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Effects of fire severity on understory community regeneration and early succession after burning of moist pine forest

Effekte der Feuerstärke auf die Regeneration der Waldbodenvegetation nach Brand in einem feuchten Kiefernwald

Zbigniew Dzwonko*, Stefania Loster & Stefan Gawroński

Institute of Botany, Jagellonian University, ul. Kopernika 31, 31-501 Kraków, Poland
**Corresponding author, e-mail: ubdzwonk@cyf-kr.edu.pl*

Abstract

The interaction between fire severity (measured as the degree of organic soil layer consumption) and species regeneration strategy has been suggested to explain early post-fire vegetation dynamics in coniferous forests. To test this hypothesis we analyzed 14 years of succession on permanent plots after a wildfire in moist Scots pine (*Pinus sylvestris* L.) forest on muck-peat soil in southern Poland. Plots were established at heavily, partly and slightly burned sites, as well as in unburned forest. In the first three post-fire years, establishment was best for vascular plant invaders (regenerating from seeds transported after the fire) on heavily burned plots, seed bankers on partly burned plots, and vegetatively regenerating sprouters on slightly burned plots. In the third year after the fire, cover of bryophyte species was significantly higher on heavily burned plots than on less burned plots. This initial response of species strongly influenced the composition of understory vegetation in subsequent years. During the 14-year period the changes in vegetation were greatest on heavily burned plots, less on partly burned plots, and least on slightly burned plots. Birch woods developed on all burned sites, but the understory vegetation differed significantly in composition and cover between heavily burned and less burned plots. On the more severely burned plots, strong competition from developing tree invaders hindered understory growth. On slightly burned plots, where herb sprouter cover increased most markedly, bryophytes disappeared over the course of nine years. The results indicate that the spatial variability of fire severity in moist pine forest leads to long-lasting heterogeneity of post-fire forest communities, whose diversity will persist for decades.

Keywords: disturbance, fire severity, permanent plots, regeneration strategies, Scots pine forest, secondary succession

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Fire history investigations in Central Europe suggest that fire had a pronounced effect on prehistoric vegetation, especially during the Neolithic, when slash-and-burn forest clearance was an important practice (TINNER et al. 2005). The opening of vegetation cover through the use of fire is widely observed in the Iron Age and Middle Ages, probably corresponding to

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the spread of permanent cultivation on largely open landscape (ROBIN & NELLE 2014). In Central Europe, in contrast to Southern and Northern Europe, fires are not the most important factor shaping the contemporary forest vegetation (ELLENBERG 1988, FISCHER et al. 2013), although fires may play an essential role in regions where pine forests grow on poor sandy soil (ADÁMEK et al. 2015, DITTRICH et al. 2016). Although more than half of Poland is habitat for mesophilous broadleaved woods, coniferous forests presently dominate; most of them are Scots pine (*Pinus sylvestris* L.) forests. This is because the coniferous forests growing on very poor soils were not extensively cleared for agriculture, and coniferous trees, mainly Scots pine, are still preferred for economic reasons (MATUSZKIEWICZ 1999). According to *Forest Fires in Europe 2009* (SCHMUCK et al. 2010), Poland ranks third (after Portugal and Spain) with respect to the average number of forest fires per year, and eighth in terms of area of burned forest. The number of fires is highest between March and September. Forest fires are usually associated with periods of low precipitation, particularly during prolonged drought accompanied by high temperature, but human activity is the main and immediate cause of fires (SZCZYGIEŁ 2012). In burned areas, forests are often artificially regenerated by plowing the soil and sowing tree seeds or planting seedlings. In recent decades, Polish forestry practice has accorded increasing importance to natural forest regeneration. Although the relation between the general development of tree stands and habitat conditions at burned sites has been recognized (e.g., HAWRYŚ et al. 2004, ZWOLIŃSKI et al. 2004, DOBROWOLSKA 2008), little is known about the responses of understory vegetation to variation of fire severity in the coniferous forests of Central Europe, nor about the role of this vegetation in forest regeneration.

In boreal coniferous forests, fire severity has a significant impact on regeneration and initial succession; it can determine species abundance and community composition for years and even decades after a fire (WANG & KEMBALL 2005, JOHNSTONE & CHAPIN 2006, RUOKOLAINEN & SALO 2009, BERNHARDT et al. 2011, HOLLINGSWORTH et al. 2013). Fire is a primary determinant of understory vegetation, which can be a major driver of post-fire forest conditions. Dense understory reduces light availability at the forest floor and hinders the germination, growth and survival of cohorts of young plants (MESSIER et al. 1998, AUBIN et al. 2000). In the long term, understory vegetation can also affect soil processes that regulate the nutrient supply to trees (NILSSON & WARDLE 2005).

Fire *severity* is a term usually applied to the degree of organic material consumption or vegetation mortality – the direct effects of fire (ROWE 1983, BOBY et al. 2010). In most studies of fire in boreal forests, the degree of fire severity is graded based on measurements or visual assessments of vegetation and organic soil consumption. The amount of organic material consumed by a fire is one of the most important components of the fire regime influencing post-fire regeneration patterns. It may affect both the availability of plant propagules and the properties of post-fire soil (ROWE 1983, SCHIMMEL & GRANSTRÖM 1996, CERTINI 2005, SMITHWICK et al. 2005). *Severity* depends on the intensity and duration of a fire (SCHIMMEL & GRANSTRÖM 1996, CERTINI 2005, WANG & KEMBALL 2005).

Fire *intensity* is the rate at which a fire produces thermal energy. Studies of coniferous boreal forest species indicate that grasses, herbs, dwarf shrubs and bryophytes usually die even in a low-intensity fire because of their small size and their lack of protection by thick bark. The response of underground parts of plants depends much on the soil temperature (FLINN & PRINGLE 1983, GRAMSTRÖM & SCHIMMEL 1993). That temperature falls sharply with soil depth: lethal temperature does not occur below 2–3 cm beneath the burn boundary

(SCHIMMEL & GRANSTRÖM 1996). This means that in an intense aboveground fire the underground parts of plants occurring slightly deeper in the soil can survive. The depth distribution of seeds and rhizomes in the soil determines their ability to survive deep-burning fires.

More severe fires create more open places devoid of vegetation, litter and part of the organic soil layer, where wind-dispersed seeds can easily germinate and may develop seedlings originating from reproductive plants occurring in the near or more distant vicinity of the burned area, as well as from locally occurring plants that survived the fire. The relationship between fire severity in coniferous forests and the development of vegetation and its succession has been studied in detail in Fennoscandian boreal forests (SCHIMMEL & GRANSTRÖM 1996, SKRE et al. 1998, RUOKOLAINEN & SALO 2009) and in boreal and subalpine forests of North America (TURNER et al. 1997, PURDON et al. 2004, WANG & KEMBALL 2005, BERNHARDT et al. 2011). The majority of these studies concern forest ecosystems on poor podzolized soils with a thinner or thicker mor layer on mineral soil. Experiments by SCHIMMEL & GRANSTRÖM (1996) demonstrated that the initial succession in boreal Swedish forests depends strongly on the relationship between the depth of the burned organic soil layer and the mode of plant regeneration: with depth of burn, species that depend on post-fire seed dispersal increase in importance, and rhizomatous sprouting species decrease in importance, and seed bank species may have an advantage at relatively deeply burned sites when the buried seed bank is exposed and some competitors are killed off. Similarly, WANG & KEMBALL (2005) suggested that initial regeneration of the understory community in Canadian boreal mixed woods after fire is largely controlled by interactions between fire severity and species regeneration strategy. Establishment is best for invaders on severely burned sites, seed bankers on lightly burned sites, and sprouters on scorched sites.

These relationships may apply generally to some Central European lowland coniferous forests that grow on soil with a thick layer of organic matter. To examine this possibility we analyzed 14 years of observational records of plant colonization and development of understory vegetation on permanent plots after a wildfire in a moist pine forest on muck-peat soil in southern Poland. This forest was subjected to fire varying in intensity and duration, resulting in a mosaic of fire severity within the burned area. We addressed the following questions: (1) what is the relation between fire severity and the rate and pattern of understory vegetation regeneration; (2) do species with different regeneration strategies respond differently to variation of fire severity, and if so, to what extent; and (3) what are the mechanisms responsible for the dynamics of post-fire understory communities.

2. Materials and Methods

2.1 Study area

The study area lies near the town of Chrzanów in the southern part of the Silesian Upland, southern Poland, in the Kroczymiech Forest District (50°07'54"N, 19°19'30"E; 259 m a.s.l.). The vast forest complex within this area is composed largely of moist pine forest (*Molinio coeruleae-Pinetum* W. Mat. et J. Mat. 1973 association) with dominant *P. sylvestris* and with admixture of *Betula pendula*, *B. pubescens* and *Picea abies*. In the field layer, *Deschampsia flexuosa*, *Molinia caerulea*, *Vaccinium myrtillus* and *V. vitis-idaea* predominate. In the ground (bryophyte) layer, *Brachythecium rutabulum*, *Pleurozium schreberi* and *Pohlia nutans* prevail. These are remnants of ancient natural forests which have been managed for a long time. Drainage work started in the wettest parts of the forest complex in the 1920s. The main drainage work was done in the 1950s, causing lowering of the water table and drying of the topsoil. At present the soil is most often muck-peat (Sapri-Dystric Histosol) with a thicker

or thinner layer of muck (amorphous peat) on sand. The habitat conditions of these forests were described in more detail by DZWONKO et al. (2015). In June 1992, a wildfire described as an underground, surface and crown fire occurred on 20 ha of moist pine forest. The duration of the initially severe fire varied through the area. At the most severely affected sites the muck layer smoldered from June until mid-September. This variation resulted in a mosaic of differently burned field layer vegetation, ground layer vegetation and soil organic matter. In the spring of 1993 we estimated organic soil consumption at points near pine stumps in more burned places, measuring height from the top of the remaining organic soil to the root collar of tree stumps. We used the root collars as an indicator of the pre-fire level of the organic layer because in the unburned forest the root collars of pine trees were, as a rule, at the top of the organic soil. According to these measurements, in heavily burned places the muck layer was consumed to 20 cm depth on average, maximally to 40 cm depth. In all places the tree and shrub layers were completely destroyed. For the purpose of the long-term study, an area covering 0.35 ha was left unmanaged. Only the burned trunks and fire-damaged trees were removed. The fire markedly altered soil properties. Total nitrogen (N) was most reduced in more severely burned areas. A fire-severity-dependent increase of calcium (Ca), phosphorus (P), potassium (K), magnesium (Mg) and the sum of basic cations persisted two or three years after the fire. From the beginning of post-fire succession, *B. pendula* was dominant at all sites, with a small share of *P. sylvestris*. The rate of tree species colonization and birch development and the cover of all trees were highest on more severely burned sites and lowest on slightly burned sites (DZWONKO et al. 2015).

2.2 Data collection and analysis

In the spring of 1993, 50 permanent plots (5 m x 5 m) were established systematically throughout the area designated for research and in the adjacent unburned forest. The plots were spaced at 5 m intervals in four rows 5 m apart. Three rows were more than 140 m long and one was 90 m long. Fire severity was graded for each plot at the time of demarcation. As fire severity refers to the degree of organic material consumption and vegetation mortality, the percentage cover of burned soil organic matter, approximate depth of muck consumption and the cover of surviving vegetation were assessed visually and recorded. We graded fire severity in three classes: (1) heavily burned: over 50% of muck layer surface (85% on average) deeply consumed, field layer vegetation cover less than 20%; (2) partly burned: 20–50% of muck layer surface (34% on average) consumed (not deeply), vegetation cover 20–40%; and (3) slightly burned: less than 10% of muck layer surface (3% on average) lightly consumed, vegetation cover greater than 40%. Similar classes have been used to characterize fire severity in various studies of boreal forests (e.g., WANG & KEMBALL 2005, BERNHARDT et al. 2011). Twenty-four plots were at heavily burned sites, nine at partly burned sites, nine at slightly burned sites, and eight in unburned forest. Each May from 1993 to 2006 (except for 2005), for each plot we estimated the percentage cover (at 10% estimation intervals) of all vascular plant species in the field (less than 1.5 m high), shrub and tree layers, and bryophytes in the ground layer. For these plots we had also assessed the effects of fire severity on soil properties and the development of trees and shrubs (DZWONKO et al. 2015).

We classified the vascular plant species in three regeneration strategy groups, based on our observations and information from the literature (ROWE 1983, SCHIMMEL & GRANSTRÖM 1996, WANG & KEMBALL 2005). We also divided them into seven dispersal groups, and into five groups according to growth form and lateral vegetative spread (Table 1). The values and categories of these traits were determined for each species using the databases of FITTER & PEAT (1994), GRIME et al. (2007) and KLEYER et al. (2008). Among the bryophytes, species adapted to fire disturbance were distinguished according to ESSEEN et al. (1992), RYÖMÄ & LAAKA-LINDBERG (2005) and HYLANDER & JOHNSON (2010). Nomenclature follows TUTIN et al. (1964–1980) for vascular plant species, and OCHYRA et al. (2003) and SZWEYKOWSKI (2006) for bryophytes.

Canonical correspondence analysis (CCA, CANOCO program, TER BRAAK & ŠMILAUER 1998) with time as explanatory variable was used to assess changes in field layer species cover in the study area over the 14 years from 1993 to 2006. We tested only the first CCA axis because only this axis was

Table 1. Regeneration strategy types and traits of plants used in this study.

Tabelle 1. In dieser Studie verwendete Strategietypen der Regeneration und Pflanzenmerkmale.

Strategy/Trait	Short description
Regeneration strategy	
Invader	Highly dispersive pioneer species
Sprouter	Regeneration mainly from surface or buried buds
Seed banker	Regeneration from buried seeds
Dispersal mode	
Hovering anemochore	Diaspores with pappus of less than 1.5 mg in weight or diaspores without pappus of less than 0.1 mg in weight
Light anemochore	Diaspores with pappus of less than 3 mg in weight or without pappus ones no more than 0.5 mg in weight
Heavy anemochore	Winged diaspores of less than 3 mg in weight or unwinged ones no more than 1.5 mg in weight
Endozoochore	Diaspores with fleshy fruits
Epizoochore	Diaspores adhesive with awns, spiny calyx teethes or mucilage
Dyszoochore	Nuts or related type of hard-coated diaspores
Myrmecochore	Seeds with elaiosomes
Growth form	
Annual and biennial	
Perennial with single or several shoots	
Perennial with compact rhizomes	Perennial with compact unbranched rhizomes or forming small tussock less than 15 cm in diameter
Perennial with short vegetative spread	Perennial attaining diameter of 15-100 cm
Perennial with long vegetative spread	Perennial attaining diameter more than 100 cm

constrained – it explained the total variance of fitted species data. Permutation tests under a reduced model with the split-plot design option were done in each case. As the analyses covered 8 to 24 time series, to avoid problems with autocorrelation we ran 999 permutations restricted to the same cyclic shifts within parallel time series (cf. TER BRAAK & ŠMILAUER 1998). The total changes in community composition were characterized by the length of the gradient for the first axis of detrended canonical correspondence analysis (DCCA) with detrending by segment and with time as explanatory variable. To learn whether the role of fire severity as a determinant of species composition and cover decreases during succession, such that the post-fire understory communities would converge to a state similar to that of unburned forest, we carried out PERMANOVA non-parametric multivariate analysis of variance (ANDERSON 2001; PAST program, HAMMER et al. 2001) comparing dissimilarities between plots within every year with 9999 permutations. The Bray-Curtis index and its equivalent for presence-absence data (Sörensen's coefficient) were used to calculate dissimilarity matrices. We then calculated the correlation ratio η^2 (ZAR 2010), which expresses the proportion of total variability of plots that is accounted for by the effect of differences among the groups of plots. η^2 was used as a measure of the fire-severity-explained variability of communities in each year. To estimate the differences between the vegetation characteristics of the study sites within years, we employed non-parametric analysis of variance, the Kruskal-Wallis test, and multiple comparisons according to the Conover (CONOVER 1999). Between-year differences in vegetation characteristics at the same sites were analyzed by the Friedman test and by pair-wise comparisons after Conover. These analyses were performed using BrightStat (STRICKER 2008). Non-parametric analyses were applied, as the compared vegetation characteristics did not show normal distributions and their variances were not homogeneous.

3. Results

3.1. Temporal variation of community composition

We recorded 88 vascular plant species and 16 bryophyte species during the 14-year study period (Supplement S1). CCA with time as explanatory variable revealed significant changes in the cover of species in the understory vegetation on all study sites (Table 2). Comparisons of gradient length along the first DCCA axes indicate that the greatest changes occurred on heavily burned plots, less on partly and slightly burned plots, and least in unburned forest. During the study period the heavily burned plots had the fewest persistent species, but many more immigrant species appeared there than on less burned plots (Table 3). Considerably fewer species became extinct on slightly burned than on more severely burned plots.

According to PERMANOVA the species composition of the understory vegetation differed significantly between the compared plots after 14 years of succession, though one year after the fire it did not differ between partly and slightly burned plots, and from the fourth to the tenth year it did not differ between heavily and partly burned plots (Table 4). In species cover the plots in all study sites differed considerably during the first nine post-fire years. Thereafter, species cover on the partly and slightly burned plots became similar. The decreasing values of the correlation ratio (η^2) in successive years indicate a temporal decrease in the differences in understory vegetation composition between burned plots and unburned forest (Pearson correlation coefficient for η^2 and years from the second post-fire year: $r = 0.32$ for burned sites, $p > 0.3$; $r = -0.78$ for all sites, $p < 0.01$), and a temporal decrease in the differences in species cover between the variously burned plots and between burned plots and unburned forest ($r = -0.94$ for burned sites, $p < 0.001$; $r = -0.70$ for all sites, $p < 0.05$).

3.2. Plant regeneration strategy and vegetation changes

Among the vascular plants, invaders formed the largest group on all burned plots, including 14 tree and shrub species and 47 herbaceous species. We recorded 19 sprouters and 8 seed bankers. The two latter groups were represented only by dwarf shrubs and herbs. The majority of the observed species had low cover. Only 12 vascular plant species (3 invaders, 8 sprouters, 1 seed banker) and 4 bryophytes had highest mean cover exceeding 2.5% on burned plots (Supplement S1). In the first post-fire year there were significantly fewer

Table 2. Results of CCA with time as explanatory variable. Eigenvalue (λ_1) corresponds to the first axis. *r* indicates species-environment correlations. *p* denotes the probability of no changes in species cover in understory vegetation on the study sites during 1993–2006. Gradient length corresponds to the first DCCA axis.

Tabelle 2. Ergebnisse der CCA mit Zeit als erklärender Variable. Der Eigenwert (λ_1) entspricht der ersten Achse. *r* bezeichnet Art-Umwelt-Korrelationen, *p* die Wahrscheinlichkeit fehlender Änderungen im Deckungsgrad des Unterwuchses der Untersuchungsflächen zwischen 1993 und 2006. Die Gradientenlänge entspricht der ersten DCCA-Achse.

	λ_1	*r*	*p*	Gradient length
Heavily burned site	0.25	0.86	0.037	1.62
Partly burned site	0.11	0.86	0.036	1.06
Slightly burned site	0.08	0.66	0.038	0.80
Unburned forest	0.04	0.64	0.037	0.59

Table 3. Vascular plant species turnover in understory vegetation on the plots in 1993-2006. Values are mean species numbers. Persistent species: present from 1993 to 2006. Extinct species: present in 1993 and extinct before 2006. Immigrant species: absent in 1993 but later appearing and present until 2006. Transient species: absent in 1993 later appearing and extinct before 2006. Within rows, values bearing the same letter do not differ significantly at $p > 0.05$.

Tabelle 3. Gefäßpflanzen-Fluktuation im Waldunterwuchs der Probeflächen zwischen 1993 und 2006. Die Werte sind mittlere Artenzahlen. Persistente (bleibende) Arten: vorhanden von 1993 bis 2006. Ausgestorbene Arten: 1993 vorhanden, ausgestorben vor 2006. Eingewanderte Arten: 1993 fehlend, später auftauchend und vorhanden bis 2006. Transiente (vorübergehende) Arten: 1993 fehlend, später auftauchend und ausgestorben vor 2006. Innerhalb der Reihen unterscheiden sich Werte mit dem gleichen Buchstaben nicht signifikant bei $p > 0{,}05$.

	Heavily burned site	Partly burned site	Slightly burned site	Unburned forest	*p*
Number of plots	24	9	9	8	
Persistent species	6.7	8.9^{A}	9.0^{A}	10.9^{A}	< 0.001
Extinct species	7.5^{A}	8.2^{A}	5.2	1.5	< 0.001
Immigrant species	7.6	5.1^{A}	3.3^{A}	3.8^{A}	< 0.001
Transient species	4.8^{A}	3.8^{AB}	3.6^{AB}	1.9^{B}	< 0.050

species on heavily burned plots than on partly and slightly burned plots (Fig. 1). Irrespective of fire severity, species richness increased significantly in the second year after the fire (Friedman and Conover tests, $p < 0.001$), and until the end of observations did not differ markedly between the variously burned plots.

The number and cover of all invaders significantly increased at burned sites shortly after the fire (Friedman and Conover tests, $p < 0.01$), reaching the highest values in the second and third years (Table 5). In those years the number of invasive species was similar on the variously burned plots but their cover differed notably, being highest on heavily burned plots, lower on partly burned plots and lowest on slightly burned plots. Such great differences in cover of invaders resulted from abundant colonization of more severely burned plots by light-anemochorous trees, mostly *Betula pendula* and *B. pubescens* (Fig. 2). The highest mean cover of light- anemochorous trees was 38.9% on heavily burned plots, 21.4% on partly burned plots and 6.4% on slightly burned plots. In the second and third post-fire years the cover of herbaceous invaders was similar on all burned plots but their number of species was considerably higher on heavily and partly burned plots than on slightly burned plots (Table 5). Among the invasive herbs, species most effectively dispersed by wind (hovering anemochores) prevailed. The most frequent herb colonizer was *Epilobium angustifolium*. Much less frequent were other perennial species such as *Agrostis capillaris*, *Deschampsia caespitose*, *Eupatorium cannabinum*, *Rumex acetosa* and *Taraxacum officinale*, as well as annuals including *Conyza canadensis*, *Senecio vernalis* and *S. vulgaris*. From the fourth post-fire year fire onwards, the cover of invaders in the understory vegetation decreased significantly on heavily and partly burned plots (Friedman and Conover tests, $p < 0.01$). In that period, fast-growing woody invaders began to form a shrub layer, increasingly shading the understory vegetation; this proceeded most intensively on the heavily burned plots (Fig. 1, 2).

As early as the second year after the fire, significantly more seed bankers (e.g., *Calluna vulgaris*, *Moehringia trinervia*, *Scrophularia nodosa*, *Stellaria longifolia*) grew on the partly burned plots than on the heavily and slightly burned plots (Table 5). The highest

Table 4. Results of PERMANOVA used to test differences in the composition and cover of vascular plant species in understory vegetation on different sites: Hb – heavily burned site, Pb – partly burned site, Sb – slightly burned site, Uf – unburned forest. η^2 is the correlation ratio. p denotes the probability of no difference between all sites. Within rows, sharing of the same letter indicates no significant difference between sites at $p > 0.05$, based on pair-wise tests with the Bonferroni correction.

Tabelle 4. Ergebnisse der PERMANOVA zum Test auf Unterschiede in der Zusammensetzung und dem Deckungsgrad von Gefäßpflanzen im Waldunterwuchs unterschiedlicher Standorte: Hb – stark verbrannt, Pb – geringer verbrannt, Sb – leicht verbrannt, Uf – nicht verbranntem Wald. η^2 ist das Korrelationsverhältnis. p bezeichnet die Wahrscheinlichkeit fehlender Unterschiede zwischen allen Standorten. Innerhalb der Reihen unterscheiden sich Werte mit dem gleichen Buchstaben nicht signifikant bei $p > 0{,}05$; basierend auf paarweisen Tests mit Bonferroni-Korrektur.

	Presence/absence of species							Cover of species						
Year	Hb	Pb	Sb	Uf	η^2 (%) burned sites	η^2 (%) all sites	p	Hb	Pb	Sb	Uf	η^2 (%) burned sites	η^2 (%) all sites	p
1993	A	B	B	C	15.9	23.8	< 0.001	A	B	C	D	26.2	36.5	< 0.001
1994	A	B	C	D	20.9	38.9	< 0.001	A	B	C	D	30.1	41.6	< 0.001
1995	A	B	C	D	16.1	37.2	< 0.001	A	B	C	D	33.8	44.8	< 0.001
1996	A	A	B	C	15.7	37.5	< 0.001	A	B	C	D	30.8	40.6	< 0.001
1997	A	A	B	C	16.0	36.5	< 0.001	A	B	C	D	25.4	35.9	< 0.001
1998	A	A	B	C	15.0	32.7	< 0.001	A	B	C	D	24.4	34.8	< 0.001
1999	A	A	B	C	14.4	31.6	< 0.001	A	B	C	D	23.8	34.6	< 0.001
2000	A	A	B	C	16.1	34.5	< 0.001	A	B	C	D	21.8	33.1	< 0.001
2001	A	A	B	C	17.8	35.4	< 0.001	A	B	C	D	22.0	35.2	< 0.001
2002	A	A	B	C	18.9	35.7	< 0.001	A	B	B	C	18.2	36.3	< 0.001
2003	A	B	C	D	19.7	33.4	< 0.001	A	B	B	C	18.9	37.3	< 0.001
2004	A	B	C	D	19.8	32.5	< 0.001	A	B	B	C	17.7	34.4	< 0.001
2006	A	B	C	D	18.1	29.0	< 0.001	A	B	B	C	17.2	33.8	< 0.001

cover of seed bankers on partly burned plots was noted in the ninth and tenth post-fire years, when plants of *C. vulgaris*, the most abundant species of this group, reached their greatest height (Fig. 1). In later years the cover of these species decreased significantly (Friedman and Conover tests, $p < 0.001$) on all burned sites until the end of observations, but remained highest on partly burned plots.

The cover of sprouters increased significantly ($p < 0.01$) on burned sites as early as the third post-fire year; it increased most on slightly burned plots (Fig. 1). From the beginning of observations, the cover of sprouters was lower on heavily burned than on less burned plots. The abundance of these species (e.g., *Calamagrostis arundinacea*, *Deschampsia flexuosa*, *Molinia caerulea*, *Pteridium aquilinum*, *Vaccinium myrtillus*) increased markedly on heavily burned plots in subsequent years but was lower than on less burned plots until the end of observations. These species regenerated almost exclusively vegetatively; only a few seedlings of them were found. Seedlings of anemochorous *M. caerulea* emerged in the second and third years after the fire as a result of local seed dispersal from plants that survived the fire. These seedlings were most abundant on heavily and partly burned plots but their average cover did not exceed 3%. Sparse seedlings of endozoochorous *V. myrtillus* were found on these plots from the fifth year, when the shrub layer was formed.

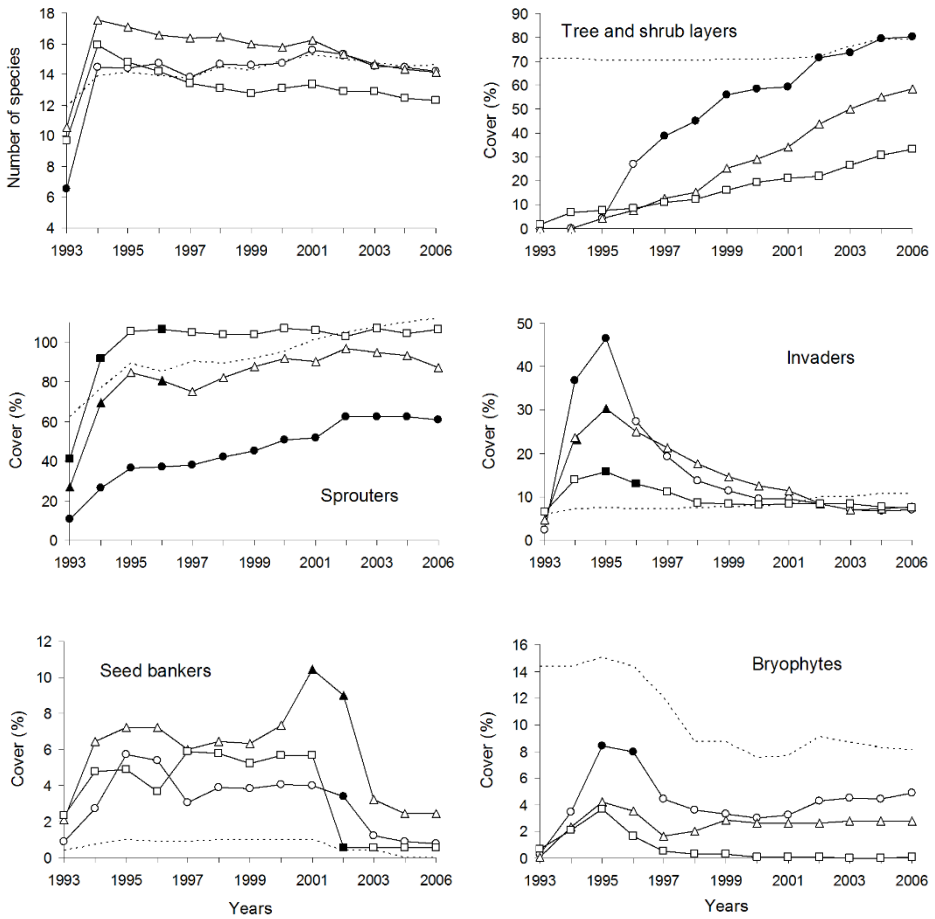

Fig. 1. Mean number of vascular plant species, mean total cover of the tree and shrub layers, and total cover of invaders, sprouters, seed bankers and bryophytes in the understory on heavily (○), partly (△) and slightly (□) burned plots, and in unburned forest (- - -) during 1993–2006. Empty symbols in the same year indicate no significant difference at $p > 0.05$.

Abb. 1. Mittlere Zahl der Gefäßpflanzen, mittlere Gesamtdeckung der Baum- und Strauchschicht und Gesamtdeckung von Einwandernden, sich vegetativ Regenerierenden, sich aus der Samenbank Regenerierenden und Moosen im Walduntersuchs von stark (○), geringer (△) und leicht (□) verbrannten Probeflächen sowie nicht verbranntem Wald (---) zwischen 1993 und 2006. Leere Symbole im gleichen Jahr bezeichnen keinen signifikanten Unterschied bei $p > 0{,}05$.

Bryum pallescens and *Polytrichum formosum* were the most abundant mosses on burned plots. The number and cover of bryophyte species were highest in the third post-fire year (Table 5). At that point their cover was significantly higher on heavily burned than on less burned plots. Cover of fire-favored bryophytes (*Ceratodon purpureus*, *Funaria hygrometrica*, *Marchantia polymorpha*, *Polytrichum commune*, *P. juniperinum*) showed the same relation. On slightly burned plots, where herb sprouter cover increased most, bryophytes disappeared almost completely from the third to ninth post-fire years (Fig. 1). Their number and cover decreased less on partly burned plots and least on heavily burned plots.

Table 5. Highest mean number of species and mean cover of species groups (with mean cover greater than 3%) in understory on the plots in 1993–2006 (m), and number of years (t) after the fire when they occurred. p denotes the probability of no differences between the sites. Within rows, values bearing the same latter do not differ significantly at $p > 0.05$.

Tabelle 5. Höchste mittlere Artenzahl und mittler Deckungsgrad von Artengruppen (mit mittlerer Deckung > 3 %) im Waldunterwuchs der Probeflächen von 1993 bis 2006 (m), und Zahl der Jahre (t) nach dem Feuer, in dem sie vorkamen. p bezeichnet die Wahrscheinlichkeit fehlender Unterschiede zwischen den Standorten. Innerhalb der Reihen unterscheiden sich Werte mit dem gleichen Buchstaben nicht signifikant bei $p > 0{,}05$.

	Heavily burned site		Partly burned site		Slightly burned site		Unburned forest		p
	t	m	t	m	t	m	t	m	
Number of plots		24		9		9		8	
Number of species									
All invaders	2	8.1	3	9.2	2	7.6	14	6.8	*n.s.*
Herb invaders	2	5.2 ^{A}	2	5.0 ^{A}	2	2.9 ^{B}	3	1.1 ^{B}	< 0.001
Sprouters	11	8.3	10	8.0	2	8.1	9	8.8	*n.s.*
Seed bankers	2	1.5 ^{A}	2	2.4	2	1.2 ^{AB}	2	0.8 ^{B}	< 0.01
Bryophytes	3	2.5	3	2.4	3	3.1	3	4.1	*n.s.*
Cover of species (%)									
All invaders	3	46.6	3	30.3	3	15.7 ^{A}	12	10.6 ^{A}	< 0.001
All anemochores	3	45.6	3	26.6	3	13.6	7	2.6	< 0.001
Light anemochores	3	39.3	3	21.6	3	8.9 ^{A}	10	1.6 ^{A}	< 0.001
Endozoochores	14	1.4 ^{A}	14	1.9 ^{AB}	11	3.6 ^{B}	12	7.3	< 0.001
Herb invaders	2	6.8 ^{A}	3	6.6 ^{A}	3	7.2 ^{A}	7	1.4	< 0.01
All anemochores	2	6.1 ^{A}	2	4.8 ^{A}	3	6.9 ^{A}	7	0.9	< 0.01
Hovering anemochores	2	5.3 ^{A}	2	4.2 ^{A}	3	4.0 ^{A}	1	0.4	< 0.001
Annuals and biennials	2	2.8	2	1.2 ^{A}	3	2.2 ^{A}	7	0.6 ^{A}	< 0.01
Perennials with veg. spread	2	2.8 ^{A}	3	5.7	3	4.7 ^{A}	2	0.8	< 0.01
Sprouters	11	62.6	10	96.7 ^{A}	4	106.7 ^{A}	14	112.0 ^{A}	< 0.001
All anemochores	10	55.6 ^{A}	10	78.3 ^{B}	3	83.2 ^{B}	9	66.0 ^{AB}	< 0.05
Heavy anemochores	10	42.7 ^{A}	10	64.9 ^{B}	11	71.0 ^{B}	3	38.8 ^{A}	< 0.01
Endozoochores	14	9.3 ^{A}	11	21.1 ^{AB}	9	26.1 ^{BC}	12	45.0 ^{C}	< 0.001
Compact perennials	11	10.0 ^{A}	3	10.6 ^{A}	5	13.1 ^{A}	12	30.6	< 0.01
Perennials with short veg.	10	38.0 ^{A}	10	58.3 ^{B}	11	64.1 ^{B}	12	22.4 ^{A}	< 0.01
Perennials with long veg.	3	15.3	3	39.7 ^{A}	3	39.7 ^{A}	14	56.6	< 0.001
Seed bankers	3	5.8 ^{AB}	9	10.4 ^{A}	5	5.9 ^{B}	3	1.0	< 0.01
Anemochores	3	5.6 ^{AB}	9	10.4 ^{A}	5	5.9 ^{B}	3	1.0	< 0.01
Perennials with veg. spread	3	4.9 ^{AB}	9	10.1 ^{A}	5	5.8 ^{B}	6	1.0	< 0.01
All bryophytes	3	8.4 ^{A}	3	4.2 ^{B}	3	3.7 ^{B}	3	15 ^{A}	< 0.01
Fire-favoured bryophytes	3	4.5 ^{A}	3	1.0 ^{AB}	2	0.7 ^{B}	1	0.3 ^{B}	< 0.001

Fig. 2. a) Unburned forest; **b)** Part of the burned area in June 1993; **c)** The heavily burned site in June 1993; **d)** Seedlings of birches on the heavily burned site in May 1994; **e)** Young birches on the heavily burned site in June 1996; **f)** Vegetation on the heavily burned site in June 2000. (Photos: 2.a–d Z. Dzwonko; 2.e–f S. Gawroński).

Abb. 2. a) nicht verbrannter Wald; **b)** Teil des verbrannten Bereichs im Juni 1993; **c)** Die stark verbrannte Fläche im Juni 1993; **d)** Keimlinge von Birken auf der stark verbrannten Fläche im Mai 1994; **e)** Junge Birken auf der stark verbrannten Fläche im Juni 1996; **f)** Vegetation der stark verbrannten Fläche im Juni 2000 (Fotos: 2.a–d Z. Dzwonko; 2.e–f S. Gawroński).

4. Discussion

4.1. Species responses to fire severity

We found that the early development of vegetation after burning of the studied temperate moist pine forest was determined by the interaction between fire severity and the regeneration strategy of species. Similar findings have been reported from boreal coniferous forests occurring on podzolic soils with a distinct organic layer (SCHIMMEL & GRANSTRÖM 1996, WANG & KEMBALL 2005, HOLLINGSWORTH et al. 2013). As expected, invaders regenerating-

from seeds transported after the fire were favored on more severely burned plots. Among the tree species this mainly involved *Betula pendula*, whose seedlings emerged a year after the fire, most abundantly on heavily burned plots (DZWONKO et al. 2015). The main sources of birch seeds were a few fruiting trees that had survived in less burned places. According to various authors, the seed rain of *B. pendula* ranges from a few thousand to tens of thousands of seeds per square meter, and most seeds fall within 40–50 m of the source (cf. ATKINSON 1992). In other parts of southern Poland and in many regions of Western and Northern Europe, *B. pendula* is often a pioneer that dominates after fire in pine and mixed forests (ATKINSON 1992, ESSEEN et al. 1997, REYES et al. 1997, DOBROWOLSKA 2008). During the first two years after the fire, significantly more herbaceous invaders colonized the heavily and partly burned plots than the slightly burned plots. The seeds of invasive herbs originated mostly from a few plants that grew in open habitat near the burned sites. The critical stage in recruitment of anemochorous plants producing small lightweight seeds (e.g., birch, most invasive herbs) is germination and establishment of contact with a stable soil moisture regime. For seedling survival the radicle must penetrate the organic layer (SCHIMMEL & GRANSTRÖM 1996, GREENE et al. 2007, HESKETH et al. 2009). Seedling establishment and plant development can be strongly promoted by a disturbance that removes this soil layer and eliminates the existing herbaceous vegetation.

In contrast to the invaders, sprouters showed decreasing cover with increasing fire severity, and seed bankers appeared most abundantly on the partly burned plots. The species of this last group (*Calluna vulgaris*, *Luzula pilosa*, *Moehringia trinervia*, *Scrophularia nodosa*) are known to form a long-term, persistent seed bank (KLEYER et al. 2008, KWIATKOWSKA-FALIŃSKA et al. 2014). Observations and experiments in boreal forests have shown that most seeds of *C. vulgaris* and *L. pilosa* are located in the lower part of the organic (mor) layer and the upper part of the mineral soil (SCHIMMEL & GRANSTRÖM 1996, RYDGREN & HESTMARK 1997). While in coniferous forests the depth of underground regenerative plant structures forming the vegetative (or bud) bank tends to be species-specific, for the majority of species they lie within the organic layer rather than in the mineral soil (FLINN & WEIN 1977, GRANSTRÖM 1982, GRANSTRÖM & SCHIMMEL 1993, RYDGREN & HESTMARK 1997). According to GIOVANNINI et al. (1988) substantial consumption of organic matter begins at 200–250° C and becomes complete at ca. 460° C. These temperatures are far above the range of physiological tolerance of plant organs: generally, shoots and rhizomes of understory species die at temperatures of 60° C or slightly less, and the seeds of various species most often die at 65–75° C (FLINN & PRINGLE 1983, GRANSTRÖM & SCHIMMEL 1993). It is reasonable to assume that most seeds buried in the forest floor were consumed by fire in the heavily burned plots, while in slightly burned plots the disturbance was not enough to stimulate germination of seeds stored deeper in the muck layer. Sprouters' vegetative organs buried in organic soil layer would have been consumed by the fire. Most buds on underground vegetative organs would have been rendered nonviable in heavily burned plots, fewer in partly burned plots, and fewer still in slightly burned plots. Our results support the model of SCHIMMEL & GRANSTRÖM (1996), which posits a positive relation between depth of burn and the initial success of invaders, the opposite relation for sprouters, and an advantage for seed bankers after a relatively deeper-burning fire.

Unlike in boreal forests, bryophytes did not play a major role in the studied moist pine forest. Their average cover did not exceed 20%. As in boreal forests, however, the response of these species strongly depended on fire severity. Such bryophytes as *Ceratodon pur-*

pureus, *Fumaria hygrometrica*, *Marchantia polymorpha* and *Polytrichum juniperinum*, which appeared on heavily burned plots as early as the first year after the fire, are considered to be pioneer species in post-fire succession (ESSEEN et al. 1992, RYÖMÄ & LAAKA-LINDBERG 2005, HYLANDER & JOHNSON 2010). They appear quickly after a fire, especially in fresh and moist places where the organic layer has been consumed. ROWE (1983) classified these bryophytes as invaders since they tend to be shade-intolerant and colonize burned areas via wind-dispersed spores. *Pleurozium schreberi*, which was most abundant in unburned forest, did not appear at all on heavily burned plots. This pleurocarpous moss favors closed-canopy forests and is known to be slow in recolonizing after a fire (RYÖMÄ & LAAKA-LINDBERG 2005, RUSKOLAINEN & SALO 2006, MAROZAS et al. 2007). *Pleurozium schreberi* was present on slightly burned plots, where it could survive the fire in small-scale refugia (cf. HYLANDER & JOHNSON 2010).

4.2. Vegetation dynamics

Although species richness remained similar between the fire severity classes from the second post-fire year onwards, fire severity continued to affect species composition and cover through the whole 14-year study period. After rapid changes of vegetation during the first four years after the fire, much slower changes in communities were noted at all the burned sites in the next ten years. It is well known that burning of organic matter markedly alters soil properties. Both the extent and duration of these changes depend on fire severity (GONZÁLEZ-PÉREZ et al. 2004, CERTINI 2005). In the topsoil of the studied sites a fire-severity-dependent increase of Ca, P, K, Mg and the sum of basic cations persisted two or three years after the fire (DZWONKO et al. 2015). It may thus be supposed that this fertilization was an important factor in the rapid and abundant development of vegetation on the burned plots during the first three post-fire years. This seems to be a more general dependence. In some boreal and other coniferous forest types, rapid post-fire reestablishment of vascular plants has been reported, with substantial increases in vegetation cover during the three to four years following a fire (SKRE et al. 1998, TURNER et al. 1999, WANG & KEMBALL 2005, FORNWALT & KAUFMANN 2014).

Our results clearly show that the interaction between fire severity and the regeneration strategy of species in early stages of post-fire regeneration also had a decisive impact on the later development of forest vegetation. During the whole study period, sprouter cover was significantly lower on heavily burned than on less burned plots. The poorer colonization and development of tree species on slightly burned than on severely burned plots were due to strong competition from herb sprouters. On slightly burned plots, most sprouters survived the fire and grew abundantly shortly after it, thanks to nutrient enrichment of the substrate and better access to light after the trees and shrubs had burned. As herb sprouter cover was very low after the fire on heavily burned plots, competition from it was weak. There the abundantly developing trees that colonized the bare substrate hindered the growth of herbs. In forests on muck soil, severe fire is thus likely to generate dense stands with high canopy cover, restricting subsequent tree recruitment and understory development. In lightly burned areas, on the other hand, open-canopy stands can establish, providing increased opportunities for delayed tree seedling recruitment and the development of multi-aged forests with dense understory. These conclusions are in accord with some observations and experimental findings from boreal forests (ARSENEAULT 2001, JOHNSTONE at el. 2004).

4.3. Concluding remarks

In this study we showed that regeneration of understory vegetation after burning of a temperate moist pine forest was strongly dependent on fire severity, via the interaction between fire severity and the regeneration strategy of species. In burned areas a mosaic of birch wood patches was created as a result of the spatial variability of fire severity, with patches differing in tree density and in the cover and composition of understory vegetation. It is not known how long birch can dominate after a fire on mesic soils in Central Europe. In boreal Fennoscandia, according to ESSEEN et al. (1992), pioneer broadleaved trees such as *Betula* ssp. usually dominate the stand for 80–150 years following a fire, after which conifers take over. At local scale in Central Europe, many trees and shrubs colonize recent coniferous stands quicker than herbaceous forest species do, which can be explained by their effective dispersal via wind and animals (WULF & HEINKEN 2008). Other observations suggest that natural regeneration of understory communities on sites strongly disturbed by fire may be very slow due to the poor dispersal ability of many forest species, especially when those sites are isolated from undisturbed forests (DZWONKO 2001, WULF & HEINKEN 2008). Only a few coniferous forest species (e.g., *Vaccinium myrtillus*, *Dryopteris carthusiana*) can migrate to adjacent places at a rate faster than 1 m yr^{-1} (ORCZEWSKA & FERNES 2011). This implies that the observed spatial heterogeneity of the post-fire forest communities is long-lasting and may persist for at least a few decades, so our findings may have important practical implications, providing an argument for management practices that promote natural forest regeneration rather than artificial reforestation after a fire. The mosaic of unburned forest patches and forest stands that results from the variability of fire severity may be beneficial, helping to maintain the diversity of species and community types at local landscape scale.

Erweiterte deutsche Zusammenfassung

Einleitung – Waldbrände können die Vegetation in Regionen Mitteleuropas, in denen Kiefernwälder auf nährstoffarmen sandigen Böden wachsen, beeinflussen. In Polen dominieren heute Nadelwälder mit einem hohen Anteil der Waldkiefer (MATUSZKIEWICZ 1999). Die Bedeutung der Standortfaktoren für die Entwicklung von Waldbeständen auf Brandflächen ist allgemein anerkannt. Wenig bekannt hingegen ist die Reaktion der Bodenvegetation auf unterschiedliche Schweregrade des Feuers in mitteleuropäischen Nadelwäldern bzw. deren Rolle bei der Wald-Regeneration. Es wird angenommen, dass die Wechselwirkung zwischen dem Schweregrad des Feuers (gemessen als Ausmaß der Umsetzung der organischen Auflage) und artspezifischen Regenerationsstrategien die frühe Vegetationsdynamik nach Bränden erklärt (SCHIMMEL & GRANSTRÖM 1996, WANG & KEMBALL 2005). Dies dürfte grundsätzlich auch auf mitteleuropäische Nadelwälder zutreffen, die auf Böden mit einer mächtigen Humusauflage wachsen. Um dieser Vermutung nachzugehen, analysierten wir die Pflanzen-Besiedlung und Entwicklung der Bodenvegetation auf Dauerflächenbeobachtungen über 14 Jahre in einem feuchten Waldkiefern-Wald (*Molinio coeruleae-Pinetum*) auf Schwemmton-Böden in Süd-Polen.

Material und Methoden – Die Studie wurde zwischen 1993 und 2006 in der Nähe von Chrzanów im südlichen Teil des Schlesischen Berglandes durchgeführt. Im Juni 1992 brannten Untergrund, Bodenoberfläche und Baumkronen eines feuchten Kiefernwaldes auf einer Fläche von 20 ha. Im Frühling 1993 wurden Dauerbeobachtungsflächen auf einer Teilfläche von 0,35 ha etabliert, die stark, mäßig und leicht sowie nicht verbrannte Bereiche umfasste (d. h. vier Behandlungsvarianten mit insgesamt 50 Plots à 25 m^2). Jeweils im Mai von 1993 bis 2006 wurden in jedem Plot die Deckung der Gefäßpflanzen in der Kraut-, Strauch- und Baumschicht sowie diejenige der Bodenmoose geschätzt. Veränderungen in der Artenzusammensetzung und der Deckungsgrad der einzelnen Pflanzenarten in Bezug auf Zeit und Schweregrad des Feuers wurden mittels Kanonischer Korrespondenzanalyse (CCA) und

PERMANOVA analysiert. Unterschiede in den Vegetationscharakteristika der Behandlungsvarianten innerhalb der Jahre wurden mittels Kruskal-Wallis-Test überprüft. Friedman-Tests wurden herangezogen, um Unterschiede zwischen den verschiedenen Jahren zu analysieren.

Ergebnisse – Während der 14 Jahre wurden 88 Gefäßpflanzenarten und 16 Moosarten erfasst (Anhang S1). Die Veränderungen im Deckungsgrad der Arten waren am größten auf den stark verbrannten Flächen, geringer auf den mäßig und leicht verbrannten und am geringsten auf den nicht verbrannten Flächen (Tab. 2). Über die Zeit nahmen die Unterschiede in Artenzusammensetzung und Deckungsgrad der Bodenvegetation zwischen verbrannten und nicht verbrannten Flächen ab (Tab. 4). Unabhängig vom Schweregrad des Feuers stieg der Artenreichtum im zweiten Jahr signifikant an und unterschied sich am Ende der Untersuchungsreihe kaum zwischen den Behandlungsvarianten (Abb. 1). In den ersten drei Jahren nach dem Brand etablierten sich Gefäßpflanzen in den stark verbrannten Flächen am besten durch Diasporeneintrag, während sie sich in den mäßig verbrannten Flächen überwiegend aus der Samenbank regenerierten. Vegetative Regeneration herrschte auf den leicht verbrannten Flächen vor. Im dritten Jahr nach dem Brand war die Moosdeckung auf den stark verbrannten Flächen signifikant höher als auf den mäßig und leicht verbrannten Flächen. Diese anfängliche Reaktion beeinflusste die Zusammensetzung der Bodenvegetation in den Folgejahren. Innerhalb von 14 Jahren entwickelten sich Birkenvorwälder auf allen Brandflächen, aber die Bodenvegetation unterschied sich signifikant zwischen den stark und den weniger stark verbrannten Flächen (Tab. 5). In stark und mäßig verbrannten Flächen behinderte starker Konkurrenzdruck durch Pionierbaumarten das Wachstum der Pflanzen im Unterwuchs. Auf leicht verbrannten Flächen, in denen die Deckung der Kräuter mit vegetativer Regeneration am markantesten zunahm, verschwanden die Moose innerhalb von neun Jahren.

Diskussion – In dieser Studie zeigten wir, dass die Regeneration der Bodenvegetation nach Brand in einem feuchten Kiefernwald stark vom Schweregrad des Feuers abhängt. Unsere Ergebnisse entsprechen den Befunden in borealen Nadelwäldern auf podsolierten Böden mit einer ausgeprägten Humusauflage (SCHIMMEL & GRANSTRÖM 1996, WANG & KEMBALL 2005, HOLLINGSWORTH et al. 2013). Die frühe Vegetationsdynamik wurde bestimmt durch die Wechselwirkung von Schweregrad des Feuers und Regenerationsstrategie der Pflanzenarten. Wie erwartet wurden ausbreitungsstarke Arten, deren Diasporen auf die Flächen eingetragen wurden, auf den am stärksten verbrannten Flächen begünstigt. Arten, die sich aus der Samenbank des Bodens regenerierten, erschienen am zahlreichsten auf den mäßig verbrannten Flächen, die Anzahl dieser Arten war jedoch niedrig. Die Deckung der Arten mit vegetativer Regeneration nahm mit dem Schweregrad des Feuers ab. Unsere Ergebnisse unterstützen das Modell von SCHIMMEL & GRANSTRÖM (1996). Dieses nimmt einen gegenläufigen Zusammenhang an zwischen der Brandtiefe und den anfänglichen Erfolgen von ausbreitungsstarken Arten (positiv) und Arten mit vegetativer Regeneration (negativ) sowie einen Vorteil für Arten mit Regeneration aus der Samenbank nach mäßig tiefreichenden Bränden. Auf der Brandfläche bildete sich ein Mosaik von Birkenvorwäldern, die in Baumdichte und Bodenvegetation variierten als Ergebnis räumlich differenzierter Schweregrade des Feuers. Es ist nicht bekannt, wie lange Birken nach einem Brand auf Böden mittlerer Nährstoffversorgung in Mitteleuropa dominieren können. Im borealen Fennoskandien dominieren Pionierbaumarten wie *Betula* spp. die Bestände nach Waldbränden gewöhnlich für 80–150 Jahre (ESSEEN et al. 1992), danach übernehmen wieder Nadelbäume. Andere Beobachtungen legen nahe, dass die natürliche Regeneration stark verbrannter Bereiche aufgrund der eingeschränkten Ausbreitungsfähigkeit von Waldpflanzen sehr langsam verlaufen kann, insbesondere wenn diese Flächen größere Abstände zu ungestörten Wäldern aufweisen (DZWONKO 2001, WULF & HEINKEN 2008, ORCZEWSKA & FERNES 2011). Dies lässt vermuten, dass die beobachtete räumliche Differenzierung der Waldgesellschaften nach dem Brand langfristig angelegt ist und mindestens einige Jahrzehnte Bestand haben dürfte. Unsere Ergebnisse liefern Argumente für die Anwendung von Waldnutzungsformen, die die natürliche Waldverjüngung nach Brand begünstigen. Das Mosaik aus nicht verbrannten Waldflächen und von Waldbeständen, die aus der räumlichen Variabilität des Schweregrades des Feuers hervorgehen, dürfte die Erhaltung der Diversität von Arten und Waldgesellschaften auf Landschaftsebene begünstigen.

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Supplements

Supplement S1. Highest mean cover (%) of species in understory on the plots in 1993–2006, and number of years (t) after the fire when they occurred.

Beilage S1. Höchste mittlere Deckung (%) von Arten im Waldunterwuchs der Probeflächen von 1993 bis 2006, and Zahl der Jahre (t) nach dem Feuer, in denen sie vorkamen.

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Supplement S1. Highest mean cover (%) of species in understory on the plots in 1993–2006, and number of years (t) after the fire when they occurred. For species with highest mean cover greater than 2.5%, results of the Kruskal-Wallis test and Spearman correlations (r) between cover and time (* $p < 0.01$) are given. Within rows, values bearing the same letter do not differ significantly at $p > 0.05$. Dispersal mode: An1 – hovering anemochore, An2 – light anemochore, An3 – heavy anemochore, D – dyszoochore, En – endozoochore, Ep – epizoochore, M – myrmecochore. Growth form: A – annual or biennial, Cp – perennial with compact rhizomes, Sp – perennial with single shoot, Vs – perennial with short vegetative spread, Vl – perennial with long vegetative spread. F – fire-favored bryophyte.

Beilage S1. Höchste mittlere Deckung (%) von Arten im Waldunterwuchs der Probeflächen von 1993 bis 2006, and Zahl der Jahre (t) nach dem Feuer, in denen sie vorkamen. Für Arten mit höchster Deckung > 2,5% sind Ergebnisse des Kruskal-Wallis-Tests und von Spearman-Korrelation (r) zwischen Deckung und Zeit (* $p < 0,01$) gegeben. Innerhalb der Reihen unterscheiden sich Werte mit dem gleichen Buchstaben nicht signifikant bei $p > 0,05$. Ausbreitungstyp: An1 – schwebende Anemochore, An2 – leichte Anemochore, An3 – schwere Anemochore, D – Dyszoochore, En – Endozoochore, Ep – Epizoochore, M – Myrmekochore. Wuchsform: A – Ein- oder Zweijährige, Cp – Ausdauernde mit kompaktem Rhizom, Sp – Ausdauernde mit Einzelspross, Vs – Ausdauernde mit kurzer vegetativer Ausbreitung, Vl – Ausdauernde mit weiter vegetativer Ausbreitung. F – von Feuer gefördertes Moos.

Species	Dispersal mode	Growth form	Heavily burned site			Partly burned site			Slightly burned site			Unburned forest			p
			t	%	r	t	%	r	t	%	r	t	%	r	
Number of plots				24			9			9			8		
Vascular plants															
Invaders															
Betula pendula	An2	Sp	3	34.58	-0.32*	3	17.89	-0.36*	1	2.89A	-0.26*	1	0.63A	-0.06	< 0.001
Betula pubescens	An2	Sp	4	3.66A	0.14	4	2.33AB	0.18	3	2.44AB	0.07	1	1.00B	-0.02	< 0.05
Populus tremula	An2	Vl	3	0.87		9	1.44		2	1.11		12	0.13		
Pinus sylvestris	An3	Sp	5	1.00		14	1.33		3	0.56		11	0.38		
Frangula alnus	En	Sp	10	0.46		12	0.67		10	1.89		10	1.50		
Sorbus aucuparia	En	Sp	14	0.33		11	0.67		11	1.11		10	3.00		
Prunus serotina	En	Sp	14	0.63		9	0.56		10	0.56		12	2.50		
Quercus robur	D	Sp	12	0.38		11	0.44		10	0.33		12	0.75		
Picea abies	An2	Sp	11	0.25		3	0.11		1	0.11		4	0.63		
Sambucus nigra	En	Sp	1	0.04		1	0.11		1	0.11		1	0.13		
Coryllus avellana	D	Sp	3	0.21			-			-		6	0.13		
Salix cinerea	An2	Sp	7	0.46		2	0.44		2	0.11			-		
Prunus avium	En	Sp		-		9	0.11			-			-		
Quercus rubra	D	Sp		-			-		8	0.11		10	0.13		
Sambucus racemosa	En	Sp		-			-			-		2	0.25		
Quercus petraea	D	Sp		-			-			-		1	0.13		
Epilobium angustifolium	An1	Vl	2	1.25A	-0.50*	3	2.33A	-0.57*	2	2.67A	-0.42*	1	0.38	-0.35*	< 0.01
Deschampsia caespitosa	An2	Cp	4	0.25		2	0.11		3	2.78		1	0.13		
Luzula multiflora	M	Cp	2	0.50		3	2.22		7	0.33		6	0.25		
Cerastium fontanum	An2	A	1	0.04		2	0.11			-		3	0.25		
Holcus lanatus	Ep	Cp	1	0.08		4	0.11			-		2	0.13		
Poa trivialis	Ep	Vl	10	0.13		1	0.11			-		1	0.13		
Conyza canadensis	An1	A	3	2.04		2	0.67		3	1.89			-		
Senecio vernalis	An1	A	2	0.50		2	0.22		2	0.22			-		
Taraxacum officinale	An1	Sp	2	0.50		2	0.44		2	0.11			-		
Eupatorium cannabinum	An1	Cp	2	0.38		2	0.67		1	0.22			-		
Cirsium vulgare	An2	Sp	1	0.42		2	0.22		2	0.33			-		
Arabidopsis thaliana	An1	A	1	0.13		2	0.22		2	0.11			-		
Juncus effusus	Ep	Cp	10	0.13		2	0.33		3	0.11			-		
Cardaminopsis halleri	Ep	Vs	1	0.04		2	0.11		1	0.11			-		
Senecio nemorensis	An1	Sp	2	0.04			-		2	0.22			-		
Agrostis canina	An1	Vl	1	0.04			-		1	0.11			-		
Cucubalus baccifer	En	Sp	1	0.04			-		2	0.11			-		
Agrostis capillaris	An1	Vl	1	0.42		2	0.33			-			-		
Senecio vulgaris	An1	A	2	0.21		1	0.22			-			-		
Cirsium arvense	An1	Vl	1	0.08		2	0.22			-			-		
Rumex acetosa	An3	Sp	4	0.21		3	0.11			-			-		
Senecio jacobaea	An1	A	1	0.04		2	0.11			-			-		
Lysimachia vulgaris	An2	Vs	2	0.21			-			-			-		
Juncus bufonius	Ep	A	1	0.13			-			-			-		
Leontodon autumnalis	An1	Sp	1	0.13			-			-			-		
Sonchus oleraceus	An1	A	2	0.13			-			-			-		
Rumex acetosella	An2	Vs	3	0.08			-			-			-		
Hieracium sabaudum	An1	Sp	1	0.08			-			-			-		
Erigeron annuus	An1	A	1	0.08			-			-			-		
Stellaria pallustris	An3	Vs	1	0.08			-			-			-		
Matricaria perforata	An2	A	1	0.04			-			-			-		
Achillea millefolium	An2	Vl	1	0.04			-			-			-		
Capsella bursa-pastoris	An2	A	1	0.04			-			-			-		
Chenopodium album	Ep	A	1	0.04			-			-			-		
Polygonum aviculare	En	A	1	0.04			-			-			-		
Hypochoeris radicata	An1	Sp	1	0.04			-			-			-		
Galium aparine	Ep	A	2	0.04			-			-			-		
Poa annua	An2	A	3	0.04			-			-			-		
Stellaria media	An2	A	3	0.04			-			-			-		
Hieracium acuminatum	An1	Sp	6	0.04			-			-			-		
Hieracium pilosella	An1	Vl	6	0.04			-			-			-		
Trifolium pratense	An3	Sp	10	0.04			-			-			-		
Poa compressa	An2	Vl		-		2	0.11			-			-		
Solidago gigantea	An1	Vs		-		5	0.11			-			-		
Festuca rubra	Ep	Vs		-		1	0.22		1	0.89			-		
Mycelis muralis	An1	Sp		-			-		1	0.22			-		
Festuca gigantea	Ep	Sp		-			-		2	0.22		3	0.13		
Cirsium palustre	An2	A		-			-			-		7	0.63		
Sprouters															
Molinia caerulea	An3	Vs	10	6.67A	0.53*	10	58.33B	0.60*	11	63.89B	0.49*	12	21.25A	0.08	< 0.001
Vaccinium myrtillus	En	Vl	14	6.71A	0.52*	11	17.44AB	0.23	14	20.78B	0.14	12	41.25	0.68*	< 0.001
Trientalis europaea	An3	Vl	3	7.79	0.16*	3	13.89A	-0.16	2	15.00A	-0.22	2	20.00A	-0.14	< 0.001
Deschampsia flexuosa	An2	Cp	12	6.13A	0.54*	8	4.00A	0.25*	8	10.56A	0.19	11	27.50	0.40*	< 0.01
Calamagrostis epigejos	An2	Vl	4	6.63A	-0.23*	5	16.78	-0.42*	3	9.78A	-0.03	1	3.38	-0.04	< 0.01
Calamagrostis arundinacea	An2	Cp	11	2.96A	0.43*	2	6.11A	0.07	2	3.89A	-0.02	6	0.13	0.19	< 0.05
Rubus sp.	En		10	1.38A	0.12	10	3.89AB	0.06	5	5.89B	0.03	3	2.88A	0.15	< 0.05
Pteridium aquilinum	An1	Vl	14	2.67	0.34*		-		10	3.33	0.16	14	0.75	0.15	n.s.
Athyrium filix-femina	An1	Cp	1	1.96		1	1.33		2	1.00		1	0.75		
Vaccinium vitis-idaea	En	Vs	10	1.17		3	0.11		1	0.22		8	0.88		
Dryopteris carthusiana	An1	Cp	4	1.04		10	1.33		2	1.44		12	1.50		
Rubus idaeus	En	Vl	4	0.33		3	0.33		2	1.22		9	0.75		
Vaccinium uliginosum	En	Vl	8	0.04		2	0.22		4	0.11		1	0.13		
Veronica officinalis	An2	Vs	5	0.13			-			-		3	0.25		
Melica nutans	M	Cp	4	0.08		1	0.11			-			-		
Eriophorum vaginatum	An1	Vs	5	0.08			-			-			-		
Milium effusum	An3	Vs	9	0.04			-			-			-		
Convallaria majalis	En	Vl		-			-		3	0.11			-		
Potentilla erecta	An3	Sp		-			-		7	0.11			-		
Oxalis acetosella		Cp		-			-			-		9	1.88		
Dryopteris dilatata	An1	Cp		-			-			-		1	0.13		
Seed bankers															
Calluna vulgaris	An1	Vs	3	4.87AB	-0.1	9	10.11A	-0.05	5	5.78B	-0.12	6	1.00	-0.06	< 0.01
Moehringia trinervia	An2	A	1	0.75		1	1.67		1	1.33		2	0.50		
Stellaria longifolia	An1	Sp	1	0.38		1	0.44		8	0.11		1	0.13		
Luzula pilosa	M	Cp	9	0.04			-			-		6	0.13		
Scrophularia nodosa	An1	Sp	3	0.58		3	0.56		3	0.33			-		
Solanum dulcamara	En	Sp	2	0.13		2	0.11		3	0.11			-		
Carex cura	Ep	Cp	10	0.17		2	0.11			-			-		
Carex pilulifera	M	Cp		-		2	0.11			-			-		
Bryophytes															
Bryum pallescens			4	4.13A	-0.12	3	2.00AB	-0.25*	2	0.89BC	-0.46*	3	0.25C	-0.18	< 0.001
Polytrichum juniperinum F			5	2.33	0.15*	3	0.44	-0.02	3	0.33	-0.25*	1	0.25	0.00	n.s.
Atrichum undulatum			2	0.08		3	0.22		3	0.33		3	0.38		
Brachythecium rutabulum			10	0.04		3	0.11		3	0.89		1	1.38		
Pohlia nutans			9	0.04		1	0.11		1	0.11		3	1.63		
Polytrichum formosum			14	4.25A	0.61*	7	2.56AB	0.36*		0.00C		5	0.38BC	0.10	< 0.01
Dicranella heteromalla			6	0.25		11	0.11			-		1	0.88		
Pleurozium schreberi				-		3	0.11		3	0.78		1	10.63		
Plagiomnium rostratum				-		2	0.11		3	0.11		1	0.13		
Ceratodon purpureus F			3	3.04A	-0.19*	3	0.22AB	-0.16	3	0.11AB	-0.12		0.00B		< 0.05
Marchantia polymorpha F			2	0.75		2	0.22		3	0.11			-		
Funaria hygrometrica F			2	0.67		2	0.33		2	0.57			-		
Polytrichum commune F			2	0.04			-			-			-		
Sphagnum sp.			1	0.04			-			-			-		
Bryum amblyodon				-			-		3	0.22			-		
Pseudoscleropodium purum				-			-		3	0.11			-		
Brachythecium rivulare				-			-			-		1	0.25		
Plagiomnium undulatum				-			-			-		1	0.13		
Plagiothecium laetum				-			-			-		1	0.13		

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