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SPRING FEN VEGETATION AND WATER CHEMISTRY IN THE WESTERN CARPATHIAN FLYSCH ZONE

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Abstract: In the western part of the Carpathian flysch zone, aquifers host several springwater chemistry types. Four vegetation types, distinguished along the poor-rich gradient (tufa-forming and peat forming brown moss fens, moderately rich and poor *Sphagnum* fens), have been compared with respect to the main habitat factors. Water calcium and magnesium concentrations, pH and conductivity as well as the soil organic carbon content were the properties measured that showed the strongest correlation with the main vegetation gradient (the poor-rich gradient). Further, significant differences in iron, sodium, potassium, sulphate and phosphate concentrations were also found between pairs of related vegetation types. The range of calcium concentrations is wide (2–300 mg/l). The calcium concentration in tufa-forming springs is higher than values usually reported from northern and western Europe. Tufa formation is influenced not only by high calcium concentrations, but also by the total chemical composition of springwater and both climatic and topographic conditions. There is a great excess of cations over Cl^- and SO_4^{2-}, balanced by HCO_3^- and CO_3^{2-} in springs with the most intense tufa precipitation. Unusually high calcium concentrations combined with high iron concentrations were found in peat-forming brown moss fens. Rich *Sphagnum*-fens with calcitolerant *Sphagnum* species are distinctively low in phosphates. The Western Carpathian poor fens dominated by *Sphagnum flexuosum* have water and soil calcium concentrations comparable to those reported from rich fens of some other areas. The springwater of these fens are rich in iron, phosphates and sulphates. The poorest spring fens with *Sphagnum fallax*, *S. magellanicum*, *S. papillosum* and *S. auriculatum* are not only poor in calcium, but also in iron, sodium and potassium.

INTRODUCTION

There are two principal approaches to vegetation research in springs and mires in Europe. The first focuses on the variation of mire and spring vegetation in relation to environmental gradients (MALMER 1986, ØKLAND et al. 2001); the second uses a phytosociological approach, prevailing in Central and Eastern Europe, and classifies vegetation according to diagnostic plant species. Some plant associations defined in the latter way (e.g. DIERSSEN 1982, STEINER 1992) may therefore not reflect environmental differences clearly (see also RYBNÍČEK 1985, MARTINČIČ 1997). Unfortunately, classifications based on species combinations that indicate particular parts of environmental gradients (e.g. SUCCOW 1974, RYBNÍČEK et al. 1984) have not been generally accepted, as made clear by vegetation surveys of some Central and Eastern European countries (MATUSZKIEWICZ 1982, POTT 1992, STEINER 1993, SOLOMAKHA 1995, COLDEA 1997). Gradient analysis of spring and mire vegetation has demonstrated that the same main local gradients are important over a wide geographic area. This mainly concerns the so-called poor-rich vegetation gradient (MALMER 1962, 1986), which stresses vegetation differences from extremely rich fens through rich fens and poor fens to strongly acid and extremely poor bogs (see the Scandinavian works by SJÖRS 1952, PERSSON 1962, MÖRNSJÖ 1969). In Central Europe, similar studies on the poor-rich gradient are restricted to the Alps (WAUGHMANN 1980, GERDOL 1995); in contrast, outside the Alps, water chemistry has rarely been investigated (e.g. BALÁTOVÁ-TULÁČKOVÁ 1974, RYBNÍČEK 1974, HÁBEROVÁ 1976). In the Carpathians, mire and spring vegetation has been described, for example, by PAWŁOWSKI et al. (1960), COLDEA (1997), HÁBEROVÁ & HÁJEK (2001) and VALACHOVIČ (2001), but the knowledge of relationships between spring and mire vegetation and water or soil chemistry has remained insufficient. Nevertheless, Carpathian mires, where rich calcareous spring fens prevail, are sufficiently different in their species composition from those of Northern Europe and the Alps to merit thorough studies.

Improved knowledge of Carpathian spring fens and their vegetation is also needed from a conservation-biological point of view. In recent years, such ecosystems are increasingly threatened by direct human impact (drainage, eutrophication, building, afforestation) and by cessation of traditional mowing for hay-making (HALADA et al. 1997, DEVÁNOVÁ & DEVÁN 2000, STANOVÁ 2000) that sometimes causes the disappearence of fen species and increases the representation of meadow species. The same situation, however, often results in the development of monodominant *Molinia arundinacea* or *Eriophorum angustifolium* stands, which cannot be regarded as belonging among the meadow communities.

Spring fens in the extreme West Carpathians were considered for this study. They are of small extent (from several square meters to, rarely, 0.2 ha) and lack a superficial structure. A substantial number of springs have started depositing sediment (cold-water travertine or peat) first after settlement and deforestation of wooded springs (RYBNÍČEK & RYBNÍČKOVÁ 1995 and unpublished pollen diagrams from the southern part of our study area). They are regularly mowed in late summer or, as it has occurred over the past years, are occasionally disturbed by pasture. The spring fens under study could be, according to their floristic composition (DUDA 1950, URBANOVÁ & KUDERAVÁ 1996, HÁJEK 1998, HÁJKOVÁ & HÁJEK 2000), classified into (a) extremely rich tufa-forming (petrifying) spring fens of the *Carici flavae-Cratoneuretum* association (the *Caricion davallianae* alliance), (b) extremely rich spring fens with enhanced organic matter content and without tufa formation of the *Valeriano-Caricetum flavae* association (the same alliance), (c) rich spring fens of the *Sphagno warnstorfiani-Eriophoretum latifolii* association (*Sphagno-Tomenthypnion*), or (d) acid poor fens of the *Carici echinatae-Sphagnetum recurvi* (*Sphagno recurvi-Caricion canescentis*). Spring fens, so circumscribed, are well supplied by water and well separated from each other.

The aims of this study are (a) to find the main gradients in the vegetation composition of the Western Carpathians spring fens and relate them to environmental factors such as water chemical conditions and soil organic carbon content; (b) to compare the chemical composition of springwater among main spring fen vegetation types; (c) to describe the distribution and occurrence of species along these gradients.

Nomenclature: MARHOLD (1998) for vascular plants, FREY et al. (1995) for bryophytes (except *Sphagnum auriculatum* – see DANIELS & EDDY 1995).

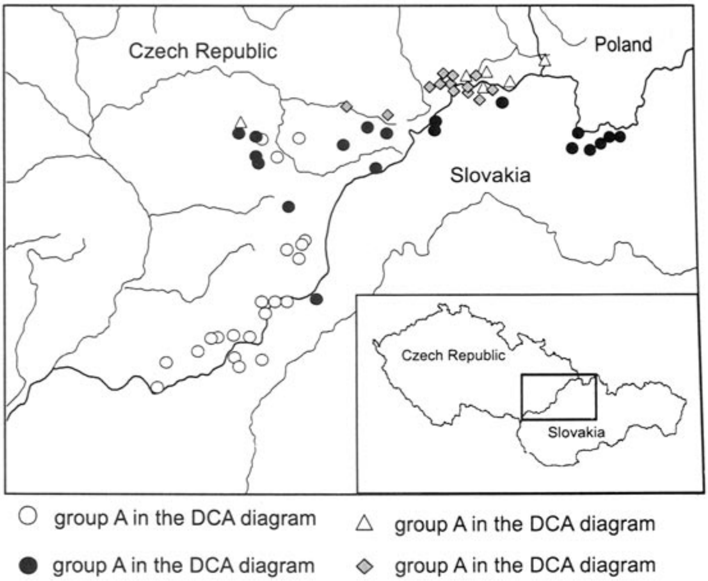

Fig. 1. The distribution of studied spring fens in the flysch borderland between the Czech Republic and Slovakia. For further explanations see text and Fig. 2.

MATERIAL AND METHODS

The study area

The study was performed in the borderland between the Czech Republic and Slovakia (Fig. 1), on the margin of the Western Carpathians. The study area forms part of the so-called Carpathian flysch zone. Flysch is bedrock where in each geological stratum (bed) claystone and sandstone alternate. Beds differ from one another in both chemistry and claystone : sandstone ratio (BUDAY 1967, PESL & ŽŮRKOVÁ 1967). Each bed mostly occupies a narrow strip running from south-west to north-east (POPRAWA & NEMČOK 1988). The chemical composition of the ground water reflects the bedrock chemistry (RAPANT et al. 1997). Marls, claystone, limestone and calcareous sandstone prevail in the south-western part of the study area (the Bílé Karpaty Unit), where springwater is extremely mineral-rich and often saturated by CO_2 (POPRAWA & NEMČOK 1988). The chemistry of the springwater supports cold water travertine (tufa) formation (see e.g. PENTECOST 1992, 1996). Towards the north-east, the group of flysch beds belonging to the Rača and Bystrica Units occurs. The northern part of the borderland is mostly of decalcified, iron-cemented sandstone from the Silesian Unit (MENČÍK & TYRÁČEK 1985).

Studied fens occupy the following range of altitudinal levels: from 390 m (spring fen "U Baladů" in south-west) to 905 m (spring fen "Biely Kríž" in north-east). The annual mean precipitation increases from south-west (station Bošáca: 713 mm, in vegetation period April-September 383 mm) to the north-east (station Vyšní Mohelnice: 1327 mm, in vegetation period 795 mm); the annual mean temperature varies between ca. 5.4 °C (station Bílá-Salajka, north-eastern part) and 8.4 °C (station Bojkovice, south-western part).

The western-most Carpathians are situated in the contact zone of three phytogeographical units, namely the Carpathian, the Pannonian and the Hercynian regions (GRULICH 1997).

Vegetation data sampling

The majority of available fens were studied. The sites extremely distant from roads and tracks were excluded from the study to reduce the delay of starting laboratory analyses. In 70 springs, the occurrence and cover of species were recorded on the nine-grade scale of VAN DER MAAREL (1979) for both vascular plants and bryophytes. Vegetation relevés were subjectively placed on central, well-hydrated and well-developed parts of spring fens. Only one relevé was analyzed per spring fen. The sample size was 16 m^2, with the exception of several sites of small extent where sample size was only 8–10 m^2. A comparison of relevés of various size in larger fens confirmed only minute differences in number of species among plots larger than 1 m^2 (HÁJKOVÁ, in prep.).

Water and soil sampling

August was chosen as a suitable month for obtaining representative values for the concentrations of major elements in the spring fens. The differences in water chemistry among the sites of main vegetation types are the most significant in this period (HÁJEK & HEKERA, unpubl.). Among 70 springs sampled once, a subset of 10 reference sites located throughout the study area was selected and sampled three times a year in 1999 and 2000. Water samples were taken from the micro-sites best supplied by water in the central parts of the springs. For ion concentration determination, conservants were added to divide samples after sampling: for metallic elements, 0.5 ml of concentrated HNO_3 per 100 ml of sample; for anions, 3 ml of chloroform per 1000 ml (see HORÁKOVÁ et al. 1989). Water conductivity at 20 °C, pH at 20 °C and redox potential were measured in situ using portable instruments (CM 101 and PH 119, Snail Instruments). Conductivity caused by H^+ ions in acid waters was subtracted (SJÖRS 1952). The water redox-potential was measured (and presented) with a platinum electrode with argentochlorid reference electrode in a 3M KCl solution. Soil samples were taken from the rhizosphere (5–30 cm) on 35 sites.

Water and soil analysis

Since most of the water samples were turbid due to colloidal suspensions, filtration or centrifugation was necessary. We determined concentrations of sulphates, phosphates, nitrates, ammonium ions and chlorides by DR 2000 spectrophotometry following colour reactions with reagents supplied by the HACH company (ANONYMOUS 1993). Metallic cation (Ca, Mg, Si, K, Na and Fe) concentrations were determined using a GBC AVANTA atomic absorption spectrometer (ANTANASOPOULOS 1994). Since the localities are isolated and distant from the laboratory, alkalinity cannot be estimated by HCl titration due to delay of starting analyses. Soil samples were dried at laboratory temperature (ZABÍRAL 1995), crushed and sifted through a sieve with 2 mm mesh width. Frame analyses were made on the fine-soil fraction.

The oxidizable carbon concentration was determined by oxidation with potassium dichromate in sulphuric acid. Oxidative mixture redundancy was determined via volumetry

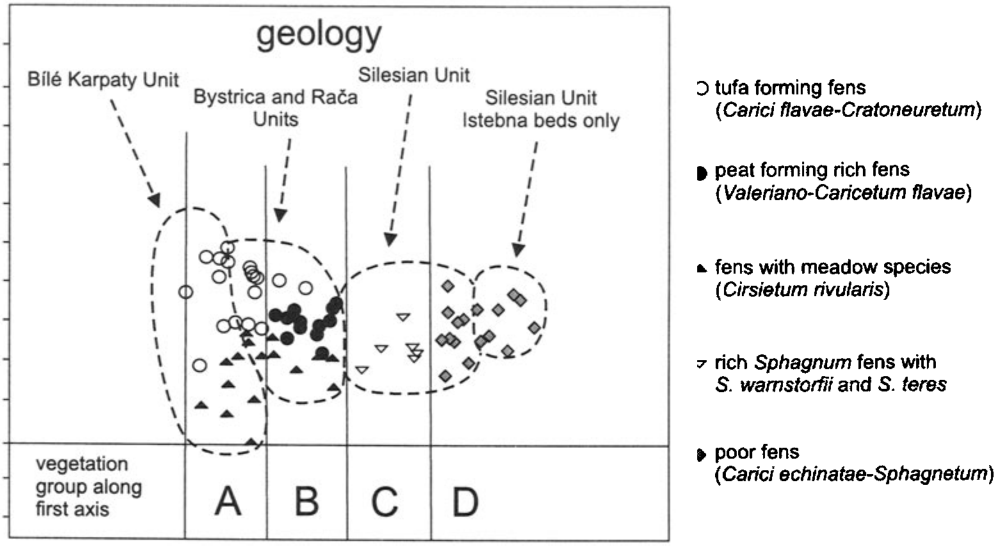

Fig. 2. DCA diagram of all investigated sites, classified according to the species composition (five communities) and divided along the first axis into four main groups (A–D). The groups of sites occurring on the same bedrock are bordered by dashed lines.

with Mohr's salt (JAVORSKÝ 1987). Organic nitrogen concentrations were determined after mineralization with sulphuric acid, conversion to ammonium ions and subsequent distillation with water vapour (ANONYMOUS 1990) on a Kjeltec System Instrument (TECATOR). Determinations of metallic cation (Ca, Mg, Na, K) and phosphorus pentoxide concentrations in soil samples were made after extraction in a Mehlich II solution (MEHLICH 1978) using a DR 2000 spectrophotometer and an AVANTA atomic absorption spectrometer.

Data analysis

Several scarce-distributed species, found on identical sites as their related taxa, were coupled with these related taxa to aggregate species before starting numerical analyses. *Drepanocladus revolvens* thus includes *D. cossonii*, *Chiloscyphus polyanthos* includes var. *pallescens* and *Campylium stellatum* includes var. *protensum*.

The Kolmogorov-Smirnov test confirms the normal or uniform distribution of all measured variables; therefore no transformation was done. Environmental data were correlated with each other using Kendall's correlation coefficient. Principal components analysis (PCA) was used for indirect ordination of environmental data (with centering and standardization by species).

The species-by-sample matrix was subjected to detrended correspondence analysis (DCA), using default options with downweighting of rare species. Three types of vegetation matrices were used in DCA: (a) only vascular plants; (b) only bryophytes; (c) both vascular plants and bryophytes. Ordination site scores obtained were correlated each other and with environmental factors using Pearson's correlation coefficient. The first DCA axis resulted from ordination of complete vegetation matrix (vascular plants + bryophytes) was arbitrarily

Table 1. The characteristics of site groups A-D obtained after dividing first DCA axis. * – *Carici rostratae-Sphagnetum sphagnetosum teretis*, *Sphagno warnstorfii-Eriophoretum latifolii* and *Caricetum goodenowii* (with *Sphagnum teres*). [1)] – occur only in respective group > 50%; species found most commonly in non-wetland habitats are omitted.

Group A tufa-forming fens	Group B peat-forming fens	Group C rich *Sphagnum*-fens	Group D poor *Sphagnum*-fens
Indicator species [1)]			
Cratoneuron commutatum, *Philonotis calcarea*, *Juncus inflexus*, *Carex flacca* combined with *Caricetalia davallianae* species	*Hypnum pratense*, *Philonotis fontana*, *Drepanocladus revolvens*, differential species with respect to the first group: *Aulacomnium palustre*, *Carex echinata*, *Agrostis canina*, *Epilobium palustre*	*Sphagnum warnstorfii*, *S. teres*, with low frequency also *S. contortum*, *S. subnitens*	*Sphagnum fallax*, *S. flexuosum*, *Polytrichum commune*, *Calliergon stramineum*, *Drosera rotundifolia*
Phytosociology			
Carici flavae- *-Cratoneuretum* *Cirsietum rivularis* p.p.	*Valeriano-Caricetum flavae* *Cirsietum rivularis* p.p.	several associations with small distribution in study area*	*Carici echinatae-* *-Sphagnetum*
Substratum			
tufa	peat, anmoor, tufa is very scarce	peat, anmoor	peat, anmoor
Variability			
meadow species prevail over fen and spring species in the lower spart of the 2nd axis	as Group A	as Group A	vegetation varies along 2nd axis from mineral (*Sphagnum subsecundum*) to organic soils

divided into four sections of identical length. As a result we obtained four groups of sites, which roughly corresponds to the phytosociological classification. The means of environmental variables among these groups and between related groups were compared using non-parametric Kruskal-Wallis and Mann-Whitney tests.

The CANOCO 4 package (TER BRAAK & ŠMILAUER 1998) was used for multivariate analyses.

RESULTS

The sites, classified according to species composition, are arranged along the first two axes in the DCA diagram (Fig. 2) and characterized in Table 1. The groups (A–D) distinguished are in good accordance with phytosociological classification, position in flysch beds and chemical element concentration in springwater (Table 2). Due to the chemical composition of the aquifers, the spring fen plant communities are rather uniform in each geological bed (Fig. 2). The Bílé Karpaty Unit is the most mineral-rich, particularly in calcium and magnesium. The mineral-poorest beds occur in the Silesian Unit. Within it, the Istebna bed is the poorest one, especially in potassium.

Table 2. Pearson correlation coefficients (r) and significance (P) of correlation among DCA site scores of entire data set (1st axis: DCAall1; 2nd axis: DCAall2), bryophyte subset (DCAbr1, DCAbr2), vascular plant subset (DCAva1, DCAva2) and environmental factors. The first 13 factors are those determined in water. Explanations: cond. – conductivity; C_{org} – soil organic carbon content; redox – water redox potential; alt. – altitude; N_{org} – soil organic nitrogen content. * – $P < 0.05$, ** – $P < 0.01$, *** – $P < 0.001$.

	DCAall1		DCAall2		DCAbr		DCAbr2		DCAva1		DCAva2
	r	P	r	P	r	P	r	P	r	P	P
DCAall2		n.s.									
DCAbr1	**0.97**	***		n.s.							
DCAbr2		n.s.		n.s.		n.s.					
DCAva1	**0.99**	***		n.s.	**0.92**	***		n.s.			
DCAva2		n.s.	**0.93**	***		n.s.		***		n.s.	
Ca	**-0.80**	***		n.s.	**-0.72**	***		n.s.	**-0.82**	***	n.s.
Mg	**-0.73**	***		n.s.	**-0.69**	***		n.s.	**-0.73**	***	n.s.
Fe		n.s.		n.s.		n.s.	**-0.31**	**		n.s.	n.s.
K	**-0.33**	**		n.s.	**-0.39**	***		n.s.	**-0.30**	*	n.s.
Na	**-0.49**	***		n.s.	**-0.55**	***		n.s.	**-0.47**	***	n.s.
Si	**-0.29**	*		n.s.	**-0.33**	**		n.s.	**-0.27**	*	n.s.
SO_4	**-0.30**	*		n.s.	**-0.27**	*		n.s.	**-0.31**	**	n.s.
PO_4		n.s.		n.s.		n.s.		n.s.		n.s.	n.s.
NO_3		n.s.		n.s.		n.s.		n.s.		n.s.	n.s.
NH_3	**0.40**	***		n.s.	**0.39**	***		n.s.	**0.37**	**	n.s.
Cl		n.s.		n.s.		n.s.		n.s.		n.s.	n.s.
pH	**-0.63**	***		n.s.	**-0.60**	***		n.s.	**-0.62**	***	n.s.
cond.	**-0.77**	***		n.s.	**-0.74**	***		n.s.	**-0.77**	***	n.s.
C_{org}	**0.65**	***		n.s.	**0.66**	***		n.s.	**0.63**	***	n.s.
redox		n.s.		n.s.		n.s.		n.s.		n.s.	n.s.
alt.	**0.68**	***		n.s.	**0.63**	***		n.s.	**0.70**	***	n.s.
slope	**-0.25**	*		n.s.	**-0.25**	*		n.s.	**-0.24**	*	n.s.
soil Ca	**-0.77**	***		n.s.	**-0.70**	***		n.s.	**-0.81**	***	n.s.
soil Mg		n.s.		n.s.		n.s.		n.s.		n.s.	n.s.
soil K	**0.51**	**		n.s.	**0.57**	***		n.s.	**0.49**	**	n.s.
soil Na		n.s.		n.s.		n.s.		n.s.		n.s.	n.s.
P_2O_5		n.s.		n.s.		n.s.		n.s.		n.s.	n.s.
N_{org}	**0.59**	***		n.s.	**0.62**	***		n.s.	**0.58**	***	n.s.

The site scores along the first DCA axis of the entire data set strongly correlate with the first-axes site scores of both subsets (vascular plants, bryophytes) (Table 2). The first axes clearly show the poor-rich gradient. The following variables increase in this order from the poor to the rich end of the poor-rich gradient (w=water; s=soil): wCa, sCa, conductivity, wMg, pH, wNa, wK, wSO_4, wSi and slope; following ones decrease: altitude, organic C, organic N, sK and wNH_3. Conductivity, pH, soil Ca and water concentrations of all metallic cations related to the poor-rich gradient are mutually strongly correlated ($P < 0.001$). The range of water calcium concentrations is wide (2–300 mg/l). The water calcium and magnesium concentrations present the steepest trend along the poor-rich gradient. The water concentrations of monovalent metallic ions (Na, K) and silicon are not so steep (see also Fig. 3). The calcium-richest springs have rather low concentrations of these ions; this is particularly the case of springs originating in claystone and limestone aquifers of the Bílé

Table 3. The mean values of environmental variables, standard deviations and significance of comparing means for 4 groups distinguished along the first DCA axis. The highest values are in bold print. Significance levels of Kruskal-Wallis (K-W) and Mann-Whitney (U) tests: *** $P < 0.001$; ** $P = 0.001–0.01$; * $P = 0.01–0.05$.

	group A	group B	group C	group D	Significance levels			
	brown moss fens		*Sphagnum*-fens		K-W	U-test		
	tufa-forming	peat-forming	rich	poor	A–D	A, B	B,C	C, D
number of samples	26	21	6	17	70	47	27	23
altitude (m)	480 (64)	569 (116)	600 (104)	**689** (104)	***	**	n.s.	n.s.
pH	**7.6** (0.5)	6.9 (0.32)	6.3 (0.47)	5.5 (0.73)	***	***	*	*
conduct. (μS/cm)	**516** (109)	364 (147)	145 (86)	53.1 (31.8)	***	***	**	**
water redox (mV)	**-27** (114)	-61 (110)	-71 (96)	-44 (129)	n.s.	n.s.	n.s.	n.s.
slope (^{0})	**4.2** (4)	2.1 (2.8)	1.5 (1.6)	2.3 (1.3)	*	*	n.s.	n.s.
water Ca (mg/l)	**231** (90)	106 (77)	26.8 (13.7)	7.0 (3.9)	***	***	**	***
water Mg (mg/l)	**11.4** (4.8)	6.4 (5.3)	1.8 (0.78)	0.68 (0.27)	***	***	**	***
water Fe (mg/l)	28.6 (18.7)	**51.2** (39.4)	**51.3** (32)	39.3 (45.2)	n.s.	*	n.s.	n.s.
water K (mg/l)	3.4 (2.2)	**4.1** (2.8)	1.8 (0.8)	1.8 (1.5)	**	n.s.	*	n.s.
water Na (mg/l)	10.1 (7.2)	**11** (8.7)	3.4 (1.1)	1.4 (0.9)	***	n.s.	***	***
water Si (mg/l)	19.6 (13.6)	**25.8** (21.9)	14.6 (10.1)	8.96 (4.8)	**	n.s.	n.s.	n.s.
water SO_4 (mg/l)	**45.3** (33.2)	17.9 (12.2)	19 (12.2)	23.1 (13.6)	**	***	n.s.	n.s.
water PO_4 (mg/l)	0.07 (0.04)	**0.13** (0.16)	0.03 (0.03)	**0.15** (0.17)	*	n.s.	*	**
water NO_3 (mg/l)	0.69 (1.1)	0.42 (0.75)	0.48 (0.34)	**1.0** (0.74)	**	n.s.	n.s.	n.s.
water NH_3 (mg/l)	1.9 (0.95)	1.9 (1.1)	**4.9** (4.5)	3.4 (1.4)	***	n.s.	n.s.	n.s.
water Cl (mg/l)	**6.1** (9.5)	4.8 (4.5)	4.8 (2.8)	**6.2** (4.5)	n.s.	n.s.	n.s.	n.s.
organic C (%)	5.6 (2.1)	11.3 (6.4)	10.1 (4.8)	**18.2** (7.8)	***	***	n.s.	*
number of samples	12	9	4	10	35	21	13	14
soil Ca (mg/100 g)	**3046** (1239)	1020(671)	291 (88.4)	325 (286)	***	**	**	n.s.
soil Mg (mg/100 g)	42.7 (10.9)	**60.8** (26.2)	43 (13.7)	36.9 (15.8)	n.s.	n.s.	n.s.	n.s.
soil K (mg/100 g)	6.9 (5.5)	14.1 (4.8)	11.1 (6.9)	**23.4** (16.4)	*	*	n.s.	n.s.
soil Na (mg/100 g)	4.79 (1.5)	**13.1** (7)	6.8 (3.9)	6.1 (4)	*	**	n.s.	n.s.
soil P_2O_5 (mg/100 g)	**0.99** (0.32)	0.94 (0.5)	0.54 (0.14)	0.83 (0.77)	n.s.	n.s.	n.s.	n.s.
organic N (mg/100 g)	546 (154)	1343 (434)	1144 (658)	**1536** (604)	***	***	n.s.	n.s.

Karpaty Unit. For example, the tufa-forming spring near the Tlstá hill (the Bílé Karpaty Mts.; left of group A in Fig. 2) has 322 mg/l of Ca, but only 1.05 mg/l of Na, 0.78 mg/l of K and 7.4 mg/l of Si. On the contrary, the peat-forming spring near the Dubcová hill (the Hostýnské hills; upper left of group B), situated on sandstone aquifers has the following concentrations: Ca 82 mg/l, Na 44.4 mg/l, K 8.3 mg/l and Si 31.2 mg/l. In brown moss fens, a high standard deviation among soil calcium concentrations is noticeable. Soil calcium was high only on springs completely covered by tufa. Calcium, magnesium and sodium concentrations in water are significantly higher in rich *Sphagnum* fens than in poor *Sphagnum* fens (Table 3). However, several poor *Sphagnum* fens have soil and water Ca concentrations comparable to the rich fens. The poorest spring fens with *Sphagnum fallax*, *S. magellanicum*, *S. papillosum* and *S. auriculatum* are not only poor in calcium, but also in iron, sodium and potassium.

The second axis of the entire data set correlates with the second axis of the vascular plants subset, but not with second axis of the bryophyte subset (Table 2). The vegetation gradients indicated by the second axes are not correlated with measured variables. Only the second

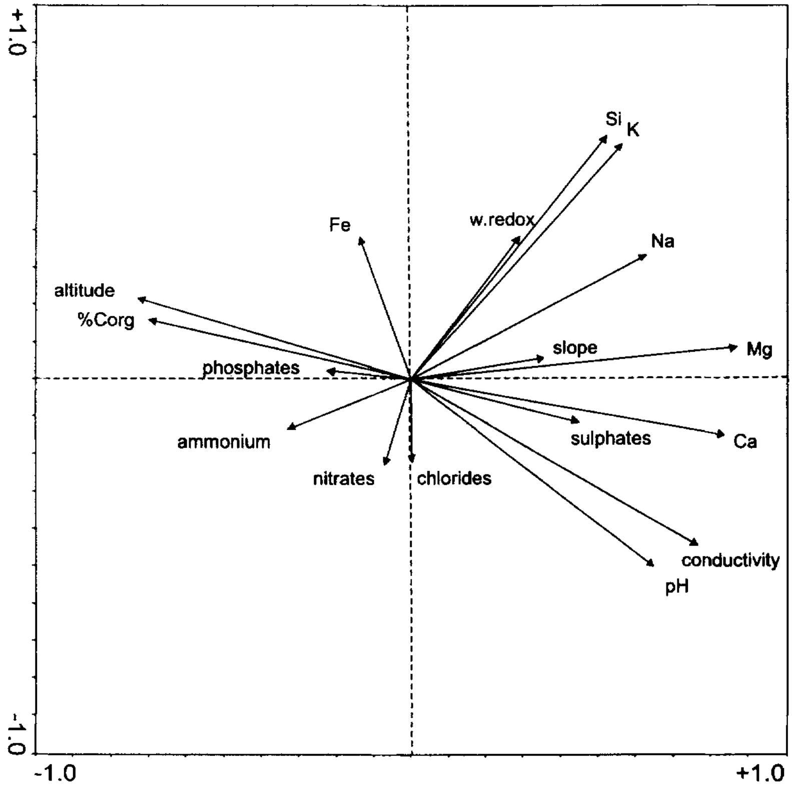

Fig. 3. PCA ordination of environmental variables. Only variables measured on all 70 springs (water chemical properties, organic carbon, altitude, slope) are presented.

"bryophyte axis" significantly correlates with the water iron concentration (Table 2). Iron is also correlated with the second axis of PCA ordination of environmental variables (Fig. 3). The iron concentration is lowest at both poles of the poor-rich gradient (Table 3). Iron is correlated only with silicon ($P < 0.001$). The precipitates of ferric ions have been recorded on iron-rich sites.

Other variables measured do not correlate with any of the DCA axes. There are, however, significant differences in phosphate, nitrate and soil sodium concentrations among the four main vegetation groups (see Table 2); these are summarized by the PCA ordination (Fig. 3). Chlorides correlate positively with nitrates ($P < 0.001$) and ammonium ($P < 0.01$); water redox potential correlate positively with sulphates ($P < 0.02$) and negatively with ammonium ($P < 0.05$); soil phosphorus pentoxide correlates positively with several metallic cations (sCa, wCa, wMg, wK) and pH ($P < 0.05$).

The DCA ordination of the bryophyte subset (Fig. 4) shows the two independent gradients: first is the poor-rich gradient, and the second is related to the iron concentration in water (see Table 2). The poor-rich gradient is related not only to chemical factors, but also to the geographical position. In particular, species with an optimum on the rich part of the gradient (score -1.45 to 0, see Table 4) occur mostly in the southwestern tufa-forming fens. In contrast,

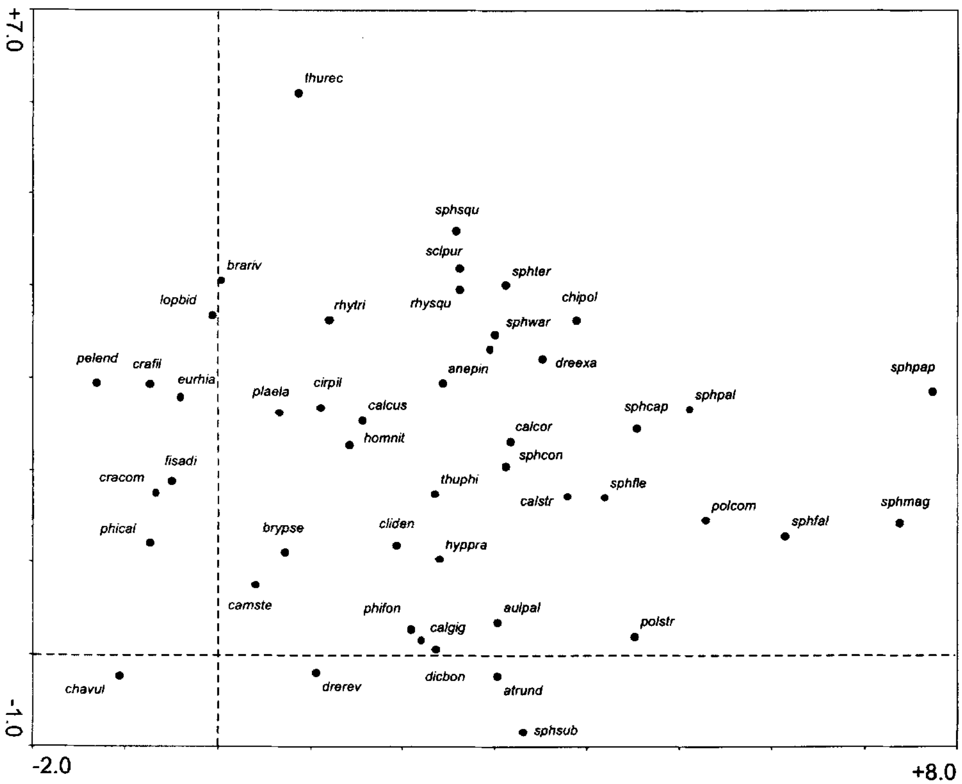

Fig. 4. Species optima along the first two DCA axes in an ordination of a bryophyte subset. Species list: *Aneura pinguis* (anepin); *Atrichum undulatum* (atrund); *Aulacomnium palustre* (aulpal); *Brachythecium rivulare* (brariv); *Bryum pseudotriquetrum* (brypse); *Calliergon cordifolium* (calcor); *Calliergon giganteum* (calgig); *Calliergon stramineum* (calstr); *Calliergonella cuspidata* (calcus); *Campylium stellatum* (camste); *Chara vulgaris* (chavul); *Chiloscyphus polyanthos* (chipol); *Cirriphyllum piliferum* (cirpil); *Climacium dendroides* (cliden); *Cratoneuron commutatum* (cracom); *Cratoneuron filicinum* (crafil); *Dicranum bonjeanii* (dicbon); *Drepanocladus exannulatus* (dreexa); *Drepanocladus revolvens* incl. *D. cossonii* (drerev); *Eurhynchium hians* (eurhia); *Lophocolea bidentata* (lopbid); *Fissidens adianthoides* (fisadi); *Homalothecium nitens* (homnit); *Hypnum pratense* (hyppra); *Pellia endiviifolia* (pelend); *Philonotis calcarea* (phical); *Philonotis fontana* (phifon); *Plagiomnium elatum* (plaela); *Polytrichum commune* (polcom); *Polytrichum strictum* (polstr); *Rhytidiadelphus squarrosus* (rhysqu); *R. triquetrus* (rhytri); *Scleropodium purum* (sclpur); *Sphagnum capillifolium* (sphcap); *S. contortum* (sphcon); *S. fallax* (sphfal); *S. flexuosum* (sphfle); *S. magellanicum* (sphmag); *S. palustre* (sphpal); *S. papillosum* (sphpap); *S. squarrosum* (sphsqu); *S. subsecundum* (sphsub); *S. teres* (sphter); *S. warnstorfii* (sphwar); *Thuidium philibertii* (thuphi); *T. recognitum* (thurec)..

species that are absent in the south-western part of the study area (*Geum rivale*, *Dicranum bonjeanii*, *Philonotis fontana*, *Calliergon giganteum*, *Hypnum pratense*, *Aulacomnium palustre*, *Carex echinata*, *Epilobium palustre*, *Agrostis canina*) have their ordination scores above 1.38. These species can be used as differential species between tufa-forming (*Carici flavae-Cratoneuretum*) and peat-forming brown moss fens (*Valeriano-Caricetum flavae*).

Sphagnum species occur over the whole gradient. The calcitolerant *Sphagnum* species (*S. warnstorfii*, *S. teres*, *S. contortum*, in one site also *S. subnitens*) grow together with rich-fen species. These species, as well as the *Drepanocladus* species (*D. exannulatus*, *D. revolvens*, *D. cossonii*), can be found on springs with Ca+Mg concentrations > 10 mg/l. In contrast, oligotrophic species of bog lawns and pools (*Sphagnum magellanicum*, *S. papillosum*, in one site also *S. auriculatum*) occur in the poorest fens in the study area (Ca+Mg 2–5.6 mg/l in summer); *Sphagnum subsecundum* was found just in poor fens on non-organic soils.

DISCUSSION

In the Western Carpathian flysch range, the poor-rich gradient is controlled mainly by the properties of the springwater, namely pH, conductivity and concentrations of Ca and Mg. Similar patterns are known from other parts of Europe (e.g. SJÖRS 1952, PERSSON 1962, MALMER 1962, WAUGHMANN 1980, ØKLAND 1989, MARTI 1994, GERDOL 1995). However, such patterns are found only when the chemistry gradient is long enough; if only raised bogs are studied separately, pH is not always correlated with conductivity and calcium concentrations (cf. BRAGAZZA 1997, BRAGAZZA & GERDOL 1999). A unimodal change of iron concentrations along the poor-rich gradient, found by WAUGHMANN (1980) in Germany and SEEPONEN et al. (1978) in Finland, is also indicated by our dataset (Table 3).

The species distribution along the poor-rich gradient also corresponds to results obtained from other regions, namely from northern Europe and northern America (FRANSSON 1972, VITT & SLACK 1974, 1983, PAKARINEN & RUUHIJÄRVI 1978, PAKARINEN 1979, SLACK et al. 1980, GERDOL 1995).

All conclusions presented here are based on the premise of the crucial importance of the chemical characteristics of mire habitats. However, altitude and geographical position correlate with the main chemical gradients in our study area. Beds rich in Ca, Mg and SO_4^{2-} are situated in the south-west and at low altitudes, while mineral-poor beds lie in the northern areas at higher altitudes. Iron-rich beds occupy the eastern areas. The occasional occurrences of poor fens at low altitudes and rich fens in north-eastern areas, dependent on bedrock, confirm the prevailing influence of springwater chemistry on fen species composition. Climatic conditions can have increasing importance in the transitional types between tufa--forming and organic-matter-depositing rich fens, where the precipitation regime influences instantaneous calcium concentration in waters and the temperature regime influences the intensity of tufa precipitation.

Organic matter

In our study area, the extremely low organic matter content in soils was recorded, surprisingly not only in tufa-forming rich fens, but also in stands with calcitolerant *Sphagnum* species (Table 3, column C). The low organic carbon content in other than tufa forming spring fens can be caused by running water, which is more readily oxygenated (SPARLING 1966), further by a falling water table in dry periods, high nitrogen content in peat (AERTS et al. 1992, MALMER 1962, OHLSON & ØKLAND 1998) and perhaps even short time elapsed in the Holocene (RYBNÍČEK & RYBNÍČKOVÁ 1995). Generally, the organic matter content is lower in rich fens than in poor fens and bogs (ØKLAND 1989, HEIKKILÄ 1987, WAUGHMANN 1980).

Table 4. The species occurrence along the poor-rich gradient (first DCA axis of entire data set).

	First axis eigenvalue 0.54		First axis eigenvalue 0.54		First axis eigenvalue 0.54
Chara vulgaris	-1.45	*Pinguicula vulgaris*	0.70	*Galium palustre*	2.41
Carex davalliana	-1.14	*Drepanocladus revolvens*	0.70	*Potentilla erecta*	2.45
Dactylorhiza incarnata	-0.95	*Calliergonella cuspidata*	0.72	*Chaerophyllum hirsutum*	2.46
Molinia arundinacea	-0.90	*Cruciata glabra*	0.73	*Carex pallescens*	2.47
Carex lepidocarpa	-0.83	*Equisetum palustre*	0.75	*Cardamine pratensis*	2.53
Carex paniculata	-0.81	*Valeriana simplicifolia*	0.75	*Anemone nemorosa*	2.57
Equisetum telmateia	-0.80	*Listera ovata*	0.78	*Lotus corniculatus*	2.58
Valeriana dioica	-0.76	*Vicia cracca*	0.78	*Luzula campestris*	2.59
Potentilla reptans	-0.75	*Caltha palustris*	0.79	*Rhinanthus minor*	2.64
Ophrys holubyana	-0.75	*Homalothecium nitens*	0.82	*Cirsium palustre*	2.65
Carex distans	-0.68	*Linum catharticum*	0.96	*Menyanthes trifoliata*	2.69
Hypericum tetrapterum	-0.65	*Festuca pratensis*	0.96	*Galium uliginosum*	2.7
Taraxacum sect. *Palustria*	-0.59	*Eleocharis quinqueflora*	0.97	*Aulacomnium palustre*	2.73
Cratoneuron filicinum	-0.49	*Angelica sylvestris*	0.99	*Juncus conglomeratus*	2.75
Salix rosmarinifolia	-0.48	*Primula elatior*	1.01	*Carex nigra*	2.78
Philonotis calcarea	-0.47	*Scleropodium purum*	1.01	*Danthonia decumbens*	2.80
Juncus inflexus	-0.46	*Leucanthemum vulgare*	1.02	*Carex rostrata*	2.82
Eupatorium cannabinum	-0.45	*Cirriphyllum piliferum*	1.04	*Sphagnum warnstorfii*	2.87
Mentha aquatica	-0.43	*Filipendula ulmaris*	1.08	*Calliergon cordifolium*	2.87
Lythrum salicaria	-0.38	*Alchemilla glabra*	1.08	*Luzula multiflora*	3.03
Cratoneuron commutatum	-0.37	*Thuidium recognitum*	1.13	*Sphagnum teres*	3.08
Eurhynchium hians	-0.35	*Lycopus europaeus*	1.13	*Carex echinata*	3.1
Tussilago farfara	-0.35	*Aneura pinguis*	1.17	*Anthoxanthum odoratum*	3.11
Carex flacca	-0.35	*Rhytidiadelphus triquetrus*	1.22	*Epilobium palustre*	3.17
Myosotis laxiflora	-0.31	*Ranunculus acris*	1.29	*Atrichum undulatum*	3.22
Lysimachia nummularis	-0.28	*Briza media*	1.37	*Sphagnum contortum*	3.27
Cirsium oleraceum	-0.28	*Geum rivale*	1.38	*Agrostis tenuis*	3.28
Pellia endiviifolia	-0.25	*Achillea millefolium*	1.38	*Juncus effusus*	3.29
Carex tomentosa	-0.24	*Prunella vulgaris*	1.44	*Polygala vulgaris*	3.3
Succisa pratensis	-0.22	*Climacium dendroides*	1.51	*Ranunculus flammula*	3.35
Mentha longifolia	-0.19	*Trifolium pratense*	1.51	*Lotus uliginosus*	3.38
Gymnadenia densiflora	-0.17	*Lysimachia vulgaris*	1.54	*Chiloscyphus polyanthos*	3.39
Agrostis stolonifera	-0.17	*Alchemilla vulgaris* s.str.	1.55	*Dactylorhiza fuchsii*	3.7
Jacea pratensis	-0.1	*Lychnis flos-cuculi*	1.59	*Sphagnum subsecundum*	3.7
Triglochin palustre	-0.03	*Cardamine amara*	1.64	*Agrostis canina*	3.72
Fissidens adianthoides	-0.03	*Dicranum bonjeanii*	1.68	*Carex demissa*	3.83
Blysmus compressus	-0.01	*Holcus lanatus*	1.75	*Drepanocladus exannulatus*	3.85
Scirpus sylvaticus	0.08	*Carex panicea*	1.77	*Viola palustris*	3.89
Gladiolus imbricatus	0.2	*Philonotis fontana*	1.83	*Carex canescens*	3.90
Campylium stellatum	0.24	*Thuidium philibertii*	1.88	*Calliergon stramineum*	3.96
Ajuga reptans	0.27	*Calliergon giganteum*	1.9	*Pedicularis sylvatica*	3.96
Brachythecium rivulare	0.28	*Hypnum pratense*	1.93	*Sphagnum flexuosum*	4.06
Epipactis palustris	0.29	*Rumex acetosa*	1.93	*Juncus bulbosus*	4.06
Sanguisorba officinalis	0.32	*Leontodon hispidus*	1.96	*Nardus stricta*	4.13
Polygala amarella	0.32	*Cerastium holosteoides*	2.10	*Equisetum sylvaticum*	4.2
Epilobium parviflorum	0.41	*Plantago lanceolata*	2.12	*Drosera rotundifolia*	4.43
Bryum pseudotriquetrum	0.42	*Dactylorhiza majalis*	2.13	*Sphagnum capillifolium*	4.44
Deschampsia cespitosa	0.42	*Mentha arvensis*	2.14	*Polytrichum commune*	4.49
Lathyrus pratensis	0.42	*Myosotis nemorosa*	2.16	*Sphagnum palustre*	4.52
Parnassia palustris	0.43	*Equisetum fluviatile*	2.16	*Hieracium laevigatum*	4.53
Lophocolea bidentata	0.44	*Rhytidiadelphus squarrosus*	2.18	*Vaccinium myrtillus*	4.62
Carex flava	0.46	*Equisetum arvense*	2.19	*Sphagnum fallax*	4.75
Eriophorum latifolium	0.51	*Eriophorum angustifolium*	2.19	*Sphagnum magellanicum*	5.08
Juncus articulatus	0.53	*Lysimachia nemorum*	2.30	*Sphagnum papillosum*	5.19
Cirsium rivulare	0.56	*Festuca rubra*	2.38	*Vaccinium vitis-idaea*	5.36
Plagiomnium elatum	0.60	*Crepis paludosa*	2.39		
Ranunculus repens	0.68	*Alchemilla crinita*	2.41		

High calcium concentrations in poor fens

The Western Carpathian poor fens dominated by *Sphagnum flexuosum* have water and soil calcium concentrations comparable to those reported from rich fens of some other areas. Rich fen vegetation dominated by *Homalothecium nitens*, *Sphagnum warnstorfii* and *Drepanocladus revolvens* have often been found with calcium concentrations of about 10–15 mg/l and with water conductivity at ca. 50–100 μS/cm (see SJÖRS 1952, GLASER at al. 1981, MALMER 1986, MALMER at al. 1992, MARTINČIČ 1995, 1997). We found these concentrations in the water of several poor fens dominated by *Sphagnum flexuosum* and *Drosera rotundifolia*. Enhanced iron, phosphate and sulphate concentrations were found in the waters of these fens. We have analyzed only a small number of these sites and therefore it is difficult to consider which of these ions is the most responsible for developing poor *Sphagnum* fen vegetation on relatively Ca-rich sites.

Iron concentrations in flysch springs recorded in this study are rather high; the water iron concentrations reported in literature (e.g. RYBNÍČEK 1974, BALÁTOVÁ-TULÁČKOVÁ 1974) are lower than in our study area. Iron, respectively mixture of ferric oxides and calcium carbonate, can immobilize calcium in fens. PRÁT (1960) analyzed the chemical composition of some poor-fen mosses intolerant of calcium which he have found in mineral-rich habitats. The springs he studied were rich in calcium, sodium and iron and the amount of iron was several times higher than the amount of calcium. The poor-fen species he found on these sites (e.g. *Calliergon stramineum*, *Sphagnum recurvum* agg., *S. palustre*, *Polytrichum commune*, *Drepanocladus exannulatus*) are iron-tolerant, accumulating iron in their phytomass.

An enhanced phosphate supply can cause increasing resistance of *Sphagnum recurvum* agg. to divalent metallic cations (KOOIJMAN & KANNE 1993). When *Sphagnum recurvum* agg. is not restricted by a high calcium level, it grows fast and forms dense carpets eliminating calcitolerant *Sphagnum* species. In competition, acidification also plays an important role (KOOIJMAN & BAKKER 1994). Enhanced sulphate inputs also decrease pH (e.g. RYBNÍČEK 2000). RYBNÍČEK (1974) found moderately rich fen communities with a strong representation of calcitolerant *Sphagnum* species in fens with calcium concentrations lower than in our study, but phosphate concentrations were low (0.03–0.06 mg/l). In the same area, NEUHÄUSL (1975) reports high calcium concentrations in *Sphagnum* sect. *Cuspidata* dominated stands (up to 36 mg/l), but under high nitrogen concentration. On the other hand, Ca+Mg concentrations (6–14 mg/l) increased by aerial liming have caused the extinction of *Sphagnum* sect. *Cuspidata* on non-fertilized mountain bogs in the Jeseníky Mts., not far from our study area (RYBNÍČEK 1997). HEDENÄS & KOOIJMAN (1996) recorded a change of rich fen vegetation into *Sphagnum fallax*- and *Calliergon stramineum*-dominated poor fen vegetation over the last 50 years. One of the discussed reasons is the influence of nitrogen-enriched rain water.

High calcium concentration in rich fens

In our study area, extremely rich fen vegetation of the *Caricion davallianae* alliance develops in springs with calcium concentrations between 50–300 mg/l. Lower values are found in several stands in the northern part of the study area. Not far from the Western Carpathians (to the north-west), rich fen species occur on non-sloping fens with fluctuating water tables, where the calcium concentration is about 50–80 mg/l (BALÁTOVÁ-TULÁČKOVÁ 1974). Extremely rich fens can be found, however, in springs with calcium concentrations of about 30–50 mg/l in areas with magnesium-rich groundwater on dolomite bedrock (PERSSON 1962, MARTINČIČ 1995, 1997).

This study found the minimum calcium concentration needed for occasional calcite precipitation to be about 90 mg/l and for forming reinforcement tufa deposits to be about 250 mg/l. On the other hand, summer concentrations of 150 mg/l (in some cases up to 250 mg/l) need not result in tufa formation. From western and northern Europe, various authors (BELL & LODGE 1962, PIETSCH 1984, BOYER & WHEELER 1989, PENTECOST 1992) have reported lower calcium concentrations in *Cratoneuron commutatum*-springs (to 150 mg/l) than in our study area. The reasons of differences in calcite precipitation in sites with the same summer calcium concentration can be as follows:

(1) Total chemical composition of springwater. In most tufa-forming springs, Ca and Mg are the main elements (70–95% of all cations), while in the peat-forming springs, they make up only 20–60% of all cations. Tufa-forming springs have 12.6 times more cations than sulphates and chlorides, while peat-forming springs have only four times more cations than sulphates and chlorides. According to MALMER (1963), the excess of cations over Cl^- and SO_4^{2-} is balanced by HCO_3^-. Calcium and HCO_3^- have often been found strongly correlated (GORHAM 1953, WASSEN et al. 1990). Thus, Ca^{2+}, HCO_3^- and CO_3^{2-} are the dominant ions in the water of tufa-forming springs. This feature not only affects calcite saturation ratio in springwater and the crucial chemical processes during tufa precipitation, but also can influence the growth of some plant species. The dependence of *Cratoneuron commutatum* occurrence upon the iron concentration as well as the divalent to monovalent cation ratio is indicated by BELL & LODGE (1962).

(2) Rainfall regime. This plays an important role during tufa formation, especially when combined with the slope inclination of the spring fen. In contrast to the south-west, the north-eastern areas are rich in summer rainfall. Thus, rain water often mixes with the groundwater, particularly in fens developed on moderate slopes. This was recorded in an extremely calcium-rich peat-forming brown moss fen (*Valeriano-Caricetum flavae*) during an extremely moist period, when the calcium concentration was about 40 mg/l. After a dry June and April, the calcium concentration steeply increased (to 150 mg/l). On the contrary, the calcium concentration of the poorest mineral tufa-forming spring (*Carici flavae--Cratoneuretum*) was stable during both extreme periods (about 80 mg/l). The mixing of groundwater with rainwater, together with lowered pH, causes carbonates to dissolve (ALMENDINGER & LEETE 1998).

(3) Air temperature. When the difference between water and air temperature is highest, tufa precipitation is most intense (JÄGER & LOŽEK 1968). Only a few carbonate grains were found in calcium-rich springs situated in cold tributary valleys of the Vsetínská Bečva River in the central part of the study region. Downstream in a warmer area, calcium-rich springs of the same water chemistry are completely covered by tufa.

(4) Holocene development. Tufa deposition culminated in the Boreal and Atlantic (JÄGER 1969, LOŽEK 1972). Recently the intensity of carbonate precipitation is decreasing because of changes in CO_2 atmospheric and soil concentrations (ALMENDINGER & LEETE 1998) and dwindling of springs. These changes lead to an increase of standing crop and litter, which produce CO_2 from root respiration and from aerobic decay (BOYER & WHEELER 1989,

ALMENDINGER & LEETE 1998). Thus, the amount of tufa or peat deposited during the Holocene is the important feature.

(5) The source type of spring. When water flows on a flat surface, resulting in a number of small springs with equalized partial pressures of CO_2, carbonate precipitation is more intense than when only one or a few springs occur. In north-eastern fens, we have observed persistent albeit slight tufa precipitation; this takes place only small spring source.

Major nutrients (N, P, K)

Base saturation and pH are the main factors which vary along the poor-rich vegetation gradient. pH is the factor that explains best the grouping of mire and spring vegetation when large data sets from a wide area are analyzed (GORHAM & JANSSENS 1992, CHARMAN 1993). Besides the direct influence of hydrogen ions, major nutrient availability (see CLYMO 1983, LARCHER 1984) is an important factor. However, the total amount of major nutrients in soil and water do not reflect the poor-rich gradient, as also reported by WAUGHMANN (1980). In our study area, major nutrients influence species composition only on smaller parts of the examined fens.

Among all metallic cations, potassium has a unique position because it is utilized in large amounts both by vascular plants (KOERSELMAN et al. 1990, GÜSEWELL et al. 2000) and mosses (PAKARINEN & TOLONEN 1978, AULIO 1980, GERDOL 1990). The water concentration of potassium is higher towards the rich end of the gradient, but the soil concentration has an inverse trend. This is caused by potassium leaching from aerobic soils with high calcium concentrations (MALMER 1962, SEEPONEN et al. 1978, HEIKKILÄ 1987, KRUK 1998) and also by the regular mowing of rich fens. *Sphagnum*-dominated, mostly unmowed, poor fens accumulate potassium, which under anaerobic conditions is strongly bound in soils (HEIKKILÄ 1987).

Among the nitrogen forms, the summer ammonium concentration significantly grows towards the poor end of the gradient. In most *Sphagnum*-sites, a pH of 5 to 6 and moderately decreased water table are suitable conditions for ammonifying bacteria (GROOTJANS et al. 1985, WAUGHMANN 1980).

Soil P_2O_5 concentrations in typical *Calthion* meadows have been reported to be higher than in spring *Calthion* meadows investigated in our study area (cf. BALÁTOVÁ-TULÁČKOVÁ 1987). In our study, *Calthion* and *Caricion davallianae* stands do not differ significantly in soil phosphorus. It can be explained by soil phosphorus binding in an unavailable form as hydroxyapatite, as was reported from tufa-forming springs in Great Britain (BOYER & WHEELER 1989).

Sulphates and chloride

While metallic cations show an apparent co-occurrence, based on their presence in aquifers, the variability in springwater anion composition reflects both bedrock chemistry and human influences on the wide surroundings. In the flysch Carpathians, a large amount of chloride occurs naturally in springwater originating in deep beds. In this case, the concentration is stable. The highest concentrations of sulphates are in tufa-forming springs. On the richest-sulphate tufa-forming springs, *Carex distans* and *Juncus inflexus* have the greatest cover (see also HÁJEK 1998).

The sulphate concentration and water redox potential are correlated. A reduction of sulphates to pyrite can, in some cases, immobilize iron (see MÖRNSJÖ 1969, DIERSSEN & DIERSSEN 2001) and thus make the establishment of some iron-intolerant meadow species possible (SNOWDEN & WHEELER 1993).

Conservation notes

All studied sites are unique not only from a vegetation point of view, but also due to the specific water chemistry which underlies the high diversity of those communities that change their species composition along the poor-rich gradient, such as vascular plants, mosses, algae (POULÍČKOVÁ et al. 2001) and molluscs (HORSÁK, in prep.). The low organic matter content and high nitrogen content in poor fen soils can lead to nitrogen being released during dry periods and consequently to vegetation changes. We consider the rich *Sphagnum* fens with calcitolerant *Sphagnum* species (*S. warnstorfii*, *S. teres*, *S. contortum*, *S. subnitens*) as critically endangered vegetation types in the study area, because they are often replaced by *Sphagnum flexuosum* poor fens if the phosphate and sulphate inputs increase. The poor *Sphagnum* sites with *Drosera rotundifolia*, having conservation priority, are less threatened. The traditional management (mowing) of rich fens should continue to prevent succession, major nutrient accumulation and the dissolution of carbonates precipitated.

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