

Biological control of beech and hornbeam affects species richness via changes in the organic layer, pH and soil moisture characteristics

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Summary

1. Litter quality is an important ecosystem factor, which may affect undergrowth species richness via decomposition and organic layers directly, but also via longer-term changes in soil pH and moisture. The impact of beech trees with low-degradable and hornbeam trees with high-degradable litter on biodiversity and soil characteristics was studied in ancient forests on decalcified marl, a parent material sensitive to changes in pH and clay content, and characteristic of large parts of western Europe.

2. Vegetation analysis clearly separated beech and hornbeam plots, and showed that species richness was consistently lower under beech. Low species richness under beech was associated with low pH, high mass of the organic layer and low soil moisture, which were all interrelated.

3. Development of the organic layer was affected by, not only litter quality, but also by pH levels and soil moisture. Under hornbeam, older organic matter increased from almost zero to 1 kg m⁻² in drier and more acid soil. Under beech tree litter decay was generally slow, but slowed further in acid soils, where older organic matter amounted to 4 kg m⁻².

4. Soil moisture and pH levels were strongly related, possibly due to long-term soil development. Under hornbeam, which is more palatable to soil organisms, moisture, bulk density, clay content and pH were high. Acidification and clay eluviation may be counteracted by earthworms, which bring base cations and clay particles back to the surface, and stimulate erosion, so that the impermeable, clay-rich subsoil remains close to the surface. Soils remain base-rich and moist, which further stimulates litter decay and species richness.

5. The unpalatable beech showed low pH and clay content, and high porosity, air-filled pore space and depth to the impermeable subsoil. Acidification and clay eluviation may proceed uninhibited, because earthworm activity is low, and erosion limited by protective litter covers. This may lead to drier and more acid soils, which reduce litter decay and species richness even further.

6. Trees with low and high litter quality may thus act as an ecosystem engineer, and not only affect ecosystem functioning via mass of the organic layer, but also via longer-term changes in soil characteristics, which in turn affect species richness of the understorey.

Key-words: biodiversity, clay migration, drainage, Luxembourg, plant-soil interactions

Introduction

Litter quality is one of the most important factors influencing forest ecology (e.g. Swift, Heal & Anderson 1979; Ponge 2003). Differences in litter quality result in a different accu-

mulation of organic matter on the forest floor, and other humus forms (Ponge 2003). Litter quality may not only affect organic layers, but habitat factors such as pH levels and base status. Under species with high-degradable litter, there is a lack of dense organic layers. Availability of base cations may be relatively high, because they are retrieved from deeper soil layers by tree roots or earthworm

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excrements (e.g. Jongmans *et al.* 2003; Mohr & Topp 2005). Under species with low-degradable litter, dense organic layers accumulate on the forest floor, and may even promote soil acidification (Neiryck *et al.* 2000; Aubert *et al.* 2004). Litter quality may also affect soil moisture, although studies on this topic are scarce. Water storage in dense organic layers, i.e. under species with low-degradable litter, can be considerable (Rode 1999), and possibly reduce the amount of water reaching the mineral soil below. Under species with readily degradable litter, high earthworm activity may improve water holding capacity due to excrements enriched in clay and organic matter (Pulleman *et al.* 2005). However, earthworms and other soil animals may also increase macroporosity and drainage (Oades 1993; Neiryck *et al.* 2000; Cammeraat 2002), and even mitigate oxygen stress to some extent (Lee & Foster 1991).

Considering the potential effects on habitat conditions, undergrowth species composition is probably affected by litter quality as well. Under trees with high-degradable litter, undergrowth diversity seems to be generally higher than under less palatable species (van Oijen *et al.* 2005; van Calster *et al.* 2008). An increase in undergrowth diversity may especially affect spring ephemerals such as *Anemone nemorosa* L., which are target species for ecological restoration in the Netherlands (van Oijen *et al.* 2005). Under trees with readily degradable litter, species diversity may increase due to the absence of dense litter layers, or increased base status. Under trees less palatable to soil organisms, species richness may be reduced due to dense litter layers, which may hamper undergrowth species physically, and also chemically via reduced base status (Aubert *et al.* 2004; van Oijen *et al.* 2005) or allelopathic effects of phytotoxic components (Hane *et al.* 2003). Because photosynthesis is already hampered by low light levels on the forest floor, undergrowth species may also be sensitive to drought stress. However, whether high or low litter quality would improve soil moisture status or not, is not clear. Nevertheless, litter quality seems to affect habitat conditions and species diversity in many interactive ways.

The objective of this study was to evaluate the impact of litter quality on species richness via changes in the organic layer, pH and soil moisture. As these factors are interrelated, but longer-term changes in habitat conditions cannot be tested with experiments, we used an indirect approach. We studied ancient forests in Luxembourg, dominated by hornbeam (*Carpinus betulus* L.) and beech (*Fagus sylvatica* L.) trees, which are common species in Europe, but differ clearly in litter quality (e.g. Swift, Heal & Anderson 1979; Aubert *et al.* 2003, 2004) with hornbeam generally having a higher initial N-content, lower lignin : N ratios, is preferentially eaten by earthworms and often disappears from the forest floor in a few months whilst beech litter, in contrast, is less palatable, and in most cases accumulates in organic layers. The forests are located on decalcified marl, which is characteristic of large parts of western Europe, and occurs in many countries including Belgium, Luxembourg and Germany (Cammeraat 2002). This parent material is very suitable for detecting changes in habitat conditions as it is relatively sensitive to

changes in pH and drainage conditions, as soils are buffered by cation exchange rather than calcite dissolution, and the pH-regime (4–7) is favourable to clay-dispersion and transport (Duchaufour 1982; van den Broek 1989).

We used a three-step approach, and first analyzed undergrowth diversity and habitat factors under the hornbeam and beech. We then examined how development of the organic layer was correlated with litter quality, pH and moisture. As a last step, we analyzed regulation of soil moisture characteristics such as clay content and depth to the clay-rich subsoil. With this knowledge, we tried to explain how directly important litter quality is to undergrowth diversity via the forest floor, but also indirectly via longer-term changes in pH and moisture, which develop in a complex and interactive way.

Materials and methods

SITE DESCRIPTION

The three forests are located in Luxembourg, near Diekirch, in Mesozoic Keuper marl with gentle slopes. The forests were already shown on a 1777 map, and, except for some harvesting, mainly undisturbed by man (Cammeraat 2002). Dispersal is probably not a limiting factor in the distribution of forest species. The climate is mesic, with mean temperatures of 0.8 °C in January and 17.2 °C in July and rain fall of 788 mm with precipitation throughout the year. The forests are dominated by hornbeam (*Carpinus betulus* L.) or beech (*Fagus sylvatica* L.), intermixed with common oak (*Quercus robur* L.). Vegetation types ranged from *Stellario-Carpinetum* under Hornbeam to *Milio-Fagetum* under Beech (van der Werf 1991). Humus forms ranged from Vermimull to Mullmoder, and soil type from stagnic luvisol to luvic planosol. The soil is characterized by lateral eluviation of clay, over a more or less impermeable Bw-horizon rich in swelling clays (van den Broek 1989; Cammeraat 1992, 2002). We focussed on hornbeam and beech, because they clearly differ in litter quality (Swift, Heal & Anderson 1979; Aubert *et al.* 2003, 2004). Initial N-content was $9.0 \pm 0.5 \text{ mg g}^{-1}$ for beech, and $13.3 \pm 0.6 \text{ mg g}^{-1}$ for hornbeam. Preliminary experiments further supported higher litter decay for hornbeam than for beech in both field and laboratory. Oak litter contributes to total litter input as well, but further analysis showed that oak was not important to species diversity and habitat factors.

FIELD SURVEY

Data were collected in May (spring) and/or directly after leaf fall at the end of November or beginning of December (autumn). In each sampling period, five hornbeam and five beech plots were selected in the interior of each of the three forests, according to stratified random sampling. Each time, a new set of random plots was chosen. Plots were c. 7 × 7 m and located in between tree stems. Plots were surrounded by 3–5 trees, of which at least three mature trees belonged to the particular species.

In spring 2003 and 2004, in each plot, tree cover was estimated to calculate the relative contribution of beech to the total of beech and hornbeam combined (B : H ratio). Plant species in the undergrowth were listed, and their cover values visually estimated as a percentage of the total number of species. Species names were used according to van der Meijden (2005). Spring ephemeral species, which are target species to ecological restoration in the Netherlands (van Oijen *et al.* 2005), were recorded separately. In each plot, presence of seedlings

with more than just cotyledons was noted as well. Hornbeam and beech plots were generally within 10–20 m distance to each other, so that access of diaspores was not a limiting factor. Many ancient forest species are endangered in northwest European countries (Brunet, von Oheimb & Diekmann 2000; van Oijen *et al.* 2005), even though they may be still relatively common in central Europe. We therefore combined Dutch and Luxembourgian red lists, and classified species as 'red list' when appearing on at least one of the lists (Colling 2005; van der Meijden 2005). In each plot, depth of the impermeable, clay-rich subsoil (Bw) was measured as an indicator of the soil profile affected by clay eluvation. Depth of the Bw was determined with a traditional auger in 2003, but later we used a special small auger of 25 cm (Cammeraat 1992), and combined triplicate measurements to one mean value. As spring 2003 values did not differ from later periods, we assumed that the two methods were comparable. In each plot, the organic layer was sampled in the central part within a 25 × 25 cm square. The mineral topsoil was sampled within the square, in three metal rings, 5 cm height and of known volume, which generally comprised the Ah completely. The three soil samples were bulked for further analysis. Soil moisture was considered to be at field capacity, because dry soil conditions are rare in spring (and autumn), and there had been light rain in the days before sampling. In spring 2003, light availability at the forest floor was measured. However, since light levels were consistently lower under hornbeam than under beech, this could not explain higher species number, so measurements were not repeated in later years, and data not shown.

In autumn 2004 and 2005, fresh litter and older material in the organic layer was sampled in each plot, in 25 × 25 cm squares. Fresh litter and older organic matter were separated, and used to calculate litter decay values according to Olson (1963). As older organic material does not necessarily correspond to the fresh litter just fallen, this does not reflect actual rates of decomposition, but may nevertheless be suitable as general indication of differences in litter decay. Litter was divided in hornbeam, beech and oak; other species were negligible. The relative contribution of beech litter to the total of beech and hornbeam combined (B : H ratio) was calculated. Depth to the clay-rich subsoil was also measured. Soil moisture was assumed to be at field capacity due to light rain in the days before sampling, and the mineral topsoil was sampled as described earlier.

LABORATORY ANALYSIS

Samples of organic layer and mineral topsoil were dried for 48 h at 70 °C and weighed. For autumn samples, the amount of fresh litter and organic matter remaining from the previous year(s) was used to calculate decomposition values according to Olson (1963). pH of the mineral topsoil was determined in demineralized water with 1 : 2.5 weight : volume ratio. For the 120 mineral soil samples collected at field capacity, dry bulk density and volumetric moisture content were calculated. With bulk density, porosity was calculated, based on rock particle density of 2.65 g cm⁻³ (Scheffer 1982). Air-filled pore space was calculated by subtracting volumetric moisture content from porosity. Corrections for soil organic matter, which ranged around 5% for both hornbeam and beech, were not applied, but since particle density is substantially lower than for mineral soil, this would have led to lower porosity and even lower air-filled pore space than the 10% estimated for the wettest soils. C and N content were measured with a CNS analyzer (Westerman 1990). Distribution of dry macro-aggregates was measured by sieving over 16, 8, 4, 2, 1, 0.5, 0.25, 0.125 and 0.106 mm sieves (Cammeraat & Imeson, 1998). Because we focussed on the general pattern, rather than detailed aggregate distri-

bution, we combined fractions smaller and larger than 4.8 mm, as small and large macro-aggregates respectively. Potential clay dispersion was analyzed by overnight shaking of 0.5 g samples in 40 mL demineralized water, and measurement of turbidity after 24 h (van den Broek 1989). Clay dispersion was expressed in nephelometric turbidity units (NTU). The more elaborate analysis of clay content was conducted on the 60 samples of spring and autumn 2004. Actual clay content was measured with a Sedigraph 5100 X-ray based particle size analyzer. The grain size distribution of the samples was measured directly after insertion into the measurement cuvette, and again after addition of Na-pyrophosphate dispersant and application of ultrasonic energy to destruct pseudo-silt clay particle assemblages. Total clay content was expressed as percentage of all soil particles < 2 mm.

STATISTICAL ANALYSIS

Potential effects of sampling year, forest site on species richness, characteristics of organic layer and mineral topsoil were tested with two-way ANOVA, using sampling year (repeated measurement) and forest site as independent factors (SAS Inc. 1985; Cody & Smith 1987). Differences between sampling years and forest sites were generally not significant, and data from different years and forests were combined.

Relations between species composition and environmental variables were tested using data from the 60 plots sampled in spring. Because sampling year (repeated measurement) had no effect on species richness, and general species composition seemed more or less the same, vegetation data of different years were combined. Species composition of the relevés under beech and hornbeam was analyzed using Twinspan cluster analysis, with standard cut levels (Hill 1979). The relationship between species richness and mass of the organic layer, pH and soil moisture was tested with linear regression, for hornbeam and beech combined and separately. Like almost all parameters, species richness, pH and soil moisture were normally distributed. Mass of the organic layer had some extreme values for beech at low pH, but we chose to use actual values rather than log-transformed ones, because interpretation was clearer this way. Most variables showed homoscedasticity of variance, and errors were not autocorrelated. For mass of the organic layer, errors were also not autocorrelated, but variance was heteroscedastic, and lower for the more extreme values. To test which of the factors pH, mass of the organic layer and soil moisture were most important to species richness, and to which extent other factors could explain additional variation, stepwise multiple regression was applied.

Development of the organic layer was tested with data from the 60 plots sampled in autumn. Relationships between older organic matter of the previous year(s) and B : H litter input ratio, pH and moisture content of the mineral topsoil were analyzed with linear regression, for hornbeam and beech combined and separately. To test which of the three factors was most important to older organic matter, and to which extent other factors could explain additional variation, stepwise multiple regression was applied.

Soil moisture characteristics were analyzed with data from the 120 plots sampled in spring and autumn. To test potential effects of tree species and pH on soil moisture, bulk density, porosity, air-filled pore space, aggregate distribution, clay content, potential clay dispersion and depth of the clay-rich subsoil, hornbeam and beech samples were divided over three pH-classes: 6–7, 5–6 and 4–5. As hornbeam was preferentially found at relatively high pH, and beech at low, sample sizes per pH-class were different. We therefore used the General Linear models procedure rather than ANOVA (Cody & Smith 1987), with tree species and pH-class as independent factors. Differences between

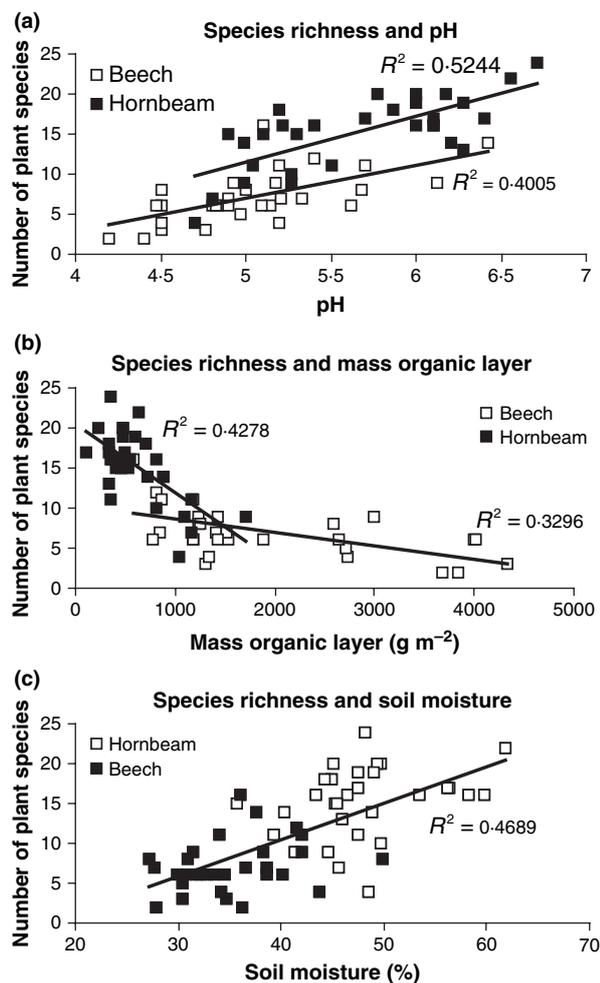


Fig. 2. Number of plant species in the undergrowth under hornbeam and beech in Luxembourg forests on decalcified marl in relation to habitat conditions ($n = 60$). (a) Species richness and pH of the mineral topsoil, (b) species richness and mass of the organic layer (g m^{-2}) and (c) species richness and moisture content of the mineral topsoil (%). For beech and hornbeam, correlations with species richness are significant ($P < 0.05$) for pH and mass of the organic layer. For soil moisture, correlations with species richness were not significant for beech and hornbeam separately, but only when the two were combined.

more than 20. However, when mass of the organic layer increased, species richness under hornbeam strongly decreased. Under beech, mass of the organic layer was always high, and generally above 1000 g m^{-2} . Species richness, which was already low to start with, further decreased with higher mass of the organic layer. Species composition was not affected by C-content of the mineral topsoil, which ranged around 4.6–5.1% for hornbeam and beech respectively. However, species richness increased when C : N ratio of the mineral topsoil decreased from 18:1 in low pH beech plots to 13:7 in high pH hornbeam plots.

Species richness was further affected by soil moisture, as well as variables related to this (Figure 2). The number of undergrowth species significantly increased with soil moisture when hornbeam and beech were combined ($R^2 = 0.4689$), if

not for the individual species separately. Hornbeam had clearly higher soil moisture than beech. Species richness also increased with a rise in large aggregates and bulk density, and decreased with depth of the impermeable, clay-rich subsoil and air-filled pore space. However, species composition was not affected by potential clay dispersion.

The above results suggest that pH, mass of the organic layer and soil moisture all three affected species richness of the understorey. Stepwise multiple regression suggested that pH was most important, and explained 60% of the variance in species richness. Mass of the organic layer explained an additional 7% of the variance, but soil moisture was of no importance. Soil moisture already strongly correlated with the other factors ($R^2 = 0.50$ with pH and 0.43 with mass of the organic layer).

DEVELOPMENT OF THE ORGANIC LAYER

Mass of the older organic layer, measured immediately after leaf fall and consisting of older litter from the previous year(s), was strongly affected by the relative contribution of hornbeam and beech litter (Figure 3). In accord with expectations, older organic matter was rare under hornbeam, especially at low B : H ratios. When B : H ratio increased to values above 0.80, mass of the older organic layer under hornbeam increased, but still remained far below values found under beech. Low mass under hornbeam correlated with high Olson decomposition values, which were generally above one, and indicated that most of the litter disappeared within a year. Under beech, mass of older organic layer was high in all cases, and varied independently of the already high B : H ratio, possibly due to differences in pH and moisture.

When the organic layer was correlated with pH or moisture content of the mineral topsoil, hornbeam showed a significant increase in older litter below pH 6, or moisture content of 40%. Under beech, where older organic matter was much higher to start with, the effect of progressive soil acidification was even stronger. Below pH 5, older organic matter increased to values close to 4000 g m^{-2} , which corresponds with a dense layer of several cm thickness. However, litter accumulation under beech was not affected by soil moisture, probably because moisture content was low anyway.

Litter quality and habitat conditions such as pH and soil moisture are probably interrelated. Stepwise regression suggested that pH was the most important, and explained 54% of the variance in older organic matter. The additional effect of litter quality was indeed relatively low, and B : H ratio explained only 4% more of the variance. Soil moisture had no additional explanatory value.

SOIL MOISTURE AND SOIL CHARACTERISTICS

Soil moisture was significantly higher under hornbeam than under beech, but decreased under more acid conditions for both species (Table 2). Under hornbeam, soil moisture decreased from high to low pH from 52% to 43%, and under beech even from 40% to 33%. Bulk density and the amount

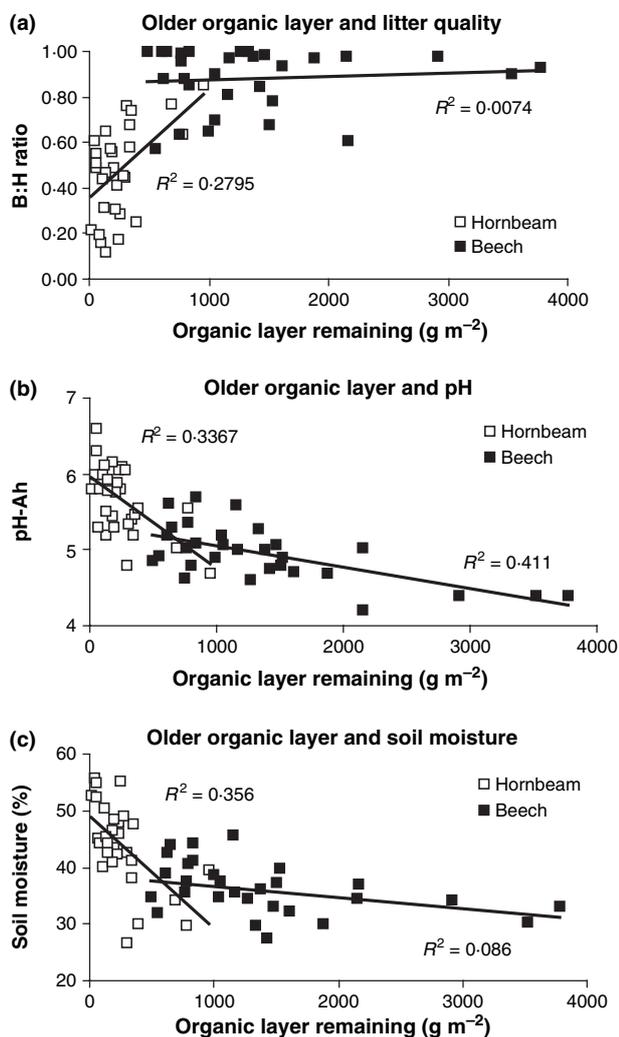


Fig. 3. Relationship between the older organic layer from previous years and litter quality or pH under hornbeam and beech in Luxembourg forests on decalcified marl ($n = 60$). (a) Older organic layer and B : H ratio in litter input. (b) Older organic layer and pH of the mineral topsoil. (c) Older organic layer and soil moisture content (%). Except for older organic layer and B : H ratio or soil moisture under beech, correlations were significant ($P < 0.05$).

Table 2. Characteristics of 120 mineral topsoil samples under hornbeam and beech, divided over three pH-classes. The number of replicates per pH-class varied between species: under hornbeam, $n = 17$ for pH 6–7, $n = 35$ for pH 5–6 and $n = 8$ for pH 4–5; under beech, $n = 2$ for pH 6–7, $n = 25$ for pH 5–6 and $n = 33$ for pH 4–5. Clay content was based on 60 samples, and number of replicates per class was lower accordingly

	Hornbeam pH 6-7	Hornbeam pH 5-6	Hornbeam pH 4-5	Beech pH 6-7	Beech pH 5-6	Beech pH 4-5
Soil moisture (%) *, †	52 (5) ^c	44 (7) ^b	43 (3) ^b	40 (3) ^b	39 (5) ^b	33 (4) ^a
Bulk density (g cm ⁻³)*, †	1.00 (0.10) ^b	0.99 (0.10) ^b	0.88 (0.15) ^a	0.72 (0.06) ^a	0.94 (0.09) ^{ab}	0.78 (0.17) ^a
Large aggregates (%) *, †	83 (10) ^d	68 (15) ^c	66 (14) ^{bc}	82 (7) ^{cd}	61 (15) ^b	53 (14) ^a
Clay content (%) *, †	31 (3) ^c	27 (3) ^b	25 (4) ^{ab}	27 (4) ^{ab}	24 (3) ^a	22 (4) ^a
Clay dispersion (NTU)	83 (38) ^a	75 (36) ^a	82 (39) ^a	94 (9) ^a	71 (36) ^a	69 (35) ^a
Porosity (%)*, †	62 (4) ^a	62 (4) ^a	67 (6) ^b	73 (2) ^b	64 (4) ^{ab}	71 (7) ^b
Air-filled pores (%) *, †	10 (6) ^a	19 (7) ^b	24 (4) ^{bc}	33 (5) ^{cd}	26 (7) ^c	38 (9) ^d
Small aggregates (%) *, †	17 (10) ^a	32 (15) ^b	34 (14) ^{bc}	18 (7) ^{ab}	39 (15) ^c	47 (14) ^d
Depth of Bw (cm)*	10 (4) ^a	12 (4) ^a	11 (5) ^a	14 (5) ^{ab}	17 (4) ^b	18 (5) ^c

* = significant effect of species on a particular response parameter; † = significant effect of pH-class on a particular response parameter ($P < 0.05$). Mean values and standard deviations are given for each group; different letters indicate significant differences between individual mean values for a particular parameter ($P < 0.05$).

of large aggregates showed a similar decrease over this gradient. Also, even though potential clay dispersion did not differ, clay content decreased from 31% under hornbeam at high pH to 22% in the most acid beech plots. Consistent with the general decrease in bulk density and clay content, porosity increased from 62% at high pH under hornbeam to 71% at low pH under beech. This may look like a small change, but air-filled pore space increased over this gradient from 10%, which is close to the aeration limit, to 38%, which reflects much better oxygen supply. Depth of the impermeable clay-rich subsoil may be of further importance to soil moisture and species richness. Under hornbeam, at high pH, the clay-rich subsoil was found only 10 cm below the soil surface, but depth increased to 18 cm in low pH beech plots.

These patterns in soil moisture characteristics were supported by correlations between them (Table 3). Soil moisture showed positive correlations with bulk density, the amount of large aggregates and clay content, which also showed positive correlations between each other. High clay content and high amount of large aggregates may reflect that soil aggregates are generally kept together by clay. Clay content and large aggregates were also positively correlated with clay dispersion, which reflects high potential for clay eluviation. Correlations between soil moisture and bulk density, even if positive, were relatively low, possibly because bulk density may increase with high clay content, but be reduced by digging earthworms.

In accord with the positive correlations with clay content, large aggregates and bulk density, soil moisture was negatively correlated with porosity, air-filled pore space, small aggregates and depth of the clay-rich subsoil. These factors were interrelated as well, and showed positive correlations between each other. A high amount of air-filled pores may reflect low soil moisture, but also high porosity due to low clay content. A large amount of small aggregates may reflect high porosity as well, together with an increase in contact surfaces, from which clay may disappear. In addition, high depth of the clay-rich subsoil may reflect the presence of a water-stagnant layer deeper in the soil surface, which may lead to

Table 3. Correlation matrix between soil characteristics in hornbeam and beech plots in Luxembourg mixed forests on decalcified marl. Correlations are generally based on $n = 120$, but those with clay content on $n = 60$

	Soil moisture	Bulk density	Large aggr.	Clay content	Clay dispersion	Porosity	Air-filled pores	Small aggr.	Depth Bw
Soil moisture	–	0.41	0.69	0.62	NS	–0.41	–0.89	–0.69	–0.31
Bulk density	0.41	–	0.29	0.35	NS	–1.00	–0.78	–0.29	–0.21
Large aggregates	0.69	0.29	–	0.70	0.51	–0.29	–0.62	–1.00	–0.32
Clay content	0.62	0.35	0.70	–	0.55	–0.35	–0.58	–0.70	–0.44
Clay dispersion	NS	NS	0.51	0.55	–	NS	NS	–0.51	NS
Porosity	–0.41	–1.00	–0.29	–0.35	NS	–	0.78	0.29	0.21
Air-filled pores	–0.89	–0.78	–0.62	–0.58	NS	0.78	–	0.62	0.31
Small aggregates	–0.69	–0.29	–1.00	–0.70	–0.51	0.29	0.62	–	0.32
Depth Bw	–0.31	–0.21	–0.32	–0.44	NS	0.21	0.31	0.32	–

Only significant correlations are given ($P < 0.05$); NS = not significant. To help interpretation, correlation coefficients were given for both bulk density and porosity, and for large as well as small aggregates, even if they were complementary.

increased drainage, and drier and more aerated topsoils, instead of water stagnation and oxygen stress.

Discussion

UNDERGROWTH DIVERSITY AND THE ORGANIC LAYER

As shown by van Oijen *et al.* (2005) and van Calster *et al.* (2008), species richness was clearly affected by litter quality. Species richness was generally lower under beech than under hornbeam, especially with respect to valuable species for nature conservation, such as red-list species and spring ephemerals. Lower species number under beech was at least partly due to differences in litter decay. As predicated (Swift, Heal & Anderson 1979; Ponge 2003), mass of the organic layer was much higher under beech than under hornbeam. Even at high pH, with high earthworm activity (Pop 1997), Olson decay values suggest that the organic layer consisted of several generations of beech litter, while hornbeam litter usually disappeared within a year.

Under trees with low-degradable litter, dense litter layers may act as a physical barrier, and retrieval of base cations from deeper layers by tree roots and earthworms may be low (Jongmans *et al.* 2003; Mohr & Topp 2005). Beech litter may even promote soil acidification (Neirynek *et al.* 2000; Aubert *et al.* 2004). Dense litter layers and retarded decomposition could potentially also reduce establishment of species by low nitrate, because many forest species preferentially take up nitrate to ammonium (Falkengren-Grerup 1995; Bijlsma, Lambers & Kooijman 2000). In addition, allelopathic effects may play a role. For European beech, data are unfortunately not available, but Hane *et al.* (2003) clearly described the negative impact of beech leaf leachates on sugar maple seedlings for American beech.

UNDERGROWTH DIVERSITY AND PH

Under both hornbeam and beech, species richness decreased when pH was lower. These patterns are in accord with the general decrease in species richness from calcareous to acid

forests (van der Werf 1991; Brunet, Falkengren-Grerup & Tyler 1997). Low species richness at low pH may be due to lower nitrate availability at low pH (Falkengren-Grerup 1995; Bijlsma, Lambers & Kooijman 2000), or toxic levels of ammonium or aluminium (van den Berg *et al.* 2005; Zvereva, Toivonen & Kozlov 2007).

The decrease in pH may be partly attributed to differences in litter quality, as beech is known to acidify its surroundings (Neirynek *et al.* 2000; Aubert *et al.* 2004). However, a shift in pH from 7 to 4 is probably too large to be caused by only one generation of beech. More likely, such differences in pH have been inherited, and reflect past changes in habitat conditions. Possibly, hornbeam and beech have different habitat preferences with respect to pH, even though both species can grow in soils ranging from calcareous to acidic (van der Werf 1991; Brunet, Falkengren-Grerup & Tyler 1997). Possibly, hornbeam seedlings are restricted to hornbeam habitats by phytotoxic components in beech litter (Hane *et al.* 2003). Hornbeam may also avoid the most acid soils, where foliar Al-contents were 2.6 times higher than for beech (A.M. Kooijman, unpublished data). However, beech seedlings were found everywhere, and seemed not to be restricted by pH.

UNDERGROWTH DIVERSITY AND SOIL MOISTURE

In accord with e.g. Ellenberg *et al.* (1974), undergrowth diversity clearly decreased from high to low moisture content. Species with relatively high Ellenberg values for wetness were only present at high soil moisture. In forests, high soil moisture may be an advantage, because photosynthesis is already hampered by low light levels at the forest floor. However, high moisture may also lead to oxygen stress. At high soil moisture, air-filled pore space was only 10%, which is close to the aeration limit (Zou *et al.* 2000). Oxygen stress may also explain part of the habitat differentiation between beech and hornbeam. Beech is generally found in relatively dry places, with soil moisture below 40% (Bolte, Czajkowski & Kompa 2007), but hornbeam can occur in wet soils as well (van der Werff 1991). Beech seedlings may establish in the relatively wet soil under hornbeam, but further growth is probably

hampered by oxygen stress. Low oxygen levels may be further depleted after heavy rain, when water tables rise over the impermeable subsoil, and come close to, or reach the surface for more than a day (Cammeraat 2002). This suggests that, even if profiting from higher water availability, hornbeam and species-rich undergrowth probably have to deal with low aeration and oxygen stress during part of the year. In contrast, species-poor undergrowth, with air-filled pore space of more than 40% even at field capacity, may be restricted by drought stress rather than oxygen. Beech can stand dry conditions rather well (Bolte, Czajkowski & Kompa 2007), but undergrowth species are probably reduced by prolonged dry periods, especially when adapted to oxygen stress.

INTERRELATED ENVIRONMENTAL FACTORS

Species diversity under beech and hornbeam was thus clearly affected by the organic layer, pH and soil moisture, which were all interrelated. Mass of the organic layer not only differed with B : H ratio, but with pH and moisture as well. Also, pH and soil moisture may be affected by the organic layer via higher or lower acidification capacity (Aubert *et al.* 2004) and water storage (Rode 1999).

Soil moisture and pH may be even more closely related, via clay eluviation and changes in porosity. In marl, clay dispersal can occur between pH 6.5 and 4, when calcite has dissolved and clay particles are no longer stabilized by high Ca-content, but not yet flocculated by high concentrations of Fe and Al (Duchaufour 1982; van den Broek 1989). High pH may thus reduce clay dispersion. However, in this study, potential clay dispersion was not affected by pH at all. Possibly, at high pH, clay dispersion is reduced by high calcium, but stimulated by clay content, which is also still high. Similarly, at low pH, a potential decrease in clay dispersion by lower amounts of available clay may be compensated by lower calcium and lower aggregate stability. It is thus possible that lower pH is not the cause of increased eluviation and loss of clay, but merely reflects the same process. If increased porosity and drainage lead to increased eluviation of clay, they lead to increased leaching of base cations and lowering of pH as well.

Both pH and soil moisture clearly differed between beech and hornbeam. Clay content and pH may have been higher under hornbeam, because earthworms bring soil from deeper layers to the surface, and excrements are usually enriched in clay and base cations (Jongmans *et al.* 2003; Pulleman *et al.* 2005). In this way, earthworms may counteract clay-eluviation from the topsoil. Bulk density may potentially decrease with high earthworm activity (Lee & Foster 1991; Neirynek *et al.* 2000), but in our study, values actually increased, due to higher clay content. Furthermore, earthworms, and larger soil animals such as moles, may reduce matrix flow and leaching of clay particles and base cations, due to rapid drainage of water via pipe flow in larger channels (Cammeraat 2002). Under beech, earthworm activity is low due to the relatively unpalatable litter (Westernacher & Graff 1987). Clay eluviation and leaching of base cations may be higher than under hornbeam,

due to increased matrix flow, and may also proceed uninhibited, because there are no earthworms to counteract it.

Litter quality effects may be further enhanced by erosion (or not) of the topsoil. In the study area, slope denudation may be relatively high (Duijsings 1985; Cammeraat 1992), but topsoil erosion probably mainly occurs under hornbeam. Under beech, the organic layer may form a protective cover all year round (Greene & Hairsine 2004). Under hornbeam, however, soil is bare during part of the year, and topsoil particles may disappear due to splash erosion (van Hooff 1983). Also, if topsoil particles are removed, the clay-rich subsoil, which was already closer to the surface under hornbeam, may come even closer, and locally lead to overland flow after heavy rain. Overland flow may happen a few times a year, when precipitation exceeds 20–30 mm day⁻¹ (Cammeraat 1992), and further increase topsoil erosion. Thus, at least in soils sensitive to clay-eluviation and erosion, litter quality may be a very important factor to both soil moisture and pH.

BEECH AND HORNBEAM AS ECOSYSTEM ENGINEERS

Soil development takes time. Development of 20 cm of clay-impooverished topsoil, as found in the most acid beech plots, may take 3500–9400 years (van den Broek 1989). This comes close to the time that beech has been present in the area (Slotboom 1963). It is not certain that beech has actually dominated the most acid soils all the time, but considering the counteractive effects of beech and hornbeam on soil development and erosion, it is not unlikely.

Initial soil differences may have caused one or the other tree to establish. However, once beech had established, the soil became protected from erosion (Greene & Hairsine 2004), and started to acidify. Acidification may have some clear advantages, such as an even denser organic layer, which may reduce competition by phytotoxic components (Hane *et al.* 2003), and improve N-availability to the vegetation. Net N-mineralization may increase with mass of the organic layer, but also, under acid conditions, with the shift in microbial communities from bacteria to fungi, with probably lower N-requirements (Kooijman, Kooijman-Schouten & Martinez-Hernandez 2008; Kooijman & Martinez-Hernandez 2009). In addition, under acid conditions, beech may profit from its preference for ammonium (Gessler *et al.* 1998). Prolonged soil development may further lead to eluviation of clay and improved drainage, which is suitable for beech, with soil moisture generally below 40% (Bolte, Czajkowski & Kompa 2007), and further reduces competition with other species. Beech thus seems to be an efficient ecosystem engineer, creating suitable conditions for itself, and unsuitable conditions for other species.

The main limit to beech may be high soil moisture, which is kept high by hornbeam. Under anoxic conditions, beech seedlings may not survive, and hornbeam may remain the dominant species. Since hornbeam litter is highly palatable, earthworm activity is high, which improves erosion, counteracts acidification and eluviation of clay, keeps the impermeable subsoil close to the surface, and leads to high water tables and oxygen stress after heavy rain. This is good for un-

derstorey species richness, but not for beech. Hornbeam may thus be as efficient as ecosystem engineer as beech, even if in a completely different way. Both species seem to affect ecosystem functioning and species richness, not only via the organic layer, but also via longer-term changes in soil conditions.

Acknowledgements

We would like to thank Pim Jungerius, Jan Sevink and Koos Verstraten for fruitful discussions, and Leo Hoitinga, Greet Kooijman and Bert de Leeuw for support in field and laboratory.

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Received 2 February 2009; accepted 5 August 2009
Handling Editor: Gareth Phoenix