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Effect of tree species and soil properties on nutrient immobilization in the forest floor

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Abstract

To investigate the effect of tree species and soil properties on organic matter accumulation and associated nutrients, an area-based sampling of the forest floor was carried out in a 28 years old species trial including Norway spruce, Douglas fir, beech, and common oak at two sites, a poor and sandy soil, and a fertile loamy soil.

The accumulation of C, N and P in the forest floor was significantly higher at the sandy site than at the loamy site under all species. At the loamy site, oak was characterized by lesser accumulation of C, N and P than the other species. Remarkably, the C/N-ratios showed no substantial differences, whereas the C/P-ratios were significantly higher at the sandy site for all species. pH was significantly lower at the sandy site for all species, and among the species, pH was lower in the conifer forest floors than in the broadleave forest floors. The concentration of ammonium, nitrate and phosphate in the soil solution was much higher at the loamy site under all species showing a stronger microbial activity. It is therefore hypothesized that the differences in accumulation rates were, at least partly, caused by differences in the mineralization regimes. Strong root infiltration in the forest floors at the sandy site compared to almost none at the loamy site, is probably responsible for the differences in mineralization rate due to competition between the organic matter decomposers and the tree-roots/mycorrhiza for nutrients.

Introduction

The forest floor, defined as dead organic matter above the mineral soil, is an important link in the biogeochemical cycle of nutrients in forest ecosystems and essential for the nutritional status of forest stands. Nutrients are supplied in organic matter by litterfall and rendered available following mineralization by saprophytic microorganisms. Litter production rates exceeding mineralization rates lead to accumulation of organic matter and nutrients in unavailable forms. The various nutrients are held in different kinds of compounds, and consequently, the nutrient release over time exhibit different patterns due to different degradability (Staaf and Berg, 1982). As a result of incomplete mineralization, organic acids causing increase in soil acidity are produced, and in turn podzolization may be initiated. These effects may be considered adverse, whereas an increase in the weathering rate of soil minerals due to effects of the organic acids may be considered positive (Lundström and Öhman, 1990).

The effect of vegetation on accumulation and properties of the forest floor has for more than a century attached scientific interest. Müller (1879) defined two types of organic matter, mull and mor, and related formation of the two types to fertile and poor soils, respectively. Subsequent observations have shown differences in accumulation and properties of the forest floor under various species (Binkley and Valentine, 1991; Bockheim and Leide, 1991; Bockheim et al., 1991; Ovington, 1953, 1954; Perala and Alban, 1982). The differences have been attributed to various factors such as environmental factors, e.g. climate (Meentemeyer and Berg, 1986; Witkamp and Van Der Drift 1961), nutrient content of the litter (Blair, 1988; Staaf and Berg, 1982), the C/N ratio (Pastor et al., 1984), and the lignin/N ratio (Aber and Melillo, 1982; Gower and Son, 1992). The nutritional status of the foliage and thereby also the litter, is, to some extent, influenced by soil properties (Fernandez and Struchtemeyer, 1984; Liu and Trüby, 1989), and the general observation is that low fertile soils often are characterized by accumulation of large mor-like litter layers whereas fertile soils are characterized by mull and only minor litter layers. Since the so-called mull-forming tree-species dominate on fertile soils and the so-called mor-forming tree-species dominate on nutrient poor soils, it is not clear to which extent site specific factors, e.g., the nutrient status, influence or overrule the species specific differences in accumulation of organic matter and nutrients in the forest floor.

In this study, accumulation of C and associated nutrients in the forest floor are examined in 28 years old monoculture stands of beech, oak, Norway spruce and Douglas fir, on two sites, a relative fertile loamy soil, and a relative poor sandy soil. To obtain quantitative estimates on accumulated elements, area-based sampling of organic matter above the mineral soil was carried out. The accumulation of C, N and P is discussed in relation to C/N and C/P ratios, inorganic N and P in soil solutions relative to total N and P, pH, and root intensity in the forest floors. The availability of Ca, Mg and K was estimated by sequential extraction by water, 1 M NH_4NO_3, and total digestion. The forest floor was investigated, because this layer was considered the most sensitive to the effects of vegetation-soil interaction. In the long-term perspective changes in the mineral soil also may be expected.

Material and methods

Site description

Two sites were used, Ulborg in Western Denmark (56 18'N, 8 25'E) and Christianssaede on the island of Lolland in Southern Denmark (54 47'N, 11 22'E). The Ulborg soil, afterwards called the sandy soil (Typic Haplohumod), has been formed on Saale-glacial till; the Christiansaede soil, afterwards called the loamy soil (Mollic Hapludalf), has been formed on Weichsel-glacial till. Some characteristics of the soils are given in Table 1. Both sites are almost level and the spatial variation within the sampling area seems relatively small. On both sites a tree species trial in monoculture including Norway spruce (*Picea abies*), Douglas fir (*Pseudotsuga menziesii*), beech (*Fagus sylvatica*), and oak (*Quercus robur*) was established in 1964 by The Forest and Landscape Research Center (Holmsgaard and Bang, 1977). Each stand is about 0.5 ha. Both sites were formerly deforested, farmland at the loamy site and heathland at the sandy site. Ploughing depth at the loamy site was about 20 cm. Before planting the sandy soil was ploughed to 40 cm depth and the former O, A, E, Bh and Bhs horizons were turned upside-down, but remained almost unmixed. The data in Table 1 is from pits just outside the trials. The ploughing implies that all organic matter now present in the forest floors originate from the present stands. The mean annual temperature is 8°C at both sites, the mean precipitation is 840 mm at the sandy site and 620 mm at the loamy site.

Sampling procedure

Prior to litterfall in October 1991 area-based samples of the forest floor were collected in spruce, Douglas fir, oak and beech on the two sites excluding lignified roots, cones, and larger twigs. Ten litter samples were collected randomly in each plot by dropping a frame covering 25 × 25 cm. The samples were kept in tight plastic bags at 5°C until handling in the laboratory. Characteristics of the forest floors may be seen in Table 2. Although care was taken to exclude mineral material contamination was unavoidable. Since silicate minerals partly dissolve and release base cations during acid digest four additional samples of only the top litter layer without mineral grains from each stand at the sandy site were collected and used in a sequential extraction of base cations.

To isolate the soil solution, samples containing natural moisture were transferred to centrifuge tubes with 2mm holes in the bottom and a cup beneath the tube (Davies and Davies, 1963). The centrifugation was carried out at 4000g for 30 minutes. Afterwards the solid material was air-dried and milled.

Soil solutions

Soil solutions were filtered (HVLP <0.45 μm) and the following analyses carried out: pH by potentiometry; Ca, Mg, K and Al by flame atomic absorption spectrometry (AAS); nitrate, sulphate and chloride by ion chromatography; ammonium by the Berthelot-reaction (Hinds and Lowe, 1980); phosphate by the molybdenum blue method (Murphy and Riley, 1965) and dissolved organic C as CO_2 by IR spectrometry following oxidation in a 600°C oven (Shimadzu TOC 500).

Organic matter analyses

pH (1:10) in 0.01M $CaCl_2$ suspensions was determined potentiometrically. Exchangeable cations were deter-

Table 1. Soil properities

		pH_{CaCl_2}	Ca^{2+}	Mg^{2+}	K^+	C	N	P	Clay	Silt	Sand	$CaCO_3$
			---- $cmol_+ \, kg^{-1}$ ----			--- $mg \, g^{-1}$ ---			---------- % ----------			
Christianssaede, loamy soil												
A1	0–5	3.8	4.6	0.6	0.12	28	2.1	0.11	12	10	78	
A2	5–25	5.2	9.3	0.4	0.10	15	1.7	0.11	12	11	77	
Bt	25–50	6.2	12.2	0.6	0.18	4	0.5	0.24	15	18	67	
Btg	50–73	7.5	(21.7)	0.5	0.12			0.38	18	20	62	0.6
Ckg	73–110	7.7		0.3	0.07				9	16	75	28
Ulborg, sandy soil												
A	0–18	2.7	0.99	0.67	0.23	107	3.3	0.06	2	3	95	
E	18–30	3.4	0.03	0.01	b.d	4	0.1	0.02	1	2	97	
Bh	30–34	3.5	0.20	0.13	0.09	70	2.4	0.01	11	4	85	
Bhs	34–40	4.1	0.06	0.04	0.04	36	1.3	0.02	6	4	90	
Bs	40–60	4.4	0.02	b.d	0.01	12	0.1	0.02	3	3	94	
BC	60–100	4.5	0.01	b.d	b.d	3		0.01	1	2	97	
C	100–130	4.4	0.01	b.d	b.d	1		0.01	1	3	96	

b.d: below detection limit,
Ca^{2+}, Mg^{2+}, K^+: 1*M* NH_4CH_3COO, pH 7.
C, N: dry combustion.
P: 0.1*M* H_2SO_4.
clay, silt and sand: sedimentation of $CaCO_3^-$ and organic matter-free sample.
$CaCO_3$: volumetric.

mined by extraction with 1*M* NH_4NO_3 (Stuanes et al., 1984), modified by four times extractions and centrifugation. Concentrations of Ca, Mg, K and Al were determined by AAS. Extractable acidity at pH 8.1 was determined by use of the m-nitrophenol/nitrophenolat method (Piper, 1944). Total C was determined by dry combustion and weighing of evolved CO_2 (modified LECO method). Total N was determined by dry combustion and mass spectrometry (EA 1108- Elemental analyzer, Carlo Erba). Total P was determined after ashing (550°C) and dissolution in 6*M* H_2SO_4 (70°C) by the molybdenum blue method (Murphy and Riley, 1965).

Sequential extraction of Ca, Mg and K

Samples from beech and oak were chopped coarsely with a knife whereas the spruce and Douglas fir samples were used as collected. Water extractable cations were determined by extraction of 18.00 g (wet weight) organic material with 150 mL demineralized water for 17 hours before separation and further wash on a suction paper filter. After water extraction, exchangeable cations in the organic material were determined by extraction with 150 mL 1*M* NH_4NO_3 for other 17 hours before separation and further wash with 200 mL 1*M* NH_4NO_3 on the suction filter. The remaining cations were determined following concentrated H_2SO_4/H_2O_2 digestion. Concentrations of Ca, Mg, and K in the extracts were determined by AAS.

Statistics

Effects of tree species and of site were tested by a two way F-test (Anova in SAS). Specific species effects were tested by t-tests.

Results

Mobility of Ca, Mg and K in the forest floor

Only minor parts of Ca and Mg (< 10%) but about 40% of K in the forest floor were water extractable (Table 3). However, the major part of Ca (71–83%), of K (90%) and of Mg (93–100%) were held at exchange site (NH_4NO_3 extractable) and immediately available for the vegetation.

Table 2. Characterization of the forest floors

	Thickness cm	Border to mineral soil	Composition/ decomposition	Roots	Flora	Activity of earthworms
Loamy site						
Norway spruce	1–4	Sharp	Needles (red to brown) and twigs	Sparse	None	None
Douglas fir	1–4	Sharp	Needles (brown to black) and twigs	None	None	Sparse
Oak	almost absent		Scattered oak and herb leaves, mineral soil nearly stripped	None	Extremely vigorous herblayer, stinging nettle, elder, grass	Intense
Beech	1–6	Sharp	Leaves and bud-scale, severe by depth comminution	None	None	Intense
Sandy site						
Norway spruce	2–6	Sharp	Slightly decomposed needles (brown), twigs and branches	A lot	None, except widespread moss	None
Douglas fir	3–8	Sharp	Loose slightly decomposed needles (redyellow, redbrown, black), twigs, branches	Dense on transition to min.soil	None, except moss on stumps	None
Oak	4–10	Clear, a zone of transition	Leaves and roots, by depth increas-sing comminution and fermentation	A lot (oak and grass)	Bent grass, moss, toadstool	None
Beech	2–10	Clear, a zone of transition	Leaves and bud-scale, by depth increa-sing comminution	Dense on pas--sage to min. soil	Sparse moss toadstool	None

Table 3. Extractability of Ca, Mg and K in the forest floor from the sandy site (Ulborg). Values, i.e. H_2O- and NH_4NO_3-extractable content are given as percentage of the total content

	Ca		Mg		K	
	H_2O	NH_4NO_3	H_2O	NH_4NO_3	H_2O	NH_4NO_3
Beech	1	83	4	100	42	95
Douglas	3	73	9	95	37	88
Oak	3	78	8	100	42	93
Spruce	5	71	10	93	37	88

Accumulation of C, N, P, Ca, Mg and K

The accumulation of C, N, P, K and Mg showed strong site differences, but only minor species differences (Table 4). The accumulation of Ca was only significantly different between the two sites for Douglas fir and oak. Generally, about 2–3 times more of the various elements under spruce, Douglas fir and beech, and 7–30 times more under oak, were accumulated on the sandy soil than on the loamy soil. Among the species, oak accumulated significantly lesser on the loamy soil than the other species. On the sandy soil oak accumulated the same amount as the other species except for

Table 4. Accumulation of C, N, and P, and exchangeable Ca, Mg and K

	C	N	P	Ca	Mg	K
	mg ha^{-1}	kg ha^{-1}				
Loamy site						
Beech	3.78^{a}	143^{a}	9^{b}	87^{a}	6^{a}	7^{a}
Douglas	4.68^{a}	174^{a}	13^{ab}	75^{a}	5^{a}	7^{a}
Oak	0.4^{b}	14^{b}	2^{c}	10^{b}	1^{b}	2^{b}
Spruce	5.2^{a}	214^{a}	16^{a}	110^{a}	6^{a}	8^{a}
Sandy site						
Beech	11.2^{ab}	467	22^{ab}	132^{a}	28^{a}	22
Douglas	12.0^{a}	515	27^{a}	120^{ab}	21^{ab}	15
Oak	8.7^{b}	417	20^{b}	70^{c}	16^{b}	19
Spruce	11.7^{a}	443	24^{ab}	85^{bc}	20^{b}	18
Site differences						
Beech	***	***	**		***	**
Douglas	***	***	***	*	***	***
Oak	***	***	***	***	***	***
Spruce	***	***	**		***	***

Values in a column - by site - with the same letter (or no letter) do not differ significantly at 5%, level. Site differences on 5% 1% and 0.1% level are indicated by *, ** and ***, respectively.

less C than Douglas fir and spruce, less P than Douglas fir and less Ca than Douglas fir and beech.

Properties of the forest floor

The forest floors exhibited significant differences for some but not all parameters among the various species and the two sites (Table 5). To allow for mineral soil contamination of the litter samples, values in Table 5 are expressed per g C. The Ca concentration in the loamy soil forest floors was significantly higher than in the sandy soil forest floors, whereas the Mg concentration, except for oak, behaved oppositely. K exhibited no significant differences except for higher concentration in the oak forest floor at the loamy site. pH was higher in the loamy soil forest floors than in the sandy soil forest floors. Among the species, beech and oak forest floors were higher in pH than spruce and Douglas fir on both sites. Remarkably, the C/N ratios showed only small differences among the species on the two sites and between the sites. The C/P ratio was significantly lower in the loamy soil forest floors than in the sandy soil forest floors. Except for smaller C/P ratio in the oak forest floor, the species differences were negligible.

Composition of soil solutions

Except for Mg, the concentrations of the various nutrients were significantly higher at the loamy site than at the sandy site for all species (Table 6). Especially the differences in phosphate, ammonium and nitrate were notable. pH was also higher at the loamy site, roughly 1–1.3 unit for beech and oak, and 0.3–0.7 unit for Douglas fir and spruce. On both sites, pH was higher in beech and oak than in spruce and Douglas fir. Among the species, oak at the loamy site was different from the other species in Ca, Mg, K and phosphate. On the sandy site, beech was remarkably lower in nitrate and ammonium than the other species, whereas the values for Douglas fir were relatively high.

Discussion

Considerations on nutrient immobilization in the forest floors are important for N and P, but also, although to a lesser extent, for Ca, whereas Mg and K were found readily available.

The different amounts of C, N and P accumulated in the forest floors are caused by differences in rates of litter production and decay (Olson, 1963). Decay rate and mineralization constants cannot be calculated since litter production data are available only for spruce and beech at the sandy site, and steady-state in accumulated organic matter hardly exists in the only 28 years old first generation stands. Nevertheless, since litter production and quality as substrate for saprophytic organisms depends on soil fertility (Miller, 1984) litter production may be higher at the loamy site than at the sandy site, and the substantial differences in organic matter accumulation may be attributed to differences in the decay rates. Clearly, the decay rate under oak was higher than under the other species at the loamy site, and the decay rates were higher at the loamy site than at the sandy site under the various species. The very fast decay under oak at the loamy site - the forest floor litter layer was almost absent - is probably due to effects of earthworms (Table 2). Earthworms may also be partly responsible for the differences between the two sites but hardly for the complete differences. Rather, differences in the saprophytic activity in the forest floors at the two sites may be responsible for the differences in accumulation. The significantly higher concentration of nitrate, ammonium and phosphate in the soil solution, and, in particular, the ratios of miner-

Table 5. Exchangeable Ca, Mg, K, and Al, titratable acidity, pH in $CaCl_2$, and C/N and C/P ratios

	Ca^{2+}	Mg^{2+}	K^{+}	Al^{3+}	H^{+}	pH	C/N	C/P
	$\mu mol_{+}\ gC^{-1}$							
Loamy site								
Beech	1.31^{a}	0.15^{b}	0.06^{b}	0.01^{c}	2.7^{b}	5.1^{b}	27^{ab}	431^{a}
Douglas	0.83^{b}	0.09^{c}	0.04^{c}	0.08^{a}	3.8^{a}	4.1^{b}	29^{a}	383^{ab}
Oak	1.31^{a}	0.27^{a}	0.14^{a}	0.02^{c}	2.9^{b}	5.2^{a}	28^{ab}	267^{c}
Spruce	1.12^{a}	0.10^{c}	0.05^{c}	0.06^{b}	3.2^{ab}	4.3^{b}	25^{b}	344^{b}
Sandy site								
Beech	0.65^{a}	0.23^{a}	0.05	0.04^{b}	3.6^{b}	3.9^{a}	24^{a}	514
Douglas	0.54^{ab}	0.16^{b}	0.04	0.12^{a}	4.4^{a}	3.5^{bc}	24^{a}	455
Oak	0.43^{bc}	0.17^{b}	0.06	0.11^{a}	3.7^{b}	3.6^{b}	21^{b}	458
Spruce	0.39^{c}	0.16^{b}	0.04	0.11^{a}	4.1^{ab}	3.4^{c}	26^{a}	485
Site differences								
Beech	***	**		***	**	***		*
Douglas	***	***				***	*	*
Oak	***	***	***	***	*	***	***	***
Spruce	***	***		**	*	***		***

Values in a column - by site - with the same letter (or no letter) do not differ significantly at 5%, level. Site differences on 5%., 1%, and 0.1% level are indicated by *, ** and *** respectively.

Table 6. Composition of soil solutions, in mmol dm^{-3} except pH

	Ca	Mg	K	NH_4	Al	pH	NO_3	PO_4	DOC
Loamy site									
Beech	1.27^{b}	0.35^{b}	0.86^{b}	0.42	0.09	5.1^{a}	0.49^{b}	0.11^{b}	52^{ab}
Douglas	1.08^{b}	0.41^{b}	1.04^{b}	0.36	0.08	4.1^{c}	0.80^{b}	0.14^{b}	57^{ab}
Oak	3.07^{a}	1.35^{a}	4.76^{a}	0.58	0.11	5.1^{a}	1.70^{a}	0.22^{a}	142^{ab}
Spruce	1.00^{b}	0.48^{b}	1.03^{b}	0.45	0.10	4.3^{b}	2.49^{a}	0.15^{b}	106^{ab}
Sandy site									
Beech	0.66	0.52^{ab}	0.43^{ab}	0.02^{b}	0.05	4.0^{a}	0.07^{d}	0.01	47
Douglas	0.69	0.67^{ab}	0.34^{b}	0.10^{a}	0.07	3.8^{b}	0.89^{a}	0.01	42
Oak	0.40	0.46^{b}	0.44^{44}	0.05^{b}	0.06	3.8^{a}	0.41^{c}	0.01	34
Spruce	0.59	0.77^{a}	0.51^{a}	0.04^{b}	0.06	3.6^{c}	0.68^{b}	0.01	50
Site differences									
Beech			**	***		***	***	***	***
Douglas	*	*	***	***		**		***	
Oak	***	***	***	***	**	***	***	***	
Spruce		*	**	***		***	**	***	

Values in a cohmn - by site - with the same letter (or no letter) do not differ significantly at 5%, level. Site differences on 5% 1% and 0.1% level are indicated by *, ** and ***, respectively.

Table 7. Ratios between dissolved inorganic and total nitrogen and phosphorus

	N (diss/total) x 1000	P x 1000
Loamy site		
Beech	1.76[c]	7.19
Douglas	2.52[bc]	9.00
Oak	4.21[ab]	9.02
Spruce	5.04[a]	7.50
Sandy site		
Beech	0.18[d]	0.90
Douglas	1.59[a]	0.64
Oak	0.66[c]	0.51
Spruce	1.08[b]	0.66
Site differences		
Beech	***	***
Douglas		*
Oak	***	***
Spruce	***	***

Values in a column - by site - with the same letter (or no letter) do not differ significantly at 5% level. Locality differencies on 5%, 1% and 0.1%, level are indiceted by *, ** and *** respectively.

alized N and P to total N and P (Table 7) indicate higher saprophytic activity in the loamy soil forest floors.

Several factors may be responsible for the higher saprophytic activity in the forest floors at the loamy site compared to the sandy site: The P content or C/P ratio, the pH and the Ca concentration were all in favour at the loamy site. On the other hand, the C/N ratios generally claimed to be a key factor, were slightly higher in the forest floors at the loamy site suggesting that N may not be a limiting factor. The rather low C/N ratios may originate from N-deposition due to air pollution in excess of net biomass accumulation.

To account for the total N and P contents at the sandy site, other sources of N and P must have been supplied in addition to N and P in above ground litter (compare 443 kg N and 24 kg P ha^{-1}) accumulated, and an average yearly flux in litterfall (1985–1989) of 20.2 kg N and 1.0 kg P ha^{-1} in spruce on the sandy site, flux data from Bille-Hansen (1993, pers. comm.). The most obvious source is root litter, considering that roots were densely present in the forest floor on the sandy site, but almost absent in the forest floor at the loamy site (Table 2). An additional effect of the roots may result from nutritional competition between the roots including associated mycorrhiza fungi, and the free saprophytic microorganisms, the so-called Gadgil-effect (Gadgil and Gadgil, 1971, 1975). This effect has also been demonstrated on sandy soils comparable to the sandy soil from Ulborg used in this study (Oksbjerg, 1954). The root competition effect was also hypothesized by Aber et al. (1983) and has been described in agricultural soils, reviewed by Dormaar (1990). The reason why the forest floors are heavily infiltrated by roots at the sandy site but not at the loamy site can undoubtedly be attributed to the differences in the mineral soils as rooting media. In the loamy soil the nutritional status is high and root growth in the mineral soil is intense also due to favorable moisture regime and clay content (Table 1). The sandy soil is poor in nutrients, especially P, Ca, K, and undoubtedly most micronutrients, and the coarse texture result in low water holding capacity.

Despite the significant soil effect, species effects, and especially for oak at the loamy site, were also found. The two conifers, spruce and Douglas fir, seemed to acidify the forest floors (pH in $CaCl_2$, pH in soil solution and extractable acidity) more than the two broadleaves as often found (Alban, 1982; Binkley and Valentine, 1991; Ovington, 1953). However, the higher acidity has not led to differences in accumulation of organic matter. The often held believe, that Douglas fir resembles a broadleave in respect of easily decomposable litter, is not substantiated by results in this study of young stands.

This investigation focused on accumulation of carbon and nutrients in the forest floor in young stands. Obviously, information on accumulation and conditions in the forest floor only is a part of the organic matter interaction between vegetation types and soil types. Distribution differences in accumulation of carbon between the forest floor and mineral soil layers may be expected, especially between different soil types.

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