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ORIGINAL PAPER

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Ecological background of crown condition, growth and nutritional status of *Picea abies* (L.) Karst. in the Bavarian Alps

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Abstract Using a representative sample of stands from a cross section through the Bavarian portion of the northern Calcareous Alps, this study evaluates the plausibility and significance of causal hypotheses for an explanation of the poor crown condition of Norway spruce in mountain forests: (1) ozone exposure in conjunction with (a) drought and (b) ample water supply; (2) soil-borne nutrient deficiency; (3) drought; and (4) tree age. Site index and, in a subset of stands, foliar nutrient concentrations are considered as additional indicators of tree vigour. According to principal component analysis and multiple regression, crown condition was controlled by soil chemistry (transparency increased towards shallow calcareous soils), stand age and, to a smaller degree, by an interaction between ozone exposure and drought. Site index was best explained by a model including elevation, soil chemistry and drought. Tree nutrition clearly reflected the main soil chemical gradient, and P, N and Fe deficiencies were found in transparent stands, which had markedly smaller needles. The similar distributions of crown transparency, site index and nutrition present a strong argument for the hypothesis that soil chemistry has constrained the vigour of spruce trees in the Calcareous Alps for a long time. By leaving unproductive stands to age naturally, forest management has accentuated the pattern of crown condition. In the heterogeneous alpine landscape, possible effects of recent increases in ozone exposure have to be viewed extremely carefully against the background of these natural and anthropogenic covariables.

Keywords Forest decline · Mountain forest · Site ecology

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Introduction

The Bavarian Alps fall into the natural distribution area of Norway spruce [*Picea abies* (L.) Karst.] and, through much of the region, this coniferous tree species is predominant over European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) both in present-day situations and in the estimated natural vegetation. In the monitoring of forest conditions since 1984, spruce consistently showed a markedly poorer crown condition than in those areas, where the species has been established in the place of natural deciduous forest (Kennel 1990; Anonymous 1997). A number of ecological case studies lead to the formulation of several explanations for poor crown condition of spruce in the Calcareous Alps (Table 1).

The ozone hypothesis, as a specification of the photooxidant hypothesis, originated from work at Wank Mountain near Garmisch-Partenkirchen (Liu and Payer 1996; Maier-Maercker and Koch 1995). While Norway spruce is generally regarded as a rather ozone-resistant species (Matyssek et al. 1997), spruces at Wank Mountain exhibited increased fall of green needles after episodes with AOT40 doses above 500 nl l^{-1} h^{-1}. That effect was most pronounced at sites with good water supply. Liu and Payer observed unspecified damage of photosynthetic tissues caused by O_3, which is damped by stomatal closure at dry sites (see also a study of *Picea sitchensis* seedlings by Dobson et al. 1990). In contrast, Maier-Maercker and Koch (1995) saw a causal link between green needle fall at Wank Mountain and a malfunction of stomata, which could be reproduced experimentally in O_3 exposition chambers (Maier-Maercker and Koch 1991). Both variants of the hypothesis predict an increase in crown transparency with ozone exposure, which follows elevation above sea level rather closely in the region (Paffrath and Peters 1988). Both suggest an interaction with water availability, but with opposite tendencies. According to Liu and Payer (1995), high ozone dose in conjunction with ample water supply should cause transparency, while Maier-Maercker and

Table 1 Hypotheses explaining crown transparency of Norway spruce in the Calcareous Alps

Hypothesis	References	Region	Observations	Null hypothesis	Indicator variable(s)
Ozone	(Liu and Payer 1996; Maier-Maercker and Koch 1995)	Wank	Needle fall occurs at high AOT doses	No relationship between ozone exposure and transparency	Elevation a.s.l.
Ozone + good water supply	(Liu and Payer 1996)	Wank	Green needle fall occurs if high AOT doses are coupled with ample water supply	No relationship between interaction ozone × water availability and transparency	Elevation × moisture index
Ozone + drought	(Maier-Maercker and Koch 1995)	Wank	Ozone disturbs stomatal closure	No relationship between interaction ozone(1−water availability) and transparency	Elevation (1−moisture index)
Soil-induced nutrient deficiency	(Bosch 1986; Polle et al. 1992; Flückiger and Braun 1995; Haupolter 1999)	Mangfall-gebirge, Wank, Switzerland, Tyrol	High transparency coincides with K, N, P and Mn deficiency, fertilisation improves crown status	No increase in transparency with decreasing availability of N, P, K and Mn and increasing pH	C/N, C/P, exchangeable concentrations of K and Mn, Mn saturation, pH in main rooting zone
Drought	(Webster et al. 1996; Vacik and Lexer 1998)	Switzerland, Lower Austria	High transparency coincides with hallow carbonate soils	No increase in transparency with decreasing moisture	Moisture index
Tree age	(Thomsen and Nellemann 1994; Klap et al. 1997)	Europe	Old trees have more transparent crowns (regression models)	No increase in transparency with increasing stand age	Stand age

Koch (1995) predict highest transparency at high ozone and drought conditions. A statistical test of both predictions not only has to look at elevation (as a surrogate of ozone dose), but also at the interaction terms (products) between elevation and water balance as potential causes of crown condition.

Poor soils and nutrient deficiency as a cause of 'decline' of spruce in the Calcareous Alps were first reported by Bosch (1986) in the Mangfall section of the Bavarian Alps. In that study, strongly discoloured and transparent spruces of low site index (IV.5) had low foliar concentrations of K, Mn, N and P, which was interpreted as a typical limestone chlorosis caused by ion antagonism and high pH (Zech 1969). Low foliar contents of P, N and Mn were also found at the Wank research site (Polle et al. 1992) and regarded as an important cause of low vitality (Liu and Payer 1995). Haupolter (1999) reported similar deficiencies from the Tyrolian Loisach valley and showed that adjacent spruce trees without marked transparency had normal nutrient levels. Flückiger and Braun (1995) induced a re-vitalization of a strongly transparent spruce forest on dolomite in the Swiss Alps by fertilisation. Without distinguishing a separate drought hypothesis Rehfuess (1995) coined the term 'Kalkalpen-Erkrankung' for this syndrome of spruce in the Calcareous Alps. The nutrition hypothesis in the strict sense predicts that crown transparency and discoloration should, other things being equal, coincide with low availability of N, P, K and Mn, whereas more fertile soils should lack the symptoms.

The explanation that drought causes higher crown transparency of spruce on limestone soils was put forward as the result of two independent regression studies, in Switzerland (Webster et al. 1996) and Austria (Vacik and Lexer 1998), both of which had no variables available to discern this explanation from the nutrition hypothesis (Rehfuess 1995). The drought hypothesis predicts that, other things being equal, low water availability should coincide with high transparency.

Last, but not least, Thomsen and Nellemann (1994) and Klap et al. (1997) presented strong evidence for the importance of tree age for transparency in Norway spruce. This is of special significance in the Alps with their wide range of stand ages and high proportion of very old protective forest stands (Ewald and Reuther 1999). The assumption that, other things being equal, transparency will be higher in old stands is here referred to as the senescence hypothesis.

Crown transparency is a relatively unspecific indicator of tree vitality and is often only loosely related to current production (Hüttl 1991; Dobbertin 1996). Marked growth decline was, so far, only found in spruce trees with very high transparency (Franz et al. 1987). The relationship between stand age and height (site index) is an accepted indicator for the mean long-term conditions of growth. If the level of crown transparency were higher at poor sites, as suggested by Ellenberg (1995), one would expect a close relationship with site index and both indicators of tree vitality should follow the same long-term ecological factors.

This study aimed at validating the relevance of the cited hypotheses by using a representative field data set and at supporting these findings by more precise nutritional data. The following questions were addressed: (1) which causal hypothesis performs best in explaining the crown transparency pattern of Norway spruce in the landscape? (2) Do crown transparency and site index follow the same ecological gradients? (3) Is high crown transparency accompanied by nutrient deficiencies? (4) Can nutritional status be explained by site properties? (5) Which nutritional deficiencies and imbalances can cause low vitality?

Materials and methods

Study sites

The 78 Norway spruce stands form part of a larger transect in the region called 'Werdenfelser Land' (Fig. 1) extending from the Flysch pre-Alps (forest region 15.4/1, Walentowski et al. 2001) across the central part of the Bavarian Limestone Alps (15.5) to the Wetterstein Mountains (15.8). Covering a high proportion of the stratigraphic units occurring in the Bavarian Alps (Anonymous 1983), the transect is quite representative of the larger region. The forests are subject to a cool, humid mountain climate with a summer peak in precipitation. Lower elevations (700 m) receive ca. 1,200 mm and stands close to the timberline (1,600 m) receive ca. 1,700 mm annual precipitation. In the same elevation interval, mean annual temperature drops from 7°C to 3°C (Anonymous 1996a). Montane, mixed deciduous–coniferous forests are classified as Luzulo–Fagetum (strongly acid loam soils), Galio–Fagetum (acid, base-rich loam soils), Galio–Abietetum (base-rich hydromorphic soils), Aposerido–Fagetum (moist carbonate soils) and Seslerio–Fagetum (dry carbonate soils, Ewald 1997). Above the limit of European beech at 1,400 m, subalpine spruce forest (Adenostylo glabrae-Piceetum) prevails (Ewald 1999).

Survey of crown condition and ecological factors at 78 sites

Plot locations were chosen in a stratified random design based on existing forest inventories to ensure that stands

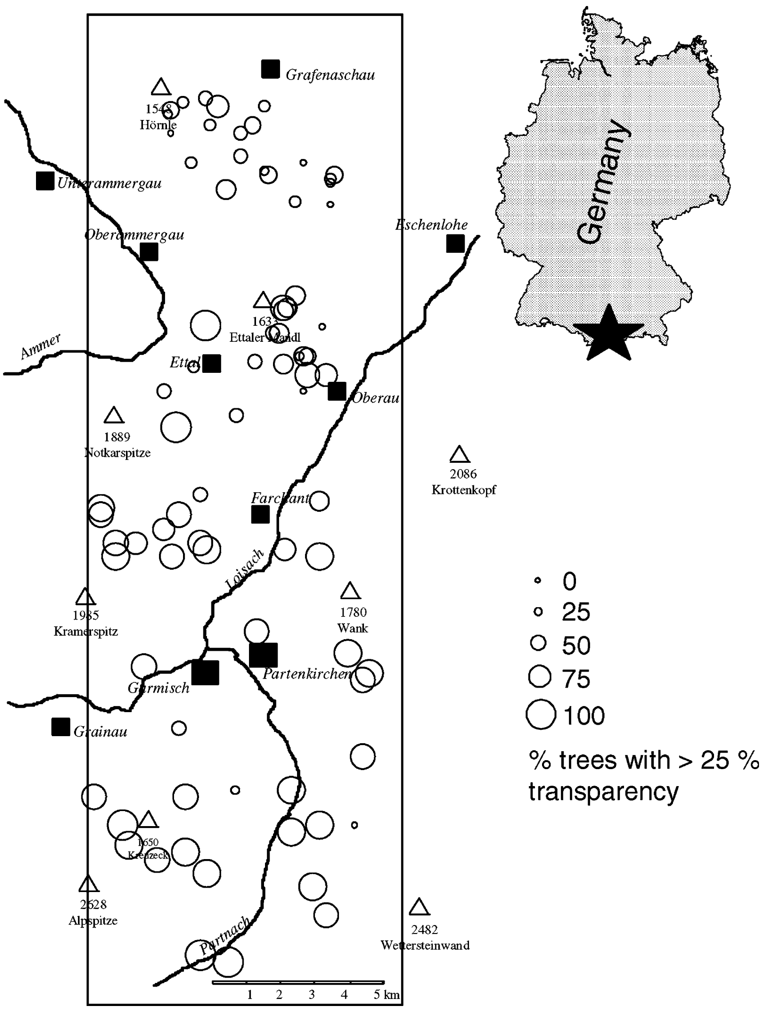

Fig. 1 Map of the transect showing 78 study sites; crown condition of *P. abies* shown by bubble size

older than 60 years were equally represented in terms of species mixture (pure spruce vs. spruce–beech stands), elevation, parent material, water balance and slope exposition (for details see Ewald et al. 2000). The selection procedure attempted to minimise intercorrelations among stratification criteria by drawing a multivariately balanced sample. On 78 plots, the crown transparency of 20 dominant Norway spruces was assessed in August 1997, following the official monitoring protocol. Estimates of stand age and site index were taken from the Bavarian State Forest Administration's inventory database. Each plot was characterised in terms of relief (elevation, slope exposition, inclination and position on slope). The slope exposition angle (*Exposit*) was transformed to a favourability index (Beers et al. 1966)

$$\text{Aspect} = \cos(\text{Aspect}_{\max} - \text{Exposit}) + 1 (\text{with Aspect}_{\max} = 202.5^\circ,\ \text{SSW}),$$

which takes values of 2 for sunny slopes and 0 for shaded slopes.

Soil augerings (diameter 3.5 cm, maximum depth 60 cm) were performed at four points around the plot centre and used to measure depth of free carbonate (HCl probe) and record the horizon properties (texture, density, humus and stone content) needed to estimate available water storage capacity (*AWSC*), according to the tables in Anonymous (1996b). All fine humus (duff) horizons were assigned a storage capacity of 20% volume. Quadruplicate soil measurements were aggregated by calculating medians.

The point of departure was AWSC, for calculating a master index of overall moisture (*MI*) by empirically weighting soil type, elevation, slope favourability and position (details in Ewald et al. 2000), resulting in a continuous variable taking values between 2.4 (moderately dry) and 10 (wet). For statistical tests of the ozone hypotheses two interaction terms were calculated by multiplying elevation (as a surrogate for ozone exposure) by moisture (*MI*) and by its complement, the drought index (*DI*). Both interactions were rescaled to lie between 0 and 100:

$$\text{ELEV} \times \text{MOIST} = \frac{\text{ELEV} - \text{ELEV}_{\min}}{\text{ELEV}_{\max} - \text{ELEV}_{\min}} \times 10 \times \frac{\text{MOIST} - \text{MOIST}_{\min}}{\text{MOIST}_{\max} - \text{MOIST}_{\min}} \times 10$$

$$\text{ELEV} \times \text{MOIST} = \frac{\text{ELEV} - \text{ELEV}_{\min}}{\text{ELEV}_{\max} - \text{ELEV}_{\min}} \times 10 \times \frac{\text{MOIST}_{\max} - \text{MOIST}}{\text{MOIST}_{\max} - \text{MOIST}_{\min}} \times 10.$$

Composite soil samples of the four augerings were taken from L-horizons and Of-horizons (pooled), Oh-horizons (where present) and from the uppermost 10 cm of mineral soil (Ah-horizons or Aeh-horizons), oven-dried and partly ground. The following chemical variables were measured by standard laboratory procedures for litter (L-layers and Of-layers) and topsoil (mineral soil, if Oh > 10 cm Oh-layer): contents of organic C, P and N (in the following expressed as the two ratios C/N and C/P), pH in $CaCl_2$ and NH_4Cl-exchangeable K and Mn. Cation exchange capacity and base saturation were not calculated, because as an acid extractant NH_4Cl dissolves Ca-carbonates and Mg-carbonate, leading to an overestimation of exchange sites in limestone soils. Depth of free carbonate (median) was used as an indicator of mineral soil quality at greater depth. Soil chemical variables were standardised and subjected to principal component analysis (Anonymous 1999) yielding four orthogonal soil nutrient factors.

Relationships between crown transparency (median and percentage of trees with >25% transparency) and ecological variables were evaluated by Spearman rank correlation and stepwise multiple regression. The contribution of single significant predictors to the explanation of crown transparency was estimated by partial regression (variance partitioning, Whittaker 1984).

Nutritional analysis at 12 intensive sites

From the larger pool of 78 sites, 12 stands were selected for analysis of tree nutrition in order to represent the major soil chemical and altitudinal gradients. Of the 20 spruces surveyed for crown condition the 10 closest to the plot centre were subjected to needle sampling. Current-year needle samples were taken from the seventh whorl. Needles were dried, weighed (100-needle weight), ground and analysed for total content of C, N (combustion in O_2 flow, Leco CHN-analyser), P, K, Ca, Mg, Mn, Fe, Cu, Zn and Al (pressure extraction, ICP/OES). Bivariate correlations between site and nutritional variables were assessed by Spearman coefficients.

Results

Regional patterns of crown transparency and ecological conditions

The sample spanned a range of crown transparency in Norway spruce that is representative and typical for the Bavarian Alps (Table 2). An increase in crown transparency from the Flysch pre-Alps in the north to the high Calcareous Alps in the south is visible in the sample (Fig. 1). However, a large amount of small-scale variance was observed in the geologically diverse central and southern portion of the transect, where extreme crown transparency existed in close vicinity to densely foliated spruce stands. The soils of the 78 sites stands were positioned in a space of four principal components conveying 76% of the total measured variance. Factor 1 ordered the plots by decreasing depth of free carbonate,

Table 2 Descriptive statistics of study variables from 78 Norway spruce stands

	Minimum	Maximum	Mean	SD
Median transparency (%)	7.5	65.0	27.7	11.4
Proportion of trees >25% transparency (%)	0.0	100.0	48.0	32.0
Site index: stand height at 100 year (m)	12.8	42.4	27.2	6.8
Elevation (m) (ELEV)	690	1,570	1,106	245
Moisture index (MOIST)	2.4	10	6.0	2.0
Interaction elevation × moisture (ELEV × MOIST)	0.0	68.0	22.1	17.9
Interaction elevation (1−moisture) (ELEV × DROUGHT)	0.0	86.1	25.2	19.3
Stand age (year) (AGE)	67	307	139	51
Depth of free carbonate (cm)	0.0	60.0	28.5	23.5
pH litter	3.4	5.6	4.5	0.5
pH topsoil	3.0	6.8	4.7	1.1
C/N ratio litter	20.7	32.6	25.8	2.9
C/N ratio topsoil	7.2	28.1	19.8	3.1
C/P ratio litter	136.0	602.0	359.2	126.5
C/P ratio topsoil	26.0	1,214.3	317.0	268.5
K_{ex} litter (μmol g^{-1})	0.0	33.2	17.6	6.8
K_{ex} topsoil (μmol g^{-1})	0.0	20.1	4.9	3.5
Mn_{ex} litter (μmol g^{-1})	1.4	43.8	12.4	9.5
Mn_{ex} topsoil (μmol g^{-1})	0.3	27.9	5.2	4.8

which was accompanied by a decrease in exchangeable Mn and increases in pH, C/P and C/N ratios (Table 3), and is in the following referred to as 'carbonate factor'. Contrary to the nutritional hypothesis exchangeable K tended to increase along this gradient.

Mean crown transparency and the proportion of Norway spruces with transparency >25% increased significantly with increasing carbonate factor (Spearman's $\rho=0.64/0.62$), high stand age ($\rho=0.58/0.60$), low moisture supply ($\rho=-0.41/-0.40$) and at high values of the elevation–drought interaction ($\rho=0.37$, 0.39). This means that relatively dry sites had higher crown transparency if situated at higher elevations. There was also a significant positive correlation between percentage transparency >25 and elevation ($\rho=0.23$).

Table 3 Results of a principal components analysis of soil chemical variables; maximum factor loadings of variables in *boldface*; principal components 1–4 are in the following referred to as soil nutrient factors

	Soil nutrient factors			
	NF 1	NF 2	NF 3	NF 4
Eigenvalue	4.27	1.65	1.23	1.17
Variance (%)	38.84	14.99	11.14	10.60
Cumulative (%)	38.84	53.83	64.97	75.56
Free carbonate	**−0.87**	0.02	0.07	−0.09
Mn_{ex} litter	**−0.76**	0.37	0.18	−0.04
C/N topsoil	**0.74**	−0.31	0.09	−0.08
C/P topsoil	**0.72**	−0.03	0.56	0.14
C/P litter	**0.70**	0.30	0.28	−0.18
pH litter	**0.60**	0.47	−0.41	−0.05
K_{ex} topsoil	**0.45**	0.42	0.41	0.39
C/N litter	0.24	**0.63**	0.07	−0.51
Mn_{ex} topsoil	−0.58	**0.61**	0.07	−0.08
pH topsoil	0.62	0.22	**−0.66**	0.10
K_{ex} litter	−0.20	0.32	−0.10	**0.81**

Practically no spruce stands with high transparency were encountered at sites with low carbonate content (Fig. 2), whereas stands on limestone and dolomite soils almost consistently had 30% mean transparency or more. The plot of transparency against age was curvilinear. Old stands were consistently more transparent and the dependence seemed to flatten out. The relationship was linearised by a square root transformation of the age variable ($\sqrt{\text{AGE}}$ step 2) which was used in multiple regression.

Stepwise multiple regressions included carbonate factor, stand age (square root) and elevation–drought interaction as predictors of both variants of spruce transparency, explaining 49% and 50% of the variation, respectively (Table 4). Variance of the model for transparency >25% was partitioned into 17% explained by the carbonate factor, 10% by age and 6% by the interaction term, with 17% being jointly attributable to all predictors (Fig. 3).

There was a close relationship between crown transparency as measured in 1997 and site index. Stands that had reached low heights for their age had markedly more transparent crowns (Spearman's $\rho=0.62$ and $\rho=0.60$, respectively). Slow-growing stands also tended to be older than those with vigorous growth ($\rho=0.60$). Low site index was also related to the carbonate factor ($\rho=0.62$), low water storage capacity ($\rho=0.35$), sun-exposed ($\rho=0.31$) and steep slopes ($\rho=0.30$) and high elevation ($\rho=0.23$). Stepwise multiple regression selected the carbonate factor, elevation and water storage for a model explaining 53% of the variation in site index. When models of crown transparency were run against the same set of predictors, water storage capacity was not significant, but the carbonate factor and elevation jointly explained 40% and 44% of crown transparency, respectively.

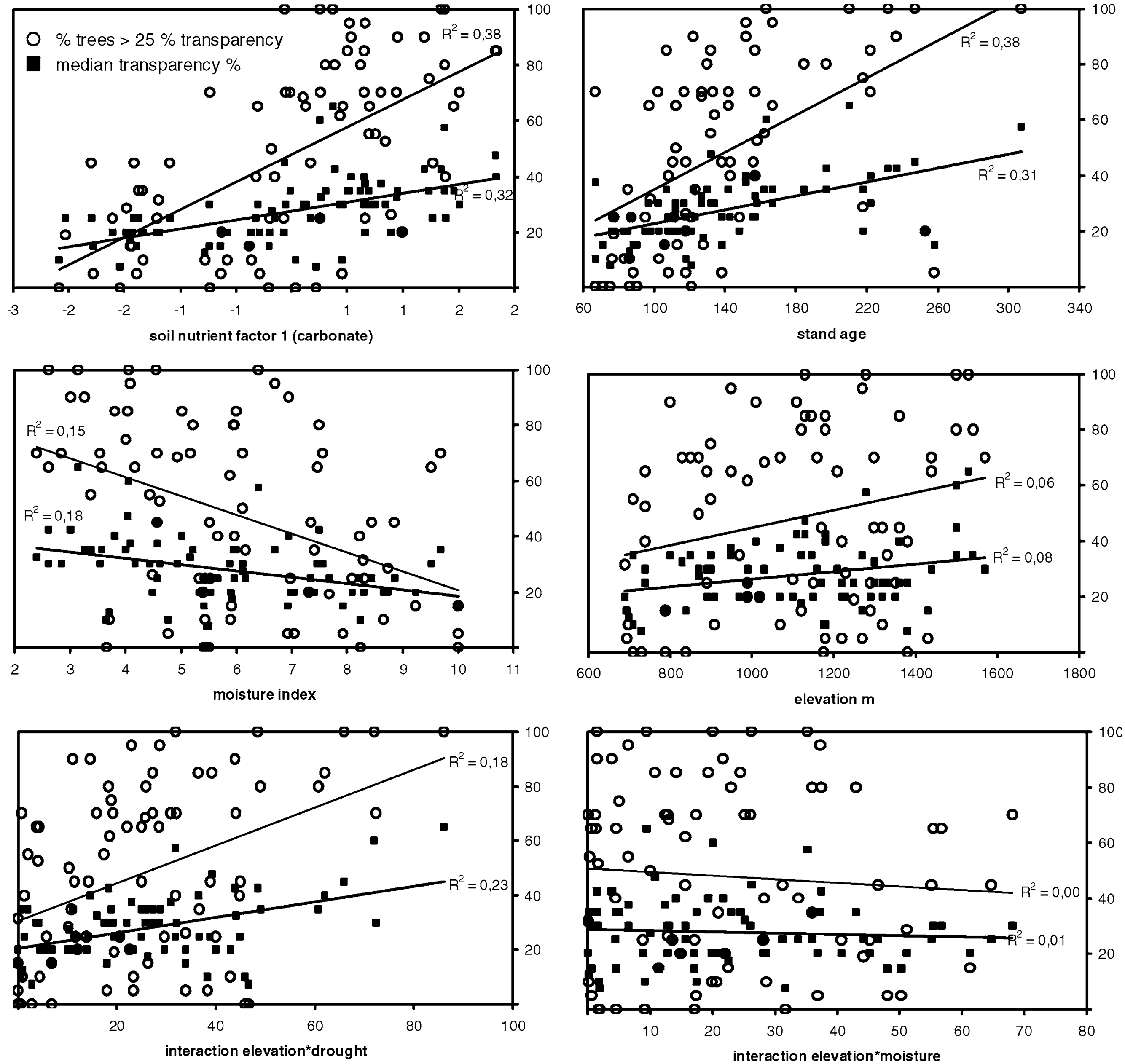

Fig. 2 Scatter plots of crown transparency (median transparency and percentage of 'significantly damaged' trees) against predictor variables with linear regression lines

In summary, crown transparency was predicted to an accuracy of 50% from chemical soil properties related to carbonate depth, stand age and the elevation–drought interaction. Site index could be modelled even better from carbonate factor, elevation and water storage. Both indicators of tree vitality followed very similar ecological gradients in the studied sample.

Nutritional status of Norway spruce at 12 study sites

Foliar concentrations of most elements were well above the conventional limits of deficiency (Anonymous 1996a, b; Table 5). While elements P, N, K and Mg were more abundant in young spruce needles, Fe, Ca and Al had accumulated in older needles. Deficient concentrations in 1-year-old needles, which were found regularly for P, N and twice for Fe, were invariably associated with low needle weights and high crown transparency. Four of the stands with low P also had disharmonious N/P ratios (Hüttl 1991).

While crown transparency was not significantly related to any single foliar element level, there was a tight relationship with needle weight (Table 6). There was also a remarkable positive relationship between site index and needle weight. Foliar concentrations were related to soil nutrient factors derived in PCA. The carbonate factor was particularly closely mirrored in tree nutrition by increasing Ca, decreasing P and Mn

Table 4 Results of stepwise multiple regression of crown condition and site index against ecological predictor variables, abbreviations as in Table 2

Dependent: median crown transparency					
R^2_{corr}	0.487				
F-value	25.3				
P	0.000				
	b	SD	β	T	P
Intercept	2.324	5.826		0.399	0.691
$\sqrt{\text{AGE}}$	1.851	0.510	0.336	3.630	0.001
NF 1	3.870	1.051	0.339	3.681	0.000
ELEV × DROUGHT	0.154	0.053	0.260	2.934	0.004
Dependent: proportion of trees >25% transparency					
R^2_{corr}	0.497				
F-value	26.3				
P	0.000				
	b	SD	β	T	P
Intercept	−16.719	16.171		−1.034	0.305
NF 1	13.675	2.918	0.427	4.686	0.000
$\sqrt{\text{AGE}}$	4.946	1.416	0.320	3.493	0.001
ELEV × DROUGHT	0.291	0.146	0.175	1.993	0.050
Dependent: stand height at 100 years					
R^2_{corr}	0.578				
F-value	36.2				
P	0.000				
	b	SD	β	T	P
Intercept	39.058	3.029		12.895	0.000
ELEV	−0.014	0.002	−0.515	−6.945	0.000
NF 1	−3.110	0.621	−0.459	−5.011	0.000
MOIST	0.648	0.311	0.191	2.082	0.041

(marginally significant also N) and smaller needles (Table 6).

Discussion

Representing the larger landscape of the Bavarian Alps and its environmental gradients, this study allowed a regional test of causal hypotheses (Table 1) that had been largely derived from local case studies and experiments. Bivariate and partial relationships of crown transparency and ecological variables support the relevance of soil chemical gradients resulting from the vastly differing developmental status of soils (nutrition hypothesis, Rehfuess 1995), of stand age (senescence) and of an interaction between elevation and drought, which could be a result of disrupted stomatal closure at high ozone exposure (Maier-Maercker and Koch 1995). On the other hand, there is no evidence for particular stress at moist high elevation sites, which casts considerable doubt on the significance of Liu and Payer's (1996) variant of the ozone hypothesis. While crown transparency is also higher at relatively dry sites, this gradient can be fully replaced by soil chemistry. This suggests turning around the argument of Webster et al. (1996), who interpreted a positive pH-dependence in Switzerland as a result of lower water capacity of calcareous soils, and to assume a direct effect of chemistry on the vitality of Norway spruce in the Alps.

Site index of spruce stands, as a long-term integrative indicator of vigour, follows the same chemical gradients in the region, but is complemented by elevation and water storage capacity. Using mapped soil information by Freyer (1986), Lang (1991) found a very similar model for site index in Berchtesgaden National Park (situated 135 km east of the study area), with vigorously growing spruce stands on acid silicate substrates and slow-growing stands on limestone and dolomite, which often had thick organic layers. In that study, the soil component even surpassed elevation as a predictor of growth. Likewise, in the Tyrolean Loisach valley, subalpine spruce stands on deeply weathered loam (Terra fusca) were more vigorous than low-elevation stands on shallow calcareous soils (Haupolter 1999). The trend for stands of low site index to be older, which was also found by Lang (1991), demonstrates that logging intensity and rotations have adapted to site conditions. As a consequence, senescence is an important additional explanation of poor crown condition in the protective forests at unproductive sites of the Alps.

The commonalities in the present-day pattern of crown condition, site index and stand age provide circumstantial evidence that the gradients of crown condition as monitored in the Bavarian mountain forests since 1984 have long been in existence and are not

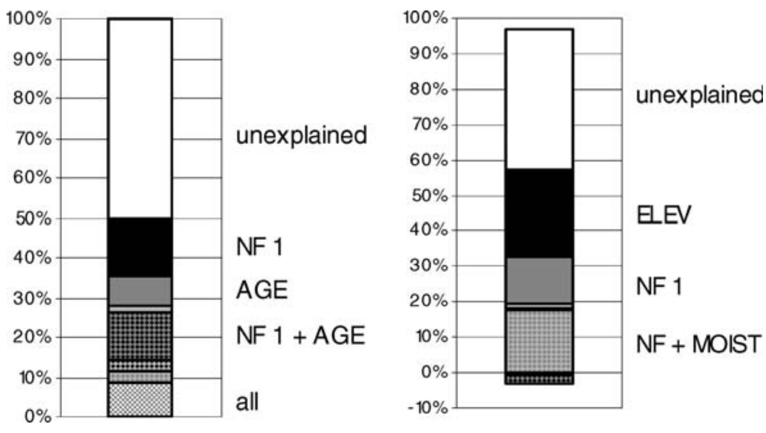

Fig. 3 Partitioning of variance in crown transparency (% of trees >25%, *left*) and in site index of study stands (height at age 100, *right*), abbreviations as in Table 2

Table 5 Diagnostics of spruce nutrition in 12 study plots

Variable	Deficiency threshold	Plot ID											
		156	262	305	26	341	137	13	89	39	94	109	389
N (mg g^{-1})	13	13.5	14.2	14.1	13.3	13.1	**12.4**	13.2	13.6	**12.3**	13.2	**12.4**	13.7
P (mg g^{-1})	1.2	1.52	1.60	1.67	1.25	**1.04**	1.85	**0.84**	1.65	**0.85**	**0.98**	1.28	**1.18**
K (mg g^{-1})	3.5	4.91	4.49	4.99	4.23	4.31	6.33	3.58	6.40	5.68	3.93	4.69	4.77
Mg (mg g^{-1})	0.75	1.00	1.06	1.07	1.63	1.32	1.25	1.01	1.21	1.09	1.28	1.12	1.67
Mn (μg g^{-1})	50	337	570	207	67	127	88	127	148	191	175	98	131
Fe (μg g^{-1})	20	32	23	21	35	27	29	37	**15**	28	32	**18**	31
Ca (mg g^{-1})	1	4.50	3.70	3.71	3.95	4.65	3.73	5.89	4.05	6.27	5.68	4.06	3.91
Al (μg g^{-1})		31	41	30	19	2	12	38	12	13	35	13	25
C (%)		51.4	51.3	51.6	51.7	52.0	51.5	51.6	51.6	51.1	52.1	52.1	51.9
100-needle weight (g)		0.52	0.49	0.52	0.47	0.47	0.49	0.52	0.47	0.49	0.30	0.33	0.34
Median transparency (%)		15	25	25	25	25	30	35	35	35	43	58	60
% trees >25% transparency		5	35	40	40	45	68	65	80	90	80	100	100

Columns are ordered by increasing proportion of transparent crowns. Deficiency thresholds from Anonymous (1996a, b); deficient concentrations are marked in *boldface*

caused by new factors. Thus, it is plausible that chemical soil conditions have always constrained tree growth through their influence on photosynthetically active needle mass. Compared to this robust natural pattern, the contribution of recent increases in ozone exposure, as indicated by the significance of the elevation–drought interaction, is small. Further research on stress caused by ambient ozone will have to concentrate on interactions with natural soil-borne stress factors.

Nutritional status in 12 selected stands supports the hypothesis that Norway spruce faces a variety of problems in acquiring nutrients from soils of the Calcareous Alps. The broad chemical gradient behind the crown transparency pattern is accompanied by decreasing fo-

Table 6 Spearman rank correlation (ρ) and significance levels (P, $n = 12$) between nutritional variables, vitality indicators and site quality; coefficients with $P < 0.05$ in *boldface*

	Al	Ca	Fe	K	Mg	Mn	P	N	100-Needle weight
Percent trees >25%									
ρ	−0.302	0.232	−0.176	0.316	0.281	−0.348	−0.348	−0.552	**−0.689**
P	0.340	0.468	0.585	0.316	0.376	0.268	0.268	0.063	**0.013**
Median transparency									
ρ	0.004	0.229	−0.075	0.068	0.255	−0.294	−0.398	−0.398	**−0.713**
P	0.991	0.473	0.816	0.833	0.425	0.354	0.200	0.200	**0.009**
Stand age									
ρ	0.280	−0.063	−0.098	−0.091	0.098	−0.035	0.105	0.119	−0.545
P	0.379	0.846	0.762	0.779	0.762	0.914	0.746	0.713	0.067
Stand height at 100									
ρ	0.253	−0.225	0.288	−0.235	−0.274	0.207	0.372	0.375	**0.758**
P	0.428	0.483	0.364	0.462	0.389	0.519	0.234	0.229	**0.004**
Elevation									
ρ	0.322	−0.483	−0.448	0.245	−0.007	0.448	0.469	**0.580**	−0.133
P	0.308	0.112	0.145	0.443	0.983	0.145	0.124	**0.048**	0.681
Moisture									
ρ	0.350	−0.308	−0.154	−0.343	0.175	0.042	0.364	0.322	−0.133
P	0.265	0.331	0.633	0.276	0.587	0.897	0.245	0.308	0.681
NF 1									
ρ	−0.245	**0.601**	0.119	−0.266	0.098	**−0.643**	**−0.636**	−0.545	**−0.587**
P	0.443	**0.039**	0.713	0.404	0.762	**0.024**	**0.026**	0.067	**0.045**
NF 2									
ρ	−0.573	0.455	0.224	0.441	−0.182	−0.259	−0.126	−0.573	0.112
P	0.051	0.138	0.484	0.152	0.572	0.417	0.697	0.051	0.729
NF 3									
ρ	0.399	−0.063	−0.014	**−0.797**	−0.336	−0.126	−0.147	−0.028	0.070
P	0.199	0.846	0.966	**0.002**	0.286	0.697	0.649	0.931	0.829
NF 4									
ρ	−0.259	−0.161	**−0.629**	0.112	−0.308	0.224	0.238	0.056	0.336
P	0.417	0.618	**0.028**	0.729	0.331	0.484	0.457	0.863	0.286

liar levels of Mn, P and N and appears to shape the overall pattern of nutrition. In the present study, stands for nutrition analysis were not selected based on visible deficiency symptoms like yellowing, but were chosen solely to provide a representative gradient of crown condition and sites. This is a crucial difference to the majority of previous nutritional studies which concentrated on few spatially autocorrelated stands with visible decline symptoms and few control stands (Bosch 1986; Polle et al. 1992; Haupolter 1999). Choosing relatively few sites from an environmentally heterogeneous pool, without preconceived bias, results in high variability and makes it difficult to obtain statistically significant relationships.

Notwithstanding, the representativity of nutrition data in the present study can be demonstrated by comparing the results to the large systematic sample of Gulder and Kölbel (1993). According to their inventory, P and N deficiencies were the most widespread deficiencies in the Bavarian Alps. The present study conforms to this, but indicates that both symptoms are not necessarily combined in the same stands and that no single deficiency is a necessary or sufficient condition of poor crown condition. In addition, two high elevation sites had deficient Fe levels, which is also typical for the Calcareous Alps according to Gulder and Kölbel. Likewise, sufficient to good K-supply fits into the broad regional statistics, but presents a contrast to the results from the Mangfall area (Bosch 1986) and the Wank site (Polle et al. 1992). Interestingly, the lowest concentrations of K in the present study (3.6 mg g^{-1}) were observed in a stand at the foot of Wank Mountain that is subject to recent forest pasture. It is plausible that K, as an element with a high turnover rate, should be particularly prone to exports of ground vegetation by grazing livestock. In accordance with Gulder and Kölbel (1993), Ca and Mg levels were consistently high.

In conclusion, this study provides strong evidence for the importance of soil chemistry and stand age in controlling crown condition of spruce, and for the close relationship of transparency with other vitality parameters like height growth and needle size. Low nutrient availability owing to low total stocks (young soils with small accumulation of weathered residuals), to low solubility (high pH and Ca concentrations) and to fixation in organic accumulations are starting points in understanding the causal path from alpine carbonate soils to poor tree vitality. As a phenomenon that is widespread in Europe's calcareous mountain forests, which seriously limits silvicultural options and which figures prominently in the statistics of forest condition, it deserves further scientific study.

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