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ECOLOGICAL ASSESSMENT OF THE CHANGES IN SPECIES COMPOSITION OF MOUNTAIN SPRUCE FORESTS' BRYOPHYTE LAYER IN THE KARKONOSZE MTS AFTER HUGE DIEBACK IN 1970-1980

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ABSTRACT. General ecological demands of bryophytes forming forest floor in two stages of tree stands development (healthy in 1967 and dead in 2007) of mountain spruce forests in the Karkonosze Mts were compared to estimate what changes in an ecological spectrum of the forest floor's bryoflora appeared after spruce stands diedback. Bryo-floristical data for comparative analyses were compiled from the literature (phytosociological tables, descriptions and list of the species stations). Bryophytes general ecological characterization was determined on the basis of Dierssen's paper. Analysis showed that the species composition and richness of bryophytes forming forest floor changed visibly. The total number of species increased by about 50% but 30% of the previous bryoflora disappeared. As it was expected the number of colonists (especially pioneer colonists sensu During 1992) and species preferring drier habitats has increased in died forests. However the highest increase in species number showed bryophytes of rather wide ecological amplitudes. The share and number of stenotopic species have not changed considerably: only one obligatory epixylic species and one xerophyte appeared; the number of photophytes increased insignificantly, from four to seven. Some species related to humus and/or rotten wood became more frequent.

KEY WORDS: bryophytes, species composition changes, plant's response to forest dieback, mountain spruce forests, Karkonosze Mts

INTRODUCTION

In 1970-1980 spruce forests in the Polish part of the Karkonosze Mts suffered huge dieback due to so called "spiral disease" caused mainly by air and soil pollution. According to Dunajski (2004, 2007) during that period 75% of forests of the Karkonosze National Park (KNP) which in 1970s were in optimal stage of spruce stand development died. This author estimated that presently only 30% of the upper mountain forest belt area in KNP is covered with forests of well developed tree crowns.

It can be assumed that such drastic changes in forest structure might have influenced bryophyte species composition and frequency in forest floor, because just tree stands create an unique microclimate conditions inside forest communities. A density of tree canopy decides of the light amount reaching the forest floor as well as of air humidity and moisture degree of substratum so the tree crowns disintegration changes ecological conditions inside a forest considerably. One can expect also an increase of the litter and decayed wood fragments' amount what would promote expansion of epixylous and humicolous bryophytes.

The questions to solve were risen: how did bryophytes respond to changes in forest structure? Has bryophyte species composition of forest floor changed visibly after dieback of spruce stands? What changes in an ecological spectrum of the died forests bryoflora appeared? To answer these questions general ecological demands of bryophytes forming forest floor in two stages of tree stands development (healthy and dead) of mountain spruce forests in the Karkonosze Mts were compared. The analyses' results and conclusions are presented in the paper.

MATERIALS AND METHODS

Bryo-floristical data for comparative analyses were obtained from literature: bryophyte species composition of the healthy spruce stands was compiled on the basis of synthetic phytosociological tables and descriptions of *Calamagrostio villosae-Piceetum* Schlüter 1969 (= *Piceetum hercynicum* Tx. 1937) in KNP elaborated by Matuszkiewicz and Matuszkiewicz (1967) while bryoflora of died spruce stands was based on recently published data by Dunajski and Fudali (2007). Both in 1967 and

2007 bryophytes were recognized for phytosociological relevés, so these data concern exclusively liverworts and mosses picked up from the ground, naked or covered with humus, litter or another organic matter. The scope of the research compared was also similar; it was carried out on the whole area of the Karkonosze National Park's upper forest belt – data concerning bryophytes of spruce stands before dieback were reported in 32 phytosociological relevés (Matuszkiewicz and Matuszkiewicz 1967) while data concerning the bryophyte layer species composition in died spruce stands were gathered from 35 research plots (Dunajski and Fudali 2007).

General ecological demands of bryophytes in relation to light moisture and substratum reaction and type were determined on the basis of Dierssen's ecological characterization of European bryophytes (Dierssen 2001), classification of bryophyte growth types as suggested by Gimingham and Birse (1957) and assignation to life-history strategy (sensu During 1992) as Dierssen (2001) proposed. Nomenclature of liverworts follows Szweykowski (2006), mosses by Ochyra et al. (2003).

RESULTS AND DISCUSSION

Comparison of bryophyte species richness and composition between forests with healthy tree stands (1967) and died trees (2007)

Differences in bryophyte species number and composition between both stages of the tree stand condition are visible (Table 1): in forests of healthy tree crowns the number of 33 species (including 11 liverworts) was reported while in forests of died trees – 48 (15). 21 species occurred in both stages and they seem to be a persistent element of forest floor in these habitats. Some of them: *Barbilophozia lycopodioides*, *Cephalozia bicuspidata*, *Dicranodontium denudatum*, *Plagiofthecium curvifolium*, *Sphagnum capillifolium* and *S. girgensohnii* has shown increase of the localities number in the forests with died tree stands.

Among species reported for the first time in 2007 ("newcomers") three had not the species status in 1967: *Calypogeia integristipula* was not separated from *C. neesiana* (Frahm and Frey 1983), *Rhizomnium magnifolium* was treated as variety of *R. punctatum* and *Rhytidiadelphus subpinnatus* as subspecies of *R. squarrosus* (Ochyra et al. 2003). Is highly probable that records of *Calypogeia neesiana*, *Rhizomnium punctatum* and *Rhytidiadelphus squarrosus* from the paper by Matuszkiewicz and Matuszkiewicz (1967) refer to currently distinguished as separate species *Calypogeia integristipula*, *Rhizomnium magnifolium* and *Rhytidiadelphus subpinnatus*. Because of these doubts in further analysis these six species were omitted. Thus the number of species noted only in one of the stages compared amounted 33 (9; 24 respectively).

Ecological character of species not confirmed in 2007 and "newcomers"

Among nine species not confirmed in 2007 dominate perennials (8 species) preferring wet or well drained

Table 1. General ecological character (according to Dierssen 2001) of liverworts and mosses occurring in the forest floor in healthy and died three stands of mountain spruce forests in Karkonosze Mts

Healthy spruce stands (1967)	Died spruce stands (2007)	Name of species	Growth type	Life-history strategy	General ecological scale of species (according to Dierssen 2001) in respect to:			
					substratum type	substrate acidity	moisture	light
1	2	3	4	5	6	7	8	9
LIVERWOTS								
*	*	*Anastrepta orcadensis*	O	p	HUM	c ac	m H	c Sc-m Ph
*	*	*Barbilophozia floerkei*	P	ps	HUM	h ac-sub	m H-M	c Sc-m Ph
*	*	*Calypogeia azurea*	P	c	HUM, P	h-c ac	m H-M	c Sc
*(III)	*!	*Cephalozia bicuspidata*	P	cp	HUM, DW, P	h-m ac(sub)	c H-M	m Sc-m Ph
*	*	*Lepidozia reptans*	P	cp	DL, HUM	h-m ac	M	c Sc-m Ph
*	*	*Mylia taylori*	P	p	R, P	c-m ac(sub)	h-m H	c Sc-h Ph
*	*	*Ptilidium ciliare*	P	l	HUM, LIT, DW	h-m ac(sub)	c H-c X	m-h Ph
*(III)	*!	*Barbilophozia lycopodioides*	P	pc	HUM	h ac-sub(b)	M	m Sc-m Ph
*	.	*Bazzania trilobata*	P	pc	HUM (more type), DW	h ac	c H-M	c Sc
*	.	*Calypogeia muelleriana*	P	c	HUM, DL	h-m ac	M	c Sc-m Ph
.	*	*Barbilophozia attenuata*	P	cp	DL, HUM	h ac	m H-M	c Sc-m Ph
.	*	*Barbilophozia hatcheri*	P	cp	HUM	h-m ac	M-m X	m Sc-c Ph
.	*	*Blepharostoma trichophyllum*	P	c	HUM, DW	c ac-sub	M	h Sc-c Ph
.	*	*Lophocolea heterophylla*	P	cp	DW, TRUNK, R	c ac-sub	m H-M	h-c Sc
.	*	*Lophozia sudetica*	P	c	MIN, R	h ac-sub	m H-m X	m Sc-h Ph

1	2	3	4	5	6	7	8	9
.	*	*Lophozia ventricosa*	P	cp	HUM, DL, P	c-m ac	m H-M	c Sc-h Ph
?	*!	*Calypogeia integristipula* (= *C. neesiana* var. *meylanii*)	P	c	HUM, DL, P	h-c ac	c H-M	h Sc
(?*)	.	*Calypogeia neesiana*	P	c	HUM	h ac-sub	m H-M	h Sc-m Ph
MOSSES								
*(V)	*!	*Buckiella undulata*	P	pc	HUM (mor type)	h-m ac	H	c Sc-m Ph
*	*!	*Dicranodontium denudatum*	O	pc	HUM, DW	h-c ac	m H-M	m Sc-m Ph
*(V)	*!	*Dicranum scoparium*	O	pc	HUM, DW, R, TRUNK	h-m ac(sub)	m H-M	c Sc-c Ph
*(III)	*!	*Plagiothecium curvifolium*	P	pc	HUM (mor type), LIT, DW	c-m ac	m H-M	h Sc-m Ph
*(III)	*	*Pleurozium schreberi*	P	pc	HUM	c ac(sub)	M	c Sc-m Ph
*(V)	*!	*Polytrichastrum formosum*	O	pc	HUM	h-c ac	M	m Sc-m Ph
*(V-II)	*!	*Polytrichum commune*	O	pc	HUM	h-m ac(sub)	c H-M	m Sc-h Ph
*	*	*Sciuro-hypnum starkei*	P	ps	HUM, DW	c ac-sub	m H-M	m-h Ph
*(III)	*!	*Sphagnum capillifolium*	O	l	P (poor fens)	h-m ac(sub)	m H-M	m Sc-m Ph
*	*	*Rhytidiadelphus loreus*	P-O	pc	MIN, R, DL	h-m ac	m H-M	m Sc-m Ph
*(III)	*!	*Sphagnum girgensohnii*	O	l	P (coniferous woodlands)	h-m ac	m H	m Sc-m Ph
*	*	*Sphagnum squarrosum*	O	l	P (minerotropic fens)	c ac-sub	h-c H	m Sc-h Ph
*	*	*Straminergon stramineum*	O	pc	among *Sphagnum*	c-m ac(sub)	h-m H	m-h Ph
*	.	*Dicranum fuscescens*	O	pc	HUM, TB, DW	h-m ac(sub)	M- m X	m Sc-c Ph
*	.	*Hylocomiastrum umbratum*	P	pc	R	m ac	m H-M	c Sc-m Ph
*(IV-III)	.	*Hylocomium splendens*	P	pc	MIN	h ac-sub	M	c Sc-m Ph
*	.	*Mnium hornum*	O	l	HUM, DL, MIN, TB	c-m ac	h H-M	Sc-m Ph
*	.	*Rhytidiadelphus triquetrus*	P-O	pc	MIN	m ac-sub	m H- m X	m Sc-c Ph
*	.	*Sphagnum magellanicum*	O	l	P (poor fens)	m ac-sub	m H	m Sc-m Ph
*	.	*Thuidium tamariscinum*	P	p	MIN, DL	m ac-sub	M	c-m Sc
.	*	*Cynodontium polycarpon*	O	c	HUM	h ac	M-c X	m Sc
.	*	*Dicranella cerviculata*	O	c	HUM, DW, MIN	c ac(sub)	m H-M	m Sc-c Ph
.	*	*Dicranella heteromalla*	O	c	HUM, TB, DW, MIN	h-m ac(sub)	M	m Sc-m Ph
.	*	*Kiaeria blytii*	O	cp	R	c ac	M	m Ph
.	*	*Orthodicranum montanum*	O	pc	TRUNK, DW, R	c-m ac(sub)	M-m X	c Sc-c Ph
.	*	*Orthodicranum tauricum*	O	pc	DW, TB, TRUNK, R	c ac	M-m X	m Sc-m Ph
.	*	*Plagiothecium cavifolium*	P	ps	CLAY, HUM, ROOTS	c ac-sub	m H-M	m Ph
.	*	*Plagiothecium denticulatum*	P	pc	HUM, DW	c-m ac(sub)	m H-M	m Sc-m Ph
.	*	*Plagiothecium laetum*	P	ps	HUM, TB, DW	c-m ac	M	m Sc
.	*	*Plagiothecium platyphyllum*	P	pc	MIN, R	m ac-sub	c H	c Sc-m Ph
.	*	*Pohlia nutans*	O	cp	MIN, TB, DW	h-m ac-sub	m H-m X	m Sc-h Ph
.	*	*Pohlia sphagnicola* (cfr.)	O	pc	among *Sphagnum*	h ac	m H	h Ph
.	*	*Polytrichastrum alpinum*	O	pc	MIN, R, ROOTS	h ac-sub	m H-M	m Sc-m Ph
.	*	*Polytrichum juniperinum*	O	ps	MIN	h-m ac(sub)	m-c X	h Ph
.	*	*Polytrichum pallidisetum*	O	ps	HUM	h ac	m H-M	m Sc-c Ph

1	2	3	4	5	6	7	8	9
.	*	*Sphagnum fimbriatum*	O	l	P (boggy woodlands)	h ac-sub	m H-M	c Sc-m Ph
.	*	*Sphagnum riparium*	O	l	P (oligotrophic fens)	h-m ac	h-c H	m Sc-h Ph
.	*!	*Tetraphis pellucida*	O	cp	DW	c ac	m H-M	h-c Sc
?	*	*Rhizomnium magnifolium* (= *R. punctatum* var. *elatum*)	O	l	R	m ac-sub	h-c H	m Sc
(?*)	.	*Rhizomnium punctatum*	O	l	R, DW, MIN	c ac-sub	c-m H	c-h Sc
?	*	*Rhytidiadelphus subpinnatus* (= *R. squarrosus* subsp. *calvescens*)	P-O	pc	MIN	m ac	m H-M	m Sc-m Ph
(?*)	.	*Rhytidiadelphus squarrosus*	P-O	pc	MIN	m ac-sub	M	m Sc-m Ph
33	48	....	...	...	....	....	....	....

Explanation of abbreviations: (*) – species was reported, (.) – species was not reported, (?) – species which taxonomical status changed during period studied and they were omitted in analyses of ecological requirements, (III, V) – grade of the phytosociological constancy, (!) – occurred frequently; growth type: O – orthotropic, P – plagiotropic; life history strategy: c – colonist, cp – pioneer colonist, l – long lived shuttle, p – perennial, pc – competitive perennial, ps – stress tolerant perennial; substratum type: DL – decayed logs, DW – pieces of decayed wood, HUM – humus layer covering soil or rocks, LIT – coniferous or ferns litter, MIN – mineral soil, P – peat, R – rock, TB – tree bases, TRUNK – tree trunks; reaction: c ac – considerably acidophilous (pH 4.1-4.8), h ac – highly acidophilous (pH 3.4-4.0), m ac – moderately acidophilous (pH 4.9-5.6), sub – subneutral (pH 5.7-7.5); moisture: c H – considerably wet, h H – very wet, m H – moderately wet, M – well drained (mesophytic), m X – moderately dry, c X – considerably dry; light: c Sc – considerably shaded, m Sc – moderately shaded, m Ph – moderately illuminated, c Ph – considerably illuminated, h Ph – in full light.

habitats (7) (Table 1). In relation to light requirements the most (8) are euryphotophytes tolerated mainly shaded to moderate light habitats (6) and only two of them are recognized as obligatory sciophytes. With respect to the substratum reaction's requirements five of them are eurytopic species of a rather wide amplitude (from acid to subneutral habitats) while the rest are acidophilous. They show differentiated preferences to substratum type and incidence of polysubstrata species was rather insignificant (2). Two species, *Hylocomium splendens* and *Thuidium tamariscinum*, are considered to be sensitive to atmospheric pollutions (Dierssen 2001).

With respect to 24 "newcomers" the analysis of their ecological character show similar share of colonists and perennials (12:12). Regarding moisture degree requirements a dominance of species preferring waterlogged and well drained habitats is marked (18-72%) and only one obligatory xerophyte was noted. Other species are eurytopic in relation to the habitat moisture with amplitudes from wet or well-drained to moderately dry places. In relation to light requirements only eight of them (33%) show narrow ecological amplitudes (two occur exclusively in shaded habitats, two – in semi-shades and four – in full light) while others are euryphotophytes tolerated a wide range of light intensity (from moderately shaded to moderately illuminated – 4; from moderately shaded to full light – 6; from considerably shaded to moderately illuminated – 3; from considerably shaded to full light – 3). Regarding species' substratum preferences these bryophytes show differentiated demands and substratum specialization (14 species are related to only one substratum type) but the most share (71%) have species occurring on humus and/or small pieces of decayed wood (nine exclusively associated with these substrata and eight polysubstrata). Only one of the "newcomers", *Tetraphis pellucida* (related to rotten wood), showed quite frequent occurrence; the others occur very rarely.

With regard to growth type the number and percentage incidence of orthotropic species increased markedly in forests with died spruce stands. This observation is convergent with opinion that ratio of orthotropic to plagiotropic mosses depends on a sites' degradation in cities (Żarnowiec 1996). It seems that environmental disturbances also promote establishment and development of bryophytes of orthotropic forms.

CONCLUSIONS

1. After dieback of spruce stands the species composition and richness of bryophytes forming forest floor changed visibly. The total number of species increased by about 50% but nearly 30% of the previous bryoflora disappeared. Among nine species not confirmed in 2007 six are generally considered to be eurytopic in relation to substratum reaction (they occur in wide range from considerably or moderately acid to subneutral habitats) but the same, two of them: *Hylocomium splendens* and *Thuidium tamariscinum* are claimed to be sensitive to atmospheric pollutions. In their case the disappearance supposed could be caused directly by pollutants (and environment acidification) not by changes in forest microclimate generated from tree stand disintegration. In relation to other ecological requirements the species not confirmed in 2007 do not show common features differentiated them from others.

2. Among bryophytes persistent in the habitats of the mountain spruce forest some humicolous and epixylous species (*Cephalozia bicuspidata*, *Barbilophozia lycopodioides*, *Dicranodontium denudatum*, *Plagiothecium curvi-

folium) showed clear increase in the localities number after tree stands dieback.

3. As it was expected the number of colonists (especially pioneer colonists sensu DURING 1992) and species preferring drier habitats has increased in spruce forests after dieback. However, the highest increase in species number showed bryophytes of rather wide ecological amplitudes in relation to light (especially those occurring in moderately shaded to full light habitats), moisture degree (mainly higro- to mezophytes), substratum reaction and substratum specialization (polysubstrata species occupying among others humus, rotten wood, tree bases). The share and number of stenotopic species have not changed considerably: only one obligatory epixylic species and one xerophyte appeared; the number of photophytes increased insignificantly, from four to seven.

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