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The impact of forest management on changes in composition of terricolous lichens in dry acidophilous Scots pine forests

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Abstract: This study focuses on dry acidophilous Scots pine forests, well known for their high biodiversity of cryptogams. We hypothesized that dense forests and heavy management were responsible for changes in species diversity, decreasing trends in lichen cover and increasing moss cover. This hypothesis was tested in three types of Scots pine forests maintained under three different management regimes: 1) managed forests (forest plantations regenerated by planting), 2) semi-natural forests (forest plantations regenerated naturally), both located in the Borská nížina lowland in SW Slovakia, and 3) natural forests (primordial vegetation without visible management actions from the association *Cladonio-Pinetum* Juraszek 1928), located in the Bory Tucholskie National Park, NW Poland.

We observed that the cover of the canopy tree layer had the most significant influence on the diversity of lichens. Managed forests are planted and maintained to achieve denser tree stocking, and although the environmental conditions created appear optimal for moss species, they are less suitable for terricolous lichens.

Key words: biodiversity, Central Europe, *Cladonio-Pinetum*, lichenized fungi, lichen ecology

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Introduction

Scots pine (*Pinus sylvestris* L.) is a Euro-Asian coniferous tree species with the broadest natural distribution range of all tree species in the world. The northernmost occurrence of natural Scots pine forest reaches Scandinavia and stretches more than 3500 km south to Sierra Nevada in Spain. It is found from the Atlantic Ocean in Scotland in the west, throughout all Europe and Siberia, to the Pacific Ocean at the Sea of Okhotsk in the east (Solon 2003). In Europe, the Scots pine occurs in various climatic zones: oceanic, sub-oceanic, sub-continental, continental, mountain and Mediterranean (Ellenberg 1988). It is conditioned by its wide ecological amplitude. It flourishes on nutrient-rich peat bogs, on nutrient-poor dry sands, in localities featuring annual precipitation exceeding 1700 mm, and also in areas with a dry climate and annual precipitation of *c.* 200 mm (Kelly & Connolly 2000). The optimal average annual temperature for growth is 0–12°C (Krippel 1965). The distribution of Scots pine forests in particular regions of Europe depends not only on the stress resistance of the trees in extreme habitat conditions, but also on its capability in competitive relationships with other trees, and on Holocene migrations (Solon 2003).

The typical dry acidophilous Scots pine forests, classified as the association *Cladonio-Pinetum* Juraszek 1928, are distributed in sandy areas of Central Europe. Although these forests are naturally poor in nutrients, they are generally rich in terricolous lichens, especially *Cladonia* species, due to their xerophilous character. Juraszek (1928), who described the association, did not state the characteristic species of *Cladonio-Pinetum*,

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however she listed species composition of vascular plants with decreasing frequency: *Pinus sylvestris, Festuca ovina* agg., *Carex ericetorum* Pollich, *Arctostaphylos uva-ursi* (L.) Spreng., *Calluna vulgaris* (L.) Hull, *Corynephorus canescens* (L.) P. Beauv., *Thymus serpyllum* L., *Quercus robur* L., *Acetosella vulgaris* Fourr., *Juniperus communis* L., and cryptogams: *Cladonia rangiferina* (L.) Weber ex F. H. Wigg., *Cladonia arbuscula* (Wallr.) Flot. em. Ruoss ssp. *squarrosa* (Wallr.) Ruoss, *Polytrichum piliferum* Hedw., *Dicranum polysetum Sw.*, *Cetraria islandica* (L.) Ach., *C. aculeata* (Schreb.) Fr., *C. stellaris* (Opiz) Pouzar & Vězda, *C. uncialis* (L.) Weber ex F.H.Wigg. and *C. gracilis* (L.) Willd. The main distribution area of this association occurs in Poland (Sokołowski 1965; Matuszkiewicz & Matuszkiewicz 1973, 1996; Ermakov & Morozova 2011), Germany (Heinken & Zippel 1999; Heinken 2007), the Netherlands (Emmer & Sevink 1994), partly in Finland, Norway, Latvia, Lithuania (Solon 2003) and also in Estonia (Zobel *et al.* 1993). The precise occurrence of this association in Slovakia and the Czech Republic is still not clear (Husová & Andresová 1992; Šomšák *et al.* 2004; Mikuška 2005; Kučera *et al.* 2006; Bouda 2009; Stefańska-Krzaczek 2010). Although *Cladonio-Pinetum* forests are widespread (Kelly & Connolly 2000), they have become threatened over a large part of the continent (Celiński *et al.* 1997; van Tol *et al.* 1998; Prieditis 2002; Danielewicz & Pawlaczyk 2004; Szczygielski 2007) so that they are now included in the NATURA 2000 network (Kabucis *et al.* 2000; Kolbek & Chytrý 2010). Numerous studies have confirmed that anthropogenic impact is a major factor influencing quantitative societal values such as the biodiversity of vascular and especially non-vascular plants, and also natural ecological processes. Intensive forest management leads to even-aged, mono-dominant forests with remarkably low species diversity, especially in cryptogams. The result of this practice is a lack of various microhabitats suitable for the development of diverse cryptogam synusias, including such habitats as dead, large and decaying pine stumps and trunks (Daniëls 1993). Thus, the age of a forest is of great importance for cryptogam diversity (cf. Meier *et al.* 2005).

In Central Europe, the natural *Cladonio-Pinetum* is a rare and seriously endangered plant community dominated by Scots pine and cryptogams. This threat is increased by the human impact of forest management. The majority of European Scots pine forests are considered not to be natural. They are either intensively managed economic forests or mildly managed semi-natural forests. Many of the localities assigned in the past to the *Cladonio-Pinetum* association have been affected by forest management (Juraszek 1928; Fałtynowicz 1983, 1986; Lipnicki 2003); only small remnants are believed to be natural (Lipnicki 2003). The management actions and subsequent changes often led to the degradation of the natural forest ecosystem, which is usually a very difficult situation to remedy by compensatory actions. The natural status of the *Cladonio-Pinetum* Slovakian forests has been discussed in the past (Ružička 1953, 1960*a*, *b*, *c*; Krippel 1965; Šomšáková 1988) and also recently (Hegedüšová *et al.* 2004; Šomšák *et al.* 2004; Valachovič 2005). Some authors currently tend to consider these forests to have had a natural origin, and they disagree with the assumption that the *Cladonia*-rich pine forests are a post-management successional stage of acidophilous pine forests (Heineken & Zippel 1999; Danielewicz & Pawlaczyk 2004).

The Borská nížina lowland in the south-western part of Slovakia is one of these sites. The cultivation of *Pinus sylvestris* here dates back as far as 1460 AD (cf. Ptačovský 1959), and intensive forest management and cultivation in this area has occurred since the first half of the 17th century (Kalivodová *et al.* 2008).

Forest management on sandy soils in Borská nížina has its own specifications (FMP 2005). After clear cuts, the sandy soil is cleared of stumps, larger roots and other debris which are stock piled. Seedlings of *Pinus sylvestris* are planted in lines and cultivated using herbicides and fertilizers, following hoeing and weed removal. The management thinning and cleaning is repeated two or three times. While felling of the managed

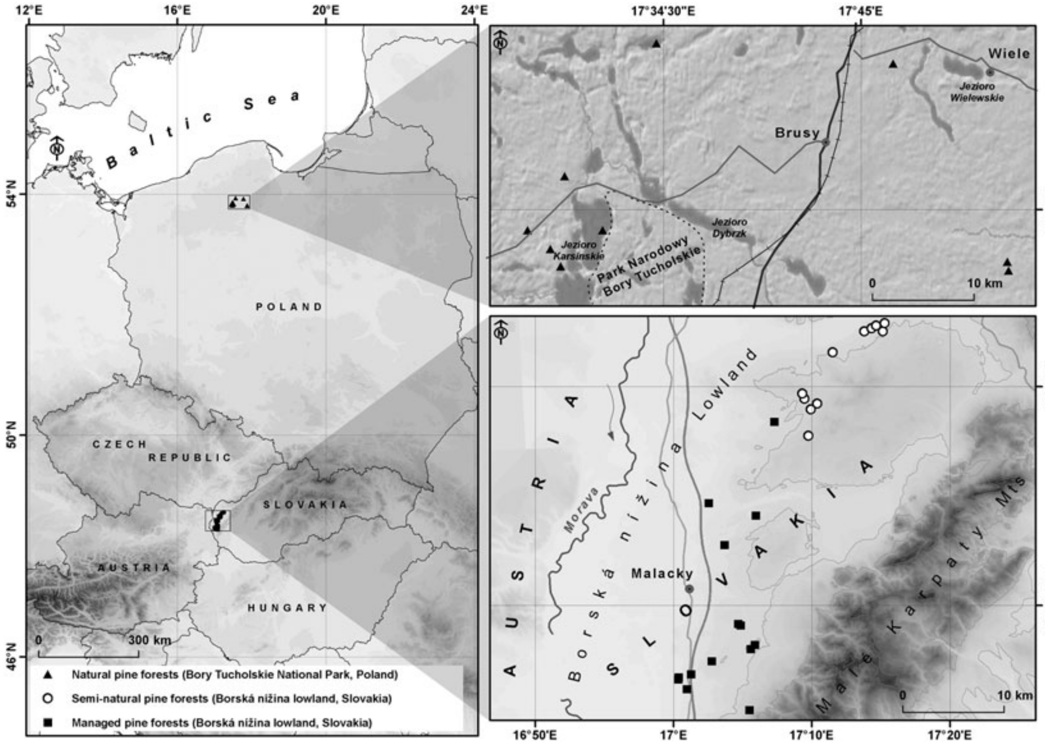

FIG. 1. Localities of the Borská nížina lowland (Slovakia) and Bory Tucholskie National Park (Poland).

forests is repeated approximately every one hundred years after clear cuts, semi-natural forests are left for natural regeneration, as soil protection is considered to be of the utmost importance.

Pine-dominated communities on sandy soils, such as *Cladonio-Pinetum*, have often been considered to have lichen-moss mats (Brodo 1961; Crittenden 1991, 2000). Here, the mechanisms that can influence these mats and their species diversity are examined. It was also important to confirm similarities between *Cladonio-Pinetum* in the Bory Tucholskie National Park and semi-natural pine forest localities in Slovakia, for consequent improvement in their conservation.

The aims of this study were: 1) to describe the species composition; 2) to discuss the variability of species richness and diversity of the cryptogam layer in dry acidophilous Scots pine forests, with particular attention to terricolous lichens; 3) to address the most significant ecological characteristics which influence the species diversity of the terricolous lichens; and 4) to determine the impact of different management actions and processes in individual *Cladonio-Pinetum* forest types on the species composition and diversity in the area studied.

Materials and Methods

This research was conducted between 2006 and 2011 in the two selected regions of Borská nížina lowland in Slovakia and Bory Tucholskie in Poland (Fig. 1). The Borská nížina lowland lies in the south-western part of Slovakia in the region of Eupannonicum (Futák 1980). It is characterized by a sub-continental climate with an average annual temperature of *c.* 9–9·6°C. July is the hottest month here, with a temperature of 19·6–20·2°C, and the growing season is *c.* 250 days long. The average annual precipitation is 550–650 mm, 300–320 mm of which falls during the growing season (Krippelová & Krippel 1956). The soil pH on top of the sand dunes in the upper horizon is very acidic, at 4·1–4·6 (Kollár *et al.* 2011).

TABLE 1. *Different management actions and processes in individual forest types*

	Forest type		
	Managed forests	Semi-natural forests	Natural forests
Forest plantation	+	+	–
Natural forest formation	–	–	+
Regeneration by planting	+	–	–
Regeneration naturally	–	+	+
Clear cuts every 100 years	+	–	–
Clearing to the bare sand every 100 years	+	–	–
Wood debris stock-piled	+	–	–
Herbicides and fertilizers after planting	+	+	–
Hoeing and weed removal after planting	+	+	–
Thinning and cleaning	+	+	–

Bory Tucholskie is a sub-oceanic region with an annual precipitation of *c.* 600 mm, a mean annual temperature of 7·1°C, and a growing season of about 200 days (Woś 1999). The average pH of the contact area between the humus and mineral horizons is 4·8 (Fałtynowicz 1986).

A total of three types of habitat were selected due to the different management actions and processes among the following forest types: 1) managed forests (forest plantations regenerated by planting), 2) semi-natural forests (forest plantations regenerated naturally) and 3) natural forests [primordial vegetation without visible management from the association *Cladonio-Pinetum* (Juraszek)] 1928). While the Borská nížina lowland encompasses the first two types of forests with different management actions, its natural status is still under discussion. Comparison with forests which are reliably natural is useful in the assessment of the natural status of these forests (see Table 1 for differences in management actions for individual forest types). Therefore, the Bory Tucholskie National Park was chosen, and plots from this locality were added to the dataset. A total of 35 localities with the occurrence of dry acidophilous pine forests (*Dicrano-Pinion*) were studied from both regions. Of these forests, 14 were managed, 11 were semi-natural and 10 were natural. Hence, a total of 35 phytosociological relevés of 400 m^2 and 350 micro-samples with a 0·25 m^2 area were examined in the field. There was 1 relevé and 10 micro-samples in each locality.

All relevés were made using standard procedures of the Zürich-Montpellier School (Braun-Blanquet 1964; Westhoff & van den Maarel 1978). The modified 9-degree Braun-Blanquet's sampling scale (Barkman *et al.* 1964) was used and data were stored in the TURBOVEG database (Hennekens & Schaminée 2001), prior to processing in JUICE 6.4 (Tichý 2002). Micro-samples were divided according to current management techniques in the area. This gave 140 micro-samples of managed forests, 110 from semi-natural forests, and 100 from natural pine forests. Canonical correspondence analysis (CCA) performed in the CANOCO 4.5 program package analyzed and depicted the relationships between the floristic composition of the relevés and the environmental variables (ter Braak & Šmilauer 2002). These variables comprised: the lichen cover, moss and herb layers, litter cover and depth, the A0 and A1 soil horizon depths, the forest age and the density of the tree canopy cover, and the Shannon-Wiener diversity index. The complete model of the Monte-Carlo permutation test was performed using 499 random permutations to assess the effectiveness of each environmental variable in the ordination model.

Statistica 9.0 (http://www.statsoft.com/) was used for correlation analysis, and box and whisker plots were constructed for the following selected environmental variables: diversity and cover of vascular plants, mosses and lichens, the frequency of selected geographical elements and life forms, canopy cover in relation to particular vegetation and also the existing management types. The significant statistical differences were tested by the Tukey post-hoc test using multiple comparisons following a one-way ANOVA, and statistical differences are depicted in the diagrams by the letters a, b and c.

The nomenclature of vascular plants follows the checklist of Marhold & Hindák (1998), and the cryptogams are as in the checklist by Bielczyk *et al.* (2004).

Several species and sub-species from problematic groups of the genus *Cladonia* spp. were not distinguished (Hennipman & Sipman 1978; Hammer 1995; Stenroos & Depriest 1998). The content of individual groups was as follows: *Cladonia cariosa* group (Pino-Bodas *et al.* 2012): *C. acuminata* (Ach.) Norrl., *C. cariosa* (Ach.) Spreng., *C. symphycarpia* (Flörke) Fr.; *Cladonia chlorophaea* group (Ahti 1966; Ferry & Pickering 1989; Kotelko & Piercey-Normore 2010): *Cladonia chlorophaea* (Flörke et Sommerf.) Spreng., *C. merochlorophaea* Asahina, *C. pyxidata* (L.) Hoffm.; *Cladonia gracilis* group (Piercey-Normore *et al.* 2004; Fontaine *et al.* 2010): *Cladonia coniocraea* (Flörke) Spreng., *C. cornuta* (L.) Hoffm., *C. gracilis*; and *Cocciferae* group (Burgaz 2009; Steinová 2009; Osyczka 2011): *Cladonia coccifera* (L.) Willd., and *C. pleurota* (Flörke) Schaer. (Ahti 1980).

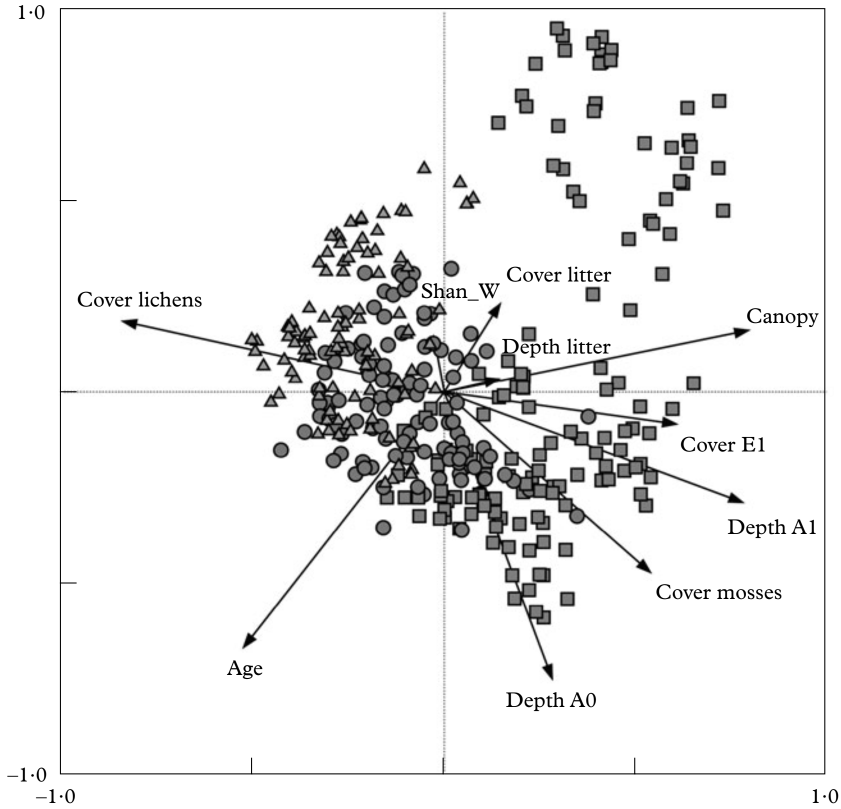

FIG. 2. Ordination diagrams of CCA analysis of 350 micro-samples from dry acidophilous Scots pine forests. ■, managed forests; ●, protected forests; ▲, natural forest from Bory Tucholskie National Park. Eigenvalues: 0·546 on the 1st axis and 0·357 on the 2nd axis.

Results

Results of data analysis show that forest management techniques seriously influence the environmental characteristics of Scots pine forests. These affect the cover of the tree canopy layer, with a considerable resultant negative impact on lichen diversity (Figs 2 & 3). The first, horizontal axis was positively correlated with the cover of mosses, vascular plants and soil depth, and negatively correlated with increasing values of lichen cover. Therefore, the relevés from Bory Tucholskie are clearly grouped on the left-hand side of the diagram. These relevés represent open dry forests which are rich in lichens, especially *Cladonia crispata* (Ach.) Flot., *C. chlorophaea*, *C. gracilis, C. rangiferina, C. scabriuscula* (Delise) Nyl. and *C. stygia* (Fr.) Ruoss. Managed forests, with the occurrence of species such as *Cladonia macilenta* Hoffm. ssp. *macilenta* and *C. pyxidata*, can be distinguished on the right side of the gradient. These forests are characterized by a thicker soil profile, denser canopy, and a less dry environment, which result in higher moss cover. Semi-natural forests occupy their transitional position between the natural and managed forests.

The box and whisker plots (Fig. 4A–H) depict the diversity of cryptogams (mosses and lichens), vascular plants and the frequency of selected geographical elements and life forms within individual forest types. In addition, they indicate the range of values of canopy cover and statistical differences between individual vegetation types. While

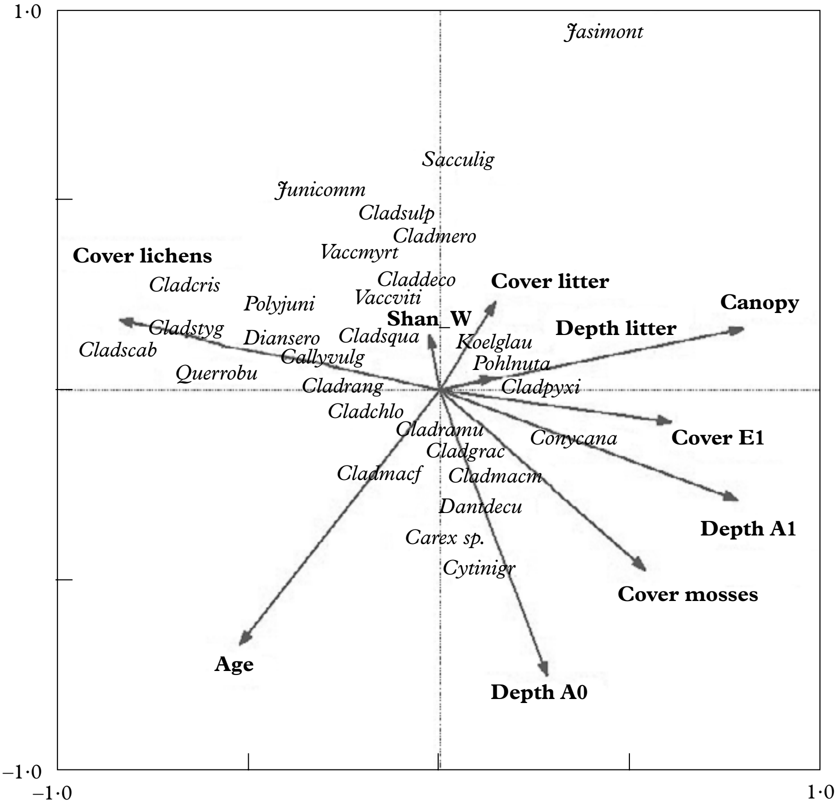

FIG. 3. Ordination diagrams of CCA analysis based on 350 micro-samples.
The abbreviations of species in the diagram are as follows: Jasimont-*Jasione montana,* Sacculig-*Saccomorpha uliginosa,* Junicomm-*Juniperus communis,* Cladsulp-*Cladonia sulphurina,* Cladmero-*Cladonia merochlorophaea,* Vaccmyth-*Vaccinium myrthylus,* Vaccviti-*Vaccinium vitis-idaea,* Claddeco-*Cladonia decorticata,* Cladsqua-*Cladonia squamosa,* *Keolglau-Koeleria glauca,* Pohlnuta-*Pohlia nutans,* *Cladpyxi-Cladonia pyxidata,* Conycana-*Conyza canadensis,* *Cytinigr-Cytisus nigricans,* Carex species, Dantdecu-*Danthoria decumbens,* Cladmacm-*Cladonia macilenta* ssp. *macilenta,* Cladmacf-*Cladonia macilenta* ssp. *floerkeana,* Cladgrac-*Cladonia gracilis,* Cladramu-*Cladonia ramulosa,* Cladchlo-*Cladonia chlorophaea,* Cladrang-*Cladonia rangiferina,* Callvulg-*Calluna vulgaris,* Querrobu-*Quercus robur,* Diansero-*Dianthus serotinus,* Cladstyg-*Cladonia stygia,* Cladscab-*Cladonia scabriuscula,* Polyjuni-*Polytrichum juniperinum,* Cladcris-*Cladonia crispata*

primal dry pine forests are naturally loose and significantly more diverse in lichen species than secondary forests, the managed forests are planted to achieve denser tree formation, and these environmental conditions are therefore more suitable for mosses and some vascular plants.

A significant participation of boreal elements is characteristic in natural *Cladonio-Pinetum* forests because the association is situated mainly in the boreal zone (Fig. 4E). Since fruticose lichens with a branching thallus, such as *Cladonia* sp. and *Cetraria* sp., need a longer period for optimal growth, their occurrence in managed forests is limited by time (Fig. 4G).

The most significant influence on the diversity of lichens was the density of the tree canopy (Figs 4H & 5). Natural and semi-natural dry Scots pine forests are significantly more diverse in lichen species than managed forests, and are naturally loose according to the various age of trees represented there which formed the gaps between the trees.

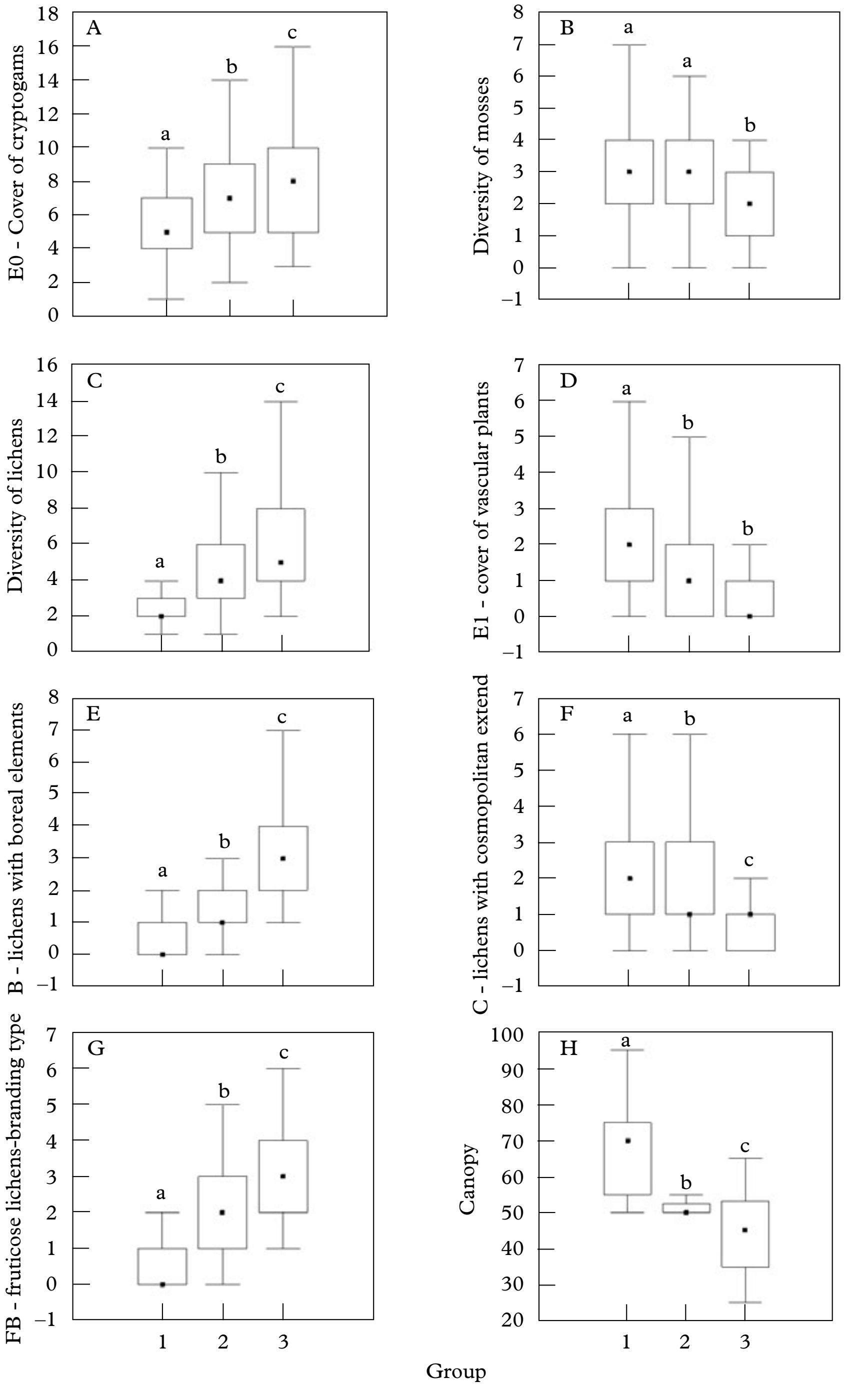

FIG. 4. Diversity of cryptogams (mosses and liverworts), vascular plants, frequency of selected geographical elements and life forms within individual forest types. 1 = managed forests; 2 = protected forests; 3 = Bory Tucholskie National Park. ● median, whiskers represent 25–75% of non-outlier range.

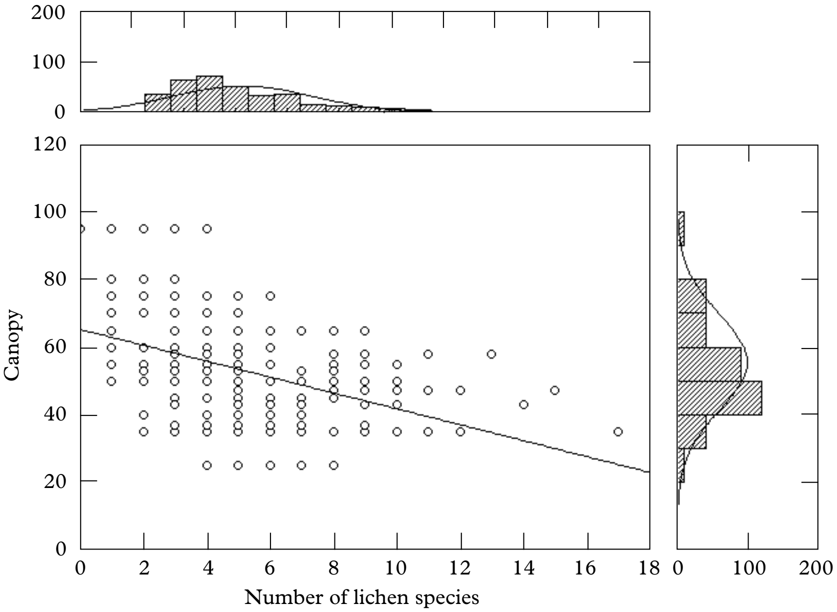

FIG. 5. Relationship between density of tree canopy cover (%) and number of lichen species in acidophilous Scots pine forests. The top and right hand boxes show the distribution of the values of both variables.

Discussion

Lichens and mosses respond differently to the effect of the canopy layer (Figs 4H & 5). Both groups of cryptogams exhibit the ability to acclimatize to a wide range of light and temperature conditions (Canters *et al.* 1991; Sulyma & Coxson 2001; Bruun *et al.* 2006; Dynesius & Zinko 2006). However, the fact that lichens are more common at open sites suggests that lichens and mosses prefer different light environments. The main lichen species occurring at open sites are: *Cladonia arbuscula* (Wallr.) Flot. em. Ruoss ssp. *mitis* (Sandst.) Ruoss, *C. chlorophaea*, *C. coniocraea*, *C. cornuta*, *C. crispata*, *C. furcata* (Huds.) Schrad., *C. merochlorophaea* and *C. rangiferina* in lichen-rich forests on dry acid sand in Estonia (Kösta & Tilk 2008). We observed that *Cladonia crispata, C. rangiferina*, *C. scabriuscula* and *C. stygia* flourish in stands with lower canopy cover, which is typical in natural and semi-natural forests (Fig. 2). *Cladonia rangiferina* is a taxon with the highest ability to increase its cover when the lichen volume increases (Oksanen 1986). While lichens overgrow mosses under conditions of high light and low moisture (Sedia & Ehrenfeld 2003), moss cover increases with increasing canopy cover, an abundance of vascular plants and increased litter accumulation, as illustrated in Fig. 2 (Coxson & Marsh 2001).

However, increased litter accumulation also allows several lichen species to colonize free niches. These include *Cladonia diversa* and *Placynthiella icmalea* (Ach.) Coppins & P. James (Hasse & Daniëls 2006), *Cladonia chlorophaea*, *C. coccifera, C. cornuta* and *C. glauca* Flörke (Magnusson 1982), and also *Cladonia merochlorophaea* and *C. subulata* (Magnusson 1983). Those are mainly lichen cup-forming species which are not typical for *Cladonio-Pinetum* forests, and it was obvious from our study that these form a rather fruticose lichen-branching type (Fig. 4G).

Our study suggests that mosses thrive on soils with a thicker organic layer, that is, an A0 layer (Figs 2 & 3), whereas lichens are prevalent in habitats where there is no developed organic layer. Moreover, lichen mats appear to inhibit the development of such layers (Sedia & Ehrenfeld 2003). Species of the family *Cladoniaceae* are known to produce very low litter input beneath the mats

(Haapasaari 1988), which could result in the absence of vascular plants from lichen-rich forests (Fig. 4B–D). There is also the possibility that patches containing a mixture of *Cladonia* spp. can inhibit the germination or establishment of vascular species, most likely through both chemical and physical processes (Hobbs 1985). Since the presence of an organic layer is crucial for the supply of nutrients, particularly nitrogen (Hyvärinen & Crittenden 1998; Ellis *et al.* 2003; Hauck & Wirth 2010; Hogan *et al.* 2010; Freitag *et al.* 2011), the different effects of lichens and mosses on the accumulation of organic matter may certainly play an important role in the lichen-mosses-vascular plant interactions.

We concur with the theory that the cover of lichens is higher in natural pine forests and semi-natural forests (Lesica *et al.* 1991; Uotila *et al.* 2005), and this is also supported by the results of canonical correspondence analysis (Figs 2 & 3). The most abundant species were the branching types of fruticose lichens forming the mats (Fig. 4G), such as *Cladonia arbuscula* ssp. *mitis*, *C. arbuscula* ssp. *squarrosa*, *C. rangiferina* and *C. stellaris* (Väre *et al.* 1995; Tømmervik *et al.* 2003; Olofsson *et al.* 2010), and management actions negatively affect them. The semi-natural stands were rich in *Cladonia* lichens and dwarf shrubs until tree-canopy closure, while the abundance of mosses was lower in these semi-natural stands (Uotila *et al.* 2005); this situation is clearly depicted in Fig. 2. Väre *et al.* (1995) suggested that it is natural to assume an increase in minute cup lichens, such as *Cladonia* sp., which occurs when the impact of maintenance pressure increases. In our study, this increase is visible in *Cladonia pyxidata* (Fig. 3). The *C. pyxidata* taxon is well noted as an apophyte occurring in anthropogenic stands (Olech 1998), and it is one of the cosmopolitan lichens which can be found on anthropogenic bare soil habitats (Fig. 4F).

Due to forest management, the abundance of grasses increased. A perfect example is *Avenella flexuosa* (L.) Drejer, which is a species commonly prominent after clear-cutting (Uotila *et al.* 2005). On the other hand, *Vaccinium myrtillus* L. disappeared and the abundance of *Vaccinium vitis-idaea* L. and *Pleurozium schreberi* (Brid.) Mitt. decreased rapidly (Nieppola 1992). It is obvious from our study (Fig. 4D) that forest management increases the abundance of vascular plants at the expense of lichen diversity (Fig. 2).

The differences in the biodiversity of lichens between managed and natural forests may not be clearly apparent when these forests are of similar age and microclimatic conditions. This especially involves the presence of similar canopy tree cover, and hence similar light conditions (Esseen *et al.* 1996). An increase in the following species is apparent in stands which are *c.* 100 years old (from 50–150 years): *Cladonia arbuscula* ssp. *mitis*, *C. rangiferina*, *C. stellaris* (Opiz) Pouzar & Vězda and *C. uncialis* (L.) Weber ex F. H. Wigg. (Coxson & Marsh 2001). In contrast, the species *Cladina* sp. and *Cladonia* sp. appear to flourish more frequently in some types of young managed forests (Söderstörm 1988; Glenn *et al.* 1998; Meier *et al.* 2005). This suggests that the management may open up and desiccate the stands, thus resulting in increased lichens on the stands. However, this may happen only where the climax stadium of the pine forests does not belong to the association *Cladonia-Pinetum*, which are naturally dry and contain fewer nutrients. Here, the lichen mats have persisted in xeric sites for more than 300 years, and the limiting factors of soil moisture and temperature have prevented mosses and vascular plants from taking hold (Fig. 4B & D) (Brulisauer *et al.* 1996).

Peterken (1999) suggested several types of forest management which would maintain a forests' natural appearance, and simultaneously retain functional integrity of the ecosystem. These suggestions included 1) maintenance of the continuity of young-growth, 2) retention of old trees in stands and an increase in the volume of dead wood, and 3) application of additional mixed planting to enhance natural regeneration. In terms of our research here, we consider that Peterken's (1999) concept of natural forestry is extremely advisable. As we have suggested, high insolation is a key environmental factor, characteristic of natural forests of the *Cladonio-Pinetum* association, and therefore the sparse character of the forest as a result of natural forestry is important. This has been proven in the semi-natural forests where open gaps occur during natural regeneration. Finally, it is important for the *Cladonio-Pinetum* association, which occurs on poor acidic sands, that tree growth is inhibited and that the tree canopy is not closed.

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References

Ahti, T. (1966) Correlation of the chemical and morphological characters in *Cladonia chlorophaea* and allied lichens. *Annales Botanici Fennici* **3:** 380–390.

Ahti, T. (1980) Nomenclatural notes on *Cladonia* species. *Lichenologist* **12:** 125–133.

Barkman, J. J., Doing, H. & Segal, S. (1964) Kritische Bemerkungen und Vorschläge zur quantitativen Vegetationsanalyse. *Acta Botanica Neerlandica* **13:** 394–419.

Bielczyk, U., Lackovičová, A., Farkas, E., Lökös, L., Liška, J., Breuss, O. & Kondratyuk, S. Y. (2004) *Checklist of Lichens of the Western Carpathians*. Kraków: W. Szafer Institute of Botany, Polish Academy of Sciences.

Bouda, F. (2009) *Lišejníky reliktních borů*. (*Lichens of the relict pine forests*). M. Sc. thesis, Charles University, Prague.

Braun-Blanquet, J. (1964) *Pflanzensoziologie* (*3ème édition*). Wien, New York: Springer-Verlag.

Brodo, I. M. (1961) A study of lichen ecology in Central Long Island, New York. *American Midland Naturalist* **65:** 290–310.

Brulisauer, A. R., Bradfield, G. E. & Maze, J. (1996) Quantifying organizational change after fire in lodgepole pine forest understorey. *Canadian Journal of Botany* **74:** 1773–1782.

Bruun, H. H., Moen, J., Virtanen, R., Grytnes, J-A., Oksanen, L. & Angerbjörn, A. (2006) Effects of altitude and topography on species richness of vascular plants, bryophytes and lichens in alpine communities. *Journal of Vegetation Science* **17:** 37–46.

Burgaz, A. R. (2009) El género *Cladonia* en la península Ibérica. Supergrupo *Cocciferae*. *Botanica Complutensis* **33:** 9–28.

Canters, K. J., Schöller, H., Ott, S. & Jahns H. M. (1991) Microclimatic influences on lichen distribution and community development. *Lichenologist* **23:** 237–252.

Celiński, F., Wika, S. & Parusel, J. B. (1997) Czerwona lista zbiorowisk roślinnych Górnego Śląska. *Raporty, Opinie* **2:** 38–68.

Coxson, D. S. & Marsh, J. (2001) Lichen chronosequences (postfire and postharvest) in lodgepole pine (*Pinus contorta*) forests of northern interior British Columbia. *Canadian Journal of Botany* **79:** 1449–1464.

Crittenden, P. D. (1991) Ecological significance of necromass production in mat-forming lichens. *Lichenologist* **23:** 323–331.

Crittenden, P. D. (2000) Aspects of the ecology of mat-forming lichens. *Rangifer* **20:** 127–139.

Danielewicz, W. & Pawlaczyk, P. (2004) Śródlądowy bór chrobotkowy. In *Poradniki Ochrony Siedlisk i Gatunków Natura 2000 – Podręcznik Metodyczny. Tom 5. Lasy i bory.* (W. Herbich, ed.): 289–296. Warszawa: Ministerstwo Środowiska.

Daniëls, F. J. A. (1993) Succession in lichen vegetation on Scots pine stumps. *Phytocoenologia* **23:** 619–623.

Dynesius, M. & Zinko, U. (2006) Species richness correlations among primary producers in boreal forests. *Diversity and Distributions* **12:** 703–713.

Ellenberg, H. (1988) *Vegetation Ecology of Central Europe.* Cambridge: Cambridge University Press.

Ellis, C. J., Crittenden, P. D., Scrimgeour, C. M. & Ashcroft, C. (2003) The natural abundance of ^{15}N in mat-forming lichens. *Oecologia* **136:** 115–123.

Emmer, I. M. & Sevink, J. (1994) Temporal and vertical changes in the humus form profile during a primary succession of *Pinus sylvestris. Plant and Soil* **167:** 281–295.

Ermakov, N. & Morozova, O. (2011) Syntaxonomical survey of boreal oligotrophic pine forests in northern Europe and Western Siberia. *Applied Vegetation Science* **14:** 524–536.

Esseen, P-A., Renhorn, K-E. & Pettersson, R. B. (1996) Epiphytic lichen biomass in managed and old-growth boreal forests: effect of branch quality. *Ecological Applications* **6:** 228–238.

Fałtynowicz, W. (1983) Zmiany biomasy runa Boru Chrobotkowego (*Cladonio-Pinetum* Juraszek 1928) pod wpływem nawożenia mineralnego doniesielnie naukowe – Changes in the ground cover biomass of a *Cladonia*-pine forest (*Cladonio-Pinetum* Juraszek 1928) after mineral fertilization (Research contribution). Zeszyty naukowe wydziału biologii i nauk o ziemi uniwersytetu gdańskiego. *Biologia* **4:** 109–121.

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

Ferry, B. W. & Pickering, M. (1989) Studies on the *Cladonia chlorophaea* complex at Dungeness, England. *Lichenologist* **21:** 67–77.

FMP (Forest Management Plans) (2005) *Department of Forest Management.* Military Forests and Estates of the Slovak Republic, state enterprise. Malacky: Branch plant Malacky Press.

Fontaine, K. M., Ahti, T. & Piercey-Normore, M. D. (2010) Convergent evolution in *Cladonia gracilis* and allies. *Lichenologist* **42:** 323–338.

Freitag, S., Hogan, E. J., Crittenden, P. D., Allison, G. G. & Thain, S. C. (2011) Alterations in the metabolic fingerprint of *Cladonia portentosa* in response to atmospheric nitrogen deposition. *Physiologia Plantarum* **143:** 107–114.

Futák, J. (1980) Fytogeografické členenie 1: 1 000 000. In *Rastlinstvo, živočístvo a fenológia: Atlas SSR VII* (P. Plesník, ed.): 88. Bratislava: Vydavatel'stvo Slovenskej Akadémĕ Vied.

Glenn, M. G., Cole, M. S., Webb, S. L. & Hale, C. M. (1998) Corticolous lichens and bryophytes: preliminary surveys of old growth and managed northern hardwood stands in Minnesota. In *Lichenographia Thomsoniana* (M. G. Glenn, R. C. Harris, R. Ring & M. S. Cole, eds.): 407–421. Ithaca, New York: Mycotaxon Ltd.

Haapasaari, M. (1988) The oligotrophic heath vegetation of northern Fennoscandia and its zonation. *Acta Botanica Fennica* **135:** 1–219.

Hammer, S. (1995) *The Biogeography and Ecology of Species in the Lichen Genus* Cladonia *in the Columbia River Basin.* Boston: Boston University Press.

Hasse, T. & Daniëls, F. J. A. (2006) Species responses to experimentally induced habitat changes in a *Corynephorus* grassland. *Journal of Vegetation Science* **17:** 135–146.

Hauck, M. & Wirth, V. (2010) Preference of lichens for shady habitats is correlated with intolerance to high nitrogen levels. *Lichenologist* **42:** 475–484.

Hegedüšová, K., Škodová, I. & Mikuška, B. (2004) Boriny a travobilinné porasty Borskej nížiny – Pine forests and grassland vegetation of the Borska nížina lowland. *Bulletin Slovenskej Botanickej Spolocnosti* **10:** 51–56.

Heinken, T. (2007) *Sand- und Silikat-Kiefernwälder (Dicrano-Pinion) in Deutschland – Gliederungskonzept und Ökologie.* Potsdam: University of Potsdam Press.

Heinken, T. & Zippel, E. (1999) Die Sand-Kiefernwälder (*Dicrano-Pinion*) im norddeutschen Tiefland: syntaxonomische, standörtliche und geographische Gliederung. *Tuexenia* **19:** 55–106.

Hennekens, S. M. & Schaminée, J. H. J. (2001) TURBOVEG, a comprehensive data base management system for vegetation data. *Journal of Vegetation Science* **12:** 589–591.

Hennipman, E., Sipman, H. J. M. & Vijsma E. (1978) *De Nederlandse Cladonia's (Lichenes).* Zeist: KNNV.

Hobbs, R. J. (1985) The persistence of *Cladonia* patches in closed heathland stands. *Lichenologist* **17:** 103–109.

Hogan, E. J., Minnullina, G., Sheppard, L. J., Leith, I. D. & Crittenden, P. D. (2010) Response of phosphomonoesterase activity in the lichen *Cladonia portentosa* to nitrogen and phosporus enrichment in a field manipulation experiment. *New Phytologist* **186:** 926–933.

Husová, M. & Andresová, J. (1992) Das *Cladonio rangiferinae-Pinetum sylvestris* des Landschaftsschutzgebietes Křivoklátsko (Mittelböhmen) und seine Stellung im phytozönologischen System. *Folia Geobotanica et Phytotaxonomica* **27:** 357–386.

Hyvärinen, M. & Crittenden, P. D. (1998) Relationships between atmospheric nitrogen inputs and the vertical nitrogen and phosphorus concentration gradients in the lichen *Cladonia portentosa. New Phytologist* **140:** 519–530.

Juraszek, H. (1928) *Pflanzensoziologische Studien über die Dunen bei Warschau.* Warszawa: Uniwersytet Warszawski. *Bulletin de l'Académie polonaise des sciences et des lettres, Classe des sciences mathématiques et naturelles, Série B* **1927:** 565–610.

Kabucis, I., Bambe, B., Eņğele, L., Laime, B., Pakalme, M., Smaļinskis, J. & Urtáns, A. (2000) *Biotopu rokasgrámata. Eiropas Savieníbas aizsargájamie biotope Latvijá.* Riga: Latvijas Dabas Fonds Press.

Kalivodová, E., Bedrna, Z., Bulánķová, E., David, S., Ďugová, O., Fedor, P., Fenďa, P., Gajdoš, P., Gavlas, V., Kalivoda, H., *et al.* (2008) *Flóra a Fauna Viatych Pieskov Slovenska.* Bratislava: VEDA Press.

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

Kolbek, J. & Chytrý, M. (2010) L8 Suché Bory – dry pine forests. In *Katalog Biotopů České Republiky. Ed. 2* (M. Chytrý, T. Kučera, M. Kočí, V. Grulich & P. Lustyk, eds.): 331–334. Praha: Agentura ochrany přírody a krajiny ČR Press.

Kollár, J., Balkovič, J., Mazúrová, A. & Šimonovič, V. (2011) Phytocoenological and production evaluation of the natural oak and secondary pine forests of the Borská nížina lowland. *Ekológia* **30:** 369–380.

Kösta, H. & Tilk, M. (2008) Variability of bryophytes and lichens on a forested coastal dune Tõotusemägi in Southwestern Estonia. *Forestry Studies/Metsanduslikud Uurimused* **49:** 71–80.

Kotelko, R. & Piercey-Normore, M. D. (2010) *Cladonia pyxidata* and *C. pocillum*; genetic evidence to regard them as conspecific. *Mycologia* **102:** 534–545.

Krippel, E. (1965) Posglaciálny vývoj lesov na Záhorskej nížine. *Biologické Práce* **11**(3)**:** 5–99.

Krippelová, T. & Krippel, E. (1956) *Vegetačné Pomery Záhoria. I. Viate Piesky.* Bratislava: VEGA Press.

Kučera, T., Peksa, O. & Košnar, J. (2006) K problematice původu acidofilních borů na Třeboňsku – About the origin of acidophilous Scots Pine forests in the Třeboňsko Basin (South Bohemia). In *Biotopy a Jejich Vegetační Interpretace v ČR* (T. Kučera & J. Navrátilová, eds): 91–106. Praha: Česká Botanická Společnost.

Lesica, P., McCune, B., Cooper, S V. & Hong, W. S. (1991) Differences in lichen and bryophyte communities between old-growth and managed second growth forests in Swan Valley, Montana. *Canadian Journal of Botany* **69:** 1745–1755.

Lipnicki, L. (2003) *Porosty Borów Tucholskich: Przewodnik do oznaczania gatunków listkowatych i krzaczkowatych.* Charzykowy: Park Narodowy 'Bory Tucholskie'.

Magnusson, M. (1982) Composition and succession of lichen communities in an inner coastal dune area in southern Sweden. *Lichenologist* **14:** 153–163.

Magnusson, M. (1983) Composition and succession of bryophytes and lichens in an outer coastal dune area in Southern Sweden. *Cryptogamie, Bryologie Lichénologie* **4:** 335–355.

Marhold, K. & Hindák, F. (1998) *Checklist of Non-vascular and Vascular Plants of Slovakia.* Bratislava: VEDA Press.

Matuszkiewicz, W. & Matuszkiewicz, J. M. (1973) Przegląd fitosocjologicyny zbiorowsk leśnych Polski. Cz. 2. Bory sosnowe. *Phytocoenosis* **2**(4)**:** 273–356.

Matuszkiewicz, W. & Matuszkiewicz, J. M. (1996) *Przegląd fitosocjologiczny zbiorowisk leśnych Polski (Synteza). Phytocoenosis* **8:** 1–79.

Meier, E., Paal, J., Liira, J. & Jüriado, I. (2005) Influence of tree stand age and management on the species diversity in Estonian eutrophic alvar and boreo-nemoral *Pinus sylvestris* forests. *Scandinavian Journal of Forest Research* **20:** 135–144.

Mikuška, B. (2005) Syntaxonómia dubovo-borovicových kultúrnych lesov na Borskej nížine – Syntaxonomy of the cultural oak-pine forests in the Borská nížina Lowland. *Bulletin Slovenskej Botanickej Spolocnosti* **27:** 157–169.

Nieppola, J. (1992) Long-term vegetation changes in stands of *Pinus sylvestris* in southern Finland. *Journal of Vegetation Science* **3:** 475–484.

Oksanen, J. (1986) Succession, dominance and diversity in lichen-rich pine forest vegetation in Finland. *Holarctic Ecology* **9:** 261–266.

Olech, M. (1998) Apophytes in the lichen flora of Poland. *Phytocoenosis* **10:** 251–255.

Olofsson, J., Moen, J. & Østlund, L. (2010) Effects of reindeer on boreal forest floor vegetation: does grazing cause vegetation state transitions. *Basic and Applied Ecology* **11:** 550–557.

Osyczka, P. (2011) The genus *Cladonia*, group *Cocciferae*, in Poland. *Herzogia* **24:** 209–227.

Peterken, G. F. (1999) Applying natural forestry concepts in an intensively managed landscape. *Global Ecology Biogeography* **8:** 321–328.

Piercey-Normore, M. D., Hausner, G. & Gibb, E. A. (2004) Group I intron-like insertions in SSU rDNA of *Cladonia gracilis* and *C. rangiferina*. *Lichenologist* **36:** 365–380.

Pino-Bodas, R., Burgaz, A. R., Martín, M. P. & Lumbsch, H. T. (2012) Species delimitations in the *Cladonia cariosa* group (*Cladoniaceae,* Ascomycota). *Lichenologist* **44:** 121–135.

Prieditis, N. (2002) Evaluation frameworks and conservation system of Latvian forests. *Biodiversity and Conservation* **11:** 1361–1375.

Ptačovský, K. (1959) Poznámky ke květeně bratislavského okolí. *Biologické Práce Slovenskej Akadémie Vied* **5:** 88.

Ružička, M. (1953) Poznámky k histórii a terajšiemu stavu borovicových lesov na Záhorskej nížine. *Biologia* **9:** 210–218.

Ružička, M. (1960*a*) *Geobotanické pomery lesov v oblasti pieskov na Záhorskej nížine.* Ph.D theis, Slovak Academy of Science, Bratislava.

Ružička, M. (1960*b*) Pôdne ekologické pomery lesných spoločenstiev v oblasti viatych pieskov na Záhorskej nížine. *Biologické Práce Slovenskej Akadémie Vied* **6:** 7–88.

Ružička, M. (1960*c*) Prehľad rastlinných spoločenstiev na Záhorskej nížine. *Biologia* **15:** 653–662.

Sedia, E. G. & Ehrenfeld, J. G. (2003) Lichens and mosses promote alternate stable plant communities in the New Jersey Pinelands. *Oikos* **100:** 447–458.

Söderström, L. (1988) The occurrence of epixylic bryophyte and lichen species in an old natural and managed forest stand in northeast Sweden. *Biological Conservation* **45:** 169–178.

Sokołowski, A. W. (1965) Zespoły leśne nadleśnictwa Laska w Borach Tucholskich – forest associations of Laska Forestry District in Bory Tucholskie (Tuchola Forest). *Fragmenta Floristica et Geobotanica* **11:** 97–119.

Solon, J. (2003) Scots pine forests of the *Vaccinio-piceetea* class in Europe: forest sites studied. *Polish Journal of Ecology* **51:** 421–439.

Stefańska-Krzaczek, E. (2010) 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.

Steinová, J. (2009) *Revize skupiny* Cladonia coccifera *ve střední Evropě s důrazem na území ČR*. M. Sc. thesis, Charles University, Prague.

Stenroos, S. K. & DePriest, P. T. (1998) SSU RDNA phylogeny of *Cladoniiform* lichens. *American Journal of Botany* **85:** 1548–1559.

Sulyma, R. & Coxson, D. S. (2001) Microsite displacement of terrestrial lichens by feather moss mats in late seral pine-lichen woodlands of North-central British Columbia. *Bryologist* **104:** 505–516.

Szczygielski, M. (2007) Zmiany charakterystyki fitosocjologicznej borów świeżych Peucedano-Pinetum w Puszczach: Piskiej i Augustowskiej na przestrzeni 50 lat. *Studia i Materiały Centrum Edukacji Przyrodniczo-Leśnej* **9:** 153–167.

Šomšák, L., Šimonovič, V. & Kollár, J. (2004) Phytocoenoses of pine forests in the central part of Záhorská nížina Lowland. *Biologia* **59:** 101–115.

Šomšáková, V. (1988) Viazanosť machov na borovicové porasty viatych pieskov Záhorskej nížiny. *Acta Facultatis Rerum Naturalium Universitatis Comenianae, Botanica* **36:** 27–58.

ter Braak, C. J. F. & Šmilauer, P. (2002) *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination.* Ithaca, New York: Microcomputer Power Press.

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

Tømmervik, H., Høgda, K. A. & Solheim, I. (2003) Monitoring vegetation changes in Pasvik (Norway) and Pechenga in Kola Peninsula (Russia) using multi-temporal Landsat MSS/TM data. *Remote Sensing of Environment* **85:** 370–388.

Uotila, A., Hotanen, J.-P. & Kouki, J. (2005) Succession of understorey vegetation in managed and semi-natural Scots pine forests in eastern Finland and Russian Karelia. *Canadian Journal of Forest Research* **35:** 1422–1441.

Valachovič, M. (2005) Lesné biotopy Borskej nížiny. *Záhorie* **3:** 32–38.

van Tol, G., Dobben, H. F., Schmidt, P. & Klap, J. M. (1998) Biodiversity of Dutch forest ecosystems as affected by receding groundwater levels and atmospheric deposition. *Biodiversity and Conservation* **7:** 221–228.

Väre, H., Ohtonen, R. & Oksanen, J. (1995) Effects of reindeer grazing on understorey vegetation in dry *Pinus sylvestris* forests. *Journal of Vegetation Science* **6:** 523–530.

Westhoff, V. & van der Maarel, E. (1978) The Braun-Blanquet approach. In *Classification of Plant Communities* (R. H. Whittaker, ed.): 287–399. The Hague: Dr W. Junk Publishers.

Woś, A. (1999) *Klimat Polski.* Warszawa: Wydawnictwo Naukowe PWN Press.

Zobel, K., Zobel, M. & Peet, R. K. (1993) Change in pattern diversity during secondary succession in Estonian forests. *Journal of Vegetation Science* **4:** 489–498.