Species richness and above-ground biomass of poor and calcareous spring fens in the flysch West Carpathians, and their relationships to water and soil chemistry

Druhová bohatost a nadzemní biomasa prameništních slatinišť flyšových Západních Karpat a jejich vztah k chemismu vody a půdy

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Species richness and above-ground biomass of vascular plants and bryophytes of poor acidic fens (the *Sphagno recurvi-Caricion canescentis* alliance), rich *Sphagnum* fens (the *Caricion fuscae* and *Sphagno warnstorfii-Tomenthypnion* alliances) and calcareous spring fens (the *Caricion davallianae* alliance including tufa-forming spring fens) were studied. The study area was in the western parts of the Outer Carpathians in the border region of the Czech and Slovak Republics. The numbers of species were recorded in plots ranging from 0.00196 to 16 m^2 and correlated with chemical factors and above-ground biomass. The chemical properties of springwater (mainly pH, conductivity, Ca^{2+}, Mg^{2+}) were the main factors influencing the species richness of vascular plants. Tufa-forming calcareous fen communities (*Carici flavae-Cratoneuretum*) had the highest species richness of vascular plants. In contrast, the highest species richness of bryophytes occurred at pH-neutral sites, in peat forming calcareous fen communities (*Valeriano-Caricetum flavae*) and in those with *Sphagnum warnstorfii* and *S. teres*. Bryophyte species richness of small plots was correlated with the iron concentration in the springwater. The differences in species richness of calcareous fens were related to the mowing regime. Litter mass had a negative effect on the species richness of vascular plants. Mosses responded to high amounts of litter or vascular plant biomass by a significant decrease in biomass. Two types of *Sphagnum* fens: (a) strongly dominated by *Sphagnum flexuosum* or *S. palustre* (rich in phosphates) and (b) polydominant (poor in phosphates), were also compared. In the former, the slope of the regression for the dependence of bryophyte species richness on plot size was less steep.

K e y w o r d s : bryophytes, Central Europe, diversity, mires, scale-dependent species richness, springwater chemistry, standing crop, wetlands

Introduction

There are spring fen communities with different species richness in the Western Carpathian flysch zone (Hájek 1998, Hájková & Hájek 2000, Hájek & Hájková 2002). Their bryophyte and vascular plant species composition is mainly influenced by groundwater chemistry, especially pH, conductivity and mineral richness (Hájek et al. 2002), which reflect the bedrock chemistry (Rapant et al. 1997). It is unknown whether acidity and mineral richness, or other factors, affect species richness and the amount of above-ground biomass and whether bryophytes and vascular plants respond to these factors in different ways. Relationships between species richness, above-ground biomass and environmental factors are plot size sensitive (Oksanen 1996, Pastor et al. 1996, Marañón & García 1997) and therefore their study necessitates using a series of various plot sizes.

In the southwestern part of our study area (the Bílé Karpaty Mts), the scale-dependent species richness of calcareous sub-xeric meadows was studied by Klimeš (1997). However, there is no data on bryophyte- and vascular plant species richness, above-ground biomass or their inter-relationships in spring fen vegetation for this or adjacent areas. Many authors have explored these relationships in Europe and North America. The relationships between species richness and above-ground biomass were investigated by Wheeler & Giller (1982), Wheeler & Shaw (1991), García et al. (1993), Gough (1994), Bergamini et al. (2001) and Virtanen et al. (2001), that between species richness and soil chemistry by Janssens et al. (1998) and the relationships between available nutrients and above-ground biomass by Vermeer & Berendse (1983). Some of these authors studied both low-sedge fen communities with a low productivity and highly productive communities on fertile sites such as tall-sedge and reed communities or communities strongly dominated by *Filipendula ulmaria* or *Molinia coerulea* agg. (e.g. Wheeler & Giller 1982, Boyer & Wheeler 1989, Wheeler & Shaw 1991). In such cases, they recorded differences in biomass among communities which were related to species richness. The spring fen communities that we studied in the Western Carpathian flysch zone all had a low productivity. We wanted to determine whether the same species richness-biomass relationships occurred in spring fen habitats. Because vegetation in most of these spring fens developed under specific past mowing regimes, it was expected that species richness and above-ground biomass would differ between stands, which are still being and are no longer mowed.

The principal aims of this study are: (i) to present information on the species richness and above-ground biomass of bryophytes and vascular plants in four major vegetation types in the Western Carpathian flysch zone (*Carici echinatae-Sphagnetum, Sphagnum warnstorfii-S. teres* community, *Valeriano-Caricetum flavae*, *Carici flavae-Cratoneuretum*); (ii) to describe the species-area relationships for different vegetation types; (iii) to determine the environmental factors that coincide with species richness in spring fen vegetation; (iv) and to find and compare factors that influence species richness in two contrasting fen habitats, the calcareous- and the poor acidic.

Study area and localities

The spring fens studied are located in the Western Carpathian flysch zone, in the border region between the Czech and Slovak Republics. This includes the Bílé Karpaty Mts in the southwest, the Hostýnské and Vsetínské Mts. in the central part and the Moravskoslezské Beskydy Mts, the Turzovská Vrchovina Mts. and the Kysucké Beskydy Mts in the north-east (Fig. 1). Alternating deposits of sandstone and claystone of different calcium contents are typical of flysch beds. The study area belongs to four geological units. The claystones, marls and calcified sandstones of the Bílé Karpaty Unit prevail in the south-western part. Here, the springwater is mineral-rich and often saturated by HCO_3^- ions, which often results in tufa formation. The Bystrica- and Rača Units in the north-eastern part of the study area are characterized by moderately calcified claystones and sandstones. The northern part of the area belongs to the Silesian Unit, which is composed of decalcified, sometimes iron-cemented sandstones.

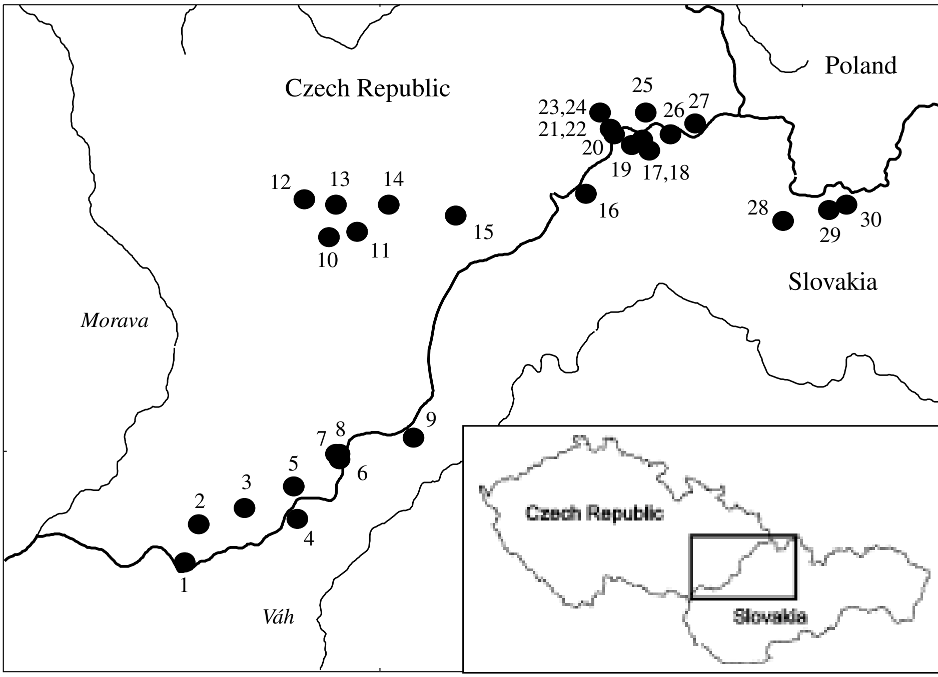

Fig. 1. – Location of the study sites in the border region of the Czech and Slovak Republics. Coordinates: NE corner 49°40'N + 19°15'E; SW corner 48°35'N + 17°05'E. Notes and descriptions of the habitats are in Appendix 1.

The fens studied in the south-western part are located at lower altitudes (calcareous fen "U Baladů", 390 m a.s.l.) than those in the north-eastern part (poor fen "Biely kríž", 905 m a.s.l.). The annual mean precipitation increases from the south-west (Bošáca: 713 mm, in the vegetation period April–September 383 mm) to the north-east (Vyšní Mohelnice: 1327 mm, in the vegetation period April–September 795 mm). The annual mean temperature varies between 5.4 °C (NE, Bílá-Salajka) and 8.4 °C (SW, Bojkovice).

Thirty localities distributed along the entire geographical gradient (from the south-west to the north-east) were selected for this study (Fig. 1). They included different bedrocks ranging from mineral-rich to mineral-poor springs (Hájek et al. 2002). All localities were designated as sloping or sub-sloping helocrene springs of uniform surfaces without distinct superficial structures. Small streams, which can dry up in summer occur in some of the spring fens. In some poor fens, very low hummocks of the peat mosses *S. capillifolium* and *S. palustre* occur. For a detailed description of localities and vegetation types see Appendix 1.

Methods

Vegetation data sampling

A complete list of bryophyte and vascular plant species was recorded at all 30 localities from 1999 to 2000. The following plot sizes were used: 0.00196 (d = 5 cm); 0.00785 (d = 10 cm); 0.07 (d = 30 cm); 0.25 (0.5 × 0.5 m); 1.00 (1 × 1 m); 4.00 (2 × 2 m) and 16.00 (4 × 4 m) m^2.

The three smallest plots (to 0.07 m^2) were circular and were replicated three times at each locality; then the mean number of species was determined. The quadrate plots that were larger than 0.25 m^2 were replicated only once at each locality. Species cover was estimated using a nine-grade scale (van der Maarel 1979). Plots were sampled in an independent, non-nested design (Podani 1984). The plots were randomly placed and separated from each other, within the prevailing vegetation type in terms of species composition and dominants. Clearly different streams and hillocks, when they occurred, were not included.

Biomass sampling

Above-ground biomass for each locality was harvested from one randomly placed 0.07 m^2 circle plot in July 2002. The material was divided into bryophyte biomass (B), living standing crop (SC) and litter mass (L), including dead standing crop. Only the upper, living parts of peat mosses were collected, which were distinct from the semi-decomposed lower parts. Biomass was dried (60 °C) to a constant weight and expressed in $g \cdot m^{-2}$.

Water and soil sampling

Water samples were taken in August from micro-sites in the central parts of the springs to determine the amount of dissolved ions entering the fen ecosystem. Water conductivity and pH, both standardized at 20 °C, were measured in situ using portable instruments (CM 101 and PH 119, Snail Instruments). Conductivity due to H^+ ions in acid water was subtracted (Sjörs 1952). For ion concentration determination, conservants were added to divided samples: for metallic elements (Ca^{2+}, Mg^{2+}, total Fe, K^+, Na^+, total Si), 0.5 ml of concentrated HNO_3 per 100 ml of sample; for anions and ammonium (SO_4^{2-}, PO_4^{3-}, NO_3^-, NH_3^+, Cl^-), 3 ml of chloroform per 1000 ml (Horáková et al. 1989). A mixed soil sample was taken from the rhizosphere (5–30 cm) at each locality and analysed for Ca^{2+}, Mg^{2+}, K^+, Na^+, P_2O_5, organic C and organic N. For details of the water and soil analyses see Hájek et al. (2002).

Data analysis

Vegetation data (16 m^2) was subjected to detrended correspondence analysis (DCA) with downweighting of rare species (ter Braak & Šmilauer 1998). The first DCA axis resulting from this ordination was arbitrarily divided into four sections to obtain groups of samples that corresponded to distinct vegetation types (see Hájek et al. 2002: Table 1). The first group consists of communities of the *Carici echinatae-Sphagnetum* association found on acidic, mineral-poor fens (A). The next group consists of moderate-rich fens with calcitolerant *Sphagnum*-species (B), of which there are only three cases rare in the study area. The third group consists of calcium-rich fens accumulating organic peat (the *Valeriano-Caricetum flavae* association) and the fourth of the *Carici flavae-Cratoneuretum* association, which is characterized by the accumulation of calcareous tufa (cold-water travertine) instead of organic peat. The two latter groups include vegetation types transitional between typical fens and wet meadows corresponding to the *Cirsietum rivularis eriophoretosum latifolii* subassociation.

Independent of this classification, the calcium-rich fens were divided into (i) regularly mowed and (ii) unmowed for 2–3 years; the *Sphagnum*-fens were divided into (i) monodominant communities (*Sphagnum flexuosum* or *S. palustre* > 75% cover) and (ii) polydominant communities.

Table 1. – The number of species of bryophytes (b), vascular plants (v) and the total number of species (b+v) for the four largest plot areas (16 m^2, 4 m^2, 1 m^2 and 0.25 m^2) at all of the localities. The five topmost values in each column are in bold font. Capital letters (A–D) indicate groups of habitats, delimited according to their position in the DCA ordination diagram (Fig. 2, Appendix 1). Numbers of localities correspond to Fig. 1.

Localities	16b	16v	16b+v	4b	4v	4b+v	1b	1v	1b+v	0.25b	0.25v	0.25b+v
A 17 Zajacovci	4	13	17	6	15	21	4	11	15	4	6	10
19 PR Polková	6	23	29	2	13	15	5	10	15	3	8	11
20 Jančíkovci	5	7	12	4	8	12	5	7	12	3	5	8
21 Biely kríž horní	4	14	18	5	11	16	4	10	14	5	8	13
22 Biely kríž dolní	5	9	14	5	9	14	4	9	13	4	5	9
24 PR Obidová	5	16	21	5	10	15	5	9	14	4	7	11
26 Korcháňovci	4	12	16	3	12	15	3	10	13	3	7	10
27 PP Vřesová stráň	4	21	25	2	22	24	2	16	18	2	11	13
B 12 Rajnochovice	7	27	34	4	19	23	4	15	19	4	16	20
23 PR Obidová	**12**	29	41	**10**	28	**38**	5	23	28	5	**20**	25
25 Horní Lomná	7	27	34	7	21	28	**8**	18	26	4	15	19
C 10 Pivovařiska	8	**46**	54	7	**36**	43	5	**30**	35	4	**25**	29
15 Hrubé Brodské	**10**	44	**54**	**9**	39	**48**	**8**	32	**40**	**6**	24	**30**
16 Kelčov	**9**	30	39	7	24	31	**7**	18	25	**6**	16	22
18 Cudrákovci	**9**	26	35	**9**	25	34	**8**	23	31	**7**	18	**25**
28 Lány	**9**	31	40	**9**	28	**37**	7	**25**	**32**	8	**20**	**28**
29 Grigovci	6	33	39	6	31	**37**	6	**25**	31	5	18	23
30 Vychylovka	8	34	**42**	5	28	33	**8**	20	28	4	15	19
9 Vlárský průsmyk	7	27	34	6	20	26	5	14	19	3	13	16
D 1 Machová	8	28	36	7	24	31	5	19	24	4	14	18
11 U Sládků	7	33	40	6	24	30	5	22	27	2	14	16
13 Kateřinice	8	16	24	6	14	20	4	11	15	3	9	12
14 Jasénka	5	15	20	5	14	19	6	12	18	4	10	14
2 U Baladů	7	21	28	5	17	22	3	13	16	5	11	16
3 Hrnčiarky	7	**44**	51	3	**32**	35	3	23	26	4	15	19
4 PP Grúň	6	34	40	6	23	29	4	20	24	3	13	16
5 Hrubý Mechnáč	6	32	38	5	31	36	6	19	35	4	17	21
6 PR Hutě	4	**37**	41	4	**32**	36	5	**26**	**32**	3	17	20
8 U Kročila	7	**44**	51	6	**36**	42	5	**29**	34	4	**23**	27
7 U Ondryša Machaly	7	34	41	6	26	32	5	24	29	5	17	22

The slope of the regression line expressing the relationship between species richness and plot size (b coefficient in the formula $N = a + \log A^b$; N is number of species, A is plot size, a and b are the coefficients) was calculated for 30 localities. The relationships between species richness, chemical quality of the environment, biomass (B, SC, L) and slope of the regression line were tested using Pearson's correlation coefficient and partial correlation. The non-parametric Mann-Whitney test was used to statistically evaluate differences between pairs of site groups for which there were few replicates (Tables 4, 5). The linear dependence of number of species on the plot size on a log-scale (Rosenzweig 1995) was determined for the following groups of localities: (a) polydominant *Sphagnum*-fens; (b) monodominat *Sphagnum*-fens; (c) mowed calcareous fens and (d) unmowed calcareous fens. A scatter plot was made of the data from all localities belonging to groups a–d, and a linear regression fitted. This procedure led to a simple comparison of species-area relationships between the vegetation types with concurrent minimization of the biases caused by the independent design, which is sensitive to stand heterogeneity (Podani 1984).

Nomenclature

The names of syntaxa were unified according to Valachovič (2001), bryophyte nomenclature follows Frey et al. (1995), and vascular plant nomenclature Marhold (1998).

Results

Comparison of species richness between sites

The comparison of species richness between sites is strongly scale-dependent (Table 1). Some sites are species-rich relative to others only at large plot sizes, and relatively species-poor at small plot sizes (e.g. Hrnčiarky, Vychylovka, Hutě). In contrast, some stands are species-rich only at small plot sizes (e.g. Lány). Some sites are species-rich in both mosses and vascular plants (e.g. Hrubé Brodské), others have only a high number of vascular plant species (e.g. Pivovařiska). Some sites are rich in bryophyte species, but only moderately rich in vascular plant species (e.g. Kelčov and Cudrákovci). Habitats in which fen and meadow species coexist have the highest species richness of both taxa in all sizes of plots (e.g. Hrubé Brodské, U Kročila, Pivovařiska).

Relationships between species richness and environmental factors

Vascular plant species richness increases significantly with increasing electrical conductivity, pH and concentration of calcium and magnesium in springwater (Table 2). It was most strongly correlated with water pH even for the smallest plots. Thus the community species richness reflects the chemistry of springwater. The calcareous spring fens, with tufa-formation, are the richest in vascular plant species (up to 46 species in 16 m^2 plots), and have the highest above-ground vascular plant biomass (Table 3). The negative correlation between the vascular plant species richness and soil organic carbon content also coincides with a major chemical gradient. The sites with the lowest calcium content (poor acidic fens) are characterized by high organic matter accumulation. Species richness and vascular plant biomass are very low on these sites (Table 3).

Whereas the species richness of vascular plants increases linearly from the poor acidic fens to the calcareous fens, the pH-neutral spring fens (pH 6–7) have the highest number of bryophytes. The bryophyte species richness of the smallest plots does not significantly correlate with the main chemical factors (pH, Ca^{2+}), but is strongly correlated and increases linearly with the total Fe concentration in the water on plots up to 1 m^2 (Table 2, Fig. 2c). However, this relationship is not statistically significant for plots larger than 1 m^2 (Fig. 2d).

Species richness of bryophytes and vascular plants does not significantly correlate with other chemical properties (K^+, Si^+, SO_4^{2-}, NO_3^-, NH_3^+, Cl^- in water; Ca^{2+}, K^+, P_2O_5 in soil) or only for some plot sizes for unknown reasons (Na^+ in water and soil; Table 2).

Differences in species richness of plots of various sizes are reflected in the slope of the regression line (Table 3). The value of this slope for bryophytes and vascular plants does not correlate with chemical properties of the springwater; no differences in this value were detected even between vegetation types (Table 3). Even though water chemistry significantly affects species richness, it has no influence on the species-area relationship.

Significant differences in bryophyte and vascular plant species richness between (i) habitats with *Sphagnum* mosses (mineral-poor part of the major gradient, groups A and B in Ta-

Table 2. – Correlations between species richness and enviromental factors (30 localities). Ca in water (mg·l^{-1}), Mg in water (mg·l^{-1}), pH and conductivity of water (µS·cm^{-1}; 20 °C), Corg: organic matter content (%), Fe in water (mg.l^{-1}), Na in water (mg.l^{-1}), Na in soil (mg.kg^{-1} of dry soil), SC: standing crop (g·m^{-2}), L: litter mass (g·m^{-2}), E_0 – bryophytes, E_1 – vascular plants. The values of Pearsons' correlation coeficient are shown for chemical factors in water and soil, partial correlation coefficients (after controlling for pH) are shown for biomass. Significance levels: * P < 0.05, ** P < 0.01, *** P < 0.001, n.s. – not significant, P > 0.05.

Factors		16 m^2		4 m^2		1 m^2		0.25 m^2		0.07065 m^2		0.00785 m^2		0.00196 m^2		
		E_0	E_1	E_0	E_1	E_0	E_1	E_0	E_1	E_0	E_1	E_0	E_1	E_0	E_1	SC
Water	Ca	n.s.	0.52**	n.s.	0.43*	n.s.	0.42*	n.s.	n.s.	n.s.	0.38*	n.s.	n.s.	n.s.	n.s.	0.57***
	Mg	n.s.	0.41*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	pH	n.s.	0.65***	n.s.	0.62***	n.s.	0.61***	n.s.	0.55**	n.s.	0.57***	n.s.	0.51**	n.s.	0.37*	0.59***
	kond	n.s.	0.57***	n.s.	0.52**	n.s.	0.48**	n.s.	0.43*	n.s.	0.48**	n.s.	0.40*	n.s.	n.s.	n.s.
	Fe	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.38*	n.s.	0.46**	n.s.	0.62***	n.s.	0.61***	n.s.	n.s.
	Na	0.38*	0.39*	n.s.	0.38*	n.s.	n.s.	n.s.	n.s.	n.s.	0.41*	0.54**	0.45**	n.s.	n.s.	n.s.
Soil	Corg	n.s.	–0.45**	n.s.	–0.42*	n.s.	–0.39*	n.s.	–0.39*	n.s.	–0.36*	n.s.	n.s.	n.s.	n.s.	–0.53**
	Na	0.38*	n.s.	n.s.	n.s.	0.56***	n.s.	0.50**	0.39*	n.s.	0.50***	0.49**	0.57***	0.52**	0.54**	n.s.
Biomass	L	n.s.	–0.55**	n.s.	–0.51**	n.s.	–0.57***	n.s.	–0.41*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	SC	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	–

Table 3. – The mean values and standard deviations (S. D.) of the species richness of the 16 m^2 and 0.00196 m^2 plots (E_0 – bryophytes, E_1 – vascular plants), slope of regression (b E_0 – for bryophytes, b E_1 – for vascular plants), standing crop (SC, g·m^{-2}), litter mass (L, g·m^{-2}), bryophyte biomass (B, g·m^{-2}), total crop (Σ, g·m^{-2}) and some abiotic factors: Ca (mg.l^{-1}), pH and conductivity (cond., µS.cm^{-1}; 20°C) of water, organic matter content (%), P_2O_5 in soil (mg.kg^{-1} of dry soil) and SO_4^{2-} in water of poor acidic fens (A), rich *Sphagnum* fens (B), peat-forming rich fens (C) and tufa-forming rich fens (D). For statistical analyses of the differences between the groups a Mann-Whitney test (U) was used; only the significance values are presented (P).

Vegetation type		16 m^2		0.00196 m^2		slope		Biomass				Abiotic factors					
		E_0	E_1	E_0	E_1	b E_0	b E_1	SC	L	B	Σ	Ca	pH	cond.	Corg	P_2O_5	SO_4^{2-}
A. Poor acidic fens	mean	4.63	14.38	1.96	1.58	0.71	0.93	145.77	79.97	521.74	747.49	6.81	5.13	37.88	20.95	7.28	25.38
	S. D.	0.70	5.15	0.73	1.04	0.09	0.02	64.68	21.70	239.23	233.14	4.16	0.32	14.01	7.32	6.61	16.83
B. Rich *Sphagnum* fens	mean	8.67	27.67	1.89	2.78	0.85	0.91	188.77	144.28	180.04	513.09	18.79	5.90	98.33	12.78	5.47	22.33
	S. D.	3.27	8.17	0.87	1.31	0.03	0.04	50.88	93.37	139.25	99.33	6.79	0.08	29.26	5.40	1.64	12.76
C.Peat-forming rich fens	mean	8.25	33.88	3.42	4.04	0.79	0.93	167.80	86.04	419.48	673.32	86.49	6.88	345.38	4.52	9.91	13.50
	S. D.	1.20	6.92	1.29	1.62	0.11	0.03	55.74	32.11	291.50	255.40	46.16	0.23	95.75	1.03	5.05	12.36
D.Tufa-forming rich fens	mean	6.55	30.73	2.24	2.52	0.75	0.92	262.63	192.74	345.40	800.77	208.06	7.65	521.64	13.71	9.97	47.55
	S. D.	1.16	9.47	0.99	1.26	0.10	0.05	100.19	139.29	246.59	135.99	91.70	0.52	101.25	5.90	3.36	37.61
P (A vs. B)	n = 11	0.011	0.014	0.917	0.051	0.052	0.836	0.683	0.307	0.066	0.082	0.041	0.307	0.014	0.153	0.918	0.014
P (C vs. D)	n = 19	0.013	0.772	0.032	0.038	0.535	0.934	0.069	0.026	0.509	0.117	0.006	0.001	0.006	<0.001	0.901	0.047
P (A+B vs. C+D)	n = 30	0.009	<0.001	0.020	0.014	0.651	0.665	0.107	0.220	0.464	0.292	<0.001	0.003	<0.001	0.001	0.030	0.863

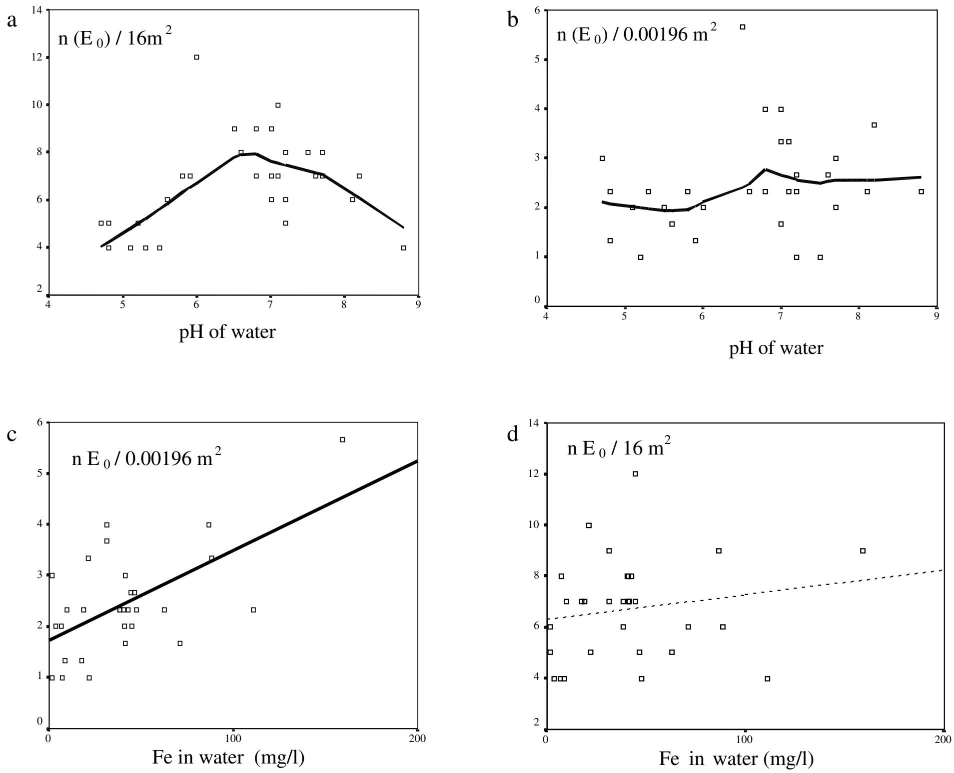

Fig. 2. – The relationship between the number of bryophyte species and pH (a, b), and Fe (c, d) in 16 m^2 and 0.00196 m^2 plots. The curves are fitted by locally weighted linear regression (a, b) and by linear regression (c: $P < 0.001$; d: $P > 0.05$).

ble 3) and (ii) those with prevailing brown mosses (mineral-rich part of the gradient, groups C and D in Table 3) were found for both large and small plots (Mann-Whitney test). Differences in the chemical factors associated with four basic vegetation types are given in Table 3.

Relationship between species richness and above-ground biomass

Differences in the ratio of bryophyte biomass to standing crop at sites with particular vegetation types were recorded (Fig. 3). This ratio correlates significantly ($P < 0.05$) with some chemical factors; positively with organic C, organic N and with soil C/N ratio and negatively with pH. On the poor acidic fens (group A in Fig. 3) this ratio is high and stable, whereas for other vegetation groups (B, C, D) it is variable due to the influence of other factors (e.g. mowing regime). The proportion of bryophyte biomass decreases from the poor acidic fens to the calcareous fens, but surprisingly, some calcareous habitats have ratios as high as the poor acidic habitats.

After the co-variation caused by the most important environmental factor (water pH) is removed, species richness of vascular plants on the larger plots correlates negatively with the amount of litter (Table 2). Increase in litter mass is associated with little increase in vascular plant species numbers with increase in plot size; the slopes of the regression lines

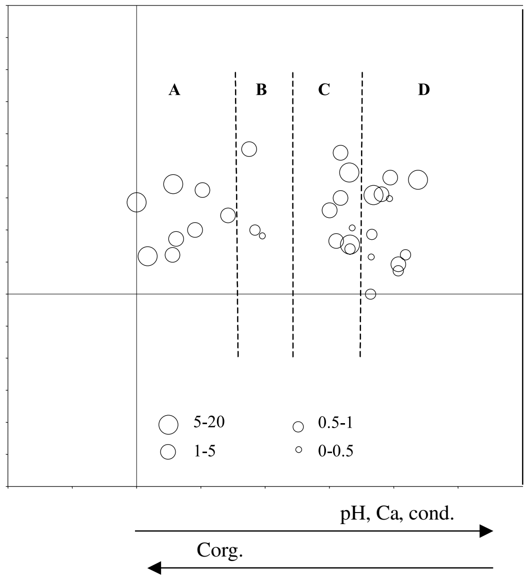

Fig. 3. – A DCA ordination diagram of the phytosociological relevés of 16 m^2 plots. The size of the symbols indicates the ratio of bryophyte biomass to standing crop. A – poor acidic fens (*Carici echinatae-Sphagnetum*), B – rich *Sphagnum* fens with *Sphagnum warnstorfii* and *S. teres*, C – peat-forming rich fens (*Valeriano-Caricetum flavae*), D – the tufa-forming rich fens (*Carici flavae-Cratoneuretum*).

have low values (Table 4). Associated with high amounts of litter or vascular plant biomass is a marked decrease in bryophyte biomass (Table 4).

Relationship between species richness and factors influencing only some vegetation types

Calcareous fen species richness (groups C and D in Table 3) is very dependent on regular mowing. The highest amounts of litter, up to 472 $g \cdot m^{-2}$, accumulated on unmowed calcareous fens. The negative effect of litter mass was reflected in the slow increase in vascular plant species number with increasing plot size (Fig. 4b). The larger plots (1–16 m^2) of mowed calcareous fens had, on average, 10 vascular plant species more than the same plots unmowed for 2–3 years (Table 5). This verified that not only the number of vascular plant species (16 m^2), but also the slope of the species-area regression relationship (b E_1) between mowed and unmowed fens differed. Bryophyte species richness did not differ, but bryophyte biomass was significantly lower on unmowed fens (Table 5).

Mowing did not determine the development of poor acidic fens. Nevertheless, they can be divided into two groups according to their species richness: (i) communities dominated by one species of *Sphagnum* moss (*Sphagnum flexuosum* or *S. palustre*) and (ii) those with a polydominant bryophyte layer. These two habitats also differ in the phosphate concentration of the springwater (Table 5; see also Hájek et al. 2002), which was significantly higher in the former. These two habitat types differ from each other in the slope of the bryophyte species-area relationship (Table 5, Fig 4a). There was no difference in vascular plant species richness associated with plot size.

Table 4. – Matrix of Pearson's correlation coefficients between the above-ground vascular plant biomass, bryophyte biomass, litter mass ($g{\cdot}m^{-2}$) and the slope of the species-area regression line (b E_0: bryophytes, b E_1: vascular plants). Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. – not significant, $P > 0.05$

	b E_1	Standing crop	Litter	Bryophyte biomass
b E_0	n.s.	n.s.	n.s.	n.s.
b E_1		n.s.	–0.56**	n.s.
Standing crop			n.s.	–0.49**
Litter				–0.40*

Table 5. – The mean values and standard deviations (S.D.) of the species richness of the 16 m^2 and 0.00196 m^2 plots (E_0 – bryophytes, E_1 – vascular plants), slope of regression line (b E_0 – for bryophytes, b E_1 – for vascular plants), PO_4^{2-} concentration in water ($mg.l^{-1}$), standing crop (SC, $g{\cdot}m^{-2}$), litter mass (L, $g{\cdot}m^{-2}$) and bryophyte biomass (B, $g{\cdot}m^{-2}$) for (1) monodominant communities with *Sphagnum* species, (2) polydominant communities with *Sphagnum* species, (3) mowed and (4) and unmowed communities on calcareous fens. For statistical analyses of the differences between the groups a Mann-Whitney test (U) was used; only the significance values are presented (P).

Physiognomic type		16 m^2		0.00196 m^2		slope		biomass			
		E_0	E_1	E_0	E_1	b E_0	b E_1	PO_4^{3-}	SC	L	B
1. Monodominant	mean	4.60	17.20	2.20	1.87	0.66	0.94	0.21	173.59	76.15	434.00
Sphagnum	S. D.	0.73	3.80	0.41	0.78	0.06	0.02	0.17	57.27	23.41	166.50
2. Polydominant	mean	6.67	18.67	1.72	1.94	0.83	0.91	0.06	144.09	115.31	424.02
Sphagnum	S. D.	2.43	8.51	0.48	0.88	0.05	0.03	0.02	66.46	73.05	324.53
3. Mowed	mean	7.33	36.50	3.00	3.61	0.78	0.94	0.12	229.85	84.58	434.09
calcareous fens	S. D.	1.48	5.82	1.01	1.18	0.12	0.02	0.21	110.13	24.08	213.40
4. Unmowed	mean	7.14	24.43	2.29	2.38	0.75	0.89	0.07	225.93	285.35	150.55
calcareous fens	S. D.	1.16	6.42	0.90	0.99	0.05	0.03	0.03	57.21	130.11	78.95
P (1 vs. 2)	n=11	0.108	0.855	0.263	0.783	0.010	0.065	0.010	0.273	0.361	0.855
P (3 vs. 4)	n=18	0.631	0.002	0.368	0.073	0.223	0.016	0.110	0.779	0.002	0.011

Discussion

The spring fen communities in the Western Carpathian flysch zone differ in both bryophyte and vascular plant species richness. The species richness of communities of the mineral-poor acidic fens is similar to that of boreal mires, which are very species-poor ecosystems (Vitt et al. 1995, Økland 1992). However, that of Carpathian poor fens has probably declined over the last decades because of increasing phosphate supply, which favours the dominant peat moss species (Hájek et al. 2002). Nevertheless, most of the fen habitats are rather species-rich. In contrast to boreal mires, the species richness of fens is increased by species from wet meadow and other adjacent communities. This is due to the small area of the studied fens, which are often found in mown meadows and exposed to disturbance and mass effect.

The species richness of mowed calcareous fens is comparable to that of the adjacent semi-dry and mesic grassland communities. As there is little data on the species richness of other treeless vegetation for exactly defined plot sizes in this area, a more detailed comparison is impossible. The only exception is the meadows in the Čertoryje Nature Reserve in the Bílé Karpaty Mts (Klimeš 1997). The species richness there exceeds that of the spring fen communities and other grassland in the area.

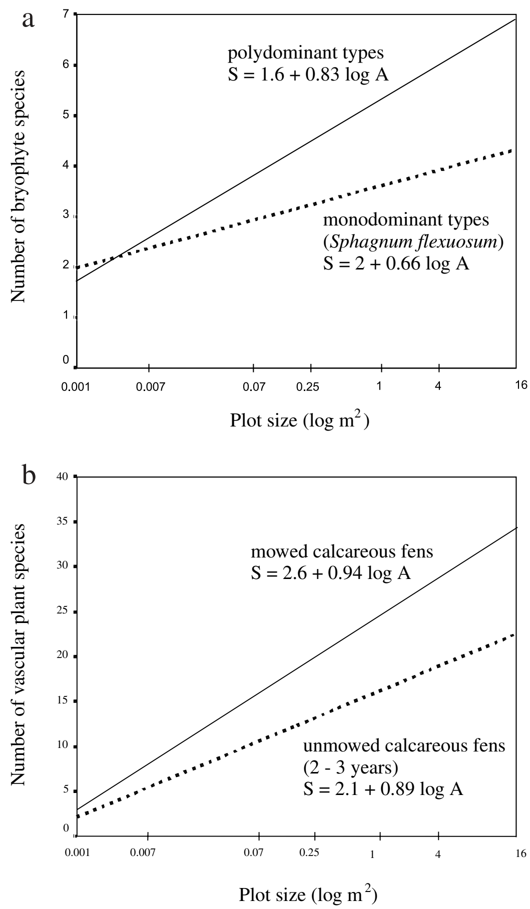

Fig. 4. – The regressions of the dependence of species number on plot size, shown for (a) the *Sphagnum* fens (groups A+B, see Appendix 1) and (b) calcareous spring fens (C+D).

Species richness and chemical factors

Calcareous fens had a higher species richness than the poor fens. An increase in vascular plant species richness with increasing pH is also reported for wetlands in the Netherlands (Vermeer & Berendse 1983) and boreal mires (Gunnarson et al. 2001). A different response was detected for bryophytes. Poor acidic fens and ombrotrophic bogs are populated by low numbers of peat moss species, of which only a few produce much biomass (Vitt et al. 1995). This is also true of the acidic fens, which were rather poor in bryophyte species. Similarly, a low bryophyte species richness was recorded in some extremely rich calcareous fens. Bryophytes growing directly in water are not able to absorb hydrogen-carbonate. The extremely high pH causes carbon to be present predominantly as HCO_3^-. This favours bryophyte specialists, such as *Cratoneuron commutatum* (Bain & Proctor 1980). The distribution of bryophyte species richness along the acidity-alkalinity gradient is therefore unimodal. A similar response of bryophyte species richness to pH, positive in poor fens and negative in rich fens, is recorded by Vitt et al. (1995).

Our results show that the total dissolved iron concentration in springwater is also potentially important for bryophyte species richness. Iron concentration and bryophyte species richness have similar unimodal distributions along the pH-gradient. Extremely high iron concentrations (up to 160 $mg \cdot l^{-1}$) were present in spring fens with a pH of about of 7, and which hosted the highest number of bryophyte species (the *Valeriano-Caricetum flavae* association). The correlation between number of bryophyte species and iron concentration is significant only for plots below 0.25 m^2. An over-supply of iron is toxic for plants (Snowden & Wheeler 1993), can adversely affect bryophyte growth, decrease their dominance and make it possible for more species to coexist on a small spatial scale. Klimeš (1997), similarly, found correlations between grassland species richness and some soil chemical factors only for small plots.

The species richness of both bryophytes and vascular plants was only marginally correlated with soil chemical factors. Soil calcium concentration was not correlated with species richness, which confirms it has little effect on vegetation compared to water calcium concentration (Hájek et al. 2002). However, the lack of a correlation may have been caused by heterogeneity in soil calcium concentration.

The species-poorest habitats were the mineral-poor acidic fens, especially those rich in phosphate. The lower species richness of phosphate-rich poor fens may be due to the increased competitive ability of *Sphagnum flexuosum*. When nutrient input increases, this peat moss becomes more tolerant of minerals and phosphorus stimulates its growth even in calcium-rich habitats (Kooijman & Kanne 1993), which results in extreme acidification (Kooijman & Bakker 1994). Acidification accelerates succession towards poor acidic fens and the fast growth of *Sphagnum flexuosum* makes the habitat unfavourable for many bryophyte species, namely the calcitolerant and stream peat mosses.

Species richness and above-ground biomass

The relation between species richness, standing crop and total above-ground biomass has often been explored, and that of biomass and species richness of both vascular plants and bryophytes evaluated (García et al. 1993, Gough et al. 1994, Bergamini et al. 2001). The unimodal relationship between vascular plant species richness and above-ground biomass was first described by Al-Mufti et al. (1977). Analyses of large data-sets for various vegetation types and various scales show this so-called humped relationship. When evaluated between vegetation types, the highest species richness is associated with moderate values of above-ground biomass. This moderate value differs between vegetation types: 400–500 $g \cdot m^{-2}$ for grasslands and wetlands (Al-Mufti et al. 1977, Vermeer & Berendse 1983), 200–300 $g \cdot m^{-2}$ for riverine and salt marshes (Day et al. 1988, García et al. 1993) and up to 1500 $g \cdot m^{-2}$ for high- and low-productive fens (Wheeler & Giller 1982). Low values are reported, for example, for lake-shore communities (80–260 $g \cdot m^2$, Wisheu & Keddy 1989). This humped relationship, which is often reported for the among-vegetation-types scale, may not be applicable to the within-vegetation-type scale, where different processes may determine the pattern of species richness (Moore & Keddy 1989, Pastor et al. 1996, Virtanen et al. 2001). At the within-vegetation-type scale, there are linear correlations between bryophyte species richness and bryophyte biomass (e.g. Bergamini et al. 2001, Virtanen et al. 2001) or no relationships (e.g. Bergamini et al. 2001 for vascular plants). In our data set, there was no relationship between above-ground biomass and species richness. In some cases, other environmental factors such as soil salinity (García et al. 1993) or flooding (Gough et al. 1994) can be more important determinants of species richness. Similarly, water chemistry and the amount of litter were the most important determinants of species richness in the studied Carpathian fens.

As the humped relationship can be a scaling artefact, plot size is relevant when interpreting results (Wisheu & Keddy 1989, Oksanen 1996, Marañón & García 1997). Further, an important factor influencing the interpretation can be the inclusion of bryophytes in the analyses. In most of the habitats studied, bryophyte biomass prevailed over the standing crop and reached up to 1000 $g \cdot m^{-2}$. Habitats studied by most authors had little bryophyte biomass (e.g. Wheeler & Shaw 1991) or bryophytes were not sampled (Vermeer & Berendse 1983, Pastor et al. 1996). When bryophytes were included (number of species and biomass), the overall species richness in the largest plots was highest where the total above-ground biomass was between 400 and 1000 $g \cdot m^{-2}$. When excluded this value decreases to 200–300 $g.m^{-2}$. These lower values are comparable with those most frequently reported (Wisheu & Keddy 1989).

High quantities of bryophyte (mainly *Sphagnum*) biomass were found in poor acidic fens; the highest values were measured in the locality Jančíkovci (1046 $g \cdot m^{-2}$). In boreal mires, the bryophyte biomass reaches 4000 $g \cdot m^{-2}$ (Malmer 1986). Thus, it is important to consider bryophytes, when studying the relationships between biomass production and species richness in mires. High quantities of bryophyte biomass were also found in rich calcareous fens dominated by brown mosses of the *Amblystegiaceae* (e.g. localities no. 30: Vychylovka – 1043 $g \cdot m^{-2}$ and no. 3: Hrnčiarky – 758 $g \cdot m^{-2}$). The values for bryophyte biomass in the literature (Sjörs 1991, de Mars et al. 1996) are low compared to our results (only up to 100 $g \cdot m^{-2}$). Only those habitats where the bryophyte layer is shaded by litter (no. 9: Vlárský průsmyk – 59.6 $g \cdot m^{-2}$) or standing crop (no. 7: U Ondryša Machaly – 60.4 $g \cdot m^{-2}$) had a comparably small amount of bryophyte biomass. Sjörs (1991) reported low quantities of bryophyte biomass (about 90 $g \cdot m^{-2}$) associated with low amounts of litter in *Scorpidium scorpioides*-communities in central Sweden. Low quantities of bryophyte biomass in calcareous fens, in some cases, can be explained by the preferential selection of unmowed and highly productive sites for research. The standing crop on our sites corresponds with those reported for other European low-sedge fen communities (Mörnsjö 1969, Boyer & Wheeler 1989, Sjörs 1991, Verhoeven et al. 1996). Comparable standing crop values are recorded by de Mars et al. (1996) for communities with *Molinia coerulea* agg. in northern Poland.

We detected an important influence of litter on the vegetation of calcareous fens. In the absence of mowing litter accumulates and negatively influences the species richness of fens and species-rich subxeric meadows in our study area (Klimeš 1997). High quantities of litter cause a decrease in the number of vascular plant species and a decrease in bryophyte biomass. Over the long-term accumulation of litter or biomass of vascular plants causes a decline in bryophyte species richness (Wheeler & Giller 1982, Bergamini et al. 2001).

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Souhrn

Zkoumali jsme vztahy mezi druhovou bohatostí cévnatých rostlin a mechorostů, množstvím jejich nadzemní biomasy a chemickými faktory prostředí na prameništních slatiništích flyšových Západních Karpat (moravsko-slovenské pomezí). Druhová bohatost byla zaznamenána na sedmi různých velikostech ploch, od 0.00196 do 16 m^2. Výsledky lze shrnout do následujících bodů:

1. Hlavním faktorem ovlivňujícím druhovou bohatost cévnatých rostlin je chemismus vody sytící prameniště. Největší význam mají pH, konduktivita vody a organický podíl v půdě, které korelují s počtem druhů i na nejmenších velikostech plochy. Z dalších faktorů jsou statisticky významné na větších velikostech plochy koncentrace Ca a Mg ve vodě (tab. 2). Druhově nejbohatší na cévnaté rostliny jsou společenstva bazických pramenišť (pěnovcových pramenišť a vápnitých slatinišť), naopak nejchudší jsou společenstva oligotrofních slatinišť.

2. U mechorostů jsme podobnou lineární závislost počtu druhů na pH a obsahu bází neprokázali. Nejvyšší druhová bohatost mechorostů je na stanovištích s pH 6–7, tedy ve vegetačních typech, které leží ve střední části hlavního gradientu (as. *Valeriano-Caricetum flavae* a spol. se *S. warnstorfii* a *S. teres*). Počet druhů mechorostů koreluje na malých velikostech ploch statisticky významně se železem, zatímco u velkých ploch se tato korelace neprokázala.

3. Při srovnávání druhové bohatosti jednotlivých porostů či společenstev je třeba výsledky vztáhnout k příslušné velikosti plochy. Při jiné velikosti plochy lze dospět k odlišným výsledkům. Jako celkově druhově nejbohatší na všech velikostech ploch se ukázaly být ty porosty, kde stanovištní podmínky dovolují společný výskyt slatinných a lučních druhů mechorostů i cévnatých rostlin (tab. 1).

4. Dalším faktorem, který má vliv především na druhovou bohatost společenstev bazických pramenišť, je kosení resp. nekosení. Není-li biomasa odstraňována kosením, dochází k jejímu hromadění ve formě stařiny. Ta potom prokazatelně snižuje druhovou bohatost cévnatých rostlin (tab. 2). Mechorosty reagují na zvýšené množství stařiny pomaleji, zpočátku pouze výrazným snížením jejich biomasy (tab. 4, 5).

5. U společenstev s rašeliníky se vyskytují dva typy porostů. Jsou to porosty s dominancí jednoho druhu rašeliníku (*S. flexuosum*, *S. palustre*), u nichž byl zjištěn zvýšený obsah PO_4^{3-} ve vodě (tab. 5) a porosty v mechovém patře polydominantní. Navzájem se liší zejména strmostí růstu počtu druhů mechorostů s plochou.

References

Al-Mufti M. M., Sydes C. L., Furness S. B., Grime J. P. & Band S. R. (1977): A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. – J. Ecol. 65: 759–791.

Bain J. T. & Proctor M. C. F. (1980): The requirement of aquatic bryophytes for free CO_2 as an inorganic carbon source: some experimental evidence. – New Phytol. 86: 393–400.

Bergamini A., Pauli D., Peintinger M. & Schmid B. (2001): Relationships between productivity, number of shoot and number of species in bryophytes and vascular plants. – J. Ecol. 89: 920–929.

Boyer M. L. H. & Wheeler B. D. (1989): Vegetation patterns in spring-fed calcareous fens: calcite precipitation and constraints on fertility. – J. Ecol. 77: 597–609.

Day R. T., Keddy P. A., McNeill J. & Carleton T. (1988): Fertility and disturbance gradients: a summary model for riverine marsh vegetation. – Ecology 69: 1044–1054.

de Mars H., Wassen M. J. & Peeters W. H. M. (1996): The effect of drainage and management on peat chemistry and nutrient deficiency in the former Jegrznia-floodplain (NE-Poland). – Vegetatio 126: 59–72.

Frey W., Frahm J.-P., Fischer E. & Lobin W. (1995): Die Moos- und Farnpflanzen Europas. – In: Gams H. (ed.), Kleine Kryptogamenflora. Vol. 4, Ed. 6. – Gustav Fischer Verlag, Stuttgart.

García L. V., Marañón T., Moreno A. & Clemente L. (1993): Above-ground biomass and species richness in Mediterranean salt marsh. – J. Veget. Sci. 4: 417–424.

Gough L., Grace J. B. & Taylor K. L. (1994): The relationship between species richness and community biomass – the importance of environmental variables. – Oikos 70: 271–279.

Gunnarsson U., Rydin H. & Sjörs H. (2000): Diversity and pH changes after 50 years on the boreal mire Skattlösbergs Stormosse, Central Sweden. – J. Veget. Sci. 11: 277–286.
Hájek M. (1998): Mokřadní vegetace Bílých Karpat. – Sborn. Přírod. Kl., Uherské Hradiště, Suppl. 4/1998: 1–158.
Hájek M. & Hájková P. (2002): Vegetation composition, main gradient and subatlantic elements in spring fens of the northwestern Carpathian borders. – Thaiszia-J.Bot. 12: 1–24.
Hájek M., Hekera P. & Hájková P. (2002): Spring fen vegetation and water chemistry in the Western Carpathian flysch zone. – Folia Geobot. 37: 205–224.
Hájková P. & Hájek M. (2000): Streuwiesengesellschaften des Gebirges Hostýnské vrchy und ihre synchorologischen Beziehungen im Bereich der mährischen Karpaten. – Linzer Biol. Beitr. 32/2: 763–789.
Horáková M., Lischke P. & Grünwald A. (1989): Chemické a fyzikální metody analýzy vod. – SNTL, Praha.
Janssens F., Peeters A., Tallowin J. R. B., Bakker J. P., Bekker R. M., Fillat F. & Oomes M. J. M. (1998): Relationship between soil chemical faktors and grassland diversity. – Plant and Soil 202: 69–78.
Klimeš L. (1997): Druhové bohatství luk v Bílých Karpatech. – Sborn. Přírod. Kl., Uherské Hradiště, 2: 31–42.
Kooijmann A. M. & Bakker C. (1994): The acidification capacity of wetland bryophytes as influenced by simulated clean and polluted rain. – Aquat. Bot. 48: 133–144.
Kooijmann A. M. & Kanne D. M. (1993): Effects of water chemistry, nutrient supply and interspecific interactions on the replacement of *Sphagnum subnitens* by *S. fallax* in fens. – J. Bryol. 17: 431–438.
Malmer N. (1986): Vegetational gradients in relation to environmental conditions in northwestern European mires. – Can. J. Bot. 64**:** 375–383.
Marañón T. & García L. V. (1997): The relationship between diversity and productivity in plant communities: facts and artefacts. – J. Ecol. 85: 95–96.
Marhold K. (1998): Papraďorosty a semenné rastliny. – In: Marhold M. & Hindák F. (eds.), Zoznam nižších a vyšších rastlín Slovenska, p. 333–687, Veda, Bratislava.
Moore D. R. J. & Keddy P. A. (1989): The relationship between species richness and standing crop in wetlands: the importance of scale. – Vegetatio 79: 99–106.
Mörnsjö T. (1969): Studies on vegetation and development of a peatland in Scania, south Sweden. – Opera Bot. 24: 1–187.
Oksanen J. (1996): Is the humped relationship between species richness and biomass an artefact due to plot size? – J. Ecol. 84: 293–295.
Økland R. H. (1992): Studies in SE Fennoscandian mires: relevance to ecological theory. – J. Veget. Sci. 3: 279–284.
Pastor J., Downing A. & Erickson H. E. (1996): Species-area curves and diversity-productivity relationships in beaver meadows of Voyageurs National Park, Minnesota, USA. – Oikos 77: 399–406.
Podani J. (1984): Spatial processes in the analysis of vegetation: theory and review. – Acta Bot. Hungar. 30: 75–118.
Rapant S., Vrana K. & Bodiš D. (1997): Geochemical atlas of Slovakia. Part Groundwater. – Slovak Geol. Mag. 3: 9–26.
Rosenzweig M. L. (1995): Species diversity in space and time. – Cambridge Univ. Press, Cambridge.
Sjörs H. (1952): On the relation between vegetation and electrolytes in north Swedish mire waters. – Oikos 2: 241–258.
Sjörs H. (1991): Phyto- and necromass above and below ground in a fen. – Holarctic Ecol. 14: 208–218.
Snowden R. E. D. & Wheeler B. D. (1993): Iron toxicity to fen plant species. – J. Ecol. 81: 35–46.
ter Braak C. J. F. & Šmilauer P. (1998): CANOCO 4. CANOCO reference manual and user's guide to Canoco for Windows. – Centre of Biometry, Wageningen.
Valachovič M. (ed.) (2001): Rastlinné spoločenstvá Slovenska, časť 3: Vegetácia mokradí. – Veda, Bratislava.
van der Maarel E. (1979): Transformation of cover-abundance values in phytosociology and its effects on community similarity. – Vegetatio 39: 97–114.
Verhoeven J. A., Keuter A., van Logtestijn R., van Kerkhoeven M. B. & Wassen M. (1996): Control of local nutrient dynamics in mires by regional and climatic factors: a comparison of Dutch and Polish sites. – J. Ecol. 84: 647–656.
Vermeer J. G. & Berendse F. (1983): The relationship between nutrient availability, shoot biomass and species richness in grassland and wetland communities. – Vegetatio 53: 121–126.
Virtanen R., Muotka T. & Saksa M. (2001): Species richness-standing crop relationship in stream bryophyte communities: patterns across multiple scales. – J. Ecol. 89: 14–20.
Vitt D. H., Li Y. & Belland R. (1995): Patterns of bryophyte diversity in peatlands of continental western Canada. – Bryologist 98: 218–227.
Wheeler B. D. & Giller K. E. (1982): Species richness of herbaceous fen vegetation in Broadland, Norfolk in relation to the quantity of above-ground plant material. – J. Ecol. 70: 179–200.
Wheeler B. D. & Shaw S. C. (1991): Above-ground crop mass and species richness of the principal types of herbaceous rich-fen vegetation of lowland England and Wales. – J. Ecol. 79: 285–301.

Wisheu I. C. & Keddy P. A. (1989): Species richness – standing crop relationships along four lakeshore gradients: constraints on the general model. – Can. J. Bot. 67: 1609–1617.

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Appendix 1. – The plant communities and habitats for which the species richness was recorded. Site numerals correspond to the numerals on the map (Fig. 1), capital letters A, B, C, D indicate habitat types as differentiated by Hájek et al. (2002); small letters indicate subtypes.

A. Poor acidic fens (*Carici echinatae-Sphagnetum*). – The following species occur with high constancy: *Carex nigra, Eriophorum angustifolium, Carex echinata, Potentilla erecta, Nardus stricta, Agrostis canina, Anthoxantum odoratum, Viola palustris, Equisetum sylvaticum*, *Vaccinium myrtillus* and *Drosera rotundifolia*. In the moss layer, *Sphagnum flexuosum*, *S. fallax* and *S. palustre* exhibit high cover; *Polytrichum commune* and *S. capillifolium* can build small hummocks.
   (a) Communities dominated by *Sphagnum palustre* or *S. papillosum*. **21** Biely Kríž (behind the hotel Kysuca, the Moravsko-sliezske Beskydy Mts) – upper part of the spring.
   (b) Communities dominated by *Sphagnum flexuosum* or *S. fallax*. **19** Polková Nature Reserve (Hlavice, the Moravsko-sliezske Beskydy Mts). **24** Obidová Nature Reserve (Vyšní Mohelnice, the Moravskoslezské Beskydy Mts). **26** Korcháňovci (Raková, the Moravsko-sliezske Beskydy Mts). **27** Vřesová stráň Nature Reserve (Mosty u Jablunkova, the Moravskoslezské Beskydy Mts).
   (c) Communities with polydominant bryophyte layer, with the species *Sphagnum capillifolium, S. fallax, S. flexuosum, S. palustre, S. magellanicum, S. papillosum, Polytrichum commune* and *Calliergon stramineum*. **17** Zajacovci (Hrubý Buk, the Moravsko-sliezske Beskydy Mts), **20** Jančíkovci (Klokočov, the Moravsko-sliezske Beskydy Mts), **22** Biely Kríž (behind the hotel Kysuca, the Moravsko-sliezske Beskydy Mts) **–** lower part of the spring.

B. Rich *Sphagnum* fens
   (a) Valley rich *Sphagnum* fen (*Carici rostratae-Sphagnetum apiculati sphagnetosum teretis*). – In this vegetation type, the following species occur with high constancy: *Carex rostrata* (high cover)*, Eriophorum angustifolium, Carex nigra*, *Potentilla erecta* and, in the bryophyte layer *Sphagnum subsecundum*, *S. teres* and *S. flexuosum*: **12** Rajnochovice – Košovi (the Hostýnské vrchy Mts)
   (b) Sloping rich *Sphagnum* fen (*Sphagno warnstorfii-Eriophoretum latifolii*). – In this vegetation type, the following species occur with high constancy: *Carex nigra, C. panicea, C. echinata, Eriophorum angustifolium, Cirsium palustre, Crepis paludosa, Potentilla erecta.* Other species occurring on the studied site with high cover: *Carex demissa, Pedicularis palustris, Aulacomnium palustre, Campylium stellatum* and *Sphagnum warnstorfii*. **23** Obidová Nature Reserve (Vyšní Mohelnice, the Moravskoslezské Beskydy Mts).
   (c) Fen meadow (*Caricetum goodenowii*). – The vascular plant species composition of this fen type is similar to the previous community; the bryophyte layer is characterized by *Sphagnum teres, Aulacomnium palustre, Calliergonella cuspidata, Hypnum pratense* and *Calliergon stramineum*. **25** Horní Lomná (the Moravskoslezské Beskydy Mts).

C. Peat-forming rich fens (*Valeriano simplicifoliae-Caricetum flavae*). – This habitat type hosts the same species group which was found in all studied fen types including poor acidic fens (*Carex nigra. C. echinata, Eriohorum angustifolium, Potentilla erecta, Carex panicea* and *Equisetum palustre*). They co-exist with the mineral-demanding rich-fen species (*Eriophorum latifolium, Valeriana simplicifolia, Carex flava, Campylium stellatum*). The bryophyte layer is well-developed and consists of *Drepanocladus cossonii, Calliergon giganteum, Philonotis fontana* and many other species.
   (a) Regularly mowed types. **16** Kelčov (Turzovská vrchovina); with subdominanting *Eleocharis quinqueflora*. **28** Stará Bystrica (Lány, Kysucká vrchovina); dominanted by *Menyanthes trifoliata* and *Carex rostrata*.

(b) Unmowed types (abandoned for 2 or more years). **9** Vlárský průsmyk (Zábava, the Biele Karpaty Mts); dominated by *Homalothecium nitens* in the bryophyte layer. **18** Cudrákovci (Hrubý Buk, the Turzovská vrchovina Mts); dominated by *Homalothecium nitens* in the bryophyte layer and noted for the occurrence of *Hydrocotyle vulgaris* (extremely rare species in Slovakia). **30** Vychylovka (open-air museum, the Kysucká vrchovina Mts); high water level makes the existence of a species-rich community possible even without mowing.

D. Tufa-forming rich fens (*Carici flavae-Cratoneuretum filicini*). – This community is characterized by extreme mineral richness and marked tufa formation. The following species occur with high constancy: *Eriophorum angustifolium, E. latifolium, Carex panicea, C. flava*, *C. paniculata, Molinia arundinacea, Valeriana dioica* and, especially, species of calcareous marls *Carex flacca, Eupatorium cannabinum, Juncus inflexus* and *Tussilago farfara*. The species often present in the bryophyte layer are *Cratoneuron commutatum* (with high cover), *Bryum pseudotriquetrum, Campylium stellatum* and *Homalothecium nitens* (dominating at sites 1 and 11).

(a) regularly mowed types. **1** Machová Nature Reserve (Javorník nad Veličkou, the Bílé Karpaty Mts). **3** Hrnčiarky Nature Reserve (Strání, the Bílé Karpaty Mts). **4** Grúň Nature Reserve (Bošáca, the Biele Karpaty Mts). **8** U Kročila (Žitková, near the Hutě Nature Reserve, the Bílé Karpaty Mts). **11** U Sládků (Semetín, the Hostýnské vrchy Mts).

(b) unmowed types (abandoned for 2 or more years). **2** U Baladů (Súchovské mlýny, the Bílé Karpaty Mts). **5** Hrubý Mechnáč (Lopeník, the Bílé Karpaty Mts). **13** Za dolní hospodou (Kateřinice, the Hostýnské vrchy Mts). **14** Jasénka (Kotrlé settlement, the Vsetínské vrchy Mts).

Transitional types: calcareous fen meadows (*Cirsietum rivularis eriophoretosum latifolii*). – These communities are positioned in phytosociological classifications between the *Calthion*- and the *Caricion davallianae* alliances. The species composition of calcareous fens is supplemented by wet meadow species such as *Cirsium rivulare, Caltha palustris, Geum rivale, Scirpus sylvaticus* and by meadow grasses *Poa pratensis, Holcus lanatus, Agrostis tenuis* and others.

(a) Tufa-forming types (habitat type A). **6** Hutě Nature Reserve (Žitková, the Bílé Karpaty Mts). **7** U Ondryša Machaly (Žitková, the Bílé Karpaty Mts); *Equisetum telmateia* and *E. palustre* dominate in both cases.

(b) Types without tufa formation (habitat type C). **10** Pivovařiska (Hošťálková, the Hostýnské vrchy Mts). **15** Hrubé Brodské (Nový Hrozenkov, the Vsetínské vrchy Mts). **29** Grigovci (Nová Bystrica, the Kysucká vrchovina Mts).