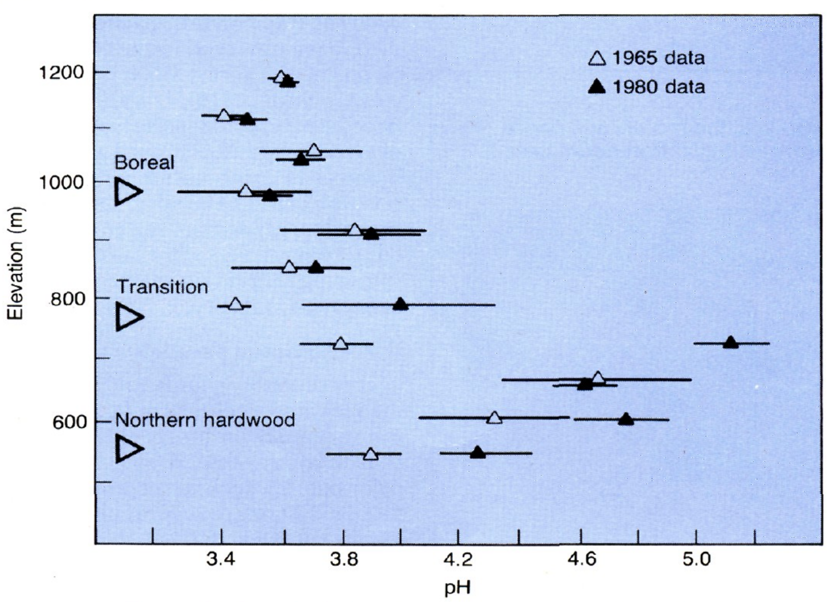
FIGURE 11
Sulfur concentrations in the foliage of red spruce increased with elevation, and the trees with higher sulfur concentrations showed visible dieback



Key
dbh = diameter at breast height
● <2 cm dbh trees at Camels Hump with visible dieback
○ <2cm dbh trees at Camels Hump in good condition
□ <2cm dbh trees at Hubbard Brook, N.H., in good condition
▲ 2–9 cm dbh trees at Camels Hump with visible dieback
△ 2–9 cm dbh trees at Camels Hump in good condition

Source: Lord (*45*) (n = 91)

FIGURE 12
In general, the soil pH in the organic horizon at Camels Hump, Vt., increased from 1965 to 1980[a]



[a] The pH (measured in water) was taken at the same sites each year. For 1965 samples, n = 33; for 1980 samples, n = 55.
Source: Siccama (*3*)

area and in a wide variety of soils having substantially different chemical properties (*3*, *14*, *40*).

- Drought or particularly warm, dry summers are associated with a loss of vigor that appears to be related to decline (*39*).
- Chemical data for the roots of declining spruce and fir suggest the possibility of a Ca deficiency in root tissue (*39*, *45*).
- Foliar chemistry indicates that, on both continents, the foliage of declining trees has 10% more sulfur than the foliage of healthy trees (*39*) (Figure 11). The cause and significance of the excess sulfur are presently unknown, but should receive more attention as research continues.
- The severity of damage increases with increasing elevation (*36*).

Prospects for ecosystem stability

Intensive soil and vegetation studies at Camels Hump, Vt., were done by Siccama in the mid-1960s (*3*) and were repeated in part in the late 1970s and early 1980s (*12*, *14*). Some information has been generated that gives insight into trends characterizing the past 20 y. Figure 12 shows that soil pH in the organic horizons did not change during that interval, a result that is expected on the basis of the high level of internal acid production in these horizons and the very large amount of atmospheric acid required to cause a notable reduction in pH (*53*). Although current data exist for the organic horizon only, we judge that these are pertinent for spruce because it is particularly shallow rooted. At low elevations, spruce seedlings are rooted primarily in the forest floor, while at high elevations, spruce of all sizes are rooted in organic soils. In many declining stands, organic horizons constitute the only soil above bedrock or felsenmeer.

It should be clear from the preceding discussion that sufficient information is not available to adequately predict the future of the high-elevation forests in which spruce has been diminished to such a large degree. Ulrich has proposed that liming the soil and reducing sulfur emissions are necessary to save the forests in West Germany (*23*). If the soil changes he observed are in fact due to anthropogenic acid additions rather than to somewhat short-term (years or decades) natural fluctuations in the soil, then the current levels of acid deposition are indeed serious. At the present time, it is not reasonable in our view to assume that the effects noted by Ulrich are happening in the montane boreal zone forests of North America because the soils here are different from those in the Solling and less vulnerable to problems of Al toxicity and because evidence generated by several other scientists studying the German forest dieback casts doubt on the Al toxicity hypothesis.

We reserve final judgment on the Al question, however, until additional information is available. For soils representative of those in which U.S. tree dieback has been observed, we need to know how acid deposition affects the levels of plant-available toxic Al species in the soil, how it affects root growth and development in spruce, and how it affects water uptake, transport, and loss from spruce. Such additional information is necessary for judging whether or not drought and acid deposition could have combined synergistically to trigger the forest decline.

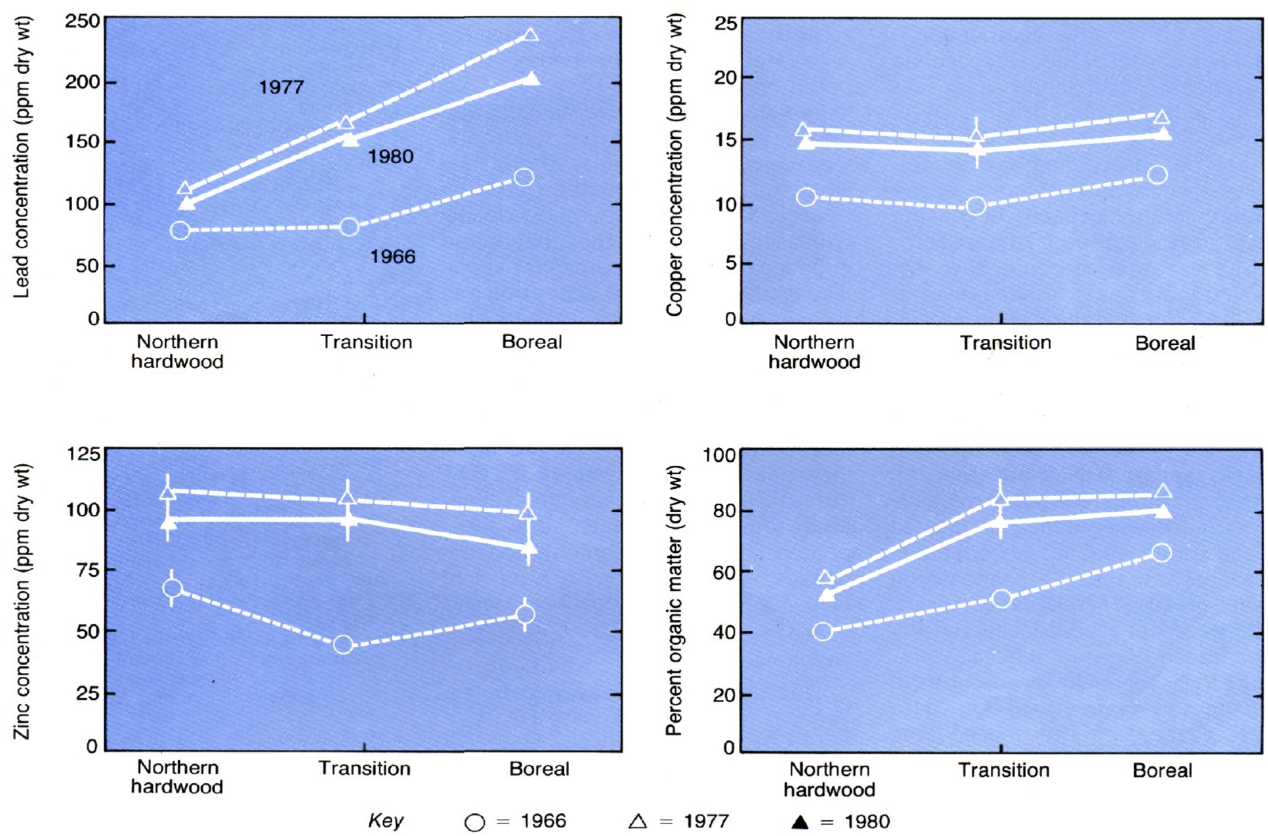
In discussing long-term ecosystem stability, it is important to point out the evidence presented by Friedland et al., which suggests both the trace-metal content of the organic horizons and the concentration of organic matter in the forest floor have increased substantially and simultaneously at Camels Hump, Vt. (Figure 13). It is unclear just what accounts for the rapid and significant increase in organic matter. This finding was not expected in the upper-elevation stands, in particular, because here the forests have been uncut and unburned for two or three centuries and the forest floor should not be aggrading rapidly. It is possible, but as yet unconfirmed, that acid deposition, trace metals, or a combination of these pollutants is interfering with litter decomposition, but this theory has not yet been thoroughly tested. If the rates of Pb accumulation in the forest floor estimated by Friedland et al. are representative of long-term trends for high-elevation forest soils, gross Pb pollution will result within a century.

To confidently assess the future of the affected North American forests, it is critical to determine the current status of reproduction. Here again, sufficient data are lacking to provide definitive insight. Table 1 indicates that balsam fir, in the small size classes, is unchanged or has increased and that, at least on Whiteface Mountain, birch has responded with dramatic increases. Only with continued monitoring of high-elevation stands can we predict whether biomass production will return to predecline levels.

To establish whether or not spruce decline is a natural phenomenon initiated or sustained by drought alone, it is important to determine if large-scale spruce mortality occurred in the past and under what climatic conditions. It is equally important to determine whether a species can persist as an important component of forests after massive, synchronous mortality has affected all size and age classes.

Sizable patches of dying or dead red spruce were noted during the 19th century. "Great destruction occurred

FIGURE 13
The concentrations of lead, copper, zinc, and organic matter on the forest floor at Camels Hump, Vt., increased between 1966 and 1980[a]



[a] Differences in 1977 and 1980 values are due to different sampling methods as described by Friedland et al. (*12*). Accumulation between 1965 and 1980 results from atmospheric deposition (*12*). For 1965, n = 33; for 1980, n = 55.

in the spruce from New York to New Brunswick" between 1871 and 1880. In 1901, Hopkins speculated that the damage was caused by the eastern spruce beetle (*Dendroctonus piceaperda*) (*54*). He cited a number of reports of spruce mortality. In some of these, beetles or other unnamed insects are mentioned, but in most cases the presence of beetles appears to be unsubstantiated. Also, beetle attack is usually related to prior stress, especially drought. It is interesting to note that the Burlington, Vt., weather records, which date back to 1832, indicate that five of the eight driest growing seasons between 1832 and 1901 occurred between 1873 and 1881. Thus, the period when spruce mortality was noted was climatically similar to the early 1960s. The relationship between dry summers and spruce mortality could be casual, but it does not seem reasonable at this time to dismiss drought as a factor sufficient to initiate decline in spruce.

McIntosh and Hurley studied the distribution of spruce and fir in the high-elevation stands of the Catskills (*55*). Their data indicate that spruce are the leading dominant only on soils that have extremely high moisture-holding capacity (>300% by weight), while balsam fir is the leading dominant on drier sites. Thus, we speculate that spruce are less tolerant of dry sites or dry conditions than fir. This could account for a selective effect of drought on spruce and for the increased spruce mortality at high elevations where the capacity of the thin soils to store moisture is diminished.

Moreover, spruce could have become more susceptible to drought after the canopy opened in response to dieback and mortality because this causes increased drying of the forest floor. Studies of birch dieback, which show that opening of the canopy by harvesting led to fine root mortality and dieback, support such a contention (*1*). Scott et al. indicated that ferns have increased in density in the gaps created by dead spruce, and our casual observations indicate that this phenomenon is widespread (*16*). Because spruce seedlings do not establish successfully under ferns (*53*), spruce in the youngest age classes could be absent until the canopy is again closed. Our data suggest that balsam fir is reproducing and could eventually create a closed canopy. Since fir is short-lived (c. 80–120 y), the long-lived spruce could become dominant again during extended periods free from closely spaced, dry growing seasons. We suggest that additional research is needed to further define the changes in species composition likely to occur in the affected forests.

Summary

The location, topography, and other characteristics of the high-elevation forests of eastern North America cause them to be receptors of high levels of acid deposition and airborne trace metals. We contend that no other major forested areas in the U.S. are subjected to such intensely acid cloud moisture, such heavy acid deposition, and such high rates of trace-metal deposition. The vulnerability of these forests to the pollutants has not been documented, but because of the spruce decline it is indeed reasonable to suspect vulnerability. In reviewing the data currently available, we find several possible pathways by which acid deposition could contribute to spruce mortality, but at this time none of these pathways are supported by convincing evidence. The framework for Al toxicity proposed by Ulrich is not consistent with the data we have generated. On the other hand, we believe that the evidence regarding a triggering effect of drought is substantiated by our data and those of others, but we do not know whether drought is sufficient to cause the dieback and decline or whether an additional stress from pollution is involved.

In viewing the spruce dieback and decline as a stress-related syndrome, we suggest the possibility of multiple stresses. Drought followed by infection by secondary organisms appears likely. Conceivably, acid deposition could enhance drought stress or vice versa. The interaction of acid deposition and secondary pathogens is also a possiblity that warrants investigation.

The prospects for ecosystem destabilization are difficult to assess in light of the available data. To adequately assess the possibility that the high-elevation forest ecosystems may be "unraveling" in response to current levels of pollutant inputs, more information is needed on population dynamics, nutrient cycling rates, nutrient pool sizes, and Al biogeochemistry.

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