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The effects of light and soil conditions on the species richness of the ground vegetation of deciduous forests in northern Germany (Schleswig-Holstein)

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Abstract

This paper reports a study carried out in 91 deciduous forests to investigate the influence of light and soil conditions on the species richness of the ground vegetation (vascular plants, bryophytes, lichens). To examine the relationships between the species richness and environmental factors all data were evaluated using univariate and multivariate (principle component analysis) methods. At all the stands investigated, the conditions of soil and light have a vegetation type specific effect on the species richness of the ground vegetation. In moist forests (alder-ash forests of the alliance *Alno-Ulmion*), species richness has a close positive correlation with soil moisture, whilst light conditions and nutrient supply have in the main no effect on species richness. On the other hand, in meso- to eutrophic beech forests (beech forests of the alliance *Fagion sylvaticae*), species richness is closely correlated with soil activity and with the base and nitrogen supply. Improving the light conditions for the ground vegetation does not increase the number of typical woodland species as most of these are shade tolerant and have very limited light requirements. Species richness in acidophytic beech and mixed beech–oak forests (beech and mixed beech–oak forests on acid soils of the order *Quercetalia roboris*) is affected mainly by the canopy closure and the interior light conditions. Soil moisture, nutrient supply and light availability must therefore be evaluated differently for their effect on the number of species of the ground vegetation and with regard to individual forest communities as they are distinguishable according to their site conditions. If the relation between species richness and environmental factors like soil conditions is analysed not with reference to individual forest communities but rather with reference to the totality of central European forests, relationships may be found which are not helpful for an explanation of the species richness of a certain forest community and thus they are only of restricted usefulness for appropriate recommendations for forest management. The consequences of the results for the effects of silvicultural treatment on deciduous forest ecosystems of the central European lowlands are discussed.

Keywords: Species diversity; Vegetation-site relationships; Site conditions; Understorey vegetation; Silvicultural treatment; Deciduous forests

1. Introduction

Although deciduous forests of the north German lowlands are still oligo- to mesohemerobic ecosystems, their species composition has changed more or less obviously over the past decades. Ecological forest

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management attempts a form of silvicultural treatment that balances the need to produce timber with a due regard for the requirements of nature conservation within forest ecosystems. In order to formulate recommendations for conservation-oriented management in forestry practice, it is helpful to have investigations which analyse the effects of silvicultural measures on the structure and species composition of forests and which describe the development of natural forests that have not been commercially used. Recent years have seen numerous studies devoted to the description and analysis of the effects of forest management on the structure and ground vegetation of the forests, as in this context the ground vegetation in particular is of great value as an indicator (Barkham, 1992; Grabherr et al., 1995, 1998; Halpern and Spies, 1995; Brunet et al., 1996; Christensen and Emborg, 1996; Graae and Heskjær, 1997; Nagaike et al., 1999). However, these investigations can only be meaningfully interpreted and proper conclusions drawn for silvicultural practice if at the same time the effect and the variability of natural conditions for growth, such as nutrient and water supply and light conditions, on the species composition and the species richness of the ground vegetation are adequately known. The variability of the forest ground vegetation within this gradient of natural site conditions, as regards soil and structure parameters, is particularly important. Roberts and Gilliam (1995) and Ehrlich (1996) have pointed out that additional research is needed to identify diversity patterns and mechanisms in respect of natural site conditions and quality (cf. also Hüttle et al., 2000).

The objective of this paper is to examine how environmental factors (light and soil conditions) affect the species richness and the species composition of the ground vegetation (vascular plants, bryophytes, lichens) of deciduous forests in northern Germany, using representative stands in Schleswig-Holstein as examples. In the foreground is the question of how the species number in the ground vegetation changes within a natural site gradient, particularly in respect of the nutrient, moisture and light gradients. Additionally we sought to compare the effect of these site gradients on diversity patterns of the ground vegetation with regard to different forest communities (moist forests with alder and ash, eu- and mesotrophic beech forests, acidophytic beech and mixed beech–oak forests). Based on this, prognoses can be formulated to describe how the species composition of the ground vegetation will change when the relevant environmental conditions are altered by silvicultural treatment.

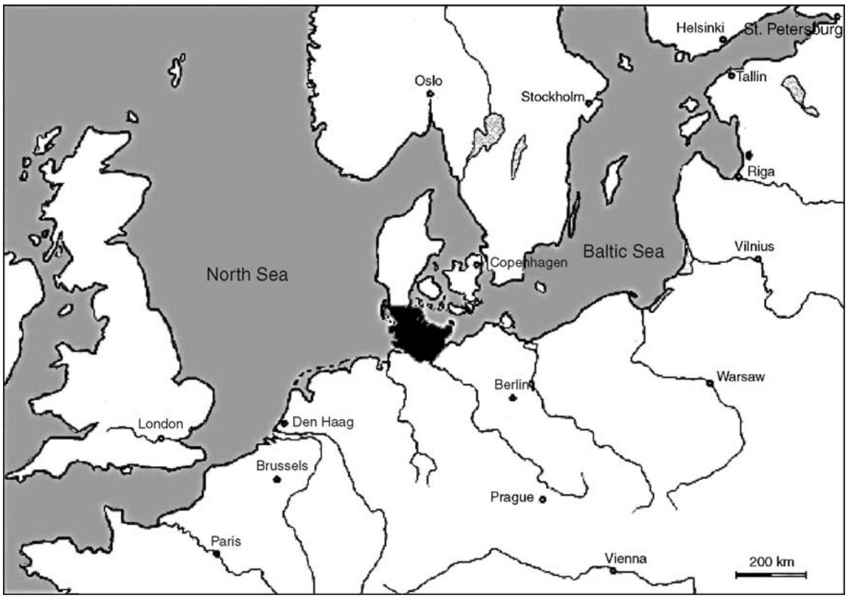

Fig. 1. Map of northern Central Europe, showing the location of the study area (Schleswig-Holstein, black area).

2. Material and methods

2.1. Study area and forest communities

Between the years 1990 and 1998, a total of 91 sample sites in different stands of deciduous forests on ancient and recent moraines in northern Germany (Schleswig-Holstein; cf. Fig. 1) was investigated (ancient moraines: moraines of the penultimate (Saale) glacial period; recent moraines: moraines of the last (Weichsel) glacial period). The study area comprises a geographic area of approximately 15700 km^2. Each sample site was square with a size of 100 m^2 and represented a stand of a forest community which is typical for the lowland of northern Germany (criteria for the selection of sample sites see below).

All deciduous forest communities, which are native in northern Germany, were investigated. These are:

- Moist forests with alder and ash (*Alnus glutinosa*, *Fraxinus excelsior*) of the alliance *Alno-Ulmion* with two subtypes: *A. glutinosa–F. excelsior* forests on wet soils (16 sample sites) and *F. excelsior* forests on moderately wet soils (17 sample sites).
- Eu- and mesotrophic beech forests (*Fagus sylvatica*) of the alliance *Fagion sylvaticae* with two subtypes: eutrophic beech forests with *Hordelymus europaeus* (*Hordelymus–Fagus* forests, 21 sample sites) and mesotrophic beech forests with *Galium odoratum* (*Galium–Fagus* forests, 20 sample sites).
- Acidophytic beech and mixed beech–oak forests (*F. sylvatica*, *Quercus robur*, *Quercus petraea*) of the order *Quercetalia roboris* with two subtypes: acidophytic beech forests with *Avenella flexuosa* (*Avenella–Fagus* forests, 6 sample sites) and acidophytic mixed beech–oak forests (*Fagus–Quercus* forests, 11 sample sites).

In each sample site the total number of species in the ground vegetation (vascular plants, bryophytes, lichens) and the canopy cover of the tree layer were recorded according to the Braun-Blanquet approach (Braun-Blanquet, 1964). As the purpose of the investigation was to determine the influence of soil and light conditions on the species richness of the ground vegetation, it was necessary that other parameters that could influence the species richness should be the same or almost the same. The following criteria thus underlay the selection of the sample sites to be investigated:

- The age of the trees ranged from 80 to 120 years.
- All the stands investigated in this study were ancient woodlands (in the sense of Rackham, 1980 and Peterken, 1996) and exist for at least since 250 years.
- The species composition of the trees at all stands was autochthonous.
- All the stands have been managed in a semi-natural manner, and no trees have been felled in the sample sites for at least 10 years.

2.2. Sampling and laboratory methods

In order to describe and to assess the soil conditions for the ground vegetation, it is important to take the soil samples in the main root horizons of the ground vegetation. In forest stands of the vegetation types *Alno-Ulmion* and *F. sylvaticae* the main root horizon for the ground vegetation is the A_h-horizon. In forest stands of the order *Q. roboris* the main root horizons are the organic layers (O_f- and O_h-horizon). For the determination of soil parameters a mixed soil sample was analysed consisting of three single soil samples.

The following soil and structural parameters were examined or determined:

- The thickness of single soil horizons (including the humus layer) within different soil profiles;
- pH (H_2O)-value, base saturation (%), and *S*-value (mval/100 cm^3) in the organic layers (O_f-, O_h-horizon) and in the A-horizon; soil sampling during October; pH-determination from Steubing (1965), the remaining parameters from Brown (1943);
- C/N ratio in the organic layers (O_f-, O_h-horizon) and in the A_h-horizon; soil sampling during October; determination with a C/N analyser;
- $CaCO_3$-content in the subsoil (G-horizon; mval/100 cm^3, only in moist forests); soil sampling during October; determination from Steubing (1965);
- Thickness of the G_r-horizon within a 2 m thick soil profile, as an expression of the soil moisture (only in moist forests);
- The mean (unweighted) indicator value for soil moisture in respect of each vegetation relevé (from

Ellenberg et al., 1992), as an expression of the water supply;

- The canopy cover as an expression of the light conditions for the ground vegetation (Malmer et al., 1978; Persson, 1980; Dzwonko and Gawronski, 1994; Christensen and Emborg, 1996);
- The number of species in the ground vegetation in spring and in summer, in order to record both the spring and the summer aspects of the vegetation and therefore the complete species composition.

2.3. Data analysis

In order to determine and describe the relations between the number of species and the site parameters just enumerated a correlation matrix for these parameters was calculated (Spearman rank correlation; statistic program SPSS). All data additionaly were evaluated by means of a PCA (statistic program SPSS) and, with reference to the syntaxa *Alno-Ulmion*, *F. sylvaticae* and *Q. roboris* and with reference to the number of species in the sampling sites, the individual sampling sites were presented in an ecogram with the aid of an ordination.

The nomenclature of phanerogams follows Rothmaler et al. (1986), of bryophytes Smith (1980) and of lichens Wirth (1980).

3. Results

As a basis for the evaluation of the correlation matrices (Tables 2–4) in Table 1 an overview is given to the mean values and the range found for each variable investigated for the three forest communities. As regards the moist forests (alder-ash forests of the *Alno-Ulmion*), the correlation matrix (Table 2) shows that a high species richness in the ground vegetation is correlated mainly with the mean Ellenberg indicator value for soil moisture. This means that the total number of species in the ground vegetation of moist forests increases as the soil moisture increases. The number of species is only weakly (the lime content in the subsoil) or not at all correlated with other site parameters that were studied. The nutrient and light supplies thus have little or no influence on the species richness.

In meso- to eutrophic beech forests (*F. sylvaticae*), the species number has the closest positive correlation

Table 1
Mean and range values for the parameters investigated for the three forest communities

	Forest communities								
	Moist forests with alder and ash (*Alno-Ulmion*)			Eu- and mesotrophic beech forests (*Fagion*)			Acidophytic beech and mixed beech–oak forests (*Querc.*)		
	$n^a = 33$			$n^a = 41$			$n^a = 17$		
	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
Number of species (ground vegetation)	38	50.3	65	20	29.8	41	23	27.1	37
Thickness of the A_h-horizon (cm)	24.0	33.9	57.0	5.0	17.0	38.0	0.0	2.2	11.0
S-value (mval/100 cm^3)	7.7	17.6	51.8	0.1	5.8	17.2	0.0	1.6	3.9
Base saturation (%)	31.0	84.5	100.0	0.5	40.2	100.0	0.0	26.7	100.0
C/N-ratio	10.9	13.2	16.2	11.8	19.1	33.7	14.5	24.7	35.5
pH (H_2O)	4.5	5.5	7.0	2.6	3.8	5.8	2.7	3.3	4.2
Mean indicator value for soil moisture	5.5	6.6	7.5	4.8	5.4	5.8	4.9	5.4	6.5
Canopy cover (%)	50.0	73.5	95.0	70.0	84.4	98.0	60.0	77.1	90.0
Lime content in the subsoil (weight %)	0.0	9.6	28.0	–	–	–	–	–	–
Thickness of the G_r-horizon (cm)	9.0	99.5	147.0	–	–	–	–	–	–
Thickness of the organic (O) layer (cm)	–	–	–	–	–	–	3.5	9.1	29.0
Thickness of the A_e-horizon (cm)	–	–	–	–	–	–	0.0	5.9	19.0
Thickness of the B_{hs}-horizon (cm)	–	–	–	–	–	–	0.0	42.2	117.0

A "–" is given, when the parameter was not investigated in a forest community.
[a] Number of site samples (n).

Table 2
Spearman rank correlation between different environmental factors and the species richness of the ground vegetation for stands of the *Alno-Ulmion* ($n = 33$)

	A_h	*S*	BS	CN	pH	LC	G_r	mM	CC
S	−0.13								
BS	−0.21	0.08							
CN	−0.06	−0.06	0.12						
pH	−0.19	0.44[a]	0.64[a]	0.18					
LC	0.05	0.48[a]	−0.07	−0.06	0.19				
G_r	0.09	0.39[b]	0.16	−0.32	0.14	0.27			
mM	−0.12	0.16	−0.13	−0.11	0.05	−0.16	0.19		
CC	0.25	−0.60[a]	−0.18	−0.08	−0.52[a]	−0.49[a]	−0.24	0.11	
ns	−0.10	0.06	−0.01	−0.15	0.10	**−0.40**[b]	0.08	**0.67**[a]	0.17

A_h: thickness of the A_h-horizon; *S*: *S*-value; BS: base saturation; CN: C/N-ratio; pH: pH (H_2O)-value; LC: lime content in the subsoil; G_r: thickness of the G_r-horizon; mM: mean Ellenberg indicator value for moisture; ns: number of species (ground vegetation) in the vegetation relevé (100 m^2); CC: canopy cover; important values in bold type.

[a] Correlation significant on the level of 0.01.

[b] Correlation significant on the level of 0.05.

with the pH-value and the base supply, but also with the thickness of the mineral humus horizon and the soil moisture (Table 3). The light supply has only little influence on the species richness in the ground vegetation.

In the acidophytic beech- and mixed beech–oak forests (*Q. roboris*), the number of species in the ground vegetation is closely correlated with the soil moisture, with the light conditions and with the thickness of the litter layer (Table 4). The number of species shows no significant correlation with any of the soil chemistry parameters that characterise the base and nutrient supply of the plants.

Table 3
Spearman rank correlation between different environmental factors and the species richness of the ground vegetation for stands of the *F. sylvaticae* ($n = 41$)

	A_h	*S*	BS	CN	pH	mM	CC
S	0.62[a]						
BS	0.56[a]	0.87[a]					
CN	−0.61[a]	−0.74[a]	−0.74[a]				
pH	0.68[a]	0.88[a]	0.82[a]	−0.71[a]			
mM	0.53[a]	0.58[a]	0.61[a]	−0.69[a]	0.57[a]		
CC	0.14	−0.04	−0.02	−0.01	−0.02	−0.21	
ns	**0.78**[a]	**0.75**[a]	**0.69**[a]	**−0.69**[a]	**0.79**[a]	**0.63**[a]	0.13

A_h: thickness of the A_h-horizon; *S*: *S*-value; BS: base saturation; CN: C/N-ratio; pH: pH (H_2O)-value; mM: mean Ellenberg indicator value for moisture; ns: number of species (ground vegetation) in the vegetation relevé (100 m^2), CC: canopy cover; important values in bold type.

[a] Correlation significant on the level of 0.01.

In the Figs. 2–4, the site and structural parameters investigated within the framework of the present study have been evaluated by means of a PCA and the individual sample sites (separated into the syntaxa *Alno-Ulmion*, *F. sylvaticae* and *Q. roboris* and with information on the number of species at the sample sites) are presented in an ordination diagram. Of the three ordination axes that were calculated (Tables 5–7), only the two axes are shown in these diagrams which gave the highest eigenvalues or which, in terms of the bivariate comparison described above, are characterised by features with which the number of species correlates maximally.

In the ordination diagram of the moist forests, the *x*-axis represents a base gradient (PCA axis 1) and the *y*-axis a moisture gradient (PCA axis 3; see Table 5). The two vegetation types that were examined (*Alnus-Fraxinus* forests and *Fraxinus* forests) differ clearly with regard to the soil moisture. It can also be recognised that stands on recent moraines have a more favourable base supply and the canopy is less closed compared with those on the ancient moraines. As is shown in Table 5, the number of species in the ground vegetation correlates significantly with the third PCA-axis ($r = 0.63$). This means that an increase in soil moisture leads to an increase in the number of species in the ground vegetation.

Table 4
Spearman rank correlation between different environmental factors and the species richness of the ground vegetation for stands of the *Q. roboris* ($n = 17$)

	O	A_h	A_e	B_{hs}	S	BS	CN	pH	mM	CC
A_h	−0.43									
A_e	0.76[a]	−0.58[b]								
B_{hs}	0.83[a]	−0.52[b]	0.91[a]							
S	−0.31	0.31	−0.31	−0.36						
BS	−0.23	0.14	−0.32	−0.47	0.79[a]					
CN	−0.70[a]	0.52[b]	−0.62[a]	−0.63[a]	0.27	−0.03				
pH	−0.13	−0.13	−0.12	−0.28	0.59[b]	0.89[a]	−0.18			
mM	0.49[b]	−0.53[b]	0.59[b]	0.52[b]	0.03	0.02	−0.44	0.03		
CC	−0.53[b]	0.17	−0.62[a]	−0.50[b]	−0.17	−0.04	0.18	0.02	−0.44	
ns	**0.55**[b]	−0.23	0.44	0.33	0.11	0.11	−0.25	0.13	**0.67**[a]	**−0.55**[b]

O: thickness of the organic layers (O_L, O_f, O_h); A_h: thickness of the A_h-horizon; A_e: thickness of the A_e-horizon; B_{hs}: thickness of the B_{hs}-horizon; S: S-value; BS: base saturation; CN: C/N-ratio; pH: pH (H_2O)-value; mM: mean Ellenberg indicator value for moisture; ns: number of species (ground vegetation) in the vegetation relevé (100 m^2); CC: canopy cover; important values in bold type.

[a] Correlation significant on the level of 0.01.

[b] Correlation significant on the level of 0.05.

The ordination of the *Fagion*-sites separates very clearly the eutrophic and mesotrophic beech forests (*Hordelymus–Fagus* and *Galium–Fagus* forests, respectively). The most important site factors in which these two vegetation types differ are the soil moisture, the nitrogen supply and the base supply. The *x*-axis (PCA axis 1) represents the base supply, whilst the *y*-axis (PCA axis 2) is an expression of the soil moisture

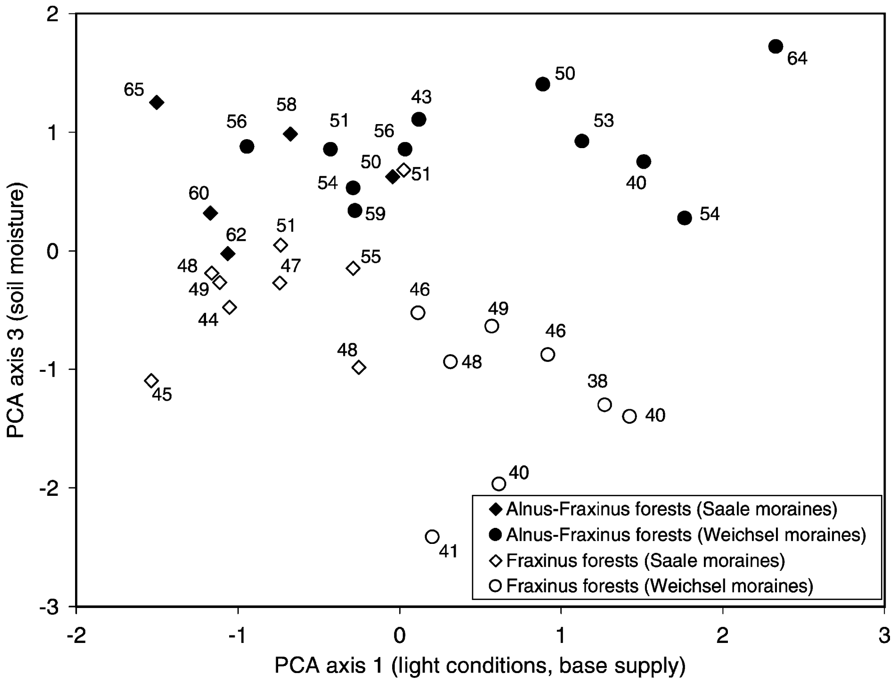

Fig. 2. PCA-ordination of stands of the *Alno-Ulmion* in northern Germany (Schleswig-Holstein). The numbers added to the plots give the number of species in the ground vegetation per 100 m^2 (size of a vegetation relevé). The number of species in the ground vegetation is closely correlated with PCA axis 3 ($r = 0.63$). Further explanation cf. text.

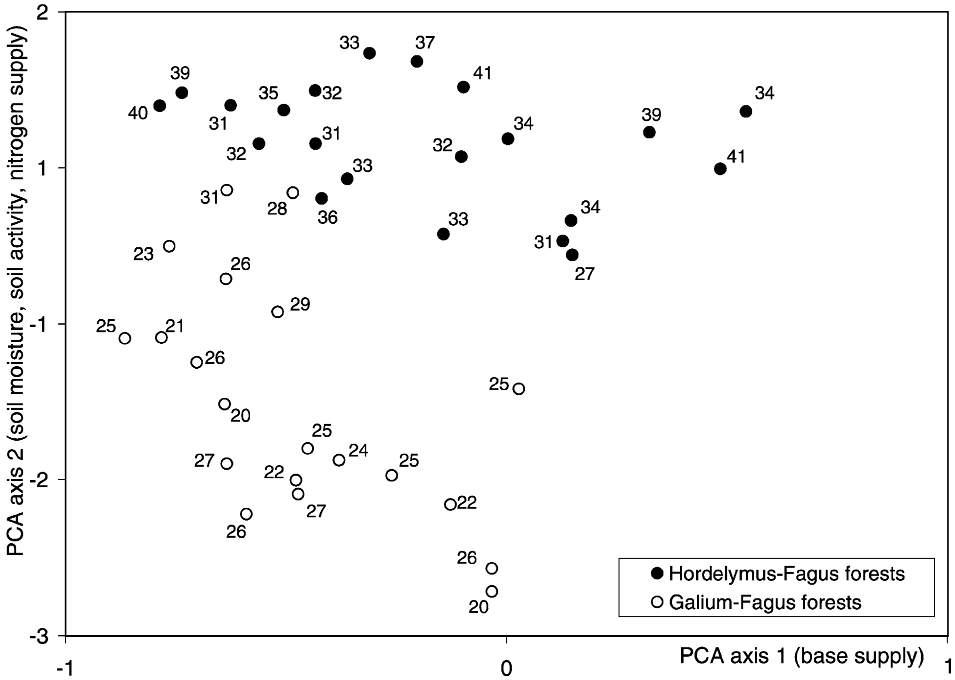

Fig. 3. PCA-ordination of stands of the *Fagion sylvaticae* in northern Germany (Schleswig-Holstein). The numbers added to the plots give the number of species in the ground vegetation per 100 m^2 (size of a vegetation relevé). The number of species in the ground vegetation is closely correlated with PCA axis 2 ($r = 0.80$). Further explanation cf. text.

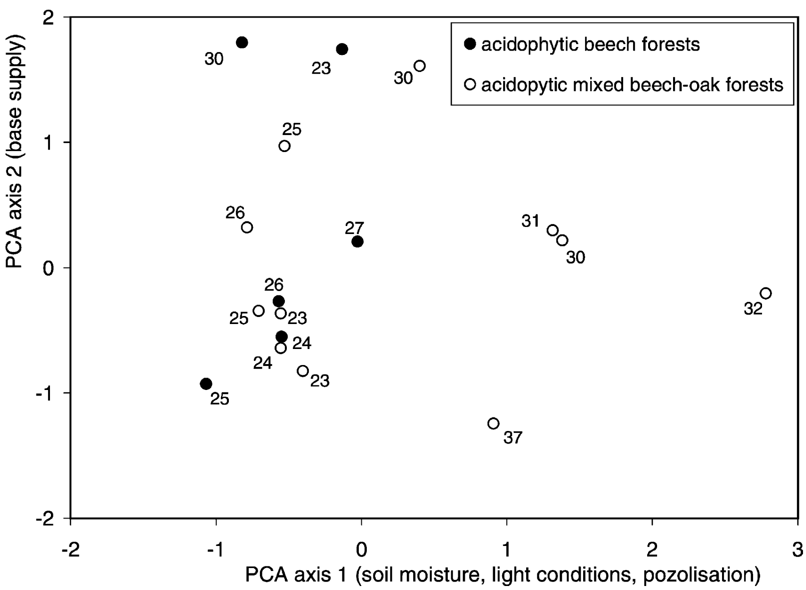

Fig. 4. PCA-ordination of stands of the *Q. roboris* in northern Germany (Schleswig-Holstein). The numbers added to the plots give the number of species in the ground vegetation per 100 m^2 (size of a vegetation relevé). The number of species in the ground vegetation is closely correlated with PCA axis 1 ($r = 0.69$). Further explanation cf. text.

Table 5
Correlation matrix of the PCA for stands of the *Alno-Ulmion* ($n = 33$)

	PCA axis 1	PCA axis 2	PCA axis 3
CC	**−0.79**	−0.25	−0.03
LC	**0.76**	−0.27	−0.31
S	**0.69**	0.05	0.41
pH	**0.56**	**0.58**	0.28
A_h	0.02	**−0.67**	0.10
BS	0.30	**0.61**	0.12
CN	−0.14	**0.59**	−0.29
mM	−0.14	0.01	**0.79**
G_r	0.32	−0.25	**0.67**
Eigenvalue	2.51	1.67	1.24
% of varianz	28	19	14
r species g.veg.	−0.26	0.11	**0.63**[a]

CC: canopy cover; LC: lime content in the subsoil; *S*: *S*-value; pH: pH (H_2O)-value; A_h: thickness of the A_h-horizon; BS: base saturation; CN: C/N-ratio; mM: mean Ellenberg indicator value for moisture; G_r: thickness of the G_r-horizon; r species g.veg.: Spearman rank correlation of the number of species in the ground vegetation with factor scores of the PCA axis; important values (>I0.5I) in bold type.

[a] Correlation significant on the level of 0.01.

and soil activity (thickness of the A_h-horizon, N-supply; see Table 6). The number of species in the ground vegetation correlates particularly closely with the PCA-axis 2 (moisture, soil activity; $r = 0.80$) but less closely with the PCA-axis 1 (base supply; $r = 0.32$; see Table 6).

Table 6
Correlation matrix of the PCA for stands of the *F. sylvaticae* ($n = 41$)

	PCA axis 1	PCA axis 2	PCA axis 3
pH	**0.91**	0.28	0.01
S	**0.90**	0.31	−0.05
BS	**0.84**	0.39	−0.06
mM	0.27	**0.88**	−0.24
CN	−0.47	**−0.77**	−0.08
A_h	0.48	**0.57**	0.40
CC	−0.07	−0.07	**0.96**
Eigenvalue	4.24	1.15	0.66
% of varianz	60	16	9
r species g.veg.	0.32[a]	**0.80**[b]	0.10

pH: pH (H_2O)-value; *S*: *S*-value; mM: mean Ellenberg indicator value for moisture; CN: C/N-ratio; A_h: thickness of the A_h-horizon; BS: base saturation; CC: canopy cover; r species g.veg.: Spearman rank correlation of the number of species in the ground vegetation with factor scores of the PCA axis; important values (>I0.5I) in bold type.

[a] Correlation significant on the level of 0.05.

[b] Correlation significant on the level of 0.01.

Table 7
Correlationmatrix of the PCA for stands of the *Q. roboris* ($n = 17$)

	PCA axis 1	PCA axis 2	PCA axis 3
mM	**0.89**	−0.01	−0.18
CC	**−0.87**	−0.06	−0.01
O	**0.85**	−0.05	−0.19
B_{hs}	**0.79**	−0.21	−0.48
A_e	**0.70**	−0.27	−0.44
BS	−0.13	**0.96**	0.20
pH	−0.10	**0.94**	−0.19
S	0.08	**0.85**	0.45
CN	−0.31	−0.08	**0.86**
A_h	−0.19	0.31	**0.82**
Eigenvalue	4.80	2.49	1.20
% of varianz	48	25	12
r species g.veg.	**0.69**[a]	0.02	−0.07

Mm: mean Ellenberg indicator value for moisture; CC: canopy cover; *O*: thickness of the organic layers (O_L, O_f, O_h); B_{hs}: thickness of the B_{hs}-horizon; A_e: thickness of the A_e-horizon; BS: base saturation; pH: pH (H_2O)-value; *S*: *S*-value; CN: C/N-ratio; A_h: thickness of the A_h-horizon; r species g.veg.: Spearman rank correlation of the number of species in the ground vegetation with factor scores of the PCA axis; important values (>I0.5I) in bold type.

[a] Correlation significant on the level of 0.01.

In the ordination diagram of stands of acidophytic beech and mixed beech–oak forests (*Q. roboris*), the PCA axis 1 represents the soil moisture, the degree of podzolisation and the light conditions for the ground vegetation, whilst the PCA axis 2 can be interpreted as an expression of the base supply (Table 7). The species richness of the ground vegetation in these stands is closely correlated with the PCA axis 1 ($r = 0.69$), and thus increases with soil moisture, degree of podzolisation and improved light conditions.

4. Discussion

The analysis of alder-ash stands (alliance *Alno-Ulmion*) shows that the species richness of the ground vegetation increases with increasing soil moisture. This can be explained by the fact that the species richness of moist forests is to a considerable extent due to the high proportion of moisture-loving or moisture-tolerant perennials which are also characteristic for moist meadows, but have their natural habitats in forests (e.g. *Crepis paludosa*, *Filipendula ulmaria*, *Ranunculus* *repens*, *Angelica sylvestris*, *Cirsium palustre*). In addition, species of reeds develop on the wettest soils and complement the species composition of the ground vegetation (e.g. *Valeriana procurrens*, *Scutellaria galericulata*, *Lycopus europaeus*). There may also be an additional water supply for the ground vegetation, mainly in forests on moraines of the Saale glacial period, originating from water seeping from small springs located in the microrelief of the soil surface. As a result, spring vegetation grows in small patches between other species of the ground vegetation (e.g. *Pellia epiphylla*, *Cardamine flexuosa*, *Chrysosplenium oppositifolium*). In moist forests, therefore, a certain level of soil moisture is not only a prerequisite for the occurrence of many species in the ground vegetation (Christensen and Emborg, 1996; Pausas and Austin, 2001) but is also responsible for a site heterogeneity that allows adapted mosses and phanerogams to develop (Standovár, 1998; Halpern and Spies, 1995). Soil moisture is a decisive environmental factor that often masks the influence of other factors on the species composition of forests, especially in the lowlands of Central Europe on soils that developed from moraines of the last and penultimate glacial periods (Graae and Heskjær, 1997). According to the studies by Davis et al. (1998), the smaller the net supply of water (gross water supply minus the demand by the herbaceous vegetation), the greater is the competitive pressure between species and individuals of the ground vegetation in forests. This may also explain why the total number of species in the field layer of moist forests rises with increasing moisture. These circumstances show that the water supply and soil moisture are the most determining site factors in moist forests and that other factors, such as the light supply or trophic differences, are of subordinate importance for species richness in the ground vegetation. Moist forests, with an average of 55 species per 100 m^2, are among the most species-rich plant communities in the north German lowlands.

In meso- to eutrophic beech forests (alliance *Fagion*), there is not only a high base supply but also at the same time a high activity level among soil organisms and a high soil moisture level that correlates with the high numbers of species in the ground vegetation (Tables 3 and 6). It should be emphasised that water and nutrient supplies as well as the pH-value are closely correlated, especially in the beech forests on moraine sites (Table 3). The majority of the mineral nutrients are released from the marly till with the ground water and are transported to the plant roots; at the same time, the mineralisation processes require a certain level of soil moisture and are assisted by high pH-values (Gönnert, 1989). The influence and the effect of soil moisture on the species composition thus has to be evaluated differently in beech forests from moist forests, where there is a fundamentally greater nutrient supply and an invariably high N-supply resulting from the leaf input of *A. glutinosa* which lives symbiotically with N-fixers. A close correlation between the soil pH-value and the species richness of the ground vegetation, especially in beech forests, has been confirmed by the investigations of other authors (Brunet et al., 1996, 1997a, b; Schmidt, 1999; Leuschner, 1999). This finding is closely linked with the phenomenon that the majority of beech forest species are categorised as NO_3^--plants and are therefore bound to sites where nitrate is the principal source of nitrogen (Ellenberg, 1996). These species are to be found on soils where nitrifiers are active due to a weakly acidic to neutral pH-value of the soil. According to Pausas and Austin (2001), calcium in particular is the most important exchangeable cation in the soil that influences soil pH-value and controls the availability of other nutrients.

The high number of species in beech forests with base rich and moist habitats may be directly connected with the thickness of the organic humus layers. Some species (such as *Ranunculus ficaria* or *Poa trivialis*) are unable to penetrate thick litter layers, or their seeds need to be in contact with the mineral soil to germinate (e.g. *Anemone nemorosa*; Sydes and Grimes, 1981a,b; Packham et al., 1992; Eriksson, 1995; Holdegger, 1996; Graae and Heskjær, 1997). As many beech forest species have adapted to unfavourable light conditions or complete their development cycles before the canopy is fully closed, the light factor in beech forests has virtually no influence on the number of species in the ground vegetation. This presupposes that the number of non-woodland species, for example the indicators of disturbance through silvicultural treatment, is low in such stands. Leuschner (1999) came to similar conclusions in an analysis of beech stands in central and north-west Germany, during which he also established a close negative correlation between the number of species and the density of fine roots from the tree layer in the humus horizons.

In acidophytic beech- and mixed beech–oak forests (order *Q. roboris*), the number of species in the ground vegetation is closely correlated positively with the soil moisture and negatively with the light supply. For a correct interpretation of these results, it is important that the site parameters too (degree of podzolisation, thickness of the humus layer, soil moisture, light conditions for the ground vegetation) are closely positively or negatively correlated respectively (Table 4). The more moist or podzolised are the forest soils (e.g. gley-podzol), the more weakly competitive *F. sylvatica* becomes, and the proportion of *Quercus* species (*Q. robur*, *Q. petraea*) in the tree layer increases. A higher proportion of *Quercus* species also means that the canopy cover is light, as these two *Quercus* species come into leaf late and form only a thin crown density, and it also means that there is a light regime favourable for the ground vegetation (see Heinken, 1995; Pallas, 2000). As Tables 4 and 7 demonstrate, this factor has a considerable influence on the species number of the ground vegetation in acidophytic beech and mixed beech–oak forests. Many characteristic species of acidophytic mixed beech–oak forests are photophilous. They die out when the crown density increases, that is to say beneath the strongly shading canopy of beech tree (see Brunet et al., 1997a). In addition, acidophytic beech forests have hardly any species that are absent in acidophytic mixed beech–oak forests, so that these beech forests are on average distinctly poorer in species than are the mixed beech–oak forests (Härdtle, 1995; Brunet et al., 1996). Trophic differences among forest communities of the order *Q. roboris* have absolutely no influence on the species richness of the ground vegetation. All the species of these forest communities are adapted to acid soil conditions and because of their preferred form of nitrogen can be termed as ammonia plants. In this regard the ordination diagram of the *Quercetalia* forest sites (Fig. 4) confirms the results of the investigations of other authors, according to which acidophytic beech forests differ little or not at all in their base and nitrogen supplies compared to acidophytic mixed beech–oak forests, so long as the humus layers are not disturbed or removed (see Gönnert, 1989; Leuschner et al., 1993; Heinken, 1995; Härdtle et al., 1996; Leuschner, 1999).

The analysis shows that, in the forest communities that have been examined, the natural factors at the sites affect the species richness of the ground vegetation quite differently. The soil moisture, the nutrient supply and the light supply have to be evaluated very differently for their effect on the number of species of the ground vegetation and in respect of the distinguishing site features of the individual forest communities. These findings confirm the results of investigations of Leuschner (1999) and Brosofske et al. (2001) into the dependence of the number of species in the forest ground vegetation on various soil conditions. It should be borne in mind that such comparisons are only possible when other factors that may influence the number of species, such as silvicultural management or the age of a forest site, can in the main be excluded. If the relation between species richness and environmental factors like soil conditions is analysed not with reference to individual forest communities but rather with reference to the totality of Central European forests, relationships may be found which are not helpful for an explanation of the species richness of a certain forest community and thus they are only of restricted usefulness for appropriate recommendations for forest management.

5. Conclusions for silvicultural management

Various conclusions can be drawn from the results described here concerning the influence of silvicultural measures on deciduous forest ecosystems that have been investigated.

In moist forests, drainage leads in the first place to a clear loss of the species characteristic of those habitats, whereas the removal of individual tree trunks and the resulting increase of light through the canopy has hardly any effect on the number of species in the ground vegetation. In this context it has to be considered that the number of species in the ground vegetation could increase as a consequence of silvicultural interventions, but then as a result of the development of new microstructures and small habitats such as logging trails, soil compaction, tiny bodies of water in tyre tracks (Barkham, 1992; Brunet et al., 1996; Christensen and Emborg, 1996; Nagaike et al., 1999; Schmidt, 1998; Oheimb et al., 1999; Oheimb, 2002).

Even in meso- to eutrophic beech forests, a moderate thinning of the canopy by the felling of trees only slightly alters the number of ground species typical for this habitat. On the other hand, measures that lead to an alteration of the trophic state, and especially of the base supply (for example, adding lime to the soil) have a much more serious effect on the species composition and thus the number of species in the ground vegetation.

In acidophytic beech- and mixed beech–oak forests, a thinning of the canopy cover by the removal of trees has particularly obvious effects on the species number and species composition of the ground vegetation, as most of the acid tolerant species of these forest communities are heliophilous and thus profit from larger gaps in the canopy. Many ground species of herbaceous plants and mosses of mixed beech–oak forests will disappear when the proportion of *F. sylvatica* in the tree layer increases in the course of succession or as a result of silvicultural improvements.

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