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

EWA STEFANIA-KRZACZEK¹* AND TOMASZ H. SZYMURA²
¹Department of Botany, Faculty of the Biological Sciences, University of Wroclaw, 6/8 Kanonia, PL-50-328 Wroclaw, Poland
²Mountain and Polar Ecosystems Laboratory, University of Wroclaw, pl. Maksa Borna 9, PL-50-328 Wroclaw, Poland
*Corresponding author: ewa.stefanska-krzaczek@uni.wroc.pl, tel. +48713754084


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 (Hannerez and Hänell 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, Ökland et al. 2003b). Clear-cutting has then a serious impact on species composition and diversity (Bräkenhielm and Liu 1998, Roberts and Zhu 2002, Ökland et al. 2003b, Moola and Vasseur 2004, Bergstedt et al. 2008, Widenfalk and Weslien 2009). Microclimate becomes favourable for early-seal species, also including alien invasive plants, which could colonise an open area (Halpem and Spies 1995, Bermúdez 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 diasporas (Dzwonko 2001). Moreover, the dominant tree species, introduced during stands re-planting, 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-

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, Bermúdez 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 (Hannerez and Hännel 1997, Uotila and Kouki 2005, Moora et al. 2007, Aavik et al. 2009). However, Scots pine is the dominant tree species in subcontinental 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 acidic 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 refuge 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 chronosequence 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 "Niederelschlesische 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 m$^3$ of volume/ha is removed and during late commercial thinnings 20–25 m$^3$ 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 m$^2$) 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 thinning. 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.

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

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 (+) 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:

\[ D = \sum (c_i/C)^2, \]

where \(c\) 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.

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 (Siegel 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 (Chytrí 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, Ókland R. H. et al. 2003a) in order to test whether stand age and canopy cover 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 \( A \)), \( A/C \) (shared variance), and \( C/A \) (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. \( A/C \) was obtained from CCA, where \( A \) and \( C \) were the environmental variables. \( A/C \) was computed as \( A/C = A \) (variation explained by \( A \) but not shared with \( C \)) and \( C/A \) the relative variation explained (or variation components divided by \( A/C \)) 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>
<thead>
<tr>
<th>Stand age classes [yr]</th>
<th>( H )</th>
<th>( p )</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;10</td>
<td>11</td>
<td>13</td>
</tr>
<tr>
<td>11–20</td>
<td></td>
<td></td>
</tr>
<tr>
<td>21–40</td>
<td></td>
<td></td>
</tr>
<tr>
<td>41–60</td>
<td></td>
<td></td>
</tr>
<tr>
<td>61–80</td>
<td></td>
<td></td>
</tr>
<tr>
<td>80–120</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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

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 oligotropa (Vain.) Coppins & P. James, P. uliginosa (Schrad.) Coppins & P. James and Tracheloopsis 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., Plaghioteicum curviliform Schliep. 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 cover in middle age class (21-40 years). Species, which reached higher values of cover, were: Deschampsia flexuosa (L.) Trin. and Placynthiella oligotropa 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 occurred 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>
<thead>
<tr>
<th>Table 3. Fidelity of species in given age classes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>Placynthiella oligotropa (Vain.) Coppins &amp; P. James</td>
</tr>
<tr>
<td>Polytrichum piliferum Hedw.</td>
</tr>
<tr>
<td>Tracheloopsis granulosa (Hoffm.) Lumbsch</td>
</tr>
<tr>
<td>Placynthiella uliginosa (Schrad.) Coppins &amp; P. James</td>
</tr>
<tr>
<td>Ceratodon purpureus (Hedw.) Brid.</td>
</tr>
<tr>
<td>Campylopus introflexus (Hedw.) Brid.</td>
</tr>
<tr>
<td>Calluna vulgaris (L.) Hull</td>
</tr>
<tr>
<td>Juncus effusus L.</td>
</tr>
<tr>
<td>Polytrichum juniperinum Hedw.</td>
</tr>
<tr>
<td>Cladonia macilenta Hoffm.</td>
</tr>
<tr>
<td>Chamaenerion angustifolium (L.) Scop.</td>
</tr>
<tr>
<td>Rubus sp.</td>
</tr>
<tr>
<td>Carex pluviosa L.</td>
</tr>
<tr>
<td>Calamagrostis epigeios (L.) Roth</td>
</tr>
<tr>
<td>Cephaloziella divaricata (Sm.) Schilff.</td>
</tr>
<tr>
<td>Cladonia subulata (L.) Weber in F.H. Wigg.</td>
</tr>
<tr>
<td>Cladonia pyxidata (L.) Hoffm.</td>
</tr>
<tr>
<td>Plagiothecium curvatumum Schliep. ex Limpr.</td>
</tr>
<tr>
<td>Lophocolea heterophylla (Schrad.) Dumort.</td>
</tr>
<tr>
<td>Cladonia chlorophaea (Flörke ex Sommerf.) Spreng.</td>
</tr>
<tr>
<td>Sciuro-hypnum oedipodium (Mitt.) Ignatov &amp; Hutten</td>
</tr>
<tr>
<td>Brachythecium rutabulum (Hedw.) Schimp.</td>
</tr>
<tr>
<td>Placynthiella kowalea (Ach.) Coppins &amp; P. James</td>
</tr>
<tr>
<td>Leucobryum glaucum</td>
</tr>
<tr>
<td>Melampyrum pratense</td>
</tr>
<tr>
<td>Dryopteris carthusiana (Vill.) H. P. Fuchs</td>
</tr>
</tbody>
</table>

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.obs = 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 ($AUC$) was due to stand age ($A/C$). Both canopy cover ($C/A$) and jointly: age and canopy cover ($A/N/C$) 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 Hänell 1997, Roberts and...
BALTIC FORESTRY

Zhu 2002, Karazija 2003, Czerepkó 2004, Moola and Vasseur 2004, Uotila and Kouki 2005). In this study the most common species were: heliophilous lichens, e.g. Placynthiella oligotropa, P. uliginosa, Trapelopsis 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 bryophytes and lichens.

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 Hänel 1997, Roberts and Zhu 2002, Otkland 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 Hänel 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 stands, 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 establishment 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 to 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 Hyländer 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 temporarily 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, Plagiothecium carvifolium and Scirypo-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 bryophyte 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-successional 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 (Orczew ska 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 raking 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-Krzaczk 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**

This study was financed by the Ministry of Science and Higher Education (N30406431/2479). The Author is grateful to Prof. Wiesław Faltynowicz for his input into the project, to Dr Monika Staniaszek-Kik and Dr Katarzyna Szczepańska for their help in identifying bryophytes and lichens, to Mr Władysław Nowak for his permission to use data available in the Bolesławiec Forest Inspectorate, to Mr Arkadiusz Sudol for his help in the explanation of forest management disturbances and to Dr Zygmunt Kački for his discussion of the problem.

**References**


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


Received 08 November 2014
Accepted 08 October 2015