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The effects of windthrow on plant species richness in a Central European beech forest

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Abstract The effects of soil disturbance caused by the uprooting of a single or a few canopy trees on species richness and composition of vascular plant species and bryophytes were examined in a temperate beech forest (*Fagus sylvatica*) in northern Germany. We recorded the vegetation in 57 pairs of disturbed and adjacent undisturbed plots and established a chronosequence of mound ages to study the effect of time since microsite formation on plant species richness and composition. We found significant differences in plant species richness and composition between disturbed and adjacent undisturbed plots. Species richness of both vascular plants and bryophytes was higher in the disturbed than in the undisturbed plots, but these differences were more pronounced for bryophytes. We suggest that three main factors are responsible for this differential response. The availability of microsites on the forest floor that are suitable for the recruitment of bryophytes is lower than for vascular plants. Establishment of bryophytes in disturbed microsites is favoured by a greater abundance of propagules in the close vicinity and in the soil of the disturbed microsites, as well as by a greater variety of regeneration strategies in bryophytes than in vascular plants. Time since mound formation was a major factor determining plant species richness and composition. A significant decrease in the mean number of species was found from young mounds to intermediate and old mounds. However, differences were observed between vascular plants and bryophytes in the course of changes through time in species richness and composition. A large number of exclusive and infrequent vascular plant species was observed on young mounds, among them several disturbance specialists. We suggest that the establishment of many vascular plant species was infrequent and short-lived due to unfavourable light conditions and a low abundance of propagules. By contrast, the development of a litter layer was the main reason for the decreased mean number of bryophytes on old mounds. Our study supports the view that groups of species differing in important life history traits exhibit different responses to soil disturbance.

Keywords Bryophytes · *Fagus sylvatica* · Pits and mounds · Small-scale disturbance · Tree uprooting · Vascular plant species

Introduction

Natural disturbances are a key factor structuring forest plant communities. In Central European

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beech (*Fagus sylvatica*) forests, small-scale disturbances due to canopy gap formation seem to be the prevailing natural disturbance regime (Tabaku 2000; Drößler and von Lüpke 2004). The majority of canopy gaps are less than 400 m^2 in size, with few gaps exceeding 1000 m^2. These canopy gaps are created by the death of single or small groups of large trees. Changes in the microclimatic conditions occur in the understorey as a result of canopy gap formation, modifications of soil properties are induced, and woody debris is added to the ground (Pickett and White 1985). Furthermore, windthrow gaps caused by the uprooting of trees lead to distinct soil disturbances. A pit and mound complex (PMC) is generally created with a depression at the former root position (pit) and an adjacent mound, where the soil falling off the decaying and displaced rootplate accumulates (Schaetzl et al. 1989). In unmanaged old-growth beech forests of northern Germany, it has been shown that uprooting is responsible for about one-third of beech tree mortality (Müller-Using and Bartsch 2003; von Oheimb et al. 2007).

Predictions on the response patterns of understorey vegetation to disturbance can be derived from the intermediate disturbance hypothesis (IDH, Connell 1978). This hypothesis states that species richness shows a unimodal (rise and fall) pattern within a range of disturbance levels (expressed e.g. by disturbance frequency or intensity), with intermediate levels of disturbance producing the highest species richness. This is because competition-intolerant species are lost by competitive exclusion if disturbance levels are very low. On the contrary, only disturbance-dependent species are present if disturbance levels are very high. In late-successional forest ecosystems, the IDH predicts that small-scale (i.e. low-intensity) disturbances such as canopy gap formation can lead to an increase of species richness (Sheil and Burslem 2003). In support of this hypothesis, various studies on the effect of canopy gap formation on understorey vegetation have found higher species richness in gaps than under a closed canopy (e.g. Moore and Vankat 1986; Stone and Wolfe 1996; Vetaas 1997). Moreover, it has been demonstrated that the response of understorey vegetation is more pronounced in windthrow gaps than in gaps without soil perturbation (Schaetzl et al. 1989; Palisaar and Poschlod 2001). Canopy gap creation with soil perturbation can be seen as representing a higher level of disturbance intensity than canopy gap creation without soil perturbation in late-successional forest communities. However, the generality of the IDH to predict local variation in species richness and composition following disturbances has been repeatedly questioned (Hubbell et al. 1999; Li et al. 2004). Hubbell et al. (1999) examined treefall gaps in a tropical forest in Panama and found no relationship between canopy disturbances and species richness of tree saplings. The authors concluded that the IDH should be rejected in favour of another model, the recruitment limitation hypothesis. This hypothesis states that differences in species richness in patches should be primarily controlled by differences in dispersal and recruitment.

According to these hypotheses, the response patterns of understorey vegetation to disturbance may be explained either by the local environmental characteristics (IDH; Connell 1978) or by neutral processes such as dispersal (recruitment limitation hypothesis; Hubbell 2001). A higher species richness in windthrow gaps with than in gaps without soil perturbation has been attributed to the influence of the distinctive soil and microclimatic characteristics of pit and mound microsites on the fine-scale pattern of understorey species distribution (Beatty and Stone 1986; Peterson and Pickett 2000). Mineral soil is exposed and the physical properties of the soil are altered in recently formed uprooting mounds. In contrast to the undisturbed forest floor, mounds tend to be exposed to higher light levels, soil temperature is higher, and soil moisture is lower (Beatty and Stone 1986). Increased moisture levels in pits with occasional standing water and thick litter accumulations have often been observed in temperate forest ecosystems (Webb 1988; Schaetzl et al. 1989). Tree uprooting therefore enhances habitat heterogeneity and provides important microsites for plant establishment. In addition to species that survived the uprooting, new species become established germinating from buried diaspores (Jonsson and Esseen 1990; Palmer et al. 2000). Low competition enables the establishment of plants after dispersal of propagules into the disturbed microsites as well as the vegetative expansion by means of clonal growth from the surrounding intact vegetation (Palmer et al. 2000). As a consequence, species well represented in the soil-buried diaspore bank, species present in the surrounding area, and species with a high colonization efficiency may increase in importance in forest patches with soil disturbance.

In Central Europe, studies have mainly focused on forest dynamics after catastrophic windthrow, especially in montane coniferous or mixed forests (e.g. Fischer et al. 2002; Wohlgemuth et al. 2002). These studies have observed an increase in both the frequency and cover of pioneer species (in particular *Rubus idaeus*) and ruderal species on disturbed soil. However, only very limited information is available on vegetation response to the uprooting of one or a few trees in beech forests, which represent the most important forest communities in natural landscapes of Central Europe. One main reason for this may be the complete lack of natural, and the low number of old-growth, beech forests in this region. We hypothesized that the uprooting of a single or a small group of beech trees would cause a significantly higher plant species richness in disturbed than in undisturbed patches of the forest floor. We also expected differences in growth-form or life strategy type spectra between forest patches with and without soil disturbances.

Most studies on the impact of soil disturbance on forest vegetation deal with only one type of organism, mainly vascular plants, and sometimes just a subset thereof, namely only tree species. However, plant response may differ not only among species within one plant group, but also among plant groups. Jonsson and Esseen (1998) showed that plant recovery in experimentally disturbed patches of an old-growth boreal spruce (*Picea abies*) forest was more rapid in bryophytes than in vascular plants. Prior to this study, responses of different groups of plant species to soil disturbance by tree uprooting have not been studied in detail in temperate deciduous forests. We assumed that in comparison to vascular plants, bryophytes would show a stronger response due to a greater variety of regeneration strategies and a larger number of propagules.

Once created, mounds and pits are not stable habitats, but show characteristic changes over time (Ulanova 2000). In a comparative study of mounds with mean ages of approximately 50, 150 and >200 years in coniferous rainforests of southeast Alaska, Den Ouden and Alaback (1996) found that the role of windthrow in the maintenance of high understorey diversity was more or less restricted to the first decades after the disturbance. With diminishing habitat heterogeneity and environmental conditions that become less favourable for plant establishment, we expected a general decline in species richness on windthrow mounds over time.

In addition to soil disturbance, increased light availability has been identified as the most important factor influencing plant establishment and performance following windthrow gap creation (Schaetzl et al. 1989). However, there is a considerable gradient in light intensity at ground level, due to differences in gap size and the ability of beech to form a dense understorey of advanced regeneration, even under a relatively closed canopy. We expected species richness in disturbed microsites to be positively related to light intensity.

The objective of this study was to examine the effects of soil disturbance, caused by the uprooting of single or a few large trees, on plant species richness and composition in a temperate beech forest. Specifically, we addressed the following questions: 1. How do plant species richness and composition differ between disturbed and undisturbed patches of the forest floor? 2. Are there differences in the responses to soil disturbance between plant species groups with different growth forms, habitat preferences, and dispersal strategies? 3. How is plant species richness and composition in disturbed microsites affected by the time period since microsite formation and the understorey light conditions?

Methods

Study area

The study was carried out in the Serrahn beech forests (Müritz National Park), Mecklenburg-Western Pomerania, North–East Germany (53°20′ N, 13°12′ E). These forests were selected for this study because they are among those Central European beech forests with the longest periods of low human interference (von Oheimb et al. 2005a) and thus allow to analyse the vegetation response to the natural disturbance regime. At Serrahn, old-growth beech forests, ranging from 200 to 235 years in age, cover an area of 330 ha. The climate is suboceanic–subcontinental with a mean annual precipitation of 593 mm and a mean annual temperature of 7.8°C. The mean height of the study area above sea level is 100 m. The soils are derived from recent moraines of the Weichsel glacial period. Predominant soil types are dystric cambisols, podzoluvisols and luvisols, developed on a parent material of loamy sand. The main humus type is moder. The potential natural forest vegetation can be assigned to acidophytic beech forests (*Luzulo-Fagetum*) on dystric cambisols and podzoluvisol soils, and to mesophytic beech forests (*Galio-Fagetum*) on luvisols (forest types according to Ellenberg 1996).

Two different approaches were taken to examine the effects of tree uprooting on understorey vegetation. To answer the questions 1 and 2, we compared disturbed and adjacent undisturbed plots. This sampling approach was devised to analyse the vegetation response to tree uprooting in a representative selection of the PMCs present in Serrahn. To answer question 3, a chronosequence of mound ages was established.

Vegetation sampling in disturbed and adjacent undisturbed plots

In the summer of 2000, 57 PMCs were randomly selected within an area of 132 ha in the central part of the Serrahn beech forests. A PMC was defined as a vertically uplifted rootplate or a mound (formed by the disintegrated rootplate) and an adjacent pit in the soil. A square sample plot of 100 m^2 was marked out around the PMC (the disturbed plot). A second sample plot of the same size with no visible evidence of soil disturbance caused by uprooting was located directly adjacent to the disturbed plot (the undisturbed plot). In this study, disturbance is thus defined as soil disturbance caused by the uprooting of canopy trees. The characteristics of the PMCs (e.g. time since PMC formation, size of pits and mounds) were not considered. The plot size of 100 m^2 was selected to include even very large PMCs and to conform with other studies conducted in temperate forests (Ellenberg 1996; Härdtle et al. 2003). Additionally, the plot size was intended to be well below the mean canopy gap size of 292 m^2 in Serrahn (von Oheimb, unpubl. data).

In each of the 57 disturbed and undisturbed plots, the presence of all vascular plants of the herb layer (<1 m tall) and terricolous bryophytes was recorded. Vernal species were recorded in spring 2001. To test for differences in light conditions between the paired plots, the total percentage cover of the tree layer (>5 m in height) and shrub layer (1–5 m) was determined in each plot and was used as an estimation of the light conditions. Percentage cover was estimated in 1% steps for cover ≤10%, and in 5% steps for cover >10%.

Nomenclature follows Wisskirchen and Haeupler (1998) for vascular plants and Dierssen (2001) for bryophytes.

Chronosequence of mound ages

The age of mounds was estimated using the stage of decomposition of the fallen tree-trunk and the root wood (cf. Webb 1988), and ages were classified on a three-stage ordinal scale. The time span for the complete decomposition of a large fallen beech trunk can be given as about 30 years, based on the data from two permanent plots in the Serrahn beech forests (von Oheimb et al. 2007). We distinguished the following three mound age classes:

- Young mounds: ranging from tight bark and no visual decay to obvious decay in the outer xylem layers of the fallen tree-trunk; high to

intermediate structural integrity of the fallen tree-trunk and the root wood (time since mound formation <12 years);
- Intermediate mounds: ranging from obvious decay in the inner xylem layers to organic debris collapsed to ground level of the fallen tree-trunk; intermediate to low structural integrity of the fallen tree-trunk, and only major root laterals in an advanced stage of decomposition (12–24 years);
- Old mounds: very few or no remnants of trunk and root wood; no structural integrity of the fallen tree-trunk; adjacent pit in the soil still visible (>24 years).

In each mound age class, 32 mounds were randomly selected for analysis of mound characteristics and vegetation. In the summer of 2000, we measured the height of the mound from the forest floor, the long axis of the mound (mound length), and the short axis of the mound (mound width). Following Webb (1988) and Palmer et al. (2000), we calculated a rough estimate of the mound area (projected vertically) as an ellipse, based on its length and width. In addition, we estimated the size of the surface area of the mound using an approximation for the calculation of an ellipsoid, based on the height, length and width of the mound (Thomsen's formula, http://home.att.net/~numericana/answer/ellipsoid.htm). We estimated the mound surface area to be one half of the surface area of an ellipsoid. Pits were not sampled in this study because they rapidly accumulate abundant litter, that in turn greatly reduce plant abundance (cf. Webb 1988).

For each mound, the presence of all vascular plants and bryophytes was recorded. Each mound was sampled in its entirety in order to document the complete flora of each mound age class. A 400 m^2 plot was established around each mound, in which the total percentage cover of the tree and shrub layer was recorded. Canopy cover of the tree and shrub layer was used as an estimation of the light conditions for the ground layer vegetation. Percentage cover was estimated in 1% steps for cover ≤10%, and in 5% steps for cover >10%. Due to the summation of the cover values of both layers the total percentage canopy cover may exceed 100%.

Definition of plant species groups

In order to interpret the results of the vegetation analysis, species were assigned to different groups according to their growth form, habitat preference, soil seed bank persistency and life strategy type. The vascular plants were classified by growth form as trees, shrubs, and herbaceous species. The herbaceous species were further classified with regard to their regional habitat preferences according to Schmidt et al. (2003). The species were assigned to one of five subgroups: H1.1—shade-tolerant forest species mainly occurring under a dense canopy; H1.2—species with a preference for forest clearings and forest edges; H2.1—species occurring in forests as well as in open vegetation; H2.2—species with a main distribution in open vegetation, but which in some cases are also present in forests; HO—species occurring in open vegetation.

Every vascular plant species was assigned a value for seed bank persistency (longevity index) according to Bekker et al. (1998), derived from the database published by Thompson et al. (1997). Species with a longevity index ≥0.35 were classified as having a persistent seed bank and species with a longevity index <0.35 as having a transient seed bank. We only included species which had at least five categorized records or four unanimous categorized records in the database (Bekker et al. 1998). Species not meeting these criteria and species not listed in the database were labelled "unknown". By using the approach of During (1992), bryophytes were assigned to a life strategy type according to Dierssen (2001).

Data analysis

Differences in the number of unique and shared plant species in disturbed and undisturbed plots were tested with McNemar's test. Differences in frequencies between disturbed and undisturbed plots as well as between mound age classes were tested with a two-tailed χ^2-test. Fisher's exact test was used when one of the expected frequencies in the contingency table was less than 5 (Zar 1999). Differences between the disturbed and undisturbed plots in the canopy cover as well as in the mean number of both all species and species groups were examined with the paired *t*-test. One-way ANOVA was used to test for differences between the three mound age classes. When differences were found among the mound age classes, subsequent multiple post-hoc comparisons were made by Turkey's HSD-test. Differences between the mean number of species of vascular plants and bryophytes per mound age class were tested for statistical significance with the unpaired *t*-test.

The relationships between the number of species in the herb and bryophyte layer and canopy cover in each mound age class were investigated using simple regression analysis. We sampled each mound in its entirety and did not use standardized plot sizes, and therefore also tested the relationship between the number of species and the sampling area (i.e. the surface area of mounds) using regression analysis. Since linear regressions yielded the highest coefficients of determination, we did not apply any data transformation. To test the interactions of mound age, canopy cover and mound area on plant species richness we performed an analysis of covariance (ANCOVA). We used plant species richness as the dependent variable, mound age as the fixed factor, and canopy cover and mound area as covariates. Separate ANCOVAs were carried out for the number of all species, vascular plant species and bryophyte species. Before each ANCOVA, we conducted simple regression analysis with the whole data set (i.e. 96 sample plots) to examine whether a linear model can adequately describe variation of species richness against each of the two covariates. Among all the pairs of species richness against canopy cover and mound area, only the relationship between vascular plant species richness and canopy cover was marginally better described by a non-linear equation than by a linear equation. Therefore, we used untransformed data for the ANCOVAs. The homogeneity-of-slopes (HOS) model was used to test for interactions between the covariates and the fixed factor. Where slopes were not significantly different, interaction terms were removed from the model, and the analysis was rerun. If at least one of the interaction terms was significant, they were kept in the model. The backward stepwise procedure was then applied iteratively to exclude insignificant variables until all variables were statistically correlated with species richness in the final model. With the exception of the ANCOVAs (PROC GLM in SAS version 6, SAS Institute Inc., Cary, USA), all statistical analyses were executed in SPSS version 11.5 (SPSS Inc., Chicago, USA).

Results

Disturbed and undisturbed plots

A total of 56 vascular plant species and 27 bryophyte species were found in all sample plots (Table 1). In the disturbed plots, 49 vascular plant species and 27 bryophyte species were recorded, while the total number of species in the undisturbed plots was 40 and 21, respectively (Table 2). More species were unique to the disturbed plots than to the undisturbed plots (16 vascular plant species and 6 bryophytes versus 7 vascular plant species and 0 bryophyte, respectively; McNemar's test vascular plants: $P = 0.093$; bryophytes: $P < 0.05$). All unique species occurred at low frequencies (≤4 occurrences, Table 1). None of the vascular plant species showed significantly higher frequencies in the disturbed plots than in the undisturbed plots, while 10 bryophyte species did exhibit higher frequencies between the plots (Table 1).

The mean number of vascular plant and bryophyte species was significantly higher in the disturbed than in the undisturbed plots (Table 2). These differences were more pronounced for bryophytes than for vascular plants. The mean number of tree and shrub species as well as herbaceous species was significantly higher in the disturbed than in the undisturbed plots (Table 2). The number of shade-tolerant forest species (group H1.1) did not differ between the paired sample plots, whereas more species which occur in forests as well as in open vegetation (group H2.1) were found in the disturbed plots (Table 2). Species with a preference for forest clearings and forest edges (group H1.2) were confined to the disturbed plots, but were present only in small numbers. The

Table 1 Frequency of vascular plant species and bryophytes recorded in disturbed and undisturbed plots, arranged in order of decreasing overall frequency (no. of plots = 57 each, plot size 100 m^2)

	Disturbed plot	Undisturbed plot	Overall	Seed longevity	Growth form/habitat preference
Vascular plants					
Fagus sylvatica	41	36	77	0.00	T
Anemone nemorosa	33	34	67	0.02	H1.1
Urtica dioica	24	17	41	0.78	H2.1
Oxalis acetosella	21	17	38	0.19	H1.1
Moehringia trinervia	20	17	37	0.69	H1.1
Calamagrostis epigejos	19	17	36	0.43	H2.1
Dryopteris carthusiana	16	11	27	– (spores)	H1.1
Juncus effusus	16	9	25	0.95	H2.1
Carex pilulifera	11	11	22	0.93	H2.1
Agrostis capillaris	12	6	18	0.66	H2.1
Taraxacum sect. *Ruderalia*	10	7	17	0.30	H2.1
Melica uniflora	6	7	13	0.00	H1.1
Poa trivialis	6	7	13	0.75	H2.1
Gymnocarpium dryopteris	6	2	8	– (spores)	H1.1
Rubus idaeus	6	1	7	0.79	S
Athyrium filix-femina	5	2	7	– (spores)	H1.1
Calamagrostis canescens	3	4	7	0.30	H2.1
Deschampsia cespitosa	3	4	7	0.27	H2.1
Viola riviniana	4	2	6	0.00	H1.1
Deschampsia flexuosa	4	2	6	0.08	H2.1
Luzula campestris	4	2	6	0.37	H2.1
Pinus sylvestris	3	3	6	0.00	T
Rumex acetosella	3	3	6	0.69	H2.1
Veronica officinalis	4	1	5	0.65	H2.1
Acer pseudoplatanus	1	4	5	0.00	T
Epilobium angustifolium	4	0	4	0.57	H1.2
Vicia angustifolia	3	1	4	–	HO
Senecio sylvaticus	3	0	3	–	H1.2
Impatiens parviflora	2	1	3	–	H1.1
Carex muricata	2	1	3	–	H2.1
Carex ovalis	2	1	3	0.50	H2.2
Cytisus scoparius	2	1	3	–	S
Carex pallescens	2	0	2	1.00	H2.1
Sagina procumbens	2	0	2	0.87	HO
Poa nemoralis	1	1	2	0.17	H1.1
Vaccinium myrtillus	1	1	2	0.12	S
Conyza canadensis	1	1	2	0.85	H2.2
Aesculus hippocastanum	1	0	1	–	T
Betula pendula	1	0	1	0.89	T
Picea abies	1	0	1	0.00	T
Quercus petraea	1	0	1	0.00	T
Sorbus aucuparia	1	0	1	0.04	T
Luzula pilosa	1	0	1	0.75	H1.1
Carex spicata	1	0	1	–	H1.2
Galium saxatile	1	0	1	0.50	H2.1
Lathyrus linifolius	1	0	1	0.00	H2.1
Persicaria hydropiper	1	0	1	0.35	H2.2
Ranunculus acris	1	0	1	0.24	H2.2
Sambucus nigra	1	0	1	0.56	S
Agrostis stolonifera	0	1	1	0.38	H2.2
Carex remota	0	1	1	0.80	H1.1
Majanthemum bifolium	0	1	1	0.00	H1.1
Poa annua	0	1	1	0.90	HO
Quercus rubra	0	1	1	–	T

Table 1 continued

	Disturbed plot	Undisturbed plot	Overall	Seed longevity	Growth form/habitat preference
Veronica arvensis	0	1	1	0.55	HO
Veronica montana	0	1	1	0.71	H1.1
Bryophytes				Life strategy type	
Hypnum cupressiforme* **	39	20	59	P	
Polytrichum formosum*	33	20	53	P	
Atrichum undulatum***	39	12	51	SSh	
Pohlia nutans**	29	14	43	Co	
Dicranum montanum*	26	15	41	P	
Dicranella heteromalla***	25	8	33	Co	
Brachythecium rutabulum*	19	9	28	Co	
Ceratodon pupureus****	20	2	22	Co	
Mnium hornum	15	7	22	PSh	
Herzogiella seligeri***	14	1	15	P	
Lophocolea heterophylla	10	4	14	Co	
Dicranum scoparium	7	5	12	P	
Polytrichum piliferum*	8	2	10	P	
Aulacomnium androgynum	6	2	8	Co	
Plagiothecium curvifolium	6	2	8	P	
Plagiothecium denticulatum	5	1	6	P	
Eurhynchium striatum	3	2	5	P	
Bryum subelegans	2	1	3	Co	
Pseudotaxiphyllum elegans	2	1	3	Co	
Leucobryum glaucum	1	1	2	P	
Pleurozium schreberi	1	1	2	P	
Eurhynchium praelongum	1	0	1	P	
Homalothecium sericeum	1	0	1	P	
Plagiomnium cuspidatum	1	0	1	P	
Plagiothecium laetum	1	0	1	P	
Plagiothecium nemorale	1	0	1	P	
Scleropodium purum	1	0	1	P	

Seed longevity: calculated value for seed bank persistency (longevity index) according to Bekker et al. (1998), derived from the database published by Thompson et al. (1997); –: unknown longevity index (spores: ferns are not included in the database). Growth form/Habitat preference: T: trees; S: shrubs; H: herbaceous species; regional habitat preference of the herbaceous species according to Schmidt et al. (2003); for explanations of the species groups see the Methods section. Life strategy type: Co: colonists; SSh: short-lived shuttle species; P: perennial stayers; PSh: perennial shuttle species. Species with significant differences in frequencies are in bold letters (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$)

mean number of vascular plant species with a transient seed bank were not different between the plots, whereas species with a persistent seed bank exhibited a significantly higher mean number of species in the disturbed plots than in the undisturbed (Table 2). Species number per life strategy type were consistently higher in the disturbed plots than in the undisturbed plots.

Neither the cover of the tree layer nor that of the shrub layer was significantly different between the pairs of disturbed and undisturbed plots (mean cover of tree layer: 56% and 61%, paired *t*-test $T = -1.868$, $P > 0.05$; mean cover of shrub layer: 9% and 12%, paired *t*-test $T = -1.708$, $P > 0.05$).

Chronosequence of mound ages

The mean vertically projected area of mounds was not significantly different between mound age classes (Table 3). By contrast, large differences were found in the mean surface areas of mounds of the different age classes. Neither the cover of the tree layer nor that of the shrub layer differed significantly between the three mound age classes in the 400 m^2 plots (Table 3).

Table 2 Total and mean number of all species as well as of different species groups in disturbed and undisturbed plots (no. of plots = 57 each, plot size 100 m^2)

	Total no. of species		Mean no. of species		*P*-value
	Disturbed	Undisturbed	Disturbed	Undisturbed	Paired *t*-test
All species	76	61	11.4	6.6	<0.001
All vascular plant species	49	40	5.6	4.2	0.002
Trees and shrubs	12	7	1.1	0.8	0.031
Herbaceous species	37	33	4.5	3.4	0.004
H1.1	11	13	2.0	1.7	ns
H1.2	3	0	0.1	0.0	0.010
H2.1	17	14	2.2	1.6	0.005
H2.2	4	3	0.1	0.1	ns
HO	2	3	0.1	0.1	ns
Transient	19	14	2.4	2.2	ns
Persistent	20	18	2.5	1.7	<0.001
Unknown	10	8	0.8	0.4	0.004
All bryophytes	27	21	5.6	2.3	<0.001
Perennial stayers	17	11	2.6	1.3	<0.001
Perennial shuttles	1	1	0.3	0.1	0.020
Colonists	8	8	2.0	0.7	<0.001
Short-lived shuttles	1	1	0.7	0.2	<0.001

For explanations of the species groups see the Methods section

A total of 79 species were observed in this study: 51 vascular plant species and 28 bryophyte species (Table 4). The two species groups exhibited large differences regarding the number of exclusive species. Young mounds had a large number of unique vascular plant species (Table 4). Of the 51 vascular plant species sampled, 21 were exclusive to young mounds, 5 were found on intermediate mounds only, and 2 were confined to old mounds. These figures were very different for bryophytes. Of the 28 species recorded, only 2 were exclusive to young mounds, 3 to intermediate, and none to old mounds. All exclusive species were very infrequent (present on at most 4 mounds). Four species each in the vascular plants and in the bryophytes differed significantly in frequency between the three mound age classes (Table 4). All these species were negatively associated with old mounds.

The total number of species was considerably higher on young mounds than on old mounds (Table 5). On intermediate mounds an intermediate total number of species was observed. When treating vascular plants and bryophytes separately, it became obvious that these differences were mainly attributable to the decrease in the number of vascular plant species with increasing mound age. The total number of bryophytes remained essentially at the same level. The mean numbers of bryophyte species were significantly higher than those of vascular plant species in all mound age classes (Table 5; unpaired *t*-test: young mounds: $P < 0.01$; intermediate mounds: $P < 0.001$; old mounds: $P < 0.001$). The mean

Table 3 Characteristics of mounds (mean and standard deviation) and cover of the tree and shrub layer (estimated on 400 m^2 plots) in three age classes

	Mean projected area (m^2)	Mean surface area (m^2)	Cover tree layer (%)	Cover shrub layer (%)	Cover tree and shrub layer (%)
Young mounds	7.2 (3.1)	16.8^a (7.3)	51.1 (30.2)	8.1 (10.2)	59.1 (33.3)
Intermediate mounds	6.8 (2.7)	11.4^b (4.4)	57.9 (30.2)	9.6 (11.0)	67.4 (32.5)
Old mounds	6.2 (3.6)	7.5^c (4.1)	63.7 (29.0)	9.5 (12.5)	73.2 (30.8)
P	ns	<0.001	ns	ns	ns

Values with different letters are significantly different between the mound age classes

Table 4 Frequency of vascular plant species and bryophytes recorded on mounds of three age classes, arranged in order of decreasing overall frequency

	Young	Intermediate	Old	Overall	Seed longevity	Growth form/Habitat preference
Vascular plants						
Fagus sylvatica	24	22	23	69	0.00	T
Moehringia trinervia***	22	8	4	34	0.69	H1.1
Oxalis acetosella	8	11	9	28	0.19	H1.1
Dryopteris carthusiana**	14	6	3	23	– (spores)	H1.1
Taraxacum* sect. *Ruderalia**	14	4	4	22	0.30	H2.1
Calamagrostis epigejos***	10	9	2	21	0.43	H2.1
Urtica dioica	7	9	2	18	0.78	H2.1
Agrostis capillaris	8	4	5	17	0.66	H2.1
Melica uniflora	2	4	2	8	0.00	H1.1
Juncus effusus	4	3	0	7	0.95	H2.1
Carex pilulifera	4	2	0	6	0.93	H2.1
Veronica officinalis	4	0	2	6	0.65	H2.1
Vicia hirsuta	3	2	0	5	0.45	HO
Pinus sylvestris	3	1	1	5	0.00	T
Carex pallescens	2	1	2	5	1.00	H2.1
Gymnocarpium dryopteris	1	4	0	5	– (spores)	H1.1
Rubus idaeus	4	0	0	4	0.79	S
Viola riviniana	3	1	0	4	0.00	H1.1
Quercus petraea	1	2	1	4	0.00	T
Deschampsia cespitosa	0	2	2	4	0.27	H2.1
Anemone nemorosa	0	0	4	4	0.02	H1.1
Vicia angustifolia	3	0	0	3	–	HO
Vicia sativa	3	0	0	3	0.34	HO
Poa trivialis	1	2	0	3	0.75	H2.1
Acer pseudoplatanus	2	0	0	2	0.00	T
Eupatorium cannabinum	2	0	0	2	0.33	H2.1
Cerastium holosteoides	1	1	0	2	0.65	H2.2
Impatiens parviflora	1	1	0	2	–	H1.1
Betula pendula	0	2	0	2	0.89	T
Luzula campestris	0	1	1	2	0.37	H2.1
Carex muricata	1	0	0	1	–	H2.1
Cerastium glomeratum	1	0	0	1	0.44	HO
Cirsium arvense	1	0	0	1	0.34	H2.2
Conyza canadensis	1	0	0	1	0.85	H2.2
Dactylis glomerata agg.	1	0	0	1	0.19	H2.2
Epilobium angustifolium	1	0	0	1	0.57	H1.2
Hypochaeris radicata	1	0	0	1	0.32	H2.2
Luzula multiflora	1	0	0	1	0.36	H2.1
Luzula pilosa	1	0	0	1	0.75	H1.1
Mycelis muralis	1	0	0	1	–	H2.1
Picea abies	1	0	0	1	0.00	T
Poa pratensis	1	0	0	1	0.39	H2.1
Rumex acetosella	1	0	0	1	0.69	H2.1
Cytisus scoparius	1	0	0	1	–	S
Senecio vulgaris	1	0	0	1	0.79	H2.2
Vicia lathyroides	1	0	0	1	0.20	HO
Calamagrostis canescens	0	1	0	1	0.30	H2.1
Fallopia dumetorum	0	1	0	1	–	H2.2
Sambucus nigra	0	1	0	1	0.56	S
Sorbus aucuparia	0	1	0	1	0.04	T
Vaccinium myrtillus	0	0	1	1	0.12	S

Table 4 continued

	Young	Intermediate	Old	Overall	Seed longevity	Growth form/Habitat preference
Bryophytes					Life strategy type	
Atrichum undulatum	30	29	28	87	SSh	
Dicranella heteromalla	26	25	21	72	Co	
Pohlia nutans**	31	23	16	70	Co	
Hypnum cupressiforme	26	22	18	66	P	
Brachythecium rutabulum**	20	21	10	51	Co	
Polytrichum formosum***	23	20	7	50	P	
Herzogiella seligeri	14	9	7	30	P	
Lophocolea heterophylla	8	8	13	29	Co	
Ceratodon purpureus***	16	10	1	27	Co	
Dicranum montanum	10	7	6	23	P	
Plagiothecium curvifolium	8	5	8	21	P	
Brachythecium velutinum	3	9	7	19	P	
Mnium hornum	4	6	8	18	PSh	
Brachythecium salebrosum	4	6	2	12	Co	
Eurhynchium praelongum	1	3	4	8	P	
Eurhynchium hians	3	3	1	7	Co	
Pseudotaxiphyllum elegans	3	1	3	7	Co	
Plagiothecium succulentum	1	5	1	7	P	
Aulacomnium androgynum	3	1	2	6	Co	
Plagiothecium laetum	3	1	1	5	P	
Polytrichum piliferum	4	0	0	4	P	
Plagiothecium denticulatum	1	2	1	4	P	
Dicranum scoparium	0	3	0	3	P	
Eurhynchium striatum	0	1	2	3	P	
Tetraphis pellucida	1	1	0	2	Co	
Isothecium alopecuroides	0	2	0	2	P	
Lepidozia reptans	0	2	0	2	Co	
Metzgeria furcata	1	0	0	1	P	

For abbreviations and explanations see Table 1. Species with significant differences in frequencies are in bold letters (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$)

number of both all species and bryophyte species was significantly higher on young and intermediate mounds than on old mounds (Table 5). The mean number of vascular plant species on young mounds was significantly higher than on both intermediate and old mounds.

The number of all species was strongly negatively related to the cover of the tree and shrub layer in all mound age classes (Fig. 1). Analysing vascular plants and bryophytes separately, however, yielded different results. While the number of vascular plant species on young mounds showed a strong negative relationship with canopy cover, no relationship was found for the number of bryophyte species. The relationship was much more pronounced on intermediate

Table 5 Total and mean number of all species as well as of different species groups on mounds of three different age classes (no. of plots = 32 each)

	Total no. of species			Mean no. of species			One-way ANOVA
	Young	Intermediate	Old	Young	Intermediate	Old	
All species	66	53	39	12.7^a	10.2^a	7.2^b	<0.001
All vascular plant species	42	27	17	5.2^a	3.3^b	2.1^b	<0.001
All bryophytes	24	26	22	7.6^a	7.0^a	5.2^b	0.001

Values with different letters are significantly different between the mound age classes

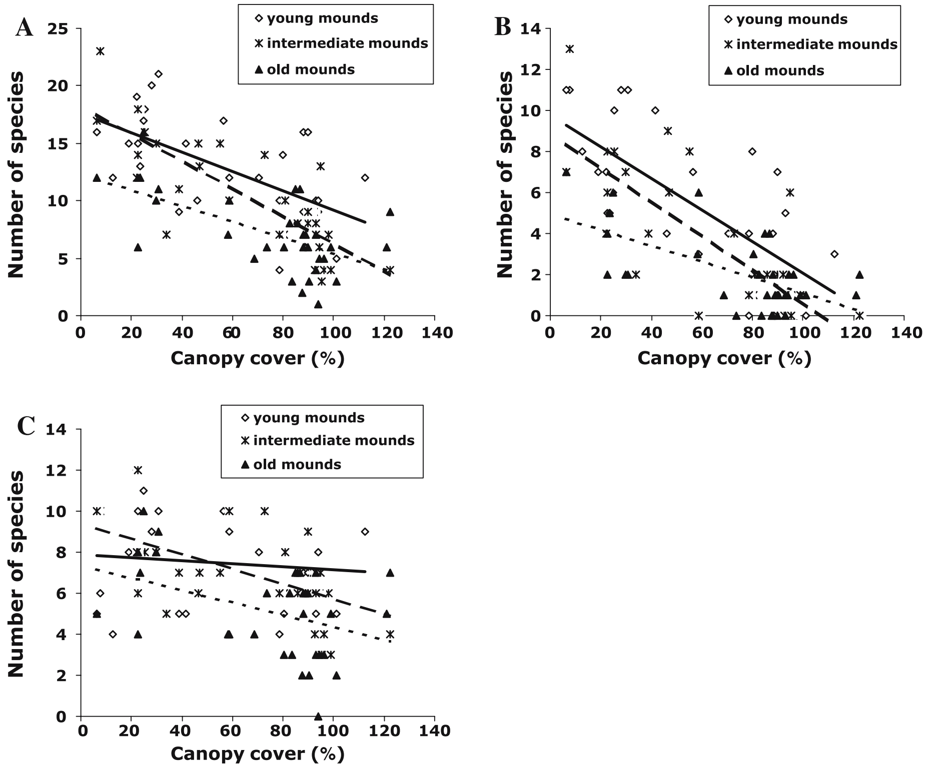

Fig. 1 Relationships between the number of species per mound and total percentage cover of the tree and shrub layer (recorded on 400 m^2 plots) in the three mound age classes. Lines are from regression analysis (solid line: young mounds, broken line: intermediate mounds, dotted line: old mounds). (**A**) All species (young mounds: $r^2 = 0.40$***; intermediate mounds: $r^2 = 0.66$***; old mounds: $r^2 = 0.43$***); (**B**) Vascular species (young mounds: $r^2 = 0.55$***; intermediate mounds: $r^2 = 0.62$***; old mounds: $r^2 = 0.43$***); (**C**) Bryophytes (young mounds: $r^2 = 0.01$; intermediate mounds: $r^2 = 0.30$**; old mounds: $r^2 = 0.19$*). *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

and old mounds for vascular plants than for bryophytes. Vascular plants and bryophytes only had similar numbers of species on young and intermediate mounds at a low canopy cover (Fig. 1). More bryophytes than vascular plant species were found on old mounds with any type of canopy cover. Simple regression analysis of the number of species on sampling area for the three mound age classes yielded very low r^2-values (all ≤0.1) and were not statistically significant (results not shown in detail).

The HOS analyses indicated that none of the interactions between covariates and fixed factor were significant for the number of all species and the number of bryophyte species. When the model was run again, we only found a significant covariate effect of canopy cover on species richness, while the other covariate mound area did not account for a significant portion of the variance in species richness (Table 6). For the number of vascular species, the HOS analysis revealed a significant interaction between mound area and mound age, indicating that mound area had different effects on the number of vascular plant species in the different mound age classes (Table 6). The slope estimates for the relationship were positive for young and intermediate mounds, and negative for old mounds. However, all slopes were not statistically different from zero (all $P > 0.05$). In all HOS models, canopy cover explained the largest amount of the variation in species numbers (Table 6).

Discussion

One of the most impressive ecological features of *F. sylvatica* is its very high competitive capacity

Table 6 Results of the homogeneity-of-slopes ANCOVAs (final models) testing for the effect of mound age (fixed factor) on the number of all species, number of all vascular species and number of bryophyte species (dependent variables), with canopy cover and mound area as covariates

Source	df	Type I SS	MS	*F*	*P*
All species ($r^2 = 0.54$)					
Canopy cover	1	885.52	885.52	81.62	<0.0001
Mound age	2	263.31	131.65	12.14	<0.0001
Error	92	998.08	10.85		
Total	95	2146.91			
All vascular plant species ($r^2 = 0.57$)					
Canopy cover	1	454.67	454.67	95.21	<0.0001
Mound area × mound age	3	120.60	40.20	8.42	<0.0001
Error	91	434.56	4.78		
Total	95	1009.83			
All bryophytes ($r^2 = 0.25$)					
Canopy cover	1	71.14	71.14	15.76	<0.0001
Mound age	2	69.49	34.75	7.70	<0.0001
Error	92	415.35	4.51		
Total	95	555.99			

For all plant species and bryophyte species, the models were rerun excluding the non-significant interaction terms between mound age and covariates

against other tree species, enabling this species to built up monodominant forests within a wide range of site conditions in Central Europe (Ellenberg 1996). However, not only the overstorey, but also the understorey vegetation in undisturbed patches of meso- to acidophytic Central European beech forests is relatively species poor (Table 2; Ellenberg 1996). This is mainly attributable to the low light levels at the forest floor, the severe root competition by *F. sylvatica* and the accumulation of a litter layer. As expected from the IDH, small-scale windthrow gaps with soil perturbation provide opportunity for the regeneration of colonizing plant species and lead to an increase in local species richness in these late-successional forests. Furthermore, our results confirm that groups of species differing with respect to important life history traits show different responses to soil disturbance (Jonsson and Esseen 1998; Rydgren et al. 1998). This study is thus giving support to the IDH, as Molino and Sabatier (2001) found in a Guianan forest, but unlike the conclusion of Hubbel et al. (1999). These differences may be explained by the different characteristics of the study forests. *F. sylvatica* is an European analogue of the shade-tolerant late-successional tree species that dominate Guianan tropical forests, whereas light demanding pioneer species are abundant in the Panamanian forests studied by Hubbel et al. (1999), possibly as a result of more intensive long-term disturbance regime (Sheil and Burslem 2003). Contrary to late-successional forests, in early successional communities any further disturbance might reduce local species richness. Dispersal and recruitment limitations are important in the Serrahn beech forests (see below), but do not preclude disturbance regime as a cause of local variation in species richness (cf. Molino and Sabatier 2001).

Response of vascular plant species

The presence of the two common shade-tolerant herb layer species *Oxalis acetosella* and *Melica uniflora* seems to be independent of soil disturbances (Tables 1 and 4). By contrast, *Moehringia trinervia* and *Dryopteris carthusiana* were favoured by tree uprooting (Table 4). While *O. acetosella* and *M. uniflora* have a transient seed bank, *M. trinervia* and *D. carthusiana* build up a persistent diaspore bank (Table 1; Rydgren and Hestmark 1997). In small-scale soil disturbance experiments in three beech forests in central Germany, Jensch (2004) found that seed germination in *O. acetosella* and *M. uniflora* was not influenced by disturbances, whereas germination of *M. trinervia* seeds was highly dependent on disturbances. Since fern gametophytes require bare mineral soil, ferns have been identified as species characteristic of PMCs in different forest ecosystems (Palmer et al. 2000). We suggest that shade-tolerant forest species (group H1.1) respond in a differential way to tree uprooting, leading to an overall absence of differences between disturbed and undisturbed plots for this group (Table 2). While some species produce large seeds that do not persist in the soil, but that enable them to establish in the presence of a litter layer, others are abundant in the soil diaspore bank and require soil disturbances and bare mineral soil for germination (cf. Jensch 2004).

Regarding habitat preferences, species that are widespread in both forests and open vegetation (group H2.1) constitute the largest group among the herbaceous species (Table 2). Some of the most frequent vascular plant species belong to this group (e.g. *Urtica dioica*, *Calamagrostis epigejos*, *Juncus effusus*, Tables 1 and 4). This species group had a significantly higher mean number of species in disturbed than in undisturbed plots (Table 2). The majority of these species are long-lived perennials, which have effective dispersal mechanisms in time and space. Due to a persistent seed bank they have been found to be abundant in many studies of the soil diaspore bank in Central European forests (Jensch 2004). The dominant colonization mechanism may therefore be the germination of seeds from the soil seed bank on exposed mineral soil (Jensch 2004; Mayer et al. 2004). Short-distance seed dispersal from nearby seed sources may only be relevant in larger gaps, since most of these shade-intolerant species rarely flower and set seed under a dense canopy or in small gaps. In the extensive beech forests of Serrahn, the colonization of disturbed microsites through seed dispersal as well as the soil seed bank replenishment of these species largely requires long-distance dispersal (i.e. >100 m). We assume that large wild mammals are the most important vectors for long-distance dispersal in these forests. Fallow deer (*Cervus dama*), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), and wild boar (*Sus scrofa*) have exhibited high densities in Serrahn for much of the past 150 years, due to its long tradition as a hunting area (von Oheimb et al. 2005a). It has been shown recently that these animals are effective epi- and endozoochorous dispersers of a wide range of vascular plant species in Central Europe, including many of the species of group H2.1 that have been found in our study (Heinken and Raudnitschka 2002; Schmidt et al. 2004; von Oheimb et al. 2005b). It has been concluded that these wild mammals primarily disperse diaspores from their preferred feeding habitats (forest meadows and openings, or forest paths) into the forests. Species with habitat preferences in both forest and open vegetation, however, do not rely only on soil disturbances caused by tree uprooting. Small-scale soil disturbances created by animals, in particular by wild boar rooting, may also allow for the establishment of these species in canopy gaps and may explain the lack of significant differences in the frequencies of the single species between the paired sample plots (Table 1).

Pioneer species such as *Epilobium angustifolium*, *Carex spicata*, or *R. idaeus* (group H1.2), which have been found to be abundant in large-scale catastrophic windthrow (Palmer et al. 2000; Fischer et al. 2002; Wohlgemuth et al. 2002) were of very limited importance in the gap-phase dynamics (Tables 2 and 4).

Response of bryophyte species

The response to uprooting was more pronounced in bryophytes than in vascular plants (Tables 1 and 2). In all mound age classes bryophytes had significantly higher mean numbers of species than vascular plants (Table 5). These results are consistent with the findings of Jonsson and Esseen (1998) and Heinken and Zippel (2004) in coniferous forests of the boreal and temperate zone, where bryophytes create dense carpets on the forest floor. Rapid response of bryophytes to gaps in the closed layer of cryptogams had been attributed to their high abundance on the forest floor, a great variety of regeneration strategies and large numbers of propagules. The cover of bryophytes is very low in undisturbed patches of temperate deciduous forests, where leaf litter is the most important factor limiting bryophyte establishment on the forest floor (Schumacher

2000). However, Central European beech forests are not generally poor in bryophytes, but they mainly occur on substrates other than the undisturbed forest floor. Schumacher (2000) found living trees and dead wood to be the most species-rich substrates. Ubiquitous species such as *Hypnum cupressiforme*, *Brachytecium rutabulum*, and *Mnium hornum* are frequently observed at the root collar and the lower areas of the trunk (Schumacher 2000). After uprooting these species are already present at the microsite and can rapidly colonize the exposed mineral soil by local propagule dispersal (distance less than 1 m) and clonal encroachment. Short-distance dispersal of epiphytic species such as *Dicranum montanum* from surrounding living trees (distance of several metres) is an also probable mechanism for colonization due to the small gap sizes. The high quantities of dead wood (over 200 m^3/ha have been observed in gaps, von Oheimb et al. 2007) make up another abundant source of bryophyte propagules in Serrahn. Besides ubiquitous species such as *H. cupressiforme* and *B. rutabulum*, which have been found to be very abundant on dead wood (Schumacher 2000), bryophytes with substrate preference on dead wood were also frequently recorded in the disturbed microsites (e.g. *Herzogiella selegeri*, *Lophocolea heterophylla*; Tables 1 and 4). For all of these species only short-distance dispersal of vegetative or generative diaspores is needed to colonize the disturbed microsites. In bryophytes, diaspores include not only spores and specialized asexual propagules, but also detached stems or buried old stem fragments (During 1997). Heinken and Zippel (2004) showed that in addition to clonal ingrowth from the edge, detached and fragmented stems played an important role in the re-colonization of experimentally disturbed plots. Frego (1996) observed detached or fragmented stems within several metres of their origin. On a local scale, possible dispersal vectors include wind, slugs, and small mammals (Kimmerer and Young 1995; Heinken and Zippel 2004). However, as shown by Heinken et al. (2001), dispersal of stem fragments is not completely limited to short distances. Long-distance dispersal may be facilitated by epizoochorous transport of stem fragments by wild mammals. The authors found several bryophyte species in the coats and hooves of wild boar and roe deer, among them *H. cupressiforme* and *Ceratodon purpureus*.

It has been shown that an extensive and species-rich diaspore bank of bryophytes occurs in forest soils (During et al. 1987; Jonsson 1993; During 1997; Rydgren and Hestmark 1997). Colonists and short-lived shuttle species dominate in the soil-buried diaspore bank, while perennials are rare or absent (During et al. 1987; Jonsson 1993). Therefore, regeneration from the diaspore bank after litter removal by uprooting seems to be of particular importance for the species of these life strategy types. The abundant species *Atrichum undulatum*, *Dicranella heteromalla*, and *Pohlia nutans* probably became established predominantly from the soil diaspore bank. These species have frequently been found in disturbed microsites of the forest floor (Jonsson and Esseen 1998; Heinken and Zippel 2004; Kimmerer 2005) and rarely occur on other substrates in beech forests (Schumacher 2000).

In conclusion, we suggest that three factors are mainly responsible for the larger differences in species richness and composition of bryophytes than vascular plants between disturbed and undisturbed patches in Serrahn. With regard to the forest floor, there is a lower availability of microsites suitable for bryophyte than for vascular plant recruitment. Vascular plants may also become established in the presence of a litter layer or in small-scale soil disturbances where the mineral soil is exposed for only a short time (less than one year). By contrast, successful bryophyte recruitment requires bare mineral soil that does not develop a litter layer for at least some years. Although the number and cover of bryophytes on the forest floor is even lower than that of vascular plants, more propagules are available in the close vicinity and in the soil of the disturbed microsite. Finally, bryophytes probably benefit from the greater variety of regeneration strategies than vascular plants.

Temporal dynamics

Comparing mounds of different age classes revealed that the time since mound formation is a major factor determining plant species richness and composition (Tables 4–6). This observation is in general agreement with the literature (e.g. Jonsson and Esseen 1990; den Ouden and Alaback 1996; Palmer et al. 2000; Ulanova 2000). However, considerable differences have been found in the development of changes in species richness and composition through time and the temporal dimensions of these changes. Compositional changes following catastrophic windthrow in two Minnesota forests were strongest during the first few years (Palmer et al. 2000). Species richness peaked 10 years after disturbance when species of various tolerances were present at the disturbed microsite. Den Ouden and Alaback (1996) suggested that the major changes in species composition on mounds occur within a time span of less than 50 years, while thereafter species diversity did not change significantly. In contrast, Ulanova (2000) recorded the highest number of herb layer species on 40–80 years old mounds and Jonsson and Esseen (1990) found a peak in bryophyte diversity on mounds approximately 100 years old. In our study the highest mean number of both vascular plant and bryophyte species was recorded on young mounds (Table 5). However, while significant differences in the mean number of species of vascular plants were found between young and intermediate as well as old mounds, the main differences occurred between intermediate and old mounds in bryophytes. We suggest that different mechanisms are responsible for these differences. A large number of exclusive vascular plant species was observed on young mounds, among them several disturbance specialists. About 12 years after mound formation both the total and the mean number of vascular plant species decreased heavily. Although the mounds showed continued within-microsite disturbances due to erosion of the soil, this did not result in a continuous presence of many vascular plant species. The majority of vascular plant species failed to build up viable populations on the mounds, their soil diaspore bank is presumably depleted on older mounds (see the strong decrease of species with a persistent seed bank over time, Table 4), and they have negligible colonization rates. In contrast, not only the total number, but also the proportions of the different species groups of bryophytes remained essentially the same over time (Table 4). Jonsson and Esseen (1990) reported that early successional bryophytes such as *P. nutans* and *Polytrichum alpinum* were still present in disturbed microsites that were 120–150 years old. We suggest that the main reason for the decrease in the mean number of bryophytes is the development of a litter layer on the mounds with time. This equally reduces the abundance of bryophytes with different life strategies. Competitive exclusion by dominant species may not be the main factor because of relatively low total cover values on the mounds (cf. Heinken and Zippel 2004; Kimmerer 2005).

Gradient of canopy cover

It has been well established that canopy gap size is a major factor determining post-disturbance plant species composition (Schaetzl et al. 1989). Canopy gap size depends on tree size and crown dimensions and whether a gap is formed by single or multiple treefalls. In Serrahn the average diameter at breast height (DBH) of the uprooted beech trees was 58 cm (von Oheimb, unpubl. data). Tabaku (2000) recorded a mean crown area of about 125 m^2 for beech trees with a DBH of 60 cm, and very large beech trees may have a crown area of over 200 m^2. All gaps in the upper canopy in the old-growth forests of Serrahn were determined using aerial photographs (von Oheimb, unpubl. data). The mean gap size was 292 m^2 and the vast majority of canopy gaps (82%) was smaller than 400 m^2, created by the mortality of one or a small group of canopy trees. In Serrahn canopy gaps are formed by multiple causes (von Oheimb et al. 2007). While about one-third of the canopy tree died by uprooting, over one-half of the trees died by snapping of the trunk. Additionally, canopy trees that died standing contribute to canopy gap formation. Such gap-phase dynamics have also been observed in other Central and south-eastern European old-growth beech forests (Tabaku 2000; Drößler and von Lüpke 2004). In an old-growth Appalachian cove forest, Busing (1994) determined a gap size of 400 m^2 as a threshold size below which shade-intolerant tree species were not able to establish. The predominantly small gap sizes in Serrahn are thus a major factor explaining the infrequent and short-lived establishment of shade-intolerant pioneer species (Collins and Pickett 1987). In addition, a dense beech understorey has become established over large tracts of the total forest area, and therefore canopy gaps often do not correspond to understorey gaps. It is mainly for these two reasons (canopy gap size distribution and establishment of beech understorey) that the disturbed and adjacent undisturbed sample plots did not differ significantly in canopy cover.

Due to the variation in both, the canopy gap size and the abundance of advanced beech regeneration, a gradient of canopy cover and thus a light gradient is reflected in the chronosequence study (Fig. 1). Härdtle et al. (2003) showed that the number of ground layer species in undisturbed patches of the forest floor was mainly affected by the canopy closure in acidophytic beech forests of northern Germany. This has been explained by the large proportion of heliophilous species among the acid tolerant species of these forest communities. In our study we demonstrated that this relationship is also true for disturbed patches of the forest floor (Fig. 1, Table 6). However, considerable differences became apparent when treating vascular plants and bryophytes separately. Vascular plants exhibited a much stronger reaction along the light gradient than did bryophytes (Table 6). The number of bryophytes on young mounds was actually independent of the canopy cover (Fig. 1). Obviously more bryophyte than vascular plant species have the ability to colonize localized disturbances under dense shade (Den Ouden and Alaback 1996). The edaphic conditions (lack of litter layer) on recently created mounds are clearly more important for bryophytes than the light conditions. Based on the results of our study we cannot state whether the gradient of litter accumulation parallels the gradient of canopy cover on intermediate and old mounds and, if so, how this might influence the number of species recorded on these mound age classes. This remains to be tested in further studies.

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