Performance of two *Picea abies* (L.) Karst. stands at different stages of decline

VI. Nutrient concentration

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Summary. A declining *Picea abies* (L.) Karst. stand produced as much foliage and branches as a healthy stand but less stemwood at a similar leaf area index and climate. Nutrient analyses revealed that most biomass components at the declining site had lower concentrations of calcium and magnesium, but similar nitrogen and potassium (except for lower potassium in younger needles) and higher phosphorus, manganese and aluminum than the respective components at the healthy site. Comparison of these data with the results from studies on the nutrition and growth of *P. abies* seedlings (Ingestad 1959) led to the conclusion that the healthy stand is in a balanced nutritional state, while trees at the declining stand have only 56% of the foliar magnesium concentration required to permit growth at a rate which could be achieved at their nitrogen status. It appears that acidic deposition, which involves an input of nitrogen and a leaching of cations from the soil, causes an imbalance in the availability of nitrogen and magnesium. Growth is eventually reduced as magnesium becomes limiting.

Key words: Forest decline, Spruce (*Picea abies*) – Nitrogen – Magnesium

The impact of sulfate and nitrate in acidic deposition on the nutritional status of forests may be positive or negative. Initially, a positive effect on growth from increased nitrogen and sulfur availability nutrition may dominate if cation capital in the soil is ample but nitrogen is limiting growth (Nihlgård 1985; Schulze et al. 1987; Tamm and Aronsson 1988). Then, a nutritional imbalance may develop when acidic deposition accelerate cation leaching from soils (Ulrich 1986) while tree growth is still promoted by an elevated nitrogen supply (Nihlgård 1985; Schulze et al. 1987). Eventually, decline in tree vigor and forest productivity is expected as nutritional deficiencies develop to a level which impair physiological processes. Therefore, when cation supply from the soil barely meets stand demands, acidic deposition is likely to cause a short term increase in growth, followed by a continuous decline in productivity (Tamm and Aronsson 1988).

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A reduction in stand productivity may result from reduced production per unit of leaf area, from loss of canopy leaf area, or both. Reduction in production rate and in leaf area may result from nutritional and non-nutritional (i.e. direct damage to needles) effects of air pollution (Johnson et al. 1982). Non-nutritional effects would most likely be the major cause of decline in areas where SO_2, NO_x and O_3 levels are high (Amundson et al. 1986, see also review by Kozlowski and Constantinidou 1986) particularly if the soil has sufficient nutrient cations. However, in areas where soils are poor in these base cations, mineral weathering cannot resupply the exchange complex, and where moderate levels of acidic precipitation have been deposited over a long period, nutritional limitation may be the main reason for decline as the nutrient cation supply by the soil becomes increasingly insufficient for proper plant function.

In this part in a series on forest decline, we report on the nutritional aspect of th decline in a mountain range in northeast Bavaria, FRG. Earlier, Oren et al. (1988a) reported that an apparently declining stand of *P. abies* (L.) Karst. with a large number of trees with yellow needles and thin crowns, produced 35% less wood than a stand with no decline symptoms (Oren et al. 1988a). The lower production could not be attributed to climatic differences, nor to the degree of site occupancy, characterized by leaf area index. Allocation to below ground production was similar at the two sites and respiration was probably higher at the healthy site because it supported more living biomass. Comparison of the annual course of non-structural carbohydrates between the stands showed that the declining stand had less carbohydrates available for growth and also used less of its carbohydrates than the healthy stand.

Non-nutritional effects of acidic precipitation and air pollution on photosynthesis were studied on green, nutritionally-sound foliage of several age classes. Lange et al. (1985, 1987) and Zimmermann et al. (1988) found no indication of impaired photosynthetic and transpiration rates at the leaf level, except in extremely chlorotic foliage. Werk et al. (1988) have also found similar transpiration in both stands at a whole tree level and excluded transpiration as a mechanism involved in the nutritional differences between the sites.

Yellowing of needles in declining forest stands has been associated with nutritional deficiencies. Zech and Popp (1983) reported that trees at the declining site had lower

calcium and magnesium in their foliage than trees at the healthy site. While such differences may be attributed to leaching from foliage (Hantschel 1987), however Osonubi et al. (1988) found that the variations of the magnesium and calcium in needles at the two sites were related to the concentration of the elements in the xylem sap. This suggested difficulties in nutrient uptake, and perhaps in magnesium retranslocation. Meyer et al. (1988) observed that calcium and magnesium uptake at the declining site was related to a lower concentration of these elements in the soil solution. In addition, a high soil aluminum concentration relative to calcium in the mineral soil appears to restrict root growth below the organic layer, thus limiting the volume of soil available for uptake.

Although Zech and Popp (1983) compared the nutrient concentrations in needles between the two study sites, their study was not designed in a way that permits to evaluate seasonal trends in element concentrations in various biomass components, and thus process-oriented cause and effect hypotheses could not be generated. To separate the effects of foliar leaching from that of low availability of nutrients as the cause of nutritional differences between the sites and of tree decline, we selected only green trees at both the declining and healthy sites. This approach is different from that of Zech and Popp (1983) who were only interested in a broad site comparison and included needles from trees at various stages of decline. We followed the element concentrations in the initially green trees over one growing period, even as a few at the declining site became progressively yellow. In this paper we evaluate the effect of nutritional differences on tree decline between trees at the two sites and identify in which biomass components and at what time during the growing season nutrient deficiency may be most restrictive to proper function and growth.

Material and methods

Two *P. abies* stands, one containing many trees with yellow needles and thin crowns and the other with only trees with green, full crowns, were selected for an intensive investigation of their carbon, water and nutrient relations. The stands are located 15 km apart (60° N latitude, 12° E longitude), near the villages of Oberwarmensteinach (the declining stand) and Wülfersreuth (the healthy stand). The two sites have similar soil, climatic and stand characteristics. Soils at both sites developed from phyllit parent material; the soil at the declining site is classified as podzol while that at the healthy site as podzolic cambisol (Oren et al. 1988a; Meyer et al. 1988).

While precipitation was only 20% higher, annual proton input was 60% more at the declining site than in the healthy one (0.094 vs. 0.158 mol m^{-2}) because of a higher sulfate concentration in precipitation at the declining site (Hantschel 1987; see Oren et al. 1988a).

In March, 1985, five, 80 m^2 circular plots were randomly established in each of the two stands. The plots, which resembled in structure the immediate surrounding stand, were used to estimate biomass and growth in various biomass components, and litter fall (Oren et al. 1988a). The plots were also used to determined the concentration of elements in the soil solution (see Meyer et al. 1988 for a description of the sampling and analysis procedures). The data generated from these ten plots were used for both site mean comparisons and as individual data points in correlation analyses. Stand level variables, including microclimate, litter-fall, and soil chemical and root characteristics were determined from plot measurements and thus represent the average conditions of all trees in the plots which, at the declining site, contained trees at various stages of decline. Aboveground variables represent the conditions of one codominant tree with a green crown in each plot. Sampling was done at predetermined stages in the annual growth cycle. The first sampling was done in April when the soil was still frozen and gas-exchange rates were low. Subsequent sampling was done in May (at bud break), in July (after needles were fully expanded), and in October (at the end of the growing season when conditions were similar to those in April).

At each sampling time, samples were collected before sunrise, from one of four adjacent branches in the lower sun crown. The samples were stored on ice, brought to the laboratory within an hour, and than stored at 4° C for less than one week. Litter traps were emptied, and roots were sampled at the same time. The roots from two organic and two mineral horizons were divided into classes of large (2–10 mm), fine (<2 mm), and dead roots (Meyer et al. 1988). Twig samples were separated into five age classes before bud-break and six classes thereafter. In October, twigs were also separated into wood and bark, and additional sampling was made of the main stem wood and bark. Samples were dried in a forced air oven for 48 h at 70° C, finely ground in a ball mill, and stored in a desiccator.

Total nitrogen was determined using the ground plant material with a C/N analyzer (Model 1500, Carlo Erba, Italy). The values obtained were about 10% higher than values from the Kjeldal method.

The concentration of other elements were determined after a pressure digestion of the ground material with 100% HNO$_3$, at 170° C for 6 hours (Schramel et al. 1980). Aluminum determination was done with an inductively coupled plasma emission spectrometer (Model Y48, Yobin Yvon Instruments SR, France). Determinations of the other elements (calcium, potassium, magnesium, manganese, and phosphorus) were made with a direct current plasma emission spectrometer (model Spectro Span 6, Beckman Instruments, USA).

Phosphorus in fine roots was not determined in the samples from April and May, and in the above ground components in May due to technical difficulties. In addition, root material was not always available in enough quantities in all categories and, therefore, in a few cases a value for a given category is missing, mostly that of nitrogen.

Needles of ages 1 to 5 years, and twigs of ages 1 and 3 years from the two sites and four sampling times were compared using analysis of variance with site, sampling time and age as main factors. Current-year needles, dead needles, large, fine, and dead roots were also compared using analysis of variance with site and sampling time as main factors. The material that was uniquely collected or divided in October (i.e. bark and wood) was compared between the sites using a simple t-test.

The aboveground plant material was not cleaned before the analyses. Most elements in needles of *P. abies* show no change in concentrations even after stripping the needle surface or washing the needles with chloroform (Krivan and Schaldach 1986; Wyttenbach et al. 1985). However, aluminum concentration in needles which were not cleaned

in any way, may be 25% to several times higher than in cleaned needles. Therefore, the aluminum values reported here for the aboveground components were used only for relative comparison, and should not be regarded as precise tissue values.

Sampling time or age may contribute significantly to the overall variation in the concentration of elements because of seasonal courses of carbohydrate concentration and increase in specific leaf weight with age. It is possible to account for the seasonal variations in soluble carbohydrates by expressing element concentration on a dry weight basis, after correcting for non-structural carbohydrates, or by including the carbohydrates as a covariate in an analysis of variance. Alternatively, it is possible to account for both the seasonal course and the increase in specific leaf weight by expressing the concentrations per unit of leaf area (Smith et al. 1981). We therefore repeated the nutrient analyses after converting the concentration to an area basis and compared the results to those based on a dry weight. The specific leaf area (or its inverse, the so-called specific leaf weight) of each needle sample was determined from a sub-sample projected area and dry weight (see Oren et al. 1988a) and was used to convert nutrient concentrations to contents per unit of leaf area.

Dead needles represent a mixture of age classes. Therefore, if a significant decrease or increase in concentration occurs with age, the retrieval of each element from needles before they were shed, which was calculated based on the difference in concentration between the five-year-old and the dead needles, may be under or over-estimated, respectively. However, because calcium content of dead needles was higher than that of the oldest living needles measured, we feel that calculated values are reliable. If needles were shed at approximately constant rate during the growing period, their average residense time in the litter traps was two to four weeks, depending on the sampling period, and leaching of elements, particularly of highly mobile elements such as potassium, may also result in some over-estimation of retrival of base cations (Staaf and Berg (1982).

Results

Clear differences in the nutritional state of trees in the two stands were observed. Mean element concentrations in different plant parts over the season at the two sites are presented in Appendix 1. The results of the statistical analyses of these data are given in Table 1.

Needles

There was no interaction between needle age (1 to 5 years) and sampling time interaction for any element (Table 1). Therefore, mean the concentrations of all ages in each sampling time, and all sampling times for each needle age are presented (Figs. 1 and 2). The concentration of magnesium was higher at the healthy site in all needle age classes and increased with needle age faster than at the declining site (Fig. 1, significant site by age interaction in Table 1). Similar results have been reported from other areas where forest decline was studied. However, it appears that absolute concentration values of a single nutrient may not necessarily indicate a declining state because concentrations in healthy trees in one stand can be lower than those in declining trees in another study area (Forschner and Wild 1987; Zöttl

and Hüttl 1986; Rehfuess and Rodenkirchen 1984). The differences between the sites (Fig. 1) were already apparent in new needles and were maintained in dead needles. Trees at the site that is better supplied with magnesium retrieved magnesium from needles before shedding them while trees at the declining site failed to do so. However, concentrations at the healthy site were still higher as the needles were shed. The difference in magnesium concentration in dead needles between the sites cannot be attributed to higher leaching from foliage at the declining site because leaching was actually higher at the healthy site (Hantschel 1987). Magnesium concentrations were higher in April than in the other months. Some of the reduction in magnesium concentration between April and May may have been caused by an increase in the soluble carbohydrates, which was higher in the healthy stand (Oren et al. 1988a). However, when magnesium was expressed as content per leaf area, the difference between the sites was even greater with needle age. Retranslocation from 1 to 5 years needles at both sites between April and May was more pronounced and some magnesium appeared to be retrieved from needles prior to shedding at the declining site too (Fig. 2, Table 1). In addition, it became clear that the decreasing magnesium concentration with needle age at the declining site (Fig. 1) was a consequence of increased needle mass.

Calcium concentration and content in needles was higher in the healthy stand and increased with age faster than in the declining stand (Figs. 1 and 2, Table 1). Thus, although no clear differences could be detected in current year needles, the differences increased with needle age. Calcium was not retrieved out of needles before shedding. While a seasonal retranslocation pattern was apparent when calcium was evaluated on a dry weight basis, it was not apparent when expressed on a needle area basis, which indicates that it was related to an increase in carbohydrates concentration in May (Tab. 1, Oren et al. 1988a). Lower calcium concentrations in declining trees compared with healthy ones have been previously reported (Forschner and Wild 1987; Zöttl and Hüttl 1986; Rehfuess and Rodenkirchen 1984). The values were generally lower than those presented here.

The needles of all age classes except the most recent had similar nitrogen concentrations at the two sites (Fig. 1; Table 1). Converting the values into an area basis removed any site, age, or seasonal differences in nitrogen content for one-year-old needles and older, while differences between new needles at the two sites became clearer (Fig. 2; Table 1). The nitrogen content in new needles was lower than that of older needles. At both sites, 25 to 30% of the nitrogen was retrieved from needles before shedding, less than previously estimated (Schulze et al. 1987). Needle nitrogen concentrations in this study are similar to values reported elsewhere for *P. abies* (Forschner and Wild 1987; Zöttl and Hüttl 1986; Rehfuess and Rodenkirchen 1984).

Twigs

Magnesium concentrations in twigs were similar to the concentrations in the needles (Fig. 3; Table 1). The major difference in comparison with needles was that concentration in the 1-year-old twigs did not decline between April and May, despite an increase in soluble carbohydrates during that period (Oren et a. 1988a), but declined after bud break until July. The concentration in the 3-year-old twigs did

Table 1. Significance values of F-test from an analysis of variance of element concentrations in needles representing age classes 1 to 5-year-old, current year needles and dead needle expressed on both weight and area basis, in 1 and 3-year-old twigs, and in large (2–10 mm), fine (<2 mm), and dead roots from the healthy and declining sites sampled 4 times during the growing season. All interaction terms with $p=0.3000$ or less are given or the lowest interaction, if none could satisfy this criteria (Interaction code: 1 = site × sampling time, 2 = site × age, 3 = sampling time × age, no higher level interactions were low enough to be included, $n=5$ per factor combination, some combinations at various times had less than 5 observations due to insufficient root material). The mean element concentrations in bark and wood of 1 and 3-year-old twigs, and in the stem in october were compared with a Student's t test ($n=5$ per site)

	Aluminum	Calcium	Magnesium	Manganese	Nitrogen	Phosphorus	Potassium
Needles							
0-yr per weight							
site	0.250	0.201	0.001	0.123	0.235	0.209	0.020
time	0.933	0.355	0.969	0.239	0.801	0.060	0.287
interaction	0.834	0.689	0.184	0.951	0.409	0.941	0.479
0-yr per area							
site	0.025	0.477	0.005	0.087	0.114	0.044	0.227
time	0.982	0.427	0.909	0.308	0.899	0.128	0.394
interaction	0.794	0.810	0.346	0.980	0.556	0.952	0.471
1 to 5-yr per weight							
site	0.001	0.001	0.001	0.001	0.536	0.001	0.055
time	0.002	0.030	0.006	0.212	0.001	0.001	0.001
age	0.001	0.001	0.006	0.001	0.001	0.005	0.001
interaction	1) 0.003	2) 0.011	2) 0.243	2) 0.659	1) 0.151	1) 0.111	2) 0.003
	2) 0.020						1) 0.161
1 to 5-yr per area							
site	0.001	0.001	0.001	0.001	0.756	0.001	0.737
time	0.001	0.180	0.001	0.333	0.360	0.001	0.001
age	0.001	0.001	0.001	0.001	0.129	0.044	0.001
interaction	1) 0.010	2) 0.006	2) 0.001	2) 0.324	2) 0.032	1) 0.076	2) 0.209
	2) 0.035						
dead per weight							
site	0.823	0.080	0.001	0.135	0.011	0.005	0.266
time	0.030	0.122	0.049	0.323	0.633	0.001	0.001
interaction	0.288	0.069	0.929	0.425	0.473	0.442	0.069
dead per area							
site	0.890	0.001	0.001	0.197	0.339	0.003	0.510
time	0.001	0.265	0.220	0.649	0.361	0.686	0.396
interaction	0.721	0.088	0.526	0.503	0.774	0.978	0.536
Twigs							
1 and 3-yr per weight							
site	0.023	0.001	0.001	0.001	0.243	0.035	0.775
time	0.001	0.030	0.005	0.642	0.001	0.001	0.171
age	0.001	0.001	0.001	0.640	0.001	0.001	0.001
interaction	1) 0.032	2) 0.202	3) 0.084	1) 0.639	3) 0.036	3) 0.148	1) 0.230
	3) 0.032		2) 0.107				
	2) 0.245						
1-yr old							
bark	0.253	0.599	0.065	0.515	0.391	0.043	0.532
wood	0.865	0.030	0.187	0.239	0.448	0.674	0.482
3-yr old							
bark	0.837	0.035	0.004	0.048	0.527	0.954	0.836
wood	0.324	0.329	0.681	0.102	0.468	0.541	0.212
Stem							
bark	0.302	0.872	0.060	0.161	0.219	0.036	0.570
wood	0.823	0.219	0.385	0.178	0.311	0.890	0.067
Large Roots (2–10 mm)							
O_{lf} horizon							
site	0.028	0.102	0.834	0.065	0.116	0.114	0.751
time	0.096	0.384	0.145	0.666	0.100	0.490	0.001
interaction	0.328	0.621	0.356	0.512	0.593	0.279	0.739
O_h horizon							
site	0.945	0.124	0.066	0.001	0.585	0.014	0.591
time	0.001	0.240	0.318	0.327	0.058	0.204	0.001
interaction	0.082	0.457	0.719	0.786	0.054	0.431	0.226

Table 1 (continued)

	Aluminum	Calcium	Magnesium	Manganese	Nitrogen	Phosphorus	Potassium
0–5 cm mineral soil							
site	0.622	0.460	0.009	0.003	0.229	0.174	0.537
time	0.364	0.004	0.687	0.980	0.252	0.773	0.070
interaction	0.815	0.001	0.230	0.539	0.796	0.028	0.430
5–20 cm mineral soil							
site	0.789	0.014	0.001	0.013	0.421	0.081	0.100
time	0.094	0.479	0.252	0.926	0.009	0.818	0.001
interaction	0.110	0.364	0.137	0.855	0.704	0.097	0.088

Fine roots (2 mm)

	Aluminum	Calcium	Magnesium	Manganese	Nitrogen	Phosphorus	Potassium
O_{lf} horizon							
site	0.324	0.114	0.470	0.002	0.887	0.003	0.158
time	0.366	0.644	0.005	0.825	0.039	0.158	0.001
interaction	0.421	0.057	0.557	0.875	0.415	0.865	0.299
O_h horizon							
site	0.873	0.014	0.042	0.001	0.039	0.001	0.491
time	0.025	0.423	0.009	0.720	0.922	0.014	0.001
interaction	0.068	0.287	0.790	0.975	0.437	0.386	0.118
0–5 cm mineral soil							
site	0.458	0.090	0.382	0.001	0.104	0.002	0.735
time	0.004	0.559	0.009	0.840	0.602	0.212	0.001
interaction	0.276	0.629	0.969	0.860	0.198	0.869	0.723
5–20 cm mineral soil							
site	0.937	0.010	0.030	0.001	0.074	0.001	0.404
time	0.055	0.952	0.000	0.473	0.164	0.030	0.001
interaction	0.813	0.552	0.378	0.535	0.491	0.656	0.958
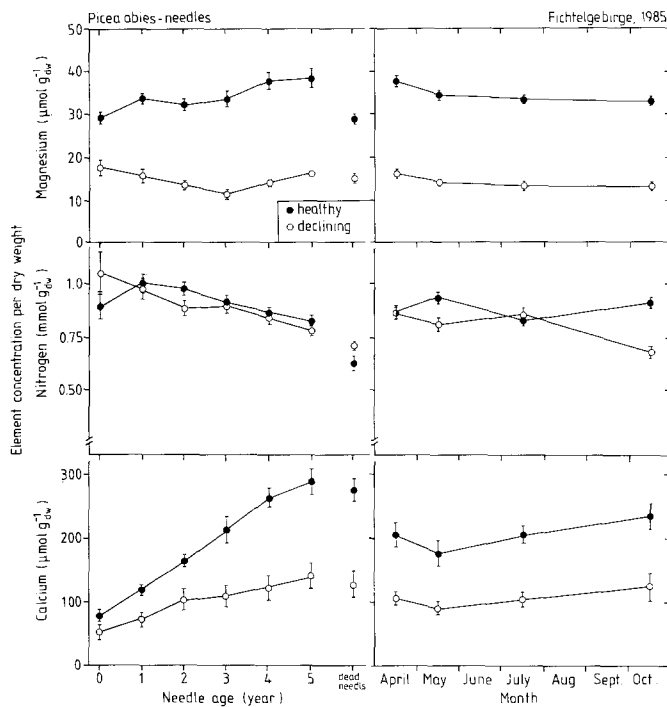
Fig. 1. Mean (± 1 s.e.) element concentrations on a dry weight basis in needles from six age classes, and dead needles from the healthy and the declining sites (left, $n = 20$) and the annual course of the mean concentrations for needles ages 1 to 5-year-old (right, $n = 25$)

Fig. 2. Mean (± 1 s.e.) element concentrations on an area basis in needles from six age classes, and dead needles from the healthy and the declining sites (left, $n = 20$) and the annual course of the mean for needles ages 1 to 5-year-old (right, $n = 25$)

not seem affected by an even larger increase in carbohydrate concentration before bud-break. This may be explained by an increase in the magnesium concentration from uptake and from retranslocation out of the needles at the same rate as the increase in carbohydrates in response to the onset of the growing period. When growth begins, the demand for magnesium by the expanding new twigs and foliage at both sites seemed to exceed the supply rate to the 1-year-old twigs, and the concentration decreased.

The concentration of calcium in twigs had a similar
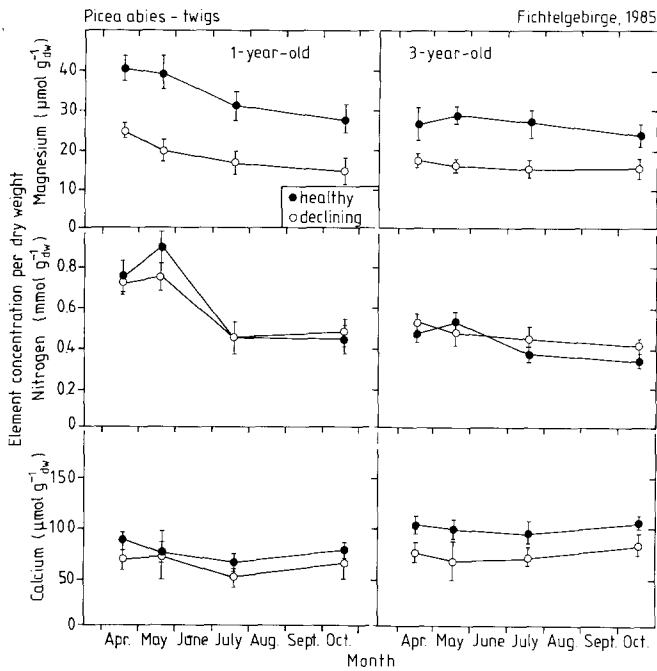
Fig. 3. Annual course of mean (±1 s.e.) element concentrations in twigs from two age classes from the healthy and the declining sites (n = 5)

Fig. 4. Mean (±1 s.e.) element concentrations in wood and bark of twig from two age classes and the stem of trees from the healthy and the declining sites in October (n = 5)

pattern to that described for the magnesium (Fig. 3; Table 1). Concentrations were higher at the healthy site, increased with age, and had a seasonal course related to changes in the carbohydrate concentrations between April and May. Life magnesium, growth was accompanied by a reduction in the calcium content of 1-year-old twigs; the reduction seems smaller than that of magnesium reflecting the more immobile nature of calcium (Kirkby and Pilbeam 1984).
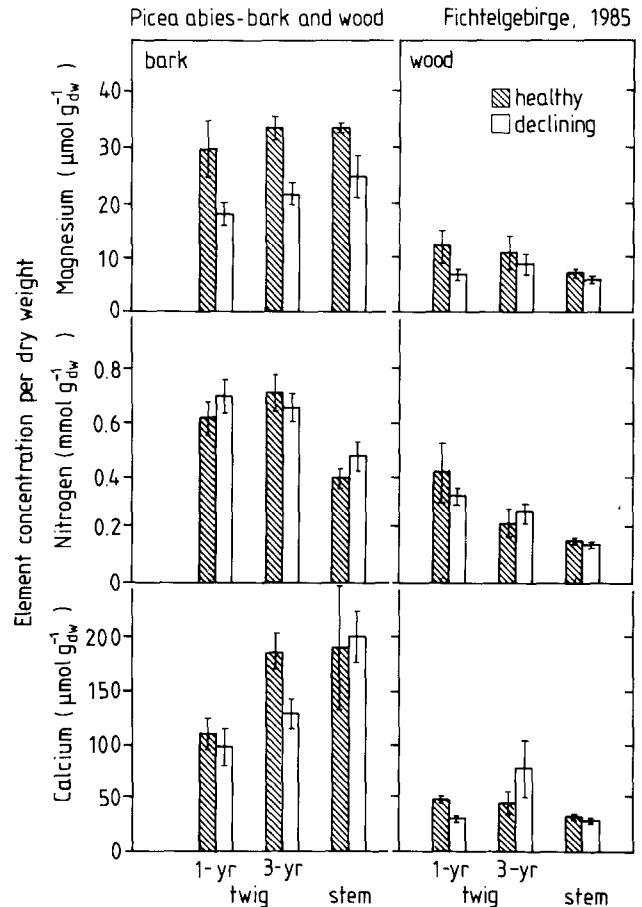
Twig nitrogen concentrations followed the seasonal pattern of magnesium (Fig. 3; Table 1). The seasonal course could also be explained in terms of the balance between supply via uptake and retranslocation and demand by the growing twigs.

Bark and wood

The source of differences between the sites in the magnesium concentrations in twigs appeared to be mostly in the bark and not the wood (Fig. 4; Table 1). Stem bark at the healthy site also had higher magnesium concentrations than the bark at the declining site but concentrations in stem wood were similar. No clear calcium concentration differences in twig or stem bark and wood between the sites were found. Nitrogen concentrations in these components were similar at the two sites (Fig. 4; Table 1).

Large roots

Differences between sites in the magnesium concentration in large roots increased with depth in the soil, perhaps indicating that the organic layer at both sites released sufficient mangesium for the uptake there, but that not enough magnesium was available at greater depths at the declining site. This may be due to a slower release of nutrients from the organic layer and a more nutrient depleted mineral soil (Fig. 5; Table 1). Calcium concentrations in large roots of

trees in the healthy stand were generally higher than in roots from the declining stand and appeared to be highest in the lower organic horizon (Fig. 5; Table 1). Except for nitrogen concentration, no clear seasonal course in element concentrations were seen in large roots (Fig. 5; Table 1).

Fine roots

The trend of magnesium concentration in fine roots was similar to, but less clear than that in the large roots (Fig. 6; Table 1). Elements concentration in fine roots represent short term conditions in the soil that may vary strongly within a short time, while the large roots probably integrated the conditions over a longer period. In addition, concentrations in fine roots may be more affected by growth than large roots. This is supported by the observation that the magnesium concentration in the large roots did not change among the sampling times in contrast to the concentration in fine root. No differences in the magnesium concentrations in fine roots of healthy and declining trees were found at another site by Zöttl and Hüttl (1986). Their values were approximately twice those in this study.

Calcium concentrations in fine roots of trees in the healthy stand were higher than in roots from the declining stand and, similar to the large roots, appear to be highest in the lower organic horizon (Fig. 6; Table 1). There was no clear seasonal course. Values for the concentrations in the fine roots were comparable to those reported by Zöttl
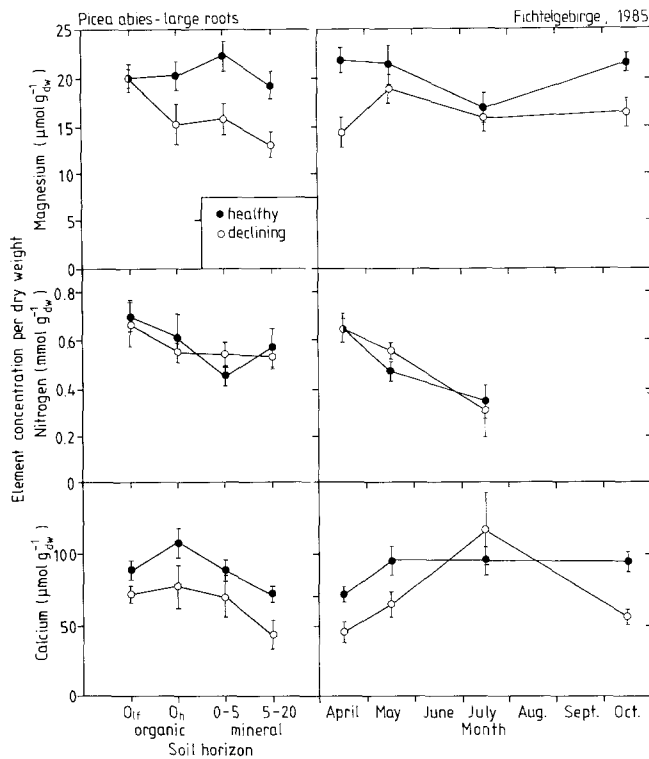
Fig. 5. Mean (± 1 s.e.) element concentrations in large roots (2–10 mm) from four soil horizons from the healthy and the declining sites (left) and the annual course of the mean concentration (right, n = 20 for most means)
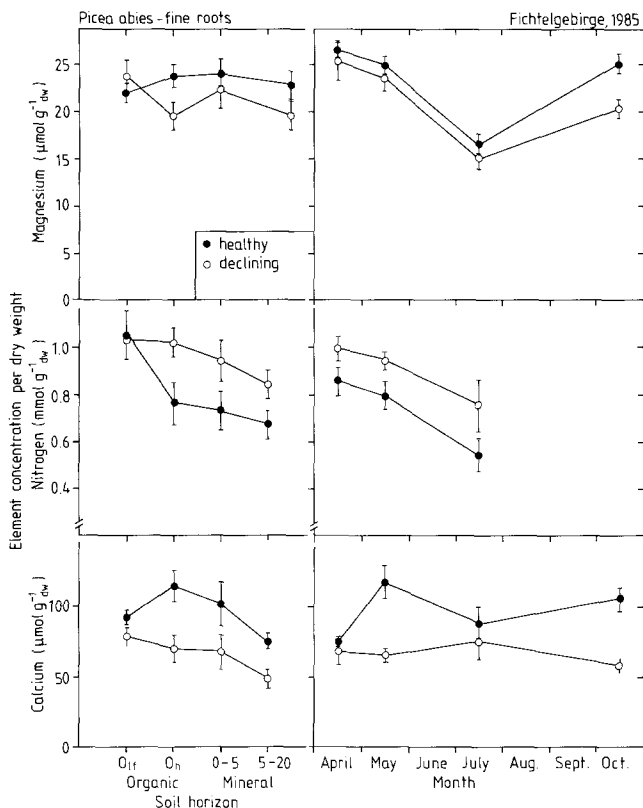
Fig. 6. Mean (± 1 s.e.) element concentrations in large roots (< 2 mm) from four soil horizons from the healthy and the declining sites (left) and the annual course of the mean concentration (right, n = 20 for most means)

and Hüttl (1986) who found no differences between declining and healthy trees.

Fine roots at the declining site appeared to have more nitrogen than roots at the healthy site, in the lower organic and upper mineral soil horizons (Fig. 6; Table 1). Nitrogen concentrations in fine roots in this study are somewhat higher than those from another study where no differences were found between healthy and declining trees (Zöttl and Hüttl 1986).

Potassium

Potassium concentrations in needles, on both a weight and an area basis, were affected differently by needle age at the two sites (Table 1; Apppendix 1). The concentration of potassium was higher in the younger needle age classes at the healthy site than at the declining site, but was similar in older needles. Site differences were not detectable when conversion to a leaf area basis was made. The seasonal trend remained significant regardless of the basis for evaluating the needle potassium. The trend reflects the withdrawal of potassium from mature needles to supply the requirements of the growing new ones, and the replenishment of potassium in mature needles once the growth is completed and supply from the roots exceeds the demand. The postassium concentrations in this study occupy the mid-range of reported values in other studies (Forschner and Wild 1987; Zöttl and Hüttl 1986; Rehfuess and Rodenkirchen 1984) which also found higher potassium concentrations in young needles than in older needles in healthy trees.

The concentration of potassium in twigs decreased with age similar to the needles. No site differences or seasonal course were found (Table 1; Appendix 1). In contrast, a decline in concentrations in all root types in all horizons was detected through the season until growth was terminated, after which concentration increased (Table 1; Appendix 1). Reported values for fine roots of declining trees in a stand in the Black Forest (Zöttl and Hüttl 1986) were higher than the potassium concentrations in the healthy stand in this study.

Manganese

The concentrations of manganese in the needles followed a similar trend to that of calcium, except that the declining site had higher concentrations than the healthy one (Table 1; Appendix 1). Manganese accumulated with needle age but, unlike calcium, not with twig age (Table 1; Appendix 1). Site differences were detected in all biomass components, including twigs and both their bark and wood, main stem, and roots of all classes (Table 1, Appendix 1).

Manganese concentrations in needles and roots of declining trees are similar to, or higher than the concentration found in healthy *P. abies* trees (Forschner and Wild 1987; Zöttl and Hüttl 1986; Rehfuess and Rodenkirchen 1984). The wide range in manganese concentrations in both needles and roots of trees at the declining site may indicate a larger variability in soil manganese compared with the healthy site (Wyttenbach et al. 1985).

Phosphorus

Phosphorus concentrations declined with needle and twig age but was more similar between twigs of the two age

classes at the end of the growing season than in April (Table 1; Appendix 1). Phosphorus content per leaf area was constant at the healthy site but increased with age at the declining site. The trend of phosphorus concentration with needle age and during the season resembles that of potassium and indicates retranslocation of phosphorus from older parts to meet the demand of the newly expanding tissues. The declining site had higher phosphorus concentrations than the healthy site in almost all plant parts (Table 1; Appendix 1).

The phosphorus concentrations in this study are within the range reported for needles in other studies (Forschner and Wild 1987; Zöttl and Hüttl 1986; Rehfuess and Rodenkirchen 1984) but those in fine roots are about half of published values (Zöttl and Hüttl 1986). In contrast to our results, phosphorus concentrations in needles in other investigations of declining trees were similar or lower than those of healthy trees (Rehfuess and Rodenkirchen 1984).

Aluminum

Aluminum concentrations increased with needle and branch age faster at the declining site than in the healthy one (Table 1; Appendix 1). The concentration also increased in roots with depth but was not different between the sites (Table 1; Appendix 1). The bark and wood of twigs in both age classes and of the stem had similar concentrations which

would indicate that surface contamination was not so high in these stands (Table 1; Appendix 1). The similarity of concentration in the younger needles and twigs from the two sites indicate that surface contamination was similar at both sites. Thus, it seems that more aluminum was transferred from the roots of trees at the declining site and slowly accumulated in the above ground parts over time. The values for needles in our study are comparable to, or lower than, aluminum concentrations reported in other studies (Forschner and Wild 1987; Zöttl and Hüttl 1986; Rehfuess and Rodenkirchen 1984).

Growth comparisons with needle element concentration were made with the data from April (Oren et al. 1988b) because the concentration in April represents the status at which the trees begin the new growing season. However, we think that it is important to investigate if such relationships would also emerge if data from other months were used. In Fig. 7a comparison between element concentrations in April to those in October is illustrated. For most elements, the correlations were very strong and indicated that the October data, for example, could be used in growth analyses with similar results to those obtained when using the April data (Oren et al. 1988b). To evaluate the relationship between element concentrations in soil solution and their concentrations in needles, a correlation between the October concentration in 3-year-old needles and soil solution was made. No needle nutrient levels, except for potassi-
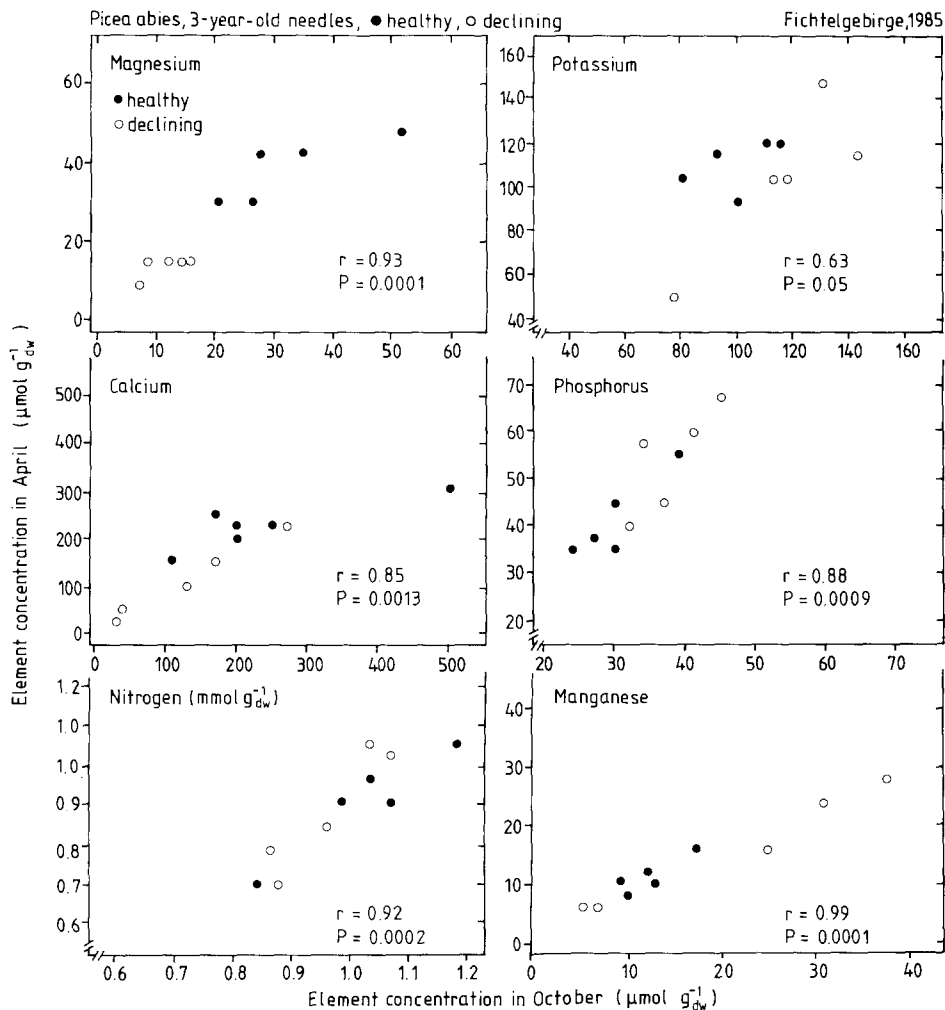

Fig. 7. Correlation between element concentrations in April and in October in needles from the ten plot at the healthy and the declining sites

um, were correlated to element concentrations in the soil solution (magnesium: $r = 0.57$, $P = 0.1084$, calcium: $r = 0.54$, $P = 0.1352$, ammonium: $r = 0.25$, $P = 0.5179$, nitrate: $r = 0.14$, $P = 0.7232$, potassium: $r = 0.83$, $P = 0.0053$, phosphate: $r = 0.39$, $P = 0.2997$), probably due to the large temporal variations in element concentrations in the soil solution or because of an inappropriate assumption that concentration in tissue and soil solution should be related.

Discussion

Element concentrations in soil solution did not seem to be related to the concentration in the trees on a plot level. However, site differences in tissue element concentrations were consistent with site differences in soil solution (Meyer et al. 1988). The supply rate of nutrients to trees in forest stands depends in part on the soil solution, but even more on the rate of of root expansion (Ingestad and Kähr 1985). The roots at the declining site were restricted from growing into the mineral horizon due to the unfavorable chemical environment there (Meyer et al. 1988) and were probably less effective in nutrient uptake.

The nutritional differences between the healthy and the declining sites in this study (Figs. 1–6) were distinct. Although these data can not provide an understanding of the decline mechanisms, they suggest, when combined with the results of the earlier publications in this series (see introduction) and with information on the mineral nutrition of *P. abies* (Ingestad 1959, 1979), that the decline is related an imbalance between the nitrogen and magnesium nutrition of the trees.

Trees that are thought to be declining due to a nutrient limitation at one site often have a higher concentration than apparently helathy trees at another site (e.g. compare magnesium concentrations in Tables 2 and 4 in Bosch et al. 1983). The absolute concentration of each nutrient may be less important than its concentration or, more importantly, its supply rate in relation to that of other nutrients. Therefore, to evaluate the results of this study, we turned to controlled studies with seedlings in which nutrient relationships were thoroughly investigated (Ingestad 1959, 1979).

Ingestad (1959, 1979) and Ingestad and Kähr (1985) have demonstrated that non-nutritional, growth-reducing stress reduces the uptake of all nutrients, including nitrogen, such that their concentrations in the plant match the growth rate of the plant. An imbalance between growth rate and nutrient uptake rate after a stress has been imposed or alleviated, resulting respectively in luxury or deficiency concentration during a non-steady state period following the perturbation, is quickly corrected as the plant adjusts the up-

take rate as necessary. If, on the other hand, the stress is imposed by reducing the nitrogen supply to the seedling to a rate which cannot support the potential growth rate, as determined by other growth factors, the growth rate would be reduced and the nitrogen concentration would recover, after a brief period of deficiency, to a level supported by the supply rate (Ingestad and Kähr 1985).

At a low nitrogen supply, concentrations of other elements in plant tissues may be higher than required for the growth rate as determined by the availability of nitrogen. However, with increasing supply of nitrogen to the plant, the demand for other elements also increase because each of them must be kept at, or above, a species-specific minimum proportion in relation to nitrogen (Ingestad 1979).

The only biomass component for which these proportions are reported are needles and fine roots (Ingestad 1959). Because a highly artificial medium was used in the seedling experiment (Ingestad 1959), roots developed there would be quite different from those in natural stands. We, therefore, chose to compare the concentration in the needles from that study to the concentration in our current-year needles.

The macro-elements concentrations which promote maximum growth rate in *P. abies* seedlings (Ingestad 1959), are presented in Table 2, along with the concentrations of these elements in the current-year needles from both our sites. (In later studies Ingestad (1979) and Ingestad and Kähr (1985) present somewhat different values which, however, present the concentration in the seedlings as a whole.) In brackets the molar ratio of each element in relations to the nitrogen in the same tissue is presented. The ratio of all the elements at the healthy site are near to, or higher than, the ratios required to maintain the maximum growth as determined by nitrogen. Thus, if growth at the healthy site is lower than the potential, according to non-nutritional factors, it is most likely reduced due to low supply of nitrogen.

The ratios of elements to nitrogen concentrations at the declining site clearly show that potassium and magnesium may be limiting to growth (Table 2). Given the nitrogen concentration in the foliage at that site, we calculated that the potassium concentration is 87 percent of that which would not limit growth (i.e. the relative value of K/N at the declining site to the optimal value, calculated from Ingestad (1959), see Table 2). However, at even lower (80 percent of optimal) concentration, Ingestad (1959) found that growth would be reduced by only 6 percent of the potential, as related to the nitrogen concentration. In comparison, magnesium limitation appears more severe than that of potassium, with only 56 percent (calculated as above for Mg/N) of the concentration that would permit growth to proceed at a rate determined by the nitrogen. At a somewhat

Table 2. Average nutrient concentrations (nitrogen in mmol g_{dw}^{-1}, other elements in μmol g_{dw}^{-1}) in current needles of seedlings growing at maximum rate (i.e. optimum concentrations, from Ingestad 1959), and of trees at the healthy and declining sites (see Appendix 1). Numbers in brackets are the molar ratios of each of the elements relative to nitrogen in the same tissue (× 100)

Source	Nitrogen μmol g^{-1}	Calcium μmol g^{-1}	Magnesium μmol g^{-1}	Potassium μmol g^{-1}	Phosphorus μmol g^{-1}
Ingestad (1959)	1.50 [100]	47.4 [3.2]	45.2 [3.0]	238 [15.9]	74.0 [4.9]
Healthy	0.90 [100]	77.0 [8.6]	29.5 [3.3]	187 [20.8]	51.9 [5.8]
Declining	1.05 [100]	54.0 [5.1]	17.6 [1.7]	145 [13.8]	57.8 [5.5]

Appendix 1. Mean annual concentration (±s.e.) of elements in various biomass components, and mean seasonal concentrations (±s.e.) of elements at each major category of biomass components in the healthy (Wülfersreuth) and the declining (Oberwarmensteinach) stands of *P. abies*. The number of replications are: needles $n=20$ (10 for 0-years-old, 15 for dead needles) by age, $n=25$ (0-year-old and dead needles not included) by season, twigs and stems $n=5$, roots $n=20$; each missing value (not determined) in the age means of any element for needles 1 to 5-years-old reduces the seasonal n of the respective element by five

Needles:	Aluminum (mol g⁻¹ dw) healthy	Aluminum decline	Calcium (mol g⁻¹ dw) healthy	Calcium decline	Magnesium (mol g⁻¹ dw) healthy	Magnesium decline	Manganese (mol g⁻¹ dw) healthy	Manganese decline	Nitrogen (mmol g⁻¹ dw) healthy	Nitrogen decline	Phosphorus (mol g⁻¹ dw) healthy	Phosphorus decline	Potassium (mol g⁻¹ dw) healthy	Potassium decline	Specific leaf weight (g m⁻²) healthy	Specific leaf weight decline
Age																
0-yr	1.6±0.13	1.8±0.09	77±9	54±14	29.5±1.2	17.6±1.9	6.1±0.6	9.1±1.7	0.90±0.06	1.05±0.10	51.9±3.1	57.8±3.6	187±6	145±8	136±6	152±7
1-yr	2.7±0.25	3.0±0.25	118±8	73±11	33.8±0.9	15.8±1.2	8.0±0.5	12.3±1.7	1.00±0.04	0.99±0.05	46.6±3.1	54.5±3.1	165±7	128±6	185±8	195±9
2-yr	3.0±0.19	5.2±0.63	164±10	104±16	32.4±1.2	12.6±0.8	9.0±0.5	16.1±1.9	0.98±0.03	0.89±0.03	38.3±2.0	48.8±3.0	109±5	103±6	198±8	211±9
3-yr	3.8±0.40	5.4±0.27	215±19	110±16	33.8±1.9	12.6±0.6	10.9±0.6	17.4±2.1	0.92±0.03	0.90±0.03	35.6±9.2	46.4±3.0	98±4	97±6	215±9	233±10
4-yr	4.1±0.26	6.5±0.33	264±16	123±18	37.8±2.0	14.2±0.7	12.7±0.5	19.3±2.3	0.88±0.02	0.84±0.02	36.4±1.8	48.7±4.3	106±5	110±8	241±11	242±11
5-yr	4.0±0.37	6.1±0.37	290±21	142±21	38.4±2.1	16.3±0.4	12.6±0.6	21.6±2.9	0.83±0.02	0.78±0.02	34.1±1.9	51.0±5.0	108±5	110±8	257±11	169±15
dead	8.7±1.23	8.5±0.90	278±24	127±23	28.9±1.1	15.0±1.1	12.2±0.7	21.9±6.2	0.62±0.03	0.72±0.02	31.3±1.1	48.5±4.1	62±5	55±5	236±12	210±10
Season																
April	4.8±0.96	5.3±0.30	209±16	108±14	38.3±1.4	16.5±0.7	10.8±0.7	16.6±2.0	0.88±0.02	0.86±0.03	44.7±1.9	57.6±2.6	132±7	118±8	234±11	248±15
May	3.1±0.16	5.5±0.54	182±19	95±13	34.7±1.7	14.1±0.7	9.2±0.5	15.1±1.8	0.94±0.03	0.81±0.03	—	—	113±5	100±5	224±12	223±8
July	3.5±0.27	5.6±0.42	211±14	108±14	34.6±1.3	13.8±0.7	11.2±0.8	17.9±2.2	0.83±0.02	0.87±0.03	36.9±1.5	51.9±3.0	99±5	92±5	216±7	240±9
October	3.3±0.18	4.5±0.89	241±23	131±20	33.4±1.6	13.3±0.8	11.4±0.5	19.7±2.3	1.03±0.02	0.97±0.03	33.0±1.5	39.4±1.4	123±6	129±5	204±9	206±9
Twig																
1-yr-old																
April	6.4±0.58	6.0±2.03	85±7	69±8	40.2±3.3	25.1±0.7	5.7±1.2	8.7±2.3	0.76±0.07	0.73±0.05	59.7±5.2	55.2±3.2	187±12	175±11		
May	5.4±0.73	5.1±0.75	75±7	73±22	39.1±4.1	20.1±2.0	4.7±0.6	10.3±4.1	0.91±0.07	0.76±0.06	—	—	178±22	194±41		
July	6.6±0.57	9.0±1.63	65±9	52±6	31.1±3.1	17.1±1.6	5.0±1.2	10.0±2.5	0.45±0.08	0.46±0.06	39.1±6.2	47.7±5.4	165±10	177±12		
October	5.7±0.33	8.5±1.68	79±5	64±11	28.4±3.7	15.0±3.2	3.8±0.2	8.6±2.0	0.44±0.07	0.49±0.05	30.0±0.6	41.4±3.2	154±7	156±9		
bark	7.3±0.65	9.5±1.60	109±12	97±16	29.6±4.5	17.5±1.9	6.0±2.1	7.6±0.9	0.61±0.06	0.69±0.06	32.6±3.4	42.9±2.5	127±24	146±15		
wood	1.6±0.65	1.8±0.33	50±4	32±2	12.2±2.8	6.8±1.1	2.9±1.1	6.1±1.6	0.41±0.11	0.31±0.03	18.6±4.9	16.0±2.4	66±16	49±3		
3-yr-old																
April	7.0±0.66	6.3±0.95	106±5	78±7	27.3±3.7	16.6±1.1	5.4±1.0	8.6±1.7	0.48±0.04	0.53±0.04	33.0±4.5	38.8±2.6	86±8	98±10		
May	5.8±0.50	5.4±1.36	101±8	68±7	29.4±1.9	16.1±0.9	4.9±0.6	8.4±1.6	0.54±0.04	0.48±0.03	—	—	107±8	95±5		
July	10.3±1.54	16.7±3.44	97±10	84±6	26.8±4.1	15.2±1.2	5.4±0.6	9.6±1.9	0.38±0.04	0.45±0.07	27.2±3.0	34.6±3.0	81±5	88±8		
October	8.5±0.63	18.0±4.22	107±4	118±25	24.1±3.3	15.8±1.6	4.1±0.4	9.5±1.7	0.34±0.03	0.42±0.03	23.9±2.4	28.1±2.0	64±6	94±5		
bark	11.6±0.52	12.1±2.44	186±16	130±15	33.7±1.6	22.4±2.1	6.3±0.7	10.3±1.4	0.71±0.05	0.65±0.05	34.3±1.4	34.2±0.5	97±6	94±7		
wood	1.4±0.45	2.1±0.46	46±10	(78)±27	10.8±2.6	9.4±1.7	2.7±0.8	4.6±0.6	0.22±0.05	0.26±0.03	13.3±3.5	15.8±1.3	31±6	43±6		
Stem																
bark	3.7±0.36	3.0±0.51	190±58	201±24	33.9±1.4	25.0±3.5	7.0±0.7	15.1±4.6	0.39±0.03	0.47±0.05	20.6±3.6	31.5±2.5	73±8	81±11		
wood	1.3±0.08	1.3±0.27	33±2	30±2	7.1±0.6	6.4±0.5	1.3±0.2	3.9±1.6	0.15±0.01	0.14±0.01	11.7±1.0	11.6±0.3	28±2	34±2		
Large roots horizon																
Of	25±5	16±3	87±7	71±6	20.0±1.4	20.0±1.0	5.1±0.8	7.3±0.8	0.50±0.06	0.67±0.09	25.8±1.8	31.8±3.0	47±5	44±4		
Oh	33±7	35±8	107±10	77±16	20.2±1.4	15.2±1.9	2.4±0.2	5.3±0.7	0.61±0.10	0.55±0.04	20.1±1.9	32.4±3.7	40±5	42±6		
0-5	62±20	58±14	89±7	70±15	22.3±1.6	15.8±1.6	2.2±0.4	6.0±1.0	0.46±0.04	0.54±0.05	24.1±1.9	31.2±5.2	40±4	48±6		
5-20	147±36	146±36	72±5	43±10	19.1±1.4	13.0±1.4	1.9±0.2	5.0±1.1	0.58±0.08	0.53±0.05	22.7±1.1	27.0±2.5	40±6	36±4		
Season																
April	128±33	79±17	73±5	47±8	21.7±1.1	14.3±1.5	2.8±0.3	5.5±1.0	0.65±0.06	0.64±0.05	—	—	52±4	40±4		
May	38±11	73±29	97±10	64±9	21.4±2.0	18.7±1.7	2.5±0.3	6.3±0.9	0.48±0.04	0.55±0.03	23.9±1.4	26.3±2.1	37±2	43±4		
July	72±8	24±8	92±10	118±25	16.7±1.5	15.8±1.4	3.4±0.9	5.6±1.1	0.35±0.07	0.35±0.11	22.2±1.1	34.2±2.5	16±3	26±5		
October	35±8	41±14	96±7	57±5	21.4±0.9	16.4±1.5	2.6±0.3	6.5±0.9	—	—	—	—	58±2	17±4		
Fine roots horizon																
Of	181±28	159±25	75±4	70±10	22.2±1.0	23.7±1.8	4.4±0.3	8.7±1.1	1.05±0.10	1.03±0.04	33.5±2.3	46.4±3.0	36±4	40±4		
Oh	87±11	110±16	118±14	65±6	23.8±1.3	19.6±1.6	2.6±0.6	5.5±0.7	0.76±0.09	1.02±0.06	30.4±1.8	42.9±1.7	38±5	41±9		
0-5	193±37	144±23	88±12	75±13	23.9±1.4	22.3±2.0	1.6±0.1	6.2±0.9	0.73±0.08	0.94±0.09	28.3±2.6	45.0±2.9	50±7	54±5		
5-20	106±19	108±18	106±9	59±4	22.8±1.5	19.6±1.4	2.4±0.2	10.1±1.2	0.68±0.06	0.84±0.06	27.5±1.7	47.1±2.2	46±5	53±6		
Season																
April					26.5±0.7	25.4±1.9	3.2±0.3	7.7±1.2	0.86±0.06	0.99±0.05	—	—	63±5	58±6		
May					24.7±1.1	23.6±1.5	2.7±0.2	6.7±0.8	0.79±0.06	0.95±0.04	27.6±1.6	41.8±1.8	35±8	43±3		
July					16.5±1.0	14.9±1.1	2.3±0.3	8.0±1.5	0.55±0.07	0.75±0.11	32.6±1.1	48.3±1.4	15±4	21±3		
October					24.9±1.0	20.3±1.0	2.9±0.4	8.0±0.9	—	—	—	—	55±3	60±2		

less limiting magnesium concentration (63 percent of non-limiting concentration) data from Ingestad (1959) show a 30 percent growth reduction. This may explain the 35 percent lower growth at the declining site compared to the healthy site. In these calculations we assumed that maximum growth occurs at a constant ratio of each element to nitrogen, regardless of the absolute level of nitrogen. This assumption seems valid based on controlled nutrition studies (Ingestad 1979, 1981).

As nitrogen input in acid rain continues to increase nitrogen supply above that in unpolluted areas and the supply of base cations is reduced due to soil leaching, the concentration ratio of magnesium to nitrogen may decrease, even in needles at the healthy site. The safety margin in the ratio at that site should permit the magnesium concentration in the needles to decrease by 10 percent before a less than optimum ratio occurs, assuming no change in needle nitrogen concentration. Should, however, the nitrogen concentration in needles increase by 20 percent, to a rather typical for *P. abies*, the ratio would drop to 90 percent of optimal without assuming a reduction in the supply of magnesium. It is clear, therefore, that a gradual decline in the ratio, associated with growth reduction at both sites, is likely to result from a continuation of current air pollution effects.

There are, however, some differences between trees and seedlings that should suggest some caution in extrapolation from seedlings to mature trees. Care must be used, for example, when growth data are extrapolated from seedlings to stands. The healthy stand in this study produced wood at a high rate, as would be expected based on its high site quality (Oren et al. 1988a). However, if data from the seedlings study were to be extrapolated to the mature stand, growth should increase by more than 10 percent as the concentration of nitrogen concentration increases to a level where the ratio of magnesium to nitrogen is near optimal. Even at that level, nitrogen concentration in needles would be only about two thirds of the optimum, and growth would be a similar proportion of the maximum. We believe that the growth rate of our healthy stand is near maximum and that any extrapolation from the seedlings studies would result in unrealistically high values. Nevertheless, the concept is still useful in the interpretation of elemental composition of foliage in relation to growth. Indeed, the general concepts of nutrition and relative supply rate of elements in relations to nitrogen which were generated from such experiments have been successfully applied in field experiments with mature trees (Ingestad 1982, 1987; Linder and Ingestad 1977; Linder and Rook 1984; Linder 1987).

Some processes, however, should be much more important for the proper functioning of mature trees in contrast to seedlings. First, highly mobile elements concentrate in the phloem and may be supplied to meet peak demands from that circulating pool which is large in mature trees but may not be so important in seedlings where the phloem pool is small relative to foliage mass. In addition, the seasonal trend in magnesium, potassium, phosphorus and, to a lesser extent, nitrogen (Table 1) indicates that retranslocation from mature tissues plays an important role in supplying the demand by newly expanding tissues (Nambiar and Fife 1987). The difference in seasonal trends in concentrations of these elements between the sites can be equated with differences in retranslocation and recharge of mature tissues because all biomass components and growth, except

for stem wood and bark biomass and stem growth, were similar at the two sites (Oren et al. 1988a).

The wood of both the main stem and twigs had a similar concentration of magnesium in the two stands, which suggests that a minimum amount of magnesium must be incorporated into the wood and that no excess magnesium is deposited there. The higher concentration of magnesium in the bark of the trees in healthy stand means that the supply of magnesium for wood production was probably better than at the declining site, resulting in a higher stem wood growth.

In the next part of this series (Oren et al. 1988b), we will provide evidance for retranslocation of elements from mature tissues as related to the supply of cations in the soil such that the production of canopy components at the declining site was not curtailed, while wood production was greatly reduced.

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