

# Impact of tree species on nutrient and light availability: evidence from a permanent plot study of old-field succession

Michaela Dölle · Wolfgang Schmidt

Received: 23 July 2008 / Accepted: 7 November 2008 / Published online: 14 December 2008  
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**Abstract** This paper compares vegetation composition, light availability, carbon and nutrient pools and Ellenberg indicator values among four old-field successional permanent plots that have received an initial treatment (ploughing, herbicide or sterilisation) prior to being left undisturbed in 1969, a second set of six plots received additional treatments (continued ploughing or mulching until 1982). On all plots species rich pioneer forests developed. Vegetation still varies among plots with different initial treatments: Sterilised plots can be distinguished from the others by dominance of *Betula pendula*, ploughed plots by *Fraxinus excelsior*, whereas herbicide-treated plots are intermediate with proportions of both species. By affecting light availability at the ground, tree species in turn influences ground vegetation and soil properties. Light availability turned out to be the dominant factor determining the composition of the vegetation in old-field succession.

**Keywords** *Betula pendula* · *Fraxinus excelsior* · Initial floristic composition · Photosynthetic active radiation · Resource-ratio-hypothesis · Soil organic carbon

## Introduction

Regular soil disturbance by ploughing and biomass removal are main characteristics of arable land use and hinder the accumulation of organic matter and nutrients in the soil (Tiessen et al. 1982). When land is no longer used for cultivation and allowed to revert to natural vegetation, ecosystem properties such as soil chemical parameters and light conditions may change significantly. Vegetation and environmental factors of abandoned old-fields in particular often change radically within relatively short time periods (Schmidt 1981; Pickett 1982).

On most sites in temperate Europe succession leads to the development of forest ecosystems. With changing structure of the vegetation, light availability to the ground flora decreases and since plant biomass is no longer removed, nutrients and carbon tend to accumulate. Later on, regrowing temperate forests develop surface organic horizons which modify the microclimate at the soil surface and the physical, chemical and biological features of the soil. The pool of nutrients contained in plant biomass increases during succession as plant biomass accumulates. Accumulation of nitrogen in the ecosystem is probably one of the main driving variables that determine the rate of succession (Tilman 1987). Since the input of nitrogen by atmospheric deposition can be at some places extremely high, its effect on natural plant communities may be crucial (Berendse 1990; Bobbink et al. 1998).

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M. Dölle (✉) · W. Schmidt  
Department of Silviculture and Forest Ecology of the  
Temperate Zones, Georg-August University Göttingen,  
Büsgenweg 1, 37077 Göttingen, Germany  
e-mail: mdoelle@gwdg.de

W. Schmidt  
e-mail: wschmid1@gwdg.de

Determining the factors that drive successional changes in ecosystems is difficult since various interacting factors influence the course of succession. It is also difficult to predict the direction of the development of a successional sere. In order to predict long-term changes in vegetation composition and structure during secondary succession, knowledge on the changes of nitrogen, other nutrients and carbon, as well as light availability and water supply in the soil are necessary. In general, successional changes in abandoned fields have been interpreted in terms of competitive ability mediated by resource availability, particularly light and nutrients (Tilman 1985, 1994; Gleeson and Tilman 1990). Tilman's (1985) formulation of the resource ratio hypothesis focuses on two plant resources: light availability at the soil surface and nutrient concentrations in the soil. Tilman (1985, 1988) viewed successional changes as a gradient from high availability of light and resource-poor soils in the beginning, to nutrient-rich soils and low availability of light later in succession.

Plants and resources interact in dynamic ways. Vegetation structure can exert large influences on the light transmittance (Binkley and Giardina 1998; Richter et al. 1994; Knops et al. 2002), as well as on water and nutrients in ecosystems (Leuschner 2002). Several authors showed that dominating tree species in forests can greatly impact soil properties (Binkley and Giardina 1998; Knops et al. 2002; Zhong and Makeschin 2004) or that different dominating plant species may have significant effects on environmental conditions, e.g. understory light supply (Bazzaz 1990; Barkman 1992; Jennings et al. 1999; Porté et al. 2004; Barbier et al. 2008), rate of nitrogen supply (Berendse 1990) or C/N ratio and N-mineralisation rate (Miles and Young 1980, Hagen-Thorn et al. 2004). Moreover, single plant species can act as ecosystem engineers who have significant effects on species diversity and ecosystem function (Wedin and Tilman 1990; Mitchell et al. 2007; Schmidt 2007).

Additionally, cultural and tillage practices before abandonment have marked consequences on overall vegetation development (Bonet 2004), and agricultural land use intensity and site history may have irreversible effects on subsequent biodiversity (Bossuyt et al. 1999; Dupouey et al. 2002). Successions may also differ due to varying climate conditions or diaspore supply in the initial stage (Schmidt 1981; 1983; Peet 1992). The initial floristic composition is a

significant factor in old-field succession, since dominants of later stages usually arrive soon after abandonment and early dominants substantially influence the further vegetation development (Egler 1954).

In the present study, we investigated long-term experimental plots of undisturbed old-field succession for 36 and 22 years. The study site in the Experimental Botanical Garden of Göttingen University was started in 1968 on a former arable field. Since that time four plots were left undisturbed to revert to natural vegetation through succession, and six additional plots were left abandoned in 1982 undergoing either experimental ploughing or mulching once per year up to this time (Schmidt 1993). The plots are located close together; hence, site-specific influences on the process of secondary succession such as soil type, climatic conditions and surrounding vegetation are basically the same. Such long-term permanent plot studies can offer, in contrast to short-term investigations or chronosequence studies, valuable insights into changes in ecosystem properties during succession.

We addressed the following questions: (1) do our findings support the resource ratio hypothesis of Tilman (1985) and if so (2) how quickly do resources change over time? (3) do our findings confirm the initial floristic composition model by Egler (1954) and thus (4) does the initial treatment of the plots, through differences in plant species composition, have lasting effects on nutrient supply, soil organic matter or light availability?

## Materials and methods

### Study site

All plots of the current study are part of an experiment located in the Experimental Botanical Garden of Göttingen University, Lower Saxony, Germany (180 m a.s.l., 51°34'N, 9°57'E; mean annual temperature: 8.5°C; average annual rainfall: 635 mm). Initiated by Heinz Ellenberg, the experiment was set up on a former arable field cultivated until 1968 on deep, calcareous and fertile soil (alluvial loamy brown earth). Regional forest vegetation is dominated by *Fagus sylvatica* (Fagion sylvaticae) which is the natural vegetation type (Bohn et al. 2003). The surrounding landscape may be characterised by a

mixture of arable fields, grasslands, ruderal communities and forests with a high diversity in mature trees as potential seed dispenser in close vicinity. A more detailed description of the study site and methods is given in Schmidt (1981; 1983; 1993).

Vegetation development and associated successional changes of 10 permanent plots were evaluated: four plots of undisturbed succession since 1969 ( $L_{S1}$ ,  $L_{S2}$ ,  $L_{H1}$ ,  $L_{C1}$ ) and six plots of undisturbed succession since 1983 ( $S_{H1-3}$ ,  $S_{C1-3}$ ), herein after referred to as short and long sere (Table 1). For vegetation sampling the plots are each subdivided into three subplots. The entire study site was farmed as crop field (wheat and sugar beet, intensive conventionally farmed) up to and including 1967, so that the long sere meets the conditions of an abandoned agricultural field. The history of the short sere differed by experimental treatment with soil disturbance once per year up to and including 1982 for the plots  $S_{H1-2}$  and  $S_{C1-2}$ , and mulching once per year for the plots  $S_{H3}$  and  $S_{C3}$  (Table 1). The plots differ in their treatment in the beginning of the experiment (1968): ploughing ( $L_{C1}$ ,  $S_{C1-2}$ ), herbicide treatment ( $L_{H1}$ ,  $S_{H1-2}$ ) or sterilised by heating ( $L_{S1}$ ,  $L_{S2}$ ) (Schmidt 1981).

### Vegetation sampling

Percentage cover of all vascular plant species on the whole subplot area (25–100 m<sup>2</sup>) was surveyed twice per year in the beginning (1969–1987) and once per year thereafter (since trees began to dominate). From 1968 until 1993, vegetation was recorded annually, afterwards vegetation relevés were conducted in 1995, 1999, 2003, 2004 and 2005. Species names for

vascular plants follow Wisskirchen and Haeupler (1998).

### Light measurement

In summer 2005, on overcast days with homogeneous diffuse light conditions, relative irradiance was measured directly in 0.5, 2 and 5-m height of the stands with PAR-sensors, type LI-190 (Licor, Nebraska, USA) fixed on a telescope bar. Nine spatial evenly distributed recordings of the absolute light intensity were done in each subplot and simultaneously on a nearby field, the open field situation. From each measurement the ratio of the absolute light intensity in the stands and in the open field was computed. For further evaluation, mean values of photosynthetically active radiation (PAR) and standard error ( $\pm$ SE) per subplot were calculated.

### Soil chemical properties

In 1969, 1973, 1977, 1989 and 2004 three randomly selected soil samples per subplot were removed to a mineral soil depth of 30 cm using an 8-cm-diameter soil auger. The soil cores were divided into 0–10 cm, 10–20 cm and 20–30 cm sections. For the year 1969 only values for the depth 0–10 cm are available. Since humus accumulation proceeded with the successional change from open vegetation to pioneer forests, samples of the litter layer (OL) were taken by a 25 × 25 cm frame in the year 2004. Soil samples of each depth per subplot were pooled. The soil was sieved with a 2-mm riddle and stones and any living plant material were removed. Samples were dried at

**Table 1** Summary of the 10 permanent plots of undisturbed old-field succession, their plot size, their assignment to the time since abandonment and resultant sere category, their initial

treatment and treatment until 1982 and group membership based on indicating tree species

Plot	Plot size (m <sup>2</sup> )	Abandoned since	Sere	Initial treatment in 1968	Treatment until 1982	Group
$L_{S1}$ , $L_{S2}$	200	1969	Long-term	Sterilisation by heating	–	Betula
$L_{H1}$	200			Herbicide treatment	–	Intermediate
$L_{C1}$	150			Ploughing (control)	–	Fraxinus
$S_{H1}$ , $S_{H2}$	200	1982	Short-term	Herbicide treatment	Ploughing	Intermediate
$S_{H3}$	200			Herbicide treatment	Mulching	Intermediate
$S_{C1}$ , $S_{C2}$	150			Ploughing (control)	Ploughing	Fraxinus
$S_{C3}$	150			Ploughing (control)	Mulching	Fraxinus

Plot letter codes—sere: *L* long, *S* short, initial treatment: *S* sterilised, *H* herbicide, *C* control (ploughing), numbers: 1+2 only ploughing, 3 mulching between 1969 and 1982

65°C (organic layer) and 105°C (mineral soil), respectively, and finely ground with a grinder. All other measurements were determined using fresh samples. Samples were analysed for  $\text{pH}_{(\text{H}_2\text{O})}$ , total carbon (C), organic C (SOC), nitrogen (N) and phosphorus (P) content. The pH values were measured with a glass electrode; concentrations of total C and N in the soil were determined by combustion (C/N analyzer, Carlo Erba Elemental Analyser). The total P was determined colorimetrically and the  $\text{CaCO}_3$  content according to Scheibler (Schlichting et al. 1995).

### Data analysis

To select the most influencing parameters, the correlation structure of the analysed soil chemical parameters, the vegetation structure and diversity, and the selected Ellenberg indicator values (weighted and unweighted) were analysed through detrended correspondence analysis (DCA) and bivariate Pearson correlations based on the cover values of the plant species (271 species) in the years where the soil properties were analysed. Since the coverage of a species is not only dependent on the site conditions but might be a specific characteristic of a certain species, the data were transformed by  $y = x^{0.25}$  to minimise differences. Axis 2 of the DCA was highly significant ( $P \leq 0.001$ ) correlated with the initial treatment of the plots ( $r = 0.717$ ). Therefore, the effect of the initial treatment on current species composition was evaluated by a second DCA of all subplot data (at this point log-transformed cover values) 36 years after abandonment for the long sere and 22 years after abandonment for the short sere. All species in all layers (128) and different environmental parameters were correlated with the ordination axes. In order to identify differences in plant species composition between the different treated plots, significant indicator species were detected by indicator species analysis (ISA). For evaluation of the current vegetation composition on the plots, according to the results of the second DCA and ISA, the initially different treated plots (ploughing, herbicide or sterilisation) were pooled together (Table 1).

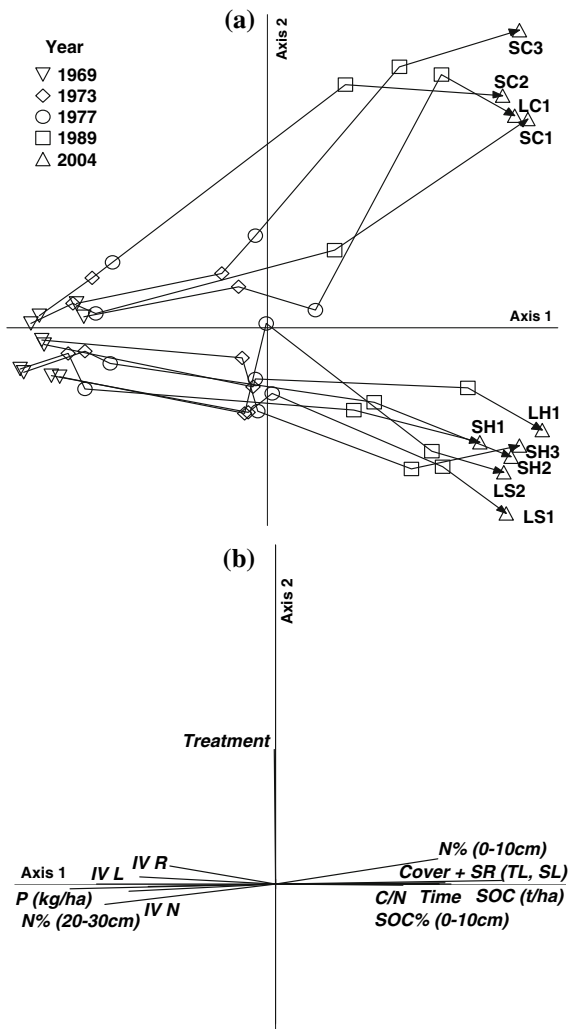
Mean Ellenberg indicator values for light, nitrogen and soil reaction (Ellenberg et al. 2001) were evaluated on the basis of cover values and presence-absence data. The variability of the time since

abandonment for the selected variables and of the different initial treatments was, if the data met the assumptions, assessed through one-way ANOVA with post hoc Scheffé-test. If the assumption of normal distribution and homogeneous variances were not fulfilled, even after log-transformation, data were tested by Kruskal–Wallis ANOVA with post hoc Mann–Whitney U-test. All statistical analyses were performed using STATISTICA 6.0 (Anonymous 1998); the ordination and correlation analyses, as well as indicator species analyses with PC Ord 5.12 (McCune and Mefford 1999). The following significance levels were used for all statistics: \*\*\*  $P < 0.001$ ; \*\*  $P < 0.01$ ; \*  $P < 0.05$ ; n.s. = not significant ( $P \geq 0.05$ ).

## Results

### Successional change

The DCA of the successional change grouped the plots along the first axis explaining 83% of the total variance and being highly significant ( $P \leq 0.001$ ) and positively correlated with the time since abandonment ( $r = 0.928$ ). A close relationship was revealed between the floristic gradient of the successional change and the changes in soil chemical properties (Fig. 1; Table 2). There was a highly significant positive correlation with the first axis of the DCA for the total amount of soil organic carbon (SOC) which increased significantly with successional age. The total nitrogen content remained almost stable in the first 10 years of abandonment, and then increased in the top 10 cm of the soil but decreased in the 10–30 cm soil. Major changes occurred between the ninth and 21st year of abandonment with an average increase over all plots of  $2.60 \text{ g N m}^{-2} \text{ year}^{-1}$  in the top 10 cm and an average decrease of  $2.55 \text{ g N m}^{-2} \text{ year}^{-1}$  in the lower soil (10–30 cm). The changes slowed down within the 22nd and 36th year of abandonment with an increase of  $1.96 \text{ g N m}^{-2} \text{ year}^{-1}$  in the top 10 cm and a decrease of  $1.88 \text{ g N m}^{-2} \text{ year}^{-1}$ . The total nitrogen pool remained stable during succession. The C/N ratio at all soil depths increased significantly with succession. The supply of phosphorus showed no significant trend in the top 10 cm of the soil, but decreased drastically in 10–30 cm soil depth,



**Fig. 1** **a** DCA of the vegetation relevés (all layers) in 1969, 1973, 1977, 1989 and 2004 of the 10 permanent plots of undisturbed old-field succession (length of gradient Axis 1: 4.87, Axis 2: 2.00;  $r^2$  Axis 1: 0.830, Axis 2: 0.026). Label points of the same plot are connected by successional vectors; serif end points are indicated by plot labels. **b** Correlation matrix of different environmental parameters with the ordination axes. Pearson  $r$  of all highly significant ( $P \leq 0.001$ ) correlated parameters ( $r \geq 0.6$ ) with Axis 1: Time (since abandonment) = 0.928, cover = 0.804 and richness (SR) = 0.782 of tree layer (TL), cover = 0.790 and richness = 0.913 of shrub layer (SL), soil organic carbon (SOC) (t/ha) = 0.819, SOC% (0–10 cm) = 0.742, nitrogen concentration (N%): in 0–10 cm = 0.787, in 20–30 cm = -0.752, C/N = 0.700, P (kg/ha) = -0.808; weighted Ellenberg indicator values: nitrogen (IV N) = -0.697, light (IV L) = -0.607, soil reaction (IV R) = -0.718, and with Axis 2: initial treatment = 0.717

resulting in a significant decrease in the total phosphorus supply. There were no clear changes in the pH values during succession.

The Ellenberg indicator values for light, nitrogen and soil reaction of the herb layers showed significant negative correlations with the time since abandonment (Fig. 1). Both weighted and unweighted indicator values for light and nitrogen significantly decreased during succession, whereas for soil reaction only the weighted evaluation showed a weak decreasing trend (Fig. 2). The weighted and unweighted values of the Ellenberg indicator values for light, nitrogen and soil reaction became more similar with increasing time since abandonment.

### Influence of the initial treatment on current species composition

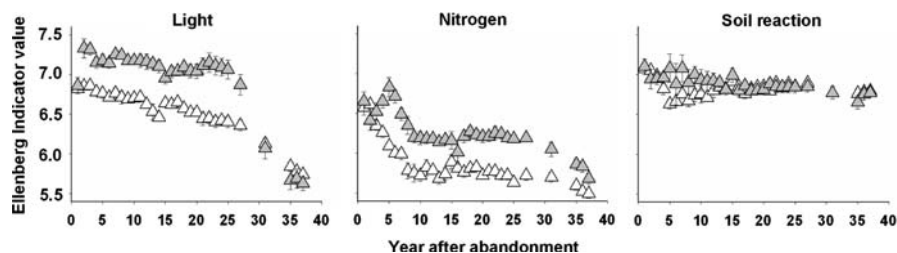
The second DCA of the current species composition grouped the plots along the first axis explaining 60% of the total variance, separating the plots according to their initial treatment in the beginning of the experiment. The axis 1 of the DCA of the current vegetation composition was highly significant ( $P \leq 0.001$ ) correlated with the coverage of *F. excelsior* ( $r = 0.789$ ) and *Betula pendula* ( $r = -0.868$ ), PAR-irradiance ( $r = -0.831$ ) and the C/N ratio of the humus layer ( $r = -0.791$ ) and of the mineral soil ( $r = -0.729$ ). The most intensively treated plots ( $L_{S1}$ ,  $L_{S2}$ : sterilised by heating) are now dominated by *B. pendula* in tree layer and have the highest PAR transmittance to the ground (Fig. 3; Table 5). In contrast, the control plots ( $SC_{1-3}$ ,  $LC_1$ : ploughing) are distinguished from the other plots by a high frequency of *F. excelsior* in the tree layer as indicating tree species for this group and significant lowest PAR-transmittance to the ground (Table 3; Fig. 3). The herbicide-treated plots ( $SH_{1-3}$ ,  $L_{H1}$ ) form an intermediate group with no certain tree species indicating this group (Table 3).

This gradient is also evident in the indicator species analyses (ISA) of the current vegetation composition (Table 3). In the *Betula* group initially sterilised by heating there is a high amount of nanophanerophytes with an Ellenberg indicator value for light of 6 (between semi-shade and partial-shade plants) or 7 (plants generally in well-lit place, but also occurring in partial shade). *Quercus robur* as late successional tree species in the herb layer is characteristic of the *Betula* group. The *Fraxinus* group, with lowest intensity of the initial treatment, had a high amount of indicator species with light indicator value of 4 (between shade and semi-shade plants).

**Table 2** Mean soil chemical parameter in 0–10, 10–20 and 20–30 cm soil depth in the years 1969 (only for 0–10 cm soil depth), 1973, 1977, 1989 and 2004 for the 10 plots (both seres estimated together) of undisturbed old-field succession

Parameter	Depth (cm)	H	1969	1973	1977	1989	2004
pH (H <sub>2</sub> O)	OL	–	–	–	–	–	8.0
	0–10	56.1***	7.8 a	7.8 a	7.6 b	7.8 a	7.6 b
	10–20	42.3***	–	7.8 a	7.6 b	7.9 a	7.6 b
	20–30	47.0***	–	7.8 a	7.6 b	7.9 a	7.7 b
SOC (t/ha)	OL	–	–	–	–	–	2.6
	0–10	85.5***	13.8 a	11.7 b	14.9 a	20.2 c	28.0 d
	10–20	81.1***	–	12.9 a	11.5 b	15.9 c	18.7 d
	20–30	56.1***	–	15.3 a	10.1 b	16.1 a	17.4 c
N (kg/ha)	OL–30	86.2***	–	39.9 a	36.7 b	52.2 c	66.7 d
	OL	–	–	–	–	–	99.2
	0–10	84.0***	1343 a	1387 b	1375 ab	1650 c	1943 d
	10–20	46.5***	–	1661 a	1618 a	1512 b	1428 c
C/N	20–30	63.7***	–	1792 a	1773 a	1568 b	1370 c
	OL–30	0.78 n.s.	–	4840	4766	4730	4837
	OL	–	–	–	–	–	26.5
	0–10	78.7***	10.2 a	8.5 b	10.9 a	12.2 c	14.5 d
P (kg/ha)	10–20	86.6***	–	7.9 a	7.2 b	10.3 c	13.1 d
	20–30	81.0***	–	8.7 a	5.7 b	10.2 c	12.8 d
	OL	–	–	–	–	–	8.3
	0–10	24.6***	662 a	728 b	707 c	688 c	666 ac
P (kg/ha)	10–20	75.9***	–	970 a	803 b	758 c	701 d
	20–30	53.3***	–	926 a	897 a	842 b	743 c
	OL–30	64.8***	–	2624 a	238 b	2288 c	2118 d

Total pool of SOC, N and P in 0–30 cm soil depth was calculated for the years 1973, 1977, 1989 and 2004, in 2004 sum includes the organic layer (OL). Significant changes within one parameter and soil depth are indicated by differing letters ( $P \leq 0.05$ ) according to Kruskal–Wallis ANOVA with post hoc Mann–Whitney U-test



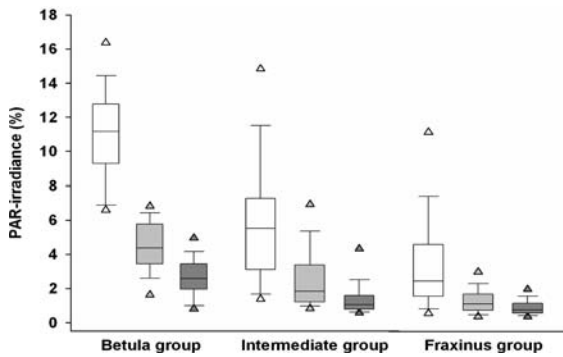
**Fig. 2** Changes in mean Ellenberg's indicator values for light, nitrogen and soil reaction in the herb layers summarised for the plots of undisturbed succession since 36 and 22 years.

Analyses were done with both data, weighted by coverage ( $\blacktriangle$ ) and presence-absence of the species ( $\triangle$ )

### PAR-irradiance

The relative irradiance in the stands significantly differed between the three groups of differing initial treatment (Fig. 3). On average, extreme low relative irradiance was measured for the Fraxinus-dominated

plots with values ranging from 3.7% ( $\pm 0.34$ ) in 5 m height to 0.9% ( $\pm 0.04$ ) in 0.5 m height of the stands. The Betula-dominated group showed with a mean of 11.0% ( $\pm 3.3$ ) in 5 m height to 2.7% ( $\pm 0.11$ ) in 0.5 m height of the stands significant higher relative irradiance intensity.



**Fig. 3** Distribution of PAR-irradiance as percentage of open field irradiance in the three groups of differing initial treatment in 5 m (□), 2 m (▣) and 0.5 m (▢) height of the stands 36 and 22 years after abandonment, respectively. For all groups and canopy height PAR values differing significantly according to Kruskal–Wallis ANOVA with post hoc Mann–Whitney U-test ( $P < 0.05$ ), 0.5 m height:  $H = 158.9^{***}$ , 2 m height:  $H = 212.0^{***}$ , 5 m height:  $H = 124.2^{***}$

**Table 3** Result of the indicator species analysis (ISA) of all species with significant indicator value (IV)  $\geq 40$  for all layers, their Ellenberg indicator value for light (L-value) and their correlation with the first and second axis of the DCA of the

Species	Layer	L-value	IV	P-value	Axis 1		Axis 2	
					r	P-value	r	P-value
<b>Betula group</b>								
<i>Betula pendula</i>	Tree	(7)	55.7	0.0002	-0.87	0.000	-0.02	n.s.
<i>Viburnum lantana</i>	Shrub	7	59.5	0.0004	-0.65	0.000	0.08	n.s.
<i>Sorbus aucuparia</i>	Shrub	(6)	49.1	0.0078	-0.35	0.042	-0.18	n.s.
<i>Lonicera xylosteum</i>	Shrub	5	39.7	0.0140	-0.34	0.045	-0.09	n.s.
<i>Betula pendula</i>	Shrub	(7)	45.3	0.0190	-0.36	0.044	-0.33	n.s.
<i>Cornus sanguinea</i>	Herb	7	40.5	0.0002	-0.41	0.014	0.11	n.s.
<i>Viburnum opulus</i>	Herb	6	47.6	0.0002	-0.76	0.000	0.30	n.s.
<i>Sorbus aucuparia</i>	Herb	(6)	56.8	0.0006	-0.75	0.000	-0.22	n.s.
<i>Viburnum lantana</i>	Herb	7	58.3	0.0008	-0.66	0.000	0.18	n.s.
<i>Euonymus europaea</i>	Herb	6	56.6	0.0032	-0.38	0.024	-0.11	n.s.
<i>Rhamnus cathartica</i>	Herb	7	57.6	0.0056	-0.56	0.000	-0.14	n.s.
<i>Cotoneaster divaricatus</i>	Herb	-	47.5	0.0110	-0.51	0.002	-0.03	n.s.
<i>Quercus robur</i>	Herb	(7)	50.0	0.0174	-0.47	0.004	-0.16	n.s.
<b>Intermediate group</b>								
<i>Rubus caesius</i>	Shrub	6	45.2	0.0154	-0.05	n.s.	0.64	0.001
<i>Rubus caesius</i>	Herb	6	54.8	0.0032	-0.12	n.s.	0.41	0.015
<b>Fraxinus group</b>								
<i>Fraxinus excelsior</i>	Tree	(4)	50.4	0.0030	0.79	0.000	-0.14	n.s.
<i>Prunus avium</i>	Shrub	(4)	49.1	0.0072	0.24	n.s.	-0.42	0.011
<i>Fraxinus excelsior</i>	Shrub	(4)	41.6	0.0210	0.66	0.004	-0.02	n.s.
<i>Daphne mezereum</i>	Herb	4	48.2	0.0032	0.41	0.016	-0.14	n.s.
<i>Hypericum hirsutum</i>	Herb	7	41.7	0.0048	0.47	0.004	-0.02	n.s.

Litter pool and soil chemical parameters

After about 20 years of abandonment, stand structure had changed to pioneer forest vegetation and typical L-mull humus had developed. Noticeable differences in the amount of litter pool and its nutrient composition occurred between the three groups of plots of differing tree species composition (Table 4). The *Betula*-dominated plots had significantly lower amounts of accumulated humus than the *Fraxinus*-dominated plots. Accordingly nitrogen, SOC and phosphorus (kg/ha) were lowest in the *Betula*-dominated plots. Nitrogen concentration (%) was lowest in the *Betula*-dominated plots, whereas SOC concentration (%) was significantly higher. The C/N-ratio was widest for the *Betula*-group.

Chemical properties of mineral soil also differed significantly between the three groups (Table 4).

vegetation composition 36 or 22 years after abandonment (Monte Carlo test of significance of observed max IV (1,000 permutations))

**Table 4** Litter pool and pH, C/N and amount of N, C and P of the litter layer (OL) and the mineral soil per 0–10, 10–20 and 20–30 cm soil depth of the plots of undisturbed succession 36

or 22 years after abandonment, respectively, for the three groups of differing initial treatment

Parameter	Depth (cm)	H (F)-value	Betula group	Intermediate group	Fraxinus group
Litter pool (kg/ha)	OL	16.1**	4318 ± 322 a	7875 ± 625 b	6450 ± 842 b
pH	OL	14.0**	7.8 ± 0.1 a	8.0 ± 0.1 ab	8.2 ± 0.1 b
	0–10	6.3*	7.5 ± 0.1 a	7.6 ± 0.1 b	7.6 ± 0.1 b
	10–20	3.2 n.s.	7.5 ± 0.1	7.7 ± 0.1	7.7 ± 0.1
	20–30	1.7 n.s.	7.6 ± 0.1	7.7 ± 0.1	7.7 ± 0.1
	∑ (OL–30)	(4.03)*	71.5 ± 2.5 a	65.4 ± 2.2 a	63.6 ± 1.3 b
SOC (%)	OL	5.8 n.s.	42.3 ± 1.2	40.3 ± 1.0	38.8 ± 0.7
SOC (t/ha)	OL	14.9**	1.8 ± 0.1 a	3.1 ± 0.2 b	2.5 ± 0.4 a
	0–10	9.1*	31.8 ± 15 a	26.9 ± 13 b	25.6 ± 14 b
	10–20	2.5 n.s.	19.9 ± 10	18.4 ± 8.2	17.8 ± 7.6
	20–30	1.7 n.s.	18.0 ± 12	16.5 ± 6.4	17.7 ± 12
	∑ (OL–30)	(4.03)*	71.5 ± 2.5 a	65.4 ± 2.2 a	63.6 ± 1.3 b
N (%)	OL	11.9**	1.4 ± 0.1 a	1.5 ± 0.1 a	1.7 ± 0.1 b
N (kg/ha)	OL	17.2***	61.2 ± 5.2 a	116 ± 10 b	108 ± 16 b
	0–10	0.1 n.s.	1918 ± 56	1925 ± 66	1985 ± 102
	10–20	4.6 n.s.	1359 ± 32	1467 ± 37	1453 ± 30
	20–30	7.6*	1261 ± 48 a	1426 ± 40 b	1414 ± 29 b
	∑ (OL–30)	(4.77)*	4598 ± 66 a	4934 ± 104 b	4960 ± 95 b
C/N	OL	20.9***	30.0 ± 0.6 a	27.7 ± 0.7 b	23.6 ± 0.5 c
	0–10	21.2***	16.5 ± 0.4 a	14.2 ± 0.4 b	13.0 ± 0.4 c
	10–20	7.0*	14.6 ± 0.6 a	12.6 ± 0.5 b	12.3 ± 0.6 b
	20–30	8.0*	14.3 ± 0.8 a	11.7 ± 0.6 b	12.5 ± 0.8 b
	∑ (OL–30)	(0.51) n.s.	2101 ± 53	2154 ± 41	2093 ± 43
P ppm	OL	6.9*	1085 ± 78 a	1328 ± 119 ab	1314 ± 59 b
P (kg/ha)	OL	14.2**	4.7 ± 0.5 a	11.1 ± 1.8 b	8.2 ± 0.8 b
	0–10	1.5 n.s.	682 ± 16	678 ± 16	641 ± 28
	10–20	2.2 n.s.	707 ± 17	711 ± 14	686 ± 11
	20–30	4.0 n.s.	714 ± 26	754 ± 19	758 ± 20
	∑ (OL–30)	(0.51) n.s.	2101 ± 53	2154 ± 41	2093 ± 43

Means ± standard error, significant differences are indicated by differing letters ( $P < 0.05$ ) according to Kruskal–Wallis ANOVA with post-hoc Mann–Whitney U-test, except for the total amount (OL–30 cm) of SOC, N and P here after one-way ANOVA with post hoc Scheffé-test

Plots dominated by *Betula* had a higher amount of SOC, higher C/N-ratio but lower total nitrogen, and a slightly lower pH value than the plots dominated by *Fraxinus* at all soil depths. The amount of phosphorus was higher in 0–10 cm but lower in 10–20 cm for the *Betula*-dominated plots.

#### Vegetation structure and diversity

Light supply on the ground had no significant effect on herb layer richness (Fig. 4b). Likewise, no influence of the tree layer canopy and thus the light supply on the ground was detected on the richness of tree

species in the herb layers. In contrast, the species richness in the shrub layers was significantly influenced by light supply (Fig. 4a).

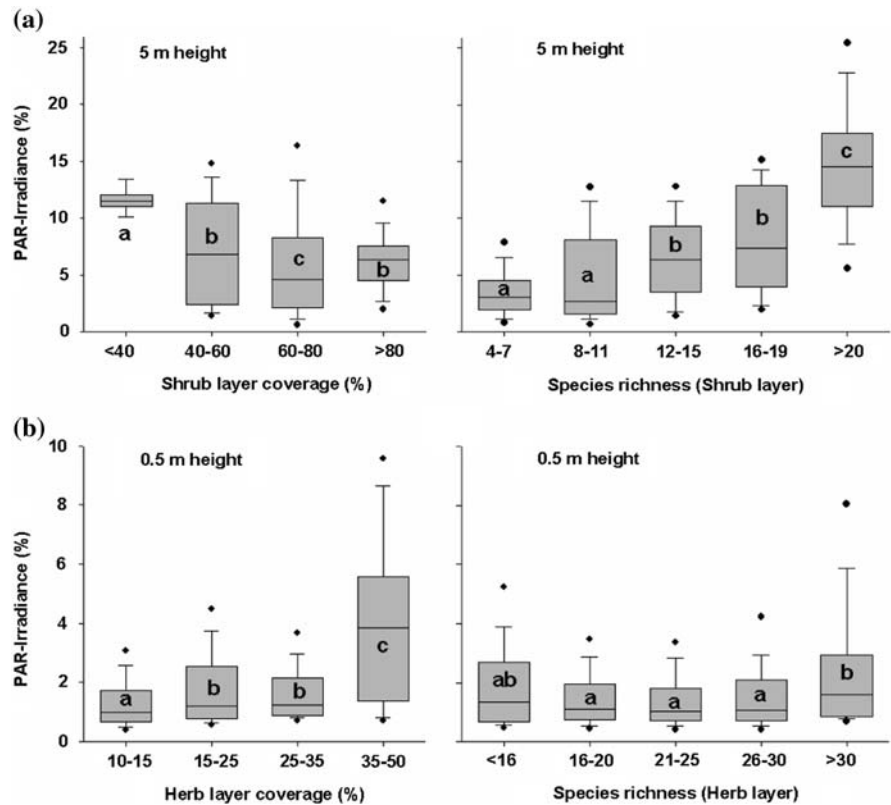
The shrub and herb layers of all plots are dominated by *F. excelsior* (Table 5). No seedlings or saplings of *B. pendula*, *Salix caprea* or *Populus tremula* were recorded in the current herb layers.

#### Ellenberg indicator values

The mean Ellenberg indicator values for light in the herb and shrub layers and for the total stands were



**Fig. 4** Distribution of PAR-irradiance 36 and 22 years after abandonment, respectively, **a** as a function of shrub layer coverage and species richness in 5 m height and **b** as function of herb layer coverage and species richness in 0.5 m height of the stands. Significant differences are indicated by differing letters (Kruskal–Wallis ANOVA with post hoc Mann–Whitney U-test  $P < 0.05$ ). For herb layer and PAR in 0.5 m height: coverage  $H = 32.3^{***}$ , species richness  $H = 12.4^*$ ; for shrub layer and PAR in 5 m height: coverage  $H = 14.0^{**}$ , species richness  $H = 58.4^{***}$



significantly higher in plots dominated by *B. pendula* (Table 6). Indicator values for nitrogen and soil reaction were slightly lower in the *Betula* group. The differences were more pronounced in the weighted evaluation, but the differences between the three groups were rather small in both cases.

## Discussion

Effects of successional changes on soil chemical properties and vegetation attributes

Impact of past land use on the patterns of changes in vegetation and soil characteristics has received considerable attention over the last decades, particularly in temperate forest ecosystems in Europe and North America (review in Flinn and Vellend 2005). On abandoned old-fields it is to be expected that nutrient and carbon levels change significantly over time as with the agricultural abandonment no fertilisation is applied anymore and the cessation of harvesting results in biomass accumulation.

In this study, soil organic carbon (SOC) increased linearly with time since abandonment ( $r^2 = 0.951$ ) with an average annual increase of  $39.6 \text{ g C m}^{-2} \text{ year}^{-1}$  in the top 10 cm during the 36 years of abandonment. Similar rates of SOC accumulation have been reported for northern ecosystems (Bormann and Siddle 1990; Bormann et al. 1995; Hooker and Compton 2003); in many cases the forest floor turned out to be a major sink for carbon after agricultural abandonment (Hooker and Compton 2003). In our study, the decrease in SOC in the top 10 cm within the first five years of abandonment and the initial decrease in the lower soil were not sustained. From the tenth year onwards the total amount (0–30 cm) of SOC showed a steady increasing rate of on average  $94.7 \text{ g C m}^{-2} \text{ year}^{-1}$ . However, SOC showed a distinct vertical gradient with an increasing difference between upper and lower soil during time. This increasing differentiation is obvious by the consequence of the perturbation by ploughing ceasing. Subsoil SOC also accumulated, presumably through mechanisms such as root turnover and exudation, sorption of dissolved organic carbon and pedoturbation. Approximately 10% of the total SOC

**Table 5** List of all tree species, their mean coverage in the tree, shrub and herb layer and the number of stems per ha and basal area ( $\text{m}^2 \text{ha}^{-1}$ ) for the tree layers for the three groups of differing initial treatment 36 and 22 years after abandonment, respectively

Species	Group (mean coverage)		
	Betula	Intermediate	Fraxinus
<b>Tree layer</b>			
n $\text{ha}^{-1}$ (dbh > 4 cm) <sup>a</sup>	4650	4530	5600
Basal area ( $\text{m}^2 \text{ha}^{-1}$ ) <sup>a</sup>	75	95	80
<i>Betula pendula</i>	50.5	20.8	1.3
<i>Fraxinus excelsior</i>	1.4	7.1	27.9
<i>Salix caprea</i>	6.2	20.4	28.3
<i>Acer platanoides</i>	2.7	14.6	6.3
<i>Acer pseudoplatanus</i>	1.8	0.8	2.1
<i>Populus tremula</i>	–	4.2	8.3
<i>Prunus avium</i>	0.5	–	1.5
<i>Sorbus aucuparia</i>	0.5	–	0.4
<i>Salix alba</i>	–	0.8	1.7
<b>Shrub layer</b>			
<i>Fraxinus excelsior</i>	6.5	27.8	29.2
<i>Betula pendula</i>	3.4	1.9	1.6
<i>Acer platanoides</i>	1.8	1.4	1.5
<i>Sorbus aucuparia</i>	1.8	1.0	0.9
<i>Acer pseudoplatanus</i>	0.7	1.5	0.7
<i>Prunus avium</i>	0.5	0.3	1.9
<i>Acer campestre</i>	0.3	0.9	0.6
<i>Populus tremula</i>	–	0.6	0.5
<i>Salix caprea</i>	0.8	0.3	0.4
<i>Carpinus betulus</i>	–	0.2	0.2
<i>Sorbus aria</i>	0.1	–	<0.1
<i>Picea abies</i>	0.4	–	–
<i>Pinus sylvestris</i>	–	0.1	–
<i>Quercus robur</i>	–	0.1	–
<i>Juglans cinerea</i>	–	0.1	–
<b>Herb layer</b>			
<i>Fraxinus excelsior</i>	1.7	2.0	1.3
<i>Sorbus aucuparia</i>	1.6	0.7	0.3
<i>Acer campestre</i>	0.6	0.6	0.2
<i>Acer platanoides</i>	0.3	0.6	0.2
<i>Prunus avium</i>	0.5	<0.1	0.4
<i>Quercus robur</i>	0.3	0.1	<0.1
<i>Acer pseudoplatanus</i>	0.1	0.1	0.1
<i>Carpinus betulus</i>	0.1	<0.1	0.1
<i>Sorbus aria</i>	<0.1	<0.1	0.1
<i>Fagus sylvatica</i>	<0.1	<0.1	<0.1
<i>Prunus padus</i>	–	–	0.1
<i>Tilia platyphyllos</i>	<0.1	–	–

<sup>a</sup> Estimated only for the plots of undisturbed succession since 36 years

accumulation occurred in the subsoil (20–30 cm). Hooker and Compton (2003) also found significant accumulation of carbon in the subsoil (20–70 cm); other studies show no significant changes (Hamburg 1984), or decreasing rates (Richter et al. 1999) or assume based on large-scale assessments or soil C models that there is no carbon accumulation in the subsoil (Turner et al. 1995; Gaudinski et al. 2000). The extent to which deeper soil layers store carbon appears to depend on several factors such as soil texture, management history, recovery time scale and vegetation development. Furthermore, in our study as in many others, the stocks were evaluated by assuming constant bulk density. Further research is required to identify the most important factors influencing patterns of carbon storage in the soil.

In accordance with other studies (Knops and Tilman 2000), the C/N ratio increased in all depths with successional age, as a result of increasing input of partly recalcitrant organic matter with high C/N ratio due to high lignin concentrations, e.g. dead woody debris in the pioneer forest stage (Berendse 1990).

The total nitrogen pool did not significantly change over time. But there was a clear redistribution of N within the soil profile. Nitrogen supply significantly decreased in the deeper soil and significantly increased in the upper soil. Hooker and Compton (2003) estimated a significant decline of nitrogen over a 115-year chronosequence after agricultural abandonment of  $1.24 \text{ g N m}^{-2} \text{ year}^{-1}$  in the mineral soil (0–70 cm), and an accumulation of nitrogen in the plant biomass and organic layer that exceeded the losses from mineral soil. Source other than plant uptake from the mineral soil, like inputs from atmospheric deposition and bacterial  $\text{N}_2$  fixation, must contribute to nitrogen accumulation in regrowing ecosystems. Nitrogen inputs by atmospheric deposition for most parts of Western Europe averages at least  $20 \text{ kg N ha}^{-1} \text{ year}^{-1}$  (Ellenberg et al. 2001). Since pioneer forests established on our study site within a relatively short time period, a high amount of accumulated nitrogen in the above- and below-ground biomass is to be expected. Schmidt (2001) reported for beech (*Fagus sylvatica*) forest ecosystem in the same region after disturbance 10 years ago, aboveground pools of up to  $15 \text{ kg N ha}^{-1}$  for the herb layer and up to  $200 \text{ kg N ha}^{-1}$  for the tree species saplings (up to 9 m in height), and rates of

**Table 6** Weighted mean Ellenberg indicator values (IV) for light, nitrogen and soil reaction in the herb and shrub layers and the total stands (all layers) of the three groups of differing

initial treatment 36 or 22 years after abandonment (1 Betula group, 2 Intermediate group, 3 Fraxinus group)

Mean IV for:	Herb layer			Shrub layer			Total stand		
	Group			Group			Group		
	1	2	3	1	2	3	1	2	3
Light	5.9 (H = 4.57, n.s.)	5.6	5.5	6.3 (H = 5.63, n.s.)	5.8	5.7	6.4 a (H = 14.1, P = 0.001)	5.9 b	5.7 b
Nitrogen	5.5 (H = 2.53, n.s.)	5.7	5.6	5.7 a (H = 9.2, P = 0.01)	6.5 b	6.3 b	5.9 a (H = 15.5, P = 0.001)	6.6 b	6.5 b
Soil reaction	6.7 (H = 1.71, n.s.)	6.8	6.8	7.0 (H = 0.50, n.s.)	7.0	7.1	6.9 (H = 5.74, n.s.)	7.0	7.0

Significant differences within one group are indicated by differing letters ( $P < 0.05$ ) after Kruskal–Wallis ANOVA with post hoc Mann–Whitney U-test

nitrogen accumulation in above- and belowground biomass of tree species regeneration of about 2–3 g N m<sup>-2</sup> year<sup>-1</sup>.

In contrast to Hooker and Compton (2003) and our findings, numerous studies report an increase of total nitrogen in the soil during succession (Woodmansee 1978; Bornkamm 1984; Stöcklin and Gisi 1989; Knops and Tilman 2000; Du et al. 2007). Possible reason for this discrepancy might be a failure of samples in the deeper soil layers, thus it is not possible to follow the profile changes over time. In their study on abandoned agricultural fields Knops and Tilman (2000) exclude pronounced profile changes due to mining of deeper soil nitrogen, since grasses are dominating on the fallows which have the highest amount of root biomass in the upper soil horizon. In our study on abandoned arable fields, vegetation structure changed rapidly from initial dominance of annuals (1–2 years) to a dominance of perennial herbs and grasses to shrub and tree colonisation five years after abandonment, and after about 20 years of succession plots exhibited pioneer forest stands (Dölle et al. 2008). Hence, early incipient and intensive root penetration to the lower soil layers is apparent (Crocker and Major 1955; Olson 1958; Tilman 1988; Berendse 1990).

Although the total amount of nitrogen in 0–10 cm soil depth increased (most important for herb layer), the Ellenberg indicator value for nitrogen for the herb layers, both weighted and unweighted decreased over time. It suggests a decline in nitrogen availability since probably more nitrogen was tied up in organic

material. More in accordance with the changes in Ellenberg indicator value for nitrogen is the broader C/N ratio in the later stages, which suggests a lower mineralisation activity. At this point data on N mineralisation rate would be more informative to describe nitrogen availability.

The mean Ellenberg indicator value for light in the herb layers showed the most distinctive decreasing rate over time. This emphasises light as being a main driving force for changes in plant species composition during succession (Tilman 1985; Pykälä et al. 2005). In forest ecosystems relative irradiance is commonly considered to be a main factor influencing the composition and diversity of the ground flora (Bazzaz 1990; Jennings et al. 1999; review Barbier et al. 2008).

The increasing convergence of the weighted and unweighted Ellenberg indicator values with increasing successional age is mainly caused by the more even distribution of the herb layer species in the pioneer forest stage (Dölle and Schmidt 2007). The herb layer coverage showed a sharp decline during time, and herb layer species in current pioneer forests ground vegetation showed a scattered composition. In contrast, throughout the early stages of succession, the herb layers were often dominated by one or a few species with high coverages (Schmidt 1981).

Soil reaction showed a slight but not continuous decrease by 0.2 pH units in 0–20 cm soil depth during succession, and a marginal decrease in the weighted Ellenberg indicator value for soil reaction emerged. Decreasing pH during succession is caused

by the increasing biomass accumulation, caused by continuous extraction of base cations from the soil and a release of protons into the soil (van Bremen et al. 1984). Acidification by acid deposition may play a role; in our study there was no perceptible indication of ongoing acidification of the soil with progressive succession. It has been shown that changes in soil reaction during succession depend on initial pH. Thus, acidification during succession varies according to soil type and initial buffering capacity (Blake et al. 1999; García et al. 2007) and only a slow decline in soil reaction on soils with high buffering capacity (like our study site) is expected (Leuschner and Gerlach 2000).

The decreasing amount of phosphorus in the soil indicates accumulation of phosphorus in the living plant biomass. Since in contrast to other main nutrients, phosphorus scarcely undergoes leaching processes and its pool in the soil is primary dependent on organic matter decomposition (Scheffer and Schachtschabel 2002), an increase especially in the lower soil is not expected. This was confirmed in our study by the more pronounced decline in the lower soil (10–30 cm), indicating relocation of phosphorus due to uptake by plant roots and storage in the plant biomass. Decreasing phosphorus supply in the soil with increasing time since abandonment of old-fields seems to be a common phenomenon (Warning 1996; Glemnitz and Wurbs 1999; Du et al. 2007).

Long-term effect of the initial plot treatment on soil chemical properties, light transmittance and vegetation attributes

The obvious divergent development of the study plots regarding the initial treatment in the beginning of the experiment was already described in Schmidt (1981). The observed gradient strongly supports the initial floristic composition model by Egler (1954) and the strong and persistent influence of the land use history on the plant community and the pathway of succession, respectively (Koerner et al. 1997; Dupouey et al. 2002; Bonet 2004; Dölle and Schmidt 2007). Which species dominate during succession can be determined by numerous factors like differences in seed dispersal, interannual differences in seed production (mast years), soil seed bank, germination requirements, relative growth rate, competition with other plant species, as well as various environmental

parameters (Hard 1975; Schmidt 1981; Tilman 1988; Zeiter et al. 2006; Standish et al. 2007).

A main question therefore is, whether or not the plant community itself can induce the changes in environmental conditions which may in turn affect these processes, and with that influence competitive interaction between the species during succession. Two main processes of competitive interaction between plant species induced by the modification of environmental conditions are facilitation and inhibition (Connell and Slatyer 1977). Both processes can intensively interact during succession (Bornkamm 1988). On one hand, the occurrence of *Quercus robur* as significant indicator for the herb layers of the *Betula* group explains facilitation, since *Q. robur* has a high demand on relative irradiance intensity in the recruitment and young-growth stage (Ellenberg et al. 2001). On the other hand, there is a lack of pioneer tree species saplings, like *B. pendula* and *S. caprea*, in all current herb layers indicating inhibition of their germination and successful establishment.

There were significant correlations between the differences in current vegetation composition and the amount of SOC and nitrogen. Effects of canopy species on soil carbon content are well in accordance with other studies (e.g. Raulund-Rasmussen and Vejre 1995; Alriksson and Eriksson 1998; Hagen-Thorn et al. 2004). The differences between the three groups were more pronounced for nitrogen. The significantly higher amount of nitrogen in the forest floor (OL) of the *Fraxinus* group can partly be explained by the significantly larger litter pool on the *F. excelsior* dominated plots. The lower amount of nitrogen in the deeper soil (20–30 cm) for the *Betula* group indicates a stronger nitrogen uptake of the *B. pendula* roots.

Mean Ellenberg indicator values for light showed a slight gradient with highest being in the *Betula* group. For the herb layers, values are comparable high in the range of half-light to semi-shade plants, although the relative PAR transmittance to the ground is at very low levels in all groups. Values for mature forest ecosystem in the same region with comparable relative irradiance intensity for the herb layer exhibited clearly lower light indicator values, about 2–4 (Schmidt 2001, 2005; Ebrecht 2005). The missing reflection of the low PAR transmittance to the ground by the herb layer is caused by scattered individuals of early successional species (Dölle et al. 2008). But

since the closed canopy of the tree layers, together with the dense shrub layers permanently reduces the light availability on the ground, such light demanding species of open landscapes get repressed and a further decline is most likely. This is in accordance with Thomas et al. (1999) who pointed out that the light-vegetation relationship might be better explained by the past light regimes rather than by current light conditions because of the slowness of plant community changes. Therewith it might be an explanation for the lack of relationship between herb layer richness and PAR transmittance to the ground, in accordance with other studies (e.g. Weisberg et al. 2003).

## Conclusion

Our study plots changed from open herbaceous to closed pioneer forest within relatively short time periods. Therewith light supply on the ground dramatically decreased over time. Nitrogen showed a clear accumulation in the upper soil but not in total, the C/N ratio significantly increased over time, and phosphorus showed a slight decreasing rate. Thus our results do not completely fit the resource ratio hypothesis proposed by Tilman (1985), but rather emphasise light as being a main influencing factor for vegetation development during succession.

Our findings clearly confirm the initial floristic composition model by Egler (1954). Differences caused by the initial treatments at the beginning of the experiment fundamentally determined the initial floristic composition and the subsequent development of vegetation on the plots. The differences in plant species composition, in particular current tree species dominants, in turn influenced light availability on the ground, as well as litter pools and nutrient supply in the soil.

**Acknowledgements** We would like to thank numerous assistants for help with the field and laboratory work since the beginning of the experiment; we especially thank Heiko Rubbert, Andrea Bauer and Andreas Parth. Many thanks also to Steffi Heinrichs and Hubertus Rölleke for critical discussion, to Bernhard Prévosto and one anonymous reviewer for valuable comments on the manuscript and to Bettina Guyon for correcting the English.

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