

Do admixed broadleaves improve foliar nutrient status of conifer tree crops?

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Abstract

We investigated three Douglas fir–red alder stands in Oregon, USA, and five Norway spruce–European beech stands in Bavaria, Germany, to test the hypothesis that admixtures of broadleaved trees improve nutritional status of conifers. At each site needle samples from 20 to 30 conifer trees with varying proportions of broadleaves adjacent to the sample trees were taken and analysed for needle mass and the macronutrients N, P, K, Ca and Mg. The neighbourhood of each tree was described by the proportion of deciduous basal area within an 8 m circle. Ordination methods (principal component analysis; redundancy analysis) were used to test the dependency of the multivariate nutritional pattern in conifers on deciduous neighbours and rank correlation and regression were used to analyse bivariate relationships between tree species composition and descriptors of needle status. The statistical analyses yielded no evidence that deciduous admixtures improve foliar nutrition of conifers. Alongside with other empirical studies this shows that beneficial effects of broadleaf admixtures on conifer nutrition are less common than postulated. Future research investigating the whole causal path relevant for tree nutrition and growth is necessary to improve our knowledge in the complex field of nutrition of mixed species forests.

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1. Introduction

Tree species differ substantially in their effects on nutrient inputs, litterfall, soil nutrient supply and rooting patterns (see overviews by Vogt et al., 1996; Rhoades, 1997; Binkley and Giardina, 1998; Rothe et al., 2001). Interactions between species resulting

from such features might be important for tree nutrition, and ultimately for understanding the role of diversity in forest ecosystems (Tilman, 1999; Xiong and Nilsson, 1999; Nilsson et al., 1999). It has been postulated repeatedly that plants growing in mixed communities should take advantage of reduced competition for nutrients due to a more effective resource utilisation and/or that one species may facilitate nutrient uptake of another (Vandermeer, 1989; Cannell et al., 1992; Olsthoorn et al., 1999). Despite these theoretical considerations empirical studies addressing nutritional interactions in mixed-species forest are comparably scarce. Reviewing the empirical evidence, Rothe and

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Binkley (2001) found that linear patterns were most common, with mixtures intermediate in nutritional status between monocultures. In several mixed systems, usually involving nitrogen-fixing species synergistic interactions were demonstrated. On the other hand even antagonistic effects have been reported, indicating that the available evidence is far too inconsistent to support generalisations. Interestingly, most studies dealt with nutritional processes rather than directly investigating the nutritional status of trees.

The present study addresses tree nutrition in two mixed forest systems of great silvicultural importance. We investigated effects of admixed European beech (*Fagus sylvatica* L.) on foliar nutrient status of Norway spruce (*Picea abies* [L.] Karst.) and of red alder (*Alnus rubra* Bong.) on Douglas fir (*Pseudotsuga menziesii* [Mirbel] Franco) across a typical range of soil types. We hypothesised that admixtures of broadleaved trees should improve nutritional status of the conifers and expected these effects to be more pronounced on less fertile soil types. In particular, we anticipated positive associations between broadleaf proportion and the foliar levels of the macronutrient elements N, P, K, Ca and Mg.

2. Material and methods

2.1. Sites

We investigated three Douglas fir–red alder stands in Oregon (USA) and five spruce–beech stands in Bavaria, Germany (Table 1). The Oregon plots are part of existing silvicultural experiments in young Douglas fir–red alder plantations, that were originally designed to cover sites with high, intermediate and low fertility. However, performance of alder at low fertility sites was so poor, that it was largely overgrown by Douglas fir, leaving only high and intermediate fertility sites to be included in this investigation. In Bavaria, we selected middle-aged, managed spruce–beech stands, in which spruce had usually been planted, while beech had often regenerated naturally. The sites were selected to include soil types ranging from extremely acid to calcareous, thus representing the whole range of soil base status, on which mixed forests of spruce and beech typically co-occur.

2.2. Sampling and analysis

We sampled Douglas fir needles in June 1999 using a shotgun (Waldport) or a pruner (Andrews, Cascade Head). Needle samples at the German sites were taken after felling spruce trees between November 1999 and January 2000. First year needles (i.e. 1998 for Douglas fir and 1999 for spruce) and third year needles (except Andrews and Cascade Head site) needles were taken from branches, that had developed in full sunlight, from the fifth to seventh whorl where possible. Needles were dried to constant mass at 45 °C. After measuring the 100 needle mass, samples were ground. Total N was measured by dry combustion (LECO CHN—analyser 1000) and P, K, Ca and Mg were measured after digestion in HNO₃ (1 ml conc. HNO₃/100 mg needles) using ICP (Perkin-Elmer Optima 3000). Nutrient contents for 100 needles were calculated by multiplication of nutrient concentrations and 100 needle mass.

2.3. Experimental design and statistics

We used a neighbourhood approach (Kelty and Cameron, 1995; Rothe, 1997) to relate foliar nutrients of a sample tree to tree species composition in its immediate neighbourhood. At each site we selected 20–30 conifer trees with varying proportions of beech or alder adjacent to the sample trees. Five trees at each site were selected in order to represent a pure stand situation, i.e. there were no other species within at least 30 m distance. At each site all sample trees were spread within an area of 1–2 ha. The trees representing the pure stand situation were taken from at least two different edges of the mixed stands in order to avoid a priori site effects. We measured DBH of all trees located within an 8 m radius from each sampling tree and calculated the proportion of deciduous basal area within the 8 m circle according to the following equation:

$$\% \text{deciduous} = \frac{\sum \text{dbh}_{\text{dec}}}{\sum \text{dbh}_{\text{con}} + \sum \text{dbh}_{\text{dec}}} \times 100$$

In addition tree species composition in the neighbourhood of each sampling tree was estimated by visual assessment of the horizontal cover by broadleaved tree crowns.

Both ordination and regression methods were used to test the null hypothesis: “The proportion of

Table 1
Characterisation of sites

Tree species	Site	Stand age	Location	Altitude a.s.l. (m)	Mean annual precipitation (mm)/ temperature (°C)	Bedrock	Soil type (FAO)	Soil fertility
Douglas fir–red alder	Andrews (forest)	12	Oregon, Cascade range, 122°13'W, 44°14'N	700	2280/9.3	Andesite	(Silty loam)	Medium
	Cascade Head	13	Oregon, Coast range, 124°00'W, 45°03'N	330	2500/13.3	Basalt	(Silty loam)	High
	Waldport	28	Oregon, Coast range, 123°55'W, 44°27'N	100	2200/14.0	Sandstone	Andic cambisol (loamy sand)	High
Norway spruce–European Beech	Eichstätt	65	Central Bavaria, 11°04'E, 48°49'N	580	800/7.0	Limestone	Stagnic luvisol (loam)	High
	Flossenbürg1	48	Northern Bavaria, 12°22'E, 49°45'N	620	750/6.5	Granite	Dystric cambisol (sandy loam)	Medium–low
	Flossenbürg2	42	Northern Bavaria, 12°23'E, 49°44'N	710	750/6.5	gneiss	Cambisol (sandy loam)	Medium
	Lohr	65	Northern Bavaria, 9°32'E, 50°02'N	450	700/7.5	Sandstone	Dystric cambisol (loamy sand)	Medium–low
	Schongau	70	Southern Bavaria, 10°44'E, 47°53'N	760	1200/7.0	Fluvioglacial sediments	Luvisol (loam)	High

deciduous admixtures does not influence foliar nutrient levels of conifers”.

Ordination was used to test the dependency of the total nutritional pattern in conifers on deciduous neighbours. The objectives were to summarise the multivariate pattern of conifer nutrition across sites (exploration) and to extract and statistically test the nutrition gradients attributable to deciduous neighbours, while avoiding the problems of multiple testing. The two datasets for Douglas fir–red alder (Oregon) and spruce–beech (Bavaria) were analysed separately. Each dataset had the proportion of broadleaved trees and site location as explaining variables and descriptors of needle status (needle mass, C, N, Ca, Mg, K, P) as dependent variable matrices. In the Bavarian dataset we also included third year needle attributes, thus doubling the number of variables in the analysis. Nutritional variables were standardised across each dataset to mean 0 and standard deviation 1. Using principal component analysis (PCA, CANOCO for Windows 4, Ter Braak and Milauer[®], 1998) trees were ordered in few dimensions (linear combinations of individual variables) according to their nutritional status. PCA also allowed a post hoc assessment of unconstrained gradients by correlations with location and the proportion of broadleaved species. Relationships between nutrition and broadleaf proportion were

tested by the constrained ordination method of partial redundancy analysis (RDA, Ter Braak and Milauer[®], 1998; Legendre and Legendre, 1998). We removed variation attributable to sites (covariable matrix of dummies coding location) and analysed the residual pattern of nutritional attributes (dependent matrix) for gradients attributable to the proportion of neighbouring broadleaves. Significance of the gradients was assessed non-parametrically by random permutations (Monte Carlo test for a design with three or five blocks (location), Ter Braak and Milauer[®], 1998).

We calculated Spearman's rank correlations to assess the bivariate relationships between broadleaf proportion and individual attributes of nutritional status (non-parametric statistics module, StatSoft, 1984–2000).

3. Results

Comparison of foliar nutrient concentrations of the Bavarian Norway spruce trees in monoculture situations (Table 2) to standard nutrient levels (Bergmann, 1993) indicated good nutrition across all five sites. Only K concentrations at the Eichstätt, Lohr and Schongau site as well as Mg at the Lohr site were in the range of light deficiency.

Table 2
Foliar nutrient concentrations of conifers in the monocultures

Tree species	Site	Needle age	Needle mass (g per 100 needles)	N (mg g ⁻¹)	P (mg g ⁻¹)	K (mg g ⁻¹)	Ca (mg g ⁻¹)	Mg (mg g ⁻¹)	
Spruce	Eichstätt	First year	0.7	14.5	1.4	4.4	6.9	1.1	
		Third year	0.7	12.8	0.9	3.0	15.6	0.8	
	FB gneiss	First year	0.5	14.9	1.5	6.5	2.2	1.1	
		Third year	0.6	14.5	1.0	4.5	2.4	0.5	
	FB granite	First year	0.4	15.1	1.5	5.3	3.9	1.1	
		Third year	0.6	14.7	1.3	4.9	5.3	0.5	
	Lohr	First year	0.5	14.9	1.4	4.3	4.2	0.8	
		Third year	0.5	12.8	1.1	3.6	4.9	0.3	
	Schongau	First year	0.5	15.5	1.7	4.2	4.2	1.5	
		Third year	0.6	12.5	1.2	3.8	5.3	0.7	
	Douglas fir	Andrews	First year	0.8	10.3	2.8	6.6	2.8	0.6
			Third year	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Cascade Head		First year	0.6	13.4	1.1	4.3	1.3	0.9	
		Third year	n.d. ^a	n.d.	n.d.	n.d.	n.d.	n.d.	
Waldport		First year	0.5	12.5	1.1	5.0	1.7	1.0	
		Third year	0.4	13.1	1.1	4.2	1.6	1.1	

^a Not determined.

Table 3
Principal components analyses of conifer nutritional status and post hoc interpretation of axes

PCA-axes	Norway spruce (Bavaria)				Douglas fir (Oregon)			
	1	2	3	4	1	2	3	4
Eigenvalues	0.244	0.187	0.139	0.116	0.863	0.605	0.474	0.181
Variance in nutrition (cumulative) (%)	24.4	43.1	57.0	68.6	42.1	59.5	74.0	84.5
Overall environment correlations	0.820	0.665	0.659	0.670	0.863	0.605	0.474	0.181
Correlation with %broadleaves	-0.086	0.069	0.027	-0.155	0.054	0.132	-0.107	-0.157

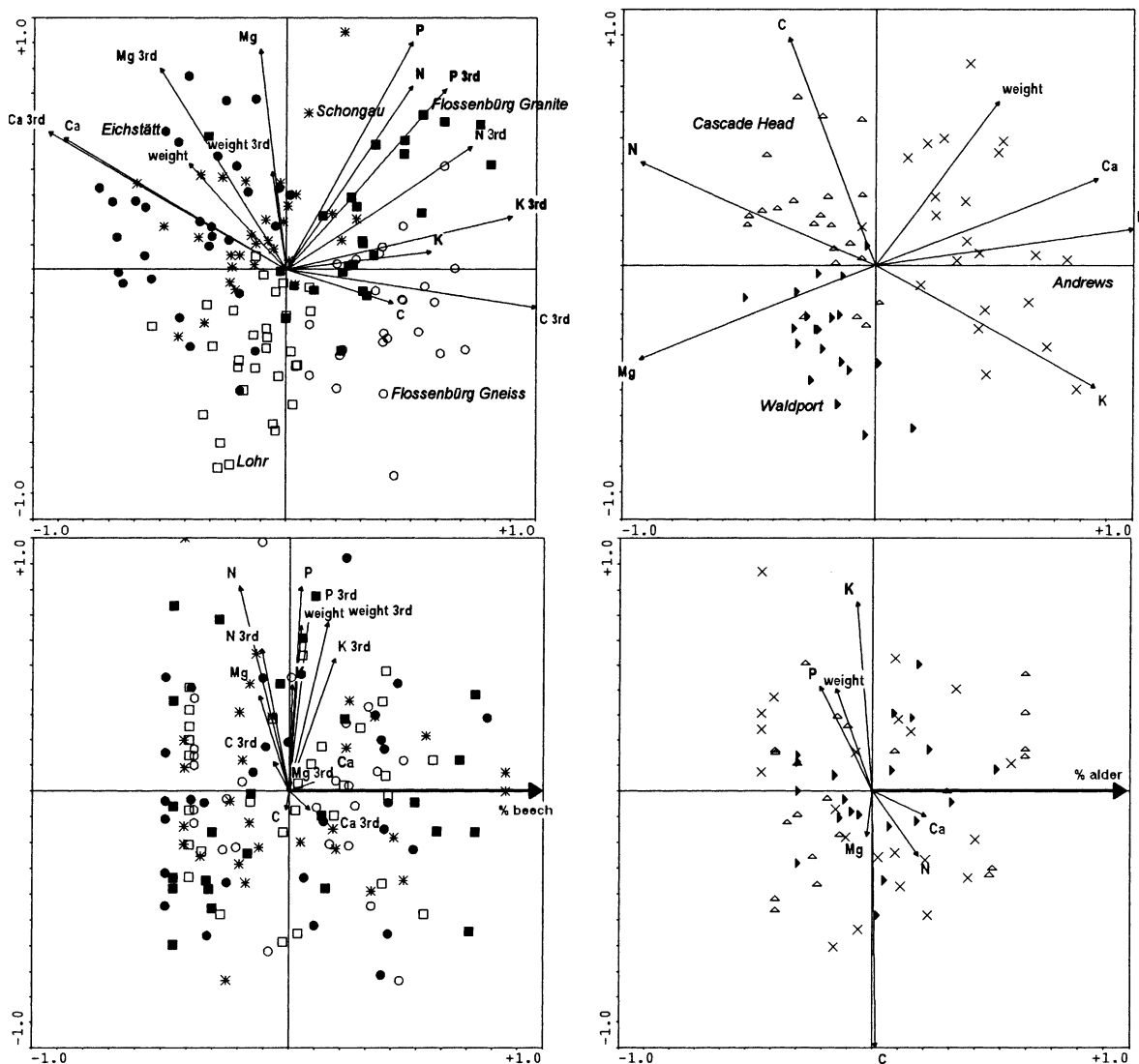


Fig. 1. Multivariate nutritional patterns in Norway spruce (five sites in Bavaria, left) and Douglas fir (three sites in Oregon, right, first year needles only) as represented by ordination axes 1 and 2; above: unconstrained PCA-axes; below: RDA-triplots showing “influence” of proportion of broadleaved neighbours.

Table 4

Partial redundancy analyses of conifer nutritional status and permutation test of the significance of broadleaf influence on nutrition pattern

Partial RDA-axes	Norway spruce (Bavaria)				Douglas fir (Oregon)			
	1	2	3	4	1	2	3	4
Eigenvalues	0.006	0.131	0.097	0.086	0.014	0.194	0.103	0.085
Variance in nutrition (cumulative) (%)	1.0	22.5	38.4	52.6	2.4	35.1	53.4	67.8
Correlation with %broadleaves	0.320	0.000	0.000	0.000	0.375	0.000	0.000	0.000
Significance level (<i>p</i> -value)	0.209				0.191			

Nutritional variation was reduced to four principal components explaining 69% of the original variance (Table 3). Corresponding first and third year needle variables behaved very similarly in PCA, with a tendency for older needles to reflect the principal

components more strongly. The position of spruces in nutritional state space was basically a function of site location. Trees sampled at Eichstätt, Schongau and Lohr contained more Ca and Mg, while the needles at the two Flossenbürg sites were richer in

Table 5

Spearman's bivariate rank correlations for the relationship between proportion of broadleaves and nutritional attributes of conifers^a

Site (number of trees)	Correlation coefficient / significant level	100 needle mass	C	N	P	Ca	K	Mg
<i>Douglas fir–red alder (Oregon)</i>								
Andrews (22)	<i>ρ</i>	–0.233	0.180	0.327	–0.776	0.204	–0.255	–0.103
	<i>p</i>	0.297	0.423	0.138	<i>0.000</i>	0.363	0.251	0.648
Cascade Head (22)	<i>ρ</i>	–0.151	–0.315	0.051	<i>0.463</i>	<i>0.444^b</i>	0.053 ^b	0.058 ^b
	<i>p</i>	0.434	0.153	0.792	<i>0.030</i>	<i>0.038</i>	0.815	0.798
Waldport (20)	<i>ρ</i>	0.243	0.088	0.111	0.291	0.106	0.180	–0.373
	<i>p</i>	0.301	0.711	0.642	0.214	0.655	0.447	0.105
Third year needles	<i>ρ</i>	0.065	–0.174	0.198	0.265	0.035	0.139	–0.035
	<i>p</i>	0.810	0.519	0.463	0.320	0.896	0.609	0.896
<i>Norway spruce–European beech (Bavaria)</i>								
Eichstätt (30)	<i>ρ</i>	–0.179	–0.124	–0.223	0.083	0.084	0.186 ^b	0.003
	<i>p</i>	0.345	0.515	0.237	0.662	0.657	0.326	0.987
Third year needles	<i>ρ</i>	–0.050	0.351	–0.041	0.165	–0.400	<i>0.467^b</i>	–0.082
	<i>p</i>	0.793	0.062	0.828	0.385	<i>0.029</i>	<i>0.009</i>	0.668
Flossenbürg Gneiss (25)	<i>ρ</i>	–0.062	–0.165	–0.321	–0.153	–0.118	–0.326	–0.231
	<i>p</i>	0.769	0.431	0.118	0.465	0.575	0.112	0.267
Third year needles	<i>ρ</i>	0.014	–0.530	–0.238	0.248	0.059	0.221	–0.183
	<i>p</i>	0.947	<i>0.006</i>	0.252	0.232	0.778	0.287	0.382
Flossenbürg Granite (25)	<i>ρ</i>	0.016	–0.190	0.040	0.269	0.132	–0.205	0.218
	<i>p</i>	0.940	0.373	0.850	0.194	0.530	0.325	0.296
Third year needles	<i>ρ</i>	–0.002	–0.256	0.051	0.209	0.352	–0.013	0.159
	<i>p</i>	0.994	0.217	0.810	0.315	0.084	0.950	0.447
Lohr (30)	<i>ρ</i>	0.177	0.049	–0.157	–0.088	0.072	0.032 ^b	0.146 ^b
	<i>p</i>	0.351	0.799	0.407	0.645	0.706	0.868	0.442
Third year needles	<i>ρ</i>	0.254	–0.101	–0.062	–0.170	0.268	–0.013 ^b	–0.001 ^b
	<i>p</i>	0.176	0.594	0.747	0.369	0.152	0.944	0.995
Schongau (30)	<i>ρ</i>	0.327	0.105	–0.149	0.056	0.230	–0.002 ^b	–0.532
	<i>p</i>	0.078	0.580	0.433	0.769	0.221	0.991	<i>0.002</i>
Third year needles	<i>ρ</i>	0.318	–0.023	–0.098	0.020	<i>0.404</i>	0.020 ^b	–0.072
	<i>p</i>	0.093	0.904	0.605	0.915	<i>0.027</i>	0.916	0.707

^a Significant coefficient values are shown in italic.

^b Elements in relatively low supply at a site (cf. Table 2).

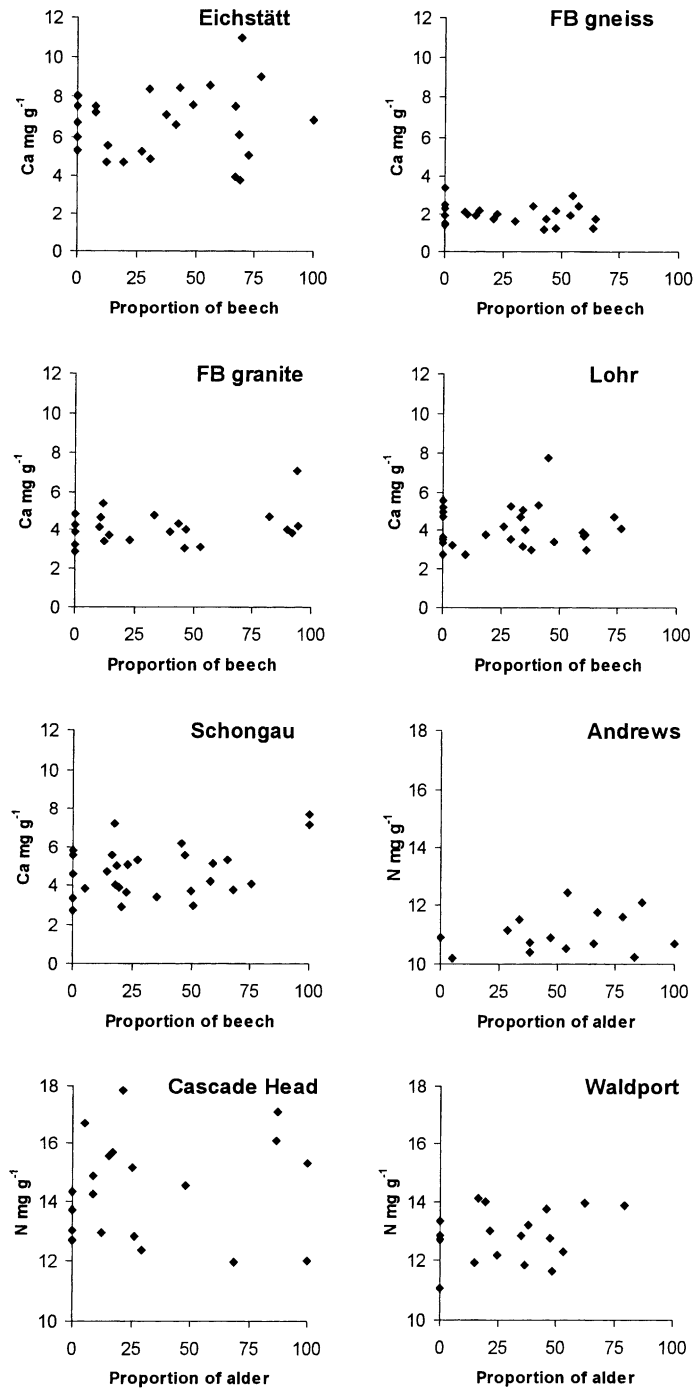


Fig. 2. Bivariate relationships between proportion of broadleaves and foliar Ca (Bavarian sites) or N (Oregon sites) concentrations of first year needles of conifers.

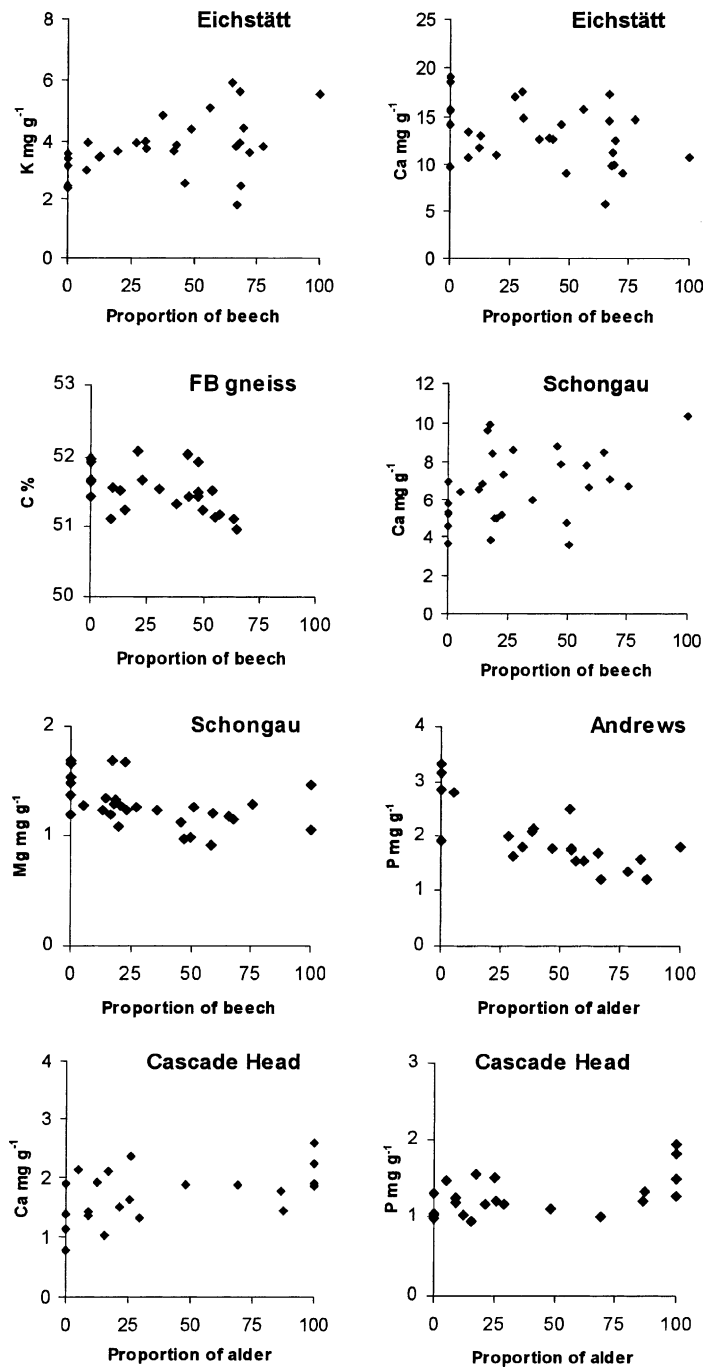


Fig. 3. Significant (see Table 5) bivariate relationships between proportion of broadleaves and foliar nutrient concentrations. The upper four graphs refer to third year needles, the lower four graphs to first year needles.

K, N and P. Also older needles at the latter sites tended to contain more carbon (Fig. 1, upper left). Correlation of beech proportion with unconstrained PCA-axes was low (Table 3, left), indicating that neighbouring tree composition was not involved in causing any of the main nutritional trends.

We found no indications of severe nutrient deficiency in Douglas fir at the Oregon sites, when comparing foliar nutrient concentrations of conifers in the monoculture situation (Table 2) to standard nutrient levels (Fisher and Binkley, 2000). N concentrations were high at the Cascade Head and Waldport site and sufficient at the Andrews site. P concentrations were sufficient at the Cascade Head and Waldport site, at the Andrews site there seems to be luxurious consumption. Ca and K were relatively low at the Cascade Head site and Mg and the Andrews site. The first four principal components represented 84% of the total variance in element contents (Table 3). Again, the pattern of tree nutrition was closely related to locations. Nutrients Ca, K and P, which reached highest levels at the Andrews site, were negatively correlated with Mg and N (Fig. 1, upper right). Douglas firs at the Waldport site differed from those at Cascade Head mainly in having less C and N in lighter needles. Low correlation of broadleaf proportion the four axes (Table 3) indicated that the nutritional pattern of Douglas firs did not strongly depend on surrounding species composition.

Constrained partial ordination (treating the study stands as blocks of a field experiment and extracting residual multivariate gradients in conifer nutrition) yielded no evidence for the hypothesis that deciduous admixtures improve foliar nutrition of conifers. Partial RDA-axes constrained by broadleaf proportion reflected only 1% (spruce in Bavaria) and 2.4% (Douglas fir in Oregon) of the original variation and was not significant at the 0.05 error level (Table 4). While nutritional status could not be attributed to a significant effect of broadleaves, at least the signs of element loadings on the constrained axes broadly corresponded to expectations (Fig. 1, below).

Bivariate rank correlations did also not detect consistent effects of the broadleaf admixtures on element levels or needle mass in the two coniferous tree crops (Table 5). Since tree species composition did not influence 100 needle mass, the results for the correlation between tree species composition and nutrient

content per 100 needles (data not shown) were well comparable to the results for nutrient concentrations. In Douglas fir effects of alder on P-status were reversed at the Andrews and at the Waldport site. The Douglas firs at Cascade Head were the only ones, where improved supply of a deficient element (Ca) may have been caused by alder admixture. When testing the many bivariate relationships for Norway spruce in Bavaria, we occasionally found significant correlations, but these were also partly conflicting (see Ca at Eichstätt and Schongau) and did not combine to a consistent pattern across sites. The only instance, where beech might have improved the status of a deficient element was K in third year needles at the Eichstätt site. Fig. 2 illustrates the absence of relationships in scatter plots of broadleaf proportion versus concentrations of first year needles for those elements, that we had expected to react most strongly: N for red alder and Ca for European beech. The scatter plots for all cases with significant coefficients (Fig. 3) shows that the trends were unstable. In most cases the significant effects disappeared when removing one or two extreme values. This indicates, that significant bivariate correlations may have been only a random effect. This is confirmed by the fact that some effects were contradicting (e.g. Ca increased and Hg decreased with beech admixture at the Schongau site) and that the (more reliable) ordination methods yielded no evidence for mixture effects.

4. Discussion

That nutrition in Norway spruce and Douglas fir trees does not appear to react consistently to the presence of broadleaved trees in their vicinity comes as no small surprise. To what extent could measurement errors and other uncontrolled sources of variation have contributed to this unexpected result?

The use of the proportion of broadleaved species within an 8 m circle to characterise stand composition is based on the observation, that tree species interactions take place on a small spatial scale (Zinke, 1962; Turner and Franz, 1985; Boettcher and Kalisz, 1990; Rhoades, 1997). Rothe (1997) analysed the relationships between tree species composition, rooting patterns, solid and liquid phase soil properties, litterfall and throughfall deposition within a spruce–beech

stand at the Höglwald experimental site (Kreutzer and Weis, 1998). He found radial effect ranges of 3–15 m depending on the individual measures. Correlation coefficients usually peaked when indices were based on a radius of 5–10 m, but differences were small within this range. Thus the proportion of broadleaves within an 8 m circle should be a sound measure to analyse effects on nutrition. This is confirmed by the fact that the alternative use of the five trees closest to the sample tree (emphasising the immediate neighbourhood) to characterise stand composition did not change the general statement (data not shown).

Another problem may result from the fact that basal area in the conifer monocultures is significantly higher than in broadleaved monocultures. Therefore the proportion of basal area tends to underestimate the area influenced by the broadleaved species (Rothe et al., 2001a). Visual estimation of the area occupied by broadleaved species resulted in a significantly higher proportion of the broadleaved species for all sites investigated (on average by about 15%) than using the proportion of basal area. Again, the use of this estimate as an independent variable did not change the results found using proportion of basal area (data not shown). It is thus unplausible, that the method of measuring species proportions accounts for the absence of correlations between tree nutrition and stand composition.

Despite several problems foliar nutrients have been used widely to characterise nutritional status of trees (Fisher and Binkley, 2000). Limitations result from the fact, that foliar nutrient concentrations vary depending on the position of the branches in the crown and both interannual and seasonal variations occur. Even when taking samples simultaneously from the same position in the crown, foliar nutrient concentrations of individual trees may vary widely. Both genetic differences and small scale site effects are likely to contribute to the variation among individual trees, but the exact causes are yet unknown. Among all sites investigated here the coefficient of variation for conifer trees growing in a monoculture situation was 7% for N, 12% for P and 20–25% for K, Mg and Ca. In any event, our negative results obtained from both multivariate ordination and bivariate correlation indicate that the presence of broadleaved trees does not cause a signal strong enough to be detectable in the inherent variability of nutritional attributes.

It has been documented repeatedly that the admixture of broadleaves (especially nitrogen fixing species) may improve soil nutrient availability (see review by Rothe and Binkley, 2001). Nitrogen fixation rates in mixed Douglas fir–red alder stands typically ranged between 5 and 15 g m⁻² per year. Interestingly, not only N availability was higher in these mixed stands, but in some cases also P and base cation (Ca, Mg, K) cycling was enhanced (Binkley, 1992; Fisher and Binkley, 2000). At the Waldport site nitrogen pools in the mixed stands with about 25% red alder was about 180 g m⁻² higher and nitrogen mineralisation in the topsoil was nearly tenfold higher than in the pure Douglas fir stands (Rothe et al., 2001b). For the two other Oregon sites no soil data were available but an influence of alder at least on nitrogen cycling is likely. For the Bavarian sites soil data were only available for the Schongau site (Rothe, 1997a; Rothe et al., 2001a). In the mixed spruce–beech stands litter and duff layers were significantly thinner and topsoil pH as well as base saturation were significantly higher than in the spruce monocultures. While total nutrient pools did not differ by stand type, although there were clear differences concerning the vertical distribution of nutrients. These findings agree well with the previous investigations of mixed stands of spruce and beech (Wittich, 1933; Wiedemann, 1942; Frank, 1994; Rothe, 1997) and comparable effects can be assumed for the other sites, where no soil investigations were performed.

However, soil nutrient pools are not necessarily linked with foliar nutrient levels. The process of nutrient uptake is highly complex and especially on nutrient rich soils the effects of increased soil nutrient availability may be small (Liebig described this effect as early as in the 19th century). It seems possible that nutrient availability at the investigated sites was too high to provoke significant tree species effects on foliar nutrients. This applies especially to N, where foliar concentrations indicated a good availability at all sites. This reasoning is in line with results of fertilisation trials, where addition of N had minor effects on sites with an inherently high N availability (Kenk and Fischer, 1988; Jacobson and Nohrstedt, 1993). Rennenberg et al. (1998) documented that spruce trees were able to actively exclude nitrate from uptake in the topsoil at a site with high N availability. Even at those sites that we selected to represent low

nutrient availability the conifer trees were well supplied with nitrogen. It may be speculated, that a long-term nitrogen deposition has improved availability even on formerly poor sites (Gundersen et al., 1998; Fenn et al., 1998), thus reducing or even reversing the concerns of managing nutrient cycles.

On the other hand effects of broadleaves on soil pools of Ca, Mg and K should have been reflected by foliar nutrient levels, as the levels of these elements were far below maximum levels reported in literature (Carter, 1992; Bergmann, 1993; Gulder and Kölbl, 1993; Ende and Evers, 1997) and at some sites we even found light deficiency. Under such circumstances, improved availability in the soil should be reflected by the trees. Fertilisation experiments have repeatedly demonstrated that foliar nutrient levels are increased by nutrient additions under conditions well comparable to those at our sites (Jacobson and Nohrstedt, 1993; Schmidt-Vogt, 1991; Hüttl, 1991). Even on the fertile Höglwald site with excellent growth rates for spruce the addition of Mg and Ca via liming significantly increased foliar nutrient concentrations (unpublished data). Both elements are taken up in a passive way and on calcareous soils a surplus uptake may even cause physiological problems (Marschner, 1995).

Nutritional interactions in mixed species stands are highly complex. Tree species composition directly influences features like nutrient input, soil nutrient availability, litterfall and rooting patterns, which then influence tree nutrition. We used a simplifying black box approach by investigating the influence of stand composition on foliar nutrient status. Since the relevant ecological parameters could not be measured directly we used the proportion of broadleaves within an 8 m circle to characterise stand composition and foliar nutrients to characterise nutrient status. Due to our simplified approach we could not analyse the effects of other sources of variation on nutritional status. Thus the negative results only document, that the effects of admixed broadleaves were too small to be detected by our methods but do not allow the statement that such effects are non-existent.

5. Conclusions

Beneficial effects of broadleaves on conifer nutrition appear to be less common than ecosystem theory

and conventional wisdom make us believe. To date only very few empirical studies were able to demonstrate such an effect (Binkley, 1992; Binkley et al., 1994; Binkley and Giardina, 1998). Conflicting results from the study of soils versus foliar status suggest that future investigations should try to analyse the whole path relevant for tree nutrition and growth. This will not only require interdisciplinary approaches, but also careful study layouts, high numbers of replicates and application of more sophisticated statistical approaches.

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