

Early development and nutrition of Norway spruce (*Picea abies* (L.) Karst.) seedlings on different seedbeds in the Bavarian limestone Alps – a bioassay

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Abstract – The development and nutrition of Norway spruce seedlings growing under controlled conditions in three different seedbed types (mineral Ah horizon, organic layer, highly decayed dead wood) obtained from two protective forest sites in the Bavarian limestone Alps was investigated for one growing season. The seedlings showed clear responses to the three natural seedbed types in biomass development and nutritional status. Their biomass was significantly lower in mineral soils and organic layers as compared to decayed dead wood. Seedlings in organic and in decayed wood substrates had significantly higher contents of N, P, K, Mn, Zn (only decayed wood), and more balanced nutrient relations as compared to seedlings grown in mineral soils. It was indicated that the acid organic layers and highly decayed dead wood represents a good seedbed for spruce natural regeneration, especially in regard to the impaired nutrient availability on alkaline dolomite sites in the Bavarian limestone Alps.

Picea abies / decayed woody debris / organic layer / mineral soil / seedbed

Résumé – Développement précoce et nutrition de semis de *Picea abies* (L.) Karst. élevés sur différents substrats dans les Alpes Bavaoises calcaires. Le développement et la nutrition de semis d'épicéa poussant en conditions contrôlées sur trois types de substrat (horizon minéral Ah, strate organique, bois mort très pourri), prélevés dans deux sites forestiers protégés dans les Alpes Bavaoises calcaires, ont été étudiés pendant une saison de végétation. Les semis ont présenté une réponse nette au trois types de substrats naturels au plan du développement de la biomasse et du statut nutritionnel. Leur biomasse était significativement plus faible sur sol minéral et strate organique comparativement au bois mort pourri. Les semis sur sol organique et substrat de bois mort pourri ont présenté des teneurs significativement plus élevées en N, P, K, Mn, Zn (seulement sur bois mort pourri), et des relations nutritionnelles plus équilibrées comparativement aux semis poussant sur sol minéral. Il a été montré que les strates organiques acides et le bois mort très pourri constituent un bon substrat pour la régénération naturelle de l'épicéa, en particulier au plan de la faible disponibilité des nutriments sur les sites dolomitiques alcalins dans les Alpes calcaires bavaoises.

Picea abies / débris décomposés de bois / strate organique / sol minéral / substrat

1. INTRODUCTION

Germination, survival, and growth depends on “safe sites” that provide the precise environmental conditions required by a particular seedling [32]. Site conditions like e.g. temperature, moisture, pathogenic fungi, or light are important factors for Norway spruce (*Picea abies* (L.) Karst.) seedling development in natural forests [5, 14, 34]. It has recently been shown that the recruitment of a new spruce generation strongly depends on the quality of the seedbed [14, 15, 46]. This applies in particular for spruce, because spruce is a species with small seeds and therefore is more substrate-restricted than other tree species [27, 35, 37].

The centre of the geographical extension of Norway spruce is located in nutrient poor, infertile environments, and spruce grows typically under acid soil conditions with thick organic

layers [50]. Mountain forests of the Bavarian Limestone Alps are characterised by a highly heterogeneous forest floor [23]. Baier et al. [9] found that the spatial distribution of spruce saplings in those forests was not random and varied among different microsite types. In addition, young, naturally regenerated Norway spruces on thick humus layers exhibited a better nutrition status than trees growing on shallow mineral soils without humus layers [7].

Potential seedbed substrates (e.g. organic layer, mineral soil, or coarse woody debris/nurse logs) are highly differentiated in physical (e.g. water storage capacity) and chemical properties. These differences in soil chemistry and plant nutrient availability are of great importance for seedling biomass responses [17, 24, 44]. Higher nutrient concentrations in spruce seedlings have been attributed to improved growth in the field, which indicates the importance of adequate nutrient supply to maintain physiological activity and growth [28]. However, the regeneration ecology of spruce on decayed wood, in particular

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Table I. Characteristics of the two study sites “Rottauer Alm” and “Fischbachkopf” (¹ according to German soil classification; ² according to FAO soil classification; ³ according to Ewald [23]).

	Rottauer Alm	Fischbachkopf
Sea level/exposition/ location/ inclination	1 100 m a.s.l./south exposed/ 47° 48' 00" N, 12° 22' 30" O/25°	1 350 m a.s.l./south exposed/ 47° 31' 04" N, 11° 20' 54" O/25° –35°
Average annual temperature	4.8 °C	2.5 °C
Average annual precipitation	1 900 mm	2 150 mm
Bedrock	Dolomite	
Soils	Rendzina, Tangelhumus ¹ Rendzic leptosols, eutric leptosols ²	
Potentially natural vegetation	Degraded moderately dry, mixed mountain forest <i>Aposerido-Fagetum caricetosum albae</i> ³	Degraded moderately fresh, mixed mountain forest <i>Aposerido-Fagetum caricetosum ferrugineae</i> ³
Forest stand	Age: 160–220 years; low canopy density; tree composition: 82% <i>Picea abies</i> , 11% <i>Abies alba</i> , and 7% <i>Sorbus aria</i> ; sparse natural regeneration; status: protective forest	Age: 150–300 years; low canopy density; tree composition: 100% <i>Picea abies</i> ; sparse natural regeneration; status: protective forest
Stand history	Former clear cuts and impact of grazing	

with regard to the benefits of decayed wood on spruce nutrition is insufficiently known [15, 22]. Furthermore, the positive properties of humus layers on seedling establishment of spruce are at the moment not fully understood [30, 31].

Increased understanding about the relationship between chemical properties of mineral soil, organic layer, and decayed woody debris on the one hand and the development and nutrition of Norway spruce seedlings on the other may have practical applications for the improvement of future methods of natural or artificial regeneration. To elucidate this relationship, we established a bioassay with Norway spruce seedlings growing for one growing season under controlled conditions on fresh, undisturbed seedbed samples. Bioassays, in which trees are grown in the problem soil under controlled environments with a variety of nutrient treatments or nutrient availabilities, can be a useful diagnostic technique, because their results are easier to interpret than soil or foliage analyses [45, 55]. This study therefore aims at analysing the influence of the three most common seedbeds in mountainous forests on Norway spruce seedling biomass development, mycorrhization, and nutrition.

2. MATERIAL AND METHODS

2.1. Study sites and soil substrate sampling

Samples of organic layers, mineral soils, and highly decayed coarse woody debris were taken from two, southern exposed mountainous (1100–1350 m a.s.l.) protective forests “Rottauer Alm” and “Fischbachkopf” (Tab. I). Stand structure, management and utilisation history (former wood pasture), soils, and the forest floor represented typical situations for reforestation sites in the Bavarian Alps.

The pasture woodlands were characterised by a low tree density, evident by large canopy openings, sparse dead wood, and a highly heterogeneous thickness of the organic layer. The spruce dominated, steep mountain slopes were located on *Aposerido-Fagetum* forest sites [23]. All soils were derived from dolomite ($\text{CaMg}(\text{CO}_3)_2$), a very pure (low clay mineral content) sediment, with a porous bedrock [11]. Soils belonged to the type “Rendzina” (according to the German soil classification; [6]) or alternatively to the type rendzic leptosols (according to the FAO classification; [18]). In addition, thick humus layers “Tangelhumus” or eutric leptosols (> 15 cm up to 35 cm, mainly built up from spruce litter) were found protected near old trees or stumps. Mineral soils with thin “mull humus” layer (up to 1 cm, only fresh litter of gramineous and herbaceous plants) or bare mineral soil without any organic layer appeared in large canopy gaps (see also [9]).

Within an area of about one hectare per site, 14 randomly distributed samples of organic layers and mineral soils were collected in May 2003. Organic layers were taken approximately 50 cm apart from the stems of old spruces. Mineral soil samples were collected in the centre of wide canopy gaps. Organic layers (abbreviation: organic) included the horizons L (= litter), Of (= fermentation), and Oh (= humification), the mineral substrate (abbreviation: mineral) consisted of Ah (= upper mineral soil, rich in humus) horizons without any organic layer [6]. As a result of intensive historic forest utilisation, decayed coarse woody debris (abbreviation: decayed wood) was exceedingly scarce. To obtain data for dead wood, we collected 7 samples within the two study sites from highly decayed coarse spruce logs (decay class V, [52]). Accumulated litter on logs influences seedling growth [31]. Therefore, we paid attention to sample pure dead wood without any litter on the logs.

All substrate samples were collected in duplicate: One intact, undisturbed fresh sample as growing substrate for spruce seedlings, and close-by, one sample for chemical analysis. A substrate cube according to the size of a polyethylene pot (103 mm long × 103 mm

wide × 64 mm deep) was carefully cut out with a knife. Thereafter, the fresh samples were packed at once into the pots. All 63 fresh soil samples (28 mineral, 28 organic, 7 decayed wood) were stored in a fridge at 5 °C until germinated spruce seeds were potted. Soil samples for chemical analyses were taken with a soil coring frame (10 cm × 10 cm × 10 cm) and filled into plastic bags.

2.2. Soil processing and soil chemistry

The 63 samples for chemical analyses were dried at 65 °C for 5 days and sieved through a 2 mm sieve. An aliquot of the mixed sample was grounded in a mill. Soil pH was measured in 1 M KCl, using a Hamilton glass electrode [12]. C and N were analysed according to the Dumas-method after complete oxidative combustion with the CHN-analyser LECO CHN-1000. Inorganic C (from all samples with a pH > 6.2) derived from carbonates was detected by a Scheibler equipment using 10% HCl-solution [49]. Total element contents of P, Ca, Mg, K, Fe, Mn, Cu, and Zn were measured after HNO₃ digestion [12] by a ICP-IES (Perkin Elmer Optima 3000).

The cations Ca, Mg, K, Na, Fe, and Mn of all three substrates were extracted with 1 M NH₄Cl for 2 h on a rotation shaker [12, 43]. The slightly acid NH₄Cl solution increases Ca and Mg concentration in alkaline mineral soils by dissolving carbonates [12]. Thus, cation exchange capacity and base saturation, which were of minor importance for this study, were not calculated. Potassium, which was of major interest for our survey, however, is extracted with this method in the same comparable extent for acid organic samples as for alkaline mineral soils.

“Plant available” phosphorus was determined for all samples with 1% citric acid extraction [49]. It has to be considered, that with this method plant available P could be slightly overestimated in alkaline soils by dissolving Ca-phosphates. All elemental concentrations in the extracts were measured by a ICP-IES (Perkin Elmer Optima 3000).

From the initially 63 samples, 6 samples of the mineral soil substrates had to be excluded after soil analyses due to exceeding high humus contents for Ah horizons, proving these samples to be transition-horizons to organic layers [6].

2.3. Plant growing conditions

The experiment was carried out one growing season from mid-May 2003 to beginning of October 2003. We used Norway spruce seeds of the provenience “No. 840 29, Bavarian limestone Alps, altitude range 900–1 300 m a.s.l.”. First, seeds were watered for 8 h (at 12-05-03) until swelling and then placed on moist vermiculite for germination. Once the radicle reached 1 cm length (after three days), seeds were cleaned with de-ionised water. Then, 50 germinated spruce seeds were evenly planted into the polyethylene pots with the intact, undisturbed fresh growing media. The pots were placed in a laboratory room with daylight (natural day-length light regime) and with a constant temperature of 20 °C. The pots were rearranged once a week to avoid possible uneven shading effects. The pots were perforated (five small borings at the bottom) for water drainage, although leaching was minimized by watering to field capacity three times a week [55].

2.4. Plant biomass and chemical analysis

At the beginning of October, in the dormancy of seedlings, 35 seedlings of each pot were randomly harvested for plant analy-

sis. About 15 seedlings were left in the pot for mycorrhizal analysis. Seedlings were carefully removed from the pot, and roots were cleaned with de-ionised water. Then, primary needles, shoots, and roots of the seedlings were separated using a scalpel, and the three parts were pooled for each pot to obtain adequate plant material for analysis. Total root length and the number of forks per root were measured using the software package WinRhizo™ (Version 4b, Regent Instruments Inc., Canada). All pooled parts were dried at 60 °C for five days, weighed, and the average dry biomass per seedling was calculated. Thereafter, needles, shoots, and roots were ground in a mill for elemental analysis. Total C and N were analysed with the CHN-analyser LECO CHN-1000. Total element concentrations of P, Ca, Mg, K, Fe, Mn, Cu, and Zn were analysed after HNO₃ digestion by a ICP-IES (Perkin Elmer Optima 3000).

2.5. Sampling and identification of ectomycorrhizae (ECM)

In mid of October 2003, the total remaining seedlings of each pot (approx. 15 seedlings) were harvested for mycorrhizal analysis. We determined species/morphotypes and exploration types of ECM. The classification of ECM fungi into exploration types, which refer to the amount, organisation and extent of the extramatrical mycelia, is an attempt to characterise the ecological relevance of ectomycorrhizal communities [3, 8]. Contact types with a smooth mantle and only a few emanating hyphae are typically sandwiched between the surrounding substrates. Short-distance types are characterised by rather short emanating hyphae and medium-distance types by rhizomorphs that are rather loosely woven and do not extend very far from the ECM.

Pots were emptied, substrate samples were soaked in water (24 h, 5 °C), and afterwards roots were carefully removed, cleaned with the aid of a dissecting microscope (Leica, Wild M5) [2], and were fixed as a specimen in FEA (formaldehyde-ethanol-acetic acid solution). All root tips (only living root tips occurred) of the pooled samples were counted and the total abundance of their ectomycorrhizal morphotypes was determined with the aid of the dissecting microscope [1]. For differentiation of morphotypes into anatomotypes, mantle-, hyphae-, and rhizomorph preparations were carried out to identify the ECM if possible, at the genus or even at the species level. This was done with a light microscope (Leica, Dialux 22) (see also Agerer [2]). Rhizomorph preparations were used particularly in regard to distinguish long-distance types and medium-distance types [4]. In a following step, ECM were classified into groups of exploration types [4]. The following characteristics were calculated: Total number of mycorrhizal root tips per root, absolute morphotype/species/exploration type abundance per root (defined as number of ECM of each type per root), relative morphotype/species/exploration type abundance per root (defined as number of ECM of each morphotype/species and exploration type per total number of mycorrhizal root tips (%)), and the degree of mycorrhization (defined as total number of ECM root tips per total number of root tips (%)).

2.6. Statistical analysis

First of all, we tested normal distribution within the dataset with the Shapiro-Wilk-Test and homogeneity of variance with the

Table II. Mean values of selected physical and chemical characteristics, total element concentrations (mg/g) and total element soil stocks (mg/cm³) of the substrates studied (C_{org} = organic C; values within columns followed by different letters are significantly different at $p \leq 0.05$).

Soil substrate	<i>n</i>	bulk density (g/cm ³)	pH range (KCl)	mean pH (KCl)	C _{org} (mg/g)	C:N ratio	Element concentrations (mg/g)									
							N	P	K	Ca	Mg	Fe	Mn	Cu	Zn	
Mineral	22	0.32 <i>a</i>	6.6–7.3	6.8 <i>a</i>	183 <i>c</i>	21 <i>c</i>	9.7 <i>b</i>	0.72 <i>a</i>	3.84 <i>a</i>	107.3 <i>a</i>	54.8 <i>a</i>	13.420 <i>a</i>	0.348 <i>a</i>	0.009 <i>a</i>	0.095 <i>a</i>	
Organic	28	0.17 <i>b</i>	2.9–6.2	4.3 <i>b</i>	429 <i>b</i>	25 <i>b</i>	17.6 <i>a</i>	0.60 <i>b</i>	0.95 <i>b</i>	26.6 <i>b</i>	5.9 <i>b</i>	3.626 <i>b</i>	0.068 <i>b</i>	0.009 <i>a</i>	0.075 <i>a</i>	
Decayed wood	7	0.13 <i>b</i>	3.5–4.1	3.7 <i>b</i>	468 <i>a</i>	48 <i>a</i>	10.2 <i>b</i>	0.40 <i>c</i>	1.07 <i>b</i>	28.0 <i>b</i>	12.7 <i>b</i>	1.961 <i>c</i>	0.060 <i>b</i>	0.008 <i>a</i>	0.079 <i>a</i>	
							Element soil stocks (mg/cm ³)									
Mineral							3.1 <i>a</i>	0.23 <i>a</i>	1.31 <i>a</i>	33.0 <i>a</i>	17.0 <i>a</i>	4.714 <i>a</i>	0.129 <i>a</i>	0.003 <i>a</i>	0.031 <i>a</i>	
Organic							2.9 <i>b</i>	0.11 <i>b</i>	0.15 <i>b</i>	4.3 <i>b</i>	0.9 <i>b</i>	0.581 <i>b</i>	0.011 <i>b</i>	0.002 <i>b</i>	0.015 <i>b</i>	
Decayed wood							1.4 <i>c</i>	0.05 <i>c</i>	0.14 <i>b</i>	3.5 <i>b</i>	1.6 <i>b</i>	0.244 <i>c</i>	0.008 <i>b</i>	0.001 <i>b</i>	0.010 <i>b</i>	

Bartlett-Test [42]. Due to differences in the homogeneity of variance and deviance from normal distribution within the samples, the non-parametric Mann-Whitney-U-Test was used to prove significant differences of the three substrate types among the two study sites, as well as among seedlings grown on them in a pairwise comparison. Due to non-significant differences among samples, the three substrates obtained from the two sites were pooled together. Then, we analysed differences of chemical properties, of biomass, and of mycorrhization or of elemental characteristics of seedlings grown in the three substrates with univariate statistical methods. Therefore, the non-parametric Kruskal-Wallis-H-test (software package SPSS 12.0 for Windows, SPSS Inc.) was used to prove significant differences of the three types. If significant differences among the three types occurred, a multiple comparison was carried out with the non-parametric Nemenyi-test (software package STATEasy 2000 for Windows, Lozan Inc.) to identify significantly different types [42]. These tests are adapted to unequal allocated data sets and offered therefore an appropriate analysis of our three types with 7 dead wood, 22 mineral soil, and 28 organic layer samples [42]. To investigate dependencies between chemical properties of substrates and nutrient contents in seedlings, the parameter free Spearman rank correlation analysis was carried out with SPSS 12.0 [42].

3. RESULTS

3.1. Soil substrate properties

Compared to rendzic leptosols in lowland ecosystems, mean contents of organic C (C_{org}) of 183 mg/g in mineral Ah horizons were still high and accordingly the bulk density was low. However, these properties are typical for soils of the Bavarian Alps derived from dolomite (Tab. II). With pH values of 6.6–7.3, mineral substrates were moderately acidic to moderately basic and within the range of carbonate buffers. Organic layers and highly decayed dead wood had a low bulk density and showed accentuated acidic pH values. C:N ratios were low in mineral soils, increased significantly in organic layers, and in dead wood.

Except for N, all mean elemental concentrations and, as a result of the higher bulk density, mean elemental stocks per soil volume were highest in mineral soils (Tab. II). In contrast, N concentration was highest in organic substrates. Unexpected were the high contents of N and of K in dead wood.

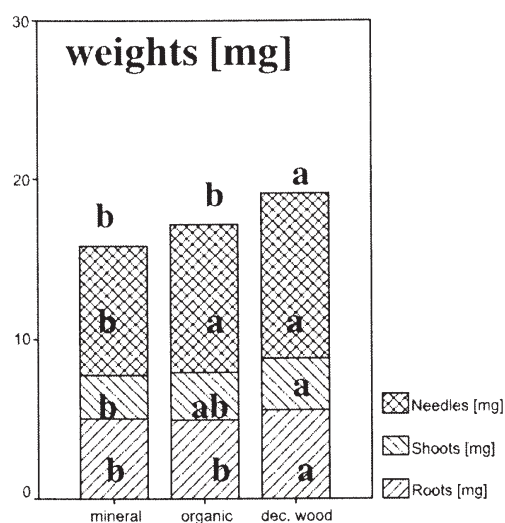
**Figure 1.** Mean values of root, shoot, and needle weights added up to total weights of seedlings in dependence on the growing substrate (different letters in plant tissues and above total weights mark significantly different values ($p \leq 0.05$) between substrates).

Table III shows mean values of NH₄Cl-extractable elements. Extractable Ca and Mg concentrations and soil stocks decreased significantly from mineral soils and organic layers to decayed wood. Because dolomite is the soil forming bedrock, the concentration of extractable Mg was high in mineral and organic substrates. In contrast to these elements, extractable K concentrations increased significantly from mineral soil to organic layers, and even more to dead wood. Consequently, the ratio of Ca and Mg to K decreased significantly by a factor of about 6, respectively. Furthermore, the mean stocks of extractable K were highest in decayed wood. Similarly to extractable K concentrations, citric acid-extractable P concentrations increased significantly from mineral soil to organic layers and dead wood. Soil stocks of extractable P were highest in organic substrates, followed by dead wood and decreased significantly in mineral Ah horizons. Thus, high pH values were accompanied in mineral soils by high (Ca + Mg)/K ratios, high soil stocks of total N and P, but with low concentrations of extractable P and K.

Table III. Mean values of extractable cations (NH₄Cl-extraction), (Ca + Mg):K ratio, and plant available P (citric acid-extraction) and stocks of extractable nutrients (values within columns followed by different letters are significantly different at $p \leq 0.05$).

Soil substrate	Ca	Mg	K	Fe	Mn	(Ca + Mg):K	P
	NH ₄ Cl-extraction ($\mu\text{mol IE/g}$)					Ratio	Citric acid-extraction (mg/g)
Mineral	368.84 <i>a</i>	155.63 <i>a</i>	3.61 <i>c</i>	0.04 <i>b</i>	0.47 <i>a</i>	146 <i>a</i>	0.026 <i>b</i>
Organic	385.61 <i>a</i>	119.55 <i>b</i>	5.62 <i>b</i>	0.13 <i>a</i>	0.53 <i>a</i>	90 <i>b</i>	0.084 <i>a</i>
Decayed wood	183.79 <i>b</i>	40.19 <i>c</i>	9.73 <i>a</i>	0.09 <i>b</i>	0.82 <i>a</i>	23 <i>c</i>	0.092 <i>a</i>
	Extractable element stocks ($\mu\text{mol IE/cm}^3$)					Extractable P stocks (mg/cm ³)	
Mineral	116.74 <i>a</i>	49.29 <i>a</i>	1.21 <i>a</i>	0.01 <i>b</i>	0.17 <i>a</i>	–	0.010 <i>b</i>
Organic	69.53 <i>b</i>	19.77 <i>b</i>	1.06 <i>b</i>	0.02 <i>a</i>	0.12 <i>b</i>	–	0.014 <i>a</i>
Decayed wood	23.63 <i>c</i>	5.32 <i>c</i>	1.28 <i>a</i>	0.01 <i>b</i>	0.11 <i>b</i>	–	0.012 <i>a</i>

3.2. Relationship between growing substrate, biomass development, and mycorrhization

Figure 1 illustrates the development of biomass for the plant components root, shoot, and needle, and for whole seedlings after the first growing season. Our results demonstrated that the seedling biomass was significantly lower in mineral soils (15.9 mg) and in organic layers (16.8 mg) as compared to decayed dead wood (19.7 mg). Seedlings growing in decayed dead wood had the highest root weight within all three tested soil substrates and significantly higher values of needle and shoot weights than seedlings in mineral soils. Also weights of spruce needles in organic substrates were significantly higher than for seedlings grown in mineral soil substrates. Seedlings in decayed wood furthermore had the significantly highest root length, as well as the highest number of root tips and forks per root (Tab. IV). Seedlings in organic and mineral soil were not distinguishable for these root characteristics. The root/(shoot + needle) ratio was significantly lower in organic seedbed compared to mineral seedbed, while decayed dead wood was intermediate.

Mean number of mycorrhizal root tips per root was highest in decayed wood, whereas the degree of mycorrhization was very low for all three samples until the harvest of seedlings, but tendentially higher in organic layers. Differences in mycorrhization data were significant for the abundance of ECM types (Tab. V). We determined the species *Cenococcum geophilum* Fr. (*C. geophilum*) and distinguished two *Tomentella*-like morphotypes TOM-01 and TOM-02. As a result of the initiated and thus rudimentary infection of root tips, numerous morphotypes were indeterminable (indet types). Corresponding to the exploration type classification according to Agerer [3], contact, short-distance, and medium-distance types could be found. Short-distance types were formed by *C. geophilum* and TOM-02, whereas the morphotype TOM-01 constituted the largest group of medium-distance types. Indet morphotypes belonged with their main proportion to contact types, but as well to the short- and medium-distance exploration types. Viewed on the distribution in soil substrates, *C. geophilum* and short-distance types favoured significantly organic and dead wood substrates. Contact types were significantly more associated with the decayed wood, and medium-distance types with mineral Ah horizons.

Table IV. Selected root characteristics and root (shoot + needle) ratio of seedlings originating from the three substrate types (values within columns followed by different letters are significantly different at $p \leq 0.05$).

Soil substrate	Root length (cm)	Number of root tips/root	Number of forks/root	Root/(shoot + needle) ratio
Mineral	14.6 <i>b</i>	40 <i>b</i>	42 <i>b</i>	0.47 <i>a</i>
Organic	14.3 <i>b</i>	43 <i>b</i>	42 <i>b</i>	0.39 <i>b</i>
Decayed wood	19.7 <i>a</i>	64 <i>a</i>	58 <i>a</i>	0.45 <i>ab</i>

3.3. Seedling nutrition in relation to chemical properties of the growing substrates

Nutrient partitioning of total contents of macro- and micro-nutrients at the end of the experiment for seedlings grown in the three tested substrates is shown in Figure 2. For a couple of elements, similar trends as for biomass were observed. Thus, seedlings in organic and in particular in decayed wood substrates had significantly higher contents of N, P, K, and Mn compared to seedlings in mineral soils. Also for Zn there were higher contents in organic layers and decayed wood, the latter being significant. For Cu there were no significant differences. In contrast, significantly higher values were observed in seedlings originating from mineral soils for Ca, Mg, and Fe compared to the other two substrates. Remarkable was the contrary total acquisition of Fe and Mn. Furthermore, Fe was preferentially accumulated in roots, while Mn in needles.

In addition to high nutrient contents or concentrations in plant tissues, harmonic, balanced nutrient relations are of great importance to insure optimal growth of spruce [36]. Nutrient relations in needles were fairly comparable with nutrient relations in whole seedlings (Tab. VI). Comparing the three seedbeds, predominantly unbalanced nutrient relations were observed for seedlings in mineral substrates. For these seedlings, only the N:P ratio was in the range of harmonic nutrition. Although N concentration was low, the high N:K ratio revealed an insufficient nutrition with K in mineral soils. On the other hand, low ratios of N and K over Ca and Mg documented the excessive supply with Ca and Mg on mineral soils derived from dolomite. In consequence of low total contents of P in seedlings in decayed wood (Fig. 2), the N:P ratio showed an inadequate P nutrition. Higher concentrations of N and K,

Table V. Mycorrhizal root tips, degree of mycorrhization, and relative and as well as absolute abundance (in italics) of species, of morphotypes and of exploration types (values within columns followed by different letters are significantly different at $p \leq 0.05$).

Soil substrate	Myc. root tips/root	Degree of myc. (%)	Abundance of species and morphotypes									Abundance of exploration types					
			<i>Cenococcum geophilum</i>			TOM-01		TOM-02		Indet morphotypes		Short-distance types		Medium-distance types		Contact types	
			Relative (%)	<i>Absolute</i>	Relative (%)	<i>Absolute</i>	Relative (%)	<i>Absolute</i>	Relative (%)	<i>Absolute</i>	Relative (%)	<i>Absolute</i>	Relative (%)	<i>Absolute</i>	Relative (%)	<i>Absolute</i>	
Mineral	5.40 <i>a</i>	14 <i>a</i>	1	0.0 <i>b</i>	72	3.9 <i>a</i>	0	0.0 <i>a</i>	27	1.5 <i>a</i>	4	0.2 <i>b</i>	72	3.9 <i>a</i>	24	1.3 <i>b</i>	
Organic	7.60 <i>a</i>	17 <i>a</i>	33	2.5 <i>a</i>	26	2.0 <i>ab</i>	10	0.8 <i>a</i>	31	2.4 <i>a</i>	43	3.3 <i>a</i>	36	2.7 <i>ab</i>	21	1.6 <i>b</i>	
Decayed wood	8.42 <i>a</i>	13 <i>a</i>	53	4.4 <i>a</i>	0	0.0 <i>b</i>	0	0.0 <i>a</i>	47	4.0 <i>a</i>	53	4.4 <i>a</i>	0	0.0 <i>b</i>	47	4.0 <i>a</i>	

combined with low concentrations of Ca and Mg resulted in ranges of harmonic element relations for N to K, Ca, and Mg as well as for K to Ca, and Mg in needles of seedlings growing in decayed wood and in organic layers. Only the N:K ratio of element contents in whole seedlings in organic layers was slightly unbalanced.

Soil characteristics had varying relevance for seedling nutrition (Tab. VII). Elemental concentrations of N in substrates was highly correlated with the seedling N content, whereas N stocks in soils were not correlated. The correlation of extractable P concentrations and stocks with the P accumulation in seedlings was high. In contrast, the total P concentration was of minor importance and even for total soil stocks, negatively correlated with the P nutrition. Similarly to P, the values of K contents in seedlings were correlated with an increasing extractable concentration of this element and negatively correlated with an increasing (Ca + Mg)/K ratio (Tabs. III and VII). Therefore, the total elemental concentration and stocks of K were of minor relevance for the K nutrition. Calcium and Mg in seedlings followed well high total soil stocks and high extractable concentrations and stocks of these elements (Tabs. II and III). A high correlation was obtained for Fe contents in seedlings and Fe concentrations in the growing substrate, whereas extractable nutrient fractions of Fe showed a negative correlation with seedling Fe nutrition. Manganese nutrition responded conversely and was negatively correlated with Mn concentrations and stocks in the substrates. In general, high pH values in the substrate corresponded with low seedling contents of N, P, K, Mn, Cu, and Zn, but with high amounts of Ca, Mg, and Fe.

4. DISCUSSION

The biomass development and nutrition of seedlings in their first growing season was strongly related to the natural seedbed substrates (Figs. 1 and 2). Our data suggest, that differences in growth of seedlings were caused by the substrate specific availability of nutritional elements.

High pH values and low soil moisture contents are the main environmental factors which impair nutrient mobility in calcareous soils [44]. Major nutritional constraints on shallow dolomite soils of the Bavarian-Tyrolian Limestone Alps are known for N, P, K, Fe, and Mn for spruce saplings as well as for adult spruce trees [7, 25, 29, 33, 58]. Shallow rendzic leptosols (rendzinas) derived from dolomite are especially characterised by the dominance of Ca and Mg on cation exchange

Table VI. Element concentration relations in needles and whole plants for seedlings grown in the three substrates (values within columns followed by different letters are significantly different at $p \leq 0.05$; grey shaded: disharmonic relations; * ranges of harmonic relations according to Hütthl [33]).

Element relations	N:P	N:K	N:Ca	N:Mg	K:Ca	K:Mg
Range of harmonic element relations*	6–12	1–3	2–20	8–30	0.8–2.4	2.2–6.4
Soil substrate	Needles					
Mineral	9.7 <i>b</i>	3.2 <i>a</i>	1.9 <i>b</i>	5.7 <i>c</i>	0.6 <i>c</i>	1.8 <i>c</i>
Organic	9.5 <i>b</i>	2.8 <i>b</i>	3.0 <i>a</i>	9.2 <i>b</i>	1.1 <i>b</i>	3.2 <i>b</i>
Decayed wood	12.9 <i>a</i>	2.6 <i>b</i>	3.9 <i>a</i>	11.6 <i>a</i>	1.5 <i>a</i>	4.4 <i>a</i>
Soil substrate	Seedling					
Mineral	9.0 <i>b</i>	3.2 <i>a</i>	1.5 <i>b</i>	3.9 <i>b</i>	0.5 <i>c</i>	1.2 <i>c</i>
Organic	9.5 <i>b</i>	3.1 <i>a</i>	3.0 <i>a</i>	9.0 <i>a</i>	1.0 <i>b</i>	3.0 <i>b</i>
Decayed wood	12.4 <i>a</i>	2.9 <i>a</i>	3.6 <i>a</i>	11.1 <i>a</i>	1.3 <i>a</i>	3.9 <i>a</i>

places and therefore by an unbalanced supply with other nutrients [26].

4.1. Soil properties and seedlings responses

The accumulation of thick organic residua uncoupled from mineral soil horizons leads to altered soil properties, especially acid soil conditions, changing solubility of nutrients, and an decreasing excess of Ca and Mg [44, 47, 48]. Hence, on dolomite sites the availability and uptake mechanisms of other nutrients than Ca and Mg highly depend on the accumulation of the organic layer [26]. In addition, downed decayed woody debris is, not for our human influenced study sites but in near to natural mountainous forests of the Bavarian Limestone Alps, an other typical structural element on the forest floor [9]. In general, the progressing decay of dead wood is accompanied by the loss of density and increasing nutrient concentrations for N, P, and K [41]. Nitrogen increases in logs due to the activity of symbiotic nitrogen-fixing bacteria and wood-decaying fungi [41]. The nitrogen fixation rate increases with decay and moisture content of dead wood [16]. In addition to soil chemistry, the water storage capacity of organic layers and highly decayed dead wood is higher than in mineral soils, and nearly comparable to peat [13, 22, 53].

Although N contents in mineral soils were as high as in dead wood, and C:N ratios were low, N availability seems quite different from dead wood substrates. In Ah horizons of rendzic leptosols, N is mainly organically bound N in stable Ca-humic compounds [44]. As a result of the reduced

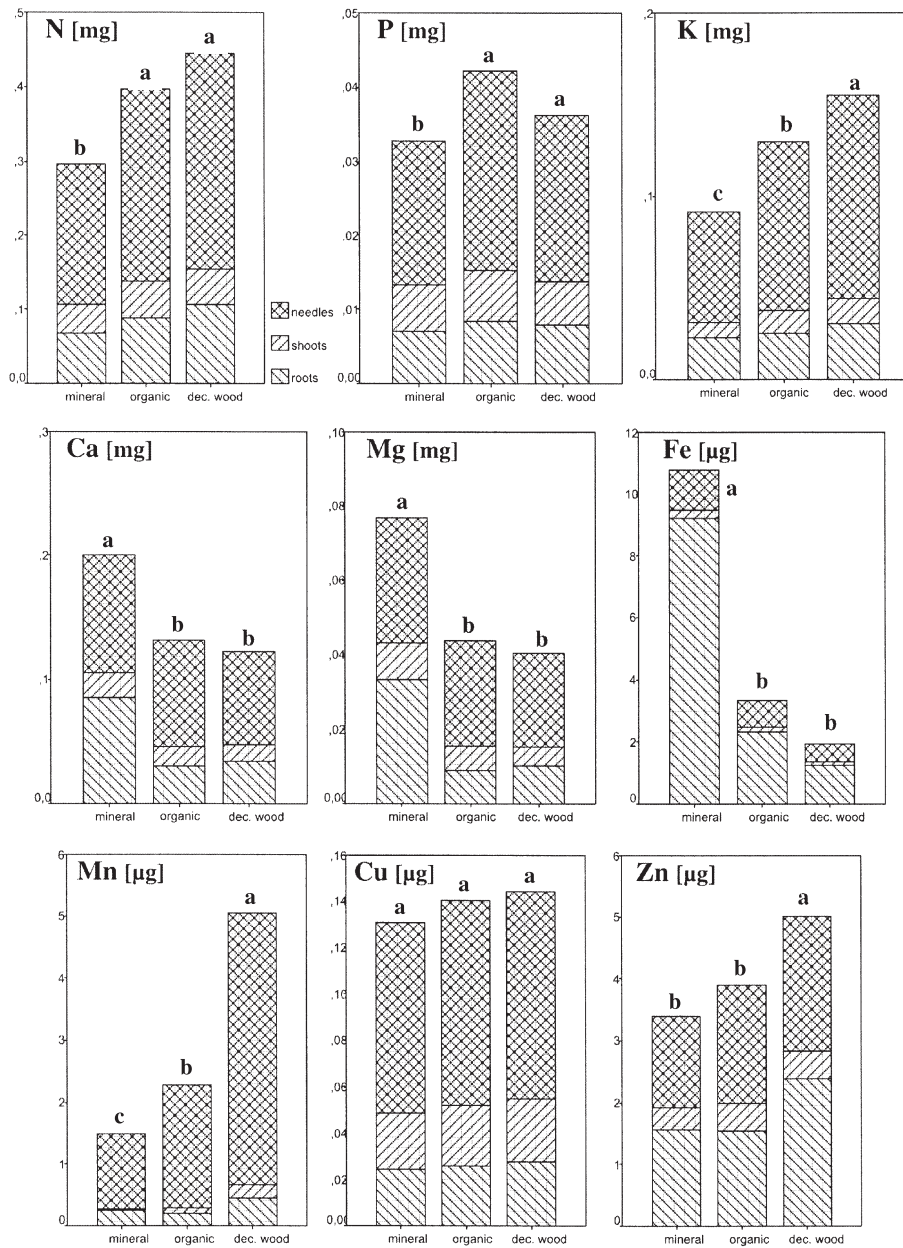


Figure 2. Partitioning of total contents of macro- and micro-nutrients in roots, shoots, and needles of the seedlings added up to total contents (pictured are mean values; different letters above total element contents mark significantly different values ($p \leq 0.05$) between substrates).

Table VII. Rank correlation coefficients matrix (Spearman ρ) between equivalent total nutrient contents in seedlings and different soil specific nutrient values, and between total nutrient contents in seedlings, (Ca + Mg/K) ratios, and pH (KCl) in soil samples (** $p \leq 0.01$; * $p \leq 0.05$; n.s. = not significant; n.d. = not determined).

Soil specific value	Total nutrient contents in seedlings								
	N	P	K	Ca	Mg	Fe	Mn	Cu	Zn
Total concentration	0.46***	-0.08 ^{n.s.}	-0.52***	0.55***	0.66***	0.66***	-0.47***	0.13 ^{n.s.}	-0.05 ^{n.s.}
Total element stocks	-0.06 ^{n.s.}	-0.22*	-0.40***	0.60***	0.70***	0.60***	-0.44***	0.06 ^{n.s.}	0.00 ^{n.s.}
Extractable concentrations	n.d.	-0.58***	0.51***	0.34**	0.57***	-0.42***	-0.02 ^{n.s.}	n.d.	n.d.
Extractable element stocks	n.d.	-0.51***	0.18 ^{n.s.}	0.60***	0.72***	-0.23*	-0.12 ^{n.s.}	n.d.	n.d.
Extractable (Ca + Mg)/K	-0.55***	-0.27*	-0.53***	0.39***	0.22*	0.26*	-0.51***	-0.33**	-0.30**
pH [KCl]	-0.77***	-0.47***	-0.70***	0.64***	0.62***	0.60***	-0.70***	-0.24*	-0.37***

mineralization of stable N in Ah horizons, the N availability is low [47]. In our case, seedlings in organic substrates and dead wood had the highest N contents. The organic layer is considered to be the most important site of mineralisation processes and nitrogen mobilisation [51]. Hence, the higher N availability of the organic layer might result from an enhanced N mineralization in fresh organic material with higher N contents [48]. Astonishing were the high contents of N in seedlings growing in dead wood. We speculate that nitrogen fixation was high due to a high moisture content in the highly decayed woody substrate. The high water storage capacity of dead wood in combination with a high amount of released, available N by bacteria would be able to explain the high N contents in spruce seedlings. However, until now the proportion of fixed nitrogen in coarse woody debris and the loss by vegetation uptake is unknown [16].

Potassium does not strongly compete for binding sites compared to divalent cations e.g. Ca and Mg which have a higher affinity to cation exchange sites [44, 48]. High Ca and Mg contents in soils result in ion-antagonism with K [38, 47, 58]. Thus, with increasing extractable (Ca + Mg)/K ratio in mineral soils, acquisition of K by seedlings decreased (Tab. VII). Our data revealed that the acid dead wood had high amounts of extractable K, but low amounts of Ca and Mg (Tab. III). Therefore, as a result of the reduced ion antagonism seedlings on dead wood showed an improved potassium uptake as compared to mineral soil horizons.

At the same time, Ca-phosphates in mineral horizons are difficult to dissolve and hence result in low plant available P in alkaline soil [48]. Hence, high total soils stocks of P were of minor relevance for P acquisition by seedlings compared to extractable P concentrations and soil stocks (Tab. VII). Therefore, the plant available P was not overestimated by the citric acid solution and our soil extraction method was efficient enough to explain the observed variation of P contents within seedlings.

Noticeable were the contrary contents as well as concentrations in plant tissues of Fe and Mn (Fig. 2). In general, the availability of Fe and Mn depends on the pH-value, the presence of chelating compounds, and redox conditions [44]. According to Baumeister and Ernst [10], Fe is characterised by a low mobility in plant tissues and by high concentrations in roots. In alkaline soils with a high organic matter content, Fe availability to roots might be enhanced by high concentrations of organic Fe chelates, but high concentrations of HCO_3^- may affect translocation from roots to needles by high pH values in the root cells [44, 48]. Manganese deficiency is common on well-aerated rendzic leptosols, because the solubility of Mn^{2+} decreases with increasing pH and high levels of CaCO_3 due to the precipitation of Mn calcite [44]. Therefore, the Mn availability increases in acid organic and dead wood substrates compared to mineral Ah horizons due to lower pH-values and probably by longer periods with anaerobic microsites in this substrates. The Mn deficiency in spruce stands might therefore decrease with an increasing organic matter build-up during stand development [39]. In summary, our results were in accordance with other findings in the Bavarian limestone Alps,

showing that Mn deficiency on shallow alkaline sites occurs more often than Fe deficiency [7, 39].

The solubility of inorganic zinc decreases with increasing pH and decreasing organic matter content [44]. This accounts for the fact that we found highest Zn contents in seedlings in dead wood. Similarly, Baier [7] found higher Zn concentrations in needles of spruce saplings growing on eutric leptosols compared to spruces on rendzic leptosols. Copper acquisition by plants is only slightly related to soil pH [48], hence Cu contents of seedlings in all three substrates varied only slightly.

Values of elemental concentrations in primary needles (data not shown) were at least twice as high as compared to nutrient thresholds for needles of adult spruce trees and therefore were deemed to be inappropriate to classify the nutritional status of seedlings. Nutrient relations are more constant in plant tissues and of importance for physiological processes [36]. Hence, we used this approved parameter for macro-nutrients as indicator to evaluate the nutritional status of seedlings (Tab. VI). In mineral soil the surplus of Ca and Mg resulted in a disharmonic nutrition as indicated by unfavourable nutrient relations. For seedlings originating from mineral soil Ca and Mg contents were highest in roots as compared to needles. This might be an indication that these seedlings attempt to avoid an excess supply with Ca and Mg by storing the surplus in roots. According to Marschner [44], in needles of spruces growing on rendzic leptosols more than 90% of Mg is water soluble, but 90% of Ca is oxalate-bound Ca. Therefore, an oversupply with Mg might be more harmful than a surplus of Ca. Until now however, these special nutritional features on Mg rich dolomite sites are not well understood [44].

4.2. Mycorrhization of the seedlings

The extramatrical mycelia of ECM radiating into the soil act as a transport system and increase the exploited soil volume [51]. We used the “exploration types” according to Agerer [3] that distinguish the extramatrical mycelia systems of ECM with regard to density, organisation and reach, assuming that they represent distinct ecophysiological strategies, e.g. for nutrient acquisition. Tedersoo et al. [54] demonstrated a clear preference of individual ECM fungi for different substrate qualities. We found significantly more mycorrhizal root tips of *Cenococcum geophilum* and of short-distance types in organic substrates and in dead wood as compared to mineral Ah horizons. By contrast, the Ah horizons were dominated by medium-distance and contact types (Tab. V). These results are in accordance with the vertical distribution of different exploration types in the organic layer and the mineral soil in a young spruce stand of the Bavarian limestone Alps [8]. Contact types, due to their smooth surface, are well equipped to explore the substrate in Ah soil horizons with its narrow pores. The same might be true for the heterogeneous dead wood. Here, loose material adequate for short-distance types alternates with woody residua of higher compaction as potential niche for contact types. Thus, the quality of the growing media might have an important effect on the ECM fungi community [20, 56]. With respect to differences in specific enzymes of

ECM exploration types to release and transport nutrients [3], the spatial niche differentiation of spruce ECM fungi between typical substrates of mountainous forests, is likely to be of importance for spruce nutrition. The inoculum potential of soils is influenced by the time span between the possibility to colonise a new seedling and the persistence of ECM fungi in soils and/or the species-specific colonisation strategies [51]. A study of Egli et al. [21] showed that ten years after a windthrow event the number of infective ECM fungi had decreased significantly. The high number of young and indeterminable morphotypes made it impossible to judge if the same reduction of species richness applies for mineral soil substrates originating from the centre of wide canopy openings distant from trees. On the other hand, *Cenococcum geophilum* is characterised by the persistence of sclerotia in soil [19] and by associations in this ecosystem with herbaceous plants as host such as *Polygonum viviparum* [51]. Hence, *Cenococcum geophilum* might have pioneering capabilities to colonise seedlings very effectively, it has been shown that this species appears to be very competitive in organic layers [8].

4.3. Seedbed qualities of the studied substrates

Compared to mineral soils with their adverse soil conditions, organic layers and dead wood might have advantages for spruce nutrition and growth. Thick litter accumulations on the forest floor are often viewed as detrimental to conifer seedling survival because they are prone to drying and prevent the root systems of the seedlings from quickly reaching mineral soil [14]. However, Hanssen [30] found a positive influence of increasing humus thickness on regeneration of spruce. We suggest that due to enhanced nutrient availability and higher water storage capacity, dead wood and organic layers represent a good seedbed for naturally regenerating spruce in mountainous forests of the Bavarian limestone Alps. Seedlings on these substrates are characterised by a higher biomass, by longer roots (for dead wood), and exhibited a better as well as more balanced nutrient supply. In addition, nutrient acquisition respectively nutrient concentrations in young plant tissues of these substrates were higher and therefore increases the rate of dry matter build-up [10]. These results are in accordance with Baier et al. [9], who found that naturally-regenerated spruce saplings preferably occurred more often clustered on dead wood and around hindrances with thick humus layers whereas spruces on exposed mineral soil without organic layers were scarce. The role of organic layers for spruce nutrition on alkaline dolomite sites is underlined by the spatial distribution of fine roots in soils. Baier [7] found on such sites the highest proportion of fine roots in the organic layer, whereas Wittkopf [57] found only 20% of fine roots in organic layers of an acid soil derived from silicate.

5. CONCLUSION

Near-to-nature mountainous forests of the vegetation type *Aposerido-Fagetum* are characterised by a great variation in humus forms and microsites [23]. Former wood pasture and clear cuts on these steep mountain slopes with shallow mineral soils led to nutrient losses, organic layer decrease, and low

amounts of coarse woody debris [33,40]. To promote natural regeneration and the growth of planted seedlings on dry, south exposed dolomite sites formerly degraded by human activities and with nowadays mull humus, we recommend the enhancement of the amount of dead wood and the establishment of the primal, acid moder humus form. In near-to-nature forest ecosystems, coarse woody debris plays a minor role in the nutrient cycles compared with other aboveground litter [41]. But under the site conditions mentioned above, highly decayed coarse woody debris is important for retaining moisture and in the long run for soil organic matter build-up. In addition, dead wood provides microsites that enhance the early establishment of spruce natural regeneration [9].

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