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Original article

On the niche breadth of *Fagus sylvatica*: soil nutrient status in 50 Central European beech stands on a broad range of bedrock types

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Abstract – The soil nutrient status of 50 Central European stands of *Fagus sylvatica* on 13 acidic to basic bedrock types was investigated with the aim (i) to define the extremes of important soil chemical and nutrient status parameters tolerated by beech forests, (ii) to investigate the dependency of these parameters on bedrock type and soil acidity, and (iii) to analyse the importance of the organic layer for the nutrient status of beech forests. Based on the parameters exchangeable cation pool ($Ca + Mg + K_{ex}$), N/P ratio of the organic layer and C/N ratio of the mineral soil, three nutrient supply classes were identified: (1) limestone and claystone soils (C/N 15–18 mol mol^{-1}, N/P 20–26 mol mol^{-1}, $(Ca + Mg + K)_{ex}$ 5–38 mol m^{-2} per 10 cm soil), (2) silicate-rich sandstone, tertiary sand, loamy loess and moraine soils (C/N 20–26 mol mol^{-1}, N/P 24–45 mol mol^{-1}, $(Ca + Mg + K)_{ex}$ 2–3 mol m^{-2} 10 cm^{-1}), and (3) soils derived from silicate-poor sandy deposits (C/N 28–34 mol mol^{-1}, N/P 47–59 mol mol^{-1}, $(Ca + Mg + K)_{ex}$ 1–3 mol m^{-2} 10 cm^{-1}). Soil chemical extremes tolerated by beech were 3–99% base saturation, 3.2–7.3 of pH (H_2O), and minima of resin-exchangeable P of 11 mol m^{-2}, and of $(Ca + Mg + K)_{ex}$ of 0.4 mol m^{-2} in the topsoil (0–10 cm). A highly variable amount of exchangeable Al in the mineral soil was identified as the key factor controlling the accumulation of C in the organic layer (OL, OF, OH). Increasing organic layer N/P ratios (19 to 59 mol mol^{-1}) from basic to acidic soils point at a growing importance of P limitation over N limitation with increasing acidity in beech forest soils.

base saturation / C/N ratio / exchangeable cations / N/P ratio

Résumé – Sur la niche écologique du hêtre *Fagus sylvatica* : statut nutritif des sols de 50 peuplements de hêtre d'Europe centrale. Le statut nutritif des sols de 50 peuplements de Hêtre (*Fagus sylvatica*) croissant sur 13 types de roches mère a été étudié dans le but de (i) définir les conditions d'alimentation édaphiques extrêmes tolérées par le hêtre, (ii) étudier les relations roche mère-conditions édaphiques, et (iii) analyser l'importance de couche organique pour le statut nutritif des forêts de hêtre. En se basant sur la réserve de cations échangeables, le rapport N/P de la couche organique et le rapport C/P du sol minéral, trois classes d'alimentation minérale ont été identifiées : (1) sols calcaire et argileux (C/N 15–18 mol mol^{-1}, N/P 20–26 mol mol^{-1}, $(Ca + Mg + K)_{ex}$ 5–38 mol m^{-2} par 10 cm de sol), (2) grès siliceux, sables tertiaires, loess limoneux et sols de moraine (C/N 20–26 mol mol^{-1}, N/P 24–45 mol mol^{-1}, $(Ca + Mg + K)_{ex}$ 2–3 mol m^{-2} 10 cm^{-1}), et (3) sols dérivés de dépôts siliceux pauvres en bases (C/N 28–34 mol mol^{-1}, N/P 47–59 mol mol^{-1}, $(Ca + Mg + K)_{ex}$ 1–3 mol m^{-2} 10 cm^{-1}). Le hêtre tolère les valeurs chimiques extrêmes suivantes : saturation en base de 3 à 99 %, pH (H_2O) de 3.2 à 7.3, valeur minimale de P échangeable de 11 mol m^{-2}, et de $(Ca + Mg + K)_{ex}$ de 0.4 mol m^{-2} dans l'horizon supérieur (0–10 cm). La quantité très variable d'Al échangeable dans le sol minéral a été identifiée comme le facteur clé contrôlant l'accumulation de C dans la couche organique (OL, OF, OH). L'augmentation du rapport N/P des humus des sols basiques aux sols acides indique dans les sols de hêtraie une limitation croissante par le P par rapport au N lorsque l'acidité augmente.

saturation en base / C/N / cations échangeables / N/P

1. INTRODUCTION

European beech (*Fagus sylvatica* L.) is exceptional among temperate tree species in forming mono-specific stands in the largest part of its distribution range. Prior to man's alteration of the forested landscape, this species dominated in an area far exceeding 300 000 km^2 in Central Europe. Moreover, *Fagus sylvatica* is remarkably tolerant against a broad range of hydrological and soil chemical factors including soil moisture, hydrogen and aluminium ion concentrations, and nitrogen availability [14, 18]. In fact, vital mono-specific beech forests are found on highly acidic quartzitic soils and on basic carbonate-rich soils, and they occur in regions with less than 550 to more than 2000 mm of annual rainfall [26, 35]. Beech forests grow on nearly all geological substrates if drainage is sufficient [18]. Thus, this species realizes a very broad ecological niche in terms of soil chemical properties and water availability. With respect to the area where this species is dominant *Fagus sylvatica* must undoubtedly be considered as the most successful Central European plant species.

In this comparative study in 50 beech forests, we explored the effect of variable bedrock types on chemical properties and the nutrient status of beech forest soils under a temperate suboceanic climate in order to quantitatively analyse the ecological niche of this species. The extraordinarily broad range of beech forest sites found in Central Europe represents an outstanding natural framework for analysing patterns and possible causes of variation in the soil nutrient status of forests. Our principal study aims were (1) to define the range (maximum and minimum) and variability of important soil chemical and nutrient

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status parameters among Central European beech forests, (2) to investigate the dependency of these parameters on bedrock type and soil acidity, and (3) to analyse the importance of the organic layer for the nutrient status of beech forests.

2. MATERIALS AND METHODS

2.1. Study sites, geology and climate

We investigated 50 mature beech stands in a restricted area of Central Germany on a broad range of bedrock types with each geological substrate being replicated four times allowing for statistical analyses of the soil chemical data. Among the five 'ecosystem state factors' defined by Jenny [15] – climate, relief, organisms, parent material and time – four could be held more or less constant in our study. This allowed us to investigate the role of the fifth factor, parent material, on soil nutrient status. Variation in climate and relief could be reduced to a minimum by selecting suitable beech stands in similar topographic positions within a limited area. The time factor had a similar influence at all studied forest sites because all soils have developed during the Holocene for about 12 000 years, and all beech stands were of similar age and belonged to 'ancient woodland' that presumably has never been clear-cut in historic time. A major strength of our study is that we compared single-species stands of the same tree species, which largely eliminates Jenny's [15] organism factor. This is important because there is increasing evidence that tree species can have a profound influence on the properties of forest floor and mineral topsoil [4, 25, 28, 36, 37].

The 50 mono-specific mature beech forests were chosen in northeastern and southern Lower Saxony (Germany) at a maximum distance to each other of 200 km. The stands were selected on a soil chemical gradient from extremely acidic sandy soils to base-rich, calcareous soils covering the whole range of soil types found under Central European beech forests. Sandy glacial deposits of the penultimate Ice Age (Saalian) cover the north of the study region (Lüneburger Heide area), whereas the south (Leine-Weser-Bergland) represents a small-scale mosaic of various Mesozoic and Kaenozoic bedrock types. Thirteen bedrock types were chosen with each being represented by four sites (one bedrock type, i.e. fluvioglacial sands, was represented by two sites only). For avoiding pseudo-replication, the minimum distance between two neighbouring sites was set at 5 km. Selection criteria for the 50 study sites were comparability with respect to stand age, stand structure, and canopy closure. Sites with significant cover layers of quaternary loess were not considered (except for the loess sites Nos. 33–36). All stands represented closed mono-specific beech forests with an age of about 100 years; small portions of other broad-leaved trees (< 5% of the stems) were only present at the sites on calcareous substrates. All study plots (20 × 20 m in size) were placed by random in stand sections with more or less homogeneous stand structure, closed canopy and comparable stem density (150–250 stems ha^{-1}). All sites were located below 520 m a.s.l. mostly in the colline and submontane belts at level to slightly sloping terrain (0–17°). All stands with impact of past compensatory soil liming were excluded from study. For a number of sites (Nos. 17, 18, 25, 27–31), however, complete absence of soil liming could not be proven. In these cases, if liming was conducted, it should have occurred at least 17 to 19 years ago, which minimises possible effects on today's soil chemical state [29].

The southern part of the study region (Leine-Weser-Bergland) represents hilly uplands ('Mittelgebirge') formed by Triassic, Jurassic and Cretaceous sediments. In certain regions, a few centimeters to several meters of Pleistocene loamy loess of the last glacial (Weichselian) covers these sediments. The soils are locally influenced by periglacial cryoturbation and solifluctuation. At least in their upper sections, all recent soil profiles are, therefore, not older than about 12 000 y. The northern part of the study region has been shaped by the deposits of the Saalian Ice Age, while being influenced by periglacial processes during the last glaciation (Weichselian). Characteristic landscape elements are large fluvioglacial sand plains. In addition, basal moraines with a high content of either sand or loam cover extended areas. Locally, sandy loess has been deposited with a thickness of several centimeters to a few meters.

The bedrock types chosen range from the Triassic to the Quaternary, thus spanning an epoch of about 240 M y. They include various types of sandstone, limestone, claystone, sandy deposits, loess, and glacial deposits (Tab. I). The soils are mainly Umbrisols (on sands, sandstones, and glacial deposits), Cambisols (on claystones, limestones, and loess), and Leptosols (on sandstones and limestones) in a variety of sub-types. None of the sites is influenced by ground water. Humus forms were classified according to Green et al. [12], soil types after ISSS-ISRIC-FAO [34].

The study region has a temperate sub-oceanic climate with annual mean temperatures of 7 to 9 °C. With only a few exceptions mean precipitation is between 600 and 950 mm y^{-1} (Tab. I). Study sites at higher elevations regularly have a somewhat higher rainfall and lower temperatures (the lapse rate is about 6 K km^{-1}).

2.2. Soil sampling and chemical analyses

First, a soil profile examination in a representative pit was carried out at every study site following the criteria of [2]. Soil samples were taken with a soil corer of 20 mm diameter in the period August to December 2000 at five randomly chosen points within the 20 × 20 m study plot in both the organic layer and the mineral soil (0–10 and 10–20 cm depth). Thus, the soil chemical data given in this paper are averages of 5 replicate samples each. To account for spatial variability, each of the five samples itself consisted of four sub-samples that were taken at random locations within a 50 cm radius around the respective sampling point. These sub-samples were mixed and used for a single analysis. Sample preparation and chemical analyses followed mainly the protocol given by "Bundesweite Bodenzustandserhebung im Wald" [6].

In the organic layer, the stocks of organic matter and carbon were determined by sampling the entire layer to the surface of the mineral soil with a soil corer (diameter 33 mm, length 100 mm), drying the material (110 °C, 48 h) and weighing it. The stock was calculated by relating the organic mass of the entire layer to corer aperture. The pH was measured in water using a 1:2.5 humus/water suspension. Total carbon and nitrogen in the humus material were determined in samples dried at 60 °C using a C/N elemental analyser (vario EL III, elementar, Hanau, Germany); total phosphorus was detected by yellow-dyeing and photometric measurement after digestion with 65% HNO_3 at 195 °C. The pools of Ca, Mg and K in the humus material were analysed by atomic absorption spectroscopy (AAS vario 6, analytik jena, Jena, Germany) after HNO_3 digestion.

Fresh mineral soil samples (0–10 and 10–20 cm depth) were analysed for pH in water using a 1:2.5 soil/water suspension. The concentrations of salt-extractable cations in the 0–10 cm horizon were determined by percolating 2.5 g of soil with 100 mL of 1 M NH_4Cl solution for 4 h. The solution concentrations of K, Mg, Ca, Mn, Al

Table I. Location, altitude, geological epoch, parent material, soil type (classification according to [25]), mean annual precipitation and temperature, and forest association of the 50 studied beech stands on thirteen different bedrock types in Lower Saxony, Germany. Precipitation and temperature were derived from weather station data that were corrected for altitude.

Site No.	Longitude (E)	Latitude (N)	Altitude (m a.s.l.)	Geol. epoch	Parent material	Soil type	Prec. (mm)	Temp. (˚C)	Assoc.	Source
1	10° 03’	51° 32’	420	l MU	Limestone	eCa-cCa	830	7.2	HF	S
2	10° 03’	51° 35’	420	l MU	Limestone	rLe	790	7.2	HF	S
3	09° 47’	51° 25’	335	l MU	Limestone	rLe	890	7.8	HF	S
4	09° 50’	51° 26’	310	l MU	Limestone	rLe	770	7.9	HF	S
5	09° 52’	51° 55’	300	u JU	Limestone	eCa-cCa	960	8.0	HF	S
6	09° 33’	52° 04’	280	u JU	Limestone	eCa-cCa	850	8.1	HF	S
7	09° 38’	52° 03’	340	u JU	Limestone	cCa-rLe	1030	7.7	CF	S
8	10° 07’	51° 52’	280	u JU	Limestone	rLe	880	8.1	HF	S
9	09° 54’	51° 58’	200	u CR	Limestone	rLe	810	8.7	CF	S
10	09° 56’	51° 58’	290	u CR	Limestone	rLe	860	8.1	HF	S
11	09° 47’	51° 55’	370	u CR	Limestone	rLe	880	7.5	HF	S
12	09° 51’	52° 01’	285	u CR	Limestone	rLe-eCa	840	8.1	HF	S
13	10° 05’	51° 31’	275	u BU	Claystone	vCa	740	8.2	HF	S
14	10° 01’	51° 28’	260	u BU	Claystone	vCa (s)	760	8.3	HF	S
15	09° 59’	51° 26’	410	u BU	Claystone	vCa	790	7.2	HF	S
16	09° 49’	51° 26’	300	u BU	Claystone	vCa	770	8.0	HF	S
17	09° 27’	52° 05’	330	m KE	Claystone	uLe-vCa	880	7.8	GF	S
18	09° 12’	52° 06’	240	m KE	Claystone	Ca-Ph	830	8.4	GF	S
19	09° 13’	52° 03’	210	m KE	Claystone	Ca	900	8.6	GF	S
20	09° 53’	51° 27’	270	m KE	Claystone	Ca	760	8.2	GF	S
21	09° 40’	51°43’	380	m BU	Sandstone	Um-uLe (p)	950	7.4	LF	S
22	09° 46’	51° 40’	260	m BU	Sandstone	Um	770	8.3	LF	S
23	09°39’	51°32’	395	m BU	Sandstone	uLe-Um	820	7.3	LF	S
24	10° 02’	51° 57’	250	m BU	Sandstone	p uLe-Um	860	8.4	LF	S
25	09° 25’	52° 11’	320	l CR	Sandstone	p Um	980	7.9	LF	S
26	09° 35’	52° 08’	220	l CR	Sandstone	p Um-uLe	940	8.6	LF	S
27	09° 42’	51° 58’	310	l CR	Sandstone	p Um-uLe	870	7.9	LF	S
28	09° 44’	51° 55’	270	l CR	Sandstone	p Um-uLe	860	8.2	LF	S
29	09° 41’	51° 26’	270	TE	Sand	Um	760	8.2	LF	S
30	09° 42’	51° 21’	520	TE	Sand	Um	810	6.5	LF	S
31	09° 45’	51° 26’	425	TE	Sand	Um	790	7.1	LF	S
32	09° 45’	51° 29’	440	TE	Sand	Um	840	7.0	LF	S
33	09° 28’	52° 07’	142	pl LL	Loess	Ph-Ca	780	9.1	GF	S
34	09° 25’	52° 03’	140	pl LL	Loess	p Ph	830	9.1	LF	S
35	09° 17’	52° 06’	180	pl LL	Loess	Ca-Ph	800	8.8	GF	S
36	10° 07’	51° 31’	250	pl LL	Loess	Ca-Ph	720	8.4	LF	S
37	10° 33’	53° 06’	80	pl SL	Loess	p Lu	610	8.4	FQ	Gö
38	10° 33’	53° 06’	80	pl SL	Loess	p Lu	610	8.4	FQ	Gö
39	10° 29’	53° 02’	90	pl SL	Loess	p Lu	610	8.4	FQ	Gö
40	10° 33’	53° 06’	80	pl SL	Loess	p Lu	610	8.4	FQ	Gö
41	09° 37’	52° 41’	50	pl LM	Glacial deposit	St-Lu	670	9.1	FQ	Gö
42	10° 29’	53° 02’	90	pl LM	Glacial deposit	St-Lu	610	8.4	FQ	Gö
43	10° 22’	53° 01’	90	pl LM	Glacial deposit	St-Lu	610	8.4	FQ	Gö
44	10° 35’	53° 04’	80	pl LM	Glacial deposit	St-Lu	610	8.4	FQ	Gö
45	09° 36’	52° 46’	50	pl SM	Glacial deposit	p Um	670	9.1	FQ	Gö
46	10° 22’	53° 01’	90	pl SM	Glacial deposit	p Um	610	8.4	FQ	Gö
47	10° 29’	53° 02’	90	pl SM	Glacial deposit	p Um	610	8.4	FQ	Gö
48	09° 19’	52° 48’	50	pl SM	Glacial deposit	p Um	670	9.1	FQ	Gö
49	10° 30’	52° 45’	115	pl FS	Glacial deposit	p Um	800	8.1	FQ	Le
50	10° 30’	52° 45’	115	pl FS	Glacial deposit	p Um	800	8.1	FQ	Le

Geological epoch: l MU = Lower Muschelkalk; u JU = Upper Jurassic; u CR = Upper Cretaceous; u BU = Upper Bunter; m KE = Middle Keuper; m BU = Middle Bunter; l CR = Lower Cretaceous; TE = Tertiary; pl LL = Pleistocene loamy loess, last Ice Age (Weichselian); pl SL = Pleistocene sandy loess, last Ice Age (Weichselian); pl LM = Pleistocene loamy moraine, penultimate Ice Age (Saalian); pl SM = Pleistocene sandy moraine, penultimate Ice Age (Saalian); pl FS = Pleistocene fluvioglacial sand, penultimate Ice Age (Saalian). Soil type (WRB): c = chromic; Ca = Cambisol; e = eutric; Le = Leptosol; Lu = Luvisol; p = podzolic; Ph = Phaeozem; r = rendzic; s = stagnic; St = Stagnosol; u = umbric; Um = Umbrisol; v = vertic. Association: CF = Carici-Fagetum; GF = Galio odorati-Fagetum; HF = Hordelymo-Fagetum; LF = Luzulo-Fagetum; FQ = Fago-Quercetum (= Luzulo-Fagetum, lowland type). Source: S = data from this study; Gö = from Gönnert; Le = from Leuschner and Rode (unpubl.).

and Fe were analysed by atomic absorption spectroscopy. Fe was assumed to be Fe^{2+}. The concentration of hydrogen ions at the cation exchangers was calculated from the observed pH change during the percolation process. The effective cation exchange capacity (CEC_e) was calculated as the sum of all extractable cations in the NH_4Cl extraction [22]. The base saturation gives the percentage portion of Ca, K and Mg in CEC_e. Plant-available phosphorus (P_a) according to [5] was extracted by resin bags that were placed for 16 h in a solution of 1 g of soil material suspended in 30 mL water [33]. P was then re-exchanged by NaCl and NaOH solutions and analysed by blue-dyeing [24] and photometric measurement. Total carbon and nitrogen in the mineral soil were determined with a C/N elemental analyser. The bulk density of the mineral soil was measured by weighing dried soil samples of 100 cm^3. C/N and N/P ratios are given in mol mol^{-1}. For most element species, analyses were only conducted in the 0–10 and 10–20 cm horizons. For C and N, a lower horizon (20–30 cm) was also investigated in order to estimate profile totals of soil carbon and nitrogen.

In about 10 profiles, the subsoil was analysed to a depth of 100 or 200 cm for establishing depth functions of soil C and N content. P_a could not be investigated at all sites due to the large number of study sites (only nine bedrock types).

2.3. Statistical analyses

In a first step, means and standard errors of the soil chemical data were calculated from each five (fluvioglacial sands: ten) samples per study site. Second, means and standard errors were calculated for the thirteen bedrock types by treating the each four (fluvioglacial sands: two) study sites of a given bedrock type as replicates. Statistical analyses were conducted with the package SAS 8.1 (Statistical Analyses System, SAS Institute Inc., Cary, NC, USA). Probability of fit to normal distribution was tested by a Shapiro-Wilk test. In the case of Gaussian distribution, mean values of the bedrock types were compared by a one-factorial analysis of variance followed by a Scheffé test. Data sets deviating from normal distribution were compared by one-way Kruskal-Wallis single factor analyses of variance. If H_0 (no significant differences among any of the bedrock types) was rejected, a non-parametric multiple comparison test after Wilcoxon was applied to locate the differences. We employed linear regression analysis to quantify the influence of various soil chemical factors on each other. Significance was determined at $p < 0.05$ in all tests. To analyse the differentiation of the 50 study sites with respect to various soil chemical parameters, a PCA analysis was applied to the standardised data of the mineral soil and organic layer (package CANOCO, version 4.5, Biometris, Wageningen, The Netherlands).

3. RESULTS

3.1. Soil types, humus profiles and soil chemistry as dependent on bedrock type

Central European beech forests grow on a broad range of soil types ranging from rendzic Leptozols and eutric Cambisols on limestone substrates to podzolic Luvisols and Umbrisols on the highly acidic glacial deposits (Tab. I). Under limestone and claystone beech forests, the typical humus form was a thin vermimull. Sandstones, Tertiary sands and loamy loess showed a variety of humus types including leptomoders, mullmoders and mormoders (Tab. II). The majority of glacial deposits and sandy loess sites were characterised by more or less thick mor profiles (raw humus) or mormoders.

We found a gradual increase in the soil acidity of the mineral topsoil (0–10 cm) from the limestone sites (pH in H_2O 5.4 to 5.6) through the claystones (4.7 to 5.3) and the sandstone, sand and loess sites (3.3 to 4.3) to the glacial sands and loams (3.3 to 3.7, Fig. 1a). The increase in acidity was paralleled by an increase in the mineral soil C/N ratio from about 16 mol mol^{-1} on the limestones to values > 30 mol mol^{-1} in some sandy glacial substrates (Tab. III). There was also a general increase in the pool of salt-exchangeable aluminium (Al_{ex}) in the mineral topsoil (0–10 cm) from limestone sites to the glacial sands. However, the variation in Al_{ex} among the four acidic glacial deposit types was very large (1.9–7.8 mol m^{-2} 10 cm^{-1}, Tab. III).

3.2. Variation in depth and quality of the organic layer and related controlling factors

The 13 bedrock types differed by a factor of more than 10 in the amount of organic dry mass on top of the soil surface (Tab. II). Only small humus amounts (1.4–2.9 kg d.m.m^{-2}) were found in beech forests on the five limestone and claystone substrates, and in those on the Pleistocene loamy moraines (plLM). The corresponding carbon pools ranged from 40 to 86 mol C m^{-2} (Fig. 2a). Soils on sandstones, Pleistocene loess or sandy moraine material contained 3.2 to 6.7 kg d.m.m^{-2} of organic matter, or 90–193 mol C m^{-2}. We found by far the largest amounts on Tertiary sands (10.0 kg d.m.m^{-2} or 221 mol C m^{-2}) and on Pleistocene fluvioglacial sands (19.2 kg d.m.m^{-2} or 531 mol C m^{-2}). The variation in organic layer dry mass was closely linked to the humus profile sequence from vermimull or leptomoder to mor (Tab. II).

According to our regression analysis, the amount of C in the organic layer was most closely related to exchangeable aluminium (Al_{ex}) in the mineral soil ($r^2 = 0.82$). Base saturation ($r^2 = 0.40$) and C/N ratio ($r^2 = 0.35$) of the mineral topsoil had a smaller influence on the C pool. The pH effect (mineral soil or organic layer) was only weak (Tabs. IV and V).

The accumulation of carbon in the organic layer was closely linked to that of nitrogen as evidenced by a coefficient of determination of 0.99 for the C pool/N pool relation (Tab. IV), and a remarkably uniform C/N ratio of the organic layer material (22.7–29.7 mol mol^{-1}) across the 13 bedrock types (Tab. II). The pools of total N in the organic layer varied between 1.5 (limestone lMU) and 18.9 mol m^{-2} (fluvioglacial sand plFS, Fig. 2). On the other hand, the C/N ratio of the organic layer was not correlated to any of the soil chemical properties investigated in the organic layer or the mineral soil (Tabs. IV and V). The accumulation of N in the organic layer was highly dependent on Al_{ex} in the mineral soil, as was found for carbon accumulation. Total nitrogen in the organic layer showed an exponential increase when the base saturation of the mineral soil fell below 50% (Fig. 3e), indicating that both Al_{ex}

Table II. Humus form, organic matter (dry mass), pH, C/N, pools of total nitrogen, total phosphorus, and of total calcium, magnesium, and potassium, and C/N, C/P, N/P, C/Ca, C/Mg, and C/K ratios in the organic layer (forest floor) of beech forests on thirteen different bedrock types (means, standard errors of four (or two) stands per bedrock type). Values relate to the entire organic layer (L, F, H layers). Different Latin or Greek letters in a row indicate significant differences among bedrock types. Data for pleistocene fluvioglacial sands according to Leuschner and Rode (unpubl.), data for pleistocene loamy moraines, sandy moraines, and sandy loess according to Gönnert [9]. Humus forms according to Green et al. [10].

Parent material			Limestones			Claystones		Sandstones		Sand	Loess		Glacial deposits		
Geological epoch			l MU	u JU	u CR	u BU	m KE	m BU	l CR	TE	pl LL	pl SL	pl LM	pl SM	pL FS
		n	4	4	4	4	4	4	4	4	4	4	4	4	2
Humus form			vm	vm	vm	vm	vm	m	lm	lm	lm	rh	m	rh	mm
Organic matter	(kg d.m.m^{-2})	mean	1.4^{C}	2.4^{C}	2.9^{BC}	1.9^{C}	2.3^{C}	6.7^{BC}	4.4^{BC}	10.0^{B}	3.2^{BC}	3.2^{BC}	1.6^{C}	5.1^{BC}	19.2^{A}
		s.e.	0.2	0.1	0.4	0.2	0.1	1.7	0.4	2.3	0.7	0.8	0.3	1.2	3.4
pH(H$_2$O) $_{(org)}$		mean	5.9^{ab}	5.9^{ab}	5.9^{a}	5.8^{abc}	5.7^{abc}	4.7^{bcde}	4.5^{cde}	4.4^{de}	5.0^{abcd}	3.4^{e}	3.8^{e}	3.5^{e}	3.6^{e}
C/N$_{(org)}$	(mol mol^{-1})	mean	29.7^{β}	$26.3^{\alpha\beta}$	$25.4^{\alpha\beta}$	$23.3^{\alpha\beta}$	$24.1^{\alpha\beta}$	$24.8^{\alpha\beta}$	$24.3^{\alpha\beta}$	$24.5^{\alpha\beta}$	$25.3^{\alpha\beta}$	29.7^{β}	22.7^{α}	$28.1^{\alpha\beta}$	$28.2^{\alpha\beta}$
		s.e.	1.6	1.0	1.9	0.7	0.6	0.5	0.7	0.7	0.4	0.6	0.5	1.4	0.4
N$_{t\ (org)}$	(mol m^{-2})	mean	1.5^{C}	2.4^{BC}	3.3^{BC}	2.2^{BC}	2.5^{BC}	7.9^{BC}	6.3^{BC}	9.1^{B}	3.6^{BC}	3.2^{BC}	1.8^{BC}	5.0^{BC}	18.9^{A}
		s.e.	0.3	0.3	0.4	0.2	0.2	2.0	0.9	1.3	0.9	1.1	0.3	1.3	3.8
C/P $_{(org)}$	(mol mol^{-1})	mean	579^{a}	979^{ab}	795^{ab}	499^{a}	940^{ab}	764^{ab}	1050^{ab}	612^{a}	1395^{ab}	679^{a}	1022^{ab}	1608^{b}	1646^{b}
		s.e.	59	182	107	29	218	76	84	79	172	81	200	187	21
P$_{t\ (org)}$	(mmol m^{-2})	mean	81^{b}	69^{b}	109^{ab}	102^{ab}	72^{b}	262^{ab}	160^{ab}	414^{a}	141^{ab}	65^{b}	40^{b}	89^{b}	322^{ab}
		s.e.	12	8	9	9	15	78	7	134	38	13	8	24	57
N$_{t\ (org)}$	(mol mol^{-1})	mean	19.3^{α}	$36.9^{\alpha\beta}$	$30.7^{\alpha\beta}$	21.5^{α}	$39.3^{\alpha\beta}$	$31.1^{\alpha\beta}$	$43.1^{\alpha\beta}$	$23.9^{\alpha\beta}$	$27.0^{\alpha\beta}$	$47.2^{\alpha\beta}$	$45.3^{\alpha\beta}$	56.8^{β}	58.5^{β}
		s.e.	1.5	6.3	2.3	0.8	9.3	3.0	3.6	3.8	3.4	6.5	9.5	4.8	1.5
C/Ca $_{(org)}$	(mol mol^{-1})	mean	72^{A}	69^{A}	60^{A}	83^{A}	104^{A}	332^{ABC}	333^{ABC}	261^{AB}	151^{A}	770^{BC}	237^{AB}	366^{ABC}	839^{C}
		s.e.	3	6	9	5	18	109	72	20	51	236	38	50	169
C/Mg $_{(org)}$	(mol mol^{-1})	mean	306^{a}	299^{a}	246^{a}	109^{a}	130^{a}	826^{a}	1116^{ab}	482^{a}	545^{a}	1224^{ab}	822^{a}	1143^{ab}	2250^{b}
		s.e.	55	80	15	9	20	208	327	109	256	189	194	187	339
C/K $_{(org)}$	(mol mol^{-1})	mean	250^{α}	352^{α}	259^{α}	145^{α}	165^{α}	541^{α}	$1042^{\alpha\beta}$	674^{α}	547^{α}	$2115^{\beta\gamma}$	$1322^{\alpha\beta\gamma}$	2502^{γ}	$1240^{\alpha\beta}$
		s.e.	47	147	41	12	76	92	151	107	115	302	313	358	126
(Ca + Mg + K)$_{t\ (org)}$	(mol m^{-2})	mean	1.0^{A}	1.0^{A}	1.9^{A}	1.5^{A}	0.8^{A}	1.4^{A}	0.6^{A}	2.0^{A}	1.3^{A}	0.3^{A}	0.3^{A}	0.6^{A}	1.4^{A}

Geological epoch: l MU = Lower Muschelkalk; u JU = Upper Jurassic; u CR = Upper Cretaceous; u BU = Upper Bunter; m KE = Middle Keuper; m BU = Middle Bunter; l CR = Lower Cretaceous; TE = Tertiary; pl LL = Pleistocene loamy loess, last Ice Age (Weichselian); pl SL = Pleistocene sandy loess, last Ice Age (Weichselian); pl LM = Pleistocene loamy moraine, penultimate Ice Age (Saalian); pl SM = Pleistocene sandy moraine, penultimate Ice Age (Saalian); pl FS = Pleistocene fluvioglacial sand, penultimate Ice Age (Saalian). Humus form: lm = leptomoder; m = mullmoder; mm = mormoder; rh = raw humus, mor; vm = vermimull. a = plant-available content; ex = exchangeable content; t = total content; min = mineral soil (0–10 cm); org = organic layer (forest floor).

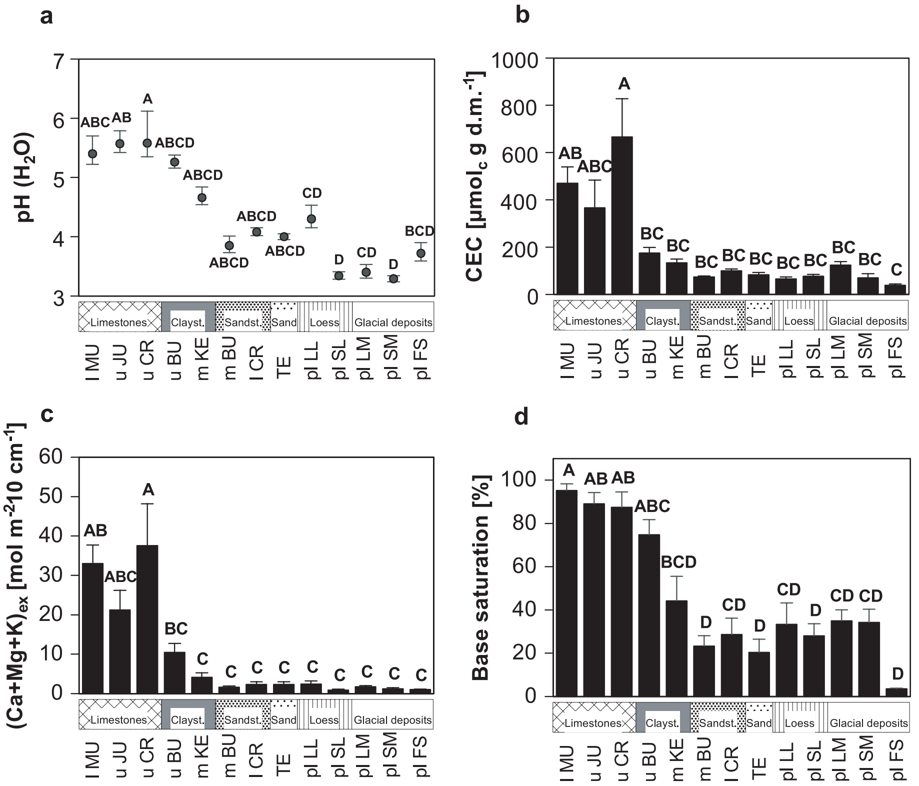

Figure 1. pH values (a), cation exchange capacity (b), pool of exchangeable calcium, magnesium, and potassium (c), and base saturation (d) in the mineral soil (0–10 cm) of beech forests on thirteen different parent materials (means and standard errors of four (two) stands per parent material). Different letters indicate significant differences among parent materials. Data for pleistocene fluvioglacial sands according to Leuschner and Rode (unpubl.), data for pleistocene loamy moraines, sandy moraines, and sandy loess according to Gönnert [10].

Table III. Soil type, C concentration, C/N ratio and pools of plant-available phosphorus or exchangeable aluminium in the mineral soil (0–10 cm) of beech forests on thirteen different bedrock types (means, standard errors of four (or two) stands per bedrock type). Different Latin or Greek letters in a row indicate significant differences among bedrock types. Data for pleistocene fluvioglacial sands according to Leuschner and Rode (unpubl.), data for pleistocene loamy moraines, sandy moraines, and sandy loess according to Gönnert [9]. Soil types according to ISSS-ISRIC-FAO [25].

Parent material			Limestones			Claystones		Sandstones		Sand	Loess		Glacial deposits		
Geological epoch			l MU	u JU	u CR	u BU	m KE	m BU	l CR	TE	pl LL	pl SL	pl LM	pl SM	pL FS
		n	4	4	4	4	4	4	4	4	4	4	4	4	2
Soil type			rLe	eCa-cCa	rLe	vCa	Ca	uLe-Um	pUm-uLe	Um	Ca-Ph	pLu	St-Lu	pUm	pUm
$C_{org\ (min)}$	(%)	mean	12.9^a	6.0^a	8.2^a	6.1^a	4.6^a	7.5^a	6.8^a	6.2^a	7.1^a	4.8^a	4.7^a	3.5^a	2.4^a
		s.e.	3.3	0.9	1.9	1.0	1.3	0.8	1.1	1.3	2.9	0.1	0.5	0.5	0.0
$C/N_{(min)}$	(mol mol^{-1})	mean	16.4^{AB}	16.5^{AB}	15.4^{A}	16.0^{AB}	17.9^{AB}	25.7^{BCDE}	24.5^{ABCDE}	23.6^{ABCD}	25.0^{ABCDE}	33.6^{E}	20.3^{ABC}	28.2^{CDE}	31.4^{E}
		s.e.	0.2	1.0	0.4	0.8	0.9	0.9	1.1	1.4	1.7	1.2	1.1	2.8	4.6
$P_{a\ (min)}$	(mmol m^{-2})	mean	563^a	418^a	298^a	521^a	599^a	475^a	607^a	386^a	416^a	n.i.	n.i.	n.i.	n.i.
		s.e.	113	76	46	65	139	73	145	65	52				
$Al_{ex\ (min)}$	(mol m^{-2}10 cm^{-1})	mean	0.4^β	0.6^β	1.5^β	1.2^β	2.7^β	2.1^β	2.1^β	2.8^β	1.7^β	1.6^β	2.6^β	1.9^β	7.8^α
		s.e.	0.3	0.3	0.7	0.3	0.8	0.3	0.2	0.3	0.2	0.3	0.2	0.5	1.7

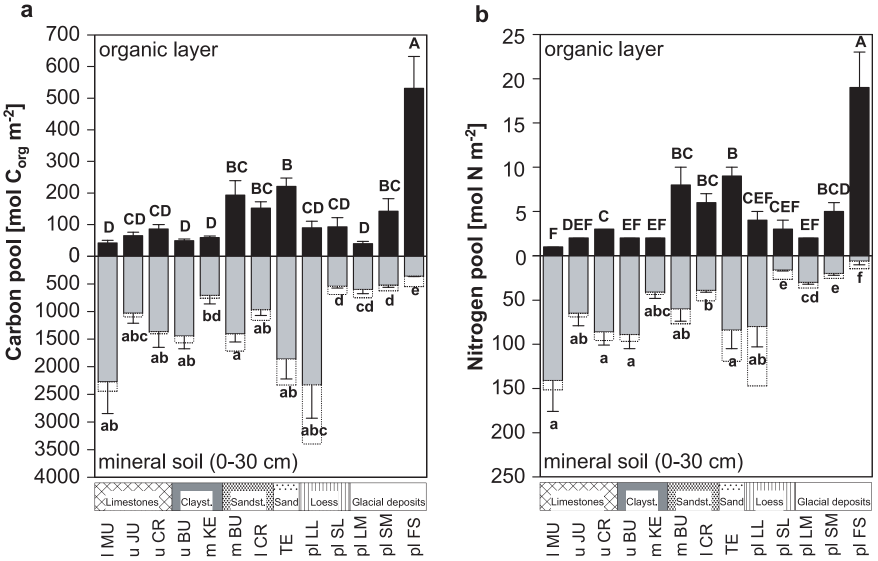

Figure 2. Carbon (a) and nitrogen (b) pools in the organic layer and the mineral soil (0–30 cm) of beech forests on thirteen parent materials (means and standard errors of four (two) stands per parent material). Values relate to the entire organic layer (L, F, H layers). Mineral soil data: filled bars: 0–30 cm, dotted bars: values extrapolated to 100 cm based on stone content and C (or N)-depth relationships derived from representative profiles. Different letters indicate significant differences among parent materials.

Table IV. Results of correlation analyses of organic layer properties in beech forests on thirteen different bedrock types. Given is a positive or negative sign for the slope *b* of the relationship, the determination coefficient r^2 and the probability of error p of linear equations ($y = a + bx$) to relate the C pool, pH value, C/N and N/P ratio, total nitrogen and total phosphorus pools, and total calcium, magnesium, and potassium pools in the organic layer to each other. All significant correlations ($p \leq 0.05$) are in bold. For units refer to Table I and Figure 1.

	Organic layer																	
	pH (H_2O)			C/N			N_t			P_t			N_t/P_t			$(Ca + Mg + K)_t$		
	b	r^2	p	b	r^2	p	b	r^2	p	b	r^2	p	b	r^2	p	b	r^2	p
Organic layer																		
C_{org}	–	**0.24**	**0.04**	+	0.06	0.22	**+**	**0.99**	**< 0.001**	**+**	**0.56**	**0.002**	**+**	**0.23**	**0.05**	+	0.09	0.16
pH (H_2O)				–	0.07	0.20	–	**0.23**	**0.05**	–	0.07	0.20	**–**	**0.56**	**0.002**	+	0.18	0.07
C/N							+	0.03	0.30	–	0.006	0.40	+	0.09	0.16	–	0.05	0.24
N_t										**+**	**0.65**	**< 0.001**	+	0.18	0.07	+	0.12	0.12
P_t													–	0.004	0.42	**+**	**0.41**	**0.009**
N_t/P_t																**–**	**0.30**	**0.02**
$(Ca + Mg + K)_t$																		

and base saturation in the mineral soil are key factors for the accumulation of C and N in the organic layer.

The total pool of phosphorus was particularly large in the organic layer of the Tertiary sands and the fluvioglacial sands (plFS, Tab. II), where large amounts of organic matter had accumulated. However, the organic layer P_t pool (and also the Ca + Mg + K pool) depended much less on the organic layer C pool ($r^2 = 0.56$ and 0.09) than did the N_t pool ($r^2 = 0.99$, Tab. IV). Other than C/N ratio, N/P of the organic layer varied considerably among the bedrock types with ratios > 45 mol mol^{-1} in the Pleistocene sandy and loamy soils, and values < 45 in all other substrates. The most influential organic layer properties that influenced the N/P ratio were the pH with a negative, and the organic layer C/Ca ratio with a positive, influence on N/P (Figs. 3a and 3b).

Among the most variable parameters were the organic layer C/Ca, C/Mg and C/K ratios which differed by factors of five to ten between the limestone and the glacial deposit sites. Organic layer pH decreased from 5.9 (limestone sites) to 3.5 (glacial deposits).

3.3. Variation of mineral soil nutrient status with bedrock type

The total pool of nitrogen in the mineral soil (0–30 cm) was much smaller in the glacial sandy and loamy substrates than in all other bedrock types. We measured 16 to 30 mol N m^{-2} in these highly acidified soils, whereas limestone, claystone and sandstone soils contained at least twice as much with maxima reaching 141 mol m^{-2} in the lMU sites (Fig. 2b). There

Table V. Results of correlation analyses of mineral soil properties (0–10 cm) to organic layer and mineral soil properties in beech forests on thirteen different bedrock types. Given is a positive or negative sign for the slope b of the relationship, the determination coefficient r^2 and the probability of error p of linear equations ($y = a + bx$). All significant correlations ($p \leq 0.05$) are in bold. For units refer to Table I and Figure 1.

	Mineral soil																				
	pH (H_2O)			C/N			N_t			CEC			Base saturation			$(Ca + Mg + K)_{ex}$			Al_{ex}		
	b	r^2	*p*	*b*	r^2	*p*	*b*	r^2	*p*	*b*	r^2	*p*	*b*	r^2	*p*	*b*	r^2	*p*	*b*	r^2	*p*
Organic layer																					
C_{org}	–	0.15	0.09	**+**	**0.35**	**0.02**	–	0.11	0.14	–	0.12	0.12	**–**	**0.40**	**0.01**	–	0.13	0.12	**+**	**0.82**	**< 0.001**
pH (H_2O)	**+**	**0.92**	**< 0.001**	**–**	**0.77**	**< 0.001**	**+**	**0.52**	**0.003**	**+**	**0.55**	**0.002**	**+**	**0.70**	**< 0.001**	**+**	**0.52**	**0.003**	**–**	**0.27**	**0.03**
C/N	–	0.01	0.35	+	0.20	0.06	+	0.003	0.43	+	0.01	0.36	+	< 0.001	0.47	+	0.04	0.20	+	0.003	0.43
N_t	–	0.16	0.09	**+**	**0.33**	**0.02**	–	0.09	0.15	–	0.13	0.11	**–**	**0.42**	**0.008**	–	0.14	0.10	**+**	**0.80**	**< 0.001**
P_t	–	0.06	0.21	+	0.13	0.11	+	< 0.001	0.46	–	0.08	0.18	**–**	**0.28**	**0.03**	–	0.10	0.15	**+**	**0.33**	**0.02**
N_t/P_t	**–**	**0.44**	**0.007**	**+**	**0.43**	**0.007**	**–**	**0.72**	**< 0.001**	**–**	**0.22**	**0.05**	**–**	**0.34**	**0.02**	**–0.24**	**0.04**		**+0.33**	**0.02**	
$(Ca + Mg + K)_t$	+	0.20	0.06	–	0.08	0.18	**+**	**0.23**	**0.05**	+	0.14	0.10	+	0.04	0.27	+	0.11	0.13	+	0.02	0.33
Mineral soil																					
pH (H_2O)				**–**	**0.71**	**< 0.001**	**+**	**0.51**	**0.003**	**+**	**0.70**	**< 0.001**	**+**	**0.81**	**< 0.001**	**+**	**0.69**	**< 0.001**	–	0.21	0.06
C/N							**–**	**0.41**	**0.009**	**–**	**0.51**	**0.003**	**–**	**0.70**	**< 0.001**	**–**	**0.49**	**0.004**	**+**	**0.27**	**0.03**
N_t										**+**	**0.48**	**0.004**	**+**	**0.45**	**0.006**	**+**	**0.55**	**0.002**	**–**	**0.23**	**0.05**
CEC													**+**	**0.74**	**< 0.001**	**+**	**0.97**	**< 0.001**	–	0.18	0.07
Base saturation																**+**	**0.78**	**< 0.001**	**–**	**0.46**	**0.005**
$(Ca + Mg + K)_{ex}$																			–	0.20	0.06

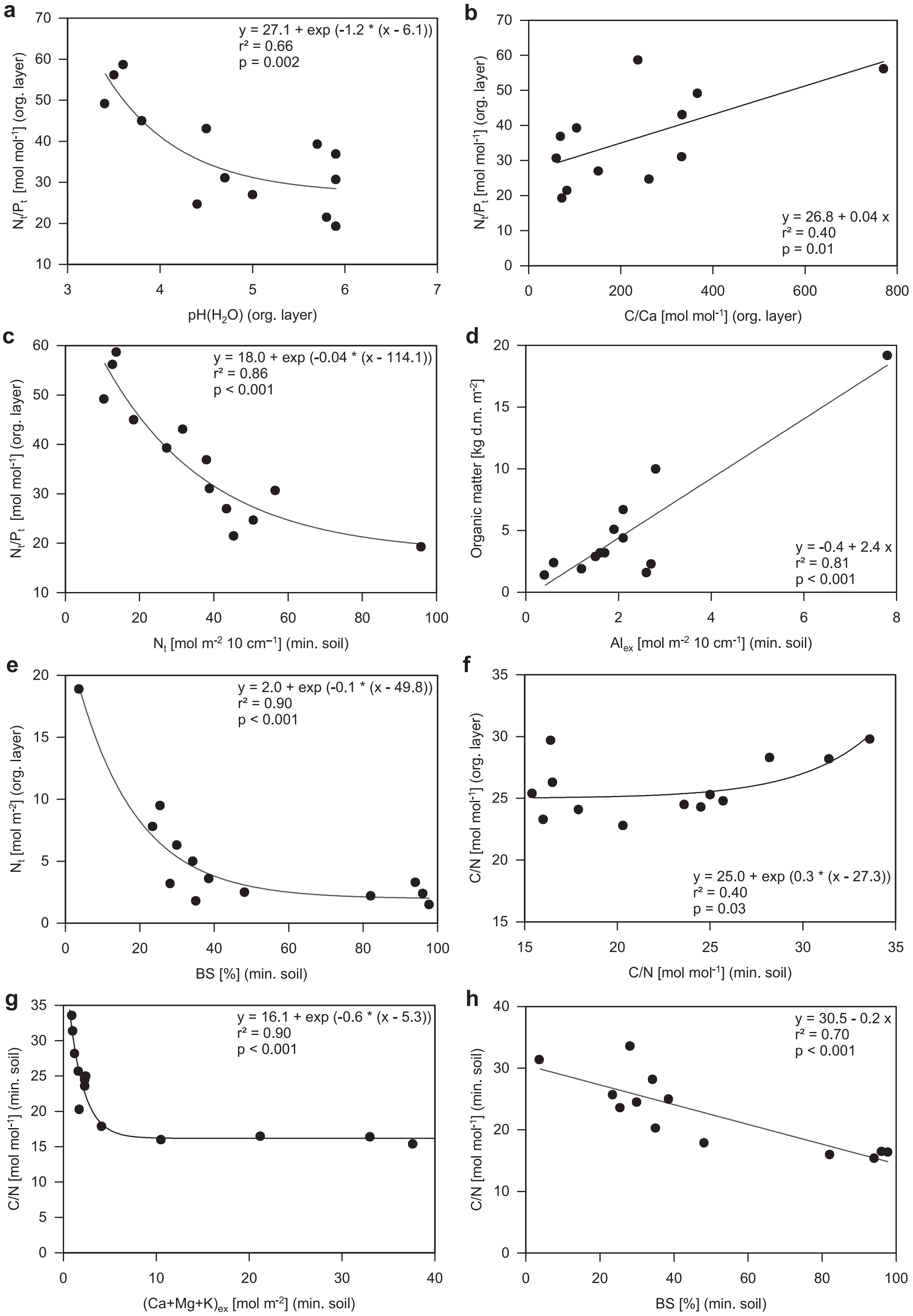

Figure 3. Some relationships between organic layer properties (a and b), between organic layer and mineral soil properties (c–f), and between mineral soil properties (g and h) in beech forests on thirteen different parent materials (means of four (two) stands per parent material). Given are the relationships between N_t/P_t ratio of the organic layer and the pH or the C/Ca ratio of the organic layer (a and b), the relationships between organic layer N/P and mineral soil (0–10 cm) N_t (c), dry mass of the organic layer and exchangeable Al in the mineral soil (0–10 cm; d), N_t of the organic layer and base saturation (e) and C/N of the organic layer or the mineral soil to base saturation, $(Ca + Mg + K)_{ex}$ or the C/N ratio of the mineral topsoil (f–h).

was a remarkable difference in the N content within the mineralogically heterogeneous group of the sandy and loamy substrates: Tertiary sands and Pleistocene loess sites contained 80 and 81 mol N m^{-2} in the 0–30 cm profile which is three to four times more than was found in the topsoil of Pleistocene sands or loams. Similarly, the variation among the three limestone substrates was also large (65–141 mol m^{-2}).

The more N occurred in the mineral soil, the smaller was the N pool in the organic layer on top of the soil because its depth decreased toward the N-rich limestone soils (Fig. 2b). Thus, similar to carbon, the soil N pool generally showed an upward shift with increasing soil acidity or decreasing base saturation. Extremes in this general trend were the limestone sites on Muschelkalk (lMU) with a ratio of about 140 for the mineral soil N pool (0–30 cm) vs. the organic layer pool. In contrast, the fluvioglacial sand (plFS) held about three times more N in the organic layer (19 mol m^{-2}) than in the upper mineral soil (6 mol m^{-2} at 0–30 cm).

Plant-available phosphorus (resin-exchangeable P, P_a) varied by a factor of two among the nine investigated bedrock types. We did not detect a significantly lower P availability in the basic calcareous substrates than in the acidic sandstone and sandy soils (Tab. III).

The pool of exchangeable Ca + Mg + K in the mineral topsoil was very small in the glacial sandy and loamy deposits, as well as in the sandstones (0.9–2.4 mol m^{-2} 10 cm^{-1}), where a base saturation < 35% was found (Figs. 1c and 1d). The $(Ca + Mg + K)_{ex}$ pool increased toward the claystones (4.1–10.5 mol m^{-2}) and further to the limestones (21.2–37.6 mol m^{-2}), which both showed much higher base saturations (44–95%).

Highly different coefficients of variation (CV) were found for the measured soil chemical parameters if their variation among the 13 bedrock types was considered. In the case of the mineral soil parameters, a relatively high between-substrate variation existed for the concentrations of $(Ca + Mg + K)_{ex}$ and H^+ (140 and 121%, respectively), an intermediate variation for cation exchange capacity (102%) and exchangeable Al (83%), and a relatively low one for N_t and base saturation in the topsoil (67 and 65%). In the organic layer, highest variation was found for H^+ (144%), an intermediate one for the N_t and P_t pools (92 and 77%, respectively) and for the C concentration (98%), and the lowest one for the base cation pool (53%).

3.4. Interrelationships between mineral soil and organic layer chemistry

Six of the seven chemical parameters studied in the mineral soil were highly correlated to each other: pH (H_2O), C/N, N_t, CEC, base saturation and exchangeable Ca + Mg + K pool (Tab. V). Most relations were significant at $p < 0.01$. Decreases in pH were correlated with highly significant decreases in the $(Ca + Mg + K)_{ex}$ pool, N_t, base saturation and also CEC. Similar relationships were found between base saturation and the mentioned parameters. The close negative relation between base saturation and C/N ratio is depicted as an example (Fig. 3h). The only mineral soil parameter with contrasting behaviour was Al_{ex} which showed a close negative relation to C/N and base saturation, but it was not significantly related to any of the other variables (Tab. V).

In the organic layer, the inter-relationship between the six measured chemical parameters was much weaker (Tab. IV). The N/P ratio of the organic material decreased exponentially with increasing pH and C/Ca ratio of this material (Figs. 3a and 3b). Remarkably, N/P in the organic material was not significantly correlated with neither N_t nor P_t in the organic layer itself, but it showed a highly significant relation to several parameters of the mineral soil including N content, C/N ratio (Tab. V and Fig. 3c), pH and base saturation of the 0–10 cm horizon (Tab. V).

4. DISCUSSION

4.1. Which soil chemical parameters are important for an ecological grouping of beech forests?

We shall focus the discussion about key chemical parameters in beech forest soils on those nutrient elements which are known to be potentially limiting for plant growth in temperate forests, i.e. the macro-elements N, P, K and Mg, with the first two being of general importance and the latter two being relevant in sandy and acidic soils [8, 9]. We also included Ca as an element closely related to the carbonate buffering system in the soil. On the other hand, Fe, S and all trace elements were not considered. In the absence of a comprehensive set of N mineralization data, we used total nitrogen and C/N ratio as rough indicators of relative N availability.

Figure 1c shows that the 50 beech forests can be sharply split into two groups based on the $(Ca + Mg + K)_{ex}$ pool in the mineral soil (1–4 and 4–38 mol m^{-2} in the 0–10 cm soil horizon). Indeed, the pool of exchangeable base cations revealed by far the largest substrate-related variation among all nutrient fractions studied (CV = 140%). A similarly large increase in $(Ca + Mg + K)_{ex}$ by a factor of 5 or more from carbonate-free soils to limestone soils was found by Hantl [13] in a survey of Northwest German forest soils. In our sample, the increase in the $(Ca + Mg + K)_{ex}$ pool was partly caused by higher cation exchange capacities (CEC) in the clay-rich limestone and claystone sites (> 130 μmol_c g $d.m.^{-1}$) compared to the majority of sandy and loamy substrates (about 40–80 μmol_c g $d.m.^{-1}$, Fig. 1b). It has to be noted, however, that our extraction method (1 M NH_4Cl) may have substantially overestimated CEC in the case of the carbonate-rich limestone substrates.

Plant-availability of P in forest soils depends on various factors including soil acidity, which determines the size of the insoluble Ca-P and Al-P fractions, the amount of organically-bound P, and mycorrhizal activity. In Central German beech forests, no clear dependence on soil type or forest community type was found for various fractions of extractable P [31]. Phosphorus bound to organic compounds is probably the most important P fraction in acidic forest soils with thick organic layers; thus, the plant-availability of P in these soils is largely dependent on the size of the soil carbon pool and the P-mineralising activity of microorganisms and mycorrhizal hyphae. Since the C pools in organic layer and mineral soil were highly variable among the bedrock types in our study, the size of the P pool did also vary considerably.

Our data indicate that important information on the relative availability of P can be deduced from the N_t/P_t ratio of the organic layer. This ratio changed more or less continuously from < 20 mol mol^{-1} in some base-rich limestone sites to > 55 in the most acidic glacial sands. Koerselman and Meuleman [16] have suggested that the foliar N/P ratio may serve as an indicator of the kind of nutrient limitation of plant growth with ratios < ca. 15 pointing at P limitation, ratios > ca. 15 standing for N limitation. If N/P is an indicator of relative growth limitation by N or P in trees as well, our data indicate that P limitation, if existent, should prevail in beech soils on Pleistocene sands and, to a lesser extent, on loess and sandstone substrates, whereas beech stands on limestones and claystones should be limited rather by N than by P. However, in the absence of experimental data on critical N/P ratios in mature beech forests, these conclusions must remain speculative.

The total N pool in the soil is mainly dependent on the N concentration in the mineral soil as reflected by the C/N ratio, but it is also influenced by the thickness of the organic layer. We found three to five times larger soil N pools in the soils on limestone, claystone or loess substrates than on sandy glacial deposits which most likely indicate higher annual N supply rates to the plants on these bedrock types. A compilation of experimentally obtained N mineralization data for various beech forests provided evidence that N supply in the mineral soil indeed increases with increasing N_t content or decreasing C/N ratio. Yet, lower mineralization rates in the mineral soil of acidic soils are partly compensated by higher supply rates from thicker organic layers [18]. As a consequence, Leuschner [18] concluded that, in recent times, Central European beech forests have rather similar N supply rates across a broad spectrum of acidic and basic soils. Accordingly, N supply seems to differentiate much less between beech forests on different bedrock types than does Ca + Mg + K or P availability. This finding is partly supported by the C/N ratios of the organic layers that were more or less similar among the 13 bedrock types, in contrast to the mineral soil C/N ratios. Similarly, Raulund-Rasmussen and Vejre [28] found only small differences in the C/N ratio of the forest floor in Danish forests stands across a large pH range which they attributed to atmospheric N deposition in recent times.

The results of the principle components analysis confirmed the prominent role of the three soil chemical variables $(Ca + Mg + K)_{ex}$ and C/N ratio of the mineral soil, and N/P ratio of the organic layer for differentiating the 50 beech forests in terms of their soil nutrient status. The PCA separated the main geological substrates along the first axis (eigenvalue = 0.474) in the sequence forests on limestones – claystones – sandstones – sand/glacial deposits (Fig. 4). This axis was related to the three mentioned variables (variable loadings: $(Ca + Mg + K)_{ex}$: 0.80, C/N: –0.87, N/P: –0.73). Based on the three parameters we were able to identify three rather clearly differentiated groups of beech forest soils:

(1) stands on various limestone and claystone substrates with low C/N ratios in the mineral soil (15–18 mol mol^{-1}), low to intermediate N/P ratios (19–39 mol mol^{-1}) and medium to high $(Ca + Mg + K)_{ex}$ pools (4–38 mol m^{-2} 10 cm^{-1});

(2) stands on moderately acidic, but more or less silicate-rich substrates (sandstones, Tertiary sands, loamy loess, loamy moraines) with intermediate C/N ratios in the mineral soil (20–26 mol mol^{-1}), variable N/P ratios (24–45 mol mol^{-1}) and low $(Ca + Mg + K)_{ex}$ pools (about 2 mol m^{-2} 10 cm^{-1}); and

(3) stands on highly acidic, silicate-poor sandy deposits with high C/N ratios in the mineral soil (28–34 mol mol^{-1}), high N/P ratios (47–59 mol mol^{-1}) and low $(Ca + Mg + K)_{ex}$ pools (about 1 mol m^{-2} 10 cm^{-1}).

Our data lead to the conclusion that the build-up of thick organic layers, as it occurs on Al-rich, acidic substrates, mainly increases the pool of N bound in organic material, whereas the enrichment of other key nutrients (P, Mg, K, Ca) is favoured by the process of organic layer carbon accumulation to a lesser extent. Beech forests with thick organic layers are, therefore, more likely affected by limitation of P (and/or Mg or K) than by N shortage. However, this conclusion must remain insecure until appropriate data on N mineralisation are available for the complete data set.

4.2. Niche breadth of *Fagus sylvatica* with respect to nutrient availability and soil acidity

The 50 beech forests from 13 different bedrock types cover nearly the entire range of site conditions that support beech growth in northern Central Europe [26]. Exceptions are sites with groundwater influence and on sand dunes which were not included in our study. However, both substrate types are only exceptionally colonized by beech forests. Thus, the maxima and minima of soil chemical parameters from our study may serve for defining the breadth of the ecological (or realized) niche of this species with respect to soil nutrient concentrations, soil acidity and Al_{ex} concentration.

Beech forests were found on soils with pH (H_2O) values between 3.2 and 7.3 and base saturations from 3.3 to 99.9%, corresponding to $(Ca + K + Mg)_{ex}$ pools of 0.4 to 60.5 mol m^{-2} 10 cm^{-1}. The C/N ratio of the mineral soil varied between 14 and 36 mol mol^{-1}. Even more impressive is the very broad range of plant-available P pools in the mineral topsoil (11–1287 mol P m^{-2} 10 cm^{-1}). On the other hand, beech can tolerate acidic soils with Al_{ex} pools as large as 9.5 mol m^{-2} 10 cm^{-1}, while calcareous soils contain only traces of exchangeable Al.

A strength of this study is that, in contrast to the majority of other forest nutrition studies, both the mineral soil and the organic layer were analysed. The latter is an important medium of fine root growth in acidic beech forests. On many bedrock types, marked differences between the mineral soil top horizon (0–10 cm) and the organic layer were found with respect to soil acidity, C/N ratio and nutrient concentrations. At least in the

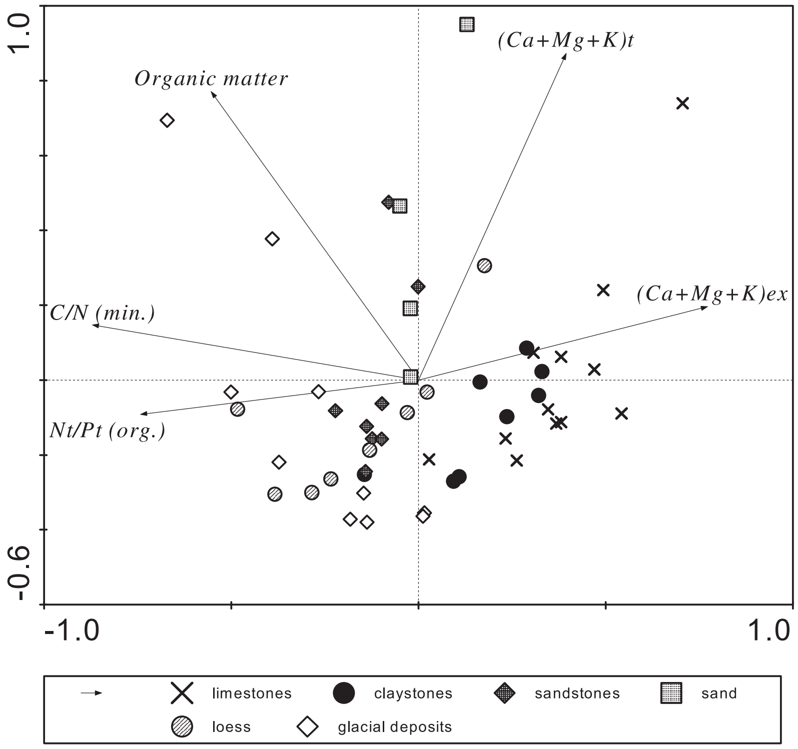

Figure 4. Plot showing the distribution of the 50 beech forests on 6 geological substrate types in PCA axes 1 and 2 together with 5 chemical variables of mineral soil and organic layer (N_t/P_t ratio, organic matter dry mass and total Ca + Mg + K pool of the organic layer, total N and exchangeable pool of Ca + Mg + K in 0–10 cm of the mineral soil). Vector length and angle are proportional to the direction and degree of their correlation with the plot ordination scores. Eigenvalues first axis: 0.474, second axis: 0.284; loadings of variables: $(Ca + Mg + K)_{ex}$: 0.80, C/N: –0.87, N/P: –0.73, $(Ca + Mg + K)_t$: 0.86, organic matter: 0.77.

acidic soils with a large portion of tree fine roots being concentrated in the organic layer, a soil chemical characterisation has to include the organic layer in order to be ecologically meaningful. As is demonstrated by the more or less uniform C/N ratio of the organic layer in our sample, analyses in the mineral soil alone would have indicated larger differences among the sites than do actually exist in the main rooting horizon.

A major disadvantage of our study is the lack of appropriate data on N availability in the soils. Although N mineralization rate was measured in several stands, a complete data set for all 50 sites (and 250 locations) could not yet be provided. Therefore, nitrogen (and, in part of the sites, phosphorus) availability can only be estimated from C/N, N/P, N_t and P_t data. This procedure is justified for Northwest German forest soils by the methodological study of Kriebitzsch [17]. Nevertheless, the respective results must be interpreted with caution.

4.3. Role of the organic layer in beech forest nutrition

In our sample, very large differences in the depth of the organic layer on top of the mineral soil (ectorganic layer sensu Emmer [7]) were found: Some limestone sites with vermimull had virtually no permanent organic layer because the leaf litter was decomposed (or dislocated) within periods of less than 12 months. In contrast, the two beech stands on highly acidic fluvioglacial sands (plFS) had up to 10 cm thick mor layers with distinct organic L, F and H horizons.

The steep gradient in organic layer thickness and C pool size across the bedrock types cannot be explained neither by differences in annual leaf litter mass, nor in leaf litter nitrogen content which both have a large influence on litter decomposition rate [3, 23, 38]. With values in the range of 295 to 391 g d.m.m^{-2} y^{-1} annual leaf litter mass was remarkably constant among the studied beech forests [21]. Even more surprising is the finding of Meier et al. [21] that the annual N return via leaf litter mass was more or less similar among the stands as well despite large differences in soil chemical properties. This observation is in line with the results of this study which show only minor variation in the C/N ratio of the organic layer in the 50-stand sample and, consequently, indicate no significant influence of the humus N content on total mass and turnover of organic matter on the forest floor.

Our correlation analysis showed that the largest influence on organic matter accumulation on top of the soil was not exerted by chemical properties of the organic layer itself. Instead, the pool of exchangeable aluminium (Al_{ex}) in the mineral topsoil was found to be the single most influential factor showing a very close relation ($r^2 = 0.82$, $p < 0.001$) to organic matter mass. Much less influential were base saturation and the C/N ratio of the mineral soil, whereas pH had no effect at all. These results exclude leaf litter supply rate and litter N content as possible causes for the different rates of C accumulation in the organic layer.

Based on these results and on additional data on fine root biomass [20] and macro- and meso-fauna activity [32] in beech forests on acidic and basic soils, we propose the following hypothetical explanation for site differences in organic matter accumulation on top of the soil.

First, litter derived from dying fine roots may be as relevant as, or even more important than, leaf litter as a source of soil organic matter [28]. This is suggested by the fact that roots were densely present in the forest floor on the acidic sites, but almost absent in the forest floor of the more fertile sites. Leuschner [19] concluded that the thick organic layers of beech forests on acidic soils represent feedback systems in which growing organic layers attract more tree fine roots, which deliver increasing amounts of C and nutrients to this compartment and thus further enhance its growth in thickness. In fact Leuschner and Hertel [20] concluded from a meta-analysis that the amount of beech fine root biomass in the organic layer increases with decreasing soil pH, thereby presumably contributing to an increase in organic layer thickness. High densities of roots and associated mycorrhizal fungi may also contribute to humus accumulation by depleting available nutrients that could alternatively be consumed by free saprophytic microorganisms during the decomposition process [10].

Second, other factors than litter N content might be responsible for a lower decomposition rate in acidic beech forest soils. Although relevant data are not existent for our beech forest sample, contents of lignin and other polyphenols in beech leaf and root litter could be higher in acidic than in basic soils which would slow down decomposition. By influencing decomposition, plants can feedback on nutrient cycles and soil properties in a manner that may be favourable for their fitness [36]. In addition, we observed substantially smaller C/P, C/Ca and C/Mg ratios in the organic layer of acidic beech forests as compared to basic sites (Tab. II) which could further reduce the activity of decomposing organisms [27].

Third, humus material also disappears from the organic layer by the burying activity of the soil macro- and meso-fauna which is generally less abundant in acidic forest soils [30]. Thus, thin organic layers could in part be the consequence of a high density of earthworms and other deep-dwelling animals which are favoured by high Ca and low Al contents of the soil [1]. The strong dependence of organic layer mass on mineral soil Al content in our study may indicate that elevated aluminium contents negatively influence the activity of soil organisms that foster decomposition or dislocation of organic substances in the organic layer.

We suggest that most likely more than one factor is responsible for the striking differences in C accumulation on top of beech forest soils. Processes or properties that control organic matter decomposition or dislocation, but that are not related to N content, must play a key role in our study. It may well be that N has lost its key influence on decomposition rate in Central European beech forests in the past decades which have experienced increasing atmospheric N inputs during the last 50 years. N deposition may have levelled off former differences in the C/N ratio and the chemical properties of the organic layer material. Nevertheless, the organic layer is most likely fulfilling important functions in the nutrition of beech forests on acidic soils, in particular with respect to N and P.

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