Species diversity across the successional gradient of managed Scots pine stands in oligotrophic sites (SW Poland)

E. Stefańska-Krzaczek

Department of Biodiversity and Plant Cover Protection, Faculty of Biological Sciences, University of Wrocław, Wrocław

ABSTRACT: The Scots pine communities are common forest types in Central Europe, however, the general model of changes resulting from cyclical management practices is still unclear. The aim of this paper is to present the changes in species diversity during the development of managed Scots pine stands and to distinguish main stages of vegetation succession. The examined stands were divided into six age classes: ≤ 10 years old, 11–20, 21–40, 41–60, 61–80, 81–120 years old. Data from our study suggest a division of the stands into three main stages of succession on oligotrophic (low nutrient) sites. The first stage is associated with the youngest stands before the canopy formation (< 10 years), the second stage with young closed-canopy stands (11–40 years) and the third stage with the maturing, pre-mature and mature stands (> 40 years). The first stage was characterised by the highest value of the Shannon index, the highest number of vascular plant species, the highest cover of lichens but the lowest cover of bryophytes. There was a group of non-forest cryptogams, exclusive for that stage. In the second stage, there was a significant decline in the Shannon index, the cover of bryophytes increased and the cover of lichens decreased. *Cladonia* species were characteristic of that succession stage. The third stage was characterised by the lowest species richness, moreover, the cover of bryophytes was highest and the cover of lichens was lowest. Common coniferous forest species were characteristic of the final stage before clear-cutting. Generally, after stand removal the communities indicated higher species diversity than previous forest communities. The final forest plant associations were not determined solely by late-successional species. Forest management appeared to substantially influence changes in diversity and the course of succession.

Keywords: clear-cutting; vegetation succession; forest management; *Leucobryo-Pinetum*; undergrowth vegetation

Scots pine monocultures are very common forests in Central Europe. Some of them are introduced in fertile sites and constitute secondary communities for broadleaved or mixed forests (Zerbe 2002; Węgiel et al. 2009). Studies conducted in these phytocoenoses are mainly focused on directional transformations resulting from broadleaved forest regeneration. Except for secondary Scots pine communities in fertile sites, Scots pine forests of Central Europe are diversified in terms of the geographical locality connected with the influence of oceanic or continental climate (Roo-Zielińska, Solon 1997; Matuszkiewicz 2001). Furthermore, they are often intensively managed, with clear-cutting, site preparation, artificial re-planting and intensive thinnings. It has been recently suggested that Scots pine communities on mineral, oligotrophic sites undergo both directional transformations (Matuszkiewicz et al. 2007) as well as short- and long-term fluctuations (Solon 2010a,b). However, the general model of changes resulting from cyclical management practices is still unclear. There are few papers related to vegetation or species associated with developmental stages of managed stands (Fałtynowicz 1986; Łaska 2006; Stefańska 2006; Stefańska-Krzaczek 2011).

In general, human disturbance in commercial forests determines biodiversity and community succession (Christensen, Emborg 1996; Uotila, Kouki 2005; Widenfalk, Weslien 2009). Clear-

Supported by the Ministry of Science and Higher Education, Republic of Poland, Project No. N30406431/2479.

cutting and soil preparation cause sudden changes in site conditions, which are optimal for ruderals (Halpern, Spies 1995; Dyguś 1997), but unfavourable for later-successional forest species (Moola, Vasseur 2004). However, artificial regeneration shortens the period of non-forest microclimate, which can benefit the regeneration of species common to forest understories. Crown closure can initiate the development of forest microclimate, but the conditions are additionally modified by pre-commercial thinnings which reduce tree density and competition between trees and improve species richness (Thomas et al. 1999; Widenfalk, Weslien 2009).

Differing patterns of species diversity can be found in forests across temporal scales: diversity may be highest in the early stages of succession, may increase with succession or be equally high during both the early post-disturbance and climax stages (Roberts, Gilliam 1995). It depends on many factors, including the site quality gradient, the nature and intensity of the disturbance and the component species.

I propose that in the Scots pine monocultures on oligotrophic sites, understorey species diversity will be greater after clear-cutting and re-planting than in the oldest stands, because of simultaneous colonization and regeneration. After crown closure and during stand maturation species diversity will probably decrease because of the disappearance of non-forest species, but a decline in the general species number will be counteracted by the occurrence of late-successional species. Based on these hypotheses, the following questions were posed:

(I) How does species diversity change after clear-cut logging and re-planting, and then during subsequent stand maturation?
(II) What are the main stages of succession?
(III) What are the indicative species of early-successional and late-successional stages?

MATERIAL AND METHODS

Study area and management practices

The research plots were located throughout the northern part of Bolesławiec Forest Inspectorate, an 11,507 hectare tract in the south-western part of Poland (15°29'29"E 51°21'20"N). In the region, the climate is suboceanic with total annual precipitation of about 600 mm and mean temperature 2.4°C in January and 14.5°C in July. The prevailing winds are from the west and south-west. The terrain is gentle and the highest altitude does not exceed 200 m a.s.l. Soils are composed mostly of fluvioglacial and glacial deposits or aeolian sands. Fifty-five percent of the total area is covered by oligotrophic forest sites (low nutrient level) with moderate supply of soil moisture (mesic), classified as fresh coniferous forest. The sites are associated with podzols built of loose sands. A potential forest association of that site type is *Leucobryo-Pinetum* and it was identified in the studied sites (Stefańska-Krzaczek 2011). The Scots pine stands of the study area were planted at a density of 10,000 saplings per ha on clear-cuts after logging slash was removed and which were ploughed to prepare the soil for tree replanting. Developing Scots pine stands were tended with pre-harvest cuttings. The early pre-commercial thinnings were performed in stands before crown closure to remove some undesirable trees. The late pre-commercial thinnings were performed in stands after crown closure (> 10 years old) to reduce density to the number of 6–7,000 stems·ha^{-1}. Commercial thinnings were performed in older stands (> 20 years old) to support the growth of a proper number of high quality trees distributed regularly in a stand. During the early commercial thinning, approximately 15 m^3·ha^{-1} was removed and during the late commercial thinnings this number reached 20–25 m^3. Finally there were about 400 stems·ha^{-1} in pre-logged stands.

Field work

The study sites were categorised according to the following age classes: Ia (≤10 years old) includes young stands before crown closure where early pre-commercial thinning is performed once; Ib (11–20 years old) includes young stands of intensive height growth after recent crown closure where late pre-commercial thinning is performed once; II (21–40 years old) includes young stands of intensive height growth where early commercial thinning is performed once in each decade; III (41–60 years old) includes maturing stands after the culmination of height growth where late commercial thinning is performed once in each decade; IV (61–80 years old) includes pre-mature stands of increasing biomass where late commercial thinning is performed once in each decade; and V (81–120 years old) includes mature stands before logging.

Each age class was represented by 20 circular plots, each with a radius of 8 m. All plots were placed in randomly selected stands growing in homogeneous site conditions. Soil diagnoses for these sites, based on soil characteristics, were taken from the current management plan. The plot locations were chosen randomly with the exclusion of ecotones and stand gaps. The cover of the forest floor species (including vascular plants, bryophytes, lichens and young trees up to 0.5 m of height) was recorded using the following seven-point 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%, (r) one specimen per plot (Braun-Blanquet 1951, adapted).

Data analysis

To examine the changes of biodiversity after clear-cut logging and during stand maturation, a set of attributes was analysed, namely: number of species, species cover, Shannon index (H), participation of species synecological groups.

The mean number of all species, the separate tree, vascular plant, bryophyte and lichen categories were calculated for each age class. The normality of distribution was checked by the Shapiro-Wilk test. In order to compare the average number of vascular plant, bryophyte and tree species, the Kruskal-Wallis test with multiple comparisons as post hoc tests was conducted. To compare the average number of lichen species and all species, analysis of variance and Fisher's least significant difference test as post-hoc test were conducted.

The mean percentage cover for vascular plants, bryophytes, lichens and young trees was calculated for each age class. The mean cover values for particular scale points were: (5) 87.5%, (4) 62.5%, (3) 37.5%, (2) 17.5%, (1) 5%, (+) 0.5%, (r) 0.1%. The mean cover of all species was not presented, because the vascular plant layer, as well as the bryophyte-lichen layer was estimated separately in the field and the sum of all species per plot might exceed 100%. The differences between means were tested using the Kruskal-Wallis test with multiple comparisons as post hoc tests. The non-parametric statistics were performed because the cover was estimated and expressed in scale points, not measured.

The Shannon index (H) (Magurran 1988) was calculated according to the formula:

$$H = \Sigma(c_i/C) \times ln\ (c_i/C)$$

where:

c_i – mean cover for i species on a plot,

C – sum of mean covers for all species.

The mean cover values for particular scale points were: (5) 87.5%, (4) 62.5%, (3) 37.5%, (2) 17.5%, (1) 5%, (+) 0.5%, (r) 0.1%.

The Shannon index was calculated for each plot, and the mean values for each age class were then calculated. The differences between means were tested using the Kruskal-Wallis and multiple comparisons as post hoc tests.

Moreover, to assess the turnover of phytocoenosis types during stand development, the mean percentage participation of defined synecological groups (Matuszkiewicz 2001) in total cover and total number of species was calculated for the stages. The following groups were distinguished: species of coniferous forest (*Vaccinio-Piceetea*), species of suboceanic heaths (*Nardo-Callunetea*) and species of sandy grasslands (*Koelerio-Corynephoretea*). The differences between means were tested using the Kruskal-Wallis test and multiple comparisons as post hoc tests. The statistical significance of differences in the aforementioned attributes of species diversity in stand age classes was used as the basis for combining the classes into principal successional stages at the study sites. The analysis of species number and cover as well as Shannon index and participation of synecological groups were repeated in these stages to demonstrate general diversity changes across the successional gradient. The differences between means were tested by the Kruskal-Wallis test except for all species number where ANOVA was used.

All statistical analysis was performed using STATISTICA (Hill, Lewicki 2007).

To identify which species were indicative of new combined successional stages, the phi coefficient was calculated for each species using presence/absence data. The calculations of the coefficient and Fisher's exact tests for the significance of differences were performed in JUICE (Tichý 2002). The values of the phi coefficient range from –1 to 1, but they are multiplied by 100 in the program, only positive values are displayed (Tichý, Holt 2006).

The taxonomic nomenclature used in this study conforms with Mirek et al. (2002), Fałtynowicz (2003), Ochyra et al. (2003), and Szweykowski (2006).

RESULTS

The quantitative age classes did not represent distinct successional stages, however, the variation in different attributes of species diversity and the proportions of each synecological group were used to divide the data into 3 stages of succession: 1 – stands before crown closure (≤10 years old stands), 2 – young closed-canopy stands (11–40 years old stands) and

Table 1. Mean number, mean cover of species and the mean Shannon diversity index *H* (± SD) in stand age classes

Stand age class (years)	≤ 10	11–20	21–40	41–60	61–80	81–120
Number of species						
All species	$22^{a} \pm 3$	$22^{a} \pm 4$	$22^{a} \pm 4$	$21^{ab} \pm 5$	$20^{bc} \pm 4$	$18^{c} \pm 4$
Trees	$2^{a} \pm 2$	$2^{a} \pm 1$	$2^{a} \pm 1$	$3^{a} \pm 1$	$3^{a} \pm 2$	$2^{a} \pm 1$
Vascular plants	$5^{a} \pm 2$	$4^{ab} \pm 2$	$3^{b} \pm 1$	$3^{b} \pm 1$	$3^{b} \pm 1$	$4^{b} \pm 1$
Bryophytes	$8^{ab} \pm 2$	$9^{ab} \pm 2$	$10^{a} \pm 2$	$10^{a} \pm 2$	$8^{ac} \pm 2$	$8^{bc} \pm 1$
Lichens	$7^{ab} \pm 2$	$7^{ad} \pm 3$	$7^{a} \pm 2$	$5^{bcd} \pm 4$	$5^{bc} \pm 3$	$4^{c} \pm 3$
Percentage cover						
Trees	$1^{a} \pm 1$	$1^{a} \pm 1$	$1^{a} \pm 0$	$1^{a} \pm 1$	$2^{a} \pm 2$	$1^{a} \pm 1$
Vascular plants	$24^{a} \pm 17$	$9^{b} \pm 15$	$5^{b} \pm 8$	$13^{abc} \pm 17$	$14^{ab} \pm 16$	$30^{ac} \pm 21$
Bryophytes	$21^{a} \pm 12$	$41^{ab} \pm 17$	$47^{bc} \pm 26$	$55^{bd} \pm 15$	$68^{cd} \pm 19$	$66^{cd} \pm 19$
Lichens	23 ± 12	$4^{ab} \pm 2$	$6^{a} \pm 6$	$3^{ac} \pm 2$	$3^{ad} \pm 2$	$2^{bcd} \pm 1$
H	$2.0^{a} \pm 0.3$	$1.6^{b} \pm 0.3$	$1.8^{cd} \pm 0.2$	$1.9^{ac} \pm 0.2$	$1.7^{bc} \pm 0.2$	$1.7^{bd} \pm 0.2$

Values within each group followed by the same letter are not significantly different according to the Kruskal-Wallis test (trees, vascular plants, bryophytes) or ANOVA (all species, lichens) at $P < 0.05$

3 – mature closed-canopy stands (> 41 years old stands) (Tables 1 and 2).

The first stage (stage 1) was characterised by the highest number of vascular plant species and higher number of lichen species and all species than in stage 3. The differences were statistically significant (Fig. 1). The cover of vascular plants did not differ in comparison with stage 3, but the cover of bryophytes was significantly lower and the cover of lichens was significantly higher (Fig. 2). In the first stage the Shannon diversity index reached the highest value of statistical significance (Fig. 3). The number of coniferous forest species (*Vaccinio-Piceetea*) was lower than in stage 3 and the difference was significant (Fig. 4). The same tendency was noted in the cover of coniferous forest species and there was also a significant difference between stage 1 and stage 3 (Fig. 5). In contrast, the number of sandy grassland species (*Koelerio-Corynephoretea*) was higher than in stage 3 and the difference

Table 2. Mean percentage participation of synecological groups (± SD) in species number and cover

Stand age class (years)	≤ 10	21–40	21–40	41–60	61–80	81–120
Coniferous forest species *Vaccinio-Piceetea*						
Total species number (%)	$28^{a} \pm 8$	$30^{ab} \pm 11$	$40^{bc} \pm 9$	$48^{cd} \pm 11$	$44^{ce} \pm 7$	$51^{de} \pm 8$
Species cover (%)	$26^{a} \pm 21$	$29^{a} \pm 26$	$47^{ab} \pm 22$	$62^{bc} \pm 23$	$76^{c} \pm 23$	$84^{c} \pm 12$
Suboceanic heath species *Nardo-Callunetea*						
Total species number (%)	$25^{ac} \pm 5$	$24^{a} \pm 5$	$26^{ab} \pm 5$	$22^{a} \pm 5$	$30^{bc} \pm 5$	$27^{ac} \pm 6$
Species cover (%)	$56^{a} \pm 24$	$56^{a} \pm 25$	$41^{ab} \pm 20$	$33^{ac} \pm 21$	$21^{bc} \pm 22$	$14^{c} \pm 11$
Sandy grassland species *Koelerio glauce-Corynephoretea canescentis*						
Total species number (%)	$20^{a} \pm 9$	$21^{a} \pm 8$	$14^{ab} \pm 6$	$8^{bc} \pm 4$	$8^{bd} \pm 5$	$7^{cd} \pm 4$
Species cover (%)	$9^{a} \pm 11$	$7^{a} \pm 7$	$7^{ab} \pm 12$	$1^{bc} \pm 1$	$1^{c} \pm 1$	$1^{c} \pm 1$
Other species						
Total species number (%)	$26^{a} \pm 8$	$25^{a} \pm 10$	$20^{ab} \pm 9$	$21^{ab} \pm 11$	$19^{ac} \pm 9$	$14^{bc} \pm 9$
Species cover (%)	$9^{a} \pm 8$	$8^{a} \pm 7$	$6^{b} \pm 6$	$3^{ac} \pm 3$	$2^{bc} \pm 1$	$1^{c} \pm 1$

Values within each group followed by the same letter are not significantly different according to the Kruskal-Wallis test at $P < 0.05$

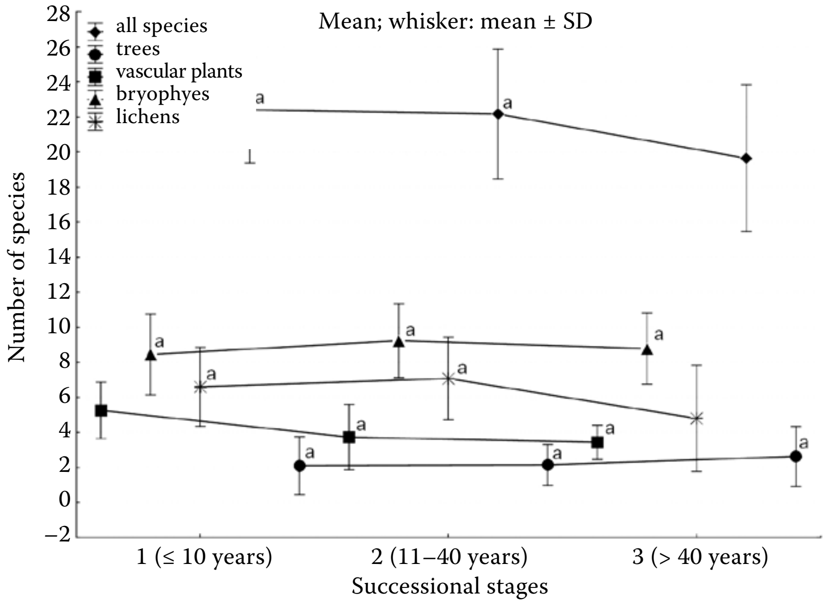

Fig. 1. Mean number of species in three successional stages

Values within each group followed by the same letter are not significantly different according to the Kruskal-Wallis test (trees, vascular plants, bryophytes, lichens) or ANOVA (all species) at $P < 0.05$

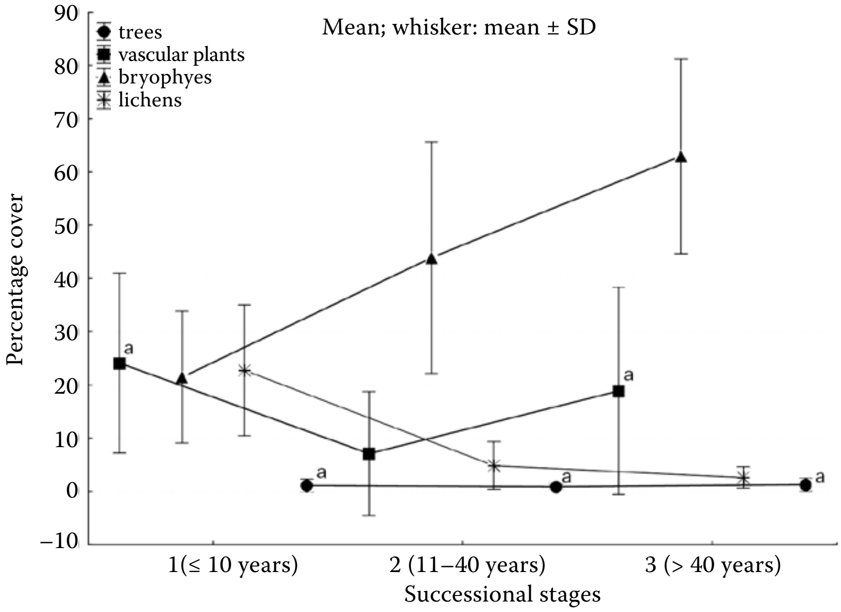

Fig. 2. Mean percentage cover of species in three successional stages

Values within each group followed by the same letter are not significantly different according to the Kruskal-Wallis test at $P < 0.05$

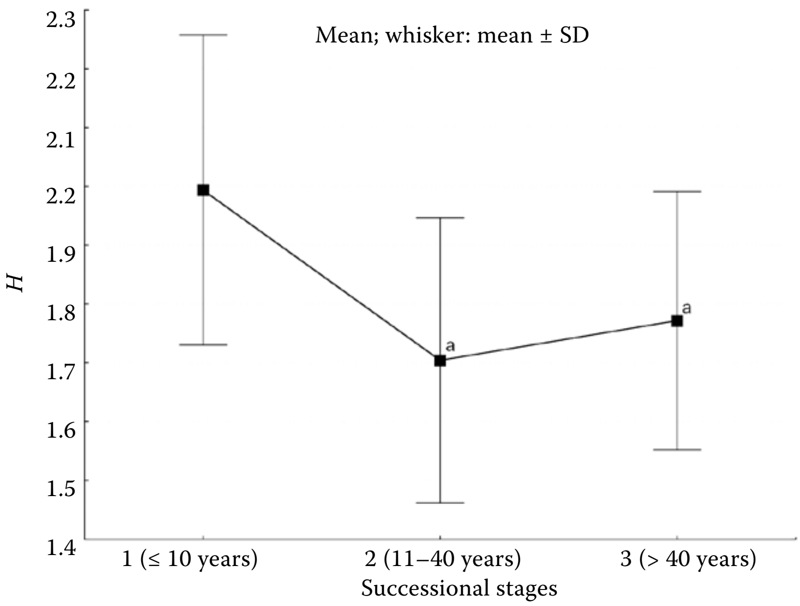

Fig. 3. Mean values of the Shannon diversity index in three successional stages

Values within each group followed by the same letter are not significantly different according to the Kruskal-Wallis test at $P < 0.05$

Table 3. Percentage frequency and fidelity (phi coefficient multiplied by 100) of species in three main successional stages. See Material and Methods for more explanations of variables

Successional stage	1 (≤10 years)		2 (11–40 years)		3 (> 40 years)	
No. of plots	20		40		60	
	Frequency (%)	Fidelity	Frequency (%)	Fidelity	Frequency (%)	Fidelity
Coniferous forest species (*Vaccinio-Piceetea*)						
Pleurozium schreberi	75	–	65	–	100	35.4
Vaccinium myrtillus	80	–	60	–	83	34.8
Cladonia gracilis	35	–	78	33.1	50	–
Dicranum polysetum	35	–	68	–	85	32.9
Leucobryum glaucum	25	–	18	–	42	21.4
Dicranum scoparium	85	–	90	–	98	17.9
Melampyrum pratense	10	–	3	–	17	16.6
Vaccinium vitis-idaea	80	–	60	–	85	14.4
Other species (frequency in stages 1, 2, 3): *Cladonia arbuscula* (30, 38, 30), *Cladonia furcata* (5, 8, 3), *Cladonia rangiferina* (10, 35, 27), *Deschampsia flexuosa* (85, 88, 88), *Dicranum spurium* (60, 88, 78), *Monotropa hypopitis* (0, 3, 0)						
Heathland species (*Nardo-Callunetea*)						
Placynthiella oligotropha	95	92.5	5	–	–	–
Calluna vulgaris	100	39.6	80	6.4	48	–
Ptilidium ciliare	35	–	60	–	87	37.8
Hypnum jutlandicum	80	–	95	–	100	21.3
Agrostis capillaris	5	–	10	16.2	–	–
Other species (frequency in stages 1, 2, 3): *Carex pilulifera* (20, 15, 5), *Cladonia chlorophaea* (35, 63, 55), *Cladonia deformis* (15, 33 18), *Cladonia pyxidata* (35, 30, 33), *Pohlia nutans* (95, 100, 95)						
Sandy grassland species (*Koelerio glauce-Corynephoretea canescentis*)						
Polytrichum piliferum	90	**75.7**	23	–	2	–
Cladonia subulata	15	–	73	58.2	13	–
Ceratodon purpuraeus	75	52.9	38	–	3	–
Spergula morisonii	35	45.1	5	–	–	–
Rumex acetosella	25	33.2	5	–	2	–
Corynephorus canescens	25	32.2	8	–	–	–
Cephaloziella cfr. *divaricata*	45	–	65	29.3	23	–
Cladonia cervicornis ssp. *verticillata*	–	–	10	26.3	–	–
Cladonia pleurota		–	8	22.6		–
Cladonia macilenta	85	–	95	16.5	82	–
Other species (frequency in stages 1, 2, 3): *Cladonia coccifera* (5, 5, 3), *Cladonia phyllophora* (0, 13, 5), *Cladonia uncialis* (0, 10, 3)						

Table 3 to be continued

Successional stage	1 (≤ 10 years)		2 (11–40 years)		3 (> 40 years)	
No. of plots	20		40		60	
	Frequency (%)	Fidelity	Frequency (%)	Fidelity	Frequency (%)	Fidelity
Accompanying species						
Trapeliopsis granulosa	95	80.9	18	–	5	–
Calamagrostis epigeios	70	56.1	25	–	3	–
Placynthiella uliginosa	65	51.2	8	–	22	–
Cladonia cornuta	–	–	20	37.8	–	–
Polytrichum juniperinum	75	31.5	60	10.2	23	–
Campylopus introflexus	40	29.6	28	8.5	–	–
Placynthiella icmalea	55	29.6	30	–	20	–
Cladonia fimbriata	–	–	23	28.5	8	–
Cladonia crispata	5	–	25	25.9	8	–
Campylopus flexuosus	–	–	–	–	8	23.9
Brachythecium salebrosum	–	–	8	22.6	–	–
Peltigera didactyla	–	–	8	22.6	–	–

Other species (frequency in stages 1, 2, 3): *Aulacomnium palustre* (0, 0, 2), *Brachythecium rutabulum* (0, 18, 13), *Brachythecium starkei* (0, 0, 2), *Cetraria islandica* (20, 13, 27), *Cladonia coniocraea* (5, 10, 2), *Cladonia digitata* (0, 3, 3), *Cladonia glauca* (5, 8, 0), *Cladonia ochrochlora* (5, 5, 13), *Cladonia portentosa* (0, 3, 2), *Dicranella heteromalla* (20, 25, 32), *Festuca ovina* (0, 3, 5), *Gnaphalium sylvaticum* (0, 3, 0), *Herzogiella seligeri* (0, 0, 3), *Hieracium pilosella* (0, 3, 0), *Holcus mollis* (5, 0, 0), *Hypnum cupressiforme* (0, 0, 3), *Juncus effusus* (5, 3, 0), *Lophocolea bidentata* (0, 0, 2), *Lophocolea heterophylla* (0, 23, 17), *Orthodicranum flagellare* (5, 0, 5), *Orthodicranum montanum* (0, 8, 5), *Placynthiella dasaea* (40, 38, 47), *Plagiothecium curvifolium* (0, 8, 10), *Polytrichastrum formosum* (5, 18, 20), *Rorippa palustris* (5, 0, 0), *Sciuro-hypnum oedipodium* (0, 23, 20), *Urtica dioica* (0, 3, 0), *Veronica officinalis* (5, 0, 0)

zero fidelity value – given to species with significance 0.05 according to Fisher's exact test

was significant (Fig. 4). Similarly, the cover of these species was higher and there was also a significant difference (Fig. 5). The number of heathland species (*Nardo-Callunetea*) was similar in stage 1 and stage 3 (Fig. 4), however, the cover of these species was significantly higher than in stage 3 (Fig. 5). Non-forest species, especially cryptogams, were characteristic of stage 1: *Ceratodon purpureus, Placynthiella oligotropha, P. uliginosa, Polytrichum piliferum* and *Trapeliopsis granulosa* (Table 3). These species manifested high fidelity, which meant that they were exclusive for the first stage of succession.

The second stage (stage 2) was characterised by a significant decrease in the vascular species number compared to stage 1. The number of all species and lichen species was still higher than in stage 3 and the differences were statistically significant (Fig. 1). The cover of bryophytes was significantly higher than in stage 1, and the cover of lichens was significantly lower, likewise the cover of vascular plants (Fig. 2). The Shannon index was significantly lower than in stage 1 (Fig. 3). Similarly to stage 1, the number of coniferous forest species was still lower than in stage 3, the number of sandy grassland species was higher and the differences were statistically significant (Fig. 4). The cover of coniferous forest species was significantly lower than in stage 3 and the cover of sandy grassland species was significantly higher, likewise heathland species (Fig. 5). *Cladonia* species were characteristic of the second stage, however, site conditions were optimal especially for *C. subulata* (Table 3).

The third stage (stage 3) was characterised by the lowest number of all species and lichen species

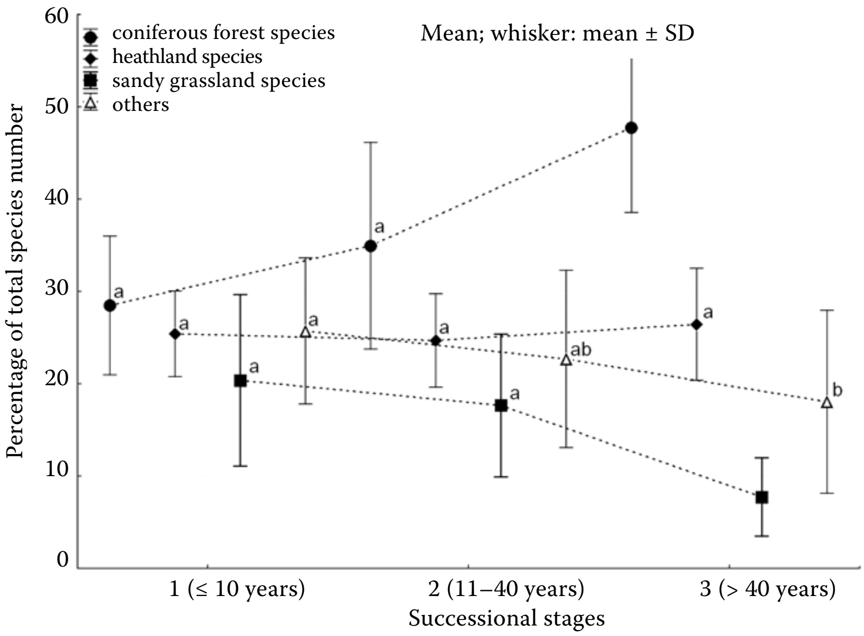

Fig. 4. Mean percentage participation of synecological groups in species number

Values within each group followed by the same letter are not significantly different according to the Kruskal-Wallis test at $P < 0.05$

and the differences were significant. The number of vascular plant species was similar to stage 2, there were no significant differences between stage 2 and stage 3 (Fig. 1). The cover of bryophytes in stage 3 was highest and the cover of lichens was lowest during succession and there were significant differences between stages 1 and 3 as well as stages 2 and 3. The cover of vascular plants was significantly higher than in the second stage, but did not significantly differ from the cover in stage 1 (Fig. 2). The Shannon index was higher than in the second stage, but there was no significant difference, however the Shannon index was significantly lower than in the first stage (Fig. 3). The number of coniferous forest species was highest and the number of sandy grassland species was lowest across the temporal gradient and the differences were statistically significant (Fig. 4). Moreover, the cover of coniferous forest species was highest and the cover of sandy grassland species was lowest with statistical significance (Fig. 5). The number of heathland species (*Nardo-Callunetea*) was similar to stage 1 (Fig. 4) but their cover was lower (Fig. 5). The species characteristic of the third stage were *Dicranum polysetum, Pleurozium schreberi, Ptilidium ciliare* and *Vaccinium myrtillus*, although their fidelity was not very high

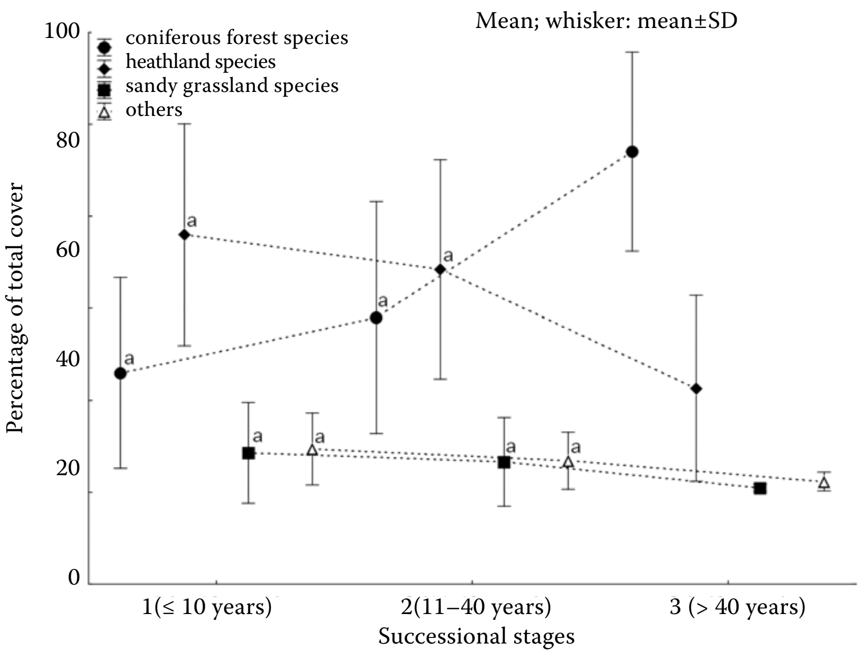

Fig. 5. Mean percentage participation of synecological groups in species cover

Values within each group followed by the same letter are not significantly different according to the Kruskal-Wallis test at $P < 0.05$

and they were also quite frequent in stage 1 and 2 (Table 3).

DISCUSSION

Species diversity after clear-cutting has been found to be lower than prior to clear-cutting in some cases (Hannerz, Hånell 1997; Bråkenhielm, Liu 1998). Others have described an increase in species diversity in the early phases of succession (Haeussler et al. 2002; Uotila, Kouki 2005; Widenfalk, Weslien 2009). In the present study, as it was hypothesised, species diversity was found to be higher after clear-cutting than before, resulting from a combination of residual forest species common to intact forests and pioneers. Clear-cutting and site preparation promote non-forest species characteristic of the respective site, but this increase of biodiversity does not mean that the ecosystem is improved. Various authors have concluded that the impact of management practices is negative for forest diversity, because it can eliminate rare and sensitive species. Those species ecologically limited to a narrow set of intact forest conditions have not had enough time to recover during a relatively short time since the last disturbance (Battles et al. 2001; Roberts, Zhu 2002; Moola, Vasseur 2004; Sullivan et al. 2008). In the oldest age classes in this study, species diversity is low even if individual moss and lichen species are included. Species characteristic of the late succession stage distinguished in this study are generally common in Scots pine forests (Matuszkiewicz 2001) and they are not confined to the oldest stands but also present in the first stage of succession. Low species diversity of the final stage of succession is then related to the absence of specific species, exclusive for old stands. Thus, the hypothesis that a decline in species richness after crown closure can be counteracted by the occurrence of late-successional species could not be supported. Vascular plants of the *Vaccinio-Piceetea* class, which could be considered as late-successional species, are representatives of *Lycopodiaceae* and *Pyrolaceae*, which are in the middle of their range in the study area (Hultén, Fries 1986). Nevertheless, these species are suggested to prefer continental and sub-continental conditions (Solon 1998), therefore suboceanic climate may be unfavourable for their recruitment in the region. Regardless of this fact, human disturbance related to the silviculture can be a threat to the occurrence of these species especially that there are no fragments of ancient Scots pine woodlands in the region which could serve as reservoirs. Some researchers have concluded that the proximity of such banks of diasporas is crucial for the effective late-seral species regeneration (Dzwonko 1993; Graae, Heskjær 1997; Jakubowska-Gabara, Mitka 2007; Orczewska, Fernes 2011). In this case the maintenance of these species in managed forests requires paying attention to each individual locality and keeping local conditions untouched during management practices (Gorzelak 2009). It is crucial, because, as it was aforementioned, current rotation ages are often shorter than the time required for their recover. As a consequence the vegetation of managed forests may remain permanently altered compared to natural forests (Hart, Chen 2006).

The formation of the canopy layer is described as a critical moment for vegetation, because of a reduction in light intensity (Økland et al. 2003). A significant decrease both in Shannon index and cover of vascular plants in the second stage of the study sites supports this statement. However, the stand shield appears to be favourable for the development of bryophytes (Andersson, Hytteborn 1991; Nelson, Halpern 2005). They become abundant in the second stage of succession in the studied sites. The young closed-canopy stands are also optimal for *Cladonia* species. Intensive transpiration of a young tree stand decreases the level of groundwater, while intensive thinnings result in drying out of the top soil layers (Puchalski, Prusinkiewicz 1990), which is probably beneficial for *Cladonia* species development. Therefore, young managed Scots pine stands in the habitat of *Leucobryo-Pinetum* can play an important role to maintain the diversity of *Cladonia* species which withdraw together with the disappearance of *Cladonio-Pinetum* phytocoenoses in Central Europe (Matuszkiewicz et al. 2007).

In general, the succession process in managed forests is constrained by human interference. For example, some successional phases after afforestation of the abandoned farmlands exhibit lower species richness than in spontaneous succession (Faliński et al. 1993). Nevertheless, the introduction of pine trees causes a decline in the number of non-forest species and an acceleration of forest species development. The slow process of canopy formation is replaced by tree planting and the forest microclimate develops quite early. According to Faliński (1986), forest species enter the community when the forest vertical structure is developed. In the studied area the stratification forms after about 10 years, when the crowns join together. Moreover, the introduction of trees in the area where the forest community has existed also promotes forest species development and forest community rebuilding. In the area where non-forest communities have existed for a long time, forest species become significant in the forest floor after 50 years (Kawecka 1990).

In summary, stand age classes did not represent distinct successional stages, however, the variation in different attributes of species diversity suggested a division of the stands into 3 stages of succession: stands before crown closure, young closed-canopy stands and mature closed-canopy stands. Stands before crown closure showed higher species diversity than mature closed-canopy stands. Each stage of the succession was distinguished by specific species composition but the first stage was unique because of a group of species with very high fidelity. The final forest communities were not determined by the exclusive late-successional species. Forest management (logging, reforestation and thinnings) was an important factor in the diversity changes and course of succession.

Acknowledgements

The author is grateful to Prof. Wiesław Fałtynowicz for his input to the project, to Dr. Monika Staniaszek-Kik for her help in identifying bryophytes, to Dr. Katarzyna Szczepańska for her help in identifying lichens, to Mr Władysław Nowak for his permission to use the data available in the Bolesławiec Forest Inspectorate and to Mr. Arkadiusz Sudoł for his help in the explanation of forest management disturbances.

References

Andersson L.I, Hytteborn H. (1991): Bryophytes and decaying wood – a comparison between managed and natural forest. Holarctic Ecology, ***14***: 121–130.

Battles J.J., Shlisky A.J., Barrett R.H., Heald R.C., Allen-Diaz B.H. (2001): The effects of forest management on plant species diversity in Sierran conifer forest. Forest Ecology and Management, ***146***: 211–222.

Braun-Blanquet J. (1951): Pflanzensoziologie – Grundzüge der Vegetationskunde. Wien, Springer Verlag: 631.

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

Christensen M., Emborg J. (1996): Biodiversity in natural versus managed forest in Denmark. Forest Ecology and Management, ***85***: 47–51.

Dyguś K.H. (1997): The influence of clear cutting on the structure, floral and phytocenotic richness and on ecological process in a forest ecosystem. Polish Ecological Studies, ***23*** (3–4): 89–106.

Dzwonko Z. (1993): Relations between the floristic composition of isolated young woods and their proximity to ancient woodland. Journal of Vegetation Science, ***4***: 693–698.

Faliński J.B. (1986): Sukcesja roślinności na nieużytkach porolnych jako przejaw dynamiki ekosystemu wyzwolonego spod długotrwałej presji antropogenicznej. [Vegetation succession on abandoned farmland as a dynamics manifestation of ecosystem liberal of long continuance anthropopression.] Wiadomości Botaniczne, ***30***: 25–50. (in Polish with English summary)

Faliński J.B., Cieśliński S., Czyżewska K. (1993): Dynamic-floristic atlas of Jelonka reserve and adjacent areas. Distribution of vascular plant species, bryophytes and lichens on the abandoned farmlands during secondary succession. Phytocoenosis, 5, Supplementum Cartographiae Geobotanicae, ***3***: 3–139.

Fałtynowicz W. (1986): The dynamics and role of lichens in a managed *Cladonia*-scotch pine forest (*Cladonio-Pinetum*). Monographiae Botaniceae, ***69***: 5–96.

Fałtynowicz W. (2003): The Lichens, Lichenicolous and Allied Fungi of Poland – an Annotated Checklist. Kraków, W. Szafer Institute of Botany, Polish Academy of Science: 435.

Gorzelak P. (2009): Nowe stanowisko widlicza spłaszczonego *Diphasiastrum complanatum* L. (Lycopodiaceae) na Dolnym Śląsku i możliwości jego ochrony z punktu widzenia leśnika. [A new locality of *Diphasiastrum complanatum* L. (Lycopodiaceae) in Lower Silesia and possibilities of its protection from the viewpoint of a forester.] Acta Botanica Silesiaca, ***4***: 125–133 (in Polish with English summary).

Graae B.J., Heskjær V.S. (1997): A comparison of understorey vegetation between untouched and managed deciduous forest in Denmark. Forest Ecology and Management, ***96***: 111–123.

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

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

Haeussler S., Bedford L., Leduc A., Bergeron Y., Kranabetter J.M. (2002): Silvicultural disturbance severity and plant communities of the southern Canadian boreal forest. Silva Fennica, ***36***: 307–327.

Hart S.A., Chen H.Y.H. (2006): Understory vegetation dynamics of North American boreal forests. Critical Reviews in Plant Sciences, ***25***: 381–397.

Hill T., Lewicki P. (2007): STATISTICS: Methods and Applications. Electronic Statistics Textbook. Tulsa, StatSoft: 800.

Hultén E., Fries M. (1986): Atlas of North European , Vascular Plants. North of the Tropic of Cancer. Königstein, Koeltz Scientific Books: 1172.

Jakubowska-Gabara J., Mitka J. (2007): Ancient woodland species in a landscape park in central Poland. Acta Societatis Botanicorum Poloniae, ***76***: 239–249.

Kawecka A. (1990): Dynamika fitocenoz sztucznych sośnin na gruntach porolnych w Suwalskim Parku krajobrazowym. [Dynamics of phytocenoses of artificial pine stands on post-agricultural grounds in Suwałki Landscape Park.] Prace IBL, ***711***: 3–34. (in Polish with English summary)

Łaska G. (2006): Tendencje dynamiczne zbiorowisk zastępczych w Puszczy Knyszyńskiej. [Dynamic Tendencies of the Secondary Communities in the Knyszyńska Forest.] Białystok–Poznań, Politechnika Białostocka, Instytut Inżynierii i Ochrony Środowiska, Bogucki Wyd. Naukowe: 503. (in Polish with English summary)

Magurran A. E. (1988): Ecological Diversity and its Measurement. Princeton, Princeton University Press: 179.

Matuszkiewicz W. (2001): Przewodnik do oznaczania zbiorowisk roślinnych Polski. [Guide for Identification of Plant Communities in Poland.] Warszawa, PWN: 537. (in Polish)

Matuszkiewicz J. M., Solon J., Orzechowski M., Kozłowska A., Różański W., Szczygielski M., Matejczuk G., Lorens B., Kowalska A. (2007): Geobotaniczne rozpoznanie tendencji rozwojowych zbiorowisk leśnych w wybranych regionach Polski. [Geobotanical Identification of the Development Tendencies in Forest Associations in the Regions of Poland.] Warszawa, PAN: 976. (in Polish with English summary)

Mirek Z., Piękoś-Mirkowa H., Zając A., Zając M. (2002): Flowering Plants and Pteridophytes of Poland. A checklist. Kraków, W. Szafer Institute of Botany, Polish Academy of Science: 442.

Moola F.M, 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.

Nelson C.R., Halpern C.B. (2005): Short-term effects of timber harvest and forest edges on ground-layer mosses and liverworts. Canadian Journal of Botany, ***83***: 610–620.

Ochyra R., Żarnowiec J., Bednarek-Ochyra H. (2003): Census Catalogue of Polish Mosses. Kraków, Polish Academy of Science, Institute of Botany: 372.

Orczewska A., 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***: 75–85.

Økland T., Rydgren K., Økland R.H., Fernes M., Storaunet K.O., 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.

Puchalski T., Prusinkiewicz Z. (1990): Ekologiczne podstawy siedliskoznawstwa leśnego. [Ecological Basis of Forest Site Science.] Warszawa, PWRiL: 619.

Roberts M.R., Gilliam F.S. (1995): Patterns and mechanisms of plant diversity in forested ecosystems: Implications for forest management. Ecological Applications, ***5***: 969–977.

Roberts M.R., 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.

Roo-Zielińska E., Solon J. (1997): Effects of geographical location on species composition, vegetation structure, diversity and phytoindicative characteristics in pine forests. Environmental Pollution, ***98***: 347–360.

Solon J. (1998): Różnorodność gatunkowa borów i borów mieszanych na transektach badawczych: klimatycznym (wzdłuż 52°N, od 12° do 32°E) i „śląskim". [Species diversity of pine and mixed pine forests along climatic (52°N, 12°-32°E) and „silesian" transect.] In: Breymeyer A., Roo-Zielińska E. (eds): Bory sosnowe w gradiencie kontynentalizmu i zanieczyszczeń w Europie Środkowej –badania geoekologiczne. [Pine forests in Central European gradient of continentality and pollution – geoecological studies.] Dokumentacja Geograficzna, ***13***: 113–130 (in Polish with English summary).

Solon J. (2010a): Florystyczne i ekologiczne zmiany charakteru runa na powierzchniach obserwacyjnych w latach 2003–2008. [Floristic and ecological changes of the undergrowth vegetation on monitoring plots in 2003–2008.] In: Wawrzoniak J. (ed.): Stan uszkodzenia lasów w Polsce w 2008 roku na podstawie badań monitoringowych. [Damage of Polish Forests in 2008 on the Basis of Monitoring Research.] Biblioteka Monitoringu Środowiska: 44–48.

Solon J. (2010b): Poziome zróżnicowanie runa powierzchni monitoringowych w roku 2008 oraz zmiany w latach 1998–2008. [Vertical diversity of the undergrowth vegetation in 2008 and changes in 1998–2008.] In: Wawrzoniak J. (ed.): Stan uszkodzenia lasów w Polsce w 2008 roku na podstawie badań monitoringowych. [Damage of Polish Forests in 2008 on the Basis of Monitoring Research.] Biblioteka Monitoringu Środowiska: 49–52.

Stefańska E. (2006): Zmiany składu gatunkowego fitocenoz w przebiegu sukcesji wtórnej na siedlisku boru świeżego w Borach Dolnośląskich. [Species composition changes during stand succession process on the mesic pine forest site in the Bory Dolnośląskie.] Badania Fizjograficzne nad Polską Zachodnią B, ***55***: 105–117. (in Polish with English summary)

Stefańska-Krzaczek E. (2011): Plant communities of Scots pine stands in the south-eastern part of the Bory Dolnośląskie forest (SW Poland). Acta Botanica Silesiaca, Monographiae, ***6***: 3–98.

Sullivan T.P, Sullivan D.S., Lindgren P.M.F. (2008). Influence of variable retention harvests on forest ecosystems: Plant and mammal responses up to 8 years post-harvest. Forest Ecology and Management, ***254***: 239–254.

Szweykowski J. (2006): An Annotated Checklist of Polish Liverworts and Hornworts. Kraków, Polish Academy of Science, Institute of Botany: 114.

Thomas S.C., Halpern C.B., Falk D.A., Liguori D.A., Austin K.A. (1999): Plant diversity in managed forests: Understory responses to thinning and fertilization. Ecological Applications, ***9***: 864–879

Tichý L. (2002): JUICE, software for vegetation classification. Journal of Vegetation Science, ***13***: 451–453.

Tichý L., Holt J. (2006): JUICE Program for Management, Analysis and Classification of Ecological Data. [Program Manual.] Brno, Vegetation Science Group, Masaryk University: 98.

Uotila A., 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.

Węgiel A., Jaszczak R., Rączka G., Strzeliński P., Sugiero D., Wierzbicka A. (2009): An economic aspect of conversion of Scots pine (*Pinus sylvestris* L.) stands in the Polish Lowland. Journal of Forest Science ***55***: 293–298.

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

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.

Received for publication February 7, 2012
Accepted after corrections June 28, 2012

Corresponding author:
Dr. Ewa Stefańska-Krzaczek, University of Wrocław, Faculty of the Biological Sciences, Department of Biodiversity and Plant Cover Protection, 6/8 Kanonia, 50-328 Wrocław, Poland
e-mail: stefla@biol.uni.wroc.pl