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Impact of *Tilia platyphyllos* Scop., *Fraxinus excelsior* L., *Acer pseudoplatanus* L., *Quercus robur* L. and *Fagus sylvatica* L. on earthworm biomass and physico-chemical properties of a loamy topsoil

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Abstract

Impact of hardwoods of different humus forms on earthworm biomass and physico-chemical properties of the topsoil of a loamy acid brown forest soil after a time-span of 60–65 years was examined in the Forest of Halle near Brussels. Three sites were selected in which homogeneous stands of mull-forming tree species (*Tilia platyphyllos* Scop., *Fraxinus excelsior* L. and *Acer pseudoplatanus* L.) were compared with adjacent stands of *Fagus sylvatica* L. and/or *Quercus robur* L. where a mullmoder had developed. Total earthworm biomass was conspicuously higher at the sites that supported *Tilia* and *Acer* as mull-forming hardwoods. Study of soil acidity revealed that there were marked differences in pH and base saturation in the A- and E-horizon between hardwoods developing different humus forms. The topsoil beneath mull-forming hardwoods was generally higher in pH and base saturation with the largest differences being displayed between *Tilia* and *Fagus/Quercus*. C/N ratios were significantly lower in the topsoil under *Acer*. Significant differences in physical soil properties among humus form were also evident. The A-horizon under mull-forming species was higher in total porosity, aeration porosity and saturated hydraulic conductivity. The bulk density was only significantly lower under *Fraxinus*. The E-horizon of the mull stands was lower in bulk density and higher in aeration porosity but this was linked by a reduction in water-filled porosity. The study indicated that mull-forming tree species differed in ability to improve or maintain productivity of the studied soil type. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Chemical and physical soil properties; Earthworm biomass; Humus forms; Soil acidity

1. Introduction

Trees can influence soil properties due to differences in litter quality, root activity, canopy interception of atmospheric deposition, nutrient uptake and

growth (Alban, 1982; Miles, 1985). Given their ability to alter soil properties, a well-considered species conversion may be an important mitigating tool in soil rehabilitation (Miles, 1985; Nebe, 1994).

Many studies concerning effects on soil processes by tree species revealed clear differences between conifers and hardwoods in affecting soil chemistry or ecosystem biogeochemistry (Tappeiner and Alm, 1975; Fried et al., 1989; Binkley and Valentine, 1991;

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Raulund-Rasmussen and Vejre, 1995; Wilson and Grigal, 1995). Among hardwood species striking differences also exist (Norden, 1994). It is often claimed that litter from oak and beech growing on poor soils closely resembles that of conifers. Migration of humic acids and initiating podzolisation were often reported in oak–beech stands (Mackney, 1961; Hornung, 1985; Beyer et al., 1991).

Soil acidification constitutes only one aspect of species-specific influences on soil processes and soil productivity. In order to obtain a broader insight in species-related soil changes, other aspects such as biological activity and physical soil properties should be taken into consideration and be included in studies which aim to quantify the impact of tree species on soil properties.

This study aimed to compare effects of hardwood species with refractory litter (e.g., *Fagus* and *Quercus*) with allegedly mull-forming broad-leaved trees (*Tilia*, *Acer* and *Fraxinus*) on topsoil properties of an acid brown forest soil. The objective was to highlight changes in soil acidity and alterations in physical properties and earthworm distribution in order to obtain an overall-picture of induced soil changes by hardwoods of different humus forms.

2. Materials and methods

2.1. Study site

The research was conducted in the Forest of Halle situated 20 km south of Brussels. The forest covers 560 ha and is a remnant of the ancient “Coal Wood” which encircled Brussels in the early middle ages.

The forest is located on a loamy plateau and ranges in elevation from 100–128 m. Five north–south orientated valleys cut the plateau which is composed of Brusselian sand layers which were covered by eolian loam deposits from the Pleistocene. The Brusselian sand layers outcrop locally in places where loamy deposits have been eroded. Loamy soils can generally be classified as haplic alfisols (FAO, 1988). Locally they can be covered as a consequence of colluvial sediments (Holocene).

Mean annual temperature is 9.9°C, with a mean temperature of 2.4°C in the coldest month (January) and 17.4°C in the warmest (July). Total annual pre-

cipitation is 780 mm. Precipitation during the growing season (May–October) averages 418 mm. Frost period extends from mid-November to mid-April.

The Forest of Halle was managed intensively as coppice with standards for the provision of charcoal for centuries. During the first World War the forest was clear-cut and was reforested from 1930 onwards and completed in 1950. Beech (*Fagus sylvatica* L.) became the main tree species (209 ha), followed by common oak (*Quercus robur* L.) which covers 111 ha. Scots pine (*Pinus sylvestris* L., 84 ha) was favoured on sites where sandy layers were outcropping.

The herbaceous layer of the hardwood stands in Halle is dominated by Bluebell (*Hyacinthoides non-scripta* (L.) Chouard ex Rothm), with a cover ranging from 40% to 90%. Other plant species such as *Lamium galeobdolon* L., *Athyrium filix-femina* L. and *Oxalis acetosella* L. are found sparsely. The plant association is characterised as the Endymio-Carpinetum type. Further details about the vegetation analysis are given by Sioen et al. (1994).

2.2. Experimental sites

Three hardwood sites were selected in which stands of *Quercus robur* L. or *Fagus sylvatica* L. were compared with adjacent stands of allegedly soil-improving tree species (Table 1). All stands belonged to the same age class (60–65 years) except the *Fagus* stand at the first site which was planted ten years later. The basal area ranged from 18 to 35 m² ha⁻¹, and the standing crop from 169 to 387 m³ ha⁻¹.

The first site (location 50°42′05″N, 4°18′00″E) is situated at the inflexion of a plateau and consists of three adjoining stands of broad-leaved lime (*Tilia platyphyllos* Scop.), common oak (*Quercus robur* L.) and beech (*Fagus sylvatica* L.). The second site (location 50°42′00″N, 4°17′00″E) consists of two adjoining stands of common ash (*Fraxinus excelsior* L.) and common oak (*Quercus robur* L.). The third site (location 50°42′20″N, 4°16′45″E) is a beech stand which is bordered by a 50 m wide strip of sycamore (*Acer pseudoplatanus* L.). A rich understory of rowan (*Sorbus aucuparia* L.) and hazel (*Corylus avellana* L.) is present everywhere except in the beech stands.

Soils of all sites are acid brown forest soils with a degraded B-horizon and are moderately dry. The soils of all stands have an identical particle size distribution

Table 1
Characteristics of experimental plots

Site	Tree species	Age (years)	Basal area (m ² ha ⁻¹)	Standing crop (m ³ ha ⁻¹)	Humus type	Weight of forest floor (tons ha ⁻¹)	pH(H ₂ O) in the F-layer	pH(H ₂ O) in the H-layer
S1	<i>Tilia platyphyllos</i> Scop.	60	32.2	352	Vermimull	2.0	5.7	–
	<i>Quercus robur</i> L.	63	22.9	259	Mullmoder (mormoder)	31.1	4.7	4.0
	<i>Fagus sylvatica</i> L.	50	26.3	307	Mullmoder	22.3	5.3	3.9
S2	<i>Fraxinus excelsior</i> L.	62	20.9	223	Vermimull	13.7	4.9	4.4
	<i>Quercus robur</i> L.	62	18.2	169	Mullmoder	27.7	4.4	3.8
S3	<i>Acer pseudoplatanus</i> L.	65	34.7	387	Vermimull	15.2	5.1	4.5
	<i>Fagus sylvatica</i> L.	65	26.2	348	Mullmoder	35.0	4.8	3.9

with a clay content of 13–18% and a silt content of 72–76%. According to the humus classification of Green et al. (1993), humus types can be classified as vermimull (under *Tilia*, *Fraxinus* and *Acer*) or mullmoder (under *Quercus* and *Fagus*). In the stands of *Quercus* a mormoder has developed only locally. An obvious forest floor beneath *Tilia* is lacking (Table 1), while the forest floor weights of the *Fraxinus* and *Acer* stand (± 15 tons ha⁻¹) are only half of those beneath *Fagus* and *Quercus* (ranging between 22 and 35 tons ha⁻¹). Species differences in humus type are also reflected in pH differences in the F- and H-layer, pH being higher in the organic layers beneath *Tilia*, *Fraxinus* and *Acer* (Table 1).

2.3. Soil sampling

In every stand the A-horizon (dark brown, 4–8 cm deep) and E-horizon (pale brown, 12–20 cm deep) were sampled systematically in the Spring of 1993. The number of replicates per stand depended on the variables measured and ranged between 5 and 10. Prior to soil sampling the forest floor was removed within a (30 × 30) cm² square frame. The samples intended for chemical analysis were taken by means of a 10 cm bucket auger and consisted of four sub-samples.

Intact soil samples were taken from the same horizons using a cylindrical core (length = 5 cm, $\varnothing = 5.3$ cm) for determination of bulk density, total porosity, aeration porosity (pore diameter > 30 μ m), water-filled porosity (pore diameter < 30 μ m) and available water (0.2 μ m < pore diameter < 30 μ m).

A cylindrical core (length = 4 cm, $\varnothing = 8$ cm) was used to take undisturbed samples for determination of saturated hydraulic conductivity (K_s).

2.4. Earthworm sampling

In all forest stands four earthworm samplings were conducted in April 1993. The earthworms were sampled according to the combined method of Bouché and Aliaga (1986). Prior to formalin extraction, organic layers covering the (50 × 100) cm² sample surface were removed and litter-dwelling earthworms were sampled by hand-sorting. The formalin application was carried out on a surface of (50 × 100) cm². The formalin solution was applied via a watering can at 10 min intervals over a period of 40 min. Ten litres of solution were used for each extraction. After harvesting the earthworms a soil sample with a surface of (30 × 30) cm² and a depth of 20 cm was taken in the middle of the formalin-soaked surface for wet washing–sieving. The worms were fixed in formalin (37%) and then transferred to the laboratory. Biomass was defined as the weight of the worms after preservation for two months and after drying for 1 min on filter paper at room temperature.

2.5. Chemical analysis

Soil samples were dried for 24 h at 80°C and passed through a 2 mm sieve prior to chemical analysis. pH(H₂O) (1:5) and pH(KCl) (1:5; 1 M KCl) were measured with a pH-electrode. Soil samples were extracted with unbuffered BaCl₂ 0.1 N (5 g/50 ml).

The supernatant solution was analysed for Mg, Al, Fe and Mn by atomic absorption spectrophotometry. Concentrations of Ca, K and Na were analysed by flame photometry. Exchangeable acidity (H + Al + Fe + Mn) was determined by titration of an 1 M KCl extraction (5 g/50 ml) with 0.01 N NaOH to pH 7.8. Cation exchange capacity (CEC) was defined as the equivalent sum of base cations and exchangeable acidity. Base saturation was calculated as the proportion of the equivalent sum of base cations in the CEC. Organic carbon content was determined using the Walkley and Black procedure. Total phosphorus was measured colorimetrically after total destruction in HClO₄ (13%) and total nitrogen was determined by Kjeldahl digestion.

2.6. Physical analysis

For the determination of the volumetric water content between 0 and –50 kPa a vacuum suction was applied to the core samples placed on a sandbank (from 0 to –10 kPa) and a sand-caolinbank (from –20 to –50 kPa). The volumes of water content at water potential of –100, –250 and –1550 kPa were obtained by applying an overpressure to the core samples placed on a cellophane membrane filter. The saturated hydraulic conductivity (K_s , cm/day) was determined using a one-dimensional vertical flow of water.

2.7. Statistics

Statistical differences were assessed using a two-way ANOVA for every separate horizon with humus

form (H) and site (S) as factors. A square-root or logarithmic transformation was performed in order to normalise the data or to obtain homogeneity of variances. In case of interactions, the differences between the three sites were tested using the least-significant-difference procedure (LSD) at the 5% level of significance. The statistical analyses was performed with the statistical package SG-PLUS. Levels of statistical significance are * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.

3. Results

3.1. Earthworms

The presence of litter-dwellers in the organic layers was low. Formalin application expelled exclusively litter-dwelling species from the topsoil. Hand-sorting of the excavated soil volume yielded only some specimens of the endogeic species *A. limicola* from soils supporting *Tilia* and *Acer* (Table 2).

The presence of mull-forming trees resulted in a significant higher biomass of *D. octaedra*, *D. rubidus* and *A. limicola* ($P < 0.001$, $P < 0.001$ and $P < 0.05$, respectively) (Table 3). For the other earthworm species and total earthworm biomass interactions with site were denoted. Total earthworm biomass and biomass of *L. rubellus* which accounted for the largest part of total earthworm biomass, were conspicuously higher at the sites that supported *Tilia* and *Acer* as mull-forming hardwoods. The two other epigeic species *Lumbricus castaneus*

Table 2
Mean earthworm biomass of the three hardwood sites (g m⁻²) (standard deviation between brackets) ($n = 4$)

Species	Site 1			Site 2		Site 3	
	<i>Tilia</i>	<i>Fagus</i>	<i>Quercus</i>	<i>Fraxinus</i>	<i>Quercus</i>	<i>Acer</i>	<i>Fagus</i>
<i>L. rubellus</i>	8.7 (3.1)	0.1 (0.3)	0.3 (0.4)	10.1 (4.6)	4.0 (4.3)	33.4 (10.0)	0.2 (0.3)
<i>L. castaneus</i>	0.7 (0.8)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
<i>D. pygmaea</i>	0.2 (0.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
<i>D. octaedra</i>	0.5 (0.5)	0.1 (0.1)	0.1 (0.1)	1.0 (0.9)	0.2 (0.2)	1.3 (0.5)	0.0 (0.0)
<i>D. rubidus</i>	0.3 (0.3)	0.0 (0.0)	0.0 (0.0)	0.5 (0.3)	0.0 (0.0)	0.7 (0.5)	0.0 (0.0)
<i>A. limicola</i>	0.2 (0.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.4 (1.8)	0.0 (0.0)
Total	10.6 (3.1)	0.2 (0.8)	0.4 (0.5)	11.6 (4.7)	4.2 (4.2)	36.8 (11.7)	0.2 (0.3)

Table 3
Differences in earthworm biomass analysed by two-way ANOVA with humus form (H) and site (S) as factors

Species	df	H		S		H × S	
		F-ratio	P	F-ratio	P	F-ratio	P
<i>L. rubellus</i>	27	80.90	0.000***	18.05	0.000***	22.81	0.000***
<i>L. castaneus</i>	27	5.89	0.024*	6.48	0.006**	6.48	0.006**
<i>D. pygmaea</i>	27	6.78	0.016*	7.75	0.003**	8.34	0.002**
<i>D. octaedra</i>	27	25.25	0.000***	1.72	0.202ns	1.80	0.190ns
<i>D. rubidus</i>	27	29.12	0.000***	2.17	0.138ns	1.80	0.189ns
<i>A. limicola</i>	27	5.58	0.028*	2.54	0.102ns	2.54	0.102ns
Total	27	84.55	0.000***	16.57	0.000***	21.07	0.000***

and *Dendrobaena pygmaea* were only sparsely found in the *Tilia* stand.

3.2. Chemical properties

The presence of mull-forming hardwoods led to a significant higher pH(H₂O) and pH(KCl) in the A-horizon ($P < 0.001$) (Fig. 1 and Table 5). The largest differences were measured at the first site with pH values being 0.6–0.7 higher beneath *Tilia*. At the second and third site species differences in pH were not larger than 0.2 units. Interactions indicated that for mullmoder-forming trees no differences in pH among the three sites existed. The pH(H₂O) in the E-horizon was only affected at the first site, in which pH(H₂O) was 0.3–0.5 higher in the *Tilia* stand. Differences in pH(KCl) in the E-horizon were significant at all sites ($P < 0.01$) with the lowest values being measured at the second site.

Cation exchange capacities did not vary significantly among humus form and site (Tables 4 and 5). Base saturation in the A-horizon was only affected at the first site with base saturation being two or three times higher than *Tilia* ($P < 0.001$). In the E-horizon of all soils supporting mull-forming trees a significant higher base saturation was recorded ($P < 0.01$). Base saturation at the first site was significantly higher compared to the other sites ($P < 0.01$).

The mull-forming hardwoods only significantly affected C/N ratios and total N concentration in the A-horizon at the third site (resp. $P < 0.001$ and $P < 0.05$) with C/N ratios beneath *Acer* being five units lower than that of *Fagus* (Tables 4 and 5). No significant differences in C/P ratio were detected.

3.3. Physical properties

The two-way ANOVA revealed marked differences in physical properties among the three sites with physical properties being more favourable at the first and second site irrespective of the humus form of the species (Tables 6 and 7).

The bulk density in the A-horizon from soils supporting mull-forming tree species was only significantly lower under *Fraxinus* ($P < 0.001$) (Fig. 2). In the E-horizon bulk densities of soils supporting mull-forming tree species were always lower than mullmoder soils ($P < 0.05$).

Total porosity and aeration porosity of the A-horizon from mull soils were significantly higher at all sites ($P < 0.001$) (Tables 6 and 7). The differences in aeration porosity at the second and third site were especially marked in the pores with diameter ranging between 30 and 300 μm (Fig. 3) and were the largest at the second site. At the first site differences were more conspicuous in the largest pores ($>300 \mu\text{m}$). Accordingly, saturated hydraulic conductivity differed significantly among humus form ($P < 0.001$) with K_s values from mull stands being twice as large than mullmoder stands.

The lower bulk densities in the E-horizon from the mull soils were also reflected in a higher aeration porosity ($P < 0.001$) but this took place at the expense of a reduction in water-filled porosity ($P < 0.05$). The increase of macropores amounted to approximately 3% (pore diameter 30–300 μm) and was mainly offset by a volume reduction of micropores with diameter ranging between 1 and 10 μm (Fig. 3). The differences in water-filled porosity and medium size pores (pore

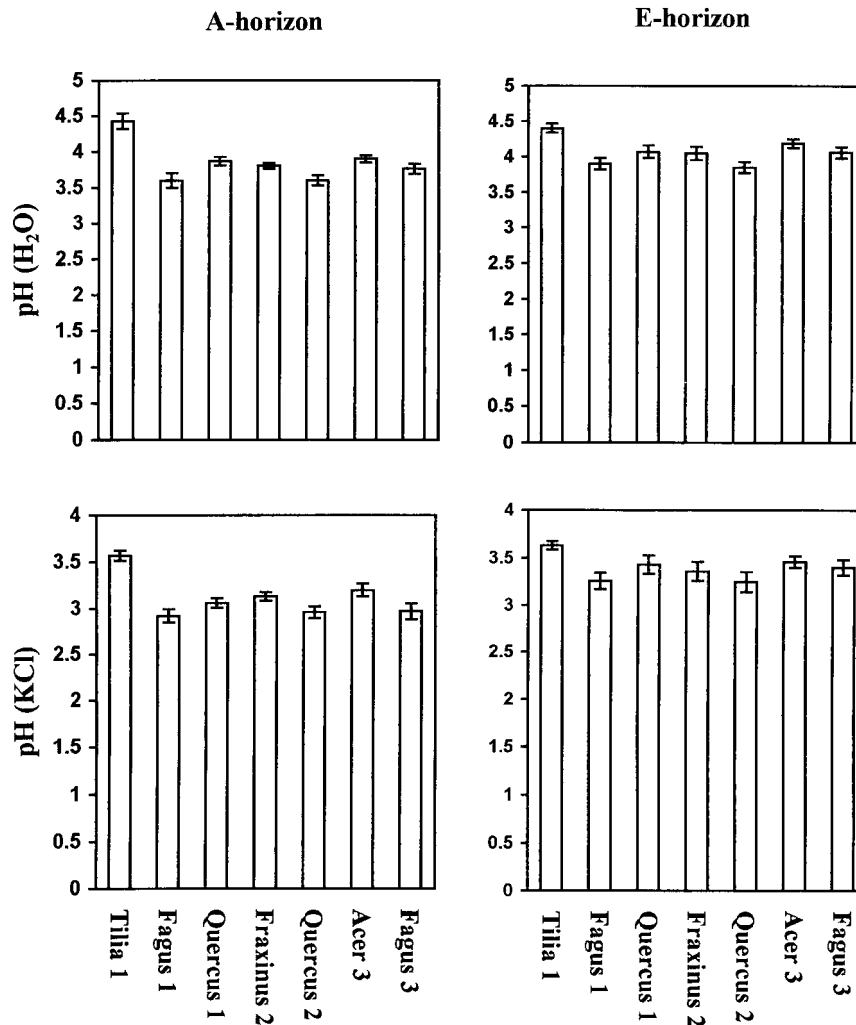


Fig. 1. Mean values ($n = 8$) of $\text{pH}(\text{H}_2\text{O})$ and $\text{pH}(\text{KCl})$ in the A- and E-horizon for all hardwoods at the three sites (standard deviation in bars).

diameter 1–10 μm) between mull and mullmoder soils were especially pronounced at the first site. Saturated hydraulic conductivity was not affected.

4. Discussion

4.1. Earthworms

Changes in vegetation may affect the earthworm distribution and biomass directly by differences in litter quality or indirectly by altering the soil proper-

ties (Boettcher and Kalisz, 1991). Earthworm sampling showed that deep-burrowing species were negligible and were replaced by litter-dwellers (epigeic species). The absence of many mineral soil-dwelling species in acid soils is often connected with low pH of the (top)soil (Nordström and Rundgren, 1974; Muys and Lust, 1992; Gemesi et al., 1995).

The distinct species differences in the biomass of the epigeic earthworms *L. rubellus*, *D. octaedra* and *D. rubidus* may be rather connected with the better palatability of the lime, ash and maple leaves than with differences in soil acidity. Nordström and Rundgren

Table 4
Chemical properties in the A- and E-horizon of the three hardwood sites (standard deviation between brackets)

Chemical properties	n	Site 1			Site 2		Site 3	
		<i>Tilia</i>	<i>Fagus</i>	<i>Quercus</i>	<i>Fraxinus</i>	<i>Quercus</i>	<i>Acer</i>	<i>Fagus</i>
<i>A-horizon</i>								
CEC (meq kg ⁻¹)	5	67 (7)	66 (9)	74 (12)	67 (9)	64 (15)	68 (7)	58 (10)
V (%)	5	54 (10)	16 (3)	25 (3)	33 (8)	21 (14)	31 (11)	24 (7)
C (%)	6	4.1 (0.8)	4.3 (1.6)	5.6 (1.6)	4.4 (1.3)	5.3 (1.2)	5.2 (1.0)	4.7 (1.0)
N (ppm)	6	3190 (590)	3430 (920)	4280 (750)	4590 (1330)	3870 (1040)	5000 (1180)	3110 (970)
P (ppm)	6	296 (72)	274 (31)	387 (151)	333 (84)	294 (16)	308 (48)	262 (41)
C/N	6	12.7 (0.6)	13.5 (1.7)	13.5 (0.6)	11.5(3.2)	14.1 (3.8)	11.7 (1.4)	16.6 (1.1)
C/P	6	140 (19)	183 (33)	137 (19)	163 (25)	180 (41)	170 (27)	176 (18)
<i>E-horizon</i>								
CEC (meq kg ⁻¹)	5	46 (8)	48 (8)	39 (4)	45 (8)	43 (7)	47 (5)	42 (10)
V (%)	5	21 (4)	9 (1)	12 (2)	9 (5)	5 (4)	15 (7)	8 (3)
C (%)	6	1.4 (0.6)	1.7 (0.5)	1.2 (0.3)	2.0 (1.3)	1.7 (0.8)	1.7 (0.5)	1.6 (0.3)
N (ppm)	6	1990 (960)	2310 (1020)	1690 (420)	2480 (1310)	1960 (1380)	1820 (760)	1390 (480)
P (ppm)	6	184 (37)	133 (26)	162 (27)	163 (75)	135 (44)	143 (44)	144 (33)
C/N	6	7.2 (3.0)	8.8 (4.4)	7.3 (2.0)	8.3 (3.3)	9.9 (3.5)	9.7 (1.8)	12.1 (2.2)
C/P	6	72 (36)	126 (10)	80 (35)	116 (34)	126 (45)	113 (30)	114 (24)

(1974) described the earthworm species *L. rubellus* as an indifferent species with regard to pH. According to the same authors *D. octaedra* and *D. rubidus* were acidophilic although their abundance decreased only

at pH higher than 5.5. Huhta (1979) reported that simple application of easily palatable litter without artificial manipulation of the pH in a Norway spruce (*Picea abies*) forest in South Finland enabled a distinct

Table 5
Differences in chemical properties in A- and E-horizon analysed by two-way ANOVA with humus form (H) and site (S) as the two factors

Chemical properties	Total df	H		S		H × S	
		F-ratio	P	F-ratio	P	F-ratio	P
<i>A-horizon</i>							
pH(H ₂ O)	55	72.17	0.000***	40.04	0.000***	17.56	0.000***
pH(KCl)	55	84.46	0.000***	20.21	0.000***	12.30	0.000***
CEC (meq kg ⁻¹)	33	2.41	0.132ns	1.14	0.334ns	3.94	0.032ns
V (%)	33	13.10	0.001**	3.51	0.044*	4.65	0.018*
C (%)	39	0.47	0.505ns	1.52	0.233ns	0.96	0.393ns
N (ppm)	39	5.50	0.025*	2.83	0.073ns	3.80	0.033*
P (ppm)	39	0.64	0.437ns	0.66	0.523ns	1.42	0.257ns
C/N	39	21.03	0.000***	1.21	0.310ns	4.07	0.026*
C/P	39	3.04	0.091ns	3.51	0.042*	0.06	0.943ns
<i>E-horizon</i>							
pH(H ₂ O)	55	20.30	0.000***	6.38	0.003**	4.41	0.017*
pH(KCl)	55	10.76	0.002**	5.92	0.005**	2.14	0.128ns
CEC (meq kg ⁻¹)	33	1.08	0.309ns	0.50	0.612ns	3.89	0.033*
V (%)	33	9.07	0.006**	5.27	0.012*	1.76	0.191ns
C (%)	39	0.23	0.641ns	0.97	0.391ns	0.19	0.829ns
N (ppm)	39	0.87	0.368ns	1.27	0.293ns	0.33	0.723ns
P (ppm)	39	2.28	0.141ns	0.77	0.473ns	0.66	0.525ns
C/N	39	0.30	0.597ns	0.72	0.493ns	0.68	0.514ns
C/P	39	0.52	0.484ns	1.83	0.171ns	0.59	0.562ns

Table 6

Physical properties in the A- and E-horizon of the three hardwood sites (standard deviation between brackets) (* K_s values for *Fagus* at the first site were not available)

Physical properties	n	Site 1			Site 2		Site 3	
		<i>Tilia</i>	<i>Fagus</i>	<i>Quercus</i>	<i>Fraxinus</i>	<i>Quercus</i>	<i>Acer</i>	<i>Fagus</i>
<i>A-horizon</i>								
Total porosity (%)	9	62 (3)	57 (2)	61 (7)	72 (3)	70 (3)	56 (5)	55(5)
Aeration porosity (%)	9	12 (4)	10 (4)	12 (3)	16 (5)	11 (3)	10 (5)	7 (4)
Water-filled porosity (%)	9	50 (4)	47 (4)	49 (7)	56 (5)	59 (2)	46 (5)	48 (5)
Available water (%)	9	41 (4)	37 (6)	40 (6)	39 (8)	40 (5)	24 (10)	27 (9)
K_s (mm h ⁻¹)	10	61 (46)	–	38 (33)	69 (39)	32 (33)	24 (12)	18 (13)
<i>E-horizon</i>								
Total porosity (%)	9	50 (2)	51 (0)	50 (2.0)	59 (5)	59 (3)	44 (7)	42 (5)
Aeration porosity (%)	9	11 (1)	9 (4)	7 (1)	11 (3)	8 (3)	9 (5)	6 (4)
Water-filled porosity (%)	9	39 (2)	42 (4)	43 (3)	49 (2)	51 (3)	35 (4)	36 (4)
Available water (%)	9	33 (2)	36 (4)	36 (3)	38 (2)	42 (3)	24 (9)	23 (8)
K_s (mm h ⁻¹)	10	11 (6)	–	7 (6)	6 (3)	5 (3)	7 (5)	7 (3)

increase in densities of *L. rubellus* and *D. octaedra*. The emergence of maple shrub in a decaying spruce forest, subject to high acidic deposition in northern Germany triggered the initial development of earthworm populations comprising *D. octaedra*, *D. rubidus*, *L. rubellus*, *A. caliginosa*, *A. rosea* and *O. lacteum* in a time-span of 28 years (Dunger, 1991). This could be ascribed to improved feeding conditions and not to changes in soil acidity or exchangeable calcium.

It is conceivable that the presence of the other species, *L. castaneus*, *D. pygmaea* and *A. limicola*, was governed more by the acidity degree of the soil. Most of these species remained exclusively in the *Tilia* soil in which more favourable conditions regarding soil acidity were met. Nordström and Rundgren (1974) described *L. castaneus* as an acidophobic species. Satchell (1955) and Standen (1979) also found a strong dependence on pH for this species. According to Muys and Granval (1997) the lower

Table 7

Differences in physical properties in A- and E-horizon analysed by two-way ANOVA with humus form (H) and site (S) as the two factors

Physical properties	Total df	H		S		H × S	
		F-ratio	P	F-ratio	P	F-ratio	P
<i>A-horizon</i>							
Bulk density (g cm ⁻³)	66	10.89	0.002**	13.11	0.000***	3.68	0.031*
Total porosity (%)	64	7.71	0.008**	124.62	0.000***	0.00	0.996ns
Aeration porosity (%)	64	8.61	0.005**	11.55	0.000***	1.65	0.201ns
Water-filled porosity (%)	64	0.78	0.390ns	31.14	0.000***	1.18	0.313ns
Available water (%)	64	0.02	0.886ns	26.42	0.000***	0.56	0.575ns
K_s (cm/day)	70	12.45	0.000**	0.07	0.931ns	0.37	0.691ns
<i>E-horizon</i>							
Bulk density (g cm ⁻³)	67	4.93	0.030*	3.22	0.047*	1.38	0.258ns
Total porosity (%)	66	0.74	0.403ns	71.24	0.000***	0.42	0.660ns
Aeration porosity (%)	66	12.50	0.000***	2.67	0.077ns	0.06	0.945ns
Water-filled porosity (%)	65	5.78	0.019*	102.41	0.000***	1.24	0.297ns
Available water (%)	66	2.05	0.158ns	46.56	0.000***	1.08	0.346ns
K_s (cm/day)	70	3.93	0.052ns	0.39	0.681ns	0.29	0.750ns

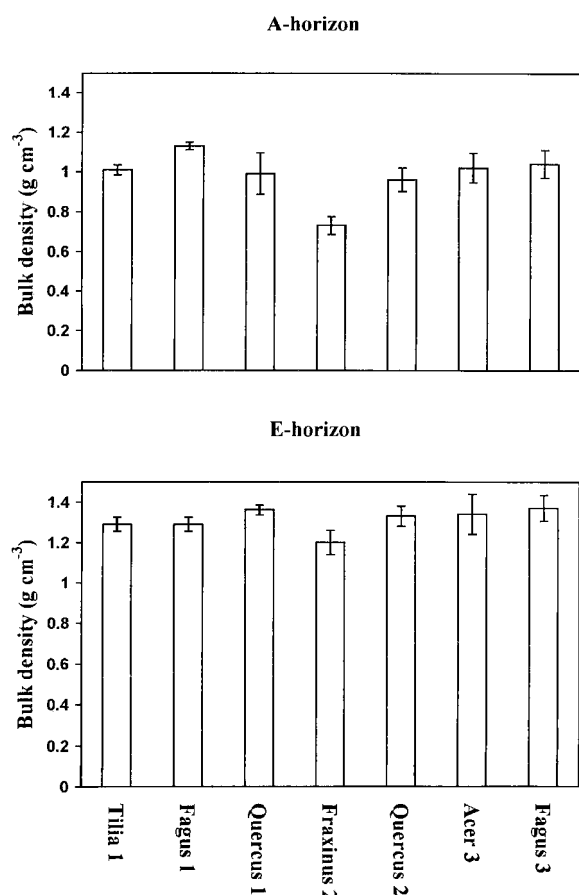


Fig. 2. Mean values ($n = 10$) of bulk density in the A- and E-horizon for all hardwoods at the three sites (standard deviation in bars).

tolerance threshold of the fairly acidotolerant endogeic species *A. limicola* in North Belgian forests soils was determined by the transition zone between the exchange and aluminium buffer range (Ulrich, 1983). Muys and Granval (1997) described the earthworm species *L. castaneus*, *D. pygmaea* and *A. limicola* as regional indicators for mull humus although they could still occur in mullmoder humus.

4.2. Chemical properties

The study of the soil acidity showed striking differences in pH and base saturation between hardwoods of different humus category with the largest differences being displayed between *Tilia* and *Fagus/Quercus* at

the first site. At the other sites the presence of mull-forming species did not lead to such pronounced decreases in acidity. The ability of *Tilia cordata* Mill. in changing chemical and physical soil properties was reported by Giott (1989). Norden (1994) studied the influence of individual hardwoods on soil acidification in South Sweden; quantifying the acidifying influence in terms of pH, CEC and using a budgetary approach (calculation of total proton load from soil budget), he decided that *Tilia cordata* Mill. acidified the soil least compared with other hardwood species (*Fagus*, *Quercus*, *Carpinus* and *Acer*).

C/N ratios in the mineral soil were only affected at the *Acer-Fagus* site. The lower C/N ratios below canopies of *Acer* may reflect differences in N nutrition (higher annual input of N in maple litter) and/or faster turnover rates of maple litter (Fried et al., 1989). Due to the rapid turnover of maple litter (Fried et al., 1989; Muys and Lust, 1992; Ogden and Schmidt, 1997), nitrogen will become less sequestered in the forest floor and can be incorporated faster in the mineral soil. Fried et al. (1989) suggested that the nutrient-rich organic matter under maple may also support larger populations of N-rich micro-organisms, which could contribute to an increase in soil N. It is conceivable that the presence of a well developed bacterial community in conjunction with a large earthworm biomass (368 kg ha^{-1}) could entail an increase of microbial biomass nitrogen in the *Acer* topsoil.

4.3. Physical properties

The study of physical soil properties revealed that the A-horizon under mull-forming tree species was higher in total porosity, aeration porosity and saturated hydraulic conductivity. Bulk density was only significantly lower below *Fraxinus*. The E-horizon of the mull stands was lower in bulk density and higher in aeration porosity but this was offset by a reduction in water-filled porosity.

The differences in physical properties could not be ascribed to the presence of more organic matter in the soil since the total C concentration as an index of organic matter in the soil did not vary consistently. A positive feedback of the actual earthworm populations on physical properties is also questionable. As yet, especially soil-dwelling species have the ability to improve soil aeration and permeability (Brais et al.,

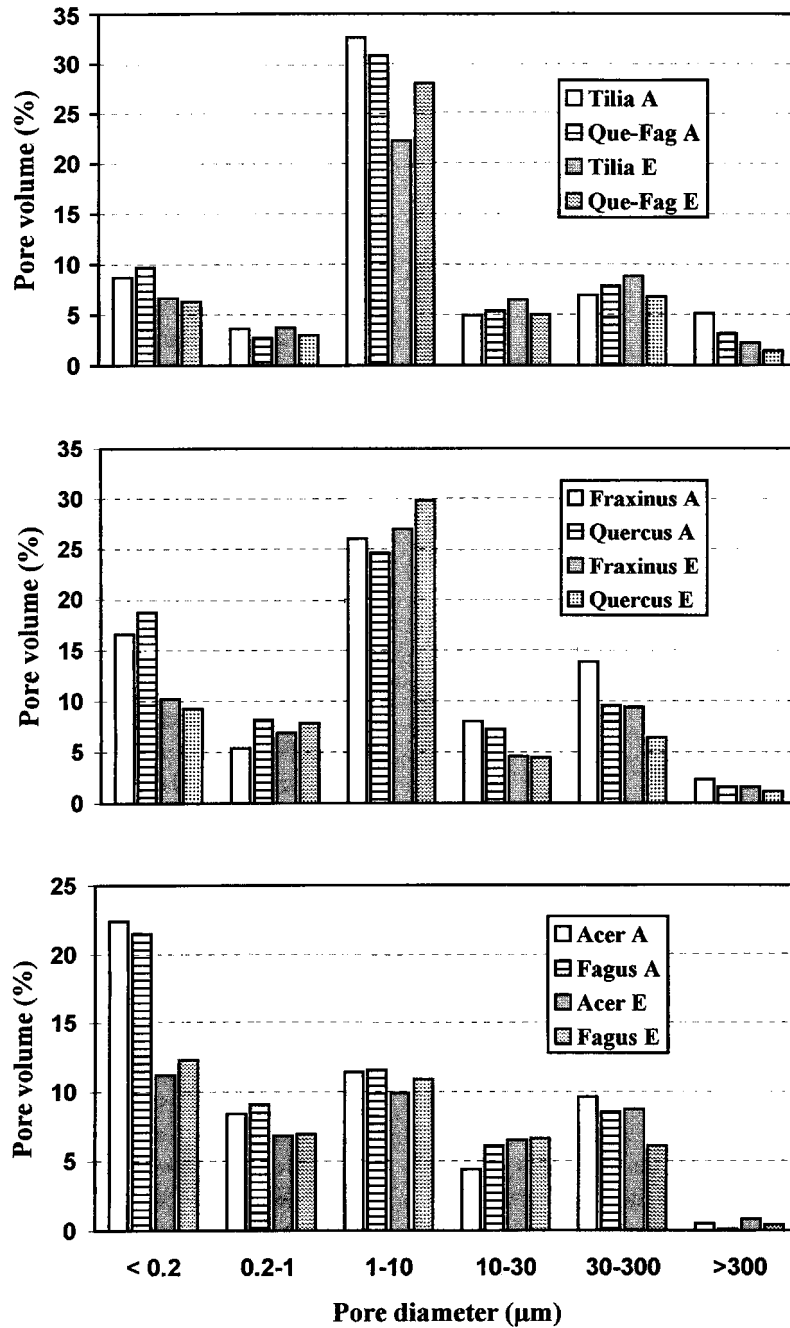


Fig. 3. Pore size distribution in the A- and E-horizon at site one (upper), site two (middle) and site three (lower).

1989; Lee and Foster, 1991). Deep-burrowing species were, however, unimportant in biomass and were replaced by epigeic species which remained mainly in the upper soil layer. The presence of *D. octaedra*,

L. rubellus and *D. rubidus* in the upper 5 cm was also reported by Abrahamsen (1972). The same author pointed out a downward movement of the latter two species up to 10 cm. However, Springett (1983) found

the burrow system of *L. rubellus* to be less stable than that of *Allolobophora*-species. At the *Fraxinus-Quercus* site, in which substantial differences in total earthworm biomass were not displayed, it was believed that the improved soil structure of the topsoil was primarily due to the mechanical loosening of *Fraxinus* roots which intensively rooted the surface soil. Challinor (1967) emphasised channels from decayed roots as an important factor in influencing infiltration rates and pore volume. Babel (1989) suggested that the higher presence of coarse pores in a Norway spruce stand was due to the combined effect of roots and enchytraeids.

5. Conclusion

The study aimed to examine differences in earthworm biomass and topsoil properties between homogenous hardwood stands of mull-forming species (*Tilia platyphyllos* Scop., *Fraxinus excelsior* L., *Acer pseudoplatanus* L.) and moder-forming hardwoods (*Quercus robur* L. and *Fagus sylvatica* L.) after a time-span of 60 years.

It was concluded that the presence of mull-forming tree species generally lead to a higher earthworm biomass and more favourable physico-chemical topsoil properties. Broad generalisations concerning effects of mull-forming tree species can, however, not be made. The study indicates that the studied mull-forming tree species (lime, maple and ash) differed in ability to improve or maintain productivity of the studied soil type. Observations of beneficial effects resulting from the presence of mull-forming hardwoods may be confined to certain soil variables only (biological activity, C/N, pH, bulk density, ...). For some species a change in certain soil properties may fail to occur or the extent of change may appear to be only little (e.g., pH). The study compels more scrutiny with regard to rehabilitation of degraded soils using mull-forming tree species.

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