The habitat factors that affect the composition of bryophyte and lichen communities on fallen logs

Jaké faktory ovlivňují složení společenstev mechorostů a lišejníků na padlých kmenech?

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The composition of cryptogam (bryophyte and lichen) communities on fallen logs was studied in two old-growth forests in the Czech Republic. Altogether, 85 species (22 liverworts, 44 mosses, and 19 lichens) were recorded. The presence and abundance of the different species on 350 logs was attributed to habitat factors (e.g. humidity, wood decay, wood softness, log diameter, bark cover, thickness of humus layer and tree species) that were recorded separately for each of the logs. The aim was to identify the factors significantly affecting the composition of cryptogam communities. For the different ecological groups of species (epiphytes, epixylic species, and ground flora) forwarded canonical correspondence analysis (CCA) selected thickness of humus layer and tree species as the factors explaining most variability. In addition, the extent of log surface covered by bark, humidity and log decay were selected as significant determinants of cryptogam community composition.

Keywords: bryophytes, Czech Republic, dead wood, epixylic species, lichens, old-growth forest, species composition

Introduction

Dead wood is an important component of temperate forests. Standing dead trees (snags), fallen logs and large branches and stumps form major structural features of ecological importance. They serve as habitats for various organisms, represent a source of mineral nutrients and energy and influence soil movement and deposition (Harmon et al. 1986). The importance of decaying logs for different groups of organisms has been intensively studied, mostly in the boreal zone (Samuelsson et al. 1994, Essen et al. 1997). Harmon et al. (1986) and Eckloff & Ziegeler (1991) have reviewed the ecological roles of dead wood in different parts of the temperate zone.

Dead wood is an important habitat for bryophytes and lichens. Some species live exclusively on dead wood (obligate or true epixylic species), others grow on logs and stumps as well as on other substrates (facultative epixylic species). Generally, the importance of dead wood for bryophytes is revealed by comparing the composition of bryophytes on logs and stumps in forests of different ages. Greater numbers of bryophyte species occur in old forests, with a continuous supply of logs in various stages of decay than in young or managed forests, where the amount and quality of dead wood is limited (Andersson & Hytteborn 1991, Lesica et al. 1991, Crites & Dale 1998, Rambo & Muir 1998, Ódor & Standovár 2001, Desponts et al. 2002). The air humidity is substantially higher in old forests than in managed forests. This seems to be important for obligate epixylic species, namely tiny and drought-sensitive liverworts, which are mostly restricted to old forests (Söderström 1988a, Laaka 1993, Vellak & Paal 1999).

The composition of the bryophyte and lichen communities on logs mirrors the successional changes in the physical and chemical properties of the wood during its decay, such as texture, density, softness, pH and water-holding capacity (McCullogh 1948, Muhle & LeBlanc 1975, Cornelissen & Karssemeijer 1987, Crites & Dale 1998, Ódor & Van Hees 2004). The composition of bryophytes and lichens is also reportedly affected by the tree species (Ježek 1959, Nakamura 1987, Stefureac 1987, McAlister 1997) and log diameter (Söderström 1988b, Andersson & Hytteborn 1991, Ódor & Van Hees 2004). The preferences of individual bryophyte species for stages of decay, surface texture, wood softness and log diameter are presented by Söderström (1988b). For example, the liverwort *Anastrophyllum hellerianum* occurs mostly on very large logs with no bark and hard wood. Noteworthy, some species of lichens (such as *Hypogymnia physodes*) affect the decay of logs thus contributing to the formation/conservation of their habitats (Rypáček 1966, Henningsson & Lundstöm 1970, Lundstöm & Henningsson 1973). This is probably not the case for bryophytes.

Most authors have previously related species composition to the above mentioned environmental and substrate factors individually. However, since those factors are inherently dependent on each other, it is imperative to take into account possible intercorrelations between those factors. This requires an appropriate analysis of the data (which is by nature multivariate) in order to identify the factors explaining the greatest proportions of the variability in species composition.

This study focuses on the composition of bryophyte and lichen communities on fallen logs in two remnants of old beech-fir forests in the Novohradské hory Mts, in SE Czech Republic. Both forests have a similar history and are integrated into larger forest-covered areas and declared reserves with a strict ban on logging in 1838. They differ in area and moisture conditions, the Žofínský prales being about 10 times larger and damper than the smaller and drier Hojná voda forest (Průša 1985).

The following questions were addressed: (i) Does the composition of cryptogams on logs differ in these two old forests that differ in dampness? (ii) Which of the habitat factors determine the composition of cryptogams on fallen logs? (iii) Which of the habitat factors determine the species composition of the different ecological groups of cryptogams? (iv) What are the preferences of the individual species of cryptogams for these factors?

Methods

Study sites

This study took place in two old forests in the Novohradské Hory Mts in the south-eastern part of Bohemia near the Czech-Austrian border. These forests are the oldest protected natural reserves in the Czech Republic, both established in 1838. They represent remnants of fir-beech mountain forest vegetation indigenous to the locality and illustrate the dynamics of a change in the tree layer. Nowadays, the dominant tree species is beech (*Fagus sylvatica* L., 79%) followed by spruce, *Picea abies* (L.) Karst. (15%). The originally dominant fir (*Abies alba* Mill.) currently represents only 5% of the tree layer. Maple (*Acer platanoides* L. and *A. pseudoplatanus* L.) and elm (*Ulmus glabra* Huds.) are scarce (under 1%). Trees are of different dimensions and ages (from 20 to 400 years), and logs are in different stages of decay (Průša 1990). The region lies at the transition between oceanic and continental climates. The climate is cold and wet, mean annual temperature is 5.5°C and annual precipitation ranges from 800 to 950 mm (Průša 1985).

The Žofínský prales forest is located at 48°39'42" to 48°40'22" N and 14°42'02" to 14°43'03" E at an altitude of between 735 and 825 m a.s.l. It covers 97.71 ha (Průša 1985). Different forest types form an heterogeneous mosaic; this is a typical feature of the reserve. Relatively abundant springs and brooks reflect the moist conditions in the mostly shaded understorey. The total number of bryophyte species recently recorded on all types of substrates in the reserve is 185 (Vacínová 1998, Kučera 2004). Currently, there are 46 epiphytic and epixylic species of lichen in this forest (Peksa et al. 2004).

The essentially smaller and sunnier Hojná voda forest is situated on a slope, 810 to 880 m a.s.l. at 48°42'30" N and 14°45'30" E. Its area covers 9 ha (Vyskot 1981). This forest represents relatively drier habitat with a small area of springs. 90 bryophyte species are recently recorded in the reserve area (Vacínová 1998, Kučera 2004). Currently, 12 epiphytic and epixylic lichens species are recorded in this forest (Peksa et al. 2004).

Field sampling

Fallen logs, at least 1 m long with diameter equal to or above 15 cm, were sampled, omitting stumps and snags. In the smaller forest, Hojná voda, all such logs found within the old forest were surveyed. In the Žofínský prales forest all such logs along a ten-meter wide NNE to SSW transect, through the old forest were examined. One plot of 0.04 m^2 (either square 20 × 20 cm or rectangle 10 × 40 cm) was sampled on each log. Rectangular plots were used on logs of smaller diameter, where the use of square plots would prevent the sampling of areas with approximately homogenous slopes. The sample plot area (0.04 m^2) is the largest approximately homogenous area (chosen with regard to habitat factors) found on a heterogeneous substrate such as decaying logs (I. Jansová, unpublished data). The sample plot was chosen randomly on each log. Presence and abundance of bryophytes and lichens was recorded in these plots between May and September 1997. Abundance classes used in this study are shown in Table 1. The species that were not identified in the field were collected and identified later. Voucher specimens are stored in PRC herbarium.

For each log sampled, certain environmental and substrate characteristics (henceforth referred to as habitat factors) were recorded: Substrate type of four levels, depends on species of tree: beech, spruce, fir and other trees including uncommon elm and maple species as well as a few indeterminable logs. The four levels of substrate type were treated as dummy variables throughout this study. Therefore, they are treated as four single factors. Logs without bark were identified to species with the help of the original map of fallen trees (Průša 1990) and by consulting the local forester (B. Švarc, pers. comm.). Recorded frequencies of individual substrate types are presented in Fig. 1. Slope, with values varying from 0 (top) to 180° (bottom of the log), and slope orientation of the sample plot either to the north (Northward) or east (Eastward) (each with values 1, 0, –1). Thickness of humus layer on the log was measured in the sample plot. Canopy was estimated as percentage of the area of the log overshadowed. Diameter of the log was measured for that part of the log on which the sample

Table 1. – Abundance scale used in assessing bryophyte and lichen cover on the sample plots ($0.04m^2$). Mean class value (in %) was used in multivariate analyses.

Class	Fraction of plot area covered	Mean class value (%)
1	Some individuals to 1/100	1
2	1/100 to 1/16	3.5
3	1/16 to 1/8	9.8
4	1/8 to 1/4	19
5	1/4 to 1/2	38
6	1/2 to 1	75.5

was taken. Decay was measured using a semi-quantitative scale modified from Söderström (1988b) as follows: (1) freshly fallen log, hard, whole, bark intact, branches present; (2) log solid, wood hard, more than 50% of bark present; (3) some patches of soft wood, more than 50% of bark missing; (4) wood softening, outline retained, bark missing; (5) log outline slightly deformed; (6) pieces of soft wood, log outline still distinguishable; (7) only log core remains; (8) log outline indeterminable, humification 100%, no evidence of hard wood. Decay refers to the condition of the whole log. Recorded frequencies of individual decay classes are presented in Fig. 2. Characteristics of the log surface (Texture) was also recorded using a semi-quantitative scale modified from Söderström (1988b) as follows: (0) bark intact; (1) smooth surface without bark; (2) small crevices; (3) crevices and rills, rough surface; (4) small pieces of wood missing; (5) large pieces of wood missing, surface irregular, large depressions; (6) humidified chippings of wood, surface still distinguishable; (7) surface indeterminable. Recorded frequencies of individual texture classes are presented in Fig. 3. Wood softness was measured as the thickness of the soft wood layer in centimetres

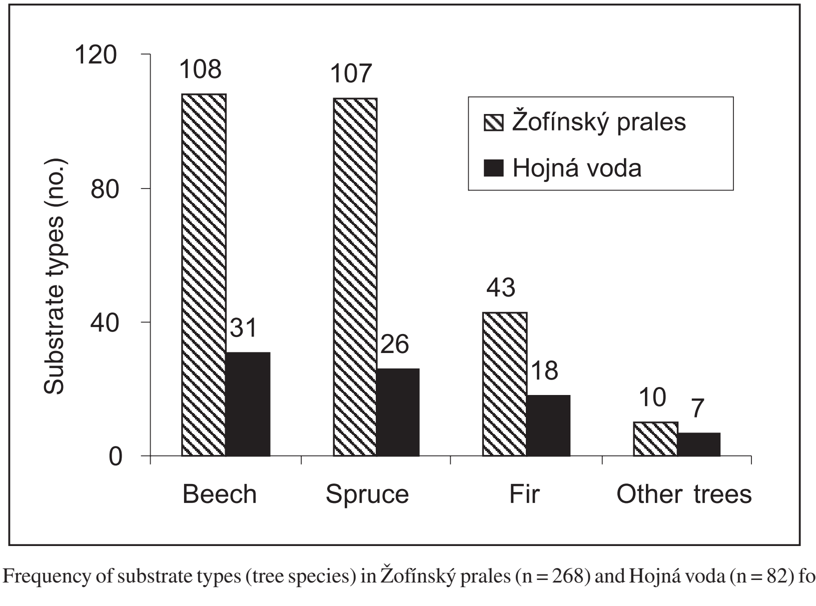

Fig. 1. – Frequency of substrate types (tree species) in Žofínský prales (n = 268) and Hojná voda (n = 82) forests.

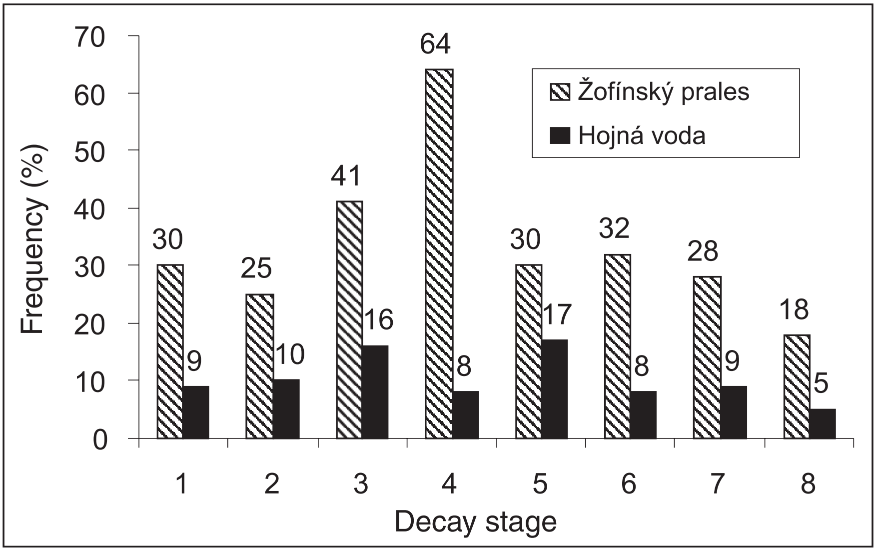

Fig. 2. – Frequency of different decay stages of logs (1 – freshly fallen log, hard, whole, bark intact, branches present; 2 – log solid, wood hard, more than 50% of bark present; 3 – some patches of soft wood, more than 50% of bark missing; 4 – wood softening, outline retained, bark missing; 5 – log outline slightly deformed; 6 – pieces of soft wood, log's outline still distinguishable; 7 – only log core remains; 8 – log's outline indeterminable, humification 100%, no evidence of hard wood) in Žofínský prales (n = 268) and Hojná voda (n = 82) forests.

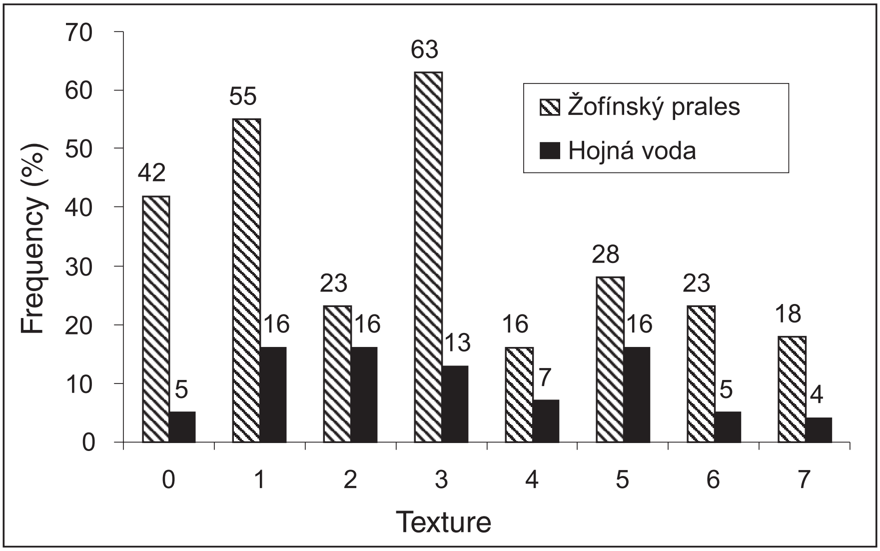

Fig. 3. – Frequency of texture classes of logs (0 – bark intact; 1 – smooth surface without bark; 2 – small crevices; 3 – crevices and rills, rough surface; 4 – small pieces of wood missing; 5 – large pieces of wood missing, surface irregular, large depressions; 6 – humidified woody chippings, surface still distinguishable; 7 – surface indeterminable) in Žofínský prales (n = 268) and Hojná voda (n = 82) forests.

and is the mean of three measurements on the sample plot. “Soft” wood was penetrable or removable with fingers. Contact of the log with the ground was estimated as a percentage of the log length. Above ground height was measured at the highest point of the elevated log from the ground. Bark cover was estimated as a percentage of the log surface. Presence or absence of branches was also recorded. Mean values of individual habitat factors are shown in Table 2.

Data analysis

Bryophytes and lichens were subdivided into three ecological groups: epiphytes (species commonly found on living trees), epixylic species (typically found on rotting wood) and ground flora (optimal habitat the ground). Species were subdivided into these groups after comparison with other studies (Söderström 1988b, Laaka 1993, Söderström 1993, Crites & Dale 1998). Some species, not mentioned in the above studies, were assigned to the groups according to Vacínová (1998). Other species (e.g. *Brachythecium* species), which occurred more frequently on other substrates than fallen logs at the studied sites (I. Vacínová, unpublished data) were assigned to ecological groups according to their substrate preferences at the studied sites (Vacínová 1998).

In the set of 17 factors there were 3 environmental (Eastward, Northward, Canopy) and 14 substrate characteristics. During sampling it became evident that the habitat factors could be intercorrelated. Strongly correlated variables bring no independent information about species composition and may be excluded from the analysis; retaining only one factor from the intercorrelated group of factors is usually sufficient for an analysis (ter Braak 1986). To determine such possible intercorrelations among habitat factors in this study, the centred and standardized analysis of principal components (PCA) was used. In this case, values of all factors (disregarding the Locality) were used as species in PCA. Factors such as Texture (correlated with Decay stage), Contact, Height, Branches (all correlated with Bark), Spruce (correlated to Beech), and Other trees (correlated with Fir) were omitted from further analyses due to their strong intercorrelation with remaining factors (analysis not shown).

Ordination techniques were used to explore the relationships between the composition of cryptogam (bryophyte and lichen) communities and habitat factors. Since an unimodal response of species to the factors was expected and supported by the Detrended Correspondence Analysis (DCA) as the gradient length was greater than 4 (ter Braak & Šmilauer 2002), it was decided to use weighted averaging techniques. DCA is an indirect gradient analysis, in which ecological gradients are derived from species composition. Canonical Correspondence Analysis (CCA), a direct gradient analysis, relates species composition to environmental variables. From previous analyses (not shown) it was apparent there was no arch effect in our species dataset that would require detrending in direct ordination (ter Braak & Prentice 1988) and thus CCA gave conclusive results. To test the significance of the explaining environmental factors used in CCA, Monte-Carlo permutation test with 999 permutations was used. All analyses were conducted with CANOCO 4.5 (ter Braak & Šmilauer 2002).

Standard CCA was used to examine the effect of site (Locality) on cryptogam composition. Factor Locality was then used as a covariable in all further analyses. Eigenvalues in particular analyses are, therefore, related to the residual variance after removing the effect of Locality. To determine which of the remaining eleven recorded habitat factors signifi-

Table 2 . – Values of recorded habitat factors. Mean values with standard deviations (SD) and frequencies are given.

Variable		Total	Žofínský prales	Hojná voda
		n = 350	n = 268	n = 82
Branches	(no. of logs)	191	158	33
Slope	(°)	37.16±36.01	38.32±36.74	42.25±33.44
Diameter	(cm)	56.43±24.42	57.31±23.98	53.59±25.74
Softness	(cm)	3.96±3.94	4.18±4.21	3.23±2.75
Height	(cm)	18.74±31.94	16.12±29.23	27.29±38.50
Contact	(cm)	72.93±40.40	74.01±41.07	69.39±38.16
Humus	(cm)	0.39±1.05	0.48±1.17	0.11±0.44
Canopy	(%)	48.62±33.93	47.71±34.54	51.62±31.87
Bark	(%)	18.86±34.06	19.51±35.30	16.74±29.76

cantly explained variability in the composition of cryptogam communities, CCA with forward selection of environmental variables was used. It showed the proportion of variance (lambda-A) that each factor explained upon its inclusion to the analysis. Further forwarded CCA analyses were used to determine the factors that significantly affected composition of epiphytes (96 samples and 27 species), epixylic species (314 samples and 25 species) and ground flora (200 samples and 33 species). Comparison of DCA and CCA eigenvalues (for first and second axes) identified the proportion of variability in species composition variability explained by factors selected by forwarded CCA; if the factors explain most of the variation in species composition (explored by DCA), eigenvalues of correspondent axes would be nearly identical (see ter Braak 1986, 1987 for discussion). The results of forwarded CCA analyses were visualized using CanoDraw ordination diagrams. The species symbols can be projected perpendicularly onto the line of the arrow representing individual factors. These projections can be used to approximate the optima of individual species for the factors (ter Braak & Šmilauer 2002).

Nomenclature of species follows Kučera and Váňa (2003) for bryophytes and Wirth (1995) for lichens.

Results

On the 350 fallen logs sampled at the two sites 85 cryptogam species (44 mosses, 22 liverworts, and 19 lichens) were found. Twenty five species were classified as epixylic, 27 species as epiphytic and 33 species as ground flora (Table 3). The most frequent species was the epixylic moss *Herzogiella seligeri* (n = 197), followed by the ground flora moss *Hypnum cupressiforme* (n = 111) and the liverwort *Chiloscyphus profundus* (syn. *Lophocolea heterophylla*) (n = 98). Highest cover (among the cryptogam species recorded more than five times) were found for *Rhytidiadelphus loreus*, *Polytrichastrum formosum*, and *Amblystegium serpens* (all belonging to the ground flora group), covering on average more than 40% of the sample plot area (Table 3). Some infrequent liverworts (n < 5) on occasion showed very high cover – e.g. *Ptilidium ciliare* (75%) and *Bazzania trilobata* (56.5%). The epiphytic moss *Neckera complanata* (n = 4) covered on average almost half of the sample plot, although epiphytes in general seldom exceeded 30% cover (Table 3).

Table 3. – Frequency and average abundance (% of sample plot area) of the recorded bryophyte and lichen species in Žofínský prales and Hojná voda forests. Ecological category: E – epiphyte, G – ground flora, X – epixylic species; S.D. – standard deviation.

Species	Ecological category	Total (n = 350)			Žofínský prales (n = 268)			Hojná voda (n = 82)		
		Frequency	Abundance	S.D.	Frequency	Abundance	S.D.	Frequency	Abundance	S.D,
Liverworts:										
Bazzania trilobata	G	2	56.50	26.16	2	56.50	26.16	0		
Blepharostoma trichophyllum	X	8	1.00	0.00	7	1.00	0.00	1	1.00	
Calypogeia suecica	X	8	7.25	7.72	8	7.25	7.72	0		
Cephalozia bicuspidata	X	7	2.29	1.60	6	2.50	1.64	1	1.00	
Cephalozia catenuata	X	4	43.25	37.17	4	43.25	37.17	0		
Frullania dilatata	E	2	9.00	0.00	1	9.00		1	9.00	
Chiloscyphus profundus	X	98	12.67	19.25	72	12.35	17.80	26	13.58	23.16
Jungermannia leiantha	X	7	5.14	6.79	7	5.14	6.79	0		
Lepidozia reptans	X	60	26.83	27.68	51	26.88	27.65	9	26.56	29.51
Lophozia incisa	X	1	9.00		1	9.00		0		
Lophozia ventricosa	X	3	16.00	19.47	3	16.00	19.47	0		
Metzgeria furcata	E	7	10.86	13.51	6	12.50	14.01	1	1.00	
Nowellia curvifolia	X	64	33.86	30.95	52	34.75	30.53	12	30.00	33.83
Plagiochila porelloides	G	3	10.67	7.64	3	10.67	7.64	0		
Porella platyphylla	E	1	1.00		0			1	1.00	
Ptilidium ciliare	G	2	75.00	0.00	2	75.00	0.00	0		
Ptilidium pulcherrimum	E	7	14.71	5.35	6	15.67	5.16	1	9.00	
Radula complanata	E	2	10.00	12.73	1	19.00		1	1.00	
Riccardia latifrons	G	10	6.90	6.74	10	6.90	6.74	0		
Riccardia palmata	G	15	11.07	12.39	15	11.07	12.39	0		
Scapania nemorea	X	1	1.00		1	1.00		0		
Tritomaria quinquedentata	G	2	6.50	3.54	2	6.50	3.54	0		
Mosses:										
Amblystegium serpens	G	6	33.00	33.23	5	37.80	34.74	1	9.00	
Atrichum undulatum	G	2	28.50	13.44	1	19.00		1	38.00	
Aulacomnium androgynum	X	14	24.86	28.05	14	24.86	28.05	0		
Brachythecium reflexum	G	5	33.80	37.75	5	33.80	37.75	0		

Species	Ecological category	Total (n = 350)			Žofínský prales (n = 268)			Hojná voda (n = 82)		
		Frequency	Abundance	S.D.	Frequency	Abundance	S.D.	Frequency	Abundance	S.D,
Brachythecium rivulare	G	1	38.00		1	38.00		0		
Brachythecium rutabulum	G	3	6.33	4.62	1	1.00		2	9.00	0.00
Brachythecium salebrosum	X	79	32.97	29.72	67	32.72	29.62	12	34.42	31.52
Brachythecium starkei	G	3	26.67	41.88	2	38.00	52.33	1	4.00	
Brachythecium velutinum	X	46	16.02	20.86	22	11.73	11.34	24	19.96	26.46
Bryum capillare	G	1	9.00		1	9.00		0		
Bryum moravicum	E	8	8.50	12.12	7	8.43	13.09	1	9.00	
Dicranodontium denudatum	X	35	25.77	29.68	33	24.94	29.07	2	39.50	50.20
Dicranum montanum	E	44	6.16	9.10	31	4.84	6.73	13	9.31	12.98
Dicranum scoparium	X	42	17.64	23.26	41	17.98	23.45	1	4.00	
Diranum polysetum	G	59	9.80	15.88	41	10.29	17.39	18	8.67	12.11
Herzogiella seligeri	X	197	24.32	27.83	140	21.66	26.71	57	30.88	29.63
Homalothecium sericeum	E	3	13.33	21.36	2	19.50	26.16	1	1.00	
Hylocomium splendens	G	12	22.08	26.78	12	22.08	26.78	0		
Hypnum andoi	E	3	31.67	38.59	3	31.67	38.59	0		
Hypnum cupressiforme	G	111	21.82	24.90	81	21.16	24.43	30	23.60	26.47
Hypnum jutlandicum	G	6	13.83	13.04	6	13.83	13.04	0		
Isothecium alopecuroides	E	8	32.75	29.35	4	49.25	32.00	4	16.25	16.13
Leucodon sciuroides	E	4	14.25	16.28	3	16.00	19.47	1	9.00	
Mnium hornum	G	2	6.50	3.54	2	6.50	3.54	0		
Neckera complanata	E	4	47.25	18.50	3	50.33	21.36	1	38.00	
Neckera pennata	E	1	4.00		0			1	4.00	
Ortotrichum stramineum	E	1	1.00		0			1	1.00	
Paraleucobryum longifolium	G	1	4.00		0			1	4.00	
Plagiomnium affine	G	1	4.00		1	4.00		0		
Plagiomnium cuspidatum	G	15	14.73	13.45	15	14.73	13.45	0		
Plagiothecium denticulatum	G	4	1.75	1.50	4	1.75	1.50	0		
Plagiothecium laetum	G	9	11.56	23.81	6	15.83	28.99	3	3.00	1.73
Platygyrium repens	E	10	10.50	11.11	9	10.67	11.77	1	9.00	
Pleurozium schreberi	G	16	20.88	25.16	15	22.20	25.46	1	1.00	
Pohlia nutans	G	5	12.80	14.31	4	15.00	15.51	1	4.00	

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		Frequency	Abundance	S.D.	Frequency	Abundance	S.D.	Frequency	Abundance	S.D,
Polytrichastrum formosum	G	25	40.28	31.03	21	39.86	30.57	4	42.50	38.24
Pterigynandrum filiforme	E	3	9.00	8.66	0			3	9.00	8.66
Ptilium crista-castrensis	G	1	19.00		1	19.00		0		
Rhizomnium punctatum	X	59	13.63	17.94	55	13.76	18.12	4	11.75	17.56
Rhytidiadelphus loreus	G	7	44.14	32.03	7	44.14	32.03	0		
Rhytidiadelphus triquetrus	G	3	31.00	38.11	3	31.00	38.11	0		
Sanionia uncinata	X	23	19.43	23.68	16	15.31	18.62	7	28.86	32.25
Sphagnum girgensohnii	G	1	1.00		1	1.00		0		
Tetraphis pelucida	X	64	28.41	29.86	46	23.11	27.61	18	41.94	31.88
Lichens:										
Cladonia cenotea	G	2	11.50	10.61	2	11.50	10.61	0		
Cladonia coniocraea	X	30	14.17	19.53	19	13.05	18.06	11	16.09	22.64
Cladonia digitata	X	26	10.81	15.42	24	10.88	15.86	2	10.00	12.73
Cladonia fimbriata	X	5	8.80	9.39	5	8.80	9.39	0		
Cladonia chlorophaea	G	4	3.00	4.00	4	3.00	4.00	0		
Cladonia sp.	G	24	2.67	2.41	21	2.62	2.52	3	3.00	1.73
Cladonia squamosa	G	1	4.00		1	4.00		0		
Hypocenomyce scalaris	E	1	1.00		1	1.00		0		
Hypogymnia physodes	E	35	17.31	21.52	24	14.54	16.97	11	23.36	29.21
Hypogymnia farinacea	E	1	1.00		1	1.00		0		
Chaenotheca ferruginea	E	2	1.00	0.00	2	1.00	0.00	0		
Chaenotheca chrysophylla	E	5	2.20	1.64	5	2.20	1.64	0		
Lecanora conizaeoides	E	2	1.00	0.00	2	1.00	0.00	0		
Lecanora sp.	E	2	1.00	0.00	2	1.00	0.00	0		
Lepraria sp.	G	4	3.75	3.77	3	3.67	4.62	1	4.00	
Parmeliopsis ambigua	E	1	1.00		1	1.00		0		
Peltigera pratextata	G	1	4.00		1	4.00		0		
Platismatia glauca	E	9	5.22	5.74	6	6.33	6.86	3	3.00	1.73
Pseudevernia furfuracea	E	4	20.00	13.93	2	21.00	24.04	2	19.00	0.00

Table 4. – Significance of habitat factors selected by forwarded CCA with Locality as covariable (a). Lambda-A indicates variance explained by the factor upon its addition to the model. Eigenvalues are shown of the first (1) and second (2) axes in forwarded CCA compared to DCA (b). ** $p < 0.01$; * $0.01 \geq p < 0.05$

(a)	All cryptogams		Epiphytes		Epixylic species		Ground flora	
	Factor	Lambda-A	Factor	Lambda-A	Factor	Lambda-A	Factor	Lambda-A
	Humus	0.26**	Beech	0.43**	Beech	0.2**	Humus	0.42**
	Bark	0.25**	Bark	0.42**	Decay	0.13**	Softness	0.15*
	Slope	0.17**	Eastward	0.21**	Slope	0.11**	Beech	0.11*
	Beech	0.14**	Canopy	0.19*	Humus	0.10**		
	Decay	0.08**	Softness	0.16*	Bark	0.06**		
	Canopy	0.08**			Eastward	0.06*		
					Canopy	0.06*		

(b)	All cryptogams		Epiphytes		Epixylic species		Ground flora	
	1	2	1	2	1	2	1	2
DCA	0.854	0.751	0.976	0.658	0.909	0.856	0.998	0.913
CCA	0.376	0.286	0.698	0.281	0.396	0.110	0.470	0.159

The total number of cryptogam species recorded on 268 logs in the Žofínský prales was 80 (40 mosses, 21 liverworts and 19 lichens). The most frequent and most abundant species were the same as above (Table 3). In the Hojná voda 46 cryptogam species (30 mosses, 10 liverworts and 6 lichens) were found on 82 logs. The most frequent species were again the same as above, but the epixylic mosses *Tetraphis pellucida*, *Brachythecium salebrosum*, and *Herzogiella seligeri* were the most abundant species covering on average about one-third of the sample plot areas (Table 3). In the Hojná voda forest an endangered moss, *Neckera pennata*, was also found.

Site effect

The cryptogam composition on logs in the two forests differed significantly (significance of the first ordination axis in CCA with F = 2.211, $p < 0.01$). This might be explained by differences in epixylic species (CCA with F = 3.696, $p < 0.01$), since the epiphytes and ground flora was not significantly different in the two localities (analyses not shown). However, the eigenvalues of the first CCA axes (0.109 and 0.105 for all species and epixylic species, respectively) were substantially less than the first axes eigenvalues for the analogous DCA's (0.857 and 0.909 for all species and epixylic species, respectively). This implies that much of the variability in species composition was not explained by the locality.

Effect of habitat factors

The factors selected by forwarded CCA taking into account all bryophyte and lichen species were Humus, Bark, Slope, Beech, Decay and Canopy, all of which were highly significant ($p < 0.01$) (Table 4a). Cryptogam species composition on logs differed along a gradient between freshly fallen logs with a large amount of bark and well decayed logs in the dense parts of the forests (Axis 1, Fig. 4). It also changed along the gradient of humus ac-

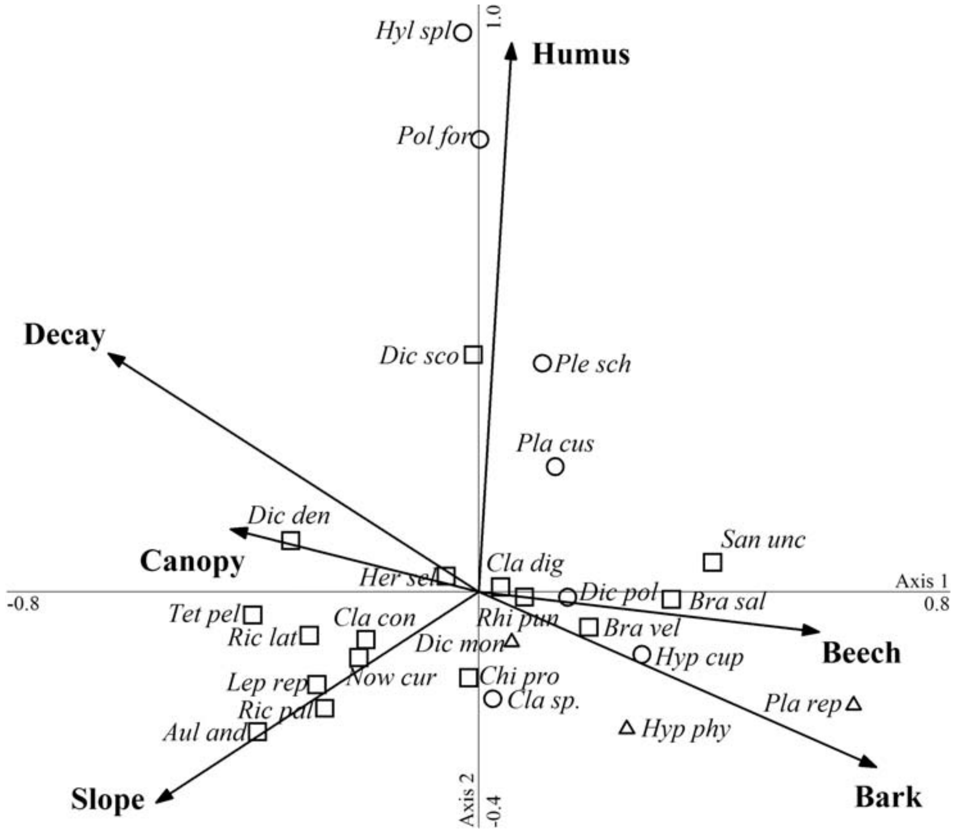

Fig. 4. – Correlation of abundances of cryptogam species on decaying logs with habitat factors (arrows), which were previously selected by forwarded CCA. Results of CCA are shown for species recorded at least 10 times. The abbreviations of names of cryptogam species are composed of first three letters of the genus and first three letters of the species names given in Table 3. Triangles indicate epiphytes, squares epixylic species, circles ground flora. First and second axes account for 41% of the variability in species data.

cumulation (Axis 2, Fig. 4). Epixylic species occurred mostly on logs in advanced stages of decay; they grew on steeper log sides without bark and humus. Ground flora species occurred on logs with a layer of humus. Epiphytes occurred more on logs with bark and no humus layer (Fig. 4). Comparison of DCA and CCA eigenvalues (Table 4b) implies that Fig. 4 accounted for 41% of the variance in cryptogam composition and so most of the variation was not explained by habitat factors.

The distribution of epiphytes on logs was mainly correlated with substrate type and amount of bark remaining on logs (Fig. 5). Beech, Bark, and Eastward were identified as highly significant ($p < 0.01$). Canopy and Softness were also selected as significant (both $p < 0.05$) for the composition of epiphyte communities (Table 4a). Since the CCA first axis eigenvalue was not far from the corresponding DCA eigenvalue (Table 4b), bark covered spruce logs and beech logs with softening wood appeared to be the two extremes delimiting the most important gradient affecting the composition of epiphytic communities on

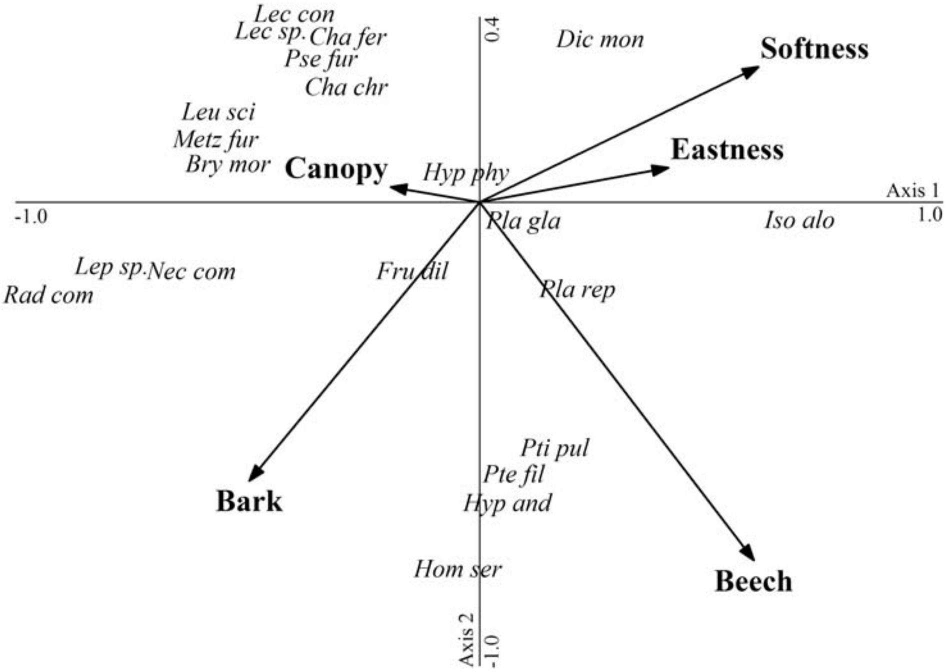

Fig. 5. – Correlation of abundances of epiphytic cryptogam species on decaying logs with habitat factors (arrows), which were previously selected by forwarded CCA. Results of CCA are shown for species recorded at least two times. Same species abbreviations are used as in Fig. 4. Species names are centered on the species scores. First and second axes account for 57% of the variability in species data.

fallen logs (Fig. 5, accounted for 57% of variation in epiphyte composition). The moss *Dicranum montanum* occurred on logs with little bark (Fig. 5). Together with *Isothecium alopecuroides*, these were the only epiphytes we found on plots without bark. *Homalothecium sericeum, Hypnum andoi, Platygyrium repens, Pterigynandrum filiforme* and *Ptilidium pulcherrimum* as well as *Isothecium alopecuroides* occurred mostly on beech logs, whereas lichens occurred mostly on logs of other tree species.

The occurrence of epixylic species was well correlated with substrate type and stage of decay of the logs (Fig. 6). Beech, Decay, Slope, Humus and Bark were identified as highly significant habitat factors for this ecological group ($p < 0.01$). Eastward and Canopy were also significant ($p < 0.05$) (Table 4a). Some species (e.g. *Brachythecium salebrosum, B. velutinum, Cladonia fimbriata, Jungermannia leiantha* and *Sanionia uncinata*) grew on logs with a high amount of bark and thus in early stages of decay (Fig. 6). On the other hand, *Dicranodontium denudatum, Cephalozia biuspidata, Riccardia latifrons* and

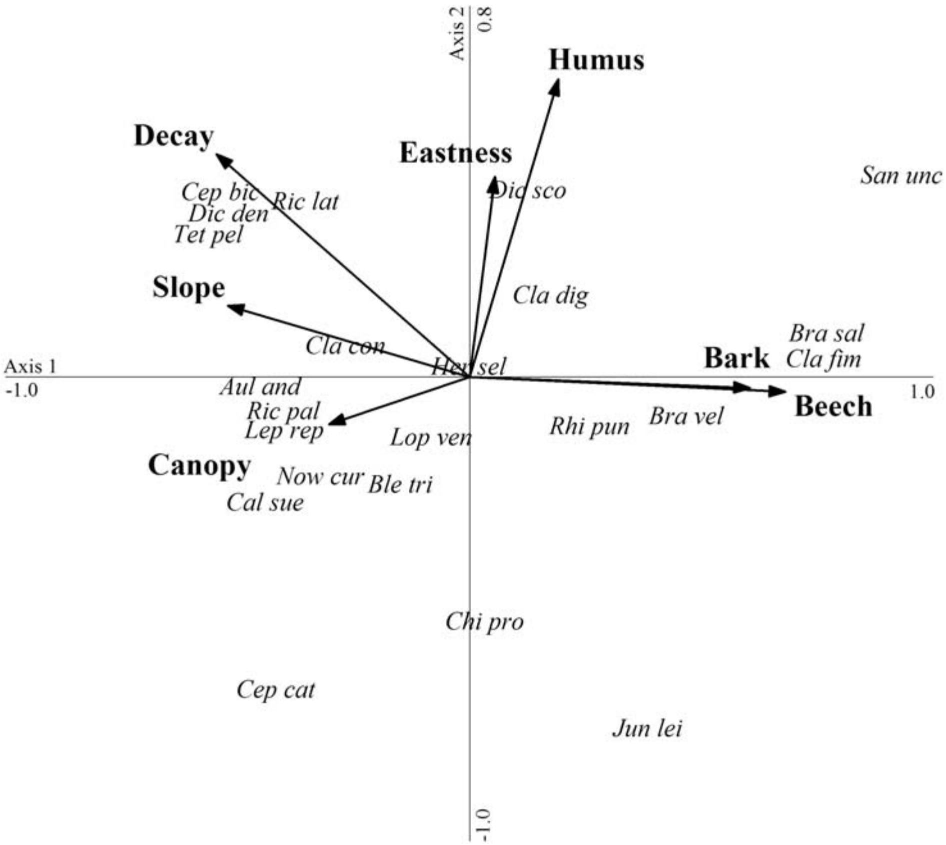

Fig. 6. – Correlation of abundances of epixylic cryptogam species on decaying logs with habitat factors (arrows), which were previously selected by forwarded CCA. Results of CCA are shown for species recorded at least twice. Same species abbreviations are used as in Fig. 4. Species names are centered on the species scores. First and second axes account for 43% of the variability in species data.

Tetraphis pellucida were most frequent on logs in the later stages of decay. The latter species also occurred mostly on steeper plots. The bryophytes *Aulacomnium androgynum, Blepharostoma trichophyllum, Calypogeia suecica, Cephalozia catenuata, Lepidozia reptans, Nowellia curvifolia* and *Riccardia palmata* grew on shaded plots. The liverworts *Cephalozia catenulata*, *Chiloscyphus profundus* and *Jungermannia leiantha* occurred on logs without humus. The mosses *Sanionia uncinata* and *Dicranum scoparium* grew even on humus (Fig. 6). The comparison of DCA and CCA eigenvalues (Table 4b) implies that most of the variability in epixylic species composition was not explained by habitat factors (Fig. 6, accounted for 43% of variation in epixylic species composition).

Ground flora species distribution was best correlated ($p < 0.01$) with humus accumulation. Softness and Beech were selected by forwarded CCA as other significant factors ($p < 0.05$) (Table 4a). Comparison of DCA and CCA eigenvalues (Table 4b) showed that habitat factors (Fig. 7) accounted only for 33% of the variation in ground flora composition. It

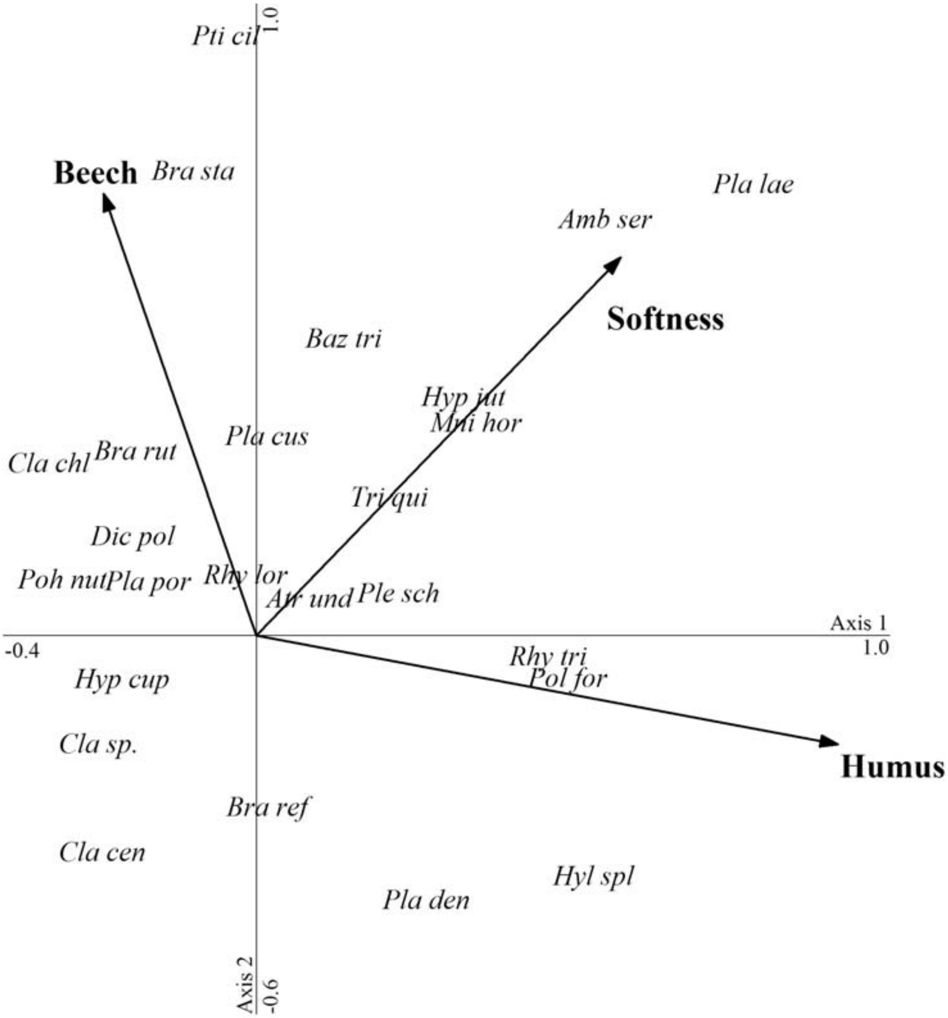

Fig. 7. – Correlation of abundances of ground flora species on decaying logs with habitat factors (arrows), which were previously selected by forwarded CCA. Results of CCA are shown for species recorded at least twice. Same species abbreviations are used as in Fig. 4. Species names are centered on the species scores. First and second axes account for 33% of the variability in species data.

implies that most of the variation remained unexplained. Species on the left hand side of the diagram (Fig. 7) did not occur on the humus layer as frequently as species on the right hand side (e.g. mosses *Hylocomium splendens, Polytrichum formosum, Rhytidiadelphus triquetrus* and *Plagiothecium* species). *Brachythecium starkei* and *Ptilidium ciliare* occurred more on beech logs. The mosses *Plagiothecium laetum* and *Amblystegium serpens* were most frequent on softer and thus more decayed wood.

Discussion

Site effect

The two forests, Žofínský prales and Hojná voda, differed in composition of log inhabiting cryptogams, although they were of the same age and both were integrated into large forest-covered landscapes. Both forests are in the same mountain range, are geographically close and have nearly the same climatic conditions. Difference in epixylic species composition might reflect the diversity of various moisture and microsite conditions in Žofínský prales compared to the more homogenous and drier Hojná voda forest (Průša 1985). Some authors (McCullogh 1948, Muhle & LeBlanc 1975) have likewise found differences in bryophyte composition among sites with different moisture conditions. Furthermore, comparisons of natural and recently managed forest stands indicate that damp conditions seem to be of primary importance for the occurrence of obligate epixylic species (Söderström 1988a, Laaka 1993, Vellak & Paal 1999). Hojná voda forest, in covering only 9 ha, is much smaller than Žofínský prales. Edge effect (proximity of contact with a different system) would be much more pronounced for this smaller forest compared to the Žofínský prales. The small area of the Hojná voda forest might also limit substrate (logs) availability and hence the occurrence of epixylic species there. In such cases, fine woody debris (branches and wood pieces of smaller diameter) may be as important as large logs (Kruys et al. 1999, Ódor & Standovár 2001). However, in this study logs and branches with diameters below 15 cm were not surveyed.

Effect of habitat factors

The results show that the presence of humus has a major impact on the composition of cryptogam communities. The communities on humus covered logs were mostly composed of ground flora species. Other ecological groups (with the exception of some epixylic mosses) did not occur where humus was present. Beech logs were inhabited by different epixylic communities than spruce logs. Similarly, differences in cryptogam communities on hardwood and conifer logs were observed previously by McAlister (1997) who proposed that pH was an important determinant of the communities, with hickory bark and wood having a high and pine bark a low pH. These results are in accord with early observations of preferences of some epiphytes for a specific tree species, reflecting the different pHs of the bark (Billings & Drew 1938). Similar preferences were also observed for some lichen species (Kermit & Gauslaa 2001, van Herk 2001).

Log diameter was previously considered an important factor affecting namely epixylic species (Söderström 1988b, Andersson & Hytteborn 1991, Rambo & Muir 1998, Ódor & Van Hees 2004). However, this factor was not found to be an important determinant of composition of cryptogam communities in our study. As only logs with a diameter of at least 15 cm and not smaller were included in the study, the range in diameters might be too small to explain the variation in our species data. On the other hand, logs with large diameter are less likely to be overgrown by ground flora and therefore more likely (both in space and time) to host epixylic species compared to thin logs (Söderström 1988b). The relationship between log diameter and presence of ground flora in our data set could be hidden in the effect of humus accumulation. Thinner logs appeared to be covered by forest litter, soil and fallen beech leaves more frequently than large logs.

Plot slope seemed to be correlated with occurrence of tiny liverworts. Perhaps they grew on steep slopes on the sides of logs to avoid the humus layer, which accumulates easier on the flat upper parts of logs. Liverworts might thus also escape competition with faster expanding pleurocarpous mosses that usually occupy the upper parts of logs (I. Jansová, unpublished). However, the large uninhabited areas on logs indicated that competition for space between bryophyte species is low (Slack 1982, 1984, McAlister 1995). Canopy and slope orientation reflected to a certain degree the moisture conditions in plots; the more shaded, the longer the logs remain moist. Areas with springs might be an exception, as the canopy is mostly open there, but air-humidity is high and suitable for ample bryophyte development. Eastern slopes of logs might be less exposed to drying sunshine compared to those facing west. Remarkably, the north/south slope orientation, which was supposed to covary with exposure to sunshine and hence moisture condition on the plots, did not have a significant effect in our data set. Therefore, it is questionable whether the slope orientation correlates with exposure to sunshine in relatively dense old forests.

Bark fragmentation was correlated with the composition of epiphytes and epixylic communities. Since logs without bark were recorded earliest at decay stage 4, the bark fragmentation gradient reflects fine-scale variation in species composition during the first three stages of decay. Previously, McAlister (1997) reported that cryptogam species composition on logs changed markedly once the bark was gone. Our results confirm that there was a change in cryptogam composition along the log decomposition gradient as found in number of previous successional studies (McCullogh 1948, Muhle & LeBlanc 1975, Cornelissen & Karssemeijer 1987, Nakamura 1987, Söderström 1988b, Rambo & Muir 1998, Ódor & Van Hees 2004). This means that changes in the species composition reflect changes in substrate characteristics caused by decay (e.g. bark fragmentation, surface roughening, increase in water-holding capacity, changes in wood density and pH). Epiphytes occurred mostly in the first two or three stages of decay in this study. In contrast to Ódor and Van Hees (2004), who suggested that the occurrence of epiphytic bryophytes on living beech trees was restricted but markedly increased on recently fallen trees, the results presented here indicate that epiphytes on logs represent remnants of the original epiphytic community on living trees, as suggested previously by Söderström (1988b). Although the epiphytes were observed to continue to grow after a tree had fallen (e.g. change in direction of stem growth in population of *Neckera crispa*), they did not grow extensively over larger areas and usually disappeared when the log was no longer covered with bark (decay stage 4). Our results also support observations by Söderström (1988b) that early and late epixylic species might be distinguished along the log decomposition gradient. Additionally, early and late species in the ground flora group might be distinguished (Fig. 7) assuming wood softness covaries with decay stage.

The delimitation of the ecological groups outlined above (epiphytic, epixylic, ground flora) is subjective (Söderström 1988b, Andersson & Hytteborn 1991, Laaka 1993, Crites & Dale 1998). Knowledge about species substrate optima (Söderström 1993) is very limited and deserves urgent attention. Furthermore, it is not clear whether the substrate optimum of the same species (e.g liverwort *Ptilidium pullcherrimum*) is the same under different climatic conditions (Laaka 1993).

This study compared the contribution of certain habitat factors to explaining differences in composition of cryptogam communities, taking into account the data for all the members of the communities. Should they be analysed separately, the results might differ from those presented here because intercorrelations among the factors would be disregarded. It is not claimed that the factors reported here were the only and primary factors affecting the composition of cryptogams. The discrepancy between the results of the CCA and DCA in this study indeed indicate that some other factors (not assessed here) also contribute to the variation in the composition of the cryptogam communities. It may be important to identify biotic factors such as disturbance and grazing that may contribute to the shaping of the communities, although this may prove extremely difficult.

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Souhrn

Složení společenstev mechorostů a lišejníků na padlých kmenech jsme studovali ve dvou zbytcích původního pralesa v Novohradských horách. Celkově jsme při tomto výzkumu nalezli v obou lokalitách (NPR Žofínský prales a NPP Hojná voda) 85 druhů kryptogam, z toho 22 druhů játrovek, 44 druhů mechorostů a 19 druhů lišejníků. Data o přítomnosti druhů a jejich pokryvnostech na 350 snímkovaných plochách na padlých kmenech jsme vztáhli k parametrům prostředí – sklonu a orientaci plochy, zástinu a charakteristice substrátu (stupni rozkladu, měkkosti dřeva, průměru kmene, pokryvu borky, mocnosti vrstvy humusu a druhu dřeviny) s cílem zjistit, zda druhové složení společenstev s těmito faktory nějak souvisí. Celkové složení vegetace je významně korelováno s více faktory, mezi nimi vrstva humusu a pokryv borky na ploše vysvětlují nejvyšší podíl variability v druhových datech. Výskyt epifytických druhů na tlejících kmenech je dán především druhem dřeviny (buk/smrk), pokryvem borky a vlhkostními podmínkami stanoviště. Epixylické druhy jsou korelovány s druhem dřeviny (buk/smrk), stupněm rozkladu kmene, sklonem plochy, mocností vrstvy humusu, pokryvem borky na ploše a opět vlhkostí. Výskyt pozemních druhů je vázán především na gradient akumulace humusu.

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