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

VII. Nutrient relations and growth

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Summary. A declining, closed-canopy *Picea abies* (L.) Karst. stand produced as much crown biomass as a healthy stand, although some trees were chlorotic due to magnesium deficiency. The production of wood per unit of leaf area in both stands was related to the foliar magnesium concentration. Although leaf area index and climate were similar at both sites, stemwood production was 35% lower in the declining than in the healthy stand. Nutritional disharmony, rather than a deficiency in a single element, was identified as the mechanism for reduced tree vigor. The role of nutrient stress in forest decline was detected by partitioning the season into three periods reflecting different phenological stages: a canopy growth period in spring, a stem growth period in summer, and a recharge period during the non-growing season. Needle growth was associated with nitrogen supply. Most of the magnesium supply required to meet the demand for foliage growth was retranslocated from mature needles. Magnesium retranslocation was related to concentration of nitrogen and magnesium in those needles before bud break. Retranslocation from mature needles during the phase of canopy production resulted in chlorosis in initially green needles if the magnesium concentration before bud break was low. Nitrogen concentration in 0-year-old needles generally remained constant with increasing supply, indicating that foliage growth was restricted by the supply of nitrogen. In contrast, magnesium concentration generally increased with supply, indicating that magnesium supply for needle growth was sufficient. Much of the magnesium required for wood production was taken up from the soil because stored magnesium was largely used for canopy growth. Uptake at the declining site was probably limited because of restricted root expansion and lower soil magnesium compared to the healthy site. For this reason only wood growth was reduced at the declining site. Because the recharging of magnesium during the non-growing period is dependent on uptake from the soil, it was more limited at the declining than at the healthy stand. However, as nitrogen uptake from the atmosphere may account for an appreciable proportion of the total uptake, and as its supply in the soil at both sites was similar, an unbalanced recharging of nitrogen and magnesium may have occurred at the declining site. If mature needles are unable to recharge with magnesium in proportion to the uptake of nitrogen, chlorosis is likely to occur during the next canopy growth period.

Key words: Forest decline – Spruce (*Picea abies*) – Nutrients – Growth

The cause of the apparent decline in some *Picea abies* (L.) Karst. stands in the Fichtelgebirge (NE Bavaria, FRG) was investigated. Some stands contained trees with a range of chlorosis and needle loss, while other stands appeared healthy (Oren et al. 1988a). One stand from each of these two types was selected for detailed study. After the exclusion of all possible causes for the decline symptoms and for the 35% lower stemwood growth at the declining site (Zimmermann et al. 1988; Werk et al. 1988; Meyer et al. 1988; Osonubi et al. 1988; Oren et al. 1988a), the only reasonable explanation remaining was nutrient stress (Oren et al. 1988b). Zech and Popp (1983) reported that the chlorosis in this area was associated with low magnesium concentration. Zöttl and Hüttl (1986) had found a similar association in the Black Forest in the southwest region of the Federal Republic of Germany.

Higher acidic deposition at the declining site, combined with higher precipitation and parent material somewhat poorer in calcium and magnesium than that at the healthy site (Hantschel 1987), have probably resulted in lower nutrient availability. The ability of the root system to exploit the mineral soil for nutrients is also impaired (Meyer et al. 1988). Low calcium-to-aluminum ratios in the mineral horizon of plots at that site was related to a reduction in root growth into deeper horizon and may have also been the cause of impaired mycorrhizal development (Meyer et al. 1988). As a result, calcium and magnesium concentrations in most tissues, including green trees, in the declining stand were lower than in tissues of trees in the healthy stand (Oren et al. 1989).

Another possible cause of the low cation concentration in needles at the declining site could be a high leaching rate of elements from the foliage, due to higher proton input than at the healthy site. However, this is unlikely because a lower concentration of magnesium was measured in the xylem sap of trees at declining site compared with those at the healthy site. This indicates that magnesium uptake, rather than canopy leaching, is the cause of lower
growth at the declining site (Osonubi et al. 1988). This is also supported by the observation that leaching was higher at the healthy site (Hantschel 1987), and that leaching could only account for a very small reduction in element concentrations in needles (Mengel et al. 1988).

Although the reduction in growth (Oren et al. 1988a) appeared to be a direct result of low soil magnesium availability, two questions remained. First, if magnesium was limiting to growth, why was growth not correspondingly reduced such that demand would not exceed supply, which would prevent needle chlorosis and loss (Schulze et al. 1988)? Second, why was stemwood production reduced while needle production still remained unaffected by the magnesium deficiency (Oren et al. 1988a)?

To address these questions, we assembled three concepts of plant nutrition into a general synthesis. The first concept is based on the information reported by Chapin and Kedrowski (1983), who found that trees normally retranslocated elements during the early part of the growing season to support the growth of new tissues, regardless of how nutrient-rich a site is, together with the results of Nambari and Fife (1987), who showed that because growth rate increases with nutrient availability, retranslocation to meet plant demand is higher at nutrient-rich sites. The second concept, based on Timmer and Morrow (1984), uses the changes in needle weight and element concentration, following an increase in nutrient availability, to assess which, if any, element was limiting stand growth. The third concept, based on Ingestad (1982, 1987), illustrates how growth rate and nutrient deficiency are related to the supply rate of elements in optimum proportions to each other.

Material and methods

Two *P. abies* stands located 15 km apart, near the villages of Oberwarthensteinach (the declining stand) and Willersreuth (the healthy stand) were chosen for the study. The sites have similar climate and support stands of similar structure, but the soil at the declining site is poorer in magnesium and calcium (Meyer et al. 1988). Precipitation was 20% higher at the declining site, and annual proton input was 60% higher than that at the healthy site (0.094 vs. 0.158 mol m$^{-2}$), due to a greater sulphate concentration in the precipitation (Hantschel 1987; Oren et al. 1988a).

In March, 1985, five, 80-m$^2$ plots were established in each of the two stands, and a single, apparently healthy (as indicated by a green crown), co-dominant tree was chosen in each plot. The plots were used to estimate biomass and growth of various plant components, amount of litterfall, and nutrient concentration in the litter, roots and soil solution (Oren et al. 1988a, b; Meyer et al. 1988). The plot measurements, including micro-climate, litter-fall, and soil chemical and root characteristics, represented the average conditions of all trees in the plots which, at the declining site, contained trees at various stages of decline. Above-ground element concentrations and needle characteristics represented the conditions of an apparently healthy tree in all the plots.

Samples were taken in April (when the soil was still frozen), in May, (at bud break), in July, (after needles growth was completed), and in October, (at the end of the growing season). More details on sampling procedure, sample preparation, and nutrients analyses of above and below-ground biomass components, are presented in Oren et al. (1988a, b) and Meyer et al. (1988).

Calculations of nutrient pools and budgets

Nutrient pools of each of the five macro-elements in each biomass component in April were calculated by multiplying the concentrations in each component (see Appendix 1, Oren et al. (1988b)) by the biomass of that component (see Table 2, Oren et al. (1988a)). The pools in the foliage were calculated multiplying the content per unit of leaf area by the leaf area. Needle production was calculated as the average between the estimate based on equations and the estimate based on needle fall, assuming steady state in leaf area index. If no significant difference between sites ($P<0.05$) was found in the biomass of a component (see Table 2, Oren et al. 1988a), or the nutrient content (needles) or concentrations (other biomass components, see Table 1, Oren et al. 1988b), a mean value was used. It was assumed that 34.5 percent of the twigs are one and two-year-old (Oren, unpublished data), for which the concentration in one-year-old twigs was used and that the rest of the twigs are three-year-old and older, for which the concentration in three-year-old foliage was used. Element concentration in branches was assumed to be similar to that in three-year-old twigs.

We also calculated the seasonal demands and supply of nitrogen and magnesium for three periods: (1) the period beginning just before the growing season (April 10) until needle and twig extension was completed (July 20), (2) the period ending at the cessation of all cambial activity, when stemwood growth is completed (October 25), (3) the period until the beginning of the next growing period. These times represent meaningful phenological stages of *P. abies* in this study area.

The processes of seasonal retranslocation and recharge and of annual accumulation of elements in mature tissues were calculated only for components that had significant seasonal trends, or age-related changes in concentrations, respectively ($P<0.05$, see Table 1 in Oren et al. 1988b). These processes were calculated from the differences in concentrations between the beginning and the end of each period (see Appendix 1, Oren et al. 1988b). The recharge of magnesium and nitrogen in all mature biomass components participating in retranslocation was assumed to reach the same concentration as that in the previous April. Retrieval of nutrients from needles before shedding was calculated as the difference between the concentration in needle litter and the mean annual concentration in the five-year-old needles.

Our study was not designed to obtain an accurate estimate of root production and our estimation was extremely low (Oren et al. 1988a). Therefore, an estimate (700 g m$^{-2}$) of fine root production was used. The estimate was derived from a detailed root study in a stand with similar characteristics, as indicated by root biomass and needle-fall data (Van Praag et al. 1988). Because no seasonal trend in root production was observed in this study, we divided the annual estimate evenly between the first two periods. The nutrient demand for fine root growth was calculated by averaging the nutrient concentration values in fine roots over all horizons during each period. We did not attempt to calculate the requirements for the production of large roots with diameter greater than 5 mm.