



# Herb-layer diversity in deciduous forests: Raised by tree richness or beaten by beech?

Andreas Mölder\*, Markus Bernhardt-Römermann, Wolfgang Schmidt

Department Silviculture and Forest Ecology of the Temperate Zones, Faculty of Forest Sciences and Forest Ecology, Georg-August-University Göttingen, Büsingenweg 1, D-37077 Göttingen, Germany

## ARTICLE INFO

### Article history:

Received 13 October 2007

Received in revised form 1 February 2008

Accepted 4 April 2008

### Keywords:

*Fagus sylvatica*

Biodiversity

Deciduous forest

Ecosystem functioning

Productivity

Shannon–Wiener Index

Ellenberg indicator values

## ABSTRACT

Where natural production capacity permits, modern silvicultural management in Central Europe frequently aims at the development of mixed broadleaved stands, instead of pure European beech (*Fagus sylvatica*) stands. It is crucial to study the effects of these tree-layer diversity variations on herb-layer vegetation, since herb-layer vegetation contributes significantly to ecosystem functioning in forests. In Hainich National Park (Thuringia, Germany), we conducted observational research in deciduous stands to investigate whether herb-layer diversity was related to canopy-layer diversity, and to ascertain possible causal mechanisms. We found that herb-layer vegetation of deciduous forest stands rich in canopy species appeared to be more diverse than herb-layer vegetation of beech-dominated stands. We surmise that herbaceous understorey diversity was indirectly influenced by canopy tree species through the medium of the altered environmental factors soil pH and litter layer thickness. Apparently, lower beech proportion had a more profound effect than the number of secondary tree species. There were no correlations between herb-layer diversity and light transmissibility of the canopy layer, indicating that the light factor was not crucial for herb-layer diversity. At least for the Hainich research sites, our results indicated that small-scale light and soil heterogeneity is insignificant for herb-layer diversity. We found several herb-layer species whose occurrence was particularly correlated with tree-layer diversity and environmental factors. Remarkably, all species positively correlated with soil pH were important for the phytosociological classification of the research sites. Beech-dominated research sites showed high tree-layer volumes, whereas research sites with high tree-layer diversity tended to feature lower tree-layer volumes. These findings could be the result of differing former silvicultural systems and varying soil clay contents affecting tree species composition. In contrast, herb-layer biomass was positively correlated with tree-layer diversity. Herb-layer productivity might be promoted in more diverse research sites by increased nutrient supply and base saturation. It is also possible that greater beech proportion interfered with herb-layer productivity. However, herb-layer biomass was also positively correlated with herb-layer diversity. Hence, our study hints that positive diversity-functioning relationships might occur in the herb-layer of the deciduous forest under investigation.

© 2008 Elsevier B.V. All rights reserved.

## 1. Introduction

One goal of modern silvicultural management is the sustainable use of natural resources, often strived for through close-to-nature forestry. However, to support economical and social functions of the forest ecosystem, the conservation of stable and productive forests with diverse tree species must be ensured (Diaci, 2006; Röhrig et al., 2006). Concerning the management of Central European deciduous forests, this frequently implies the development of mixed stands consisting of European beech (*Fagus*

*sylvatica*) and secondary broadleaved tree species (Spiecker, 2006), instead of pure beech stands, where made possible by natural production capacity (Niedersächsisches Forstplanungsamt, 2004). It is crucial to study the effects of these tree-layer diversity changes on herb-layer vegetation, since herb-layer vegetation contributes significantly to ecosystem functioning in forests (Augusto et al., 2003; Lorenz et al., 2006). Productive and species-rich herb-layer vegetation can contain a significant amount of aboveground biomass and nutrients (Yarie, 1981; Bolte et al., 2004). Unwanted nutrient discharge released by disturbances of the ecosystem can be stored in the herb-layer (Bolte, 2006), and during periods of high potential leaching, temporary storage of elements by ground-layer herbs reduces nutrient loss to ground water (Peterson and Rolfe, 1982). For these reasons, both

\* Corresponding author. Tel.: +49 551 39 4709; fax: +49 551 39 3270.  
E-mail address: [andreas.moelder@forst.uni-goettingen.de](mailto:andreas.moelder@forst.uni-goettingen.de) (A. Mölder).

productive tree and herb layers are favoured in silviculture, as long as herb-layer vegetation does not compete with tree regeneration for light, water, and nutrients (Morris et al., 1993; Coll et al., 2003). In Central Europe, there is evidence for relationships between tree species diversity and productivity from long-term experimental plots (Pretzsch, 2005). But little knowledge exists on diversity and productivity relationships between different vegetation layers in beech-dominated forests. While field experiments in artificial grasslands (e.g. Tilman et al., 1996; Scherer-Lorenzen et al., 2003) indicate positive relationships between biodiversity and ecosystem functions like productivity and nutrient uptake in meadows, synthetic forest stand approaches cannot address biodiversity-functioning issues regarding typical forest herbs. A quasi-steady state of nutrient fluxes and carbon exchange between biomass, soil, and the atmosphere, which develops in slow-growing ancient forests ecosystems, is unlikely to occur in synthetic and young forest communities (Underwood and Paine, 2007). Hence, our research was observational and focused on herb-layer diversity and ecosystem functioning in existing mature forest stands with varied tree species diversity. Besides productivity aspects, forest herb-layer species are well-known indicators of site conditions, particularly with regard to forest management and long-term differences and changes in forest site conditions (Ellenberg, 1996; Schmidt, 2005; Bernhardt-Römermann et al., 2007).

In detail, besides other factors, tree-layer composition can have an effect on ground vegetation due to its influence on many ecosystem processes, e.g. nutrient cycling, light transmittance, and soil water supply (Légaré et al., 2002; Augusto et al., 2003; Barbier et al., 2008). We are aware that relationships between tree-species effects, environmental parameters, and herb-layer diversity can be complex and difficult to analyse. Nevertheless, according to Barbier et al. (2008) we believe that it is possible to point out the main underlying processes: the effects of tree-species diversity on understorey vegetation can be on the one hand studied by the effect of tree-species richness and on the other hand by the effect of the dominant tree species. Therefore, besides possible effects of tree-layer richness, the influence of the keystone species beech will be emphasised, too.

Particularly, chemical composition of canopy-species leaf litter was found to be a key factor influencing soil acidity and thereby nutrient stocks, whereas the upper 10 cm of soil are most significantly influenced by tree-species effects (Nordén, 1994; Finzi et al., 1998; Augusto et al., 2002, 2003). Additionally, thickness of litter layer varies according to tree species (Neirynck et al., 2000; Augusto et al., 2002; van Oijen et al., 2005). A close positive correlation between soil pH and herb-layer diversity (e.g. Brunet et al., 1996; Härdtle et al., 2003; Ferretti et al., 2006; Barbier et al., 2008), as well as litter layer thinness (e.g. Graae and Heskjær, 1997; Borchsenius et al., 2004; van Oijen et al., 2005; Barbier et al., 2008) was particularly detected in forests dominated by beech, a tree species which produces less-decomposable and acidifying litter (Krauß, 1926; Ellenberg, 1996). Besides altered soil conditions, increased light transmissibility of the canopy layer was found to be another key factor promoting herb-layer diversity (Härdtle et al., 2003; Schmidt, 2005; Barbier et al., 2008). Diffuse light is transmitted differently depending on the tree species (van Oijen et al., 2005; Barbier et al., 2008); beech crowns transmit only a small proportion of daylight to the forest floor (Ellenberg, 1996; Barbier et al., 2008). Thus, it can be hypothesised that, if decreased beech proportion and increased quantity of other canopy species result in more basic soil pH, lower litter layer thickness or higher light availability, herb-layer diversity increases. Following van Oijen et al. (2005), it can further be assumed that the occurrence of

some herb-layer species is particularly bound to the environmental changes caused by varying tree-species diversity. In addition, an increased number of canopy species may form a pattern of more diverse site conditions over short distances. Following the environmental heterogeneity hypothesis (Huston, 1994), small-scale environmental differences result in increased herb-layer diversity.

Concluding, this study aims at answering the following questions:

- (1) Is there any relationship between tree- and herb-layer diversity as well as tree-layer volume and herb-layer biomass?
- (2) Does differing canopy species diversity alter soil and light conditions as well as their spatial heterogeneity and thereby herb-layer species diversity?
- (3) How pronounced is the influence of beech, a very productive and competitive tree species, on the relationships and processes stated above?
- (4) Are there herb-layer species whose occurrence is particularly correlated with tree-layer composition and environmental factors, which are apparently altered by canopy diversity effects?

## 2. Materials and methods

### 2.1. Study area

The study area was Hainich National Park, Thuringia, Germany. All research sites were situated at about 350 m elevation in the north-eastern part of Hainich National Park, close to the village of Weberstedt (51°05'28"N, 10°31'24"E), on flat plateaus above Upper Muschelkalk. The closed, homogeneous loess cover or loess-clay cover of the study area has developed as a result of loess deposition from the Pleistocene era (Greitzke and Fiedler, 1996). According to the World Reference Base (WRB) for Soil Resources, the soil type of the research sites is (stagnic) Luvisol, (st) LV. The climate can be characterised as subatlantic with subcontinental influence. Mean annual precipitation amounts to about 630 mm; the mean annual temperature is about 7.7 °C (Gauer and Aldinger, 2005). Atmospheric pollution is moderate, e.g. nitrogen deposition averages 13 kg N per hectare per year (Mund, 2004). All research sites have been permanently covered by deciduous forest for at least 200 years. The middle of the 19th century saw an initial transition from the often-irregular coppice with standards system (*Mittelwald*) to high forest (*Hochwald*), especially to the multiple aged forest system *Plenterwald*. The transition lasted until the early 20th century (I. Schmidt, personal communication). Since the study area became a military training area in 1964 and subsequently a national park in 1997, all research sites have remained free of any harvesting or thinning for over 40 years (Mund, 2004; Mölder et al., 2006). Dominant forest communities are the *Galio-Fagetum*, the *Hordelymo-Fagetum*, and the *Stellario-Carpinetum* (Mölder et al., 2006).

### 2.2. Experimental design, sampling and data analysis

#### 2.2.1. Research site selection and tree layer

For this study, field data from 21 research sites selected by expert opinion were used. Selection criteria were firstly comparable edaphic and climatic conditions (according to Barbier et al., 2008) and secondly tree-species richness and tree-layer composition. Only trees with a diameter at breast height (dbh) of at least 7 cm were considered. The research sites are described as a gradient from pure beech stands to mixed stands with up to 11 deciduous tree species (Table 1). In addition to *F. sylvatica*, major

**Table 1**  
Diversity measures and environmental factors determined for all 21 research sites

Research site	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
<b>Tree layer</b>																					
Species richness (SR)	1	3	3	4	4	4	5	5	6	6	6	6	7	7	7	7	7	9	9	10	11
Shannon–Wiener Index ( $H'$ )	0.00	0.48	0.51	0.17	0.31	0.51	0.88	0.99	0.92	0.95	1.40	1.56	0.99	1.00	1.11	1.40	1.41	1.63	1.70	1.69	1.90
Evenness $E$	0.00	0.15	0.46	0.35	0.23	0.37	0.62	0.62	0.51	0.53	0.78	0.84	0.51	0.45	0.57	0.87	0.72	0.74	0.65	0.73	0.79
Volume (m <sup>3</sup> /ha)	664	612	665	672	706	754	477	710	561	413	386	395	480	566	436	403	457	405	433	429	376
Beech proportion (%)	100	88	84	97	94	88	76	64	74	74	48	0	59	68	62	36	41	2	4	3	14
<b>Herb layer</b>																					
Species richness (SR)	20	11	14	11	19	30	34	29	15	35	26	50	45	13	45	31	33	51	55	49	53
Shannon–Wiener Index ( $H'$ )	1.90	1.15	1.67	1.75	1.86	2.53	2.82	2.40	1.36	2.66	2.41	3.26	2.99	1.30	3.10	2.46	2.62	3.30	3.34	3.32	3.30
Evenness ( $E$ )	0.65	0.50	0.65	0.76	0.64	0.75	0.81	0.72	0.52	0.75	0.75	0.84	0.79	0.52	0.82	0.72	0.76	0.84	0.84	0.86	0.84
Biomass (g/m <sup>2</sup> )	13.9	16.5	13.2	6.2	41.3	30.6	50.6	25.0	24.6	35.0	33.4	54.9	73.1	22.6	73.4	31.7	29.0	44.4	72.4	73.6	77.0
<b>Environmental parameters</b>																					
Litter layer thickness (cm)	5.3	4.5	4.5	4.6	3.8	3.4	2.2	4.5	2.4	2.3	2.2	1.9	2.8	3.1	1.6	2.7	2.6	1.9	1.9	1.9	1.9
Soil pH 0–10 cm (H <sub>2</sub> O)	4.6	5.1	4.9	4.8	5.1	5.6	5.8	4.6	5.9	5.6	6.1	6.4	6.2	5.5	6.3	5.8	6.7	6.5	6.1	6.5	6.5
Relative irradiance (%)	2.0	1.2	3.5	2.1	1.0	2.2	1.0	2.4	1.1	1.0	0.9	1.6	0.8	1.1	1.4	1.1	0.8	1.3	1.7	1.4	1.0
<b>Coefficients of variance (CV)</b>																					
CV litter layer thickness (%)	28.2	8.9	29.3	12.3	26.0	12.4	22.0	10.3	39.6	17.4	26.7	15.4	35.2	9.4	20.9	10.8	39.1	47.0	25.0	45.4	15.4
CV soil pH (%)	2.7	4.5	1.4	4.9	0.7	5.0	3.0	3.5	1.3	6.0	1.9	2.4	3.4	1.8	3.5	3.8	4.4	4.7	5.1	2.7	3.0
CV relative irradiance (%)	9.0	7.0	16.9	13.6	5.2	8.3	4.7	7.8	7.5	4.9	3.8	6.7	7.2	4.4	11.1	6.4	2.5	4.4	11.1	8.3	5.9
<b>Ellenberg indicator values</b>																					
Light	4.0	4.1	4.7	3.6	4.2	4.1	4.3	4.5	4.4	4.6	4.0	4.5	4.5	4.3	4.4	4.3	4.1	4.5	4.4	4.3	4.4
Moisture	5.2	5.8	4.9	5.2	5.7	5.4	5.3	5.4	5.3	5.5	5.5	5.4	5.5	5.5	5.4	5.4	5.4	5.5	5.5	5.5	5.4
Nitrogen	5.1	5.6	5.5	6.1	6.1	6.0	5.9	6.6	5.1	6.4	5.8	5.8	6.3	5.3	6.3	5.9	5.7	5.9	6.1	6.0	6.0
Reaction	5.6	6.1	5.6	6.2	6.7	6.7	6.8	6.8	6.7	6.7	6.8	6.6	6.8	6.0	6.7	6.6	6.7	6.5	6.7	6.7	6.6

Tree-layer species richness,  $H'$ , evenness and beech proportion (%) are based on stems/ha. Research site ranking follows tree-layer species richness.

tree species were *Fraxinus excelsior*, *Tilia cordata*, *T. platyphyllos*, *Acer pseudoplatanus*, *A. platanoides*, *Quercus petraea*, and *Carpinus betulus*. *Quercus robur*, *Prunus avium*, *Ulmus glabra*, *Acer campestre*, and *Sorbus torminalis* occurred with no more than a few individuals in any of the research sites. Each research site had a size of 2500 m<sup>2</sup> (50 m × 50 m).

Each of the research sites was characterised by loess-derived soil with a depth of approximately 60 cm, flat relief, mature stands free of harvesting for at least four decades, and homogeneous stand structure. The dominant age of the trees was about 100 years, but due to the former *Plenterwald* treatment a broad variety of age classes occurred (I. Schmidt, personal communication). To characterise the stands with respect to tree diversity at each research site, the number and the dbh of all tree specimens with a dbh of at least 7 cm was recorded. Tree-layer volume (m<sup>3</sup>/ha) can be used as a surrogate variable for tree-layer productivity (according to Hector, 1998). To calculate tree-layer volumes using the forest growth simulator SIBYLA (Fabrika, 2003), for each tree species, tree heights were measured from randomly selected specimens. For the purpose of characterising tree-layer diversity, besides tree-layer species richness (tree-layer SR), Shannon–Wiener diversity index  $H'$  [ $H' = -(\sum p_i)(\ln p_i)$ , where  $p_i$  = stems/ha] and evenness  $E$  [ $E = H'/H'_{\max}$ ;  $H'_{\max} = \ln(n)$ , where  $n$  = tree-layer SR] were calculated (Magurran, 2004). As a biotic environmental parameter, tree-layer beech proportion of each research site was determined based on stems/ha.

### 2.2.2. Herb layer

Following Mölder et al. (2006), herb-layer species richness (herb-layer SR) was estimated by vegetation relevés on 400 m<sup>2</sup> (20 × 20 m) sampling plots chosen by expert opinion in areas representative for each research site. Due to the seasonal phenology of the herb-layer vegetation, sampling was done twice for each plot in 2005 (18th–27th April and 6th July–4th August, respectively) by estimating the percentage cover of each herb-layer species. For data analysis, spring and summer relevés were combined by taking the higher percent-cover value when a species was found in both relevés. For characterising herb-layer diversity, besides herb-layer SR, Shannon–Wiener diversity index  $H'$  and evenness  $E$  [ $H' = -(\sum p_i)(\ln p_i)$ , where  $p_i$  = percentaged cover value;  $E = H'/H'_{\max}$ ;  $H'_{\max} = \ln(n)$ , where  $n$  = herb-layer SR] were calculated. To compare tree-layer diversity with herb-layer diversity, tree species were removed from the herb-layer data. Nomenclature follows Wisskirchen and Haeupler (1998).

By the use of the model PhytoCalc (Bolte, 2006), herbaceous biomass (g/m<sup>2</sup>) was calculated for each research site on the basis of vegetation relevés. This model calculates the herbaceous dry biomass from percentage plant cover and average shoot lengths. PhytoCalc was calibrated by additional measurements of plant shoot lengths. The calibration of PhytoCalc was confirmed on three research sites for species both spring- and summer-green. In each research site, ten square metres of herb-layer vegetation were harvested. The differences between harvested biomass and calculated biomass were 6.5% in research site 2, (harvested biomass: 18.5 g/m<sup>2</sup>, calculated biomass: 17.4 g/m<sup>2</sup>), 7.8% in research site 10 (25.3 g/m<sup>2</sup>, 23.4 g/m<sup>2</sup>) and 8.4% in research site 19 (22.7 g/m<sup>2</sup>, 20.9 g/m<sup>2</sup>), demonstrating that PhytoCalc calculates the herb biomass adequately, but with slight underestimation.

### 2.2.3. Abiotic environmental conditions

In four mixed samples per 400 m<sup>2</sup> sample plot, each from four sampling points, soil pH (H<sub>2</sub>O) of the upper 10 cm of soil was determined in the laboratory. Litter layer thickness was measured by ruler at 16 sampling points per sample plot, and light conditions were estimated using 200 systematically PAR (photosynthetically

active radiation) measurements per sample plot. These measurements were conducted with LI-190 Quantum Sensors (Licor, Nebraska, USA) on overcast days with diffuse light conditions from July to August 2005. For each measurement, the relative irradiance RI was calculated as  $[RI = PAR_{\text{stand}}/PAR_{\text{nearest open area}} \times 100]$ . Mean values and coefficients of variation  $[CV = \text{standard deviation}/\text{mean value} \times 100]$  (for characterising environmental heterogeneity) were computed for each sample plot. Furthermore, mean Ellenberg indicator values for light, moisture, nitrogen, and reaction (Ellenberg et al., 2001) were computed (qualitative evaluation) for each sample plot on the basis of vegetation relevés.

### 2.2.4. Statistical analysis

To investigate the interactions among tree layer, environmental factors, and herb layer, statistical analyses were conducted in two steps: firstly ordination to detect possible relationships between tree layer, environmental parameters and herb-layer and secondly regression analysis of the identified relationships. To find those diversity and environmental parameters useful for explaining differences in herb-layer species composition, multivariate analysis of the vegetation data was done with PC-ORD 5.06 (McCune and Mefford, 1999). To avoid an overestimation of common species and to adapt the data on the percent scale, vegetation data were transformed using arcsine square root transformation. Vegetation data were then ordinated using an indirect ordination method: where species response was linear (length of gradient <1.5, according to ter Braak and Prentice, 1988), a Principal Component Analysis (PCA, Goodall, 1954) was carried out; in case of unimodal species responses (length of gradient >1.5), a Detrended Correspondence Analysis (DCA, Hill and Gauch, 1980).

A bi-plot was compiled by correlating diversity and environmental parameters with the first two axes of the ordination diagram. Those environmental parameters found to be useful for explaining differences in herb-layer species composition were correlated (regression analysis) with significant diversity parameters, to determine whether herb-layer diversity is influenced by environmental parameters affected by tree-species diversity. To detect relationships between environmental heterogeneity and tree-layer as well herb-layer diversity, CV of environmental parameters were correlated with diversity parameters. A second bi-plot was compiled by correlating ground vegetation data of each sample plot with the first two axes of the ordination diagram. Those vascular plant species found to be important for explaining differences in herb-layer species composition were correlated with significant parameters revealed by the other bi-plot in order to detect relationships between species abundance and environmental as well as diversity parameters.

For regression analysis data were analysed using Statistica 6.1 (StatSoft Inc., 2004). Significance of statistic tests were noted as follow: \*\*\* $p \leq 0.001$ ; \*\* $p \leq 0.01$ ; \* $p \leq 0.05$ ; n.s.,  $p > 0.05$ .

## 3. Results

### 3.1. Relationship between tree- and herb-layer diversity measures

Regression analysis showed that tree-layer diversity measures SR,  $H'$  and  $E$  and herb-layer diversity measures SR,  $H'$  and  $E$  were significantly positively correlated throughout (Table 2). From these diversity measures, we chose tree-layer  $H'$  and herb-layer  $H'$  for use in further analyses.

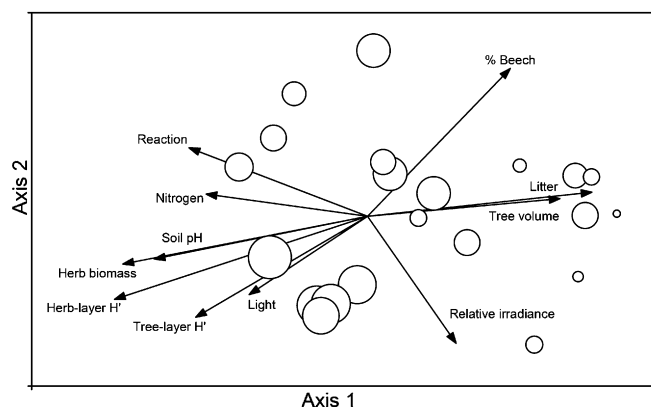
### 3.2. Relationship between diversity and environmental parameters

The DCA clearly showed that understorey vegetation differed along a diversity gradient represented by the first-axis regarding

**Table 2**  
Correlations between tree- and herb-layer diversity measures

		Tree layer								
		SR			H'			E		
		F-value	r	p-Value	F-value	r	p-Value	F-value	r	p-value
Herb layer	SR	24.82	0.75	0.000***	30.11	0.78	0.000***	13.75	0.65	0.001***
	H'	16.27	0.68	0.001***	20.61	0.72	0.000***	15.06	0.66	0.001***
	E	8.25	0.55	0.010**	9.13	0.57	0.007**	11.12	0.61	0.003**

Underlying data are shown in Table 1. *N* in all cases: 21; *r*: Pearson's correlation coefficient. SR: species richness; *H'*: Shannon–Wiener Index; *E*: evenness. \*\*\* =  $p \leq 0.001$  and \*\* =  $p \leq 0.01$ .



**Fig. 1.** DCA of the herb-layer vegetation. A bi-plot was presented by correlating diversity and environmental parameters with axes 1 and 2. Underlying environmental and diversity data are shown in Table 1. Research sites are characterised by their tree-layer Shannon–Wiener Index *H'*, indicated by circle sizes. Soil pH: soil pH 0–10 cm; herb biomass: herb-layer biomass; tree volume: tree-layer volume; % beech: relative beech proportion in tree layer; litter: litter layer thickness; reaction/light/nitrogen: Ellenberg indicator value for reaction/light/nitrogen. Matrix: 91 species, 21 relevés (axis 1: eigenvalue = 0.23, explained variance = 52%, length of gradient = 1.82; axis 2: eigenvalue = 0.07, explained variance = 15%). Correlation threshold:  $r^2 > 0.15$ .

herb-layer *H'* ( $r = -0.92$ ) and tree-layer *H'* ( $r = -0.71$ ). Also, tree-layer volume ( $r = +0.71$ ) and herb-layer biomass were correlated ( $r = -0.88$ ) with the first-axis (Fig. 1). Additionally, the first-axis showed an environmental gradient. It was positively correlated with litter layer thickness ( $r = +0.80$ ) and beech proportion in tree-layer ( $r = +0.65$ ), and negatively correlated with soil pH ( $r = -0.78$ ) as well as Ellenberg indicator values for reaction ( $r = -0.69$ ), nitrogen ( $r = -0.60$ ), and light ( $r = -0.41$ ). The second-axis was positively correlated with RI ( $r = +0.64$ ).

Regression analysis showed that tree-layer *H'* was significantly positively correlated with environmental parameters: soil pH, as well as Ellenberg indicator values for reaction and light, and negatively with litter layer thickness. Meanwhile, herb-layer *H'*

was significantly positively correlated with environmental parameters: soil pH, as well as Ellenberg indicator values for reaction and nitrogen, and negatively with litter layer thickness (Table 3). Furthermore, herb-layer *H'* was significantly negatively correlated with beech proportion in the tree-layer ( $r = -0.76$ ,  $F = 25.90$ ,  $p < 0.000$ ). Soil pH was significantly negatively correlated with beech proportion in tree layer and positively correlated with Ellenberg indicator values for reaction (Table 3). Litter layer thickness was significantly positively correlated with beech proportion in tree layer and negatively correlated with Ellenberg indicator values for reaction. The correlation between soil pH and litter layer thickness was significantly negative ( $r = -0.91$ ,  $F = 96.22$ ,  $p < 0.000$ ), and neither parameter was correlated with Ellenberg indicator for nitrogen. There were no significant correlations between beech proportion in the tree layer and Ellenberg indicator values for reaction, nitrogen, and light. It is noteworthy that there was no significant correlation between RI and Ellenberg indicator values for light. Regression analysis between CV (of soil pH, litter layer thickness, and RI) and tree-as well as herb-layer *H'* showed no significant correlations (Table 4).

### 3.3. Herb species distribution

DCA first-axis scores were negatively correlated with *Ranunculus ficaria* ( $r = -0.94$ ), *Primula elatior* ( $r = -0.89$ ), *Lathyrus vernus* ( $r = -0.87$ ), *Ranunculus auricomus* agg. ( $r = -0.82$ ), *Polygonatum multiflorum* ( $r = -0.78$ ), *Ranunculus lanuginosus* ( $r = -0.77$ ), *Pulmonaria officinalis* ( $r = -0.73$ ), *Stellaria holostea* ( $r = -0.72$ ), and *Viola reichenbachiana* ( $r = -0.71$ ). Second-axis scores were positively correlated with *Convallaria majalis* ( $r = +0.73$ ) (Fig. 2).

Cover values of these species and tree-layer *H'*, as well as environmental factors (beech proportion in tree layer, soil pH, litter layer thickness, RI, Ellenberg indicator values for reaction, light, and nitrogen) were tested for significant correlations by linear regression (Table 5). Except for *C. majalis*, there were significant positive correlations with soil pH throughout. The correlations with tree-layer *H'* (positive correlation), litter layer

**Table 3**  
Correlations between diversity and environmental parameters

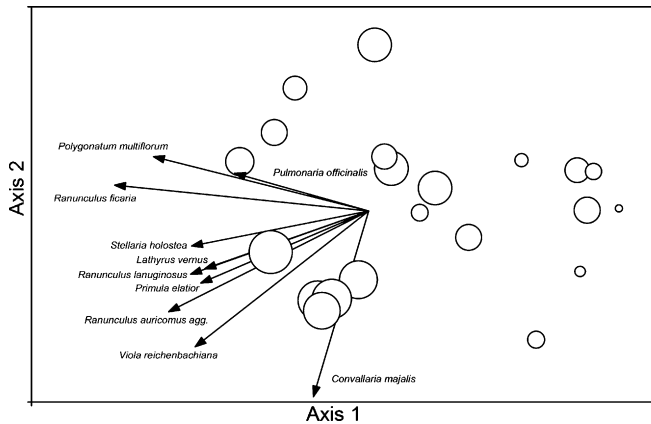
	F-value	r	p-Value		F-value	r	p-Value	
Tree-layer <i>H'</i>	46.34	0.84	0.000***	Soil pH 0–10 cm	19.78	0.71	0.000***	Herb-layer <i>H'</i>
	41.63	-0.83	0.000***	Litter layer thickness	19.02	-0.71	0.000***	
	8.60	0.56	0.009**	Ellenberg, reaction	10.36	0.59	0.005**	
	4.65	0.44	0.044*	Ellenberg, light	2.87	0.36	0.107 n.s.	
	1.05	0.23	0.318 n.s.	Ellenberg, nitrogen	9.09	0.57	0.007**	
Soil pH 0–10 cm	30.19	-0.78	0.000***	% beech	21.60	0.73	0.000***	Litter layer thickness
	10.73	0.60	0.004**	Ellenberg, reaction	17.07	-0.69	0.000***	
	0.36	0.14	0.556 n.s.	Ellenberg, nitrogen	1.05	-0.23	0.318 n.s.	

Underlying data are shown in Table 1. *N* in all cases: 21; *r*: Pearson's correlation coefficient; *H'*: Shannon–Wiener Index; % beech: relative beech proportion in tree layer; Ellenberg, reaction/light/nitrogen: Ellenberg indicator values for reaction/light/nitrogen. \*\*\* =  $p \leq 0.001$ ; \*\* =  $p \leq 0.01$ ; \* =  $p \leq 0.05$ ; n.s. =  $p > 0.05$ .



**Table 4**Correlations between variation coefficients CV (%) (of soil pH, litter layer thickness, relative irradiance) and tree- as well as herb-layer  $H'$ 

	CV soil pH			CV litter			CV relative irradiance		
	F-value	r	p-Value	F-value	r	p-Value	F-value	r	p-Value
Tree-layer $H'$	0.24	0.11	0.630 n.s.	1.34	0.26	0.262 n.s.	2.92	0.36	0.104 n.s.
Herb-layer $H'$	2.36	0.33	0.141 n.s.	1.59	0.28	0.223 n.s.	0.46	0.15	0.505 n.s.

Underlying data are shown in Table 1.  $N$  in all cases: 21;  $r$ : Pearson's correlation coefficient;  $H'$ : Shannon–Wiener Index; n.s. =  $p > 0.05$ .**Fig. 2.** DCA of herb-layer vegetation. A bi-plot was presented by correlating species data with axes 1 and 2. Research sites are characterised by their tree-layer Shannon–Wiener Index  $H'$ , indicated by circle sizes. Matrix: 91 species, 21 relevés (axis 1: eigenvalue = 0.23, explained variance = 52%, length of gradient = 1.82; axis 2: eigenvalue = 0.07, explained variance = 15%). Correlation threshold:  $r^2 > 0.5$ .

thickness (negative correlation), and beech proportion in tree layer (negative correlation) were significant in most cases. Regarding Ellenberg indicator values for reaction, three significant positive correlations were found with *L. vernus*, *P. elatior*, and *R. ficaria*. *R. ficaria* was the only species found to be significantly positively correlated with Ellenberg indicator values for nitrogen, while *C. majalis* was the only species significantly positively correlated with IR and Ellenberg indicator values for light.

### 3.4. Tree-layer volume and herb-layer biomass

Total tree-layer volume decreases with increasing tree-layer  $H'$ , while herb-layer biomass increases (Fig. 3). The highest calculated tree volume of all research sites was 754 m<sup>3</sup>/ha (tree-layer

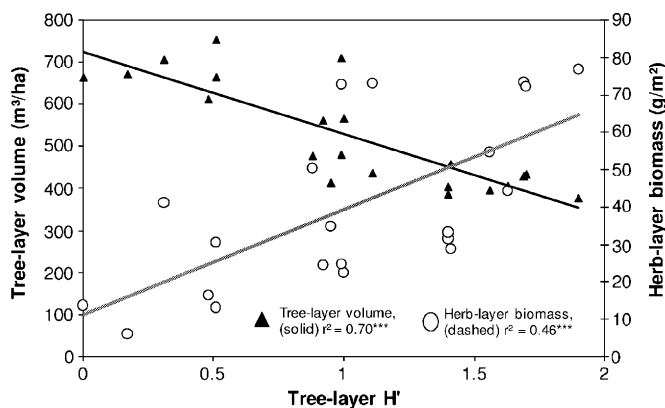
$H' = 0.51$ , beech volume 728 m<sup>3</sup>/ha), the lowest 376 m<sup>3</sup>/ha (tree-layer  $H' = 1.90$ , beech volume 59 m<sup>3</sup>/ha). The highest values of herbaceous biomass totalled 77.0 g/m<sup>2</sup> (tree-layer  $H' = 1.90$ ), and the lowest totalled 6.2 g/m<sup>2</sup> (tree-layer  $H' = 0.17$ ). Herb-layer biomass was significantly positively correlated with herb-layer  $H'$  ( $r = 0.82$ ,  $F = 40.00$ ,  $p < 0.000$ ), soil pH ( $r = 0.72$ ,  $F = 20.72$ ,  $p < 0.000$ ), Ellenberg indicator values for reaction ( $r = 0.60$ ,  $F = 10.14$ ,  $p = 0.005$ ), and Ellenberg indicator values for nitrogen ( $r = 0.46$ ,  $F = 5.04$ ,  $p = 0.036$ ), and significantly negatively correlated with litter layer thickness ( $r = -0.75$ ,  $F = 24.90$ ,  $p < 0.000$ ) and beech proportion in tree-layer ( $r = -0.66$ ,  $F = 14.60$ ,  $p = 0.001$ ).

## 4. Discussion

Our study showed that tree- and herb-layer diversity was positively correlated. In the literature, contradictory results can be found concerning diversity relationship between tree layer and herb layer. Ewald (2002), Neumann and Starlinger (2001), and Aubert et al. (2004) found weak or no correlations. In contrast, McCune and Antos (1981), Bradfield and Scagel (1984), Leuschner (1999), Ingerpuu et al. (2003), and Ferretti et al. (2006) described positive correlations between tree- and herb-layer diversity. Both Leuschner (1999) and Ingerpuu et al. (2003) regarded chemical and biological relationships between vegetation strata as responsible for positive diversity correlations.

In our study, chemical relationships were also indicated by the positive correlation between tree-layer  $H'$  and soil pH, as well as Ellenberg indicator values for reaction. The relationship between measured and indicated pH was close, according to Diekmann (2003) a result found in many studies (e.g. Lawesson and Mark, 2000). Various authors (Nordén, 1994; Finzi et al., 1998; Augusto et al., 2002; Aubert et al., 2004) concluded that beech litter leads to the more acid soil conditions with lower base saturation and nutrient supply; also oak litter results in more acid soil conditions (van Oijen et al., 2005). Additionally, beech foliage decomposes poorly, resulting in thick litter layers (Krauß, 1926; Sydes and Grime, 1981a,b). On the other hand, the litter of *F. excelsior*, *C. betulus*, *Tilia* spp., *U. glabra*, and *P. avium* results in more favourable soil conditions with higher pH and base saturation (Pigott, 1991; Nordén, 1994; Augusto et al., 2002; Aubert et al., 2004; van Oijen et al., 2005). Additionally, in more diverse research sites, nutrient pumping by trees might have an ameliorating effect on topsoil. In particular, *F. excelsior* seems to have a high propensity for nutrient pumping (Gordon, 1964). Furthermore, it must be acknowledged that soil in the stemflow area around beech trunks is often acidified by rainwater flowing down the trunk (Wittig and Neite, 1985).

We found significant correlations between soil pH as well as litter layer thickness and herb-layer  $H'$ . Many authors have regarded litter layer thickness as a factor influencing herb-layer density and composition (Graae and Heskjær, 1997; Borchsenius et al., 2004; van Oijen et al., 2005; Ferretti et al., 2006; Bernhardt-Römermann et al., 2007; Barbier et al., 2008). In particular, close correlations between soil pH and herb-layer diversity were reported for species-rich beech forests (Brunet et al., 1996, 1997; Härdtle et al., 2003; Borchsenius et al., 2004; Ferretti

**Fig. 3.** Correlations between tree-layer  $H'$  and tree-layer volume [m<sup>3</sup>/ha], as well as herb-layer biomass [g/m<sup>2</sup>]. Underlying data are shown in Table 1.  $r^2$ : coefficient of determination.  $H'$ : Shannon–Wiener Index. \*\*\* =  $p \leq 0.001$ . Tree-layer volume:  $p < 0.000$ ; herb-layer biomass:  $p = 0.001$ .

**Table 5**Correlations between herb-layer species and tree-layer  $H'$  as well as environmental parameters

	<i>Viola reichenbachiana</i>	<i>Lathyrus vernus</i>	<i>Ranunculus auricomus</i> agg.	<i>Primula elatior</i>	<i>Ranunculus lanuginosus</i>	<i>Ranunculus ficaria</i>	<i>Stellaria holostea</i>	<i>Polygonatum multiflorum</i>	<i>Pulmonaria officinalis</i>	<i>Convallaria majalis</i>
Tree-layer $H'$										
$F$ -value	16.08	13.55	12.45	10.51	8.80	8.32	4.00	2.28	1.56	1.17
$r$	0.68	0.65	0.63	0.60	0.56	0.55	0.42	0.33	0.28	0.24
$p$ -Value	0.001***	0.002**	0.002**	0.004**	0.008**	0.009**	0.060 n.s.	0.147 n.s.	0.226 n.s.	0.294 n.s.
% beech										
$F$ -value	20.63	14.68	14.26	12.37	7.83	5.44	3.77	0.87	1.62	3.30
$r$	−0.72	−0.66	−0.65	−0.63	−0.54	−0.47	−0.41	−0.21	−0.28	−0.38
$p$ -Value	0.000***	0.001***	0.001***	0.002**	0.011*	0.031*	0.067 n.s.	0.362 n.s.	0.219 n.s.	0.085 n.s.
Litter layer										
$F$ -value	9.87	14.47	13.71	11.19	5.98	17.08	6.34	6.14	4.27	0.04
$r$	−0.58	−0.66	−0.65	−0.61	−0.49	−0.69	−0.50	−0.49	−0.43	−0.05
$p$ -Value	0.005**	0.001***	0.002**	0.003***	0.024*	0.001***	0.021*	0.023*	0.053 n.s.	0.842 n.s.
Soil pH 0–10 cm										
$F$ -value	9.44	20.15	14.32	14.82	8.66	12.57	7.80	5.16	4.49	0.13
$r$	0.58	0.72	0.66	0.66	0.56	0.63	0.54	0.46	0.44	0.08
$p$ -Value	0.006**	0.000***	0.001***	0.001***	0.008**	0.002**	0.012*	0.035*	0.048*	0.722 n.s.
Reaction										
$F$ -value	1.63	4.52	1.99	4.61	1.56	7.53	1.11	2.85	4.10	1.93
$r$	0.28	0.44	0.31	0.44	0.28	0.53	0.23	0.36	0.42	0.30
$p$ -Value	0.217 n.s.	0.047*	0.174 n.s.	0.045*	0.227 n.s.	0.013*	0.305 n.s.	0.108 n.s.	0.057 n.s.	0.181 n.s.
Relative irradiance										
$F$ -value	0.16	2.39	0.34	1.43	1.49	3.33	0.41	1.44	1.63	9.87
$r$	0.09	0.33	0.13	0.26	0.27	0.39	0.14	0.27	0.28	0.58
$p$ -Value	0.698 n.s.	0.139 n.s.	0.565 n.s.	0.246 n.s.	0.237 n.s.	0.084 n.s.	0.532 n.s.	0.244 n.s.	0.217 n.s.	0.005**
Light										
$F$ -value	1.98	1.80	1.71	0.87	1.88	3.63	1.37	0.87	0.36	7.77
$r$	0.31	0.29	0.29	0.21	0.30	0.40	0.26	0.21	0.14	0.54
$p$ -Value	0.176 n.s.	0.195 n.s.	0.207 n.s.	0.362 n.s.	0.187 n.s.	0.072 n.s.	0.257 n.s.	0.361 n.s.	0.553 n.s.	0.012*
Nitrogen										
$F$ -value	0.22	2.29	1.90	2.23	1.78	9.16	0.97	2.75	1.70	0.15
$r$	0.28	0.33	0.30	0.32	0.29	0.57	0.22	0.36	0.29	0.09
$p$ -Value	0.224 n.s.	0.147 n.s.	0.184 n.s.	0.152 n.s.	0.198 n.s.	0.007**	0.336 n.s.	0.114 n.s.	0.208 n.s.	0.706 n.s.

Underlying environmental and diversity data are shown in Table 1.  $N$  in all cases: 21;  $r$ : Pearson's correlation coefficient;  $H'$ : Shannon–Wiener Index; litter layer: litter layer thickness; % beech: relative beech proportion in tree layer; reaction/light/nitrogen: Ellenberg indicator value for reaction/light/nitrogen. \*\*\* =  $p \leq 0.001$ ; \*\* =  $p \leq 0.01$ ; \* =  $p \leq 0.05$ ; n.s. =  $p > 0.05$ .

et al., 2006). These findings are closely linked with the phenomenon that the majority of (eutrophic) beech forest species are categorised as  $\text{NO}_3^-$ -plants, and therefore linked to soils where nitrifiers are active due to slightly basic to neutral soil pH (Ellenberg, 1996; Härdtle et al., 2003). Our study showed that the Ellenberg indicator value for nitrogen was significantly correlated with herb-layer  $H'$  and herb-layer biomass (see section below), but not with litter layer thickness and soil pH. This result seems to support findings by Schaffers and Šykora (2000), who endorse Hill and Carey's (1997) suggestion that the term  $N$ -values should be replaced by 'productivity values'.

Härdtle et al. (2003) detected a positive soil pH/herb-layer species richness correlation in North-German meso- to eutrophic beech forests (*Fagion sylvaticae*), but not in acidophytic beech- and mixed beech-oak forests (*Quercetalia roboris*). They emphasised that in the *Quercetalia* forests light and soil moisture are the most important factors influencing species richness, whereas in the meso- to eutrophic beech forests light is not correlated with herb-layer species richness. The latter is also true in the Hainich research sites, both *F. sylvaticae* and *Carpinus betuli* stands (Mölder et al., 2006), where the relative irradiance is not correlated with herb-layer diversity. Ellenberg indicator values for light were indeed significantly positively correlated with tree-layer  $H'$ , but Diekmann (2003) stresses that the strength of correlation between indicated and measured light values is highly dependent on the length of the gradient considered: if the light gradient is short (as in the light dataset of this study) the relation will be weak. We assumed that direct measurements of relative irradiance reflected the light condition best. It should be observed that relative irradiance values ranged between 0.8% and 3.5%, therefore the stands can be regarded as dark (Ellenberg, 1996). Many beech forest species, especially geophytes, have adapted to unfavourable light conditions or complete their development cycles before the canopy is fully closed (Ellenberg, 1996). Following Härdtle et al. (2003), the light factor has virtually no influence on herb-layer species richness in beech forests if the number of non-forest species is low in such stands. This presupposition was met on the Hainich research sites, which featured a typical forest flora with very few disturbance indicators (Mölder et al., 2006). Horizontal light variation, often regarded as a factor influencing the diversity of typical forest plants (Meusel, 1951/1952; Messier et al., 1999), was also not correlated with herb-layer diversity. The same applied for the small-scale heterogeneity of soil pH, in contrast to Bobiec (1998), who found the herb-layer to be more diverse in deciduous forests with a wider soil pH range than in forests with low soil pH variation. Although Lodhi and Johnson (1989) stressed that spatial heterogeneity of the litter layer may influence herb-layer diversity, no correlation between herb-layer diversity and the variation of litter layer thickness was found in our study. At least for the Hainich research sites, our results might be an indication for the insignificance of small-scale light and soil heterogeneity for herb-layer diversity as predicted by the environmental heterogeneity hypothesis (Huston, 1994).

Environmental factors and tree-layer  $H'$  appeared to be correlated with the occurrence of particular herb-layer species. All species positively correlated with soil pH were important for the phytosociological classification of the research sites (Mölder et al., 2006). Particularly *R. ficaria*, conspicuously the only species correlated with Ellenberg indicator values for nitrogen, is an important differential species within the species-rich and nutrient-demanding association *Stellario-Carpinetum* following Dierschke (1986). A significant negative relationship between litter layer thickness and cover of *R. ficaria*, among others, was observed. This indicates that *R. ficaria* is unable to penetrate thick litter layers (Graae and Heskjær, 1997). The abundance of *C. majalis*, a semi-

shadow plant (Ellenberg L value: 5), was correlated solely with relative irradiance and Ellenberg indicator values for light. van Oijen et al. (2005) stressed that in Dutch deciduous forests *C. majalis* is found mostly in open plots with low external crown projection. In the Hainich research sites, increased light intensity might promote the abundance of *C. majalis*, but this supposition must be seen in light of overall shady stand conditions. Our findings can be seen as an indication that the current occurrence of *C. majalis* might be a relic from former, brighter stand conditions due to silvicultural management in coppices with standards.

Research sites with both high tree-layer diversity and low tree-layer volumes mostly belonged to the *Stellario-Carpinetum* association. In spite of an obvious transition towards natural forest conditions, these research sites still showed characteristics of the ancient coppice with standards system and the multiple aged forest system *Plenterwald* (Mölder et al., 2006). Under a coppice with standards system, beech retreats rapidly (Ellenberg, 1996), and the growing stock of the canopy layer is low (Geb et al., 2004). The silvicultural system *Plenterwald* requires that a lower volume of growing stock be kept, if light-demanding tree species such as *F. excelsior* and *Acer* spp. are to be supported. For the Hainich area, it is recommended that 280  $\text{m}^3/\text{ha}$  be kept as growing stock (Röhle and Fuchs, 1999). In more diverse research sites, *T. cordata* provided a considerable portion of tree-layer volume. In the Hainich, there is a trend of higher clay content in the soil of stands with a more diverse tree layer (Guckland et al., unpublished data). Besides silvicultural conditions, heightened clay content in soils is crucial for the prominence of *T. cordata* and the decline of *F. sylvatica* (Schlüter, 1968; Pigott, 1991). Heavy, poorly aerated clay soil promotes *T. cordata* (Schlüter, 1968), while *F. sylvatica* frequently withdraws due to its avoidance of temporary water-logged sites (Czajkowski et al., 2006).

In contrast to deep-rooting tree species, herb-layer species root in the topsoil horizon; other factors are regarded as crucial for their development. The results of this study might indicate that herb-layer productivity was promoted in more diverse research sites by increased nutrient supply and base saturation. On the other hand, increasing beech proportion and biomass production in tree layer might interfere with herb-layer productivity, since beech features a dense fine root network in the topsoil and is a strong competitor for nutrients and water (Falkengren-Grerup and Tyler, 1993; Leuschner et al., 2004). Leuschner (1999) found increasing root densities in thicker litter layers of Central German beech forests, and negative correlations between herb-layer cover (as a surrogate variable for herb-layer productivity) and beech root density. This indicates that litter layer thickness might influence herb-layer cover negatively as well. In our study it was shown that herb-layer biomass was significantly negatively correlated with litter layer thickness.

Due to its profound effect on nutrient cycling, herb-layer productivity is an important part of ecosystem functioning in forests (e.g. Yarie, 1981; Peterson and Rolfe, 1982; Bolte et al., 2004; Bolte, 2006). According to theories indicating positive diversity-functioning relationships (Hooper et al., 2005), there may also be a positive effect of increased herb-layer diversity on herb-layer productivity. Similarly we found herb-layer biomass to be positively correlated with herb-layer diversity of the investigated deciduous forest. We are aware, however, that 21 research sites do not allow broad generalisations of our results. Supplementary investigations as well as experiments on different sites and forest types would be necessary to acquire more knowledge about the possible relationships described in this study. But, for instance, it is probably impossible to entirely divorce the association between species diversity and productivity from other biotic and environmental factors (Vilà et al., 2005).



## 5. Conclusions

Herb-layer vegetation of deciduous forest stands rich in canopy species appeared to be more diverse than that of beech-dominated stands. We surmise that herbaceous understorey diversity was indirectly influenced by canopy tree species by the medium of altered environmental factors soil pH and litter layer thickness. Apparently, lower beech proportion had a more profound effect than the number of secondary tree species. There were no correlations between herb-layer diversity and light transmissibility of the canopy layer, indicating that the light factor was not crucial for herb-layer diversity. At least for the Hainich research sites, our results indicated that small-scale light and soil heterogeneity is insignificant for herb-layer diversity. We found several herb-layer species whose occurrence was particularly correlated with tree-layer diversity and environmental factors. Remarkably, all species positively correlated with soil pH were important for the phytosociological classification of the research sites. Beech-dominated research sites showed high tree-layer volumes, whereas research sites with high tree-layer diversity tended to feature lower tree-layer volumes. These findings could be the result of differing former silvicultural systems and varying soil clay contents affecting tree-species composition. In contrast, herb-layer biomass was positively correlated with tree-layer diversity. Herb-layer productivity might be promoted in more diverse research sites by increased nutrient supply and base saturation. It is also possible that greater beech proportion and beech biomass production interfered with herb-layer productivity. However, herb-layer biomass was also positively correlated with herb-layer diversity. Hence, our study hints that positive diversity-functioning relationships might occur in the herb-layer of the deciduous forest under investigation.

## Acknowledgements

Our study received financial support from the German Research Foundation (DFG, Research Training Group 1086). We thank Karl-Maximilian Daenner for his support in the tree-layer data analysis. Andrea Bauer, Heiko Rubbert, and Christoph Fischer were a great help during the fieldwork. Many colleagues from the Research Training Group 1086 supported our studies with data and comments, especially Inga Schmidt, Mascha Brauns, and Karl-Maximilian Daenner. We are grateful to Dylan Leeman and Ginamarie Gemma Lopez for language correction. Finally, we thank two anonymous reviewers for their helpful comments on the manuscript.

## References

- Aubert, M., Bureau, F., Alard, D., Bardat, J., 2004. Effect of tree mixture on the humic epipedon and vegetation diversity in managed beech forests (Normandy, France). *Can. J. For. Res.* 34, 233–248.
- Augusto, L., Ranger, J., Binkley, D., Rothe, A., 2002. Impact of several common tree species of European temperate forests on soil fertility. *Ann. For. Sci.* 59, 233–253.
- Augusto, L., Dupouey, J.-L., Ranger, J., 2003. Effects of tree species on understorey vegetation and environmental conditions in temperate forests. *Ann. For. Sci.* 60, 823–831.
- Barbier, S., Gosselin, F., Balandier, P., 2008. Influence of tree species on understorey vegetation diversity and mechanisms involved—a critical review for temperate and boreal forests. *For. Ecol. Manage.* 254, 1–15.
- Bernhardt-Römermann, M., Kudernatsch, T., Pfadenhauer, J., Kirchner, M., Jakobi, G., Fischer, A., 2007. Long-term effects of nitrogen-deposition on vegetation in a deciduous forest near Munich, Germany. *Appl. Veg. Sci.* 10, 399–406.
- Bobiec, A., 1998. The mosaic diversity of field layer vegetation in the natural and exploited forests of Białowieża. *Plant Ecol.* 136, 175–187.
- Bolte, A., 2006. Biomasse- und Elementvorräte der Bodenvegetation auf Flächen des forstlichen Umweltmonitorings in Rheinland-Pfalz (BZE, EU Level II). *Ber. Forsch. zent. Waldökosyst. (Reihe B)* 72, 1–80.
- Bolte, A., Lambert, B., Steinmeyer, A., Kallweit, R., Meesenburg, H., 2004. Zur Funktion der Bodenvegetation im Stoffhaushalt von Wäldern—Studien auf Dauerbeobachtungsflächen des EU Level II-Programms in Norddeutschland. *Forstarchiv* 75, 207–220.
- Borchsenius, F., Nielsen, P.K., Lawesson, J.E., 2004. Vegetation structure and diversity of an ancient temperate deciduous forest in SW Denmark. *Plant Ecol.* 175, 121–135.
- Bradfield, G.E., Scagel, A., 1984. Correlations among vegetation strata and environmental variables in subalpine spruce-fir forests, southeastern British Columbia. *Vegetatio* 55, 105–114.
- Brunet, J., Falkengren-Grerup, U., Tyler, G., 1996. Herb layer vegetation of south Swedish beech and oak forests—effects of management and soil acidity during one decade. *For. Ecol. Manage.* 88, 259–272.
- Brunet, J., Falkengren-Grerup, U., Tyler, G., 1997. Pattern and dynamics of ground vegetation in south Swedish *Carpinus betulus* forests: importance of soil chemistry and management. *Ecography* 20, 513–520.
- Coll, L., Balandier, P., Picon-Cochard, C., Prévosto, B., Curt, T., 2003. Competition for water between beech seedlings and surrounding vegetation in different light and vegetation composition conditions. *Ann. For. Sci.* 60, 593–600.
- Czajkowski, T., Kompa, T., Bolte, A., 2006. Zur Verbreitungsgrenze der Buche (*Fagus sylvatica* L.) im nordöstlichen Mitteleuropa. *Forstarchiv* 77, 203–216.
- Diaci, J. (Ed.), 2006. Nature-Based Forestry in Central Europe. Alternatives to Industrial Forestry and Strict Preservation. University of Ljubljana, Ljubljana.
- Diekmann, M., 2003. Species indicator values as an important tool in applied plant ecology—a review. *Basic Appl. Ecol.* 4, 493–506.
- Dierschke, H., 1986. Pflanzensoziologische und ökologische Untersuchungen in Wäldern Süd-Niedersachsens. III. Syntaxonomische Gliederung der Eichen-Hainbuchenwälder, zugleich eine Übersicht der Carpinion-Gesellschaften Nordwest-Deutschlands. *Tuexenia* 6, 299–323.
- Ellenberg, H., 1996. Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. Ulmer, Stuttgart.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., 2001. Zeigerwerte von Pflanzen in Mitteleuropa. *Scr. Geobot.* 18, 1–264.
- Ewald, J., 2002. Multiple controls of understorey plant richness in mountain forests of the Bavarian Alps. *Phytocoenologia* 32, 85–100.
- Fabrika, M., 2003. Rastový simulátor SIBYLA a možnosti jeho uplatnění při obhospodarování lesa. *Lesnícky časopis* 49, 135–151.
- Falkengren-Grerup, U., Tyler, G., 1993. Soil chemical properties excluding field-layer species from beech forest floor. *Plant Soil* 148, 185–191.
- Ferretti, M., Calderisi, M., Amoriello, T., Bussotti, F., Canullo, R., Campetella, G., Costantini, A., Fabbio, G., Mosello, R., 2006. Factors influencing vascular species diversity in the CONECOFOR permanent monitoring plots. *Ann. Inst. Sper. Selv.* 30, 97–106.
- Finzi, A.C., Canham, C.D., Van Breemen, N., 1998. Canopy tree-soil interactions within temperate forests: species effects on pH and cations. *Ecol. Appl.* 8, 447–454.
- Gauer, J., Aldinger, E. (Eds.), 2005. Waldökologische Naturräume Deutschlands—Forstliche Wuchsgebiete und Wuchsbezirke. Mitt. Ver. Forstl. Standortskd. Forstpflanzenzücht. 43, 1–324.
- Geb, M., Schmidt, W., Meyer, P., 2004. Das Mittelwaldprojekt Liebenburg—Entwicklung der Bestandsstruktur. *Forst u. Holz* 59, 567–573.
- Goodall, D.W., 1954. Objective methods for the classification of vegetation. III. An essay in the use of factor analysis. *Aust. J. Bot.* 2, 304–324.
- Gordon, A.G., 1964. The nutrition and growth of ash, *Fraxinus excelsior*, in natural stands in the English Lake District as related to edaphic site factors. *J. Ecol.* 52, 169–187.
- Graae, B.J., Heskjær, V.S., 1997. A comparison of understorey vegetation between untouched and managed deciduous forest in Denmark. *For. Ecol. Manage.* 96, 111–123.
- Greitzke, A., Fiedler, H.J., 1996. Schuttdecken und Bodentypen entlang einer Catena auf Muschelkalk in Buchenbeständen des Hainich. *Arch. Nat. Schutz Landsch. Forsch.* 34, 257–268.
- Härdtle, W., Oheimb, G., von Westphal, C., 2003. The effects of light and soil conditions on the species richness of the ground vegetation of deciduous forests in northern Germany (Schleswig-Holstein). *For. Ecol. Manage.* 182, 327–338.
- Hector, A., 1998. The effect of diversity on productivity: detecting the role of species complementarity. *Oikos* 82, 597–599.
- Hill, M.O., Carey, P.D., 1997. Prediction of yield in the Rothamsted Park grass experiment by Ellenberg indicator values. *J. Veg. Sci.* 8, 579–586.
- Hill, M.O., Gauch, H.G., 1980. Detrended correspondence analysis—an improved ordination technique. *Vegetatio* 42, 47–58.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* 75, 3–35.
- Huston, M.A., 1994. Biological Diversity: The Coexistence of Species on Changing Landscapes. Cambridge University Press, Cambridge.
- Ingerpuu, N., Vellak, K., Liira, J., Pärtel, M., 2003. Relationships between species richness patterns in deciduous forests at the north Estonian limestone escarpment. *J. Veg. Sci.* 14, 773–780.
- Krauß, G.A., 1926. Über die Schwankungen des Kalkgehaltes im Rotbuchenlaub auf verschiedenem Standort. *Forstwiss. Cent. bl.* 48, 401–429 452–473.
- Lawesson, J.E., Mark, S., 2000. pH and Ellenberg reaction values for Danish forest plants. In: White, P.S., Mucina, L., Lepš, J. (Eds.), *Vegetation Science in Retrospect and Perspective. Proceedings of the IAVS Symposium, Uppsala*, pp. 153–155.

- Légaré, S., Bergeron, Y., Paré, D., 2002. Influence of forest composition on understory cover in boreal mixedwood forests of western Quebec. *Silva Fenn.* 36, 353–366.
- Leuschner, C., 1999. Zur Abhängigkeit der Baum- und Krautschicht mitteleuropäischer Waldgesellschaften von der Nährstoffversorgung des Bodens. *Ber. Reinh.-Tüxen-Ges.* 11, 109–131.
- Leuschner, C., Hertel, D., Schmid, I., Koch, O., Muhs, A., Hölscher, D., 2004. Stand fine root biomass and fine root morphology in old-growth beech forests as a function of precipitation and soil fertility. *Plant Soil* 258, 43–56.
- Lodhi, M.A.K., Johnson, F.L., 1989. Forest understory biomass heterogeneity—is “moisture complex” or associated litter the cause? *J. Chem. Ecol.* 15, 429–437.
- Lorenz, M., Fischer, R., Becher, G., Mues, V., Seidling, W., Kraft, P., Nagel, H.-D., 2006. Forest Condition in Europe. Technical Report of ICP Forests. Bundesforschungsanstalt für Forst- und Holzwirtschaft, Institut für Weltforstwirtschaft, Hamburg.
- Magurran, A.E., 2004. Measuring Biological Diversity. Blackwell Science, Oxford.
- McCune, B., Antos, J.A., 1981. Correlations between forest layers in the Swan Valley. *Montana Ecol.* 62, 1196–1204.
- McCune, B., Mefford, M.J., 1999. PC-ORD, Multivariate Analysis of Ecological Data, Version 5.01. MjM Software, Gleneden Beach, Oregon, USA.
- Messier, C., Parent, S., Bergeron, Y., 1999. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. *J. Veg. Sci.* 9, 511–520.
- Meusel, H., 1951/1952. Die Eichen-Mischwälder des Mitteldeutschen Trockengebietes, vol. 1. Wiss. Z. d. Martin-Luther-Univ., Halle-Wittenberg, pp. 49–72.
- Mölder, A., Bernhardt-Römermann, M., Schmidt, W., 2006. Forest ecosystem research in Hainich National Park (Thuringia): first results on flora and vegetation in stands with contrasting tree species diversity. *Waldökologie-Online* 3, 83–99.
- Morris, L.A., Moss, S.A., Garbett, W.S., 1993. Competitive interference between selected herbaceous and woody plants and *Pinus taeda* L. during two growing seasons following planting. *For. Sci.* 39, 166–187.
- Mund, M., 2004. Carbon pools of European beech forests (*Fagus sylvatica*) under different silvicultural management. *Ber. Forsch. zent. Waldökosyst. (Reihe A)* 189, 1–256.
- Neirynck, J., Mirtcheva, S., Sioen, G., Lust, N., 2000. 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 soil. *For. Ecol. Manage.* 133, 275–286.
- Neumann, M., Starlinger, F., 2001. The significance of different indices for stand structure and diversity in forests. *For. Ecol. Manage.* 145, 91–106.
- Niedersächsisches Forstplanungsamt, 2004. Langfristige ökologische Waldentwicklung—Richtlinie zur Baumartenwahl. Roco-Druck, Wolfenbüttel.
- Nordén, U., 1994. Influence of broad-leaved tree species on pH and organic matter content of forest topsoils in Scania, South Sweden. *Scand. J. For. Res.* 9, 1–8.
- Peterson, D.L., Rolfe, G.L., 1982. Nutrient dynamics of herbaceous vegetation in upland and floodplain forest communities. *Am. Midl. Nat.* 107, 325–339.
- Pigott, C.D., 1991. *Tilia cordata* Miller. *J. Ecol.* 79, 1147–1207.
- Pretzsch, H., 2005. The mixed stands issue—a central European perspective. In: Scherer-Lorenzen, M., Körner, C., Schulze, E.-D. (Eds.), *Forest Diversity and Function, Temperate and Boreal Systems*. Springer, Berlin Stuttgart, pp. 41–63.
- Röhle, H., Fuchs, A., 1999. Plenterwaldbewirtschaftung und Forsteinrichtung im Hainich. Betriebsinventur auf der bundeseigenen Liegenschaft Weberstedt. *AFZ/Wald* 54, 584–586.
- Röhrig, E., Bartsch, N., von Lüpke, B., 2006. Waldbau auf ökologischer Grundlage. Ulmer, Stuttgart.
- Schaffers, A.P., Sýkora, K.V., 2000. Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. *J. Veg. Sci.* 11, 225–244.
- Scherer-Lorenzen, M., Palmborg, C., Prinz, A., Schulze, E.-D., 2003. The role of plant diversity and composition for nitrate leaching in grasslands. *Ecology* 84, 1539–1552.
- Schlüter, H., 1968. Zur systematischen und räumlichen Gliederung des Carpinion in Mittelthüringen. *Feddes Repert* 77, 117–141.
- Schmidt, W., 2005. Herb layer species as indicators of biodiversity of managed and unmanaged beech forests. *For. Snow Landsc. Res.* 79, 111–125.
- Spiecker, H., 2006. Minority tree species—a challenge for multipurpose forestry. In: Diaci, J. (Ed.), *Nature-Based Forestry in Central Europe. Alternatives to Industrial Forestry and Strict Preservation*. University of Ljubljana, Ljubljana, pp. 47–59.
- StatSoft Inc., 2004. STATISTICA for Windows, Version 6. StatSoft Inc., Tulsa/Oklahoma/USA.
- Sydes, C., Grime, J.P., 1981a. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. I. Field investigations. *J. Ecol.* 69, 237–248.
- Sydes, C., Grime, J.P., 1981b. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. II. An experimental investigation. *J. Ecol.* 69, 249–262.
- ter Braak, C.J.F., Prentice, I.C., 1988. A theory of gradient analysis. *Adv. Ecol. Res.* 18, 271–317.
- Tilman, D., Wedin, D., Knops, J., 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379, 718–720.
- Underwood, A.J., Paine, R.T., 2007. Two views on ecological experimentation. *Bull. Brit. Ecol. Soc.* 38, 24–27.
- van Oijen, D., Feijen, M., Hommel, P.W.F.M., den Ouden, J., van der Waal, B.H.C., 2005. Effects of tree species composition on within-forest distribution of understorey species. *Appl. Veg. Sci.* 8, 155–166.
- Vilà, M., Inchausti, P., Vayreda, J., Barrantes, O., Gracia, C., Ibanez, J.J., Mata, T., 2005. Confounding factors in the observational productivity-diversity relationship in forests. In: Scherer-Lorenzen, M., Körner, C., Schulze, E.-D. (Eds.), *Forest Diversity and Function, Temperate and Boreal Systems*. Springer, Berlin Stuttgart, pp. 65–81.
- Wisskirchen, R., Haeupler, H., 1998. Standardliste der Farn- und Blütenpflanzen Deutschlands. Ulmer, Stuttgart.
- Wittig, R., Neite, H., 1985. Acid indicators around the trunk base of *Fagus sylvatica* in limestone and loess beechwoods: distribution pattern and phytosociological problems. *Vegetatio* 64, 113–119.
- Yarie, J., 1981. The role of understory vegetation in the nutrient cycle of forested ecosystems in the Mountain Hemlock Biogeoclimatic Zone. *Ecology* 61, 1498–1514.