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Response of Norway spruce seedlings in relation to chemical properties of forest soils

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Abstract

The response of Norway spruce seedlings to 157 samples of upper soil layers obtained from 66 forest sites with Norway spruce distributed throughout Switzerland was examined during a 4 months growth chamber study. The pH values of the soil samples ranged from 2.95 to 7.41, with 43% of the samples being acidic ($\text{pH} < 4.75$) and with high concentrations of exchangeable Al. A comparison of two soil extraction methods, the NH_4Cl -extraction representing the 'exchangeable' fraction of cations in soils and the NH_4 -acetate–EDTA-extraction representing the 'extractable' (potentially plant available) fraction, revealed similar results only for the cation K. With the NH_4 -acetate–EDTA-extraction, slightly more Al was extracted in nearly all the samples, and distinctly more Ca was extracted from samples with $\text{pH} > 6$. Seedlings growing in these soil samples showed clear differences in biomass responses, when soils were arranged in classes according to the pH, the sum of 'exchangeable' basic cations (BC), or the BC/Al molar ratio. Reduced biomass was observed at $\text{pH} < 4.75$, at $\text{BC} < 100 \text{ mmol}_c \text{ kg}^{-1}$, and at a BC/Al ratio < 1 . Additionally, a significant positive relationship occurred between root biomass and BC/Al ratio in soils with a low BC/Al ratio (< 10), indicating a potential for the use of the BC/Al ratio of soil extracts to assess the risk of Al stress. In acidic soils, Ca concentrations in the shoots were reduced but Al concentrations were enhanced. This trend was also apparent when soils were arranged according to the BC/Al ratio. Here, Ca concentrations in the shoots were steadily enhanced from BC/Al < 1 to > 1000 , whereas Al was reduced. The Ca concentrations in the shoots were similar to the 'exchangeable' amount of Ca in the soils, whereas for K and Mg an accumulation in the shoots occurred. The Al concentrations in the shoots, on the other hand, indicated a constant translocating rate of Al from the roots to the shoots independent of the 'exchangeable' amounts of Al in the soils. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: *Picea abies*; Root and shoot biomass; Shoot element concentrations; Soil basic cations/Al molar ratio; Soil extractions

1. Introduction

Temperature, moisture, light, ground cover, pathogenic organisms, and allelopathic interactions are

known as critical factors for the growth and survival of conifer seedlings in natural forests (Coates et al., 1991; Brang, 1996). In addition, soil chemical properties such as pH, soil base saturation, or nutrient are also of high importance for seedling growth. In acidic soils, Al is soluble and acts as a phytotoxic agent (Foy, 1984; Sumner et al., 1991). Inhibition of root growth

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and changes in root morphology are the principal visible symptoms of the Al-toxicity (Godbold, 1994; Horst, 1995; Kochian, 1995). Experiments with hydroponically-cultured seedlings of Norway spruce (*Picea abies* (L.) Karst.), the most important tree species in Switzerland, have shown that this species is sensitive to Al³⁺ (Jorns and Hecht-Buchholz, 1985; Godbold et al., 1988). Jentschke et al. (1991) and Hentschel et al. (1993) further found that symptoms of Al-toxicity include reductions of Ca and Mg contents in needles and roots, and of chlorophyll concentration and net photosynthesis in needles.

Over the last 10 years, the percentage of conifers with over 25% crown thinning has increased from 12% to 23% in Switzerland (Anonymous, 1996). A possible reason for this could be the high atmospheric inputs of protons, nitrogen, and sulphur in central Europe, leading to accelerated soil acidification, the loss of base cations, and the release of Al ion into soil solution as a consequence of proton-buffer processes (Matzner, 1992; Matzner and Murach, 1995). Based on present knowledge, the hypothesis relating soil changes to forest damage cannot be falsified (Matzner and Murach, 1995). In this context, the Ca/Al and the basic cation/Al (BC/Al) molar ratios of the soil solution are believed to be valuable indicators for the assessment of the ecological risk of soil acidification or potential acid soil infertility (Sverdrup and Warfvinge, 1993; Cronan and Grigal, 1995). However, chemical data of forest soils at large scales generally are generated from the solid soil matrix and not from soil solutions. Therefore, parameters for monitoring soil acidification and Al stress should be derived from the solid soil matrix.

The aim of this study was to investigate the response of Norway spruce seedlings to natural forest soils with a broad spectrum of soil chemical properties. An 'experimental monitoring' approach was applied using fresh soils sampled from sites containing Norway spruce from throughout Switzerland. Seedlings of Norway spruce, growing under controlled conditions in these soils, were harvested for biomass and element concentration analyses. The following two questions were addressed: (i) are the responses of the seedlings related to soil chemical properties, and (ii) can alternative soil indicators be derived from plant responses to estimate the risk of Al stress?

2. Materials and methods

2.1. Soil sampling and processing

Within the framework of the Swiss forest health monitoring programme, which is conducted on a 8×8 km grid, soil samples were taken in 1992 from 72 survey plots with at least 25% Norway spruce among the tree species (Ahlich et al., 1998). Each plot consisted of a circular area of 500 m². Soil samples were taken below three randomly selected Norway spruce trees (diameter at breast height >12 cm) with a soil coring cylinder (10 cm in diameter, 10 cm in height). Four soil core samples from the upper soil layers were taken in each main geographic direction (north, west, south, east) at a distance of 2 m from the stem of each tree, pooled per tree in a plastic bag, and sent to the laboratory. Each fresh soil sample was mixed, sieved through a 9 mm sieve, and placed in an individual clay pot (mean diameter 7 cm, 10.5 cm in height). The pots had previously been washed with citric acid in a washing machine. The remaining soil material from each sample was dried at 60°C for 3 days for pH measurements and elemental analysis.

2.2. Soil chemical analyses

Soil pH was measured potentiometrically in deionized water and in 0.01 M CaCl₂ with a solid:extractant ratio of 1:2 using an Orion pH meter. Carbonate was detected using a 10% HCl-solution.

Exchangeable cations were extracted with 1 M NH₄Cl for 1 h on an end-over-end shaker using a solid:extractant ratio of 1:10. Ammonium-acetate-EDTA-extractable elements were extracted after 1 h on an end-over-end shaker using a solution containing 0.5 M NH₄-acetate and 0.02 M EDTA, buffered at pH 4.65 with acetic acid (Lakanen and Erviö, 1971). The solid:extractant ratio was 1:10 and the temperature was strictly controlled at 20°C (Zimmermann, 1997). Cation concentrations in the extracts were measured by inductively-coupled plasma atomic emission spectrometry (ICP-AES; Bausch and Lomb ARL 3580 or Perkin Elmer OPTIMA 3000), with three measurements for each sample.

Total C and N contents of ground soil samples were measured using an automatic CN analyser (Carlo Erba

Instruments NA 1500). All analyses were carried out in triplicate. The exchangeable Al-concentration of nine soil samples were below the detection limit of 0.1 ppm and are not included in the data interpretation. The effective cation exchange capacity (CEC_{eff}) was calculated by summing the charge equivalents of exchangeable K, Mg, Ca and Al. Base saturation (BS) was calculated as the fraction of the basic cations K, Ca, and Mg to the CEC_{eff} .

2.3. Plant growing conditions

In each clay pot, 21 surface-sterilized seeds of Norway spruce (seeds originated from a single tree near Tägerwil in eastern Switzerland, germination rate 95%) were placed in a fixed arrangement using a grid and covered with an additional 5 mm of soil. Seeds were surface-sterilized by stirring them for 10 min in a 30% H_2O_2 solution. The clay pots were then placed in a growth chamber with the temperatures of 22°C during the 16 h period of illumination (PAR: $100 \mu\text{mol m}^{-2} \text{s}^{-1}$) and of 14°C during the 8 h of darkness, and with a constant air humidity of 70%. The pots were watered daily with demineralized water to keep the soil moist. Four months after seedling emergency, the pots were emptied, the soil removed from the roots, and the roots lightly rinsed with demineralized water. Then, shoots and roots of the living plants were divided using scissors, and the shoots and roots pooled for each pot. Shoots and roots were dried at 60°C for 3 days, weighed, divided by the number of seedlings per pot to estimate the mean seedling biomass, and then the shoots were ground for elemental analysis.

2.4. Plant chemical analyses

Total N and C was quantified using 6–8 mg of ground shoot material in a Carlo Erba NA1500 analyser. Samples were analyzed in duplicate. Calcium, K, Mg, and Al were determined using 100–250 mg of dried shoot material after ashing at 480°C for 12 h, boiling in 1 ml HNO_3 (10%)/2 ml HCl (30%) for 30 min, diluting to 10 ml with H_2O , and filtering. Measurements were made with inductively coupled plasma atomic-emission spectrometry (ICP-AES; Bausch and Lomb ARL 3580 or Perkin Elmer OPTIMA 3000). Standard reference materials (peach

leaves NIST 1547 and pine needles NIST 1575; National Institute of Standards and Technology) were included in the analyses. Differences to NIST 1547 were of 1–3% for Ca, K, Mg, and P, and of 10% for Al. Differences to NIST 1575 were of 1–3% for Ca, of 5–7% for K and P, and of 23% for Al. Potassium values for 31 shoot samples were lost due to a mishandling of the samples for ICP-analysis.

2.5. Statistical analyses

Statistical analysis were carried out using one-way analysis of variance (ANOVA). Least significance differences were calculated at $P \leq 0.05$ using Fisher's PLSD test. All tests were undertaken using StatView 4.5.

3. Results

3.1. Forest sites and soil parameters

From the totally investigated 216 soil samples of 72 survey plots, complete data sets were obtained only from 157 soil samples of 66 survey plots. The plot distribution over Switzerland is shown in Fig. 1. Thirty-five soil samples came from survey plots between 473 and 800 m above sea level, 41 between 801 and 1200 m, 53 between 1201 and 1600 m, and 28 between 1601 and 2001 m.

The pH values of the 157 soil samples ranged from 2.95 to 7.41 with a mean pH value of 5.17. Using exchangeable Al and detectable carbonate as criteria, the soil samples were ordered into three pH classes (Table 1): acidic soils (pH < 4.75) with no detectable carbonate and high concentrations of exchangeable Al (with 85% of the values being $>0.05 \text{ g kg}^{-1}$; Fig. 2), moderately acidic soils (pH 4.75–6.6) containing no detectable carbonate and low concentrations of exchangeable Al (with 86% of the values being $<0.02 \text{ g kg}^{-1}$; Fig. 2), and neutral or slightly basic soils (pH > 6.6) containing carbonate and low concentrations of exchangeable Al. Most soil samples (43%) were acidic (pH < 4.75), whereas only 17% had a neutral to basic pH (pH > 6.6).

Mean exchangeable Ca increased from acidic to neutral soils by a factor of 4.3, exchangeable Mg was highest in the moderately acidic soils, and Al

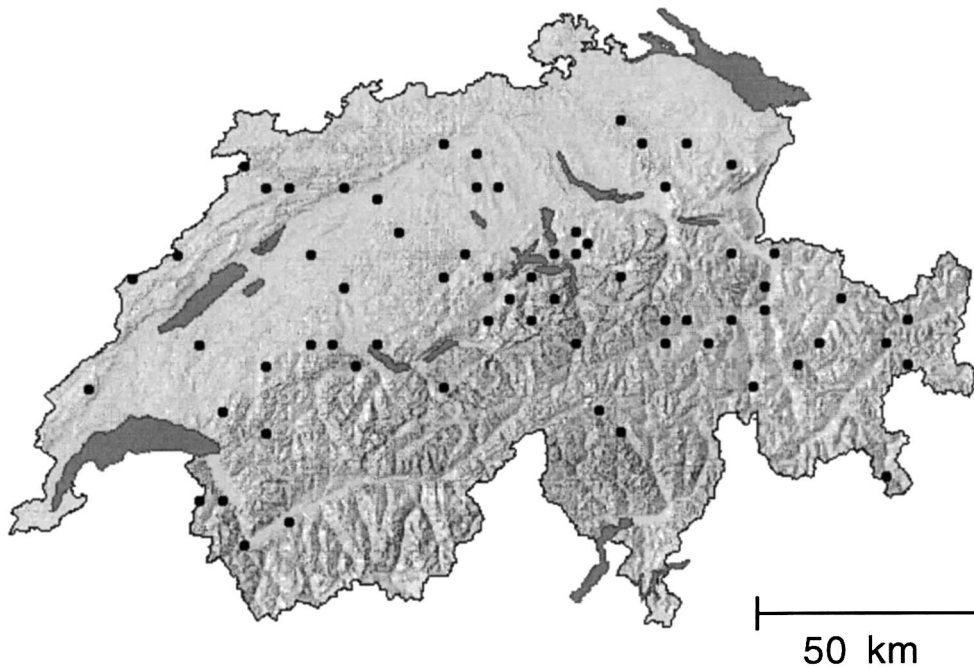


Fig. 1. Location of the survey plots in Switzerland from which soil samples were considered in the present study.

Table 1
Mean values of selected chemical properties of soil samples ordered into three soil pH classes

Soil pH class	<i>n</i>	Soil pH range	Mean soil pH	CEC (mmol _c kg ⁻¹)	BS (% of CEC)	Al (% of CEC)
<4.75	68	2.95–4.74	3.9c	153c	65.3b	34.7a
4.75–6.60	63	4.75–6.60	5.8b	331b	99.3a	0.7b
>6.60	26	6.61–7.41	7.0a	458a	99.9a	0.1b

CEC=Cation exchange capacity; BS=Base saturation.

Values within columns followed by different letters are significantly different at $P \leq 0.05$.

decreased by a factor of 64 (Table 2). Similarly, the mean values of the NH₄-acetate–EDTA-extractable Ca and Mg increased from acidic to neutral soils, whereas the extractable Al decreased (Table 2). In contrast to these cations, exchangeable and extractable K concentrations were not significantly different among the three pH classes. As with Ca, the cation exchange capacity and the BS increased from acidic to neutral soils (Table 1). A comparison of the two extracts showed that the NH₄-acetate–EDTA-extract was less efficient than the NH₄Cl-extract for K in all three pH classes, for Mg at pH<6.6, and for Ca at pH<4.75 (Table 2, Fig. 2). The NH₄-acetate–EDTA-extract was more efficient for Al in

all three pH classes. The BS and the amount of exchangeable Al were strongly pH-dependent (Figs. 2 and 3). Above pH 4.75, BS was close to 100%. In contrast, BS in the acidic soils varied between 11% and 99% and in the moderately acidic soils between 85% and 100%.

Fig. 2 shows the concentrations of K, Ca, Mg and Al in relation to the pH of the soil samples. ‘Exchangeable’ and ‘extractable’ amounts of K were not dependent on the pH of the soil; Ca increased and Al decreased with increasing pH. A highly significant linear relationship occurred with ‘exchangeable’ Ca ($r=0.7$). The highest concentrations of exchangeable Mg was in the pH-range 5.5–7.0.

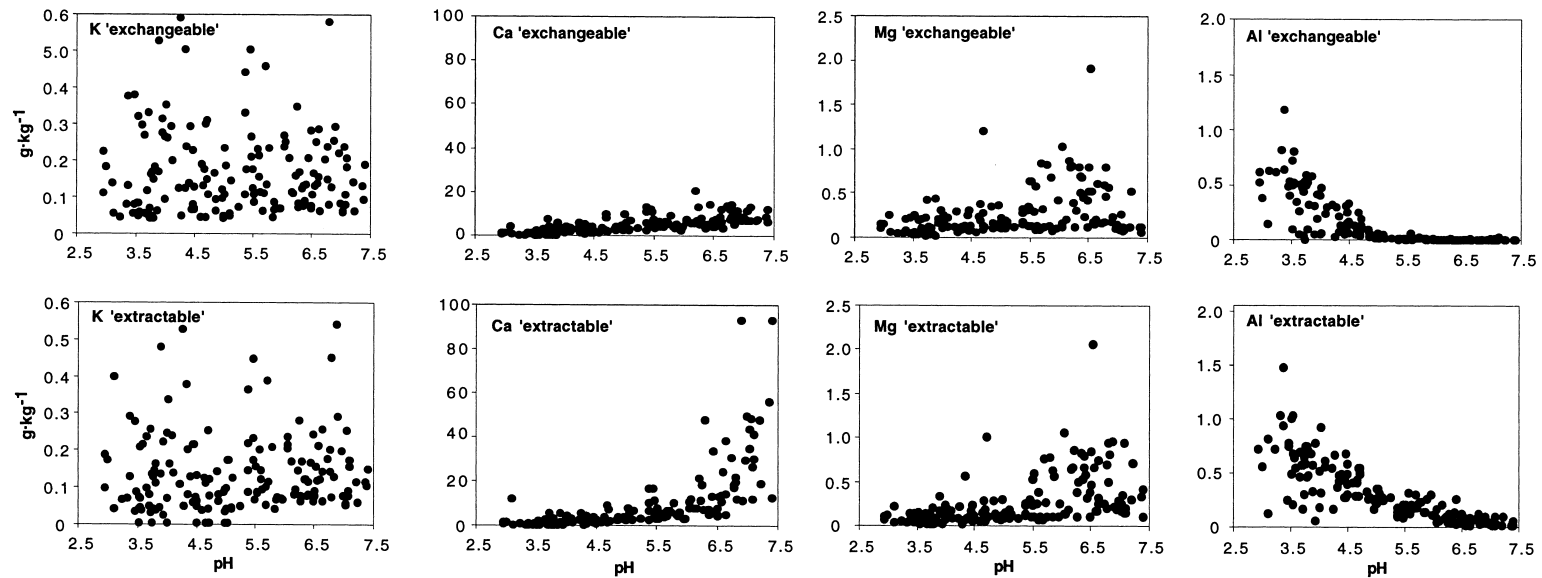


Fig. 2. Relation between soil pH and soil 'exchangeable' (NH₄Cl-extraction) and 'extractable' elements (NH₄-acetate-EDTA-extraction).

Table 2

Mean values (g kg^{-1}) of selected 'exchangeable' (NH_4Cl -extraction) and 'extractable' (NH_4 -acetate-EDTA-extraction) soil elements ordered into three soil pH classes

Soil pH class	'Exchangeable'				'Extractable'			
	K	Ca	Mg	Al	K	Ca	Mg	Al
<4.75	0.17a	2.03c	0.15b	0.32a	0.14a	1.78c	0.12b	0.54a
4.75–6.60	0.16a	5.91b	0.37a	0.01b	0.13a	7.85b	0.35a	0.17b
>6.60	0.17a	8.69a	0.24b	0.01b	0.16a	32.54a	0.40a	0.05c

Values within columns followed by different letters are significantly different at $P \leq 0.05$.

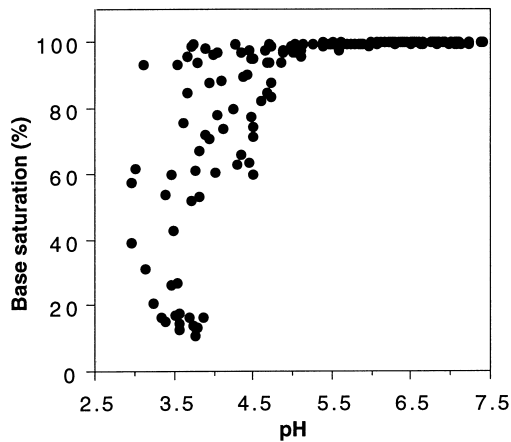


Fig. 3. Relation between soil pH and BS.

3.2. Relationships between soil and plant parameters

The mean number of living seedlings in the pots was 19 (91% of the applied seeds). The mean biomass of shoots of the spruce seedlings was 16.0 ± 4.5 mg with a minimum of 8.4 mg and a maximum of 43.1 mg, and with 91% of the values between 8 and 18 mg (data not shown). Mean root biomass and mean root/shoot ratio were significantly lower in acidic soils compared to moderately acidic soils (Table 3). Arranging the samples in six classes according to the sum of the 'exchangeable' basic cations BC ($\text{BC} = \text{K} + \text{Ca} + \text{Mg}$), significantly lower values were observed for the shoot, root, and total biomass for the two BC classes <50 and 50–100 $\text{mmol}_c \text{kg}^{-1}$ (Fig. 4). A similar trend was obtained when ranging the biomass according to the BC/Al molar ratio of the soil samples (Table 4). Here, significantly lower values were obtained for the shoot, root, and total

Table 3

Mean values of biomass (mg/seedling) and root/shoot ratios ordered into three soil pH classes

Soil pH class	Shoots	Roots	Total	Root/shoot ratio
<4.75	16.6a	11.4b	28.0a	0.71b
4.75–6.60	15.9a	12.6a	28.5a	0.80a
>6.60	14.6a	11.6ab	26.2a	0.80a

Values within columns followed by different letters are significantly different at $P \leq 0.05$.

biomass for the BC/Al class <1 compared to the classes 1–10, 10–100, and 100–1000.

Mean concentrations of Ca in the plant material increased with increasing soil pH, whereas N, P, Mg, and Al decreased (Table 5). Potassium showed no clear pH-dependence. Similarly, mean concentrations

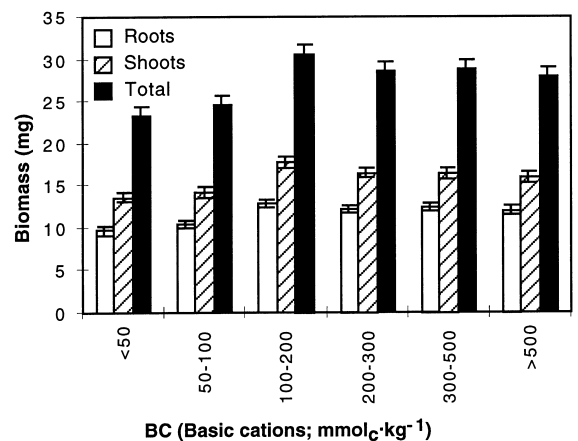


Fig. 4. Mean biomass per seedling (\pm standard error) in relation to classes of basic cation concentrations (BC; NH_4Cl -extraction) (class <50, $n=19$; class 50–100, $n=17$; class 100–200, $n=33$; class 200–300, $n=28$; class 300–500, $n=41$; class >500, $n=19$).

Table 4

Mean values of soil pH, biomass (mg/seedling), and root/shoot ratios ordered into five classes of BC/Al molar ratios (NH₄Cl-extraction)

Soil BC/Al molar ratio	<i>n</i>	Mean soil pH	Shoots	Roots	Total	Root/shoot ratio
<1	18	3.5e	13.4b	9.6b	23.0b	0.73ab
1–10	31	4.1d	16.8a	11.6a	28.4a	0.72b
10–100	24	4.5c	17.2a	12.7a	29.9a	0.76ab
100–1000	40	5.8b	16.4a	12.6a	29.0a	0.78ab
>1000	35	6.4a	15.5ab	12.3a	27.8a	0.80a

Values within columns followed by different letters are significantly different at $P \leq 0.05$.

Table 5

Mean values of selected shoot element contents (g kg⁻¹) of seedlings ordered into three soil pH classes

Soil pH class	N	P	K	Ca	Mg	Al	Shoot Ca/Al molar ratio
<4.75	20.4a	1.84a	4.92b	3.91c	1.35a	0.16a	35c
4.75–6.60	17.7b	1.67ab	5.55a	6.78b	1.41a	0.14ab	67b
>6.60	15.0c	1.50b	4.92ab	8.78a	1.18b	0.10b	118a

Values within columns followed by different letters are significantly different at $P \leq 0.05$.

Table 6

Mean values of selected shoot element contents (g kg⁻¹) of seedlings ordered into five classes of BC/Al molar ratios (NH₄Cl-extraction)

Soil BC/Al molar ratio	N	P	K	Ca	Mg	Al	Shoot Ca/Al molar ratio
<1	17.3b	1.74ab	3.62b	2.94e	1.24b	0.25a	11c
1–10	20.3a	1.68ab	5.07a	3.97d	1.32ab	0.16b	26c
10–100	20.8a	1.91a	5.52a	4.89c	1.44a	0.10bc	50bc
100–1000	17.4b	1.73ab	5.45a	6.80b	1.31ab	0.15b	62b
>1000	17.5b	1.57b	5.42a	8.22a	1.35ab	0.09c	119a

Values within columns followed by different letters are significantly different at $P \leq 0.05$.

of Ca increased and Al decreased by factors of about 3 with increasing BC/Al molar class (Table 6). In addition, the shoot Ca/Al molar ratio increased by a factor of about 11. The concentrations of K and Mg were significantly reduced at BC/Al class <1 compared to the BC/Al class 10–100, whereas N was significantly enhanced (Table 6).

The soil BC/Al molar ratio <10 was highly correlated with the soil parameters pH and BS (Fig. 5). In addition, highly significant positive correlations occurred also between the soil BC/Al molar ratio <10 and the plant parameters Ca/Al molar ratio and root biomass (Fig. 5).

A comparison of the mean values of the cations K, Ca, and Mg in each pH class of the soil samples with the mean concentration of the corresponding elements in the shoots reveals the accumulation of these ele-

ments (Fig. 6). The K or Mg concentrations in the shoots in all three pH classes did not vary significantly, independent of the amount of 'exchangeable' or 'extractable' K or Mg. The accumulation factor which relates the concentration of an 'exchangeable' cation in the soil to the concentration of that element in the shoot, varied between 29 and 35 for K and between 4 and 9 for Mg. The Ca concentration in the shoots strongly depended on the 'exchangeable' amount in the soil. It increased from soil pH class <4.75 to >6.6. The accumulation factor, in contrast, decreased from 1.9 for the soil pH class <4.75 to 1.0 in soil pH class >6.6. Compared to other macroelements, Al concentrations in the shoots were low. In the soil pH class <4.75 with the highest Al concentration in the soil, the Al concentration in the shoots were below the amount of exchangeable Al in the soil by a factor of 2. In the

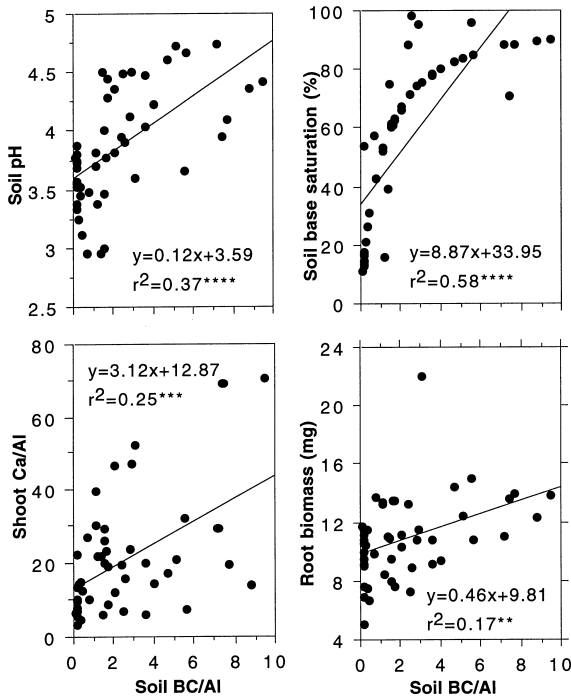


Fig. 5. Relation between the soil BC/Al molar ratio <10 (NH_4Cl -extraction) and the soil pH, the soil base saturation, the shoot Ca/Al molar ratio, and the root biomass. (****, $P \leq 0.0001$; ***, $P \leq 0.001$; **, $P \leq 0.01$) ($n=49$).

two soil classes with $\text{pH} > 4.75$, the Al concentration in the shoots exceeded the amount of exchangeable Al in the soil, indicating an accumulation with factors of 10.5 and 20.2, respectively.

In general, concentrations of the shoot nutritional elements K, Ca, and Mg were highly correlated with the soil concentrations (Table 7), independently of the soil pH classes, and independently of the extraction method. Comparing the two soil extraction methods, however, distinctly higher correlation coefficients were obtained for Ca with the NH_4Cl -extraction in the acidic soil pH class <4.75. Conversely, Mg had a higher correlation in the acidic soil pH class <4.75 after NH_4 -acetate-EDTA-extraction. Only slight or insignificant correlations between soil and shoot concentrations were obtained for Al.

4. Discussion

To estimate the optimal soil extraction method representative for plant growth responses, the methods for extracting 'exchangeable' and 'extractable' cations were compared. The extraction efficiency of the two extractants can be explained by their chemical

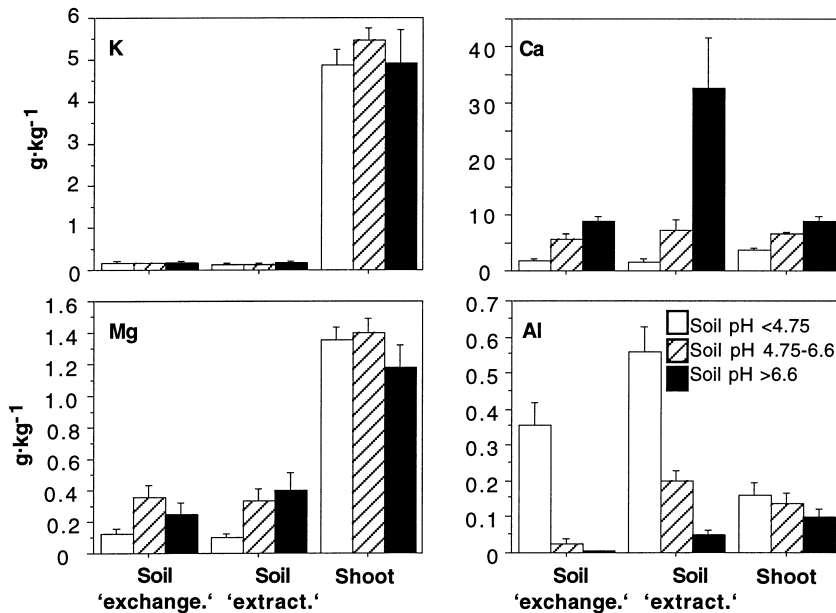


Fig. 6. Mean contents of 'exchangeable' (NH_4Cl -extraction) and 'extractable' (NH_4 -acetate-EDTA-extraction) elements in soils and of elements in shoots in relation to soil pH classes.

Table 7

Correlation coefficients (r) between equivalent shoot elements and soil 'exchangeable' (NH_4Cl -extraction) and 'extractable' elements (NH_4 -acetate–EDTA-extraction)

	Soil pH class	K	Ca	Mg	Al
Exchangeable	<4.75	0.52****	0.55****	0.36**	0.28*
	4.75–6.60	0.61****	0.75****	0.77****	0.11 ^{NS}
	>6.60	0.74***	0.43*	0.75****	0.27 ^{NS}
	All 3 pH classes	0.55****	0.82****	0.61****	0.24**
Extractable	<4.75	0.52****	0.42***	0.65****	0.15 ^{NS}
	4.75–6.60	0.62****	0.67****	0.79****	0.28*
	>6.60	0.73***	0.53**	0.78****	0.20 ^{NS}
	All 3 pH classes	0.55****	0.69****	0.62****	0.21**

****, $P \leq 0.0001$; ***, $P \leq 0.001$; **, $P \leq 0.01$; *, $P \leq 0.05$; ^{NS}, not significant.

composition. The exchanging cation of both extractants is the same (NH_4^+). The concentration, however, is 1.0 M in the NH_4Cl -extract and 0.5 in the NH_4 -acetate–EDTA-extract. In addition, the NH_4 -acetate–EDTA-extract is buffered with acetic acid at pH 4.65 and contains EDTA as a complexing agent. Both extracts are suited to the measurement of exchangeable cations, although the results may differ due to the different NH_4^+ concentrations and the buffering properties of the NH_4 -acetate–EDTA-extract. Besides the exchangeable cations, the NH_4 -acetate–EDTA-extract also affects elements that are more strongly bound in the soil but which are still thought to be available to plants (Lakanen and Erviö, 1971; Zimmermann, 1997). The extractability of such elements depends on their conditional stability constants with EDTA.

The amount of 'exchangeable' and 'extractable' K is not related to the soil pH. The K concentration in the top soil is controlled primarily by the vegetation, the nutrient cycle and the leaching conditions. The efficiency of both extracts is similar because K is not complexed by EDTA. The generally lower concentrations in the NH_4 -acetate–EDTA-extract can be explained by its lower NH_4^+ concentration. 'Exchangeable' Ca is positively related with soil pH. The extractability of the two extracts is similar at pH values <6. At higher soil pH values, the NH_4 -acetate–EDTA-extract becomes much more efficient. This is explained by the presence of even low amounts of lime in the soil matrix, which are affected by the acetic acid during the extraction procedure (Zimmermann and Blaser, 1993). 'Exchangeable' Al strongly depends on the pH of the soil, which also governs the

Al-solubility. The 'exchangeable' fraction exponentially increases below pH 4.6. Due to the strong complexation of Al by EDTA, the NH_4 -acetate–EDTA-extract is much more efficient and affects not only the 'exchangeable' fraction but also any Al that is present as non crystalline Al-compounds or that is complexed by the organic matter (Zimmermann, 1997).

The growth of Norway spruce seedlings for 4 months in these natural forest top soils indicated that various soil chemical parameters are related to biomass production. In soils with a pH < 4.75, root biomass was significantly reduced compared to moderately acidic soils, resulting in significantly decreased root/shoot ratios. When the soils were ordered according to the sum of the 'exchangeable' basic cations (BC), there were significantly lower values for root, shoot, and total biomass in the two classes with $\text{BC} \leq 100 \text{ mmol}_c \text{ kg}^{-1}$. This suggests that the growth of Norway spruce seedlings is limited by the low availability of these nutritional elements. Similarly, when using the BC/Al ratio of the 'exchangeable' fraction, significantly lower values were obtained for root, shoot, and total biomass in the class $\text{BC/Al} < 1$.

Although concentrations of some selected elements in the plants differed significantly among the three pH-classes for most of the elements, they are still sufficient for plant growth in all pH-classes (according to data published for *Picea abies* in Bergmann, 1993), with one exception of K in acidic soils, where 4.9 g kg^{-1} represents a slight deficiency (sufficient: $5.0\text{--}12.0 \text{ g kg}^{-1}$). The Ca concentrations in the shoots

increased continually with increasing soil pH class whereas Al concentrations decreased. Calcium uptake is obviously closely related to the concentration of the 'exchangeable' fraction of the soils. For Ca the NH_4Cl -extraction should be used in preference to the NH_4 -acetate–EDTA-extraction, as correlation coefficients between soil and shoot element concentrations were slightly higher for the NH_4Cl -method at $\text{pH} < 6.6$, also NH_4 -acetate–EDTA-extract is not recommended for soils containing lime. On the other hand, the Mg concentrations in the shoots and the Mg concentrations from both extracts were more or less identical related, with the exception at low pH. Here, the relation of the Mg concentrations of the shoots with the soil Mg concentrations from the NH_4 -acetate–EDTA-extract was distinctly higher than that from the NH_4Cl -extract, indicating that the efficiency of the plant roots exceeded the 'exchangeable' Mg fraction from the soils. Gonzalez Cascon et al. (1989) in their studies observed similar high significant correlations between soil elements and the growth of *Abies alba* Mill. seedlings. Water-extraction and NH_4Cl -extraction both gave more or less identical values. Low correlations, as in the present study, were only observed for the corresponding Al fractions in the soil.

The concentration of 'exchangeable' cations only reflects their plant availability to a minor extent. Considerable amounts of cations can be taken up by plants, independent of the concentrations in the soil. High accumulation factors can be calculated for K and Mg independent of the soil pH class because of the relatively low concentrations in the soils. However, it also has to be taken into account that a certain percentage of the elements originated from the seeds. Analyses of 24-day-old germlings (germinated on water agar) revealed that from the four elements K, Ca, Mg, and Al, only Mg was present in higher concentrations (three times) in the germlings compared to the shoots of 4-month-old seedlings (unpublished data), indicating that the accumulation rate of Mg effectively was about 30% lower. On the other hand, concentrations of Al in the shoots from all pH classes were similar, although the amounts of exchangeable Al in the soils of the three pH classes varied from 0.01 to 0.35 g kg^{-1} . Possibly, Al is accumulated in the roots (compare also Hentschel et al., 1993; Zysset et al., 1996), but translocated to the

shoots in constant rates and independent of soil pH and root Al concentrations.

In this study, soils with a low BC/Al molar ratio (< 10) from NH_4Cl -extracted soils had a BC/Al molar ratio that was positively correlated with the root biomass. These results agree with those of other studies (Sverdrup and Warfvinge, 1993; Cronan and Grigal, 1995; Zysset et al., 1996) showing that the growth of most plants is reduced at low BC/Al ratios. In this context, the question arises whether the BC/Al ratio of the soil extracts can be as an indicator to assess Al stress, as is done with the BC/Al ratio of soil solutions (Sverdrup and Warfvinge, 1993; Cronan and Grigal, 1995). The use of soil extracts instead of soil solutions would have several advantages, enabling (a) the sampling of soils on a large scale representative for whole areas, (b) the recognition of 'hotspots' in terms of soil acidification and Al stress, and (c) the validation of parameters by plant responses (bioindication). In a study done by Joslin and Wolfe (1989), significant correlations were also obtained between the Ca/Al ratio of SrCl_2 -extracted soils (suitable for plant-available Al; Joslin and Wolfe, 1988) and the foliar biomass, the root and foliar tissue concentrations, and the root branching of northern red oak (*Quercus rubra* L.) seedlings.

The soil base saturation and the Ca/Al molar ratio of the foliage are considered to be alternative indicators for Al stress (Cronan and Grigal, 1995). In the present study, six soil samples from four survey plots had a BS below 15%, the value which is considered as critical. These six soil samples were characterized by a BC/Al molar ratio < 0.2 , a soil $\text{pH} < 3.9$, and shoot Ca/Al molar ratios < 11 of the seedlings grown in these soils (a value < 12.5 represents a 50% risk of adverse impact on growth or nutrition; Cronan and Grigal, 1995). The forest sites of these soil samples are all located on the Swiss Plateau (between the Jurassic Mountains and the Alps; elevation 475–686 m above sea level).

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References

- Ahlich, K., Rigling, D., Holdenrieder, O., Sieber, T.N., 1998. Dark septate hyphomycetes in Swiss conifer forest soils surveyed using Norway-spruce seedlings as bait. *Soil Biol. Biochem.* 30, 1069–1075.
- Anonymous, 1996. Forest condition in Europe. Results of the 1995 survey. EC-UN/ECE report, Brussels, Belgium, and Geneva, Switzerland.
- Bergmann, W., 1993. Ernährungsstörungen bei Kulturpflanzen. Gustav Fischer, Jena, Germany, p. 835.
- Brang, P., 1996. Experimentelle Untersuchungen zur Ansammlungsökologie der Fichte im zwischenalpinen Gebirgswald. *Beih. Schweiz. Z. Forstwes* 77, 1–375.
- Coates, K.D., Emmingham, W.H., Radosevich, S.R., 1991. Conifer-seedling success and microclimate at different levels of herb and shrub cover in a *Rhododendron-Vaccinium-Menziesia* community of south central British Columbia. *Can. J. For. Res* 21, 858–866.
- Cronan, C.S., Grigal, D.F., 1995. Use of calcium/aluminum ratios as indicators of stress in forest ecosystems. *J. Environ. Qual.* 24, 209–226.
- Foy, C.D., 1984. Physiological effects of hydrogen, aluminum and manganese toxicities in acid soils. In: Adams, F. (Ed.), *Soil Acidity and Liming*. Agronomy Monogr., vol. 12, ASA, Madison, WI, pp. 57–97.
- Godbold, D.L., 1994. Aluminum and heavy metal stress: From the rhizosphere to the whole plant. In: Godbold, D.L., Hüttermann, A. (Eds.), *Effects of Acid Rain on Forest Processes*. Wiley-Liss, New York, pp. 231–264.
- Godbold, D.L., Dictus, K., Hüttermann, A., 1988. Influence of aluminum and nitrate on root growth and mineral nutrition of Norway spruce (*Picea abies*) seedlings. *Can. J. For. Res* 18, 1167–1171.
- Gonzalez Cascon, M.R., Alcubilla, M., Rehfuess, K.E., 1989. Entwicklung von Tannensämlingen (*Abies alba* Mill.) in Abhängigkeit von der Basensättigung natürlicher Substrate. *Allg. Forst. J. Ztg.* 160, 233–241.
- Hentschel, E., Godbold, D.L., Marschner, P., Schlegel, H., Jentschke, G., 1993. The effect of *Paxillus involutus* Fr. on aluminum sensitivity of Norway spruce seedlings. *Tree Physiol.* 12, 379–390.
- Horst, W.J., 1995. The role of the apoplast in aluminum toxicity and resistance of higher plants: A review. *Z. Pflanzenernähr. Bodenk.* 158, 419–428.
- Jentschke, G., Godbold, D.L., Hüttermann, A., 1991. Culture of mycorrhizal tree seedlings under controlled conditions: Effects of nitrogen and aluminium. *Physiol. Plant.* 81, 408–416.
- Jorns, A., Hecht-Buchholz, C., 1985. Aluminiuminduzierter Magnesium- und Calciummangel im Laborversuch bei Fichtensämlingen. *Allg. Forstz.* 46, 1248–1252.
- Joslin, J.D., Wolfe, M.H., 1988. Responses of red spruce seedlings to changes in soil aluminum in six amended forest soil horizons. *Can. J. For. Res.* 18, 1614–1623.
- Joslin, J.D., Wolfe, M.H., 1989. Aluminum effects on northern red oak seedling growth in six forest soil horizons. *Soil Sci. Soc. Am. J.* 53, 274–281.
- Kochian, L.V., 1995. Cellular mechanisms of aluminum toxicity and resistance in plants. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 46, 237–260.
- Lakanen, E., Erviö, R., 1971. A comparison of eight extractants for the determination of plant available micronutrients in soil. *Acta Agral. Fenn.* 123, 223–232.
- Matzner, E., 1992. Acidification of forests and forest soils: Current status. In: Schneider, T. (Ed.), *Acidification Research: Evaluation and Policy Applications*. Elsevier, Amsterdam, The Netherlands, pp. 77–86.
- Matzner, E., Murach, D., 1995. Soil changes induced by air pollutant deposition and their implication for forests in Central Europe. *Water Air Soil Pollut.* 85, 63–76.
- Sumner, M.E., Fey, M.V., Noble, A.D., 1991. Nutrient status and toxicity problems in acid soils. In: Ulrich, B., Sumner, M.E. (Eds.), *Soil Acidity*. Springer, Berlin, Germany, pp. 149–178.
- Sverdrup, H., Warfvinge, P., 1993. The effect of soil acidification on the growth of trees, grass, herbs as expressed by the (Ca+Mg+K)/Al ratio. Rep. in *Ecology and Environmental Engineering 2*. Lund Univ., Dep. of Chem. Eng. II, Lund, Sweden, p. 125.
- Zimmermann, S., 1997. Wirkung einer gepufferten Ammonium-Acetat-EDTA-Extraktion auf ausgewählte Bodenbestandteile und natürliche Bodenproben. Ph.D. Thesis, Swiss Federal Institute of Technology (ETH), Zürich, Switzerland, p. 154.
- Zimmermann, S., Blaser, P., 1993. Resultate einer Pilotstudie zur Durchführung einer schweizerischen Waldbodeninventur. In: M. Kirchner, K. Rösel, M. Reuther (Eds.), *Stoffeinträge aus der Atmosphäre und Waldbodenbelastung in den Ländern von ARGE ALP und ALPEN-ADRIA*, GSF-Bericht 39, Neuherberg, Germany, pp. 179–191.
- Zysset, M., Brunner, I., Frey, B., Blaser, P., 1996. Response of European chestnut to varying calcium/aluminum ratios. *J. Environ. Qual.* 25, 702–708.