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Long-term changes in the *Leucobryo-Pinetum* community: interactions between the tree-stand, understorey and moss layer

Wieloletnie zmiany w zespole *Leucobryo-Pinetum*: interakcje pomiędzy drzewostanem i podrostem a warstwą mszystą

SUMMARY

Results of the research at 0.5 ha permanent study plots in two patches of *Leucobryo-Pinetum* community in the Roztocze National Park over a period of almost 40 years are discussed. The changes in the canopy species composition and their effect on the composition and arrangement of the moss layer were analysed. The share of pine in the number of trees decreased markedly over the study period. Instead, numerous species of trees, casting deep shade on the forest floor vegetation (fir, spruce, beech and oaks), encroached the tree-stands. A similar tendency of changes took place in the shrub layer: a decrease in the percentage contribution of light demanding and moderately light demanding tree species and an increase in the shade-tolerant ones. In contrast, the changes in the moss layer were mainly quantitative, but they were essentially related to the transformation in the tree stand. The considerable increase in the proportion of broadleaved species in the tree stand and understorey and, in consequence, a high cover of broadleaved litter greatly inhibited the development of terricolous bryophytes characteristic of coniferous forests.

STRESZCZENIE

W pracy przedyskutowano rezultaty prawie czterdziestoletnich obserwacji prowadzonych na dwóch stałych, półhektarowych powierzchniach badawczych. Zlokalizowane są one na terenie Roztoczańskiego Parku Narodowego w płatach zespołu *Leucobryo-Pinetum*. Analizie poddano zmiany składu gatunkowego drzewostanu oraz ich wpływ na skład i rozmieszczenie naziemnej warstwy

mszystej. Udział sosny w liczbie drzew spadł bardzo wyraźnie w okresie prowadzenia obserwacji. Na jej miejsce licznie wkroczyły gatunki drzewiaste silnie ocieniające glebę, jak jodła, świerk, buk i dęby. Podobne tendencje zmian miały miejsce w warstwie krzewów: spadł udział procentowy drzewiastych gatunków światłożądnych i umiarkowanie światłożądnych, przy wzroście udziału gatunków cienioznośnych. Natomiast zmiany zaobserwowane w warstwie mszystej miały głównie charakter ilościowy, ale istotnie związany z przekształceniami w warstwie drzew. Znaczący udział gatunków liściastych w drzewostanie i podroście, a w konsekwencji wzrost ilości ściółki liściastej zalegającej na dnie lasu, bardzo wyraźnie zahamował rozwój naziemnych mchów charakterystycznych dla fitocenoz borowych.

K e y w o r d s: oligotrophic pine forests, moss layer, species composition, long-term changes, deciduous litter, interactions, Roztocze National Park

INTRODUCTION

Oligotrophic pine forests are natural in Poland (17, 18) and many rare and threatened plant and animal species occur in them. Species richness and habitat diversity will be maintained as long as such forests are adequately preserved. However, directional transformations of coniferous communities are often observed (18, 28, 29, 30, 32, 33, 35, 42). It is often believed that they result from habitat eutrophication caused by industrial pollution emission, mostly nitrogen and phosphorus compounds and dusts (4, 16, 30, 31), and by climate changes (12, 13, 26) that trigger succession processes. These changes may eventually lead to a complete disappearance of such communities (23, 24). They are less frequently associated with natural processes of tree-stand development or regeneration subsequent deformation caused by different usage types. As the volume of air pollution emission (15) and the condition of coniferous forests in the Roztocze area (8) may suggest, processes similar to those described above may be taking place here. The majority of phytocenotic studies cited above deal with changes in separate layers of communities. Only few studies adopt a comprehensive approach and analyse whole phytocoenoses, including the terricolous bryoflora. Aggregations of these plants are considerably influenced by habitat conditions in communities and often visibly react to their transformations (e.g. 7, 21, 22, 27, 39). Some bryophyte species, e.g. feather mosses, may therefore be very good indicators of phytocoenotic transformations like expansion of broadleaved species in the coniferous forests.

Feather mosses like *Pleurozium schreberi* and *Hylocomium splendens* dominate in the ground cover of coniferous-dominated forest stands (19, 37), but in the same geographic regions and in the same site conditions, forest stands that have a component of deciduous trees do not develop feather moss layer (2). Mosses may be suppressed by the leaf litter from broad-leaf species such as beech, oak or aspen. The leaf litter periodically blankets the ground, thereby blocking light transmission to the mosses (36, 38). Dense deciduous leaf litter can also be an important factor limiting the growth and establishment of mosses (6, 20). The compounds released by the deciduous litter might have allelopathic effects which directly inhibit the development of mosses (14). Additionally, Startsev et al. (34) demonstrated experimentally that the leaf litter had negative effects on feather moss growth and survival caused much more damage to these bryophytes than pine litter. Therefore, the stand structure and composition may directly affect moss growth.

Suboceanic pine forests *Leucobryo-Pinetum* Mat. (1962) 1973 cover almost 19% of the forest area in the Roztocze National Park (Fig. 1A). The moss layer is well-developed in these phytocoeno-

ses (65–80% of the cover). Rare, protected and mountain species of vascular plants occur in them (8). The state of preservation of these communities in the Park may suggest that processes similar to those described above may be taking place here. Therefore, the main aim of the study was to answer the following questions:

1. To what degree does the increase of deciduous tree species share in the canopy composition affect the composition and arrangement of the moss layer?

2. Is the course of spontaneous changes in species composition directional and parallel in the analysed forest layers?

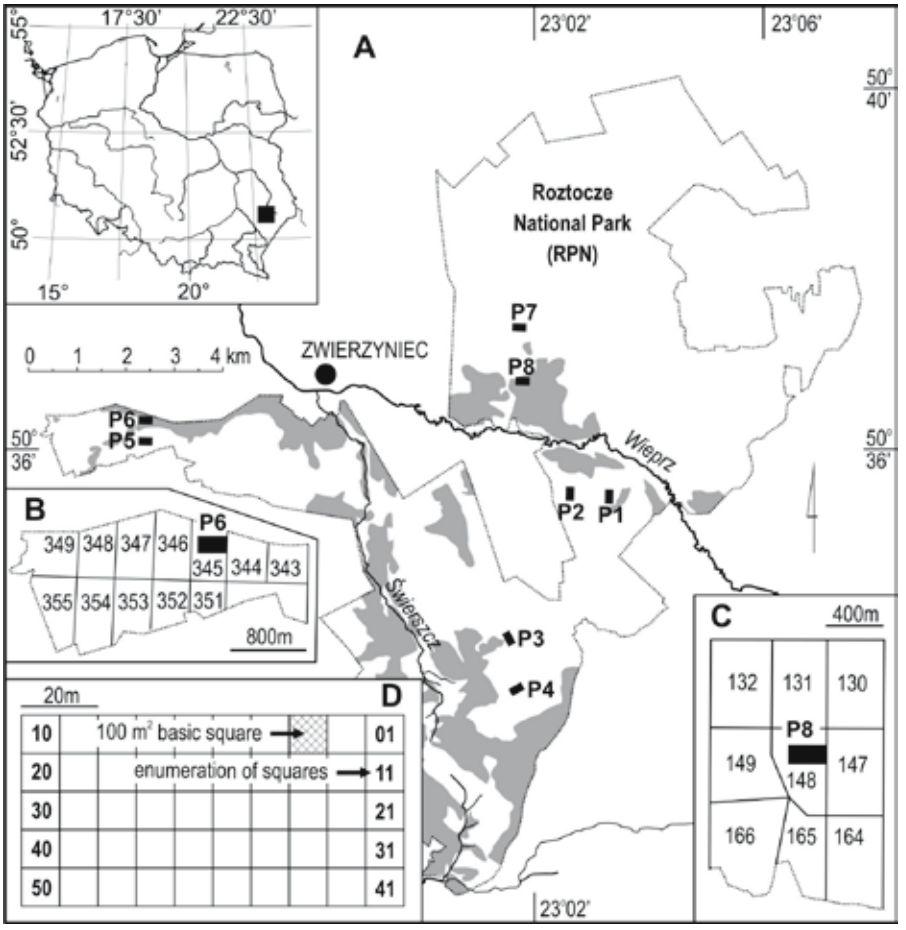

Fig. 1. Study area: A – range of occurrence of the *Leucobryo-Pinetum* forest association in the Roztocze National Park (marked in grey) and the location of permanent study plots (P1-P8); B, C – exact location of the patches studied (P6, P8) in forest sections; D – division of the study plot into squares

STUDY AREA AND METHODS

The results are a part of comprehensive comparative research on the dynamics of tree stands and the herb layer in the actively and passively protected phytocoenoses in the Roztocze National Park. These studies are conducted in permanent study plots located in several forest communities (P1-P8 plots; Fig. 1A). In this article, changes recorded at two study plots, P6 and P8 (Fig. 1B-C), representing *Leucobryo-Pinetum* forest communities, are presented. In the phytocoenoses examined, the pine stands were planted in the 1920s and they were managed subsequently by the State Forests Holding until the early 1970s. The study plots (0.5 ha) were established in the stands in 1971–1974 (9, 10) and that was the first (I) term of measurement. As separate tree-stand divisions, the plots were excluded from forest management afterwards. It activated processes of spontaneous changes in the phytocoenoses. After the plots were restored, the tree stand, understorey, and moss layer were re-examined in 1995–1998 (measurement term II) and in 2007–2009 (measurement term III). The stand measurement methods were based on the research conducted in the 1970s. Each study plot was divided into a net of squares 10 × 10 m. Observations were carried out on two levels: a 100 m^2 square, and a 0.5 ha study plot. The numbers of individuals of each species in the tree stand were calculated for each plot studied (P6, P8). The cover of the moss layer and litter was estimated as percentage participation within each square and its distribution pattern was mapped for each plot. Three litter types were distinguished: broadleaved (participation of needles below 20%), mixed (20–80%) and coniferous (above 80% of needles). A full list of terricolous bryophytes (mosses and liverworts) was made for each square and study plot. The total cover of the key bryoflora species was determined (calculated as the average percentage cover for all the squares in a plot). Changes in the cover of four mosses, characteristic of coniferous forest: *Dicranum polysetum*, *Hylocomium splendens, Leucobryum glaucum* and *Pleurozium schreberi*, were assumed as an indicator of transformations of the moss layer.

All trees with the diameter at breast height (DBH) exceeding 7 cm were considered to be forest stand trees, while the smaller ones were regarded as forest regeneration. In the latter category, individuals whose height exceeded 0.5 m were considered to be the undergrowth. Each stand tree was numbered and exact places of DBH measurement were marked in the bark of trees. Measurements of the stand trees included their diameters (measured in two perpendicular directions), heights and height of their crown base (using the Vertex VI as a measuring device). Forest regenerations were counted in the whole study plots.

RESULTS

At the beginning of the study the tree and moss layers were very homogenous and almost identical in both plots studied. The tree stand was entirely dominated by pine, and terricolous bryophytes covered 65% of the forest floor in both patches.

The course of changes in the first study plot (P6) considerably differs from the second one (P8). Therefore, each study patch is described separately.

Research plot no 6

Tree stand and litter. During almost 40 years, the mono-species tree stand with a complete dominance of pine transformed into a multi-species tree stand

with an almost 60% contribution of fir and spruce. A three-fold decrease in the share of pine was observed in that period and numerous species casting deep shade on the soil entered the tree layer. Altogether they constituted 65% in the tree-stand (Table 1). At the beginning of the study coniferous litter dominated on the forest floor and covered 35% of the research plot area. Currently, the litter covers about 36% of the research plot and it shows a mosaic pattern of distribution. The cover of broadleaved litter increased, while the cover of the coniferous one considerably decreased over the study period (Fig. 2).

Understorey. An over ten-fold decrease in the percentage contribution of spruce and an even greater decrease in the share of juniper was observed in the shrub layer. In contrast, fir and beech intensively encroached on this layer (Table 1). A two-fold increase in the abundance of alder buckthorn *Frangula alnus* and black cherry *Prunus serotina* was recorded in the last ten years. The latter took the places mostly in the range of canopy gaps or transparencies.

Moss layer. At the beginning of the observations, bryophytes occupied 65% of the study plot and *Pleurozium schreberi* was the dominant species. The cover of the moss layer did not change during the study period but participations of particular species changed significantly. The percentage share of *Leucobryum glaucum* and *Hylocomium splendens* considerably increased (Table 1). Currently, *P. schreberi* still dominate in the layer, but its cover decreased by about 15%. Two new taxa (*Ptilium crista-castrensis* and *Polytrichastrum formosum*) were recorded there. The symptoms of their spreading tendency were observed. Additionally, a few gametophytes of *Thuidium tamariscinum*, the characteristic species of the *Abietetum polonicum* forest community, were discovered.

Research plot no 8

Tree stand and litter. As in plot 6, the species composition of the tree stand changed considerably. The share of pine in the number of trees decreased by over 40% and broadleaved species, especially beech, encroached on the tree stand. A slight increase was also recorded for spruce. The number and share of fir individuals remained unchanged. Considerable changes in the stand species composition have an effect on the cover and type of litter lying on the forest floor. At the beginning of the studies, the participation of broadleaved litter in the patch was ca. 2% and coniferous litter occupied $^1/_3$ of the area. Current observations showed that broadleaved and mixed litter considerably dominated in the patch, while the share of coniferous litter was very small (Table 1). All the litter types cover nearly 60% of the plot and form large, non-partitioned patches (Fig. 2).

Understorey. Similarly to the tree layer, the share of beech increased considerably in this part of the forest (Table 1). The contribution of other species such as spruce and oaks decreased. An increase in the abundance and percentage of silver

Table 1. Long-term changes in the tree, shrub and moss layers

	Species / Percentage share in	Plot 6				Plot 8			
		1971–1972		2008–2009		1973–1974		2008–2009	
		T	S	T	S	T	S	T	S
Tree (T) and shrub (S) layers [1]	*Pinus sylvestris*	98.8	–	34.6	0.1	99.1	–	57.0	–
	Abies alba	0.6	11.3	40.1	54.7	–	1.3	0.8	1.3
	Picea abies	0.6	85.5	18.5	8.1	–	20.7	8.6	8.1
	Fagus sylvatica	–	3.1	5.7	30.3	–	16.0	27.2	45.7
	Quercus petraea	–	–	–	–	0.3	47.1	4.6	26.0
	Quercus robur	–	–	–	–	–		1.3	8.8
	Quercus rubra	–	–	–	0.25	–	12.0	0.5	5.0
	Sorbus aucuparia	–	0.1	–	0.9	–	1.1	–	0.4
	Prunus serotina	–	–	1.1	5.6		1.3	–	–
	Betula verrucosa	–	–	–	–	0.6	1.3	0.3	4.6
	Populus tremula	–	–	–	–	–	0.5	–	–
		1971–1972		2008–2009		1971–1972		2008–2009	
Moss layer [2]	*Pleurozium schreberi*	51.8		36.7		48.6		17.2	
	Hylocomium splendens	5.4		14.3		0.8		13.0	
	Dicranum polysetum	5.5		4.0		14.6		1.2	
	Leucobryum glaucum	1.9		6.9		–		0.02	
	Ptilium crista-castrensis	–		0.3		–		9.0	
	Polytrichastrum formosum	–		1.5		–		0.9	
	other species*	0.4[a]		0.1[b]		1.0[c]		0.2[d]	
	Total	65.0		63.9		65.0		41.4	

[1] Percentage participation of tree / shrub species

[2] Percentage cover of individual species

**Atrichum undulatum*[d], *Buxbaumia aphylla*[b], *Cephaloziella divaricata*[bd], *Dicranella heteromalla*[d], *Dicranum scoparium*[abcd], *Herzogiella seligeri*[bd], *Hypnum cupressiforme*[b], *Lophocolea heterophylla*[d], *Orthodicranum montanum*[d], *Plagiomnium affine*[bd], *Plagiothecium laetum*[bd], *Pohlia nutans*[abd], *Polytrichum piliferum*[a], *Scurio-hypnum oedipodium*[d], *Sphagnum capillifolium*[bd], *S. fimbriatum*[b], *Tetraphis pellucida*[b], *Thuidium tamariscinum*[b]

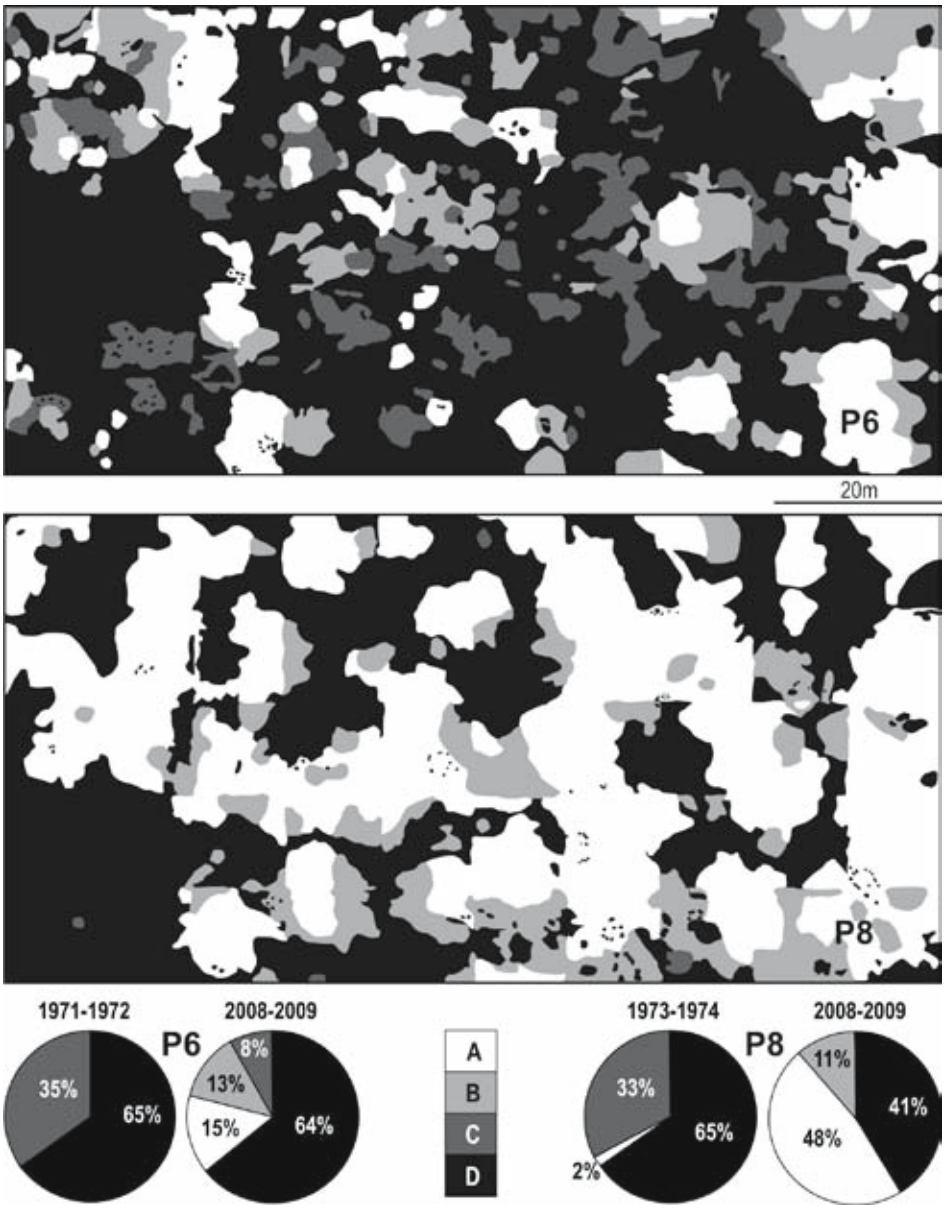

Fig. 2. The current distribution pattern of terricolous bryophytes and participation of the particular litter types at plots studied (P6, P8). A – leaf litter, B – mixed litter, C – coniferous litter, D – bryophytes

birch and downy birch before the 1990s was followed by their decrease. On the other hand, the abundance of juniper decreased throughout the study period.

Moss layer. In 1970s, the terricolous bryophytes occupied 65% of the patch and the greatest cover was noted for *Pleurozium schreberi* and *Dicranum polysetum*. After almost 40 years the moss layer covered 41% of the study plot only. A significant increase in the cover of *Hylocomium splendens* and a considerable decrease in the share of *P. schreberi* and *D. polysetum* were observed in 2009 (Table 1). Two new species were noted: *Polytrichastrum formosum* and *Ptilium crista-castrensis*. The cover of the latter one amounts to 9% of the plot studied. Currently, *P. crista-castrensis* together with *P. schreberi* and *H. splendens* is the main component of the moss layer.

DISCUSSION

Mono-species tree stands were recorded at the beginning of the study. Their composition changed considerably over the study period. The abundance and share of pine clearly declined in both plots. Species such as fir, spruce, beech and oaks enter both phytocoenoses. Similar trends of expansion of broadleaved species to pine stands in oligotrophic habitats have been observed in north-east Poland (1, 3, 12, 24, 25, 29) and in Germany (42). However, in north-east Poland these processes progress differently from those in Roztocze due to a different geographical location and a poorer tree stand composition.

It should be noticed that the dynamic development of species strongly shading the forest floor probably caused a considerable decrease in the abundance of both young and older individuals of juniper, a coniferous species that prefers full light (41).

The cover of the moss layer and its species composition were similar in both patches at the beginning of the study. During the whole study period, the cover of bryophytes did not change in the first plot (P6) and decreased by 20% in the second (P8), although no qualitative changes in both studied patches were observed. The abundance of *Pleurozium schreberi* and *Dicranum polysetum* decreased in both plots, particularly in P8 (respectively 30% and 13% drop in the cover). The considerable increase in the proportion of broadleaved species in the tree stand and understorey and, in consequence, a high cover of broadleaved litter greatly inhibits the development of terricolous bryophytes characteristic of coniferous forests (6, 14, 20, 34). This is the main factor shaping the cover of the moss layer and percentage participation of individual bryophyte species in the studied plots. Leaf litter seems to be the major cause of the paucity of bryophytes on the forest floor, especially in the second plot (P8).

In both patches, appearance and expansion of *Ptilium crista-castrensis* and *Polytrichastrum formosum* was observed. The first species has phytocoenotic optimum in *Leucobryo-Pinetum* community (5, 8, 11, 40). According to our observations, its appearance after forest management was ceased, which may be regarded as a return to the natural habitat. The second taxon in the studied patches is clearly associated with wild boar rooting places, but this phenomenon needs further, separate studies. For this reason, the expansion of *P. formosum* may be significant in the local scale only and caused by local conditions. The appearance of a small population of *Thuidium tamariscinum,* the species characteristic of *Abietetum polonicum* associations (17) in the first plot (P6), may be a signal of patch transformation towards the mesotrophic submontane fir forest, but further observations of its dynamics are needed. The comparison of long-term changes in the frequency of major moss species and the present differences in their cover between the two patches suggest divergent forest transformations. Changes in the tree species composition are reflected in the moss layer; however, based on bryophytes only, it is impossible to determine whether a directional change or a fluctuation is taking place. Bryophytes react to changes mostly quantitatively with the species composition changing slightly. Further observations of spreading and receding species will confirm whether the changes observed in the moss layer are directional.

If the observed tendency of changes in the tree species composition persists, directional transformations, as a secondary succession or potential regeneration, towards *Querco roboris-Pinetum* in plot 8 and *Abietetum polonicum* in plot 6 may be expected. This is particularly apparent in the dynamics of tree species entering the stand. It should be finally stressed that despite the directional changes in the species composition of the tree stand and the understorey, they are definitely less conspicuous in the moss layers (species composition was not changed or was changed slightly). The change in the cover of the particular species was observed, but this process is essentially related to the transformation in the tree stand.

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REFERENCES

1. Andrzejczyk T., Brzeziecki B. 1995. The structure and dynamics of old-growth *Pinus sylvestris* stands in the Wigry National Park, north-eastern Poland. Vegetatio 117: 81–94.

2. Beckingham J. D., Corns I. G. W., Archibald J. H. 1996. Field guide to the ecosystems of west-central Alberta. Natural Resources Canada. Canadian Forest Service Northwest Region, Northern Forest Center, Special report 9, Edmonton, Alberta, Canada, 540 pp.
3. Bernadzki E., Bolibok L., Brzeziecki B., Żybura H. 1996. Development of natural forest stands in the Białowieża National Park. A case study of two research plots in period 1936–1991. [In:] Biodiversity Protection of Białowieża Primeval Forests, Selected Papers. P. Paschalis, S. Zajączkowski (eds.), Warszawa: 51–61.
4. Brożek S. 1986. Wpływ pyłów emitowanych przez aglomerację krakowską na mineralizację azotu w glebach leśnych. Roczn. Glebozn. 37(2–3): 237–248.
5. Dierßen K. 2001. Distribution, ecological amplitude and phytosociological characterization of European bryophytes. Bryophyt. Bibliotheca 56: 1–289.
6. Glime, J. M. 2007. Bryophyte Ecology. Ebook sponsored by Michigan Technological University and the International Association of Bryologists. Published on-line at http://www.bryoecol.mtu.edu/
7. Humphrey J. W., Davey S., Peace A. J., Ferris R., Harding K., 2002. Lichens and bryophyte communities of planted and semi-natural forests in Britain: the influence of site type, stand structure and deadwood. Biol. Conserv. 107: 165–180.
8. Izdebski K., Czarnecka B., Grądziel T., Lorens B., Popiołek Z. 1992. Zbiorowiska roślinne Roztoczańskiego Parku Narodowego na tle warunków siedliskowych. Wyd. UMCS, Lublin, 268 pp.
9. Izdebski K., Kimsa T., Kozak K., Michna E., Popiołek Z., Stączek A., Zinkiewicz A. 1976. Influence of habitats of two forest ecosystems on productivity of pine stands in Central Roztocze. Part I. Ann. UMCS, Sec. C 31: 1–54.
10. Izdebski K., Kimsa T., Kozak K., Michna E., Popiołek Z., Stączek A., Zinkiewicz A. 1977. Influence of habitats of two forest ecosystems on productivity of pine stands in Central Roztocze. Part II. Ann. UMCS, Sec. C 32: 1–43.
11. Klama H., Żarnowiec J., Jędrzejko K. 1999. Mszaki naziemne w strukturze zbiorowisk roślinnych Makroregionu Południowego Polski. Wyd. Politechniki Łódzkiej, Filia w Bielsku-Białej, Bielsko-Biała: 236 pp.
12. Kowalski M. 1993. The development of natural forest stands in the Białowieża National Park. Fol. For. Pol., Sec. A. Forestry 35: 35–47.
13. Kożuchowski J., Degirmendžić J. 2005. Contemporary changes of climate in Poland: trends and variation in termal and solar conditions related to plant vegetation. Pol. J. Ecol. 53 (3): 283–297.
14. Legare S., Pare D., Bergeron Y. 2005. Influence of aspen on forest floor properties in black spruce-dominated stands. Plant and Soil 215: 201–220.
15. Maciejewski Z. 1995. Imisje SO_2, NO_x, związków fluoru oraz pyłu w Roztoczańskim Parku Narodowym na podstawie wyników badań monitoringu technicznego. Raport o stanie środowiska w województwie zamojskim w 1994 roku, Biblioteka Monitoringu Środowiska: 1–44.
16. Maltzan 2002. Monitoring zagrożeń i zanieczyszczenia środowiska leśnego Puszczy Białowieskiej. Kosmos 51(4): 435–441.
17. Matuszkiewicz J. M. 2007a. Zespoły leśne Polski. PWN Warszawa: 1–358.
18. Matuszkiewicz J. M. 2007b. Geobotanical identification of the development tendencies in forest association in the regions of Poland. A synthetic survey. [In:] Geobotanical identification of the development tendencies in forest association in the regions of Poland. J. M. Matuszkiewicz (ed.), PAN IG i PZ, Monographies 8: 817–847.

19. Mills S. E., Macdonald S. E. 2004. Predictors of moss and liverwort species diversity of microsites in conifer-dominated boreal forest. J. Veg. Sci. 15: 189–198.
20. Oechel W. C., Van Cleve K. 1986. The role of bryophytes in nutrient cycling in the taiga In: Forest Ecosystems in the Alaskan Taiga. A Synthesis of Structure and Function. K. Van Cleve, F. S. Chapin, P. W. Flanagan, L. A. Viereck, C. T. Dyrness (eds.), Springer, Berlin, pp. 122–137.
21. Økland T., Rydgren K., Økland R. H., 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 Ecol. Man. 177: 17–37.
22. Olsson B. A., Kellner O. 2006. Long-term effects of nitrogen fertilization on ground vegetation in coniferous forests. Forest Ecol. Man. 237: 458–470
23. Paluch R. 2001. Zmiany zbiorowisk roślinnych i typów siedlisk w drzewostanach naturalnych Białowieskiego Parku Narodowego. Sylwan 10: 73–81.
24. Paluch R. 2002. Kierunek i tempo zmian sukcesyjnych roślinności runa na obszarze ochrony ścisłej Białowieskiego Parku Narodowego. Kosmos 4: 453–461.
25. Paluch R. 2003. Wpływ zmian składu gatunkowego i fazy rozwojowej drzewostanu na roślinność runa w Białowieskim Parku Narodowym. Prace Inst. Bad. Leśn., A, 13 (950): 39–52.
26. Przybylak R. 2008. Zmiany klimatu Polski i Europy w ostatnich stuleciach. Kosmos 57 (3–4): 280–281.
27. Ross-Davis A. L., Frego, K. A. 2002. Comparison of plantations and naturally regenerated clearcuts in the Acadian Forest: forest floor, bryophyte community and habitat features. Can. J. Bot. 80: 21–33.
28. Rost-Siebert K., Jahn G. 1988. Veränderungen der Waldbodenvegetation während der letzten Jahrzehnte – Eignung zur Bioindikation von Immissionswirkungen? Forst und Holz 43 (4): 75–81.
29. Sokołowski A. W. 1991a. Zmiany składu gatunkowego zbiorowisk leśnych w rezerwatach Puszczy Białowieskiej. Ochr. Przyr. 49: 63–78.
30. Sokołowski A. W. 1991b. Changes in species composition of a mixed Scots pine-Norway spruce forest at the Augustów forest during the period 1964–1987. Fol. Forest. Pol. Ser. A, 33: 5–23.
31. Sokołowski A. W. 1995. Character and rates of successional changes in the strict reserve of the Białowieża National Park. [In:] Protection of Forest Ecosystems Biodiversity. P. Paschalis, K. Rykowski, S. Zajączkowski (eds.), Warszawa, pp. 103–111.
32. Sokołowski A. W. 1999. Sukcesja zbiorowisk leśnych w rezerwacie Starzyna w Puszczy Białowieskiej. Parki Nar. Rez. Przyr. 18 (2): 31–59.
33. Sokołowski A. W., Paluch R. 2004. Wpływ sztucznego odnowienia drzewostanów w borze mieszanym na skład zbiorowisk leśnych w Wigierskim Parku Narodowym. Sylwan 12: 48–57.
34. Startsev N., Lieffers V. J., Landhäusser S. M. 2008. Effects of leaf litter on the growth of boreal feather mosses: implication for forest floor development. J. Veg. Sci. 19: 253–260.
35. Stefańska E. 2007. Stan i tendencje dynamiczne zbiorowisk borowych Borów Dolnośląskich. Praca doktorska, Uniwersytet Wrocławski, 1–119.
36. Tarkhova T. N., Ipatov V. S. 1975. Effect of illumination and litter on the development of some moss species. Soviet J. Ecol. 6: 43–48.
37. Turetsky M. R. 2003. The role of bryophytes in carbon and nitrogen cycling. Bryologist, 106: 395–409.
38. Van Cleve K., Oliver L., Schlentner R., Viereck L. A., Dymess C. T 1983. Productivity and nutrient cycling in taiga forest ecosystems. Can. J. For. Res. 13: 747–766.

39. Vellak K., Paal J. 1999. Diversity of bryophyte vegetation in some forest types in Estonia: a comparison of old unmanaged and managed forests. Biodiv. Conserv. 8: 1595–1620.
40. Żarnowiec J. 1995. Bryopsida. In: Cryptogamous plants in the forest communities of Białowieża National Park. General problems and taxonomic groups analysis (Project CRYPTO). J. B. Faliński, W. Mułenko (eds.), Phytocoenosis 7 (N. S.), Archiv. Geobot. 4: 46–61.
41. Zarzycki K., Trzcińska-Tacik H., Różański W., Szeląg Z., Wołek J., Korzeniak U. 2002. Ecological Indicator Values of Vascular Plants of Poland. W. Szafer Institute of Botany, Polish Academy of Sciences. Kraków, 183 pp.
42. Zerbe S. 2002. Restoration of natural broad-leaved woodland in Central Europe on sites with coniferous forest plantations. Forest Ecol. Man. 167: 27–42.