Air Pollution and Forest Decline in a Spruce (*Picea abies*) Forest

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Symptoms of forest decline of spruce in Europe range from needle yellowing and loss to tree and stand mortality. In a study area in northeast Bavaria, West Germany, where forest decline was initially detected, exposure to high concentrations of gaseous pollutants, SO_2, NO_x, and ozone has had no long-lasting direct effect on needles, and pathogens have only been secondary agents. Deposition of sulfur, nitrate, and ammonium, however, have significantly modified plant nutrition and soil chemistry. Spruce roots apparently take up ammonium rather than nitrate with an antagonistic effect on uptake of Mg. Nitrate left in the soil solution is leached together with sulfate to ground water, accelerating soil acidification and decreasing Ca/Al and Mg/Al ratios in the soil solution. Soil solution chemistry affects root development, and water and nutrient uptake. Had all nutrients become equally deficient, spruce trees probably could have adjusted by retarding their growth. However, canopy uptake of atmospheric nitrogen in addition to root uptake stimulated growth and caused a nitrogen to cation imbalance to develop; this imbalance resulted in the decline symptoms.

FOREST DECLINE IN CENTRAL EUROPE HAS BEEN MANIFESTed through a combination of symptoms, especially needle yellowing and loss in conifers. It attracted public attention when the economically most important coniferous tree, Norway spruce (*Picea abies* L. Karst), exhibited symptoms of damage on a large scale and when this phenomenon could not be accounted for by known pathogens or other factors (*1*). Extensive needle damage first became apparent in the late 1970s in northeastern Bavaria, West Germany. In the early 1980s, 20 to 25% of European forests were classified as moderately or severely damaged from unknown causes (*2*). Recent surveys have indicated that some areas have partially recovered (*2*); however, severely damaged and dead trees generally have been harvested to avoid spread of secondary pathogens. Such harvesting reduced stand density and helped maintain a "healthy" appearance of German forests.

Numerous hypotheses have been developed to account for the observed decline in conifers and broadleaf species (*1, 3–5*). (i) Decline may be completely unrelated to anthropogenic pollution but result from natural climatic variation. In support of this hypothesis, the early 1980s were drier than the long-term average, and there were several unusual frost events (*1*). (ii) Fungal infections of needles have been thought to play an important role in producing forest decline symptoms and their spread; during the early phase of decline, needle loss appeared to be associated with such infections (*4*). (iii) Gaseous pollutants, especially SO_2, NO_x, and ozone, have long been known to affect forest health (*3*), and large-scale damage in forests of eastern Europe has been related to emissions of SO_2 from burning high-sulfur coal. This effect has been implicated in particular in forest decline in northeastern Bavaria bordering on Czechoslovakia and the German Democratic Republic (*3*). (iv) Cation leaching of soils by acid rain with subsequent soil acidification and enrichment of the soil solution with Al has been proposed as the major mechanism leading to forest decline (*6*). (v) Nutrient deficiencies manifested as needle yellowing have also been proposed as the main cause (*5*). However, the type of nutrient deficiency can depend on the substrate (*1*). For example, old yellow needles on acidic soils show symptoms of Mg deficiency, young yellow needles on dolomite show symptoms of Mn deficiency, and old yellow needles on limestone show K or Fe deficiencies. None of the hypotheses can account for the observed simultaneous decline of forests containing a large range of species growing on a variety of geological substrates on a large region (*3, 7*).

All of the hypotheses are based essentially on field observations without experiments. As a result, they have been evaluated on the basis of the degree of conflict with other observations, experience, or theory. Testing one theory against another has been difficult because anomalies can develop in relation to one but not to all mechanisms (*8*), and because not just one mechanism but interactions among mechanisms may account for specific decline situations. Although in most cases experiments have been made to test a particular hypothesis, these had intrinsic shortcomings in that the treatments were mostly drastic in order to achieve a response, true repetitions were not always possible, or major components of the decline situation such as root development or humus and soil stratification were not controlled in the experiment. As an alternative, a synoptic approach has been suggested for diagnosing complex problems (*8*). In this approach, the observational study is designed to incorporate as many hypotheses as possible in order to allow identification of major pathways rather than the testing of an a priori hypothesis. This approach will only elucidate reasons for forest decline, which need further experimental testing (*8, 9*).

In this article, I describe the results of a study of forest decline (*10, 11*) in a mountain range of northeast Bavaria (Fig. 1A), the Fichtelgebirge. In this study, a synoptic approach (*7*) was adopted and as many hypotheses as possible were tested on the same field plots. Decline is defined as reduced stand growth per ground area for trees with needle yellowing. At the "declining site," in contrast to the "healthy site," trees were dying for reasons other than density-related mortality (*9, 10*). The site represents the common symptoms of decline at higher elevations of the mountain ranges throughout

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Germany with acid bedrock. The study revealed that there was a network of effects (Fig. 1B) and that a combination of factors rather than one single process led to the decline phenomenon.

Above-Ground Effects of Gaseous Pollutants

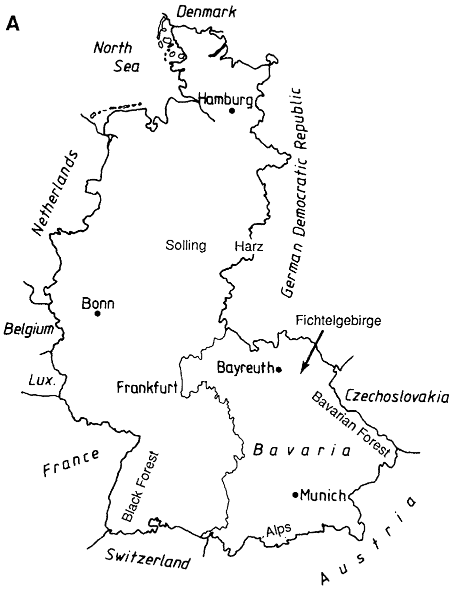
The forest region of northeast Bavaria is exposed to concentrations of gaseous SO_2 far above the level at which damage is expected (Table 1), and ozone and NO_x also reach levels at which damage might occur (*12*). Critical levels for other detected organic pollutants are unknown, although these also accumulate in cuticles of needles (*3*).

Measured levels of SO_2 are known to accumulate in chloroplasts at rates at which *p*H regulation in cells should be strongly affected (*13*) unless trees have effective mechanisms for avoiding or neutralizing this influx (Fig. 1B). Photosynthesis in green and yellow needles of different ages has been measured under field conditions in order to test for any direct damage by SO_2, ozone, or NO_x at the sites of observed forest damage (*13*). Surprisingly (Fig. 2), rate of photosynthesis does not decrease with time of exposure (up to 5 years), as expressed by needle age. In yellow needles (not shown in Fig. 2) the rate is lower than in green needles, but it also does not decrease with needle age (*13*). Lange (*14*) gave additional experimental evidence that damage by gaseous pollutants alone cannot account for the observed decline pattern in the field. In a bud-removal experiment, de-budded twigs exhibiting no extension growth were exposed to the same pollution climate as untouched neighbors on the same branch (Fig. 3). By the end of the ensuing growing season, they had regained the Mg content and maintained green color in 1-year-old needles to the level of healthy green needles in nondeclining control trees. Also, photosynthesis (not shown in Fig. 3) recovered (*14*). The experiment suggested that there is a strong long-term interaction between the decline symptom of needle yellowing and tree growth.

Table 1. Concentration of anthropogenic gases (micromol per cubic meter of air) in a stand exhibiting symptoms of forest decline (*9*). The data are based on continuous monitoring of these gases for a 3-year period as part of the air pollution monitoring network of the state of Bavaria. The United Nations Economic Commission for Europe considers 22.5 μmol ozone per cubic meter air in an 8-hour period as a critical level where harmful effects can occur to conifers (*12*). Critical levels are 1.5 and 1 μmol SO_2 and NO_x, respectively, per cubic meter of air during a 24-hour period.

Measurement	O_3		SO_2		NO_x	
	Winter	Summer	Winter	Summer	Winter	Summer
Average	0.79	1.49	0.73	0.29	0.82	0.56
± SD	±0.3	±0.3	±0.6	±0.3	±0.2	±0.3
30 min maximum	2.1	3.9	11.5	7.6	1.7	1.1
24 hour maximum	1.8	2.7	3.8	3.3	0.8	0.3

The lack of a detrimental response of needles exposed to the high concentrations of SO_2 of the study site is partially a seasonal effect, because the highest levels of SO_2 concentrations mainly occur in autumn or winter when stomata are less open or the canopy is protected by ice and snow (Table 1). However, critical levels of SO_2 also occur in summer. In this case, simultaneous uptake of NO_x and SO_2 may help prevent damage because reduction of NO_x in chloroplasts consumes hydrogen ions [(*14*), however, see also (*3*)]. Hydrogen ions may also be exchanged for cations by roots (*9*) and during uptake of ammonium by needles (*15*). Thus, damage by SO_2 may be prevented as long as base cation exchange of roots is not hindered. Additional evidence of direct damage by atmospheric pollutants, such as changes in cuticular waxes and in stomatal response, leaching of cations from needles, or accumulations of organic pesticides, was not detected or does not relate to the distribution of the decline symptoms at the study site of acute forest damage (*9*). The field measurements indicate that no long-term direct harmful effect from exposure to gaseous pollutants and pesticides can be detected despite the measured high concentrations of gaseous pollutants. However, the reversal of this statement,



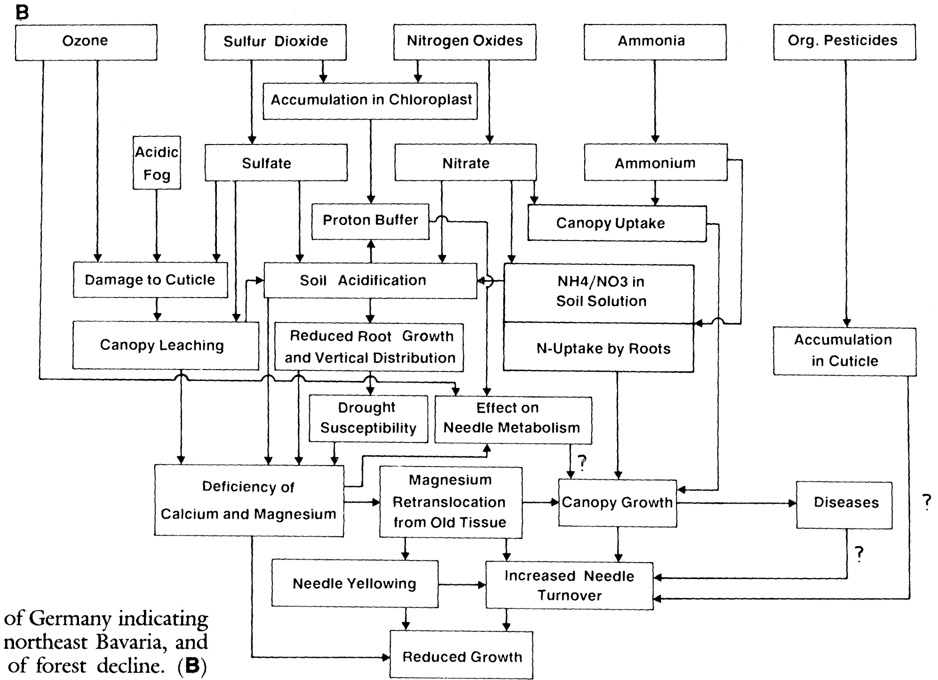


Fig. 1. (**A**) Geographic map of the Federal Republic of Germany indicating the location of the study area in the Fichtelgebirge, northeast Bavaria, and other mountain areas exhibiting similar symptoms of forest decline. (**B**) Schematic presentation of processes which led to the forest decline symptoms at the study sites (*9*). The boxes indicate the air pollutants and their effects in the soil and in the plant. The arrows indicate the main effects which were studied and discussed in this article [from (*9*)].

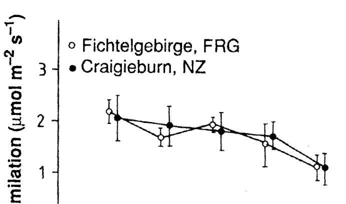


Fig. 2. Carbon dioxide assimilation rates of different age classes of *Picea abies* needles in air with 240 ppmv of CO_2 from the declining site (Fichtelgebirge, Federal Republic of Germany) and from healthy trees in an environment without any air pollution (Craigiburn, South Island of New Zealand). Error bars indicate standard errors (number of samples, $n > 30$ for the Fichtelgebirge, $n = 5$ for New Zealand) [from (*13, 16*)].

namely, that gaseous pollutants had no effect, cannot be confirmed (*13*). There is evidence from fumigation studies that even low concentrations of SO_2 produce reversible damage, which may affect the long-term performance of the needle (*16*). In addition, one may argue that the healthy "control" trees of this study have already been affected by gaseous pollutants. In order to evaluate this possibility, photosynthesis was measured in the air pollution–free environment of the South Island of New Zealand on same age spruce as in the mountain habitats in Germany. These measurements are in agreement with the data from the Fichtelgebirge (Fig. 2). The rates of photosynthesis were similar and there was no decrease in the rate with needle age.

Soil Acidification and Cation Deficiencies

In the atmosphere, the gaseous pollutants SO_2, NO_x, and NH_3 are converted into particulate sulfate, ammonium, and mostly gaseous HNO_3, respectively (Fig. 1B). Their concentrations are particularly high in fog water, for example, 19 mol of ammonium per cubic meter (Table 2). Ammonium sulfate is the major aerosol forming the atmospheric haze that is now common over much of central Europe (*17*). In contrast, in unpolluted conditions of the west coast of the South Island of New Zealand, sulfate has not been detected in fog and the concentration of nitrate has been only 5 ± 8 (average ± SD) mmol per cubic meter of fog water and that of ammonium a mere 18 ± 6 mmol per cubic meter of fog water (*17*).

The concentrations of ions in rain, fog, and aerosols affect the aerial uptake of foliage and buffering processes in the soil. However, long-term changes in the elemental balance of soils and ecosystems are related not only to concentrations of the atmospheric input but also to the total cumulative deposition over long periods of time (*6, 18*).

Soils have been progressively acidified during the last 20 to 30 years over large areas of central Europe (*18–21*). In an elaborate study, Hallbäcken and Tamm (*19*) remeasured *p*H values in soil profiles in southern Sweden that were initially studied by Tamm's father about 60 years earlier and showed that average *p*H had decreased about 0.8 (Fig. 4). Additional data collected by Falkengren-Grerup (*20*) suggest that the main change in soil *p*H took place recently, and that changes were greater in soils with a high *p*H than in those already acidified. These interpretations are supported by data (*6, 18*) for the Solling and Harz mountains of north Germany, which showed that the Ca/Al and Mg/Al ratios in the soil solution decreased strongly during the last 20 years (Fig. 4).

Soils have distinct ranges of *p*H in which specific buffering mechanisms operate (*6, 18*). Between *p*H 8.6 and 6.2, buffering is primarily by calcium-carbonate, which becomes dissolved during the buffering process. Once this reservoir becomes exhausted, the soil enters an "exchange-buffering range," which extends down to *p*H 4.2 and in which mainly clay minerals progressively exchange cations for hydrogen ions. Both cation exchange capacity and *p*H decrease with continued leaching of base cations, and exchangeable Al ions originating from silicates eventually become the dominant reactive species. At the lower end of the exchange-buffering range, aluminum hydroxosulfate immobilizes sulfate if this acid is the only input, thus terminating this part of the acidification process. However, strong acids other than sulfate alone (such as nitrate or organic acids, which may also occur naturally in soils) can continue to promote the acidification process below *p*H 4.2 and allow Al ions to enter the soil solution (*6, 18*).

Modeling all known ion exchange processes for acid soils in the Fichtelgebirge indicates that if sulfate is the only acid input, soils do not acidify below the exchange-buffering range (*9*). Even when sulfate deposition is increased dramatically, the model predicts that acidity is stored in the soil as aluminum hydroxosulfate, and that the Mg and Ca saturation does not change. However, the model predicts that soils acidify further once nitrate enters the soil solution (which occurs also as a natural process) because nitrate cannot be immobilized except by plant uptake. Excess nitrate leaching out of

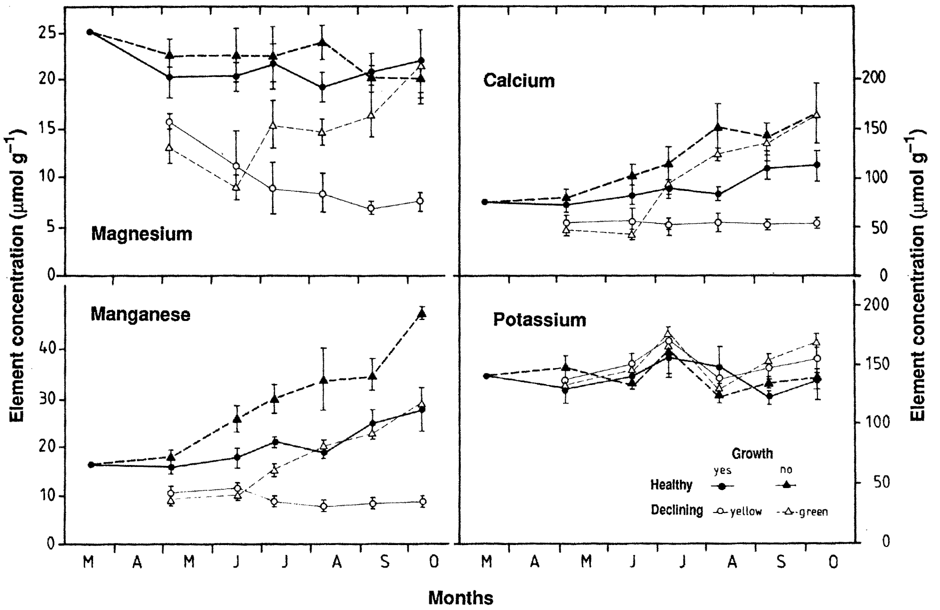


Fig. 3. Seasonal changes in element concentrations of adjacent twigs on healthy and declining trees (from March to October), which were growing during the growing season of 1987 either normally or in which growth was inhibited by bud-removal. The 1-year-old needles of twigs with removed buds on declining trees remained green while 1-year-old needles of twigs with removed buds turned yellow. Error bars indicate standard errors ($n = 3$).

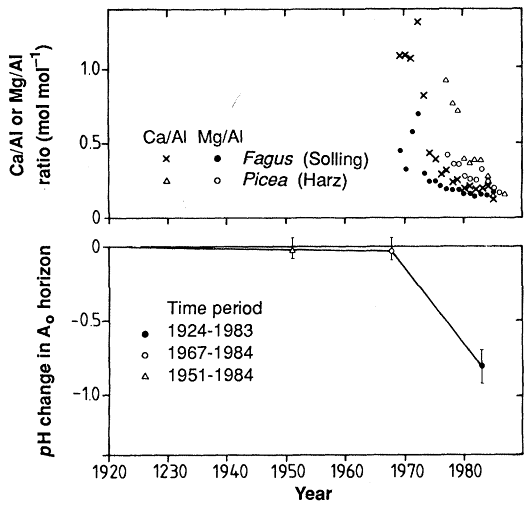


Fig. 4. Yearly average ratios of Ca and Mg to Al measured since 1968 in the Harz and Solling mountains, north Germany (**top**), and of the *p*H in the A_0 horizon from 1924 until 1985 (**bottom**). Error bars indicate standard errors (n = 41 for the period 1924 to 1983, n = 21 for period 1967 to 1984, n = 38 for period 1951 to 1984 [after (*17, 22*)].

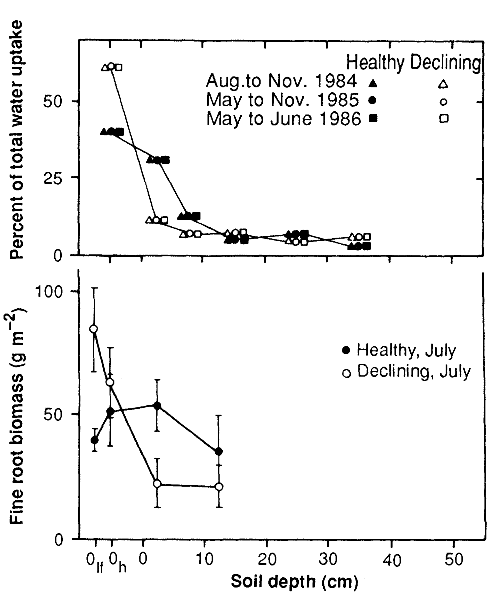


Fig. 5. Percent of total water uptake (**top**) and fine root biomass per square meter (**bottom**) for *Picea abies* in the study area in relation to soil depth. The distribution of large roots and root tips is similar to that of fine roots. Error bars indicate standard errors (n = 5) [from (7)]; O_{lf}, litter layer; O_h, humus layer.

the soil profile is accompanied by equivalent amounts of mobile cations such as Mg, Ca, and K.

Depending on the initial base saturation and acid input, the observed decreases in *p*H in central Europe suggest that sufficient acidification has occurred to pass many soils from the exchange-buffering range to the aluminum-buffering range (*6, 18, 22*). In addition, soil structure and porosity are important (*9*) because the outer skin of soil particles exposed to roots and acid soil solutions may be depleted of cations, whereas inner parts may still be at a higher level of base saturation. Such soil compartmentalization may be one reason that seasonal and yearly variations in the cation concentration of the soil solution occur (*9*).

The soil studies show that nitrate plays an important role in soil acidification (*23*). However, a major problem when assessing any possible detrimental effect of ammonium, nitrate, or sulfate on plants is that these substances are not toxic pollutants but nutrients, essential for plant growth, and are, indeed, commonly used as fertilizers in agriculture. To understand the recent history of soil acidification, we must explain why nitrate is leached from the soil profile instead of used as a fertilizer for growth. Even under nonpolluted conditions N and S compounds are continually released from dead organic matter in the litter layer by processes of mineralization and nitrate is produced naturally by microorganisms from ammonium in the process of nitrification. However, in marked contrast to atmospheric inputs of strong acids, natural processes in the N cycle are essentially balanced and do not result in a net production of hydrogen ions (*22*).

Soil acidification and the chemistry of the soil water reduces the amount of available Mg, Ca, and K in the soil solution and affects nutrient uptake and root growth (Fig. 1B). Uptake of Mg, Ca, and K may be reduced not only because concentrations are reduced, but also because of interactions among ions. For example, root uptake of Mg is suppressed in the presence of Al or ammonium ions (*24*). Effects of ammonium are particularly complicated because ammonium uptake may influence not only the uptake of Ca, Mg, and K but also inhibit that of nitrate (*15, 24*). Experiments with ammonium nitrate as a N source have shown that spruce seedlings indeed preferentially use ammonium and promote acidification of nutrient solutions as the level of available ammonium increases (*9*). Spruce seedlings growing in pots with acid soils from decline areas developed Mg deficiencies when watered with ammonium sulfate (*24*).

In the Fichtelgebirge study site, the main root horizon shows about twice as much ammonium as nitrate in the soil solution, whereas nitrate was the only N compound recovered at soil depths below the rooting zone (*9*). On the basis of extrapolations from nutrient uptake experiments in the laboratory to field conditions (*9, 15*), soil leaching of nitrate and the subsequent soil acidification, appears to result from an essentially physiological process operating at the root level, namely the preferential uptake of ammonium. Ammonium concentrations are elevated because of atmospheric inputs and because microbial nitrification is probably low under these acid soil conditions. Measurements of the natural abundance of ^{15}N in roots and soil solution are in accordance with this interpretation (*25*). Also, the high concentrations of P in needles at the study sites may be additional evidence of high ammonium uptake by spruce, because phosphate is used as a counter ion (*27*). These various processes need further experimental investigation, however.

Table 2. Mean fractional ionic charge composition of rain and aerosols in northeastern Bavaria (percent of total anionic or cationic equivalents per cubic meter ± 1 SD) and maximum (max) and minimum (min) ion concentrations in nanomoles per cubic meter of air for aerosols and millimoles per cubic meter of water for fog (*9*). The particulate mass was 14 to 167 μg per cubic meter of air.

Species	Rain (%)	Aerosol			Fog	
		(%)	min	max	min	max
		Anions				
Chloride	15.8 ± 11.7	3.5 ± 4.7	0.2	42	9	1,310
Nitrate	39.1 ± 12.4	21.2 ± 12.4	5	281	36	5,600
Sulfate	45.1 ± 10.5	75.3 ± 15.9	14	531	48	4,750
		Cations				
Ammonium	29.0 ± 8.4	62.0 ± 18.0	9	861	11	19,500
Calcium	7.7 ± 5.5	10.1 ± 7.4	0.3	67	5	1,675
Magnesium	2.1 ± 2.5	3.2 ± 2.5	0.1	25	2	290
Potassium	3.2 ± 5.4	3.3 ± 1.2	1	36	4	440
Hydrogen	49.9 ± 18.1	6.6 ± 6.5	0.4	182	1	6,600
Sodium	8.1 ± 11.0	14.8 ± 12.7	3	176	5	1,090

In addition to the direct effects of ammonium on cation and nitrate uptake (not fully represented in Fig. 1B), the chemical environment in the soil solution strongly influences root growth (*15*). For example, number of root tips under field conditions (*28*) is related to Ca/Al ratios in the soil solution and in large roots. The change in the cation composition of the soil solution (Fig. 4) is suggested to have resulted in a relocation of roots in the soil horizons. Generally, because roots transport ions from lower soil horizons to needles, which are subsequently deposited in the litter (*6, 9, 18*), the litter layer remains at a higher base saturation and *p*H than the mineral soil. Thus, the declining sites tend to have more roots in the litter layer and fewer roots in the soil below the litter than the healthy forest stands (Fig. 5). Excavations of root systems of older mature trees in declining sites indicate that roots once extended to greater depths than at present. Changes in root distribution at declining sites will obviously affect the pattern of water uptake (Fig. 5), and shallow tree roots have increased susceptibility to short-term drought in summer (*9*). These changes may account for the strong response of forests following dry years in the early 1980s and some of the recovery in recent wet years. However, present rates of acid deposition still exceed the critical loads of acidity for long-term changes of base saturation of soils on most types of parent rock material (*23*).

The Expression of Deficiency Symptoms as a Result of Nutrient Imbalance

Low supply of cations alone cannot account for the observed expression of nutrient deficiency symptoms, because if all nutrients were equally deficient for optimal growth, plants would adjust their growth within a certain range to match the supply of nutrients and show no deficiency symptoms (*29*). In order to understand the interaction between growth and cation nutrition it is necessary to

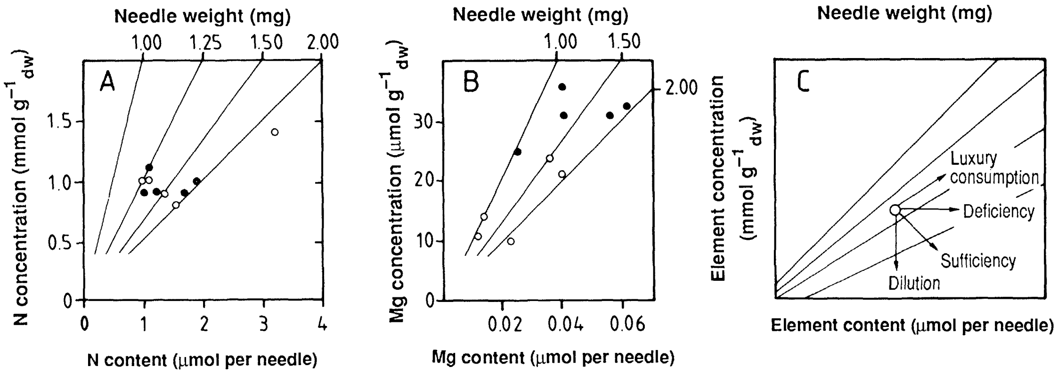


Fig. 6. Diagnosis of nutrient limitation based on the responses of single needles following a change in nutrient supply (**C**). If element concentration and element content both increase, this element is consumed luxuriously. If the element concentration remains constant but element content increases, this element was present at a deficiency level. If the element concentration decreases at constant element content, this element was diluted. Relations between needle N (**A**) and Mg (**B**) concentrations, and content, and needle weight in current year needles from ten plots of healthy and declining sites of *Picea abies*. Based on the diagnosis (C), N (A) seemed to be deficient except in one plot, in which Mg stress prevented further needle growth and N accumulated luxuriously. Mg (B) seemed to be in excess in current year needles although mature needles at the declining site showed yellowing symptoms of Mg deficiency (*9*).

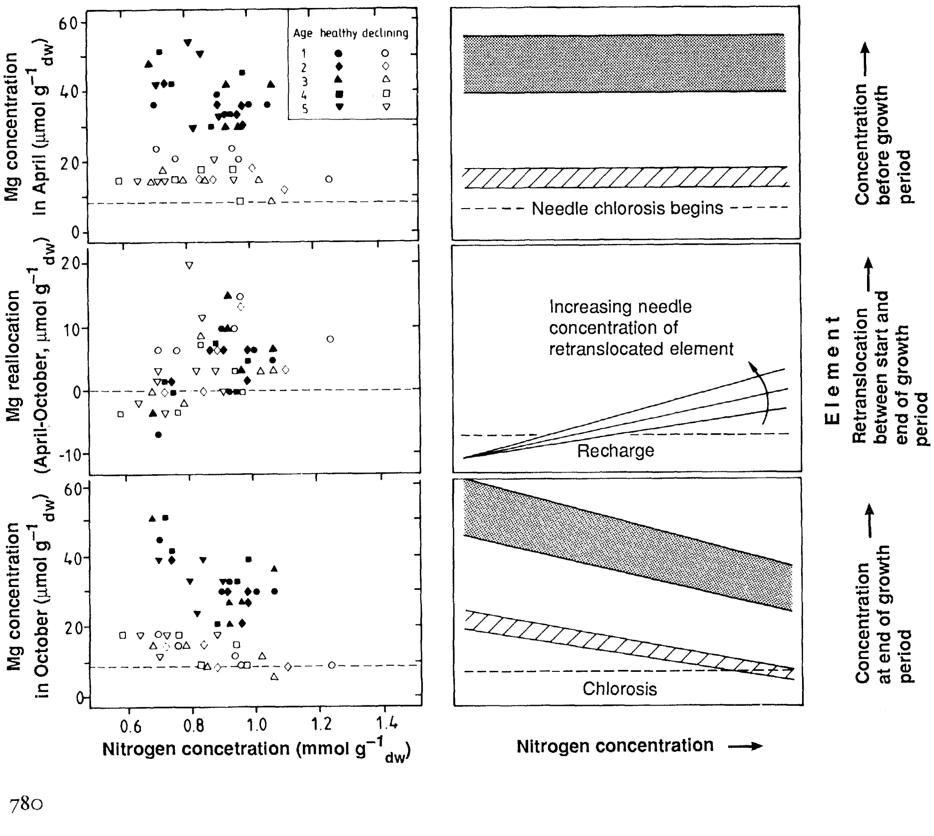
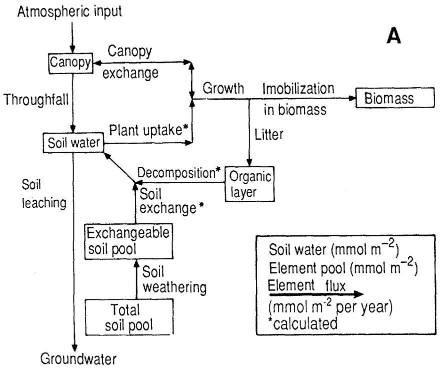


Fig. 7. (**Right**) A general description of seasonal retranslocation of a phloem-mobile element from mature needles in relation to the N concentration in those needles. Initial concentrations at the start of the growing season (top) were high (shaded area) for needles that were able to accumulate large amounts of that element before the growth phase began. They were low for needles that were not able to accumulate that element (hatched area). With beginning of canopy growth (middle), the mobile element is retranslocated out of mature needles in relation to the N concentration. More N promotes growth and increases demand for other elements. As a result, the element concentration at the end of the growth phase is inversely related to the N concentration (Bottom), and this may result in needle nutrient deficiency and yellowing. (**Left**) Measurements on *Picea abies* in the Fichtelgebirge; age is in years [from (*9*)] The Mg concentration in mature needles before growth was higher at the healthy site (top) than at the declining site. The retranslocation of Mg out of the mature needles increased with the N concentration in the needles before growth (middle) and caused Mg concentrations in some needles at the declining site to decrease below the level at which chlorosis occurs (dashed horizontal line) (bottom).



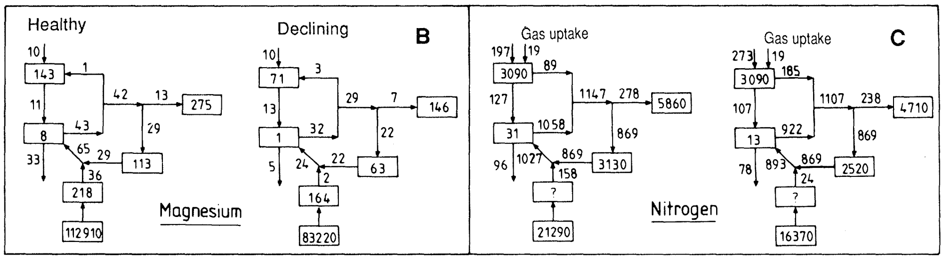


Fig. 8. Fluxes (**A**) and Mg (**B**) and N (**C**) pools in the healthy and declining forest site of the Fichtelgebirge. The data are based on five plots at each site (*9*). The boxes indicate element pools in millimoles per square meter ground as defined in the bottom part of the figure. The arrows indicate element fluxes in millimoles per square meter ground and year; * indicates values that were calculated from the mass balance. The bottom scheme defines the processes that are quantified in A and B [after (*9*)].

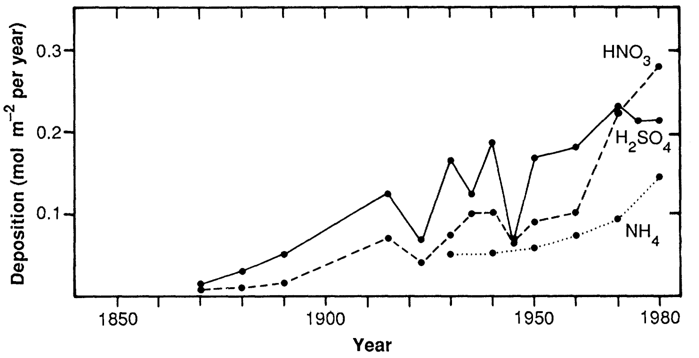


Fig. 9. The change of deposition of sulfate, nitrate, and ammonium since the year 1870. The deposition rates of sulfate and nitrate were calculated by Ulrich and Meyer (*18*) as equivalents from emission data on an area basis of Germany. The ammonium deposition data are for The Netherlands (*24*).

define precisely what is meant by deficiency or luxury consumption; plants can regulate internal concentrations in their tissues simply by adjusting organ size and number. Timmer (*26*) defined the response of leaves to added nutrients by measuring both the concentrations in leaf dry matter and the amounts of nutrients per leaf. He thereby derived more general definitions of nutrient status in terms of whether certain elements are sufficient, deficient, or at luxury levels (Fig. 6). Oren (*30*) has applied this concept to healthy and declining spruce and demonstrated that newly formed needles display nitrogen-deficiency symptoms rather than optimum supply. At the same time, Mg had been transported from old needles to new ones to such an extent that even luxury levels were reached in new needles. Trees responded strongly to addition of N by increasing their needle biomass at a rate that held the concentration in needles at a nearly constant level (*9*). This indicates that the trees under study received N far below their optimum level for growth, even though nitrate was leaching out of the soil profile, an effect likely due to selective ammonium uptake.

Only 30 to 50% of the Mg incorporated in new growth originates from concurrent root uptake (*30*); the larger proportion is reallocated from available pools in the tree biomass, especially from 1- and 2-year-old needles (Fig. 7). Before the initiation of new growth in the study area, healthy and declining trees had different levels of Mg in their old needles, but neither showed chlorosis. When new twigs start to grow, reallocation will be proportional to the supply of N and independent of the initial Mg concentration of the old needles. Hence, where initial Mg content of old needles was low (for example, in the declining plots of the study sites) mobilization of Mg from old needles leads to yellowing.

Stem growth of conifers tends to follow needle growth during the growing season (*30*) and it occurs at times when the available pools of Mg in the biomass are likely to be almost depleted. Therefore, there is a strong relation between above-ground production, which is mainly growth of wood, and the ratios of Mg or Ca to N in old needles (*9*).

It is not obvious why Mg and N nutrition are not balanced by root uptake (*9*). This imbalance results not only from preferential root uptake of ammonium interfering with uptake of other cations, but also from inputs of N through the canopy (*31*). Indeed, the mass balance of nutrients shows that aerial uptake of nitrogen (Table 3 and Fig. 8) may contribute 8 (healthy site) to 20% (declining site) of the total N requirement under conditions where uptake of other cations is hindered by ammonium uptake of the roots and cations are lost from the canopy by leaching. Uptake of N and cation leaching are the main effects of wet and dry depositions on the canopy. Experiments with ^{15}N as a tracer indicate (*25*) that there are three major pathways that atmospheric species can enter the plant. Gases, such as NO_x, enter through the stomata of the needle surface at a rate proportional to the outside gas concentration and to leaf conductance for gas diffusion (*9*). Aerial uptake in Table 3 is underestimated because direct uptake of NH_3 and HNO_3 by gas diffusion into leaves has not been considered, but may be significant in dry air (*31*). Cations such as Mg, Ca, or K cannot pass through the stomata (*9*). Gases and aerosols which are adsorbed to needle surfaces may enter through the cuticle. In this case, the ammonium uptake is constant while nitrate uptake decreases with time. Leaching of cations through the cuticle appears to be low (*25*). Another pathway for liquids is through the bark of twigs when wetted by rain or fog. In this case, the flux should be proportional to the permeability of the respective ion in bark and the concentration difference between the water-conducting element of the wood and the water outside. Thus, cations are leached from the plant interior to the outside while ammonium and nitrate enter the plant. The pathway through the bark appears to account mainly for the phenomenon of cation leaching of the tree canopy (*25*).

In summary, uptake of atmospheric N pollutants promotes canopy growth but exhausts most supplies and stem reserves of Mg in acidic soils of the Fichtelgebirge. A cation to N imbalance may potentially account for a number of nutritional deficiencies that are known to be associated with forest decline (*1, 9*), such as K deficiency on limestone and Mn or Fe deficiency on dolomite.

After the declining stands have lost a large part of their foliage and stem numbers, remaining living trees of the stand have access to a greater ground area per leaf area. Therefore, short-term recovery (see below) is expected if the trees are not too severely damaged (*32*).

The Role of Plant Diseases

Opposing the notion that forest decline is related to air pollution, several authors have proposed that decline symptoms are caused by some unknown epidemic of microorganisms or needle fungi (*4, 33*). Virus and virus-like structures are indeed widely distributed in trees, but as yet there is no concrete evidence that they are actually involved in forest decline. Although no viroids or mycoplasma-like organisms have been found in spruce, several needle fungi have been suggested to cause needle losses at the early stages of decline (*33*). These needle fungi, however, are not spread in epidemic fashion, but live inside the needle for many years without harmful effects and are still present in the remaining green needles of affected trees (*9*). What appears to have happened is that the deteriorating site conditions have allowed these needle fungi to become pathogenic at an early stage in forest decline. Also single pathogens were initially thought to have caused other types of forest decline, but now these pathogens are considered to be secondary rather than primary pests following site changes. For example, in Australia the decline of *Eucalyptus marginata* was at first thought to be the result of spread of *Phytophtora cinnamomi*, but decline is now known to have resulted initially from waterlogging conditions following habitat changes (*33*).

The Ecosystem Balance

The overall effect of major nutrient fluxes on whole plant functioning can only be viewed in the context of a complete ecosystem balance (Fig. 8). The trees of the Fichtelgebirge site appear to grow in relation to atmospheric cation inputs, while cation inputs from soil weathering are lost in amounts equivalent to soil leaching. The quantity of cations lost to the ground water is large compared to the sizes of the cation pools (*9*). At current rates of Mg flux to the ground water, the "exchangeable" pool of Mg at a healthy site could be reduced to that of a declining site in less than 2 years if Mg pools are not replenished by soil weathering. This estimate indicates that decline symptoms related to this cation are sensitive to yearly weather conditions and N inputs. Just slight changes in gain and loss will determine the balance. If the release of Mg by weathering exceeds the flux out of the exchangeable pool, which depends on the available nitrogen and on weather conditions, a declining stand may apparently recover, as was the case after recent wet years (*2*). However, any "regreening" of foliage is not an indication that the ecosystem has recovered. The ecosystem still remains at a low level of base saturation and the decline symptoms may return just as fast as apparent regreening takes place, depending on weather. Logging of timber also affects the nutrient balance. If normal harvesting practice and current acid inputs continue, the "total" pool size of Ca and Mg in healthy sites is estimated to reach that of declining sites in approximately 100 years for Ca and 800 years for Mg. This calculation demonstrates that even apparently healthy sites are not stable on hundred-year time scales. Yellowing of needles on some trees at the healthy site was first detected in 1988, although only green needles had been found in 1985, which emphasizes the lability of the exchangeable pool.

Where reduced competition among individual trees is accompanied by reduced growth per ground area of the stand, as is frequently observed at declining sites, less N is likely to be taken up from the soil, and soil cation leaching will accordingly increase because of the nitrate efflux. Decline symptoms may, therefore, return once the soil is depleted of base cations and demands for even a small leaf area cannot be met. Effects attributed to a limited supply of nutrient cations are likely to be exacerbated in dry years because soil acidification would restrict rooting depth (*9*). If inputs of N became stabilized, the forest might well reach a new steady state of low growth rate but with no decline symptoms. The more likely scenario, however, is that increasing N inputs will continue to perturb the forest ecosystem within the natural variation of weather. It is expected under these conditions that stand vigor will continue to decline because of nutrient imbalance and that tree mortality will increase because of increased susceptibility to secondary effects such as insect attack, wind, and other pathogens.

Table 3. Wet and dry deposition (millimol per square meter ground per year) of S in SO_2, and N in NO_x or NH_x in the healthy (H) and declining (D) forest sites (*9*).

	S as SO_2		N as NO_x		N as NH_x	
	H	D	H	D	H	D
Wet deposition	71	76	64	63	54	52
Aerosol deposition	11.6	20.7	6.5	11.5	19.1	34.1
Gas adsorption	19.7	51.4	54.1	112.6	—	—
Gas uptake	7.4	7.6	18.6	18.6	—	—

Historical Considerations and Outlook

The events leading to forest decline may be interpreted in terms of three overlapping phases of atmospheric deposition that have probably affected forest trees in central Europe in general [(*16, 18, 24*); Fig. 9]. During the first phase (1870 to 1900), S was the major pollutant in the atmosphere. Deposition of S initiated soil acidification, but acidification did not reach the currently observed level because sulfate was probably immobilized as aluminum-hydroxosulfate at the lower end of the exchange-buffering range. During the second phase (1900 to 1960), nitrate deposition increased steadily and probably acted at first as an effective fertilizer increasing forest productivity. This period was followed by a third phase (1960 to present) during which aerial depositions of nitrate and ammonium increased exponentially. The amount of ammonium relative to nitrate in the soil solution of acidifying soils changed because of deposition and probably also because of altered microbial nitrification at low *p*H; this change increased uptake of ammonium by trees and apparently resulted in excess nitrate remaining in the soil solution. Because nitrate is not immobilized in the soil profile, nor fully used by trees, it has become a major contributor to soil acidification and has led to the recent rapid decrease in soil *p*H. Along with a continuing stimulation of needle growth by N deposition, the deposition of ammonium and nitrate appears to have led to the expression of forest decline symptoms visible since the late 1970s. Although effective means are already being taken to reduce sulfate and nitrate deposition originating from combustion processes, it may become much more difficult to reduce the current escalating deposition of ammonium from organic sources such as city sewage dispersal, animal husbandry, and the dispersal of liquid manure (*32*) from animal enterprises.

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RNA-Protein Interactions in 30*S* Ribosomal Subunits: Folding and Function of 16*S* rRNA

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Chemical probing methods have been used to "footprint" 16*S* ribosomal RNA (rRNA) at each step during the in vitro assembly of twenty 30*S* subunit ribosomal proteins. These experiments yield information about the location of each protein relative to the structure of 16*S* rRNA and provide the basis for derivation of a detailed model for the three-dimensional folding of 16*S* rRNA. Several lines of evidence suggest that protein-dependent conformational changes in 16*S* rRNA play an important part in the cooperativity of ribosome assembly and in fine-tuning of the conformation and dynamics of 16*S* rRNA in the 30*S* subunit.

RIBOSOMES ARE LARGE RIBONUCLEOPROTEIN (RNP) structures that are responsible for translation of the genetic code (*1, 2*). As emphasized by Woese (*3*), their biological role links genotype with phenotype, and therefore the evolutionary origins of ribosomes are closely tied to the origin of life as we know

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