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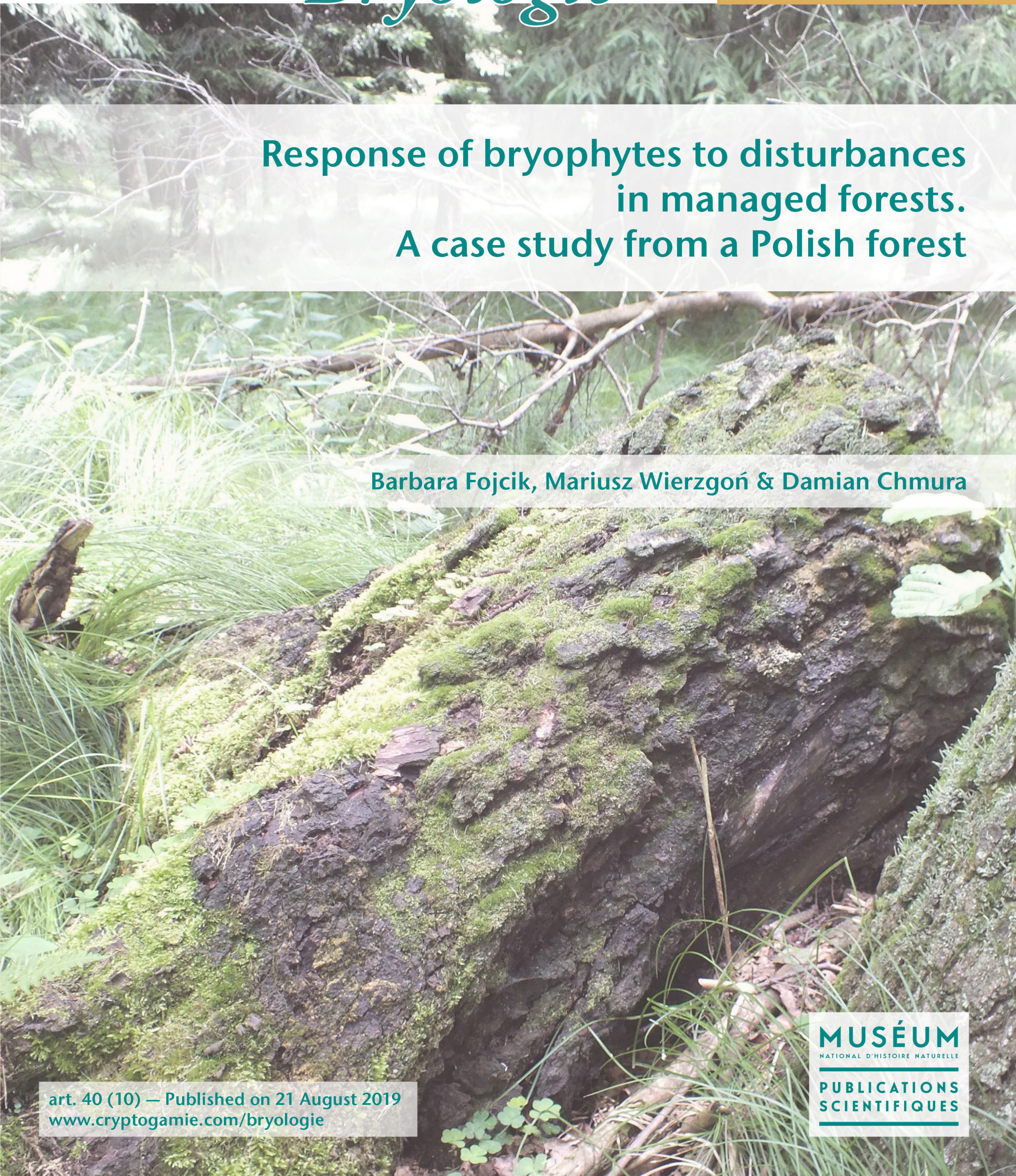

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Response of bryophytes to disturbances in managed forests. A case study from a Polish forest

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ABSTRACT
Forest management practices fundamentally impact the structure of a forest (relatively young stage of forest development, dominating stands with only one or two species of trees, planting coniferous tree species on habitats of deciduous forests, introducing alien tree species, very limited volume of dead wood). Bryophytes are especially sensitive to silvicultural practices. The aim of this study was to examine the importance of particular substrates for maintaining bryophyte species diversity in the Murckowski Forest (Silesian Upland S Poland), which is at present a managed forest. In 100 sampling plots, the structure of the forest and the species composition, frequency and abundance of bryophytes on different types of substrates (ground, tree base, tree trunk and dead wood) were analysed. In total, 54 bryophyte species were recorded (five liverworts and 49 mosses). The largest number of species was observed on dead wood (42), while the lowest number was of typical epiphytes growing on tree trunks bark more than 30 cm above the ground (18). This study confirms that dead wood is a key habitat and determines not only the number of epixylic species, but also the whole richness of bryophyte species. Maximal diameter of trees and presence of old tree stands were significant factors for species that were colonizing the tree bases.

KEY WORDS
Biodiversity,
dead wood,
epiphytes,
epixylic bryophytes,
terrestrial bryophytes,
woodland key habitats,
Murckowski Forest.

RÉSUMÉ
Réponse des bryophytes aux perturbations induites par la gestion des forêts. Exemple d'un forêt polonaise.
Les pratiques de gestion forestière ont une incidence fondamentale sur la structure d'une forêt (stade relativement jeune du développement forestier, peuplements dominants avec une ou deux espèces d'arbres seulement, plantation de conifères, espèces d'arbres sur les habitats des forêts à feuilles caduques, introduction d'espèces d'arbres exotiques, volume très limité de bois mort). Les bryophytes sont particulièrement sensibles aux pratiques sylvicoles. L'objectif de cette étude est d'examiner l'importance de substrats particuliers pour le maintien de la diversité des espèces de bryophytes dans la forêt de Murckowski (Hautes terres silésiennes, Pologne du Sud), qui est actuellement une forêt gérée. Dans 100 parcelles d'échantillonnage, la structure de la forêt et la composition des espèces, la fréquence et l'abondance des bryophytes sur différents types de substrats (sol, base d'arbre, tronc d'arbre et bois mort) ont été analysées. Au total, 54 espèces de bryophytes ont été recensées (cinq hépatiques et 49 mousses). Le plus grand nombre d'espèces a été observé sur du bois mort (42), tandis que le plus petit nombre était d'épiphytes typiques qui croissent sur des troncs d'arbres dont l'écorce dépasse 30 cm au-dessus du sol (18). Cette étude confirme que le bois mort est un habitat clé et détermine non seulement le nombre d'espèces épixyles, mais aussi toute la richesse des espèces bryophytes. Le diamètre maximal des arbres et la présence de peuplements anciens sont des facteurs importants pour les espèces qui colonisent les bases des arbres.

MOTS CLÉS
Biodiversité,
bois mort,
épiphytes,
bryophytes épixyles,
bryophytes terrestres,
habitats clés des bois,
Forêt de Murckowski.

INTRODUCTION

Almost all European forests are under managed pressures and have been strongly disturbed due to logging, fragmentation and the planting of alien tree species (Bengtsson *et al.* 2000). Management practice fundamentally impact the different elements of the structure of a forest, such as the composition of tree species, the presence of old tree specimens and decaying wood as well as the richness of plants, fungi and animals species (Nowińska *et al.* 2009; Chećko *et al.* 2015). Bryophytes are especially sensitive to silvicultural practices (Rudolphi *et al.* 2014). Even moderate management eliminates a significant number of moss and liverwort species (Vellak & Ingerpuu 2005; Caners *et al.* 2013).

In forests, bryophytes are associated with different types of substrates; they occur as terrestrial species, epiphytes and also grow on dead wood (Vanderpoorten & Goffinet 2009). All of them are subject to the strong stresses that are connected with the economic restructuring of stands (Ódor & Standovár 2001; Botting & Fredeen 2006; Madžule *et al.* 2012). In managed forests, an increase in insolation and microclimate changes, primarily a decrease in humidity, create unsuitable conditions for many bryophytes (Bell & Newmaster 2002; Fudali & Wolski 2015). A lack of old, living trees also limits the occurrence of many epiphytes (Sabovljević *et al.* 2010; Hofmeister *et al.* 2015). Because conifers are preferred in forestry, epiphytes that are attached to the barks of deciduous species are particularly vulnerable; the tree species is the most important driver of the richness and composition of epiphytic species (Király & Ódor 2010; Ódor *et al.* 2013).

The occurrence of dead wood in different stages of decay is also very important for richness of bryophytes (Evans *et al.* 2012; Hofmeister *et al.* 2015; Jonsson *et al.* 2016). Dead wood is usually harvested in managed forests, although it is one of the key habitats in the forest structure and is the substrate for many, different bryophytes (Samuelsson *et al.* 1994; Humphrey *et al.* 2003; Strazdiņa 2010). It may be overgrown not only by typical epiphytes (in the early stages of wood decomposition), but also by typical epixylic and terrestrial species (especially in the final stages of decomposition). A significantly higher total volume of dead wood distinguishes old-growth non-managed forests from managed forests (Sabovljević *et al.* 2010).

Polish managed woodlands are generally relatively young, of a similar age, with a structure that shows various forms of degeneration. The most common occurring forms of degeneration, which also have a negative effect on bryophytes, include (Kurowski 2015): 1) planting coniferous tree species on habitats of deciduous forests (in lowland Poland, this is usually pine, while in the mountains it is spruce); 2) dominating stands with one or two species of trees; 3) preserving stands at a relatively young stage of forest development, which prevents the optimal development of forest communities; 4) introducing alien tree species; in particular, the presence of *Quercus rubra* L. (red oak), which is an invasive species in Poland; and 5) dominating of grasses and sedges in herb layer cover.

Among the aspects of degeneration of the structure of the managed forests in Poland, the very limited occurrence of dead wood (due to sanitary reasons) is also mentioned (Smykała 1982). The average contribution of dead wood in the Polish state forests is about 5.6 m^3/ha, of which 2.5 m^3/ha are logs that are lying, while the rest are dead standing trees (according to the National Forest Inventory, data for years 2011 to 2015, http://www.buligl.pl/pl/web/en/forest-data-bank).

The main goal of this study was to characterize the bryoflora in the structure of managed forest stands in the Murckowski Forest (Silesian Upland, Poland). The specific purposes were: 1) to compare the bryophyte diversity on different kinds of substrates (ground, bark of trees and dead wood); and 2) to examine dependencies between elements of the forest structure and microhabitats availability and the diversity of bryophyte species.

We hypothesized that bryophyte richness and species composition in managed stands is related to forest structure and is dependent on the microhabitats availability (especially for epiphytic and epixylic species).

MATERIAL AND METHODS

Study area

The study was conducted in the Murckowski Forest (Silesian Upland, S Poland), which is an extensive forest complex (approx. 6 000 ha) that is located almost completely within the administrative borders of the city of Katowice (Silesian Upland, Upper Silesian Industrial District) (50°7'-50°13'N latitude, 18°59'-19°6'E longitude). For quite some time, local forestry has been subordinated to the needs of industry and mining. Primary deciduous and mixed forests were mainly transformed into pine forest, while spruce was only preferred in damp habitats (Myczkowski 1962). At present, managed mixed forest with *Pinus sylvestris* L., *Quercus robur* L. and *Q. rubra* (in *Querco roboris-Pinetum* (W. Mat. 1981) J. Mat. 1988 forest type) is dominant here. In addition, there are various, difficult to classify, types of secondary deciduous forest, mainly with *Quercus robur* and *Q. rubra*, locally also with *Betula pendula* Roth and *Fagus sylvatica* L. Large areas are also covered with pine monoculture. Forest areas are very diverse in age, from several-year-old plantings to tree stands over 100 years. Underwood is formed mainly by young trees and *Frangula alnus* Mill., *Prunus padus* L., *P. serotina* Ehrh. and *Sorbus aucuparia* L. Acidophilus herbaceous species spread in the undergrowth and often grow in masses.

Characteristics of study plots. The field studies covered 100 investigation plots of 100 m^2 (10 × 10 m). The sampling areas were selected in a systematic way in well-shaped stands in fresh or wet habitats, in a mixed forest (48% of the plots, 35 to 130 years old), a deciduous forest (43% of the plots, 40 to 140 years old), and a pine forest (9% of the plots, 70 to 100 years old). Most of the plots were located within the stands of the 50 to 100 year age group (71% of the plots), 23% of the plots were in the stands under 50 years old and only 6% plots were in the more than 100 years old stands. The age of stands was established according to information contained on the Polish Forest Data Bank internet portal (Bank Danych o Lasach 2018).

Sampling

The field studies were conducted from 2012 to 2015. In each sampling plot, a description of the forest structure was taken by estimating the percentage coverage of trees crown, underwood, herbs and bryophytes layer, also all plant species of each layer were described (with their coverage). The habitat offer for epiphytes was determined on each plot as the number, species and size of trees (estimated as diameter at breast height measured with a tree caliper). The habitat offer for species inhabiting dead wood was defined by size and volume of dead wood (estimated for logs and stumps with a diameter greater than 10 cm). The volume of individual logs and stumps were calculated using the formula for a truncated cone and cylinder, respectively (Humphrey & Peace 2003). The total volume of dead wood on each plot was defined as the sum of the volume of all logs and stumps.

In the sampling plots a detailed list of bryophytes was made taking into account the type of substrate. Four main types of substrates were included: 1) ground (GR); 2) tree base (TB), considering the bark at the base of tree trunks up to 30 cm above the ground, the zone of influence of a terrestrial habitat (Smith 1982), taking into account the species of phorophyte; 3) tree trunks (TT), considering the trunk bark more than 30 cm above the ground, taking into account the species of phorophyte; and 4) dead (decaying) wood (DW).

The abundance of individual bryophyte species on each sampling plot was estimated using proposed by authors categories of abundance depending on the size of the area covered by species individuals: 1) up to 10 cm^2; 2) 10 to 100 cm^2; 3) 100 to 1 000 cm^2; and 4) more than 1 000 cm^2. On each plot, the abundance was estimated separately for each substrate. For GR it was the area of the ground overgrown by bryophytes. In the case of TB and TT, the abundance resulted from the sum of coverage on all trees, whereas in the case of DW, abundance was the sum of coverage on all analysed pieces of dead wood.

The frequency of bryophyte species with size and diversity of tree reference to all plots was defined according to proposed by authors scale: 1) very rare, species present in 1 to 3 plots; 2) rare, present in 4 to 10 plots; 3) fairly frequent, present in 11 to 20 plots; 4) frequent, present in 21 to 40 plots; and 5) very frequent, present in more than 40 plots.

Statistical analysis

In order to examine the general relationships between the analysed factors (forest age, coverage of trees, underwood, herbs and bryophytes layers, number bryophyte species in general and on GR, TB, TT and DW, volume and maximum size of DW), the Spearman rank correlation test was used due to non-normality of data. Analysis of species composition was performed using ordination statistical tools, mentioned below. This was done in the R language and environment (R Core Team 2017) and the packages vegan (Oksanen *et al.* 2017), cocorresp (Simpson 2009) and indicspecies (De Cáceres & Legendre 2009). The indicator species analysis was performed and indicator value index (IndVal) for each species was computed for the specific type of habitat (GR, TB, TT and DW).

In order to examine the impact of habitat variables on structure of the bryophyte flora, the following variables were taken into account: the age of tree stand (Age), the maximal diameter at breast height (DBH.max), the volume of deadwood (DW.vol), the weighted means of Ellenberg indicator value (EIV) (Ellenberg & Leuschner 2010) for light (L), temperature (T), moisture (F), acidity (R) and nitrogen (N). The mean weighted EIVs were calculated based on the values of species occurred in the study plots.

For the bryophytes growing on GR and coexisting with vascular plants, a co-correspondence analysis (CoCa) was performed with vector fitting. This analysis permitted the relationship between two communities to be assessed. The data about the coverage of the vascular plant species from 100 sampling plots were treated as a predictor and the bryophyte data as a response. Vector fitting (999 permutations) permitted the impact of the environmental variables for the ground-inhabiting species, both bryophytes and vascular plant species, to be examined.

A redundancy analysis (RDA) was conducted for the bryophytes growing on TT and amongst the environmental variables; the EIVs for F, R and N were excluded from the analysis because they are related to the soil. For the bryophytes growing on TB and DW, RDA with Hellinger transformation was performed separately due to the large ecological gradients. The variables F, R and N were not taken into account for the epixylic bryophytes. The conditions of the most frequent species from the distinguished habitats are presented on ordination biplots. In order to exclude redundant variables variance inflation factor was computed and 999 permutations were run to examine impact of the studied environmental variables on species composition.

Nomenclature

Nomenclature for liverworts is given according to Söderström *et al.* (2016), for mosses follows to Hill *et al.* (2006), and for vascular plants complies with The Plant List (2013).

RESULTS

Characteristics of the forest structure in study plots

There were 18 species in the tree layer, among which the most common were *Quercus robur* (58% of the plots; dominant on 26%), *Pinus sylvestris* (45%; dominant on 31%) and *Quercus rubra* (39%; dominant on 23%). Although the number of species tree varied in the plots between one and five, most of them (61%) had only one or two species and they were usually pine or oak (*Quercus robur* or/and *Q. rubra*). The tree layer coverage was 60 to 100%, most often within 70 to 90% (77% of the plots).

Underwood was observed on 44% of the study area. There were 19 species, most often *Prunus serotina* (19% of the plots), *Sorbus aucuparia* (14%) and *Frangula alnus* (12%). In most areas, the coverage of the underwood layer did not exceed 10% (it occasionally reached 60%) and most often was made up of one to three species.

The herbaceous layer was composed of 1 to 20 species, but mostly 5 to 12 species (69% of the plots). It was developed to a very different degree and its coverage ranged from 0 to 100%, most often within 80 to 100% (60% of the plots). The weakest development of this layer (up to 10% of the cover) was observed in the deciduous and mixed forests with a higher proportion of *Fagus sylvatica* and *Quercus rubra* (coverage over 50%), in which a thick layer of undisturbed leaves hindered the growth of herbaceous plants. The relatively common, significant proportion of *Carex brizoides* L. was very characteristic; in the case of 36% of the research plots this sedge covered more than 50% of their area. The dominance of grasses, mainly *Calamagrostis arundinacea* (L.) Roth and *C. villosa* (Chaix) J.F. Gmel., was also observed. Unlike the other species, only *Carex brizoides* and *Calamagrostis* spp. regularly occurred in individual patches with more than 50% coverage.

It is worth noting that in the flora of the examined plots, five alien species were observed: four trees (*Fraxinus pennsylvanica* Marshall, *Prunus serotina*, *Quercus rubra*, *Robinia pseudoacacia* L.) and one herbaceous plant (*Impatiens parviflora* DC.). *Prunus serotina* and *Quercus rubra* were also relatively common, each of them was observed in more than 30% of the plots.

From 0 m^3 (14% of the plots) to more than 1 m^3 (2% of the plots) of DW were recorded on the analysed plots. In most cases, these were single logs and stumps whose volume did not exceed 0.01 m^3 (65% of the plots with dead wood).

General characteristics of the bryophytes

In total, 54 bryophyte species were recorded on different substrates: five liverworts and 49 mosses (Table 1). The most frequent were the liverwort *Lophocolea heterophylla* (Schrad.) Dumort. (95 of the plots = 95%) and the mosses: *Dicranum montanum* Hedw. (74 of the plots = 74%), *Hypnum cupressiforme* Hedw. (70 of the plots = 70%) and *Pohlia nutans* (Hedw.) Lindb. (70 of the plots = 70%) (Table 1). Species on specific types of substrate appeared with varying frequency (number of plots) and abundance. The highest mean abundance (≥3), according to abundance categories, was observed in eight of the GR species, one TB species, three TT species and five DW species. The results of the IndVal method indicated that of the 54 bryophyte species that were present, as many as 32 could be treated as indicator species for the habitats that were analysed what is reflected by probability lower than 0.05. They were characteristic for one, two and in some even for three of four analysed habitats (Table 1). The number of the bryophytes on each type of substrate is shown in Figure 1, and frequency in Figure 2.

Ground

Twenty seven species were recorded on this substrate. Most of these were identified as being rare or very rare (66% together). The most frequent species were *Dicranella heteromalla* (Hedw.) Schimp. (present in 47 plots), *Atrichum undulatum* (Hedw.) P.Beauv. (in 33 plots) and *Pleurozium schreberi* (Willd. *ex* Brid.) Mitt. (in 30 plots).

The bryophyte layer on GR developed to a very different degree and its cover ranged from 0 to 90%. On 53 plots, the cover of bryophytes was only 1% (only in 12 plots it was 30% or more). The least abundant moss layer developed in the stands, in which a thick layer of leaves lay on the forest floor as well as in stands that had compact grasses, which also limited the growth of bryophytes.

Tree bases

Thirty two species were recorded on TB. Half of them were rare or very rare (50% together), but rare species (28%) comprised

TABLE 1. — Frequency of bryophyte species in the Murckowski Forest (Silesian Upland, S Poland) (for 100 plots) and mean abundance (according to abundance category) on the different substrates studied. **Grey** cells represent habitats for which particular species are significantly associated according to indicator species analysis IndVal value (*p<0.05, **p<0.01, ***p<0.001). Abbreviations: VR, very rare; R, rare; FF, fairly frequent; F, frequent; VF, very frequent; NS, non-significant.

		Number of plots/mean abundance in plots				
Bryophyte species	**Frequency/total number of plots**	**Ground**	**Tree bases**	**Tree trunks**	**Dead wood**	**IndVal p-value**
Amblystegium serpens (Hedw.) Schimp.	F/27	–	16/2.4	2/1.5	15/2.4	0.394***
Atrichum undulatum (Hedw.) P. Beauv.	VF/41	33/3	5/2	–	14/1.9	0.547***
Aulacomnium androgynum (Hedw.) Schwägr.	R/8	–	2/1.5	–	5/1.8	0.194*
Aulacomnium palustre (Hedw.) Schwägr.	VR/1	1/2	–	–	–	NS
Brachytheciastrum velutinum (Hedw.) Ignatov & Huttunen	FF/20	1/2	14/2.2	–	6/2.2	0.309***
Brachythecium rutabulum (Hedw.) Schimp.	F/36	10/3	10 2.7	–	22/2.5	0.374***
Brachythecium salebrosum (Hoffm. ex F. Weber & D. Mohr) Schimp.	VF/65	5/2.4	5/1.8	–	47/2.9	0.575***
Callicladium haldanianum (Grev.) H.A. Crum	FF/13	–	4/2.8	1/3	8/3.1	0.235***
Calliergonella cuspidata (Hedw.) Loeske	VR/1	–	–	–	1/4	NS
Calypogeia integristipula Steph.	FF/16	1 2	13/2.2	–	6/2.3	0.301***
Cephalozia bicuspidata (L.) Dumort.	VR/1	–	–	–	1/1	NS
Ceratodon purpureus (Hedw.) Brid.	R/4	–	2/2.5	–	3/1.5	NS
Dicranella heteromalla (Hedw.) Schimp.	VF/69	47/2.7	26/1.9	–	30/2.1	0.586***
Dicranoweisia cirrata (Hedw.) Lindb.	R/5	–	–	1/3	3/1	NS
Dicranum montanum Hedw.	VF/74	–	57/2.4	32/1.9	28/2.1	0.624***
Dicranum polysetum Sw. ex anon.	R/4	–	–	–	4/1.3	0.200*
Dicranum scoparium Hedw.	VF/54	5/1.8	31/1.4	20/1.4	29/1.6	0.498***
Eurhynchium angustirete (Broth.) T.J. Kop.	R/6	5/3.4	–	–	2/2.5	0.197*
Herzogiella seligeri (Brid.) Z. Iwats.	VF/48	–	19/2.1	1/2	36/2.7	0.521***
Hylocomnium splendens (Hedw.) Schimp.	VR/2	–	–	–	2/1.5	NS
Hypnum cupressiforme Hedw.	VF/70	5/2.2	54/3.2	22/3	37/2.8	0.604***
Hypnum pallescens (Hedw.) P. Beauv.	FF/20	–	15/2.5	4/2	5/2.6	0.309**
Lepidozia reptans (L.) Dumort.	R/4	–	2/1.5	–	3/3.3	NS
Leucobryum glaucum (Hedw.) Ångstr.	VR/2	–	–	–	2/1	NS
Lophocolea heterophylla (Schrad.) Dumort.	VF/95	5/1.8	78/2.9	9/2	66/2.7	0.822***
Mnium hornum Hedw.	VR/1	–	–	–	1/2	NS
Orthodontium lineare Schwägr.	VR/2	–	2/3	–	–	NS
Orthotrichum affine Schrad. ex Brid.	VR/1	–	–	–	1/1	NS
Orthotrichum pumilum Sw. ex anon.	VR/1	–	–	1/1	–	NS
Orthotrichum speciosum Nees	VR/1	–	–	1/1	–	NS
Plagiomnium affine (Blandow ex Funck) T.J.Kop.	FF/15	14/2.7	3/2	–	8/3.1	0.317***
Plagiomnium cuspidatum (Hedw.) T.J.Kop.	R/4	–	–	–	5/1.8	0.224***
Plagiomnium undulatum (Hedw.) T.J. Kop.	VR/1	1/2	–	–	–	NS
Plagiothecium curvifolium Schlieph. ex Limpr.	VF/48	15/1.9	23/2.3	–	24/2.3	0.455***
Plagiothecium denticulatum (Hedw.) Schimp. var. denticulatum	FF/20	8/2	5/1.8	–	8/1.6	0.265*
Plagiothecium denticulatum var. undulatum R. Ruthe ex Geh.	VR/1	1/1	–	–	1/1	NS
Plagiothecium laetum Schimp.	V/66	4/1.5	56/3.1	11/1.9	39/2.4	0.657***
Platygyrium repens (Brid.) Schimp.	R/9	–	5/2.6	4/2.5	–	0.212*
Pleurozium schreberi (Willd. ex Brid.) Mitt.	VF/41	30/3.6	5/2.4	3/1	26/2.5	0.455***
Pohlia nutans (Hedw.) Lindb.	VF/70	25/2.4	45/2.2	3/1.3	40/2.2	0.606***
Polytrichastrum formosum (Hedw.) G.L. Sm.	F/25	20/2.9	2/2	–	7/2	0.391***
Polytrichum commune Hedw.	VR/1	1/2	–	–	–	NS
Polytrichum juniperinum Hedw.	R/6	5/1.4	–	–	1/2	0.197*
Pseudoscleropodium purum (Hedw.) M. Fleisch.	FF/12	11/3.2	–	–	6/2.2	0.292***
Ptilidium pulcherrimum (Weber) Vain.	FF 12	–	5/2.2	8/2.1	2/2	0.238*
Rhodobryum roseum (Hedw.) Limpr.	VR/1	1/2	–	–	–	NS
Sanionia uncinata (Hedw.) Loeske	R/7	–	1/1	–	5/2.2	0.214**
Sciuro-hypnum oedipodium (Mitt.) Ignatov & Huttunen	VF/48	29/3.2	17/2.5	–	33/3.1	0.513***
Sciuro-hypnum reflexum (Starke) Ignatov & Huttunen	VR/2	–	2/3.5	–	–	NS
Sphagnum fimbriatum Wilson	VR/2	1/3	–	–	2/2	NS
Sphagnum girgensoni Russow	VR / 2	2/3.5	–	–	–	NS
Tetraphis pellucida Hedw.	F/40	–	29/2.2	–	22/2.5	0.505***
Thuidium tamariscinum (Hedw.) Schimp.	VR/1	–	1/2	–	–	NS
Ulota crispa (Hedw.) Brid.	VR/1	–	–	1/2	–	NS

the largest group. The most frequent species were *Lophocolea heterophylla* (in 78 plots), *Dicranum montanum* (in 57 plots) and *Plagiothecium laetum* Schimp. (in 56 plots). In contrast to typical epiphytic habitats, terrestrial species were often introduced here, for example, *Plagiomnium affine* (Blandow *ex* Funck) T.J. Kop., *Pleurozium schreberi* and *Polytrichastrum formosum* (Hedw.) G.L. Sm.

Although bryophytes were observed on TB of 15 tree species, they were mainly found on *Quercus robur* (28 plots), *Betula pendula* (22 plots) and *Quercus rubra* (19 plots).

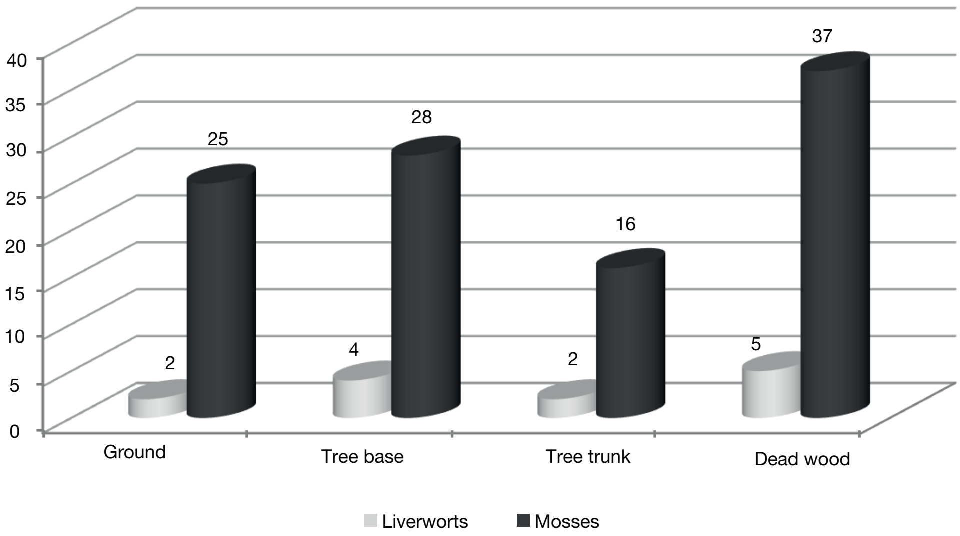

FIG. 1. — Number of bryophyte species in the four types of substrates considered.

Tree trunks

Eighteen species were recorded in typical epiphytic habitats. Most of these were identified as rare or very rare (78% together), being the largest group the very rare species (50%). The most common species were *Dicranum montanum* (in 32 plots), *Hypnum cupressiforme* (in 22 plots) and *Dicranum scoparium* Hedw. (in 20 plots).

Most of these were bryophytes that also occurred on the other types of substrates. Only a few, *Orthotrichum pumilum* Sw. *ex* anon., *O. speciosum* Nees and *Ulota crispa* (Hedw.) Brid., were obligatory epiphytes.

Epiphytes were observed on eight tree species on 41% of the plots. They mainly occurred on *Quercus robur* (in 24 plots) and *Betula pendula* (9 plots). No epiphytes were recorded on conifers.

Dead wood

There were as many as 42 species of bryophytes on DW. Most of these were recorded rarely or very rarely (61%). *Lophocolea heterophylla* (in 66 plots), *Brachythecium salebrosum* (Hoffm. *ex* F. Weber & D. Mohr) Schimp. (in 47 plots) and *Pohlia nutans* (in 40 plots) were observed most often.

The species listed from DW belong to various ecological groups such as epiphyte bryoflora residues (e.g. *Orthotrichum affine* Schrad. *ex* Brid. and *Ptilidium pulcherrimum* (Weber) Vain.), typical epixylic bryophytes (e.g. *Aulacomnium androgynum* (Hedw.) Schwägr., *Callicladium haldanianum* (Grev.) H.A. Crum, *Herzogiella seligeri* (Brid.) Z. Iwats., *Tetraphis pellucida* Hedw.), typical terrestrial species (e.g. *Dicranum polysetum* Sw. *ex* anon., *Pseudoscleropodium purum* (Hedw.) M. Fleisch. or *Sphagnum fimbriatum* Wilson) as well as a large group of multi-habitat species (e.g. *Amblystegium serpens* (Hedw.) Schimp., *Brachythecium rutabulum* (Hedw.) Schimp., *Ceratodon purpureus* (Hedw.) Brid. and *Hypnum cupressiforme*).

Interdependencies between elements of forest structure and bryoflora structure

Spearman rank correlation analysis revealed several statistically significant relationships (Table 2). The coverage of the bryophyte layer on the studied plots as well as the number of GR bryophyte species were negatively correlated with the coverage of the herbaceous vascular plants layer, although they were not very strong dependencies. At the same time, the coverage of the bryophyte and herbaceous layers were negatively correlated with the coverage of the trees layer.

The richness bryophyte species increased along with the volume of DW (Table 2). The number of epixylic species increased significantly with an increase in the volume of DW, and were also positively correlated with the maximum size of the pieces of DW in the study areas. No correlation was found between the age of the stands and the number of bryophytes on the analysed plots. No relationship was found between the number of epiphytic bryophytes and the size of the trees or the diversity of the tree species in the stands (not shown in the Table 2).

Interpretation of the ordination analyses

The ordination analyses (Table 3) demonstrated that the species composition of bryophytes on the GR is related to the species composition of the vascular plant species in the herbaceous layer and in the overstory layer. The first axis of the CoCa explained 8.6% of the variation in the bryophyte species data ($p=0.001$). Seven explanatory variables were significantly fitted onto ordination. Several species such as *Aulacomium palustre* (Hedw.) Schwägr., *Pleurozium schreberi* and *Rhodobryum roseum* (Hedw.) Limpr. were associated with older tree stands that had trees with a higher mean DBH. *Sciuro-hypnum oedipodium* (Mitt.) Ignatov & Huttunen was more confined to sites with a higher presence of large logs, whereas *Plagiothecium denticulatum* var. *denticulatum* (Hedw.) Schimp. grew in more acid sites (Fig. 3).

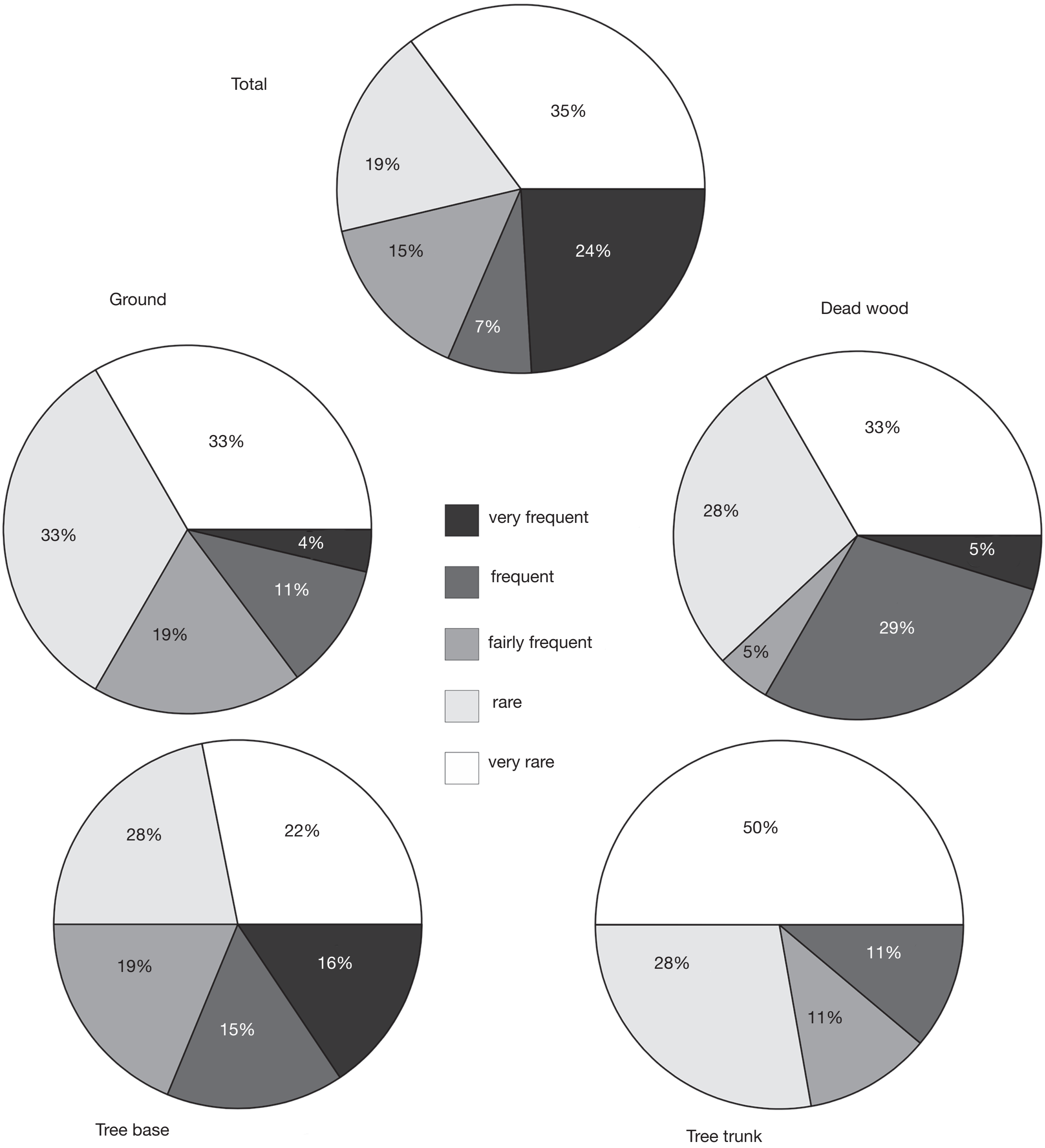

Fig. 2. — Frequency of occurrence of bryophytes generally and in the four types of substrates considered.

Amongst the epiphyte species (TT), L and T were the only important factors. As far as the former was concerned, *Dicranum scoparium* and *Platygyrium repens* (Brid.) Schimp. were more closely associated with L, while in the case of T, it was *Plagiothecium laetum* (Fig. 4).

Although DBH and presence of old tree stands were the statistically significant factors for species that were colonizing TB (Table 3), only *Tetraphis pellucida* clearly responded to those variables while majority of species seemed not to be strongly affected (Fig. 5). Along T, another significant factor, only rare species were associated.

Epixylic bryophytes such as *Atrichum undulatum* and *Herzogiella seligeri* responded positively to the volume of DW, whereas *Plagiothecium curvifolium* Schlieph. *ex* Limpr. occurred on plots with a higher DBH and *Sciuro-hypnum oedipodium* and *Tetraphis pellucida* preferred older sites (Fig. 6).

Table 2. — Values of correlations among some analysed factors of forest structure and diversity of bryoflora. Significant coefficients (p<0.05) are written in **bold**. Abbreviations: **Σ**, total number of species; **GR**, ground; **TB**, tree bases; **TT**, tree trunks; **DW**, dead wood.

	Forest age	Trees coverage	Underwood coverage	Herbs coverage	Bryophytes coverage	Σ all bryophytes	Σ GR bryophytes	Σ TB bryophytes	Σ TT bryophytes	Σ DW bryophytes	DW volume
Forest age	–	–	–	–	–	–	–	–	–	–	–
Trees coverage	-0.17852	–	–	–	–	–	–	–	–	–	–
Underwood coverage	**-0.26819**	**0.25885**	–	–	–	–	–	–	–	–	–
Herbs coverage	**0.20423**	**-0.48356**	**-0.28265**	–	–	–	–	–	–	–	–
Bryophytes coverage	0.03086	**-0.25973**	-0.04248	**-0.24691**	–	–	–	–	–	–	–
Σ all bryophytes	-0.14498	-0.05882	-0.03594	0.13710	**0.22118**	–	–	–	–	–	–
Σ GR bryophytes	-0.13792	-0.06543	0.14713	**-0.36562**	**0.80841**	**0.30266**	–	–	–	–	–
Σ TB bryophytes	-0.17362	0.17427	-0.02210	0.09155	-0.18766	**0.65882**	-0.08105	–	–	–	–
Σ TT bryophytes	-0.04428	0.07283	-0.03928	0.14753	**-0.20838**	**0.41862**	-0.10601	**0.59915**	–	–	–
Σ DW bryophytes	-0.09218	-0.11705	-0.08256	0.13551	**0.19815**	**0.65854**	0.16935	0.13747	0.03838	–	–
DW volume	-0.08352	-0.11066	-0.09748	0.09385	0.01189	**0.48375**	-0.02029	0.12287	0.10502	**0.74122**	–
DW maximum size	-0.16528	0.04341	0.14969	0.00978	0.07441	**0.29966**	0.05248	0.04162	0.00714	**0.52958**	**0.50201**

Table 3. — Values of permutation tests of ordination analyses for bryophytes from various habitat studied. Significant variables (p<0.05) are written in **bold**. Abbreviations: **CoCa**, co-correspondence analysis; **RDA**, redundancy analysis; **DBH max**, maximal trees diameter at breast height; **DW**, dead wood; **L**, Ellenberg indicator value (EIV) for light; **T**, EIV for temperature; **F**, EIV for moisture; **R**, EIV for pH; **N**, EIV for nitrogen.

Habitat	Ground	Tree trunks	Tree bases	Dead wood
Method Ordination	CoCa+vector fitting	RDA	RDA (Hellingen transformation)	RDA (Hellingen transformation)
Significance (number of permutations)	999	999	999	999
Variable:				
DBH max.	**0.015**	0.124	**0.009**	**0.035**
DW volume	**0.041**	0.754	0.199	**0.021**
DW max. size	0.264	0.674	0.640	0.960
Forest age	**0.001**	0.517	**0.032**	**0.020**
L	0.589	**0.035**	0.171	**0.012**
T	**0.005**	**0.011**	**0.005**	0.260
F	**0.017**	–	0.081	–
R	**0.001**	–	0.117	–
N	**0.001**	–	0.313	–

DISCUSSION

In managed forests the structure of ecosystems is usually disturbed and causes a reduction in biodiversity in various ways (Nowińska *et al.* 2009; Chećko *et al.* 2015). Most of the forms of degeneration that are characteristic for commercial forests have been observed in the Murckowski Forest. The tree stands are relatively young, are often formed by one or two species and are often dominated by *Pinus sylvestris* or *Quercus rubra*. Cutting and altering the structure of the tree stands that are planted usually lead to changes in the herbaceous vegetation (Bergstedt & Milberg 2001). In the analysed plots, the herbaceous layer was usually impoverished and was often limited by a thick litter layer or grass and sedge. The litter layer was particularly thick in stands with *Quercus rubra* (39% of plots). In Poland, the negative impact of *Quercus rubra* on the richness and abundance of forest floor vegetation has been and continues to be widely discussed (Fojcik & Stebel 2001; Chmura 2013; Woziwoda *et al.* 2014). A very limited share of DW was also observed in the analysed forest ecosystem (80% of the plots had none or less than 0.01 m^3). In general, the volume of DW in the managed forests of Europe is small and varies between 1 and 23 m^3/ha (Kirby *et al.* 1991). The average contribution of DW in the Polish state forests is about 5.6 m^3/ha, of which the 2.5 m^3/ha are logs that are lying, while the rest are dead standing trees (data from National Forest Inventory, https://www.buligl.pl/pl/web/en/forest-data-bank). This has a significant, unfavorable impact on the variety of epixilic bryoflora.

All of the abovementioned factors negatively affect the local bryoflora. Their impact varies according to the ecological preferences of bryophytes, especially type of substrate (GR, TB, TT or DW). The degree of the development of the GR bryophytes was mainly determined by two factors: the herbaceous layer coverage and leaf litter. As herbaceous layer is concerned there is a negative relationship between coverage of herbaceous species and total coverage of bryophytes due to competition. Such relationship was observed only in case of terrestrial bryophytes what is obvious. The excessive development of Poaceae and Cyperaceae (in our case *Calamagrostis* spp. and *Carex brizoides*) eliminates the other species of the herbaceous layer as well as bryophytes (Chmura & Sierka 2007). The development of grasses in the herbaceous layer is usually the result of the thinning of stands (Meier *et al.* 2005; Liira *et al.* 2007), which is a phenomenon that is typical for managed forests. In turn, the leaf litter of deciduous trees also negatively affects forest-floor bryophytes and herbaceous species because they form a mechanical barrier (Startsev *et. al.*

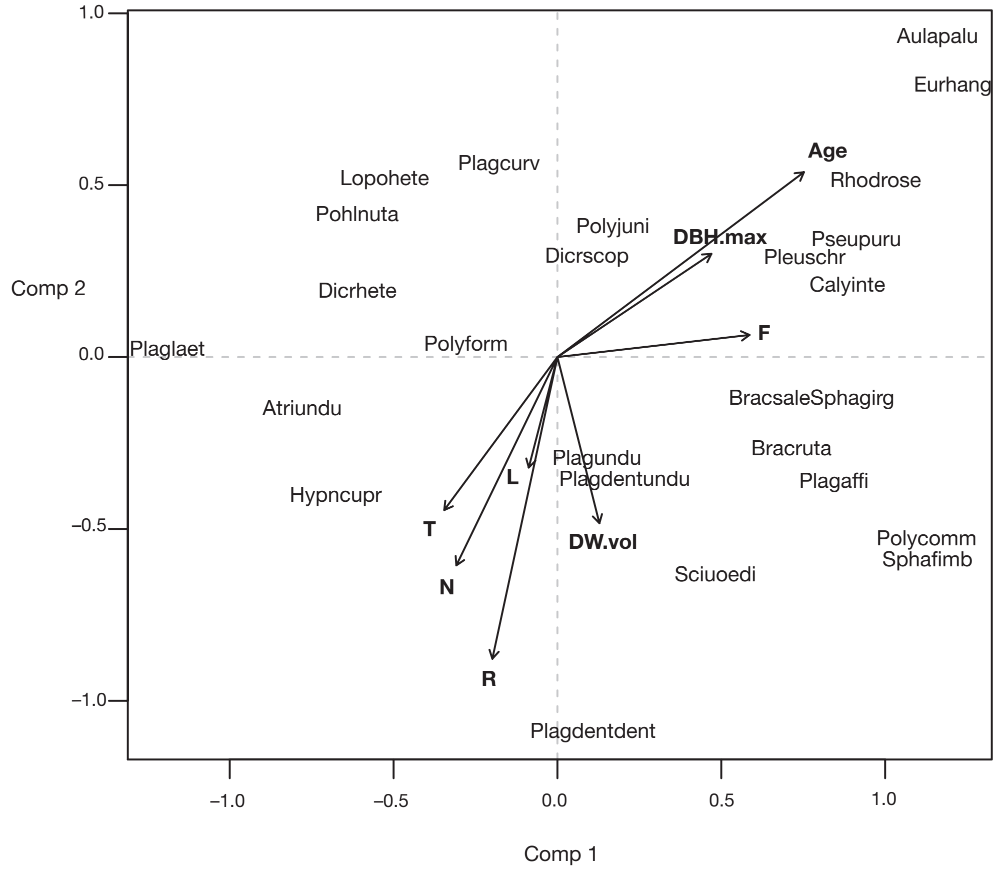

FIG. 3. — Co-correspondence analysis biplot illustrating the ordination of most frequent bryophyte species colonizing ground in relation to the statistically significant environmental variables (n=75). Abbreviations: **Age**, forest age; **DBH.max**, maximal trees diameter at breast height; **DW.vol**, dead wood volume; **L**, Ellenberg indicator value (EIV) for light; **T**, EIV for temperature; **F**, EIV for moisture; **R**, EIV for pH; **N**, EIV for nitrogen; the first four letters of species indicate genus name, next four indicate species names and next four letters subspecies names.

2008; Evans *et. al.* 2012). This is particularly the case for the stands with invasive *Quercus rubra* in Poland (Chmura 2013; Woziwoda *et al.* 2014) and such areas comprised more than 30% of the investigated plots. For terrestrial bryophyte species, which are displaced from the forest floor by the herbaceous cover and leaf litter, structural features such as TB and DW may provide an escape and a rescue habitat (Evans *et. al.* 2012). This was confirmed in this study, as some typical terrestrial species were only observed on DW (*Dicranum polysetum*, *Hylocomium splendens* (Hedw.) Schimp. and *Leucobryum glaucum* (Hedw.) Ångstr.) or on TB (*Thuidium tamariscinum* (Hedw.) Schimp.).

A less important, but statistically significant for the degree of development of the ground bryophytes coverage is the layer of trees (were negatively correlated). This is probably due to the deterioration of the light conditions on the forest floor (shading) with the increase in the density of tree crowns. Lighting is among the main factors conditioning the development of forest bryophytes and differing managed and unmanaged forests (Hannerz & Hånell 1997; Botting & Fredeen 2006).

Over time, the structure of a managed forest changes, which also reflects qualitative changes in the bryoflora (Hofmeister *et al.* 2015). The age of the stands also had a significant impact on the qualitative differences of the analysed terrestrial bryoflora, as some species such as *Aulacomnium palustre* or *Rhodobryum roseum* were observed exclusively in older stands.

Trees, as habitat for bryophytes, are usually considered in two aspects: TB and TT (Smith 1982; Fudali 2012). TB are characterised by specific ecological and habitat conditions, which are different from those that occur higher on the trunk (less light availability, higher humidity, contact with soil) (Moe & Botnen 2000; Mežaka & Znotiņa 2006). TB form a transitional zone between the terrestrial and epiphytic habitat, and therefore, a relatively large number of terrestrial species are introduced that are not observed on the TT (Fudali & Wolski 2015). Our study confirms the relatively large diversity of the bryoflora that was growing on TB (more species were only recorded on DW). At the same time, in tree stands where there were no favorable conditions for the development of the GR moss layer (because of excessive herbaceous coverage and leaf litter), the TB were sometimes the only enclaves for terrestrial species. In our study, *Sciuro-hypnum reflexum* (Starke) Ignatov & Huttunen and *Thuidium tamariscinum* were recorded only on TB, although they usually grow on GR. In case of TB the size and age of trees are also important factors encouraging presence of bryophytes.

TT were the poorest in terms of the number of bryophyte species (compared to the other analysed habitats). In the case

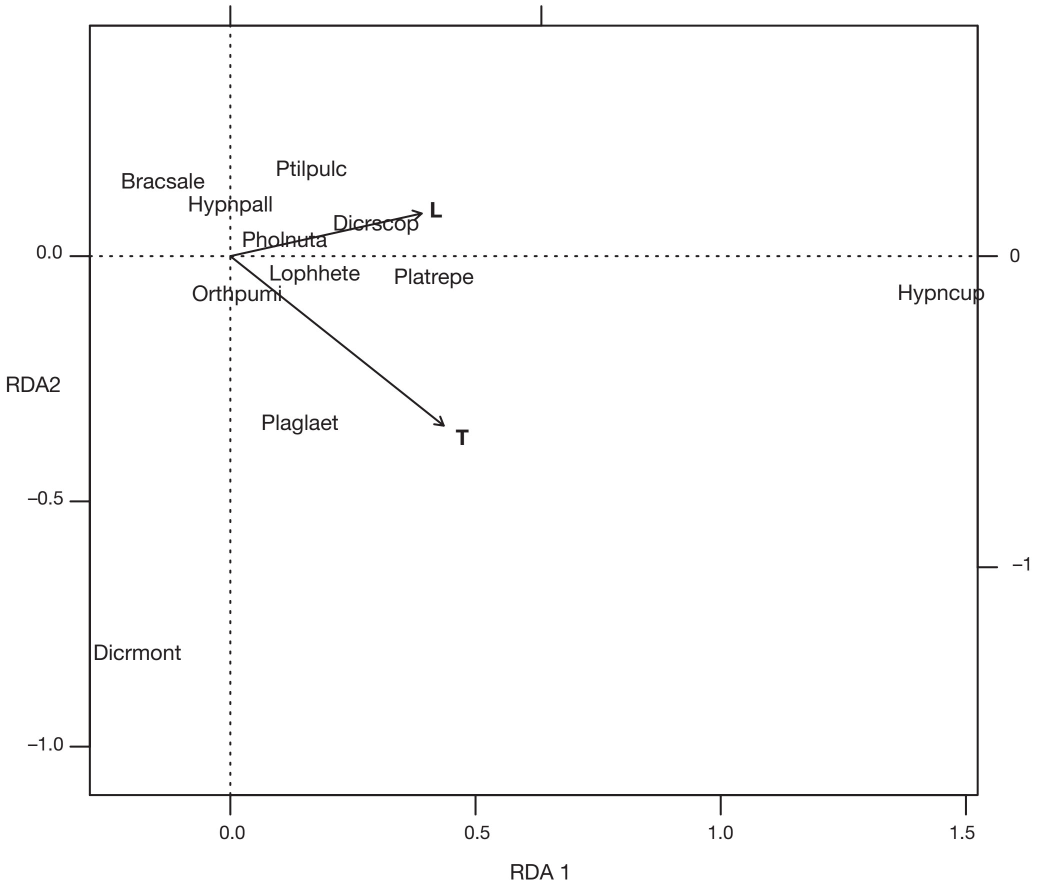

FIG. 4. — Redundancy analysis biplot illustrating the ordination of most frequent bryophyte species colonizing tree trunks in relation to the statistically significant environmental variables for the plots with the presence of tree host species (n=41). Abbreviations as in Fig. 3.

of epiphytes, tree size and the composition of the tree species in a stand are the most important determinants of species richness (Király & Ódor 2010; Nascimbene *et al.* 2013). This study does not confirm these relationships, which is probably due to the high degree of disturbance, especially the limited age range of the stands (no very young or old trees) and the limited species diversity of the stands, which were dominated by some of the preferred tree species (with a small share of others). Other authors have also documented a similar situation in managed forests (Király & Ódor 2010; Ódor *et al.* 2013).

In general, our study confirms the fact that epiphytic bryophytes are very sensitive to forest management practices (Gustafsson & Hallingbäck 1988; Friedel *et al.* 2006; Fudali & Wolski 2015). The lack of old trees is of particular importance as their trunks are characterised by a greater degree of the heterogeneity of microsites (Király *et al.* 2013; Pentecost 2014) and many rare species limit their occurrence only to old trees (Friedel *et al.* 2006). Another important factor is the location site of bryophytes on the trunk. The L and T conditions increase along with height of trees what partially was observed in our study because EIVs for L and T were significant factors in ordination analysis. There were no epiphytes on the coniferous trees in our study, which is confirmed by the preference for this group of bryophytes for deciduous trees, especially trees with a higher bark pH, that has been documented in the literature (Cleavitt *et al.* 2009; Boch *et al.* 2013).

This study also confirms that DW in forest ecosystems, especially those that heavily economically exploited, is a key habitat for bryophytes (Strazdiņa 2010; Jonsson *et al.* 2016). Not only was the largest number of species recorded here, but also in the stands in which the conditions were unfavorable for the development of the moss layer, DW was sometimes the only enclave for terrestrial species (as is the case with TB). Only on DW were recorded some typical terrestrial species such as *Calliergonella cuspidata* (Hedw.) Loeske, *Cephalozia bicuspidata*, *Dicranum polysetum*, *Hylocomnium splendens*, *Leucobryum glaucum* and *Mnium hornum* Hedw. Like other authors (Sabovljević *et al.* 2010; Evans *et. al.* 2012; Hofmeister *et al.* 2015), this study shows that the quantity and quality of epixylic bryoflora mainly depend on the volume and size of DW. This is a temporary substrate and the larger it is, the longer its decomposition takes, which means that it is available as a habitat for longer and this provides a greater variety of microhabitats (Söderström 1988; Nowińska *et al.* 2009).

In the case of epiphytic and epixylic bryoflora, the habitat offer is very important, or rather its significant limitations in managed forest (Madžule *et al.* 2012; Ódor *et al.* 2013). This particularly applies to epiphytes (TT), as demonstrated in this study (generally the least species and the largest share of very

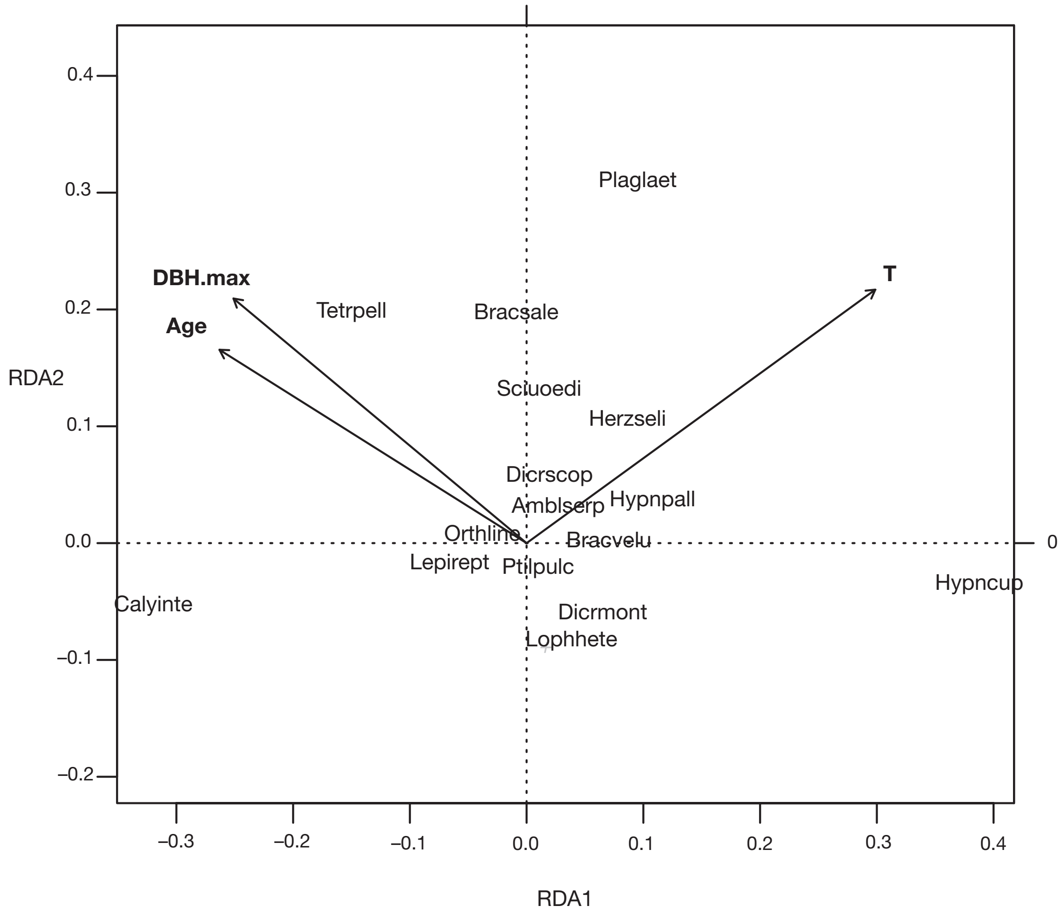

Fig. 5. — Redundancy analysis biplot illustrating the ordination of most frequent bryophyte species colonizing tree bases in relation to the statistically significant environmental variables for the plots with the presence of tree host species (n=96). Abbreviations as in Fig. 3.

rare species). DW, even with a very limited amount, is still a habitat conditioning bryophytes diversity in managed forest (which has also been confirmed by this study). Both in the case of epiphytic and epixylic bryophytes, the greater the habitat offer (especially substrate size), the greater the possibility of colonization by more species. Larger habitats provide a more valuable habitat for bryophytes, because they have greater potential surface available for colonization, improved moisture retention and greater range of microhabitats (Crites & Dale 1998; Humphrey *et al.* 2003).

The example of the Murckowski Forest described here presents the situation of bryoflora in the managed forests in Poland. Disruptions in the structure of a forest negatively affect all types of bryophytes, regardless of the type of the substrate. Liverworts are especially sensitive (Vellak & Paal 1999; Botting & Fredeen 2006). A decrease in the number of hepatic species was found to be most indicative of the intensity of forest management (Vellak & Ingerpuu 2005). Just five species of liverworts were identified in this study, of which only *Lophocolea heterophylla*, which is an epiphytic-epixylic species occurred often on pine trees (Ódor *et al.* 2013). No species of bryophytes that are characteristic of the old-growth forests in Poland were recorded in our study (Klama 2002; Stebel & Żarnowiec 2014).

In natural old-growth forest with numerous well-developed microhabitats the relationship between environment and species richness and diversity is stronger and not violated by extrinsic factors (Ódor & Standovár 2001; Hofmeister *et al.* 2015). The diversity of bryophytes in a managed forest is usually limited due to the various forms of degeneration, the lack of old trees, the lack of DW and a reduction in the number of microhabitats.

Applications for conservation

The necessity of developing and implementing the forest management methods of 'retention forestry' ('ecologically sustainable forestry') has long been indicated (Bergstedt *et al.* 2008; Gustafsson *et al.* 2012). The effective conservation of bryophytes in managed forests requires the preservation of some fundamental forest conditions: mixed stands, old trees and high DW volume (Humphrey *et al.* 2002; Caners *et al.* 2010; Sabovljević *et al.* 2010; Táborská *et al.* 2015).

Although researchers have diagnosed the causes of biodiversity loss in managed forests and pointed out the main directions for a strategy for retaining diversity, it is extremely difficult to put these recommendations into practice. While sustainable forest management is also promoted in Poland (Directorate No. 55 of the General Director of the State Forests dated 21

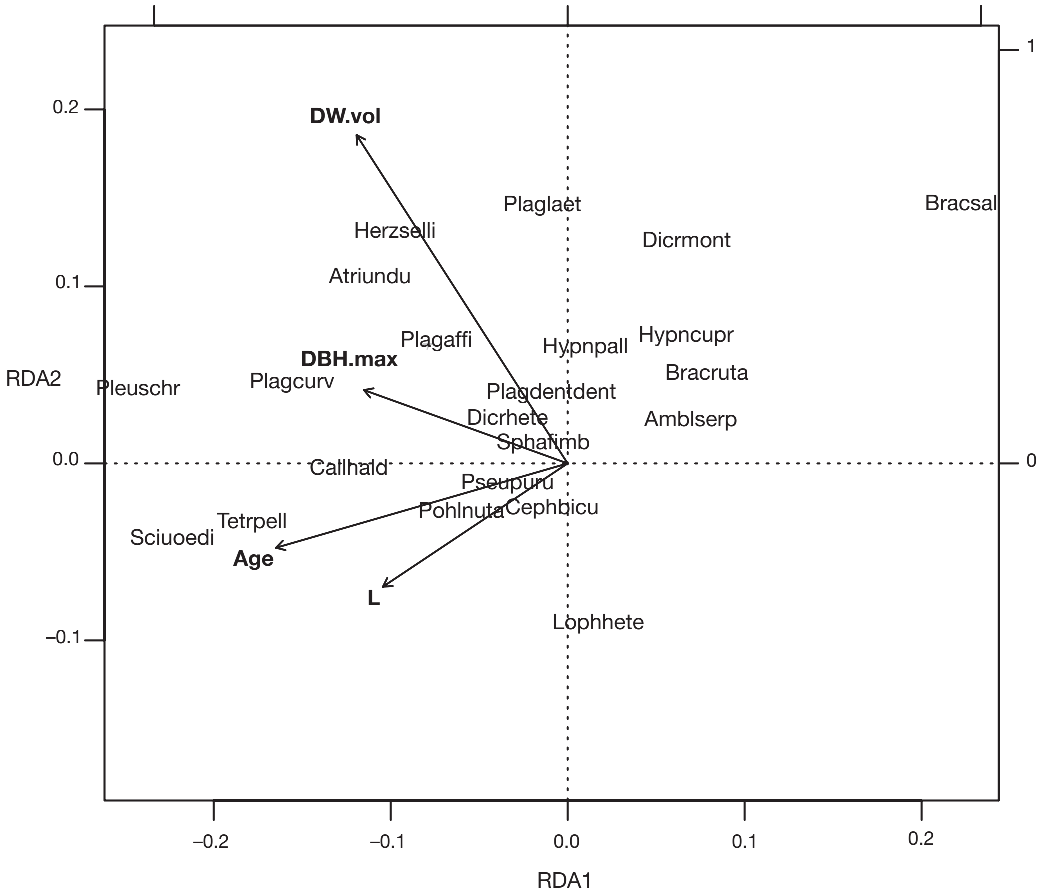

Fig. 6. — Redundancy analysis biplot illustrating the ordination of most frequent bryophyte species colonizing dead wood in relation to the statistically significant environmental variables for the plots with the presence of decaying logs (n=80). Abbreviations as in Fig. 3

November 2011), the criteria for maintaining and enhancing the productive function of the forest still appears to be favored. For many foresters, DW is still seen primarily as a hatchery for pests and that commercial forests should be excluded from specific actions that are designed to protect biodiversity (hence the reserves). As long as forest management practices do not change on a wider scale, bryophytes will continue to be one of the most threatened groups in managed forests.

CONCLUSION

Bryophyte richness in managed forest is related to specific elements of the forest structure. The development of the terrestrial bryophytes was limited mainly by two factors: the herbaceous layer coverage (especially compact graminoid plants e.g. grasses and sedges) and leaf litter. Limiting the habitat availability is the main factor negatively affecting epiphytic bryoflora. Poverty of epiphytes results from dominance of conifers tree (mainly *Pinus sylvestris*) due to frequent planting by foresters in the past for timber, as well as low species diversity of trees and lack of old deciduous trees. Despite the limited volume of DW in managed forest, this type of substrate is crucial for the richness of bryoflora. Sustainable forest management practices should be changed on a wider scale, especially with regard to the preservation of habitats for epiphytic species and the increase of DW volume in managed forests.

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