Species Diversity of Forest Floor Vegetation in Age Gradient of Managed Scots Pine Stands

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Abstract

Even-aged Scots pine-dominated plantations on nutrient-poor soils are common forest types in lowlands of Central Europe. However, the knowledge about spontaneous changes in forests floor vegetation, and correlated with it changes in species richness is still scarce. We focused our study at quantifying changes in forest floor vegetation in a 120-year chronosequence. The study was performed in the south-western part of Poland (Central Europe). Our data comprised 95 sample plots sized 200 m². The plots were located in 6 stand-age classes in homogenous forest sites.

The stands < 10 years showed the highest values for biodiversity indices. Species typical for old stands were also found in the youngest ones. The period of canopy closure resulted in decrease in species number and increase in bryophyte cover, and was followed by the increase in *Pleurozium schreberi* and *Vaccinium myrtillus* cover. The dominance of these species could be broken at middle age by *Pteridium aquilinum,* which declined in the oldest stands. Bryophytes with preference for humus-rich soil also occurred in the middle age class only. We attributed it to the soil-enriching effect of small woody debris provided by thinning. The dominance of *Pleurozium schreberi* and *Vaccinium myrtillus* in the oldest stands was correlated with the low level of biodiversity. While the oldest stands do not support any rare and specific species their conversion into a broad-leaved community could enhance spatial diversity of forest vegetation.

Key words: Central Europe, clear-cutting, *Pinus sylvestris*, rotation period, temperate zone, succession, species diversity, secondary forests

Introduction

Dynamics of vegetation in commercial forests is specific, because human-made disturbance determines both the length and the courses of succession of vegetation (Hannerz and Hånell 1997, Godefroid et al. 2005a, Marozas et al. 2005, Uotila and Kouki 2005, Moora et al. 2007, Widenfalk and Weslien 2009). The most significant anthropogenic disturbance in managed forests is clear-cutting, because it causes deep and sudden change in environmental conditions. Solar radiation becomes more intense, the level of ground water increases, top layers of the soil become dry, mineralisation of nitrogen is faster and hydrogen ions acidify the soil environment (Chojnacka-Ożga and Ożga 1999, Prescott 1997, Økland et al. 2003b). Clear-cutting has then a serious impact on species composition and diversity (Bråkenhielm and Liu 1998, Roberts and Zhu 2002, Økland et al. 2003b, Moola and Vasseur 2004, Bergstedt et al. 2008, Widenfalk and Weslien 2009). Microclimate becomes favourable for early-seral species,

also including alien invasive plants, which could colonise an open area (Halpern and Spies 1995, Bermśdez et al. 2007). Moreover, mechanical soil preparation before tree planting destroys the remaining forest floor vegetation and facilitates colonisation by non-forest species. Although some forest species can regenerate or recolonize rapidly after disturbance (Dolling 1999), sensitive and stenotopic forest species typically regenerate slowly during re-growth (Moola and Vasseur 2004, Godefroid et al. 2005b). Some of them may not recolonize for a long time (Roberts and Zhu 2002), since their regeneration depends on the proximity of sources of diaspores (Dzwonko 2001). Moreover, the dominant tree species, introduced during stands replanting, determine the course of succession (Dzwonko and Loster 1997, Dzwonko 2001), because of the significant influence of a particular tree species on soil characteristics and processes (Augusto et al. 2002). Also during the subsequent stand maturation, successional changes in understory vegetation occur, which affect species number and cover (Czerepko 2004, Gode-

froid et al. 2005b, Uotila and Kouki 2005). The changes could lead both to the increase (Qian et al. 1997, Bobiec 1998), as well as the decrease (Moora et al. 2007, Aavik et al. 2009) in vegetation heterogeneity.

Modern forest management is aimed not only at timber production, but also at protecting the biodiversity. Therefore, the changes in vegetation after clear-cutting and stand maturation have been the subject of many studies in various geographical regions (Halpern and Spies 1995, Moola and Vasseur 2004, Uotila and Kouki 2005, Bermśdez et al. 2007, Widenfalk and Weslien 2009). Coniferous forests with the dominance of pine or spruce cover a vast region in the boreal zone (Kellomäki 2000), and most of papers considering changes in vegetation after clear cuttings and along stand development in such forest, come from northern Europe (Hannerz and Hånell 1997, Uotila and Kouki 2005, Moora et al. 2007, Aavik et al. 2009). However, Scots pine is the dominant tree species in sub-continental part of Central Europe (Brus et al. 2012); in terms of percentage of forest area, it is the main species in Poland (Anon 2013) and second, after the Norway spruce, in Czech Republic and Germany (Domes 1997, Beck 2000). Previous studies considered successional changes in the introduced Scots pine stands in Central Europe, focusing rather on recovery of forest floor vegetation into more natural, typical for broad-leaved forests (Dzwonko 2001, Zerbe 2002, Czerepko 2004). They were performed in forests with relatively rich soils, in the vicinity of natural or semi-natural woodland (Dzwonko 2001, Czerepko 2004). Unfortunately, in lowlands of Central Europe, many Scots pine stands grow on relatively poor and acid soils, and the remnants of semi-natural broadleaved forests, which could serve as a source of diaspores, are scarce. Therefore, any tendencies to spontaneous recovery of broadleaved forest vegetation might not be observed. In Central Europe, most of these Scots pine stands are recently converted into the mixed forests in order to restore more natural and diversified vegetation (Kint 2005). The conversion is based on current insight into natural vegetation dynamics, which indicates that the most suitable species for poor sandy soils are *Betula pendula, Betula pubescens, Quercus robur, Quercus petraea, Fagus sylvatica* and *Sorbus aucuparia* (Zerbe 2002, Kint et al. 2006). However, it is not clear that pine stands serve as refugee for specific species and that there are any arguments against conversion of Scots pine dominated stands into mixed forests.

The aim of the study was to explore how the forest floor vegetation in Scots pine stands changes with successional age over 120 year period using a chron-osequence method. More specifically, we were interested whether components of species diversity provide any arguments for maintaining Scots pine stands. Detailed questions were posed: 1) Is species diversity supported in the old Scots pine stands? 2) Do clear-cutting and planting of Scots pine stands create a bottleneck for forest floor species or promote the increase in species diversity? 3) Is the recolonisation of the late successional species rapid or slow?

Material and Methods

Study area

The research was conducted in the south-western part of Poland (Central Europe) in the area of Bory Dolnośląskie forests (its literal meaning in English: "Lower Silesian coniferous forests", in German "Niederschlesische Heide"). It is one of the largest, solid complex of coniferous forests in the lowlands of Central Europe. The studied area distinguished itself in its history by the high percentage of forest cover and low density of inhabitants. In the period before intense forest exploitation (ca. before 1750), tree stands were predominantly mixed pine-oak-beech forests. With time the percentage of Scots pine increased, as results of forests practices, and today Scots pine prevails definitely in tree stands.

The climate is sub-oceanic. According to the data from the nearest meteorological station (Institute of Meteorology and Water Management in Wrocław), mean annual precipitation sum of 1985–2005 was 583 mm. Mean annual temperature in that period was 8.4 °C, mean temperature in the warm half year was 14.5 °C, in the cool half year- 2.4 °C. The prevailing winds are from the west and the southwest.

The terrain is gentle and the highest altitude does not exceed 200 m above sea level. Rock outcrops and shallow-soil are completely absent in the study area. Soils are composed mostly of fluvioglacial and glacial deposits or aeolian sands. 52 % of the studied area is covered by podzolic soils, 40 % by rusty soils, and only 8 % by other soil types.

Management methods

In the 1830s, the artificial Scots pine stand established after site preparation on large clear-cuts was applied as the main method of forest regeneration on these areas. Since WW II, forests are owned by the state and managed by the State Forest National Forest Holding (Bena 2001, Milnik 2010).

Recently, the stands were established artificially (10,000 saplings/ha) on clear-cuts, where logging slash was removed and which were ploughed to prepare soil for tree replanting. Pre-commercial thinnings are car-

ried out in the youngest stands (< 20 years old) to remove any less promising trees hindering the growth of the others. The early pre-commercial thinnings are carried out in stands before crown closure to remove some undesirable trees. The late pre-commercial thinnings are carried out in stands after crown closure to reduce density to the number of 6,000–7,000 stems/ha. Commercial thinnings are carried out in older stands (> 20 years old) to support the growth of proper number of high quality trees distributed regularly in a stand. During early commercial thinning, approximately 15 m³ of volume/ha is removed and during late commercial thinnings 20–25 m³ of volume/ha. Commercial thinnings are applied approximately once per decade, during this all the logs are removed; only the small branches and tree tops are left on the soil. Finally there are about 400 stems/ha in pre-logged stands. The logging is usually done in stands aged 100–120 years. Species such as *Abies alba* Mill.*, Fagus sylvatica* L.*, Picea abies* (L.) H. Karst.*, Quercus petraea* (Matt.) Liebl.*, Quercus robur* L. and *Sorbus aucuparia* L. emend. Hedl. are introduced occasionally under maturing stands as a shrub layer. The species are planted in middle-aged stands (above 40 years) to form an additional tree layer in pine dominated stands.

Data collection

The samples were taken on an area of ca 11 500 ha (15°29'29"E 51°21'20"N). The succession of vegetation was studied with a chronosequence method (Foster and Tilman 2000). The method seems to be the most suitable for measuring plant community characteristics that changed in a relatively linear fashion over time, such as plant cover and species richness (Walker et al. 2010). Moreover, it is better for trajectories that they are convergent, have low diversity and are infrequently disturbed. Admittedly, managed forests are frequently disturbed, but the same scheme of management practises works for the convergence of successional courses. The "space for time" substitution has been criticized because of the assumption of biotic and abiotic constancy over the time span. However, it is still applied, when successional trajectories exceed the life span of investigators.

Stands for examinations were selected on the basis of stratified-random sampling methods, using maps and data from forest management plans. The stratification was done according to the following two criteria: 1) mesotrophic forest site – only compartments with the stand classified as "fresh mixed coniferous forest" – according to Polish forest typology, were chosen, 2) stand age. The stands were categorised according to age classes: 1) <10 years old – includes stands before crown closure, where early pre-commer-

cial thinning was carried out once, 2) 11–20 years old – includes stands of intensive height growth after recent crown closure, where late pre-commercial thinning was carried out once, 3) 21–40 years old – includes stands of intensive height growth, 4) 41–60 years old – includes stands after the culmination of height growth 5), 61–80 years old – includes stands of increasing biomass, 6) 81–120 years old – includes the oldest stands before logging.

Overall, 95 circular plots (200 m²) were sampled (Figure 1). The subsequent age classes were represented by the following number of plots: 11, 13, 20, 19, 16 and 16. The number of plots was dependent on the number of forest stands meeting the sampling criteria.
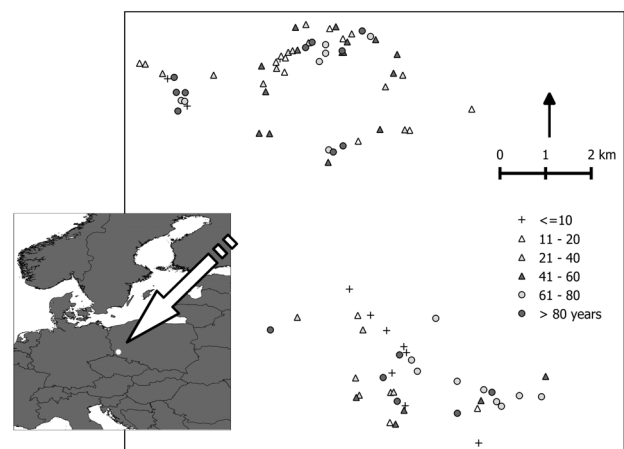

Figure 1. Location of study site and study plots in different age classes

All species of forest floor were identified in each plot including vascular plants, bryophytes and lichens. We recorded species occurring on the soil, litter, or fine wood that was in contact with the ground and formed a structural layer of forest community. Stumps and logs as habitats for distinct micro communities (of lichens and bryophytes) were not studied. The fallen logs were almost absent, as removed after the thinnings. The cover of each species was recorded using the following, slightly modified, Braun-Blanquet (1964) cover-abundance scale: (5) cover from 75.1 to 100.0 %., (4) cover from 50.1 to 75.0 %, (3) cover from 25.1 to 50.0 %, (2) cover from 10.1 to 25.0 %, (1) cover from 1.1 to 10.0 %, (+) cover up to 1.0 % or (r) one specimen per plot. Additionally, percentage of trees canopy cover was estimated visually.

Data analysis

The analyses involved only non-tree species including vascular plants, ground bryophytes and li-

chens. Tree species were not considered because they were selectively removed during thinnings, and also occasionally planted under maturing stands as a shrub layer. Consequently, the differences in tree species composition among stand age classes cannot express the uncontrolled vegetation dynamics in the course of succession. The most frequent admixture tree species in the studied plots are presented in Table 1.

$$D = \Sigma (c_i/C)^2,$$

where c_i represents the cover of species i on a plot, C represents the sum of covers of all species.

The values of the observed or computed variables were calculated for three groups of organisms: vascular plants (V), lichens (L), bryophytes (B), considered altogether, as well as for each group separately.

Table 1. The most frequent tree species in vegetation layers in the studied stands

Age classes	L	<10	11–20	21–40	41–60	61–80	80–120	<10	11–20	21–40	41–60	61–80	80–120
		percentage frequency						mean percentage cover					
Pinus sylvestris	t1	100	100	100	100	100	100	58	57	58	41	41	43
Betula pendula	t1	73	54	80	58	6		4	5	4	6	1	
Larix decidua	t1	36	46					1	5				
Quercus petraea	t1	27	15	20				0	0	2			
Picea abies	t1		15			13	6		0			1	0
Quercus robur	t1	18						0					
Quercus petraea	t2				5		25				3		3
Picea abies	t2				5	6	19				0	0	1
Pinus sylvestris	t2				5		13				0		1
Betula pendula	t2						19						1
Picea abies	s1		8	25	16	38	19		0	1	1	1	1
Quercus robur	s1	9		5		13	13	0		0		0	5
Betula pendula	s1		8			6	25		0			0	0
Pinus sylvestris	s1				5		38				0		3
Abies alba	s1					13	6					3	0
Quercus petraea	s1			5	5	6	13			0	0	0	0
Fagus sylvatica	s1					13	6					0	0
Picea abies	s2		46	50	37	38	19		4	3	2	3	1
Betula pendula	s2		92	15		6	38		6	0		0	1
Pinus sylvestris	s2		31		11	19	88		1		0	1	6
Quercus petraea	s2		8			13			0			0	
Quercus robur	s2		8	5		19	31		0	0		0	1
Larix decidua	s2		31	5		6	6		0	0		0	0
Abies alba	s2			5		13	6			0		1	0
Sorbus aucuparia	s2				5	13					0	0	
Padus serotina	s2					31	6					1	0
Pinus sylvestris	hl	55	85	80	89	81	88	0	0	0	0	0	0
Betula pendula	hl	64	69	30	32	19	38	0	0	0	0	0	0
Quercus petraea	hl	45	46	80	84	75	63	0	0	0	0	0	0
Quercus robur	hl	18	54	40	42	63	50	1	0	0	0	0	0
Quercus rubra	hl	18	31	40	16	6	13	0	0	0	0	0	0
Sorbus aucuparia	hl	18	54	35	11	38	44	0	0	0	0	0	0
Picea abies	hl		8	15	16	25	6		0	0	0	0	0
Padus serotina	hl	9	23	5		38	6	0	0	0		0	0
Frangula alnus	hl		15		5		13		0		0		0
Larix decidua	hl			5	11	6				0	0	0	

L for layers: t1 for main tree layer, t2 for lower tree layer, s1 for high shrub layer, s2 for low shrub layer, hl for herb layer; cover 0 means value <1

To examine successive changes of forest floor vegetation, the following attributes were analysed: number of species, its cover, and the Simpson Index (D) of species diversity.

Species richness, as well as cover, are the simplest measures, and were determined directly on each plot. For calculations of cover, the Braun-Blanquet (1964) scale was changed into mean values as follows: (5) 87.5 %, (4) 62.5 %, (3) 37.5 %, (2) 17.5 %, (1) 5 %, (+) 0.5 and (r) 0.1 (Faliński 2001). The species richness was calculated as an average number of species per plot in a given age class (*average N*), as well as total number of species (*total N*) – that is sum of all species found on plots in a given age class.

The Simpson Index (D) provides other information about community composition, because it is a measurement of dominance and it assesses the probability that two randomly selected individuals from a community will belong to the same species (Van Dyke 2008). It was calculated according to the following formula:

The significance of differences between age classes was tested using Kruskall-Wallis ANOVA ranks, as post-hoc test we applied multiple comparisons of average ranks (Siegell and Castellan 1988, Sokal and Rohlf 1994). We used $p = 0.05$.

To indicate species characteristic for particular stand age class, fidelity (a measure of species concentration in vegetation units) was calculated. We used the *Phi* coefficient as a fidelity measure. It takes values from -1 to +1; positive values indicate that the species and the vegetation unit co-occur more frequently than it could be expected by chance, whereas larger values indicate a greater degree of joint fidelity (Chytrż et al. 2002).

To find a pattern of changes in species cover with stand age we used the robust, nonparametric regression method LOESS (locally weighted scatter plot smoothing) with a 0.6 smoothing parameter (Trexler and Travis 1993).

To find a general pattern of vegetation, which would extract the main gradients in species composition, we used correspondence analysis (CA). To detect the impact of two known environmental variables: stand age (A) and canopy cover (C), the canonical correspondence analysis (CCA) was applied. The significance of environmental variables was tested using the Monte Carlo method with 499 permutations (ter Braak and Prentice 1988, Lepš and Šmilauer 2014). The variation partitioning approach was applied (Borcard et al. 1992, Økland R. H. et al. 2003a) in order to test whether stand age and canopy explain unique aspects of species composition. The following components of variation were calculated: $A|C$ (variation explained by A but not shared with C), $C|A$ (variation explained by C but not shared with A), $A\cap C$ (shared variance= variance jointly explained by A and C) $A\cup C$ (total variation explained by A and C). $A|C$ was obtained from CCA (as sum of all canonical eigenvalues), where A was the environmental (constraining) variable and C was the co-variable. $C|A$ was obtained from CCA, where C was the environmental variable and A was the co-variable. $A\cup C$ was obtained from CCA, where A and C were the environmental variables. $A\cap C$ was computed as $A\cup C - A|C - C|A$. The relative variation explained (or variation components divided by $A\cup C$) was reported.

Results

In general the diversity of different groups of organisms (vascular plants, lichens, bryophytes) differed significantly among age classes (Table 2). Total number of species, as well as average number of species, were higher in the first age class (<10 years) than in the oldest stands. Also the average values were higher both for all species groups altogether, as well as for individual taxonomic groups. The species richness of lichens and vascular plants decreased with stand age. The bryophytes showed a peak of species richness in mid-succession stages (21–40 years), but the mean value did not differ significantly from the first age class (Table 2).

The species composition differed among age classes: there were groups of species with high fidelity val-

Table 2. Average values, standard deviations (in parenthesis) and results of Kruskal-Wallis ANOVA ranks for average (*average N*) and total (*total N*) species number, *cover* and Simpson index of diversity (*D index*), in age classes

Stand age classes (yr)	<10	11–20	21–40	41–60	61–80	80–120	H	p
Plot number	11	13	20	19	16	16		
average N								
V	7.73 a	6.08 a	5.45 a,b	5.79 a,b	5.75 a,b	4.31 b	23.5	0.0003
B	10.73 a	11.54 a	12.25 a	10.53 a,b	9.06 b	8.63 b	23.1	0.0003
L	5.73 a	3.69 a,b	2.25 a,b,c	1.16 b,c	0.63 b,c	0.63 c	36.4	0.0000
overall	24.18 a	21.31 a,b	19.95 a,b	17.47 b,c	15.44 c	13.56 c	44.6	0.0000
cover								
V	45.29 a	18.52 b	13.48 b	28.12 a,b	27.51 a,b	40.69 a	33.5	0.0000
B	20.45 a	34.55 a,b	44.64 a,b	50.16 b,c	76.04 c	51.42 b,c	34.8	0.0000
L	18.68 a	2.54 a,b	1.11 b	0.58 b	0.24 b	0.31 b	43.1	0.0000
D index								
V	0.46 a,b	0.45 a,b	0.44 a	0.61 a,b,c	0.68 b	0.73 c	26.0	0.0001
B	0.31 a	0.36 a	0.36 a	0.50 a,b	0.81 c	0.75 b,c	48.5	0.0000
L	0.57 a	0.26 a	0.39 a	0.22 a	0.36 a	0.30 a	10.0	0.1089
total N								
V	21(-)	16(-)	15(-)	19(-)	18(-)	11(-)	-	-
B	23(-)	25(-)	34(-)	31(-)	25(-)	27(-)	-	-
L	16(-)	16(-)	12(-)	9(-)	4(-)	5(-)	-	-
sum	60(-)	57(-)	61(-)	59(-)	47(-)	43(-)	-	-

Different letters in one row indicate statistical differences between means at p = 0.05. Values are presented for vascular plants (*V*), bryophytes (*B*) and lichens (*L*), as well as for all species together (overall). Additionally, total number of species (*total N*) in a given age class is presented.

ues in a given age class (Table 3). Generally, the number of characteristic species was the highest in the youngest stands, and decreased with stand age. There was only one species *Dryopteris carthusiana* (Vill.) H. P. Fuchs, which could be considered as characteristic (*Phi* coefficient = 53.6) in the stands of medium age (60-80 years). The species characteristics for the youngest stands were mainly light demanding lichens: *Placynthiella oligotropha* (Vain.) Coppins & P. James*, P. uliginosa* (Schrad.) Coppins & P. James and *Trapeliopsis granulosa* (Hoffm.) Lumbsch, and bryophytes *Campylopus introflexus* (Hedw.) Brid.*, Ceratodon purpureus* (Hedw.) Brid. and *P. piliferum* Hedw. Bryophytes with preference for humus-rich soil as: *Lophocolea heterophylla* (Schrad.) Dumort., *Plaghiotecium curvifolium* Schlieph. ex Limpr. and *Sciuro-hypnum oedipodium* (Mitt.) Ignatov & Hutten occurred in the middle age stands (21-40 years), however with low fidelity.

The *cover* differed among different groups of organisms. In the first stage the cover of lichens was the highest, while the cover of bryophytes was simultaneously the lowest (Table 2). With time, the cover of lichens decreased, whereas bryophytes' increased. The vascular plant showed the lowest values of cov-

er in middle age class (21–40 years). Species, which reached higher values of cover, were: *Deschampsia flexuosa* (L.) Trin. and *Placynthiella oligotropha* in the youngest stands, *Pleurozium schreberi* (Willd. ex Brid.) Mitt. and *Vaccinium myrtillus* L. in older (above 41 years) and the oldest stands (Figure 2). *Pteridium aquilinum* (L.) Kuhn and *Hypnum jutlandicum* Holmen & E.Warncke in Damsholt, Holmen & E.Warncke also occured with higher abundance. The cover distribution of these species along the stand age was unimodal: they were absent (*Pteridium*) or not abundant (*Hypnum*) in the youngest stands, the most abundant in stands in medium age, and again declined in the oldest stands (Figure 2).

The eigenvalue in unconstrained ordination (CA) was similar for the first (0.549) and second (0.446) axis. The first ordination axis described 14 % of the total variation of species composition and might be interpreted as species shift from non-forest (open-canopy) to forest (closed-canopy) community (Figure 3A). The second axis described 11.3 % of the total variation and might distinguish young and disturbed forest communities and more stable communities of old stands (Figure 3A).

Table 3. Fidelity of species in given age classes

Species	Stand age classes (yr)					
	<10	11–20	21–40	41–60	61–80	80–120
Placynthiella oligotropha (Vain.) Coppins & P. James	95.6					
Polytrichum piliferum Hedw.	87					
Trapeliopsis granulosa (Hoffm.) Lumbsch	73.3					
Placynthiella uliginosa (Schrad.) Coppins & P. James	71.8					
Ceratodon purpureus (Hedw.) Brid.	65.2					
Campylopus introflexus (Hedw.) Brid.	63					
Calluna vulgaris (L.) Hull	49					
Juncus effusus L.	48.8					
Polytrichum juniperinum Hedw.	47	35				
Cladonia macilenta Hoffm.	42.1	23.6				
Chamaenerion angustifolium (L.) Scop.	32.9					
Rubus sp.	32.1					
Carex pilulifera L.	29.8	25.4				
Calamagrostis epigeios (L.) Roth	22.6	34.8				
Cephaloziella divaricata (Sm.) Schiffn.		34.6				
Cladonia subulata (L.) Weber in F.H. Wigg.		31.5				
Cladonia pyxidata (L.) Hoffm.		27.1				
Plagiothecium curvifolium Schlieph. ex Limpr.			42.5			
Lophocolea heterophylla (Schrad.) Dumort.			39.6			
Cladonia chlorophaea (Flörke ex Sommerf.) Spreng.			27.7			
Sciuro-hypnum oedipodium (Mitt.) Ignatov & Huttunen			23.7			
Brachythecium rutabulum (Hedw.) Schimp.			21.1			
Placynthiella icmalea (Ach.) Coppins & P. James			16.6			
Leucobryum glaucum				29.7		
Melampyrum pratense				25.1	26.3	
Dryopteris carthusiana (Vill.) H. P. Fuchs					53.6	

Values of *phi* coefficient are multiplied by 100. Negative values of fidelity are not shown.
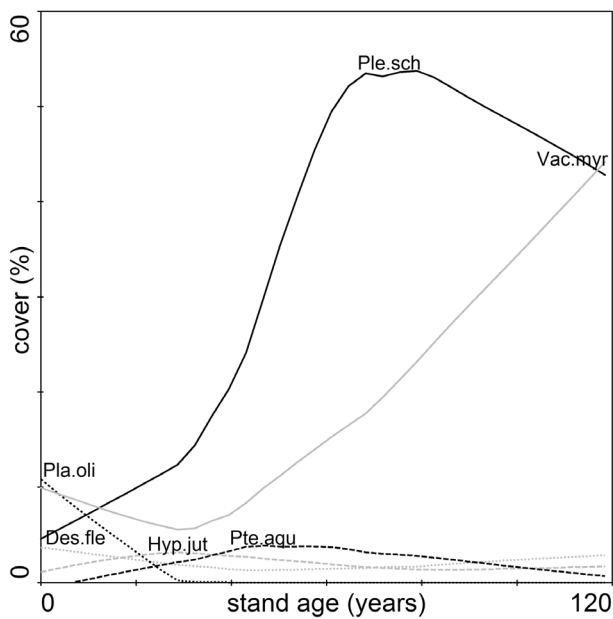
Figure 2. Changes of cover of species during 120 years of chronosequence of Scots pine stands. The regression line was fitted using LOESS (locally weighted scatterplot smoothing) with a smoothing parameter of 0.6. Des.fle = *Deschampsia flexuosa*, Hyp.jut = *Hypnum jutlandicum*, Pla.oli = *Placynthiella oligotropha*, Ple.sch = *Pleurozium schreberi*, Pte.aqu = *Pteridium aquilinum*, Vac.myr = *Vaccinium myrtillus*

In the constrained ordination (CCA) the eigenvalue of the first constrained axis was 0.301. The axis explained 7.7 % of variance in species composition and was correlated with stand *age* ($r = 0.78$). Inputting into the model another explanatory variable *canopy cover* did not improve explanatory power of the ordination model. Both the first, as well as all the axes together were statistically significant (the first axe: $F = 7.64$, $p = 0.002$ and all axes together: $F = 4.92$, $p = 0.002$). The first axis highlighted successional changes, with pioneer species or species typical to open habitats on the left side, and field vegetation dominated by *Vaccinium myrtillus,* and *Pleurozium schreberi* in old stands grouped on the right side of the graph (Figure 3B). The eigenvalue of the second axis was 0.078 and the axis explained only 2 % of species variance. The values were considerably lower than in CA, hence the second axis was determined by other, unknown ecological factors. The variation partitioning showed that the *age* and *canopy cover* variables explained 9.7 % of total variation in the model. More than half (57.7 %) of total explained variation (*A∪C)* was due to stand age (A|C). Both canopy cover (C|A) and jointly: age and canopy cover (*A∩C*) explained about one fifth of the total variation explained (21 % and 20.6 %).
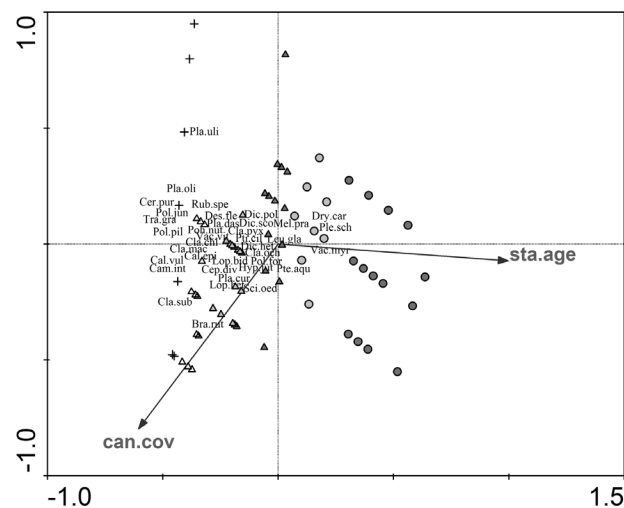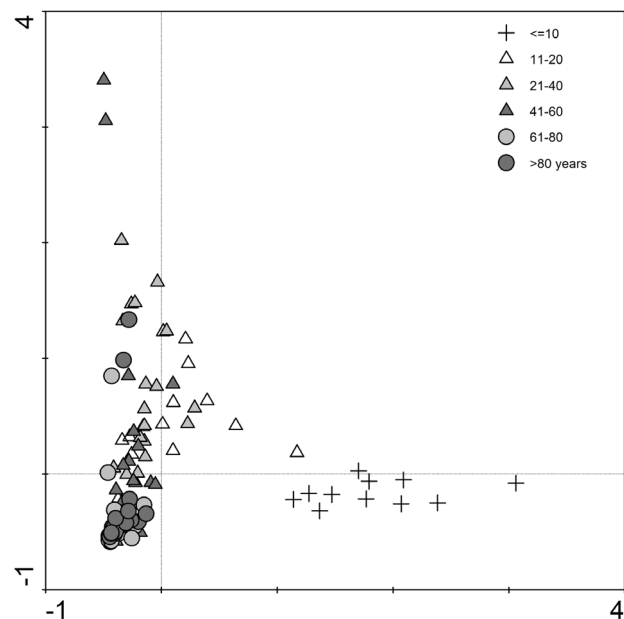

Figure 3. Ordination diagrams A) the biplot of the results of CA B) The triplot (species, samples, environmental variable) of the results of CCA. Only species with frequency of minimum 30% in one class are presented. Abbreviations of species names consist of first three letters of the genus and species. List of full names of all species is shown in Supplementary Material

Discussion

The most pronounced changes in forest floor vegetation were a rapid increase in the number of pioneer species after clear cutting. Since the disturbances created beneficial condition for this group of species, such increase was commonly observed in coniferous forests (Hannerz and Hånell 1997, Roberts and

Zhu 2002, Karazija 2003, Czerepko 2004, Moola and Vasseur 2004, Uotila and Kouki 2005). In this study the most common species were: heliophilous lichens, e.g. *Placynthiella oligotropha*, *P. uliginosa*, *Trapeliopsis granulosa*, and bryophytes, e.g *Ceratodon purpureus* and *P. piliferum*. These species are defined as disturbance-related species, which form a biological soil crust on bare soils and decayed organic matter (Belnap and Lange 2001). It was found that in Scots pine stand, after clear cutting but without site preparation, the cover of pioneer lichens was the highest relatively late, 15–20 years after cutting, whereas the cover of bryophytes rapidly decreased with time (Bråkenhielm and Liu 1998). We could conclude that the site preparation (ploughing), accompanied by high light intensity after stand removal, and accelerates the encroachment of lichens. Moreover, mechanical removal of moss patches during soil preparation diminishes dominance of typical forest bryophytes like *Pleurozium schreberi*, and also provides open surface available for pioneer lichens and bryophytes.

Along with rapid changes of light, temperature and water conditions, as well as physical damage of rhizomes caused by clear-cutting and site preparation, the number of late seral species diminished (Hannerz and Hånell 1997, Roberts and Zhu 2002, Økland et al. 2003, Moola and Vasseur 2004, Uotila and Kouki 2005). However, in the studied site the species typical for old stands were less abundant, but still able to survive the disturbance. We also did not observe a rapid expansion of any species after disturbance. Such increase in cover of strong competitive plant, which can gain control over the vegetation, was quite often observed (Hannerz and Hånell 1997, Roberts and Zhu 2002, Uotila and Kouki 2005, Dolling 1999). The potentially expansive species, like *Deschampsia flexuosa* and *C. epigejos* (L.) Roth, were most abundant in the younger age class but did not dominate the vegetation. We attributed it to site preparation (ploughing), relatively nutrient-poor, acid soil, and dense planting of Scots pine seedlings. Under these conditions, the potentially expansive species were not able to rebuild dense swards, before being over shaded by the canopy of young trees.

Survival of late seral species and pioneer species' entry caused that the first 10 years after stand establishing is a period of the highest biodiversity of forest floor. It supports results from Lithuanian Scots pine forest, where vegetation patches after clear-cuttings were the richest in species (Karazija 2003). Therefore, the forest management practices are not a "bottleneck" for plant species, although caused crucial shift in species composition, in the studied artificial Scots pine stands.

The second shift in species composition was related with the stage, when tree crowns start to join together, what takes place in the examined sites, at the stand age of about 10 years. In this period the typical forest microclimate developed (Aussenac 2000). Change in light level caused the extinction of pioneer species, most lichens, and the decrease in cover of light demanding vascular plant species, while cover of bryophyte increased. Such coincidence of increasing bryophyte cover, together with increasing canopy after clear-cutting, is a general tendency observed also in Norway spruce stands (Uotila and Kouki 2005, Schmalholz and Hylaner 2009). However, on very poor sandy soils, the decrease of bryophytes during first 20 years after clear-cutting could occur (Bråkenhielm and Liu 1998). We can conclude that the observed shift in species composition results in the decrease in species number and biodiversity indices in the studied stand. Therefore, the period of dense canopy cover could be considered as a bottleneck for species.

The subsequent changes in vegetation after the canopy closure, in most of plots were rather quantitative and manifested most in the asymptotically increase cover of *Pleurozium schreberi* and *Vaccinium myrtillus*. Results show that such domination can be temporally broken by *Pteridium aquilinum*. The development of patches of this fern caused an increase in vegetation heterogeneity of plots in middle-age class. The occurrence on only some of plots, but with a relatively high cover, we attributed to vegetative spread of this species (Dolling 1999). Lack of *Pteridium aquilinum* in the youngest stands could be easily explained by mechanical destruction of rhizomes during the ploughing. The decline of mentioned fern in the older stand age class, observed in this study, can be related with a cycle of development of this fern. With the time of *Pteridium* stands development, thickness of humus layer increased and the rhizomes lost their contact with soil (Watt 1976). Therefore, the rhizomes grow in a less favourable substrate, and they are very prone to damages caused by frost. Eventually, according to Watt (1976) *Pteridium* "becomes the victim of its own success". Similar pattern of occurrence of *Pteridium* along chronosequence was also observed by Godefroid et al. (2005a) in pure beech (*Fagus sylvatica*) stands.

The stands in middle age class (11–40 years) also support some bryophytes as e.g. *Lophocolea heterophylla*, *Plaghiotecium curvifolium* and *Sciuro-hypnum oedipodium*, which are usually considered as related to humus-rich soil and organic matter. As in managed forests, in studied stands only small amount of coarse woody debris in forest floor was observed. Fine woody debris, like those resulting from thinning in young

stand or dead branches, produce only rapidly decaying material but even this can increase bryophytes species richness (Kruys and Jonsson 1999). With time, the influx of fine dead wood decreases and *Pleurozium schreberi* and *Vaccinium myrtillus* finally dominate the ground layer, with only small number of other species co-occurring with them. These two species are known, together with symbiotic *Vaccinium* mycorrhizal fungi, to create extremely tight nutrient cycling system, where other species have little opportunity to acquire growth-limiting nutrients (Zackrisson et al. 1997, Jäderlund et al. 1998). Since these forests are protected against wild fire, the coarse woody debris is removed, and there is lack of other disturbances, which can break the domination of *Pleurozium schreberi* and *Vaccinium myrtillus* – the oldest stands are the poorest in species.

It is known that management practices are disadvantageous for maintaining rare and sensitive species (Roberts and Zhu 2002, Godefroid et al. 2005b). The evidence of past clear-cutting, manifested by the lack of some late-succesional species, could persist over 50 years for vascular plants (Moola and Vasseur 2004) and bryophytes occurring on woody debris (Dynesius and Hylander 2007). Most of species characteristic to older stands were able to survive clear cutting and site preparation; therefore, applied scheme forest management did not lead to extinction of typical forest species in this study. The only species absent in young stands is *Dryopteris carthusiana*. However, when comparing the frequency of this species in ancient and recent woods, it preferred the latter and was regarded as a good coloniser of recent forest (Orczewska and Fernes 2011). Species of natural Scots pine forests from families *Lycopodiaceae* and *Pyrolaceae* (Kelly and Connolly 2000, Matuszkiewicz 2001) could be examples of sensitive late-seral species expected in the studied sites. They were mentioned as true forest species in Lithuanian Scots pine forests in similar sites (Karazija 2003). However, plants from these families are extremely rare on the studied area. The studied site has been a subject of intense forest management for centuries, also including the litter racking up and cattle grazing to 1940s (Bena 2001, Milnik 2010); therefore, a lack of these species could be a result of former practices. Unfortunately, in the studied semi-natural areas, less intensively managed Scots pine stands persisted only on peat-bogs, and could not serve as a reference for vegetation structure.

The general pattern of vegetation changes, observed in the studied mesotrophic sites, resembles the trajectory of changes in poor, oligotrophic sites; however, these two site types differ with respect to species pool (Stefańska-Krzaczek 2012). Such similarity was

also observed in Scots pine of more continental part of Europe; however, the communities were richer in species, especially the oldest stands (Karazija 2003). While the oldest stands of studied sites do not support any rare and specific species, there are no arguments against the conversion of the managed pine stands into a broad-leaved community. It could enhance spatial diversity of forest vegetation.

Conclusions

1. The oldest age class of commercial Scots pine dominated stands did not support high species richness. Their conversion into a broad-leaved stands could then enhance spatial diversity of vegetation.

2. The coexistence of both late seral and pioneer species during the first 10 years after stand establishment results in the highest species diversity of forest floor. Therefore, the forest management practices, related to stand removal and replanting, are not a "bottleneck" for plant species. However, the period of canopy closure could be considered as a bottleneck for species, especially vascular plants and lichens.

3. Species occurring in old stands were most able to survive clear cutting and site preparation. In results recovery of the forest floor vegetation was relatively fast. However, in the studied stands we did not observe species considered commonly as typical to the ancient forests with old Scots pine stands.

Acknowledgements

References

Aavik, T., Püssa, K., Roosaluste, E. and Mora, M. 2009. Vegetation change in boreonemoral forest during succession – trends in species composition, richness and differentiation diversity. *Annales Botanici Fennici* 46: 326-335.

Anon. 2013. Forests in Poland 2010. The State Forests, Poland, 47 pp.

Augusto, L., Ranger, J., Binkley, D. and Rothe, A. 2002. Impact of several common tree species of European tem-

perate forests on soil fertility. *Annals of Forest Science* 59: 233-253.

Aussenac, G. 2000. Interactions between forest stands and microclimate: Ecophysiological aspects and consequences for silviculture. *Annals of Forest Science* 57: 287-301.

Beck, W. 2000. Silviculture and stand dynamics of Scots pine in Germany. *Investigación Agraria: Sistemas y Recursos Forestales: Fuera de Serie* 1–2000: 199-212.

Belnap, J. and Lange, O.J. (Eds) 2001. Biological soil crust: structure, function, and management. *Ecological Studies* 150, Springer-Verlag, Berlin, Heidelberg, 506 pp.

Bena, W. 2012. Dzieje puszczy Zgorzelecko-Osiecznickiej [History of the Puszcza Zgorzelecko-Osiecznicka Forest]. F.H. Agat, Zgorzelec, 344 pp. (in Polish)

Bergstedt, J., Hagner, M. and Milberg, P. 2008. Effects on vegetation composition of a modified forest harvesting and propagation method compared with clear-cutting, scarification and planting. *Applied Vegetation Science* 11: 159-168.

Bermúdez, A.M., Fernández-Palacios, J.M., González-Mancebo, J.M., Patiño, J., Arévalo, J.R., Otto, R. and Delgado, J.D. 2007. Floristic and structural recovery of a laurel forest community after clear-cutting: A 60 years chronosequence on La Palma (Canary Islands). *Annals of Forest Science* 64(1): 109-119.

Bobiec, A. 1998. The mosaic diversity of field layer vegetation in the natural and exploited forests of Białowieża. *Plant Ecology* 13: 175-187.

Borcard, D., Legendre, P. and Drapeau, P. 1992. Partialling out the spatial component of ecological variation. *Ecology* 73(3): 1045-1055.

Bråkenhielm, S. and Liu, Q. 1998. Long-term effects of clear-felling on vegetation dynamics and species diversity in boreal pine forest. *Biodiversity Conservation* 7: 207-220.

Braun-Blanquet, J. 1964. Pflanzensoziologie. Grundzüge der Vegetationskunde [Phytosociology. Basics of vegetation science]. Springer Verlag, Wien, 865 pp. (in German)

Brus, D.J., Hengeveld, G.M., Walvoort, D.J.J., Goedhart, P.W., Heidema, A.H., Nabuurs, G.J. and Gunia, K. 2012. Statistical mapping of tree species over Europe. *European Journal of Forest Research* 131(1): 145-157.

Chojnacka-Ożga, L. and Ożga, W. 1999. Thermal conditions in the intermediary zone between forest and open ground. *Sylwan* 143(6): 11-17.

Chytrż, M., Tichż, L., Holt, J. and Botta-Dukát, Z. 2002. Determination of diagnostic species with statistical fidelity measures. *Journal of Vegetation Science* 13: 79-90.

Czerepko, J. 2004. Development of vegetation in managed Scots pine (*Pinus sylvestris* L.) stands in an oak-lime-hornbeam forest habitat. *Forest Ecology and Management* 202: 119-130.

Dolling, A. 1999. The vegetative spread of *Pteridium aquilinum* in a hemiboreal forest – invasion or revegetation? *Forest Ecology and Management* 124: 177-184.

Domes, Z. 1995. The evolution of policies and institutions of the forestry sector in the Czech Republic. Economics and management of forest operations for countries in transition to market economies. Proc. FAO/AUSTRIA Seminar, Ort/Gmunden, Austria, 1994. Available in http://www.fao.org/docrep/w3722E/w3722e00.htm#Contents [10 July 2012]

Dynesius, M. and Hylander, K. 2007. Resilience of bryophyte communities to clear-cutting of boreal stream-side forests. *Biological Conservation* 135: 423–434.

Dzwonko, Z. 2001. Effect of proximity to ancient deciduous woodland on restoration of the field layer vegetation in a pine plantation. *Ecography* 24: 198–204.

Dzwonko, Z. and Loster, S. 1997. Effects of dominant trees and anthropogenic disturbances on species richness and floristic composition of secondary communities in southern Poland. *Journal of Applied Ecology* 34: 861-870.

Faliński, J.B. 2001. Przewodnik do długoterminowych badań ekologicznych. [Guide for long-term ecological research]. Wydawnictwo Naukowe PWN, Warszawa, 672 pp, (in Polish)

Foster, B.L. and Tilman, D. 2000. Dynamic and static views of succesion: testing the descriptive power of chronosequence aproach. *Plant Ecology* 146: 1-10.

Godefroid, S., Massant, W. and Koedam, N. 2005a. Variation in the herb species response and the humus quality across a 200-year chronosequence of beech and oak plantations in Belgium. *Ecography* 28: 223-235.

Godefroid, S., Rucquoij, S. and Koedam, N. 2005b. To what extent do forest herbs recover after clearcutting in beech forest? *Forest Ecology and Management* 210: 39-53.

Halpern, C.B. and Spies, T.A. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. *Ecological Applications* 5(4): 913-934.

Hannerz, M. and Hånell, B. 1997. Effects on the flora in Norway spruce forests following clearcutting and shelterwood cutting. *Forest Ecology and Management* 90: 29-49.

Jäderlund, A., Norberg, G., Zackrisson, O., Dahlberg, A., Teketay, D., Dolling, A. and Nilsson, M.C. 1998. Control of bilberry vegetation by steam treatment–effects on seeded Scots pine and associated mycorrhizal fungi. *Forest Ecology and Management* 108(3): 275-285.

Karazija, S. 2003. Age-related dynamics of pine forest communities in Lithuania. *Baltic Forestry* 9(1): 50-62.

Kellomäki, S. 2000. Forests of the boreal region: gaps in knowledge and research needs. *Forest Ecology and Management* 132: 63-71.

Kelly, D.L. and Connolly, A. 2000. A review of the plant communities associated with scots pine (*Pinus sylvestris*) in Europe and an evaluation of putative indicator/specialist species. *Investigación Agraria: Sistemas y Recursos Forestales: Fuera de Serie* 1–2000: 15–39.

Kint, V. 2005. Structural development in ageing temperate Scots pine stands. *Forest Ecology and Management* 214(1): 237-250.

Kint, V., Geudens, G., Mohren, G. M. J., and Lust, N. 2006. Silvicultural interpretation of natural vegetation dynamics in ageing Scots pine stands for their conversion into mixed broadleaved stands. *Forest Ecology and Management* 223(1): 363-370.

Kruys, N. and Jonsson, B.G. 1999. Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern Sweden. *Canadian Journal of Forest Research* 29(8): 1295-1299.

Lepš, J. and Šmilauer, P. 2014. Multivariate analysis of ecological data using CANOCO 5. Cambridge University Press, Cambridge, 373 pp.

Marozas, V., Grigaitis, V. and Brazaitis, G. 2005. Edge effect on ground vegetation in clear-cut edges of pine-dominated forests. *Scandinavian Journal of Forest Research* 20 (Suppl 6): 43-48.

Matuszkiewicz, W. 2001. Przewodnik do oznaczania zbiorowisk roślinnych Polski [Guide for identification of plant communities in Poland]. Wydawnictwo Naukowe PWN, Warszawa, 537 pp, (in Polish)

Milnik, A. 2010. Ein land wie ein Eichenblatt. Schlesische Forstgeschichte in preußischer Zeit (1741–1945) [A country like an oak leaf. Silesian forest history in Prussian times (1741–1945)]. Verlag Kessel, 632 pp. (in German)

Moola, F.M. and Vasseur, L. 2004. Recovery of late-seral vascular plants in chronosequence of post-clearcut forest stands in coastal Nova Scotia, Canada. *Plant Ecology* 172: 183-197.

Moora, M., Daniell, T., Kalle, H., Liira, J., Püssa, K., Roosaluste, E., Öpik, M., Wheatley, R. and Zobel, M. 2007. Spatial pattern and species richness of boreone-moral forest understorey and its determinants – a comparison of differently managed forests. *Forest Ecology and Management* 250(1): 64-70.

Orczewska, A. and Fernes, M. 2011. Migration of herb layer species into the poorest post-agricultural pine woods adjacent to ancient pine forests. *Polish Journal of Ecology* 59(1): 75-85.

Økland, R.H., Rydgren, K. and Økland, T. 2003. Plant species composition of boreal spruce swamp forests: closed doors and windows of opportunity. *Ecology* 84(7): 1909-1919.

Økland, T., Rydgren, K., Økland, R.H., Storaunet, K.O. and Rolstad, J. 2003. Variation in environmental conditions, understorey species number, abundance and composition among natural and managed *Picea abies* forest stands. *Forest Ecology and Management* 177: 17–37.

Prescott, C.E. 1997. Effects of clearcuttings and alternative silvicultural systems on rates of decomposition and nitrogen mineralization in a coastal montane coniferous forest. *Forest Ecology and Management* 95: 253-260.

Qian, H., Klinka, K. and Sivak, B. 1997. Diversity of the understorey vascular vegetation in 40 year-old and old-growth forest stands on Vancouver Island, British Columbia. *Journal of Vegetation Science* 8: 773-780.

Roberts, M.R. and Zhu, L. 2002. Early response of the herbaceous layer to harvesting in a mixed coniferous–deciduous forest in New Brunswick, Canada. *Forest Ecology and Management* 155: 17-31.

Schmalholz, M. and Hylaner, K. 2009. Succession of bryophyte assemblages following clear-cut logging in boreal spruce-dominated forests in south-central Sweden – Does retrogressive succession occur? *Canadian Journal of Forest Research* 39: 1871-1880.

Siegel, S. and Castellan Jr., N.J. 1988. Nonparametric Statistics for the Behavioral Sciences (2nd ed.). New York: McGraw–Hill, 399 pp.

Sokal, R.R. and Rohlf, F.J. 1994. Biometry: the principles and practice of statistics in biological research (3rd ed.). W.H. Freeman and Co., New York, 896 pp.

Stefańska-Krzaczek, E. 2012. Species diversity across successional gradient of managed Scots pine stands in oligotrophic sites (SW Poland). *Journal of Forest Science* 58(8): 345-356.

ter Braak, C.J.F. and Prentice, I.C. 1988. A theory of gradient analysis. *Advances in Ecological Research* 18: 271–313.

Trexler, J.C. and Travis, J. 1993. Nontraditional regression analyses. *Ecology* 74(6): 1629-1637.

Uotila, A. and Kouki, J. 2005. Understorey vegetation in spruce-dominated forests in eastern Finland and Russian Karelia: Successional patterns after anthropogenic and natural disturbances. *Forest Ecology and Management* 215: 113-137.

Van Dyke, F. 2008. Conservation Biology, 2nd Edition: Foundations, Concepts, Applications. Springer, 477 pp.

Walker, L.R., Wardle, D.A., Bardgett, R.D. and Clarkson, B.D. 2010. The use of chronosequences in studies of ecological succession and soil development. *Journal of Ecology* 98: 725-736.

Watt, A.S. 1976. The ecological status of bracken. *Botanical Journal of the Linnean Society* 73: 217-239.

Widenfalk, O. and Weslien, J. 2009. Plant species richness in managed boreal forests – Effects of stand succession and thinning. *Forest Ecology and Management* 257: 1386-1394.

Zackrisson, O., Nilsson, M-C., Dahlberg, A. and Jäderlund, A. 1997. Interference mechanisms in conifer-*Ericaceae*-feathermoss communities. *Oikos* 78: 209-220.

Zerbe, S. 2002. Restoration of natural broad-leaved woodland in Central Europe on sites with coniferous forest plantations. *Forest Ecology and Management* 167: 27-42.