

Sphagnum-mediated successional pattern in the mixed mire in the Muránska planina Mts (Western Carpathians, Slovakia)

Petra HÁJKOVÁ¹ & Michal HÁJEK^{1,2}

¹Department of Botany, Faculty of Science, Masaryk University, CZ-61137 Brno, Czech Republic; tel.: ++420-54-1129514, e-mail: buriana@sci.muni.cz, hajek@sci.muni.cz

²Department of Ecology, Institute of Botany, Academy of Sciences of the Czech Republic, Poříčí 3b, CZ-60300 Brno, Czech Republic

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Mixed mires, widely distributed in the boreal zone, occur only rarely in the Carpathians. The fine-scale pattern of moss species composition and species richness in the mixed mire Havraník in the Muránska planina Mts was studied using 9 transects stretching from mineral-rich pools to high, ombrotrophic hummocks. The height above water level, pH, conductivity and redox potential were measured in all of 79 sample plots (78.5 cm²). A complete exchange of species composition was recorded along the ca 3-meter transects. The sequence of cryptogamous species was as follows (*Chara*, *Drepanocladus cossonii*) < (*Bryum pseudotriquetrum*, *Campylium stellatum*, *Tomenthypnum nitens*) < (*Sphagnum teres*, *S. subnitens*, *Aulacomnium palustre*) < (*Sphagnum flexuosum*, *S. fallax*, *S. capillifolium* s.s.) < (*Sphagnum rubellum*, *Polytrichum strictum*, *Absconditella sphagnorum*). The first DCA axis reflects this long gradient and is closely connected to the height above water level and pH, which strongly decreases from more than 7 in small pools to 3–4 on high hummocks. A well-developed poor-rich mire gradient exists on this single site through *Sphagnum*-directed succession. The moss species occupying the extremes of the water level gradient (pools and high hummocks) exhibit the lowest niche breadths for pH, whereas the highest niche breadths are found in moss lawn and midhummock species. The highest species richness was found in the moderately alkaline lawns, between 10 and 30 cm above water level. This small-scale pattern of species richness found in the studied mixed mire seems to correspond with that found on a landscape scale. We also detected a distinctly bimodal distribution in pH data, about 4 in hummocks and 6–7 in the lower-positioned rich fen. Our results indicate that this mixed mire ecosystem, which developed in the Carpathians on a small area, functions in the same way as those occurring in the boreal zone over large areas.

Key words: *Sphagnum* ecology, brown mosses, niche breadth, ordination analyses, species richness, bimodal distribution of pH, Central Europe, Slovakia.

Introduction

The distribution and abundance of *Sphagnum* and

other mire mosses along environmental gradients have been studied by many authors. At landscape level, different moss species grow in bogs than in

mineral-rich fens. These two contrasting habitats differ in water sources, pH and mineral content. Their vegetation changes along several main ecological gradients (VITT & SLACK, 1984; MALMER, 1986; BRAGAZZA & GERDOL, 1999; HÁJEK, 2002; HÁJEK et al., 2002). Vertical zonation of *Sphagnum* mosses along hummock-hollow gradients and their niche diversification were often studied in European and in North American ombrotrophic bogs and oligotrophic fens (VITT et al., 1975; ANDRUS et al., 1983; BRAGAZZA, 1997; DÜNHOFEN & ZECHMEISTER, 2000). This vertical pattern was less often explored along the entire poor-rich mire gradient (TYLER, 1981; VITT & SLACK, 1984).

Boreal mixed mires are specific ecosystems, where minerotrophic and ombrotrophic structures alternate in one mire (PERSSON, 1961; KARLIN & BLISS, 1983; ANDRUS, 1986). High hummocks of *Sphagnum rubellum* or *S. fuscum* are scattered throughout the minerotrophic fens building up “miniature bogs” (BELLAMY & RIELEY, 1967). Species with completely different ecological demands can occur together on a small spatial scale and therefore such mixed mires are appropriate for studying species composition in both the extremely rich fens and the oligotrophic high *Sphagnum* hummocks. In the case of mixed mires the poor-rich mire gradient (MALMER, 1986) is developed on one site. This heterogeneity is caused by the ability of various *Sphagnum* and brown moss species to direct succession through acidification (GLIME et al., 1982; ANDRUS, 1986) and peat accumulation (KUHRÝ et al., 1993). Because of increasing acidity, the brown mosses of *Amblystegiaceae* are gradually replaced by *Sphagnum* species and peat accumulation causes the peatland surface to become more and more separated from the direct influence of mineral-rich groundwater. This succession is a general process of all mire ecosystems and is not restricted to any area or specific ecoclimatic region (KUHRÝ et al., 1993). This process was also confirmed by macrofossil analysis of *Sphagnum*-dominated peatlands which developed from lake vegetation via minerotrophic fens dominated by brown mosses during the early to middle Holocene (KUHRÝ et al., 1993; MÖRNSJÖ, 1969; JANKOVSKÁ, 1970; JANSSENS, 1983; RYBNÍČEK & RYBNÍČKOVÁ, 1968). Many botanists were interested in mixed mires (PERSSON, 1961; BELLAMY & RIELEY, 1967; TYLER, 1981; KARLIN & BLISS, 1983; ANDRUS, 1986) because of the possibility to study successional processes.

The small-scale pattern of *Sphagnum* and other mire moss distributions has not been previously investigated in the Carpathians. Only

floristic (e.g. PECIAR, 1958; RYBNÍČEK & RYBNÍČKOVÁ, 1972; ŠOLTĚS, 2001) or phytosociological data (see JURKO & PECIAR, 1959; RYBNÍČEK et al., 1984; HÁJEK & HÁBEROVÁ, 2001) have been published. The majority of Western Carpathian mineral-rich fens have a uniform superficial structure and are clearly separated from mineral-poor fens, so-called transitional mires (STANOVÁ, 2000). The occurrence of mixed mires in the Carpathians has never been reported, with the exception of a very general mention of *Sphagnum fuscum* hummocks found in calcium-rich fens in the Liptov-basin (RYBNÍČEK unpubl.). Thus, the mixed mire Havraník represents a rare phenomenon among the Carpathian mires. It is located in the Muránska planina Mts (Central Western Carpathians, Slovakia, Fig. 1) and was discovered in 2000 in the valley of a small brook. The site is composed of mineral rich pools with stonewort (*Chara*) and *Drepanocladus cossonii* alternating with hummocks of up to 70 cm height with *Sphagnum rubellum* and *Polytrichum strictum*. Flat lawns (sub-) dominated by *Tomenthypnum nitens*, *Sphagnum teres*, *S. subnitens* and *S. flexuosum* are situated between these two microhabitat extremes with regard to the height above water level. Small spruces (*Picea abies*) are established on some of the hummock tops.

The present study aims at: 1) describing the major gradient from minerotrophic pools to ombrotrophic hummocks in a Carpathian mixed mire, 2) determining the relative influence of each measured factor (height above the water table, pH, conductivity and redox potential) on the segregation of moss species along this gradient, 3) exploring how species richness changes along the major gradient, 4) quantifying the niche breadth of cryp-



Fig. 1. The position of the study site in the Slovak Republic (coordinates: 200400E; 484900N).

togams with respect to pH and height above water level and comparing it to the niche breadth of vascular plants.

Methods

Field work

Field work was carried out in early May 2001. The vegetation was sampled in 79 circle plots of 78.5 cm² (circle diameter 10 cm) along nine transects, which stretched from pools to hummocks. These transects were chosen after visual inspection to cover all the possible vegetation types, and they were from 80 to 460 cm long, depending on their steepness. Every 20 cm (for the steep transects) or 40 cm (for the flatter transects) all species of mosses and vascular plants were recorded in sample plots. The cover of all species was estimated using four-grade scale: 1 – presence (up to 5% of cover), 2 – 5 up to 30%, 3 – codominance (30 to 60%) and 4 – dominance (60 to 100%).

pH, electrical conductivity and redox potential were measured directly in the field using portable instruments (CM 101 and PH 119, Snail Instruments). They were measured in water squeezed from the bryophytes in each sample plot. Height above water level was related to water level in the pools.

Data analyses

Height above water level and pH had normal distributions and were not transformed. The conductivity and redox potential values, which had an exponential distributions, were log-transformed.

The main gradients in the data-set were detected using the multivariate analyses from the CANOCO package (TER BRAAK & ŠMILAUER, 1998). Because the major gradient was very long, we used DCA and DCCA analyses (with downweighting of rare species). Since mosses are the leading species group in a mixed mire and are generally known to be the best indicators of the various environmental parameters in mires (VITT & SLACK, 1984), primarily the bryophyte data-set was processed in ordination analyses. All bryophyte species were included in the ordinations, but only those species occurring in minimum of 3 plots were considered in the ordination diagrams. The same criteria were used for calculation of both the niche breadths and the means of ecological factors for each species. The ordination species scores obtained from DCA were correlated with each other and with environmental factors using Pearson's correlation coefficient. Principal components analysis (PCA) was used for indirect ordination of environmental data. The values of each environmental variable were standardized to mean 0 and variance 1 in this analysis.

The Monte Carlo test of significance of the first canonical axis in CCA with a single variable was used for testing the importance of each environmental variable.

Two selected environmental variables (pH and height above water level) were divided into ten classes of an identical range (pH: range = 3.7–7.4, increment

= 0.37; height: range = 0–69 cm, increment = 6.9 cm). The niche breadth of each cryptogamous and vascular plant species was calculated for both variables (for details on the method see ØKLAND, 1986 and BRAGAZZA, 1997).

Plant names were united according to MARHOLD & HINDÁK (1998) with the exception of *Absconditella sphagnum* (see GUTTOVÁ & PALICE, 2000); the nomenclature of syntaxa follows HAJEK & HABEROVÁ (2001).

Results

Gradient analysis

The vegetation of the studied mixed mire can be characterised phytosociologically as a fine-scale mosaic of the *Caricion davallianae* (pools), *Sphagno warnstorffii-Tomenthypnion* (lawns) and *Sphagno recurvi-Caricion canescentis* alliances. Their positions on the transects are indicated in Fig. 2. A total of 22 cryptogamous species (20 bryophytes, 1 lichen and 1 macroalgae species) and 26 vascular plant species were identified in the sample plots. The pH ranged from 3.7 in the hummocks to 7.4 in the fen pools, conductivity from 13 to 766 $\mu\text{S}/\text{cm}$ and redox potential from -320 to $+290$. This implies that there is a very long gradient of ecological factors in the studied mixed mire, which is reflected in the fine-scale variation in vegetation composition. The bryophyte data-set is governed by a single dominant gradient as reflected in a length of the first DCA axis (6.078). Species ordination scores (in Fig. 3 related to mean pH values) indicate that the first DCA axis can be interpreted as a major successional gradient and correlates significantly ($P < 0.001$) with all measured environmental variables. The highest correlation values are with height above water level

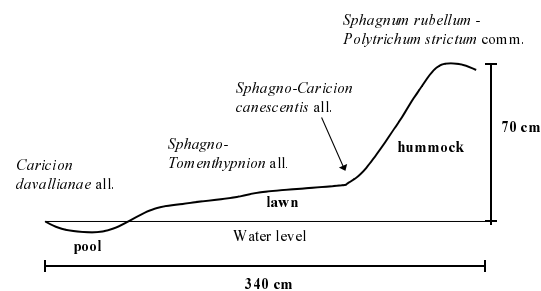


Fig. 2. Patterning of vegetation types relative to water level on one of the transects (all. = alliance; comm. = community).

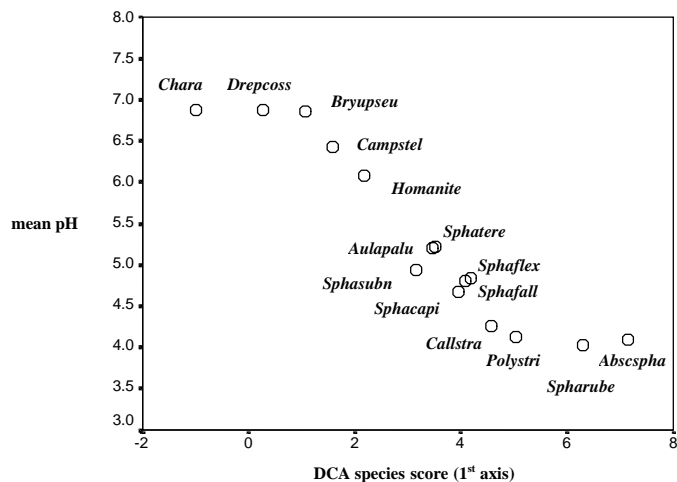


Fig. 3. DCA species scores from the first axis related to mean pH values of the sites where the species occurred. Species list: *Absconditella sphagnum* (Abscspha); *Aulacomnium palustre* (Aulapalu); *Bryum pseudotriquetrum* (Bryupseu); *Calliergon stramineum* (Callstra); *Campylium stellatum* (Campstel); *Drepanocladus cossonii* (Drepcoss); *Chara* sp. (Chara); *Polytrichum strictum* (Polystri); *Sphagnum capillifolium* s.s. (Sphacapi); *Sphagnum fallax* (Sphafall); *Sphagnum flexuosum* (Sphaflex); *Sphagnum rubellum* (Spharube); *Sphagnum subnitens* (Sphasubn); *Sphagnum teres* (Sphatere); *Tomenthypnum nitens* (Homanite).

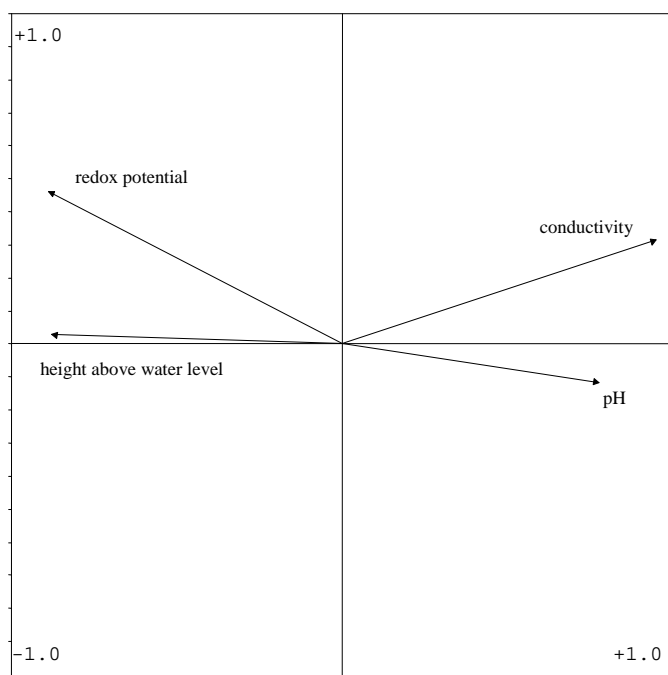


Fig. 4. PCA ordination of environmental variables (eigenvalues: the 1st axis 0.852, the 2th axis 0.146).

($r = 0.907$) and with pH ($r = -0.829$). However, all four measured factors are strongly intercorrelated ($P < 0.001$). The redox potential grows with increasing height above water level, whereas pH and conductivity decrease (Fig. 4). The first axis in the PCA of environmental factors also explains the most variability in the environmental data (85.2%), while the second axis explains only 14.6% of variation.

pH is the most important factor in the cen-

tral part of the major gradient (Fig. 3). This figure suggests that other factors are more important at both of the pH-extremes. *Chara* sp., *Drepanocladus cossonii* and *Bryum pseudotriquetrum* occurred under the same mean pH values (about 7). However, *Chara* and *Drepanocladus cossonii* populated the lower parts of the transects (fen pools) under reducing conditions, whereas *Bryum pseudotriquetrum* grows in the lawns together with *Campylium stellatum* and *Tomenthypnum nitens*.

Table 1. Environmental parameters expressed as means (\pm standard deviation) for each cryptogamous species occurring in no less than 3 sample plots. n – number of plots; HAW – height above water level; redox – redox potential; cond. – conductivity. For an explanation of species abbreviations, see species lists in Figs 3 and 5.

	n	HAW (cm)	pH	redox (mV)	cond. (μ S/cm)
<i>Abscspha</i>	3	57.7 \pm 6.60	4.1 \pm 0.22	252 \pm 32.78	49 \pm 17.72
<i>Aneuping</i>	10	17.5 \pm 3.32	6.77 \pm 0.71	2.8 \pm 106.06	403 \pm 98.64
<i>Aulpalu</i>	11	21.55 \pm 7.49	5.20 \pm 1.11	141.00 \pm 73.00	312.27 \pm 145.79
<i>Bryupseu</i>	15	13.13 \pm 5.98	6.85 \pm 0.29	-7.00 \pm 101.29	443.07 \pm 101.71
<i>Callstram</i>	10	31.70 \pm 12.11	4.25 \pm 0.36	137.40 \pm 75.46	225.90 \pm 136.14
<i>Campstel</i>	23	13.48 \pm 6.56	6.43 \pm 0.88	-14.35 \pm 120.31	410.57 \pm 148.33
<i>Chara</i>	3	0 \pm 0	6.87 \pm 0.05	-260 \pm 24.50	453.7 \pm 37.24
<i>Drepcoss</i>	29	9.48 \pm 7.36	6.87 \pm 0.24	-79.14 \pm 133.71	424.45 \pm 85.95
<i>Homanite</i>	42	16.71 \pm 8.54	6.08 \pm 1.11	46.40 \pm 108.99	370.05 \pm 139.18
<i>Hypnlind</i>	3	26 \pm 4.55	4.65 \pm 0.25	92 \pm 15.58	194.7 \pm 32.29
<i>Polystri</i>	26	44.50 \pm 13.78	4.13 \pm 0.28	205.38 \pm 58.47	104.58 \pm 72.07
<i>Sphcapill</i>	7	27.14 \pm 7.20	4.68 \pm 0.69	138.00 \pm 60.99	274.57 \pm 228.18
<i>Sphfallax</i>	18	24.39 \pm 6.17	4.80 \pm 0.93	141.11 \pm 71.00	274.33 \pm 104.29
<i>Sphflex</i>	6	22.33 \pm 6.92	4.83 \pm 0.66	81.00 \pm 51.73	252.50 \pm 69.44
<i>Spharube</i>	21	47.86 \pm 12.90	4.02 \pm 0.17	221.43 \pm 45.86	88.62 \pm 69.04
<i>Sphsubni</i>	6	20.33 \pm 4.61	4.93 \pm 0.77	101.67 \pm 72.44	390.17 \pm 133.06
<i>Sphatere</i>	19	20.95 \pm 5.97	5.22 \pm 1.11	116.26 \pm 87.57	361.21 \pm 124.67

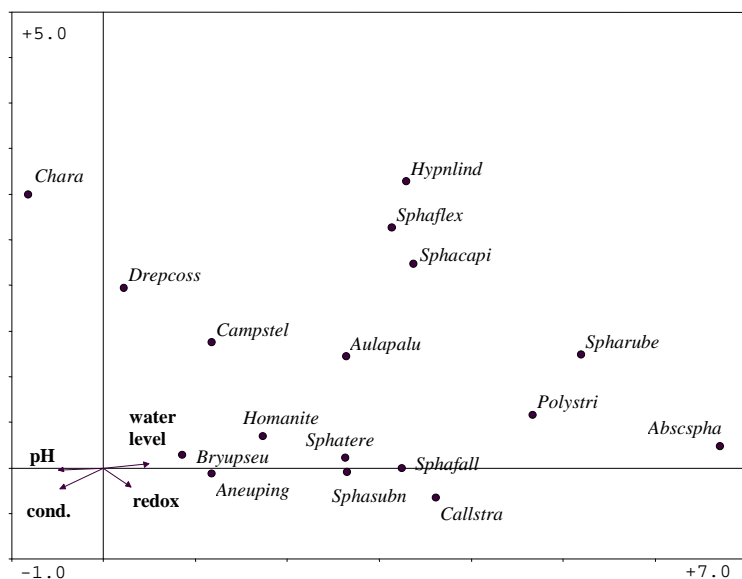


Fig. 5. DCCA ordination of the cryptogamous data set. For an explanation of species abbreviations, see species list in Fig. 3 except *Hypnum lindbergii* (Hypnlind) and *Aneura pinguis* (Aneuping).

The optima of the two latter species are, however, shifted more towards microhabitats elevated from the water level (for all mean values see Tab. 1). The first calcitolerant *Sphagnum* species, which appear along the succession gradient, are *Sphagnum teres* and *S. subnitens*, whose mean pH values are 5.22 and 4.93, respectively. Similar mean pH values are found in the microhabitats of the species *Sphagnum flexuosum*, *S. fallax* and *S. capillifolium*

s.s., among which *S. flexuosum* occurs nearer to water level. The lowest mean pH values (about 4) are connected to the occurrence of hummock-building species *Sphagnum rubellum* and *Polytrichum strictum*. They occur over the entire hummock. Only rarely the lichen *Absconditella sphagnumorum* was found on *Sphagnum* plants under extreme conditions at hummock tops. This lichen was previously published from only a few mires

Table 2. Percentage variance (PV) in cryptogamous and vascular plant species data explained by all canonical axes in single-variable CCAs. The results of the Monte-Carlo test are added, all are significant at a significance level of 0.01.

	HAW	pH	redox potential	conductivity
Cryptogamous				
PV explained (%)	16.7	16.6	13.6	13.6
Monte-Carlo test: F	15.4	15.3	12.1	12.1
Vascular plants				
PV explained (%)	6.5	7.7	5.1	5.5
Monte-Carlo test: F	4.6	5.5	3.6	3.8

in Slovakia (GUTTOVÁ & PALICE, 1999).

The direct ordination of the bryophyte data-set (DCCA), using all measured environmental data as constraining variables, resulted in a nearly identical ordering of moss species along the main gradient as DCA (Fig. 5). A second gradient related to redox potential appeared in the ordination diagram. According to the percentage variance explained by canonical axes in single-variable CCAs, the pH and height above water level seem to have the same important role (Tab. 2). The percentage of species data variance explained by these factors is 16.7 and 16.6, respectively. Two other factors (conductivity and redox potential) explain less variance (13.6%). Different results were obtained for the vascular plant data-set (Tab. 2). Here, the main factor affecting the species composition is pH (7.7% explained variance). Height above water level explains less variance (6.5%). It is noteworthy that the measured ecological factors explain much more variance in bryophyte species data than in vascular plant species data with similar species richness (22 bryophyte and 26 vascular plant species). The bryophytes (especially *Sphagnum*-species) with their ability to direct succession can better characterise the abiotic conditions of the microsite than can vascular plant species.

Niche breadth

Chara is a very specialised organism and grows only in mineral-rich pools. Therefore, the narrowest niche breadth for both factors, pH and height above water level, was found for it (Tab. 3). Similarly, *Absoconditella sphagnorum*, which was detected only on the top of hummocks, has a very narrow niche breadth for both factors. The bryophytes growing on the lawns had an average niche breadth, with the exception of *Campylium stellatum* and *Tomenthypnum nitens*, which tolerate wide ranges of pH (Tab. 3; breadth niche

Table 3. Cryptogamous habitat niche breadths for height above water level (HAW) and pH. Species are ordered according to the DCA ordination scores.

	HAW	pH
<i>Chara</i> sp.	0.100	0.100
<i>Drepanocladus cossonii</i>	0.243	0.244
<i>Bryum pseudotriquetrum</i>	0.277	0.259
<i>Campylium stellatum</i>	0.296	0.508
<i>Tomenthypnum nitens</i>	0.397	0.528
<i>Sphagnum subnitens</i>	0.207	0.280
<i>Aulacomnium palustre</i>	0.286	0.296
<i>Sphagnum teres</i>	0.299	0.236
<i>Sphagnum capillifolium</i> (s.s.)	0.203	0.248
<i>Sphagnum fallax</i>	0.295	0.296
<i>Sphagnum flexuosum</i>	0.229	0.153
<i>Calliergon stramineum</i>	0.363	0.284
<i>Polytrichum strictum</i>	0.551	0.268
<i>Sphagnum rubellum</i>	0.496	0.197
<i>Absoconditella sphagnorum</i>	0.195	0.174

0.5). Compared to the other *Sphagnum*-species, *Sphagnum rubellum* has the largest niche breadth along the water level gradient, similar to non-sphagnous mosses *Polytrichum strictum* and *Calliergon stramineum*.

The niche breadths of vascular plants calculated for the study area are more difficult to interpret. Species growing only in pools (*Eriophorum angustifolium*, *Juncus articulatus*) or rare at the locality (*Carex paniculata*, *Festuca rubra*) occupy the narrowest niches on the site (Tab. 4). Surprisingly, the widest niche breadth for pH and height above water level was found for *Drosera rotundifolia*, which is often reported from very oligotrophic and acidic sites. Here, this species grows not only on the ombrotrophic hummocks, but also in lawns, in the vegetation of the *Sphagnum warnstorfi*-*Tomenthypnion* alliance.

Table 4. Vascular plant habitat niche breadths for height above water level (HAW) and pH. Species are ordered according to the DCA ordination scores.

	HAW	pH
<i>Juncus articulatus</i>	0.132	0.100
<i>Pinguicula vulgaris</i>	0.198	0.100
<i>Blasmus compressus</i>	0.288	0.301
<i>Carex panicea</i>	0.328	0.242
<i>Triglochin palustre</i>	0.246	0.381
<i>Succisa pratensis</i>	0.302	0.220
<i>Primula farinosa</i>	0.176	0.256
<i>Festuca rubra</i>	0.134	0.241
<i>Potentilla erecta</i>	0.270	0.194
<i>Eriophorum angustifolium</i>	0.124	0.111
<i>Briza media</i>	0.287	0.235
<i>Cirsium palustre</i>	0.199	0.300
<i>Nardus stricta</i>	0.318	0.118
<i>Drosera rotundifolia</i>	0.551	0.615
<i>Carex nigra</i>	0.460	0.338
<i>Vaccinium vitis-idaea</i>	0.395	0.226
<i>Carex paniculata</i>	0.188	0.244

Species richness and pH distribution

The highest species richness was found in moderately alkaline lawns, between 10 and 30 cm above water level (Fig. 6). These are the microhabitats where brown mosses (*Amblystegiaceae*) and calcicole vascular plant species (*Primula farinosa*, *Pinguicula vulgaris*, *Carex davalliana*) can coexist with calcitolerant *Sphagnum* species. The vascular plant species intensify the extraordinary species richness in lawns, because they are not restricted here by either low pH or reducing condi-

tions. Therefore, the dependence of overall species richness on height above water level is presented (Fig. 6).

Although there is a wide range of pH on the locality, most pH values recorded were around 4 or 7 (Fig. 7). pH between 5 and 6.1 was not measured in any case.

Discussion

In the studied mixed mire, pH and height above water level were intercorrelated, pH decreased with increasing height above water level and both factors explained the same percentage of moss data variance. On ombrotrophic bogs the water chemistry gradients are of less importance than shade or drought gradients (BELLAND & VITT, 1995). Authors dealing only with bogs or oligotrophic mires found that water level depth is more important than chemical status in influencing the distribution of *Sphagnum* species (cf. KARLIN & BLISS, 1983; ANDRUS et al., 1983; BRAGAZZA, 1997; DÜNHOFEN & ZECHMEISTER, 2000). However, the water or substrate chemistry are the most important factors determining mire vegetation composition at the landscape level (the so-called poor-rich gradient), especially in fens without marked microtopography (SJÖRS, 1952; PERSSON, 1962; MALMER, 1962; KARLIN & BLISS, 1983; GERDOL, 1995; GERDOL & BRAGAZZA, 2001; HAJEK et al., 2002).

The moss species occupying the extremes of the water-level gradient (hollows and high hummocks) exhibit the lowest niche breadths for pH, whereas the highest niche breadths are exhibited

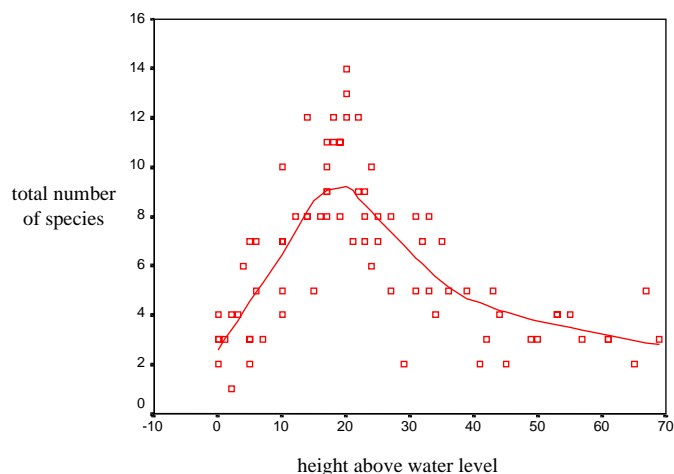


Fig. 6. The relationship between the total number of species (vascular plants + bryophytes on the area 78.5 cm²) and the height above water level. The curve is fitted by local linear regression.

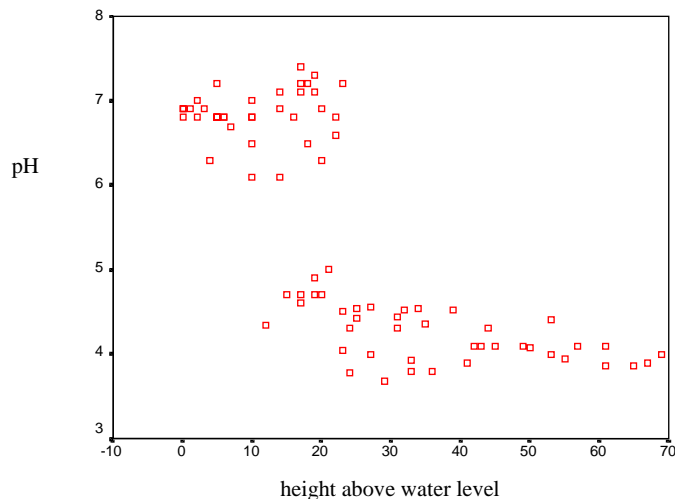


Fig. 7. Bimodal distribution of pH values related to height above water level.

by the lawn or midhummock species (VITT & SLACK, 1984; BRAGAZZA, 1997). This situation was also detected in our study. These differences in niche breadth could be caused by competition, survival strategy (e.g. type of growth) or physiological tolerance to a different range of ecological factors (for details see ANDRUS et al., 1983; ANDRUS, 1986; BRAGAZZA, 1997; DUENHOFEN & ZECHMEISTER, 2000). The hummock-building *Sphagnum* species exhibit the greatest niche breadth for height above water level, as well (ANDRUS et al., 1983; VITT & SLACK, 1984). It is caused by their physiological adaptations, which make it possible for them to survive unfavourable water and mineral conditions through hummock building (TITUS et al., 1983; HAYWARD & CLYMO, 1983; ANDRUS, 1986).

The fine-scale pattern of species richness found in the studied mixed mire seems to correspond with that found on a landscape scale (VITT et al., 1995; HÁJEK & HÁBEROVÁ, 2001; HÁJKOVÁ & HÁJEK, 2003). Analysis of phytosociological data shows that the vegetation of circumneutral fens (*Sphagno warnstorfi-Tomenthypnion* alliance especially) have the highest species richness among Slovakian mires (HÁJEK & HÁBEROVÁ, 2001). This fact was also verified in our study for a distinctly patterned locality using small sample plots.

Not only species richness but also the distribution of pH values shows the same pattern as that observed on the landscape level. GORHAM & JANSSENS (1992) described a distinctly bimodal distribution in pH data ranging from about 3–5 in bogs and 6–7 in fens. This sharp drop in pH can happen when peat accumulation isolates the fen

surface from the input of buffering minerotrophic water, containing in particular calcium bicarbonate. This bimodal distribution of pH values on a large scale was reported from the entire boreal zone, from North America (VITT et al., 1995, transitional pH range 5–5.8) and from northern Europe (SJÖRS, 1952, transitional pH range 4.4–5.8). In the mixed mire, the sharp drop in pH was detected in the lower part of hummocks, between 4 and 8 cm above water level (BELLAMY & RIELEY, 1967). The scarcity of mires with pH in the range of 5–6 has a time dimension as well and is due to the short period of existence of these mires in the developmental sequence, as was also found in palaeoecological profiles (KUHRÝ et al., 1993).

The phytosociological classification of mixed mires raises the unsolved question of whether or not to classify the high hummocks separately. We found, using very small relevé plots, a complete exchange of species composition along the ca 3-meter transects. The vegetation as well as the measured environmental factors on high hummocks, was quite different from that in the low-positioned rich fen. KARLIN & BLISS (1983) analysed the upper peat layers of hummocks on ombrotrophic bogs and mixed mires. The chemistry of the peat substrate was identical in both cases. When we accept these facts, we should assign the hummock vegetation to the ombrotrophic mire (bog) communities, although the hummocks are located in rich-fen vegetation.

Mixed mire is a very unique vegetation type within Slovakian mires and does not fall within the classical division of rich fens, poor fens and bogs. Mixed mires are connected with the boreal zone and elsewhere they are developed only on small

areas. Nevertheless, these ecosystems function in the same way even though they are smaller than those in the boreal zone. This is also supported by our results. Carpathian mixed mires represent a good starting point for further research, as well as for conservation-biological activities.

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