Ann. Bot. Fennici 41: 249–262 ISSN 0003-3847
Helsinki 27 August 2004

Environmental factors and Carpathian spring fen vegetation: the importance of scale and temporal variation

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Received 20 Oct. 2003, revised version received 16 Apr. 2004, accepted 23 Apr. 2004

Hájková, P., Wolf, P. & Hájek, M. 2004: Environmental factors and Carpathian spring fen vegetation: the importance of scale and temporal variation. — *Ann. Bot. Fennici* 41: 249–262.

The importance of scale and temporal variation in measured environmental factors is often underestimated in searching for vegetation–environmental correlations in mires. Since different ecological processes can be dominant at different spatial scales, we compared species distribution patterns along environmental gradients in Carpathian spring fens at two scales: among and within vegetation types. At the large scale, four distinct vegetation types along the poor–rich fen gradient were identified: poor *Sphagnum* fen, moderate-rich fen, extreme-rich tufa-forming fen and rich fen meadow. The results confirm that environmental factors related to water and soil mineral concentrations determine fen vegetation composition at a large spatial scale. The crucial role of base saturation for large-scale variation in mire vegetation is not always evident at a smaller spatial scale. At a within-vegetation-type scale, we found a clear pattern in water level variation which was significantly related to vegetation composition. Organic matter was detected to be the most important factor for explaining variation in rich-fen meadow vegetation. Further, periodical measurements of water level and physical-chemical properties of water (i.e. pH, conductivity, redox potential, and temperature) permitted the role of their temporal variation among vegetation types along the poor–rich fen gradient to be assessed. Water pH was the most stable variable in all vegetation types, while conductivity was more stable in the rich than in the poor and moderate-rich fens. Water temperature showed the smallest fluctuation in the extreme-rich fen. In poor and moderate-rich fens, water temperature exhibited smaller temporal variation than did conductivity. Poor and moderate-rich fens generally exhibited a lower mean water level as compared with extreme-rich habitats. Independently of vegetation type, water level decline was associated with an increase in conductivity and temperature and a parallel decrease in redox-potential. Water pH remained unchanged during water level fluctuation.

Key words: conductivity, ecology, mire, pH, poor-rich gradient, seasonal patterns, spatial scale, water chemistry, water level

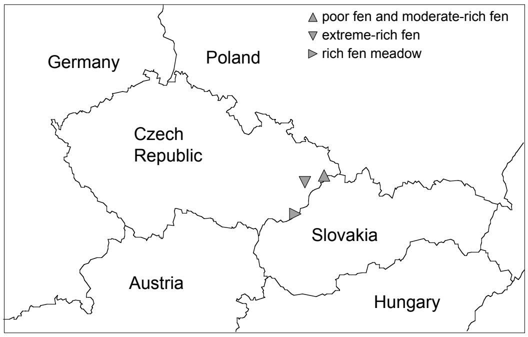

Fig. 1. Geographical position of study sites.

Introduction

Base saturation, nutrient availability and water level control the species composition of boreal and temperate fen vegetation (Karlin & Bliss 1983, Vitt & Slack 1984, Malmer 1986, Anderson & Davis 1997, Vitt 2000, Asada 2002, Hájek 2002, Kutnar & Martinčič 2003). Surprisingly, most authors exploring large-scale variation in fen vegetation measured environmental factors only once at each site (e.g. Sjörs 1952, Persson 1962, Gerdol 1995, Bragazza & Gerdol 1999, Hájek *et al*. 2002). However, chemical characteristics of water or peat may exhibit large variation due to climate and water level fluctuation during the year (Proctor 1994, Vitt *et al*. 1995, Bragazza *et al*. 1998, Tahvanainen *et al*. 2003, Hájek & Hekera 2004). Thus, it is important to know which environmental factors exhibit seasonal variation and which do not. Studies focused on seasonal variation of environmental factors have been carried out mainly in poor fens and bogs (Malmer 1962, Damman 1986, Proctor 1994, Rybníček 1997, Bragazza *et al*. 1998), and there are only a few studies dealing with seasonal variation in water chemistry along the entire rich fen-bog gradient (Vitt *et al*. 1995, Tahvanainen *et al*. 2003, Hájek & Hekera 2004). Conductivity and pH seem to be the most stable variables in these studies, and they are also the most important for characterising major vegetation types (Malmer 1986, Charman 1993, Vitt *et al*. 1995, Gerdol 1995, Mullen *et al*. 2000, Hájek *et al*. 2002). Water level is a strongly fluctuating factor which is often measured repeatedly (Malmer 1962, Persson 1962, Balátová-Tuláčková 1968, Mörnsjö 1969, Flintrop 1994, Baumann 1996 and papers cited in Grootjans *et al*. 1996), and it has been found to be the most important factor explaining vegetation variation within poor fens and bogs (Andrus *et al*. 1983, Damman 1986, Belland & Vitt 1995, Bragazza 1997, Dünhofen & Zechmeister 2000).

The evaluation of vegetation–environmental relationships in mires is scale-dependent. We can suppose that factors categorising vegetation at the landscape scale differ from those determining small-scale vegetation variation (Levin 1992, Reed *et al*. 1993, Perelman *et al*. 2001). Some mires are characterised by a fine-scale mosaic of acidic hummocks and mineral-rich fens (Bellamy & Rieley 1967, Karlin & Bliss 1983, Hájková & Hájek 2004). There is strong correlation among water level, acidity and vegetation in such patterned habitats. Little is known about such correlations in other mire types, e.g. spring fens, which lack marked superficial structures. Despite this fact, vegetation heterogeneity is observable in such fens.

In this study, we compared species distribution along ecological gradients at two spatial scales (among and within vegetation types). Four distinct vegetation types were distinguished along the entire poor–rich fen gradient in the Western Carpathians. The main objectives were to determine (i) the temporal fluctuation of pH, conductivity, redox potential and water level with respect to major fen vegetation types and (ii) the spatial variation of these environmental characteristics within vegetation types and its relation to the small-scale variation in vegetation composition.

Material and methods

Study area

The study area forms a part of the Western Carpathians in the border region between the Czech and Slovak Republics in central Europe (Fig. 1). The bedrock is composed of a group of flysch beds with alternating claystones and sandstones. The great variation in aquifer composition is consistent with the diversity of spring fen vegetation (Hájek *et al*. 2002). Four distinct vegetation types were studied at six localities (Table 1). Poor fens and moderate-rich fens are located in the Moravskoslezské Beskydy Mts. (the north-east part of the study area) on the prevailing non-calcified sandstone. Extreme-rich fen is situated in the Vsetínské vrchy Mts. on calcific flysch beds. The complex of small rich-fen meadows in the White Carpathian Mts. (the south-west part of the study area) is also saturated by extremely mineral-rich water but meadow species characterize this habitat type. The two latter mentioned fen types are also characterised by cold water travertine (tufa) formation. All studied fens occur on sloping springs and are saturated by mineral-rich or mineral-poor groundwater. They are rather homogenous with respect to their microtopogra-

Table 1. Simplified phytosociological table showing differences in species composition among vegetation types. Species which reached constancy over 30% and fidelity over 50% are included in the table. Species frequencies are expressed in percentages and their fidelity to vegetation type is indicated by an asterisk (*). Vegetation of poor fens belongs to the *Carici echinatae–Sphagnetum* association, moderate-rich fen to the *Sphagno warnstorfii–Eriophoretum latifolii* association, extreme-rich fen to the *Carici flavae–Cratoneuretum* association and extreme-rich fen meadow to the *Cirsietum rivularis* association.

Vegetation type Number of sampled sites	Poor fen 17	Moderate-rich fen 8	Extreme-rich fen 10	Rich fen meadows 13
Sphagnum papillosum	71*	–	–	–
Sphagnum fallax	71*	–	–	–
Polytrichum commune	59*	–	–	–
Equisetum sylvaticum	53*	–	–	–
Drosera rotundifolia	65*	12	–	–
Nardus stricta	94*	38	–	–
Sphagnum palustre	88*	38	–	–
Ranunculus flammula	6	88*	–	–
Cirsium palustre	6	88*	–	–
Crepis paludosa	12	88*	–	–
Viola palustris	29	75*	–	–
Calliergon stramineum	29	75*	–	–
Lotus uliginosus	12	62*	–	–
Aulacomnium palustre	–	50*	–	–
Drepanocladus exannulatus	–	50*	–	–
Philonotis fontana	–	38*	–	–
Epilobium palustre	–	38*	–	–
Hypnum pratense	–	38*	–	–
Sphagnum subnitens	–	38*	–	–
Equisetum fluviatile	18	100*	40	–
Bryum pseudotriquetrum	–	25	100*	69
Campylium stellatum	–	12	100*	54
Equisetum palustre	–	12	100*	85
Carex flacca	–	–	100*	46
Cratoneuron commutatum	–	–	90*	69
Epipactis palustris	–	–	90*	23
Eriophorum latifolium	–	–	90*	54
Eupatorium cannabinum	–	–	90*	38
Plagiomnium elatum	–	–	90*	77
Fissidens adianthoides	–	–	60*	8
Triglochin palustre	–	–	60*	–
Eleocharis quinqueflora	–	–	30*	–
Cirsium rivulare	–	–	90	100*
Juncus inflexus	–	–	30	77*
Scirpus sylvaticus	–	–	10	62*
Mentha longifolia	–	–	10	62*
Lysimachia vulgaris	12	–	–	69*
Equisetum telmateia	–	–	–	38*

phy. The climate is temperate and differs in rate of continentality among regions (Table 2). The localities of rich fens are less humid and warmer than those of other fens studied by us (Table 2).

Vegetation sampling and field work

The study was carried out during the growing seasons 2000 and 2001. Vegetation was sampled on 48 plots positioned along several short transects running from central to marginal parts of each fen, but always covering only one vegetation type. They were positioned subjectively to include the majority of observed environmental heterogeneity. The minimum distance between neighbouring vegetation sample plots was 2 m to minimize spatial autocorrelation. Exceptions were rich fen meadows developed as small patches in meadow complexes, where sample plots were not positioned on transects, but were scattered within this mosaic. At each plot, vegetation was recorded using the phytosociological relevé method (Westhoff & van der Maarel 1973) over an area of 1 m^2. The nine-degree Braun-Blanquet cover scale as modified by van der Maarel (1979) was used. Species nomenclature follows Kubát *et al.* (2002) for vascular plants and Frey *et al.* (1995) for bryophytes.

Water level was measured in the central part of each 1-m^2 site in a plastic pipe inserted into the soil with the apex at the level of the fen surface. The plastic pipe had lateral openings from the apex to the base and water level was always measured relative to the fen surface. Conductivity, pH, redox potential and temperature of water were physical-chemical properties chosen for periodical monitoring due to their great ability to reflect water alkalinity and content of bivalent minerals (Malmer 1963, Sjörs & Gunnarson 2002). Portable instruments PH 119 and CM 101 (Snail Instruments, Czech Republic) were used. Obtained values were standardized to 20 °C (pH, conductivity) and an argentochlorid reference (redox potential). Conductivity caused by hydrogen ions was subtracted (Sjörs 1952). All environmental factors were recorded 20 times at periodic intervals ca. 14 days (the first year) or 1 month (the second year) between April and October. Since the rich-fen meadow locality was geographically distant and was not monitored in the same periods as other localities, this vegetation type was excluded from some single analyses. Soil chemical factors were determined once in October 2000.

Soil samples were taken from the rhizosphere (5–30 cm) and were dried at a laboratory temperature. The oxidizable carbon concentration was determined by oxidation with potassium dichromate in sulphuric acid (for details *see* Hájek *et al.* 2002). Determinations of metallic cation (Ca^{2+}, Mg^{2+}, Na^+, K^+) and phosphorus pentoxide concentrations (P_2O_5) in soil samples were made after extraction in a Mehlich II solution using a

Table 2. Basic climatical and geographical characteristics about study localities. SK = Slovakia, CZ = Czech Republic.

Vegetation type	Poor fen	Moderate-rich fen	Extreme-rich fen	Rich fen meadows
Localities	Biely kríž, SK Jančíkovci, SK Obidová,CZ	Obidová, CZ	Jasénka, CZ	Žitková–Hutě, CZ
Coordinates	49°29´55´´N, 18°32´47´´E 49°29´26´´N, 18°33´22´´E 49°31´03´´N, 18°31´24´´E	49°31´03´´N, 18°31´24´´E	49°22´41´´N, 18°01´25´´E	48°59´25´´N, 17°54´22´´E
Altitude	730–910 m	730 m	514 m	500 m
Sediment	peat	peat, clay	tufa, marl, anmoor	tufa, marl, anmoor
Climate (mean annual values)	Bílý Kříž station 1100 mm, 4.9 °C	Bílý Kříž station 1100 mm, 4.9 °C	Vsetín station 823 mm, 7.5 °C	Strání station 828 mm, 7.6 °C
Sampled sites	17	8	10	13

DR 2000 spectrophotometer and an AVANTA atomic absorption spectrometer.

Calculation and statistical treatment

Differential species of particular vegetation types were selected according to fidelity (phi-coefficient, *see* Chytrý *et al*. 2002) using JUICE software (Tichý 2002) and are presented in a synoptic table (Table 1). SPSS software was used for all univariate statistical analyses. All measured variables, with the exception of organic carbon and soil Mg^{2+}, were normally distributed (Kolmogorov-Smirnov test). Therefore no transformations were applied. Relationships between water level and physical-chemical properties of water was tested using partial correlation with removed variation caused by different vegetation types. Means of environmental factors were compared among vegetation types with the Bonferroni post-hoc test. Temporal variation of each environmental factor was expressed as follows: (1) The arithmetic means were calculated from all values from one monitoring period separately for each vegetation type. Their time course was presented in the form of graphs. (2) The coefficients of variation were calculated separately for each variable at each measured point. Differences in these coefficients of variance between particular vegetation types were tested with the Bonferroni post-hoc test. One-way ANOVA was used for comparing temporal and spatial variation of environmental variables in each vegetation type.

Canoco 4.0 (ter Braak & Šmilauer 1998) was used for ordination analyses. Vegetation data of the entire gradient from poor to extreme-rich fens (among-vegetation-type scale) were subjected to detrended correspondence analysis (DCA) using Hill's scaling and downweighting of rare species. Pearson correlation coefficient was used to test relationships among ordination site scores and environmental variables. Redundance analysis (RDA) was applied to within-vegetation-type scale due to presumed linear response of species (short gradient in DCA). This direct ordination was used in order to calculate percentage variances in vegetation data explained by environmental variables. Only variables significant at $P = 0.05$ (Monte Carlo permutation test) were considered. Singe-variable RDAs were also used for species ordinations along selected environmental gradients.

Results

Temporal variation of environmental factors

Water pH was the most stable variable (coefficient of variance < 0.15) in all vegetation types, while conductivity was more stable in two rich fen habitats (coefficient of variance 0.1–0.2) than in poor and moderate-rich fens (Fig. 2). Temperature showed the highest stability in extreme-rich fen than in other vegetation types. When compared with other environmental factors, temperature was surprisingly more stable than conductivity and water level in poor and moderate-rich fens (compare coefficients of variance in Fig. 2). These differences in variation of pH, conductivity and temperature among vegetation types were statistically significant (Table 3). Fen types were best differentiated by pH and conductivity as implied by no mean values overlaps among three fen vegetation types (Fig. 3). The water level and especially water redox potential fluctuated considerably during the year. Variations in water level and redox potential were large in poor and moderate-rich fens and relatively stable in extreme-rich fens (Fig. 3).

Spatial variation of environmental factors

All vegetation types differed significantly in water conductivity (Table 4), which is therefore the most useful parameter for categorising fen types. Water pH also characterised particular vegetation types, but both tufa-forming types did not differ in it. Water level decreased in poor and moderate-rich fens during dry periods (Fig. 3) causing them to be significantly drier than both tufa-forming types. Differences in water temperature were in agreement with different altitudes of localities. The small-scale spatial variation in environmental factors exceeded their temporal variation within vegetation types with the excep-

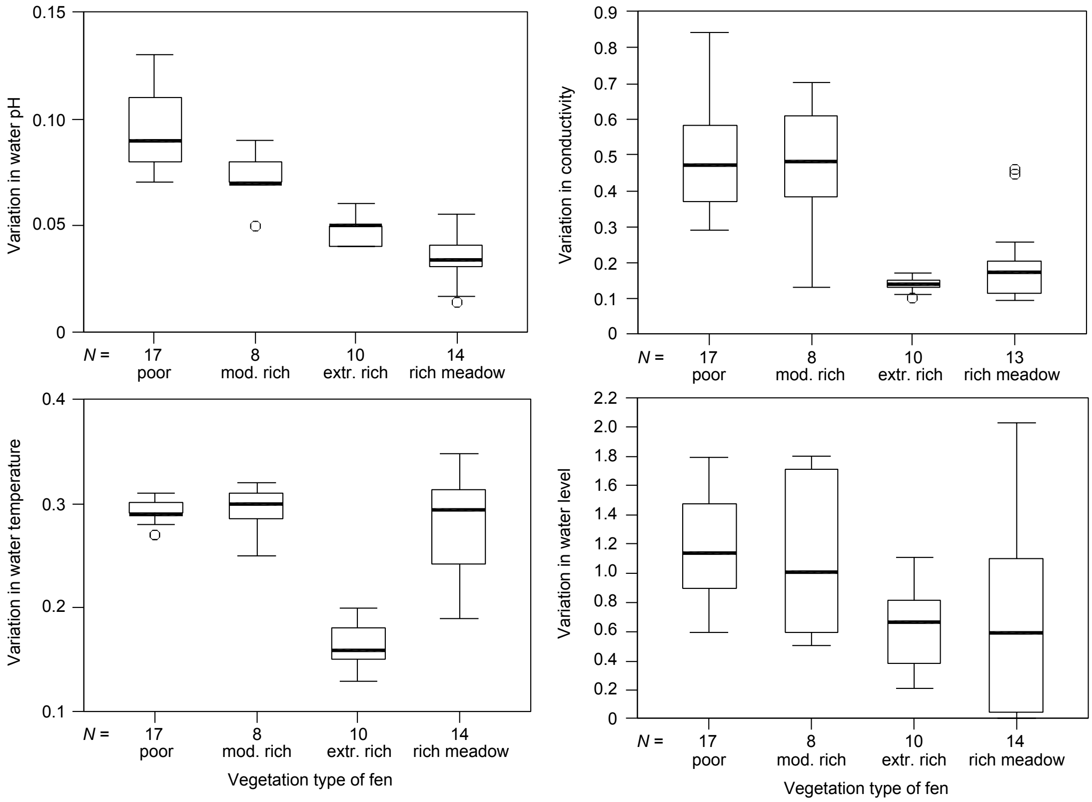

Fig. 2. Box-and-whisker plots of the coefficient of variation (CV) relative to temporal variation of environmental factors in monitored microhabitats. The box length is the interquartile range. A line across the box indicates the median. Outliers (values between 1.5 and 3 box lengths from box edges) are also presented.

tion of temperature parameter (Table 5). Among-plot variation in temperature exceeded temporal variation only in extreme-rich fen which coincided with relatively time-stable temperature values in this vegetation type. The extreme excess of spatial over temporal variation was detected for pH (poor and moderate-rich fens, rich fen meadows), water conductivity (moderate-rich fens) and water level (extreme-rich fens).

The relationships among environmental variables

We found a linear negative correlation between pH and redox potential in water with pH < 6 (Fig. 4A). There was also a nonlinear relationship between water pH and water conductivity in our data set (Fig. 4B). pH varied considerably in low-conductivity water, whereas alkaline water exhibited a wide range of conductivity. We

Table 3. Differences in coefficients of variance of environmental factors among vegetation types tested with Bonferroni post-hoc test. Only variables with coefficient of variance significantly different at $P < 0.05$ are presented. Cond. = water conductivity, t = water temperature.

	Rich fen meadow	Extreme-rich fen	Moderate-rich fen
Poor fen	Cond. (0.001)	pH (0.01), t (0.001), Cond. (0.001)	pH (0.049)
Moderate-rich fen	Cond. (0.001)	pH (0.024), t (0.001), Cond. (0.001)	
Extreme-rich fen	t (0.001)		

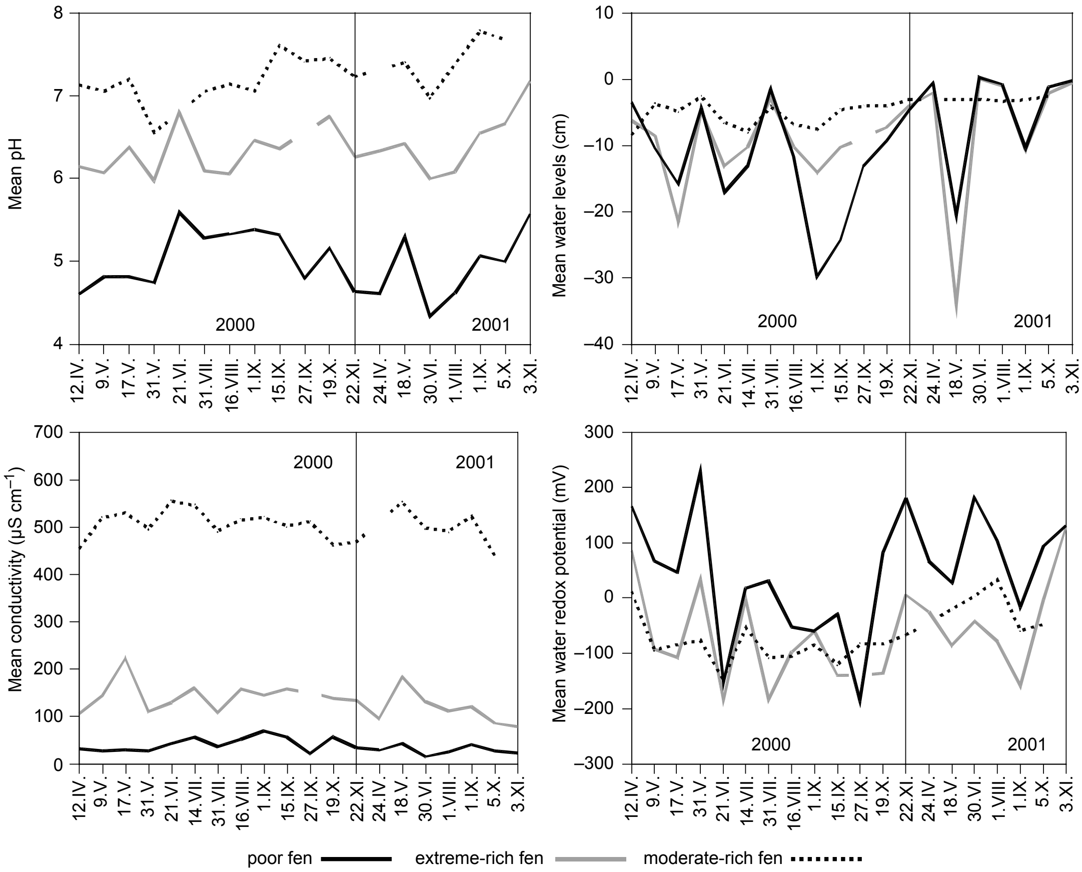

Fig. 3. Variation in mean pH, conductivity, redox potential and water level in the three fen types during two years. Only vegetation types monitored in one date are included. The discontinuity in the lines is due to the breakdown of measuring instruments.

Table 4. Multiple comparison of environmental factors among vegetation types (Bonferroni post-hoc test). Significant differences are indicated with asterisks.* $P < 0.05$,** $P < 0.01$.

	Moderate-rich fen	Extreme-rich fen	Rich fen meadows
Poor fen	pH** conductivity** redox potential**	water level** pH** conductivity** temperature** redox potential**	water level** pH** conductivity** temperature** redox potential*
Moderate-rich fen		water level** pH** conductivity** temperature**	water level** pH** conductivity** temperature** redox potential**
Extreme-rich fen			conductivity** temperature* redox potential**

found significant general relationships between water level and physical-chemical characteristics of spring water. Water level correlated significantly with conductivity, water redox potential and temperature even if variation caused by different localities was removed (Table 6). Both the conductivity and temperature increased with decreasing water level, water redox potential decreased and pH was not changed.

Environmental factors in relation to floristic composition

The first DCA axis of all vegetation samples (Fig. 5) can be interpreted as an alkalinity–acidity gradient from poor to extreme-rich fens being strongly correlated with pH (r = 0.93), conductivity (r = 0.92) and Ca^{2+} in the soil (r = 0.88). Further, soil Mg^{2+} and Na^{+}, mean temperature and mean water level correlated positively with the first DCA axis. Soil organic carbon, redox potential (mean and amplitude), pH amplitude and water level amplitude increased significantly towards poor fens (Fig. 5). Thus, fluctuation of water level, pH and redox potential were more distinct in poor fens than in extreme-rich fens, where the water regime was more stable. The plots from extreme-rich vegetation are clearly differentiated along the second DCA axis, but any measured environmental variable is not correlated with this.

The mean water level was found to be an important factor for explaining within-site vegetation variation in all of typical fen habitats (Table 7). Variability in the rich fen meadow vegetation was determined by soil organic matter. The clear species distribution pattern along the moisture gradient was, therefore, detected only in fens (Table 8). *Sphagnum fallax* and *S. flexuosum,* both belonging to *S. recurvum* agg. and growing in poor fens, replaced each other with respect to the water level. *Sphagnum flexuosum* populated streams and markedly wet carpets, whereas *S. fallax* occurred higher above water level in fairly dry carpets. The same differences were found among calcitolerant peat mosses occurring in moderate-rich fens. *Sphagnum contortum* preferred streams, *S. subnitens, S. teres* and *S. warnstorfii* occurred on higher elevated microsites, more distant from the mineral groundwater. Grasses (Poaceae) established in all fens on microhabitats with a decreasing water level. Examples are the species of dry or mesic grasslands such as *Nardus stricta* in poor and moderate-rich fens, *Festuca rubra* in moderate-rich and extreme-rich fens, *Bromus erectus*, *Danthonia decumbens* and *Briza media* in extreme-rich fens. The microhabitats with fairly constant water level in extreme-rich fens were populated by *Equisetum fluviatile*, *E. palustre*, *Eleocharis quinqueflora* and *Triglochin palustre*. *Cratoneuron commutatum* is typical stream bryophyte, unlike *Fissidens adianthoides* and *Plagiomnium elatum*. Fen meadow soils with raised organic carbon content are the habitats of wet meadow species *Scirpus sylvaticus*, *Plagiomnium elatum*, *Lythrum salicaria* and *Cruciata glabra*. On the other hand, the species occupying the second end of this fen-meadow gradient prefer or tolerate tufa substrate (e.g. *Cratoneuron commutatum*, *Eriophorum latifolium*, *Equisetum telmateia*, *Blysmus compressus*).

Table 5. One-way ANOVA of measured environmental variables in each vegetation type. The higher the F value, the higher the excess of spatial variation (among plots) over temporal variation (within plots). If F value is below 1, the temporal variation exceeds spatial variation. The differences on significance level < 0.01 are set in boldface.

	Poor fen		Mod. rich fen		Extr. rich fen		Rich fen meadow	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Water level	2.318	**0.003**	2.610	0.014	20.322	< **0.001**	6.190	< **0.001**
Conductivity	1.973	0.015	21.199	< **0.001**	5.236	< **0.001**	3.650	< **0.001**
pH	18.915	< **0.001**	15.796	< **0.001**	2.797	< **0.001**	16.523	< **0.001**
Water redox	5.890	< **0.001**	2.670	0.013	2.768	< **0.001**	1.172	0.315
Temperature	0.498	0.947	0.344	0.932	1.899	0.055	0.451	0.937

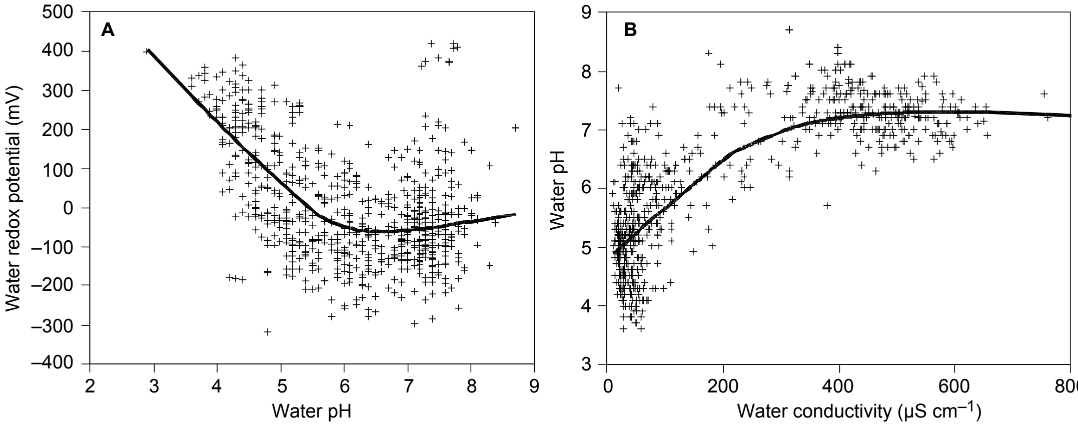

Fig. 4. The relationships between pH and water redox potential (**A**) and between pH and conductivity (**B**) in our entire data set (n = 768, 5 localities, 48 plots, 16 periods). The lines are fitted by local linear regression with 75% of points to fit in 5 iterations.

Discussion

The importance of sampling scale

Our investigation confirmed that those environmental variables which are related to concentration of mineral elements in water and soil, determine species composition of fen vegetation on the large scale, i.e. among vegetation types (Malmer 1986, Gerdol 1995, Vitt *et al.* 1995, Anderson & Davis 1997, Gerdol & Bragazza 2001, Hájek *et al.* 2002). The groundwater chemistry reflects the composition of bedrock which results in marked differences in species composition of fen vegetation types developed on calcareous and non-calcareous bedrock (Persson 1962, Anderson *et al.* 1995, Hájek *et al.* 2002). On the other hand, we found a clear pattern in small-scale vegetation variation, related to water level and soil organic matter content (Table 8). Therefore, the base saturation of springwater determined the total species composition of the fen, whereas water level and soil organic matter content were the major determinants of small-scale patterns of species distribution. Generally, small-scale variability of various fen vegetation types can also be controlled by some other environmental factors, e.g. phosphorus and nitrogen availability (Bollens *et al.* 2001) or content of toxic metallic elements, i.e. iron (Hájková & Hájek 2003).

Whereas water fluctuation appeared to be the most important factor explaining small-scale vegetation variation within typical fen habitats, organic matter content determined small-scale variation of rich fen meadow vegetation. The reason why the variation within rich fen meadows was more related to organic matter content than to water fluctuation is probably connected with two other interacting environmental factors. First, the amount of soil available phosphorus, which was significantly higher in rich fen meadows than in extreme-rich fens (t-test: $F = 4.275$, $P < 0.001$). Second, the intensity of tufa (travertine) formation, influencing the availability of phosphorus which is bound in carbonates (Boyer & Wheeler 1989). We suppose that the amount of precipitated calcareous tufa strongly correlates with the amount of soil organic matter in these habitats, because the majority of organic material is incrusted by $CaCO_3$. Therefore, enhanced organic matter content indicates less intense tufa

Table 6. Partial correlation of water level with other environmental variables. Differences among vegetation types were involved using covariables to obtain pure effect of water level decrease to changes of other fluctuating environmental variables. *** = $p < 0.001$, n.s. = not significant.

	Water level
pH	n.s.
Water conductivity	–0.225***
Temperature	–0.245***
Redox potential	0.317***

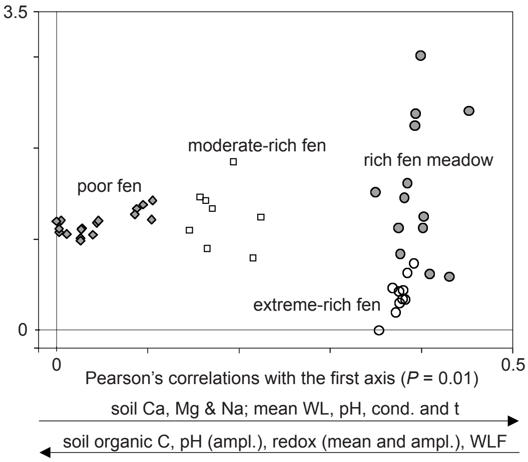

Fig. 5. DCA diagram of all sampled plots and environmental correlates with the first axis. WLF = water level fluctuation, cond. = conductivity, t = temperature, ampl. = amplitude.

precipitation in rich fen meadows resulting in local occurrence of nutrient-demanding meadow species (Table 8).

The importance of water fluctuation

We detected increasing water conductivity with decreasing water level, whereas water pH was stable during water fluctuation. This correlation is also evident from results of Baumann (1996), who studied moderate-rich and poor fens in Germany. The dependence between water level and water conductivity can be related to the increased concentration of minerals as evaporation occurs (Dickinson *et al*. 2002). The relationships among water level, water redox potential and pH found in our study can be explained by the seasonal saturation of poor fens by rain water which have high redox potential (de Mars & Wassen 1999).

Our results suggest that poor and moderate-rich fen habitats are characterised by stronger decreases of water level and stronger water fluctuations than extreme-rich fens. These results are consistent with the data from other regions. Baumann (1996) explored the water regime of poor and moderate-rich fens and found rather high mean values of water level decrease. Similar results are obtained from boreal fens (Tahvanainen *et al*. 2003), where extreme-poor fens had always deeper water level than moderate-rich fens. On the other hand, monitoring of typical extreme-rich fens has shown narrow water fluctuations with maximal decrease of 30 cm below the fen surface (Kopecký 1960, Persson 1962, Egloff & Naef 1982, Flintrop 1994). We can expect that these contrasting water regimes are not caused by geological or climatic differences. What could be the reason? Poor fens and rich fens generally differ in the vegetation structure and in the organic carbon content (Waughmann 1980, Hájek *et al*. 2002). Poor and moderate-rich fens are specific habitats dominated by peat mosses (Vitt 2000). Living peat mosses and a coarse-pored peat layer are able to retain and conduct water from a declined groundwater level (Andrus 1986, Succow & Joosten 2001). In this way the poor fen vegetation can tolerate short-term extreme decreases of groundwater level. Soils of selected extreme-rich fens are composed of clay, calcium carbonate tufa grains and only a small amount of fen peat. Here, a stronger decrease of water level below 30 cm can result in a complete desiccation of topmost soil causing hydrophytes to be gradually replaced by mesophytes (Runhaar *et al*. 1997). The vegetation of extreme-rich fens (*Caricion davallianae* alliance) shifts towards typical wet meadow vegetation (*Calthion* alliance) in such a case. Estab-

Table 7. Variation in species data explained by environmental variables within each vegetation type. Only variables significant at level $P < 0.05$ (Monte Carlo test) are presented. n.s. = not significant.

	Poor fen	Moderate-rich fen	Extreme-rich fen	Rich fen meadow
Water level (mean)	13.9%	24.4%	20.8%	n.s.
Water temperature (amplitude)	16.6%	n.s.	n.s.	n.s.
Mg in soil	15.5%	n.s.	n.s.	n.s.
Water temperature (mean)	n.s.	21.6%	n.s.	n.s.
Soil organic C	n.s.	n.s.	n.s.	15.1%

Table 8. Small-scale species distribution along the most important environmental gradients in each vegetation type as revealed by single-variable RDAs.

Poor fen		Moderate-rich fen		Extreme-rich fen		Rich fen meadow	
The most important factor							
Water level (13.9%, *P* < 0.05)		Water level (24.4%, *P* < 0.05)		Water level (20.8%, *P* < 0.05)		Soil organic carbon (15.1%, P< 0.05)	
Species (fit > 0.1)	1. RDA axis	Species (fit > 0.2)	1. RDA axis	Species (fit > 0.2)	1. RDA axis	Species (fit > 0.2)	1. RDA axis
Sphagnum flexuosum	–0.5266	*Carex nigra*	–0.8239	*Cratoneuron commutatum*	–0.7219	*Cratoneuron commutatum*	–0.7576
Ranunculus flammula	–0.4924	*Bryum pseudotriquetrum*	–0.6663	*Equisetum fluviatile*	–0.5603	*Eriophorum latifolium*	–0.5452
Cirsium palustre	–0.4924	*Equisetum arvense*	–0.6594	*Equisetum palustre*	–0.4986	*Agrostis stolonifera*	–0.5379
Viola palustris	–0.4841	*Sphagnum contortum*	–0.5901	*Eleocharis quiqueflora*	–0.4933	*Equisetum telmateia*	–0.5372
Agrostis canina	–0.3276	*Calliergonella cuspidata*	–0.5005	*Triglochin palustre*	–0.4703	*Centaurea jacea*	–0.5366
				Bryum pseudotriquetrum	–0.4669	*Blysmus compressus*	–0.4842
						Campylium stellatum	–0.4617
Drosera rotundifolia	0.3271	*Aulacomnium palustre*	0.4707	*Campylium stellatum*	0.4596	*Galium palustre*	0.4835
Sphagnum papillosum	0.3513	*Carex echinata*	0.4841	*Festuca rubra*	0.4599	*Poa trivialis*	0.5136
Sphagnum fallax	0.3588	*Prunella vulgaris*	0.5152	*Plagiomnium elatum*	0.5286	*Hypericum tetrapterum*	0.5298
Potentilla erecta	0.4466	*Dactylorhiza majalis*	0.5507	*Poa trivialis*	0.5693	*Pulmonaria obscura*	0.5298
Sphagnum palustre	0.5250	*Cirsium palustre*	0.5597	*Bromus erectus*	0.6133	*Rhizomnium punctatum*	0.5298
Nardus stricta	0.7110	*Potentilla erecta*	0.6070	*Danthonia decumbens*	0.6203	*Scleropodium purum*	0.5298
		Climacium dendroides	0.6215	*Fissidens adianthoides*	0.6460	*Scirpus sylvaticus*	0.5814
		Viola palustris	0.6243	*Juncus inflexus*	0.7322	*Cruciata glabra*	0.6474
		Nardus stricta	0.6321	*Briza media*	0.9487	*Lythrum salicaria*	0.7378
		Sphagnum warnstorfii	0.6921			*Lathyrus pratensis*	0.7650
		Sphagnum teres	0.6921			*Plagiomnium elatum*	0.8068
		Sphagnum subnitens	0.7514				
		Festuca rubra	0.7827				
		Carex demissa	0.7993				
		Leontodon hispidus	0.8063				
		Sphagnum palustre	0.8293				

lishment of meadow mesophytes is supported by improved availability of major nutrients after water level decrease (Grootjans *et al*. 1986, Venterink *et al*. 2002). In Central-European wet meadows, Balátová-Tuláčková (1968 and Balátová-Tuláčková *et al*. 1977) found water level falling deep below the surface during a great part of the year. Our rich fen meadow plots have a fairly stable water regime and the presence of wet meadow species is caused by higher content of soil available phosphorus.

The importance of pH and conductivity fluctuation

Water conductivity and, especially, pH are stable variables in time (Vitt *et al*. 1995, Hájek & Hekera 2004) showing no overlaps among particular vegetation types. Thus, we can consider these two factors useful for differentiating fen vegetation types even if single measurements are performed. In spite of relative temporal stability of pH and conductivity, there are differences in their temporal variation among vegetation types. Both tufa-forming fen habitats exhibited clearly lower variation in pH and conductivity than poor and moderate-rich fens due to a high concentration of buffering bicarbonates; a typical trait of rich-fen water (Malmer 1963, Wassen *et al*. 1990, Gorham & Janssens 1992, Vitt *et al*. 1995). Wide electrical conductivity variations in poor and moderate-rich fens coincides with wider water level fluctuation (Table 6 and Fig. 2). This marked instability of measured conductivity values in poor fens relative to rich fens is little-known and often underestimated in the vegetation-environment analyses. It remains obscured likewise in scatter constructed after averaging values from all measured microhabitats (*see* Fig. 3).

Acknowledgements

This research was supported by projects no. 206/02/0568 (Grant Agency of the Czech Republic) and MSM 143100010 (Ministry of Education of the Czech Republic). We thank Marie Derková and Petr Hekera for help with taking and analysing soil samples. Our thanks are also due to Jan Roleček and anonymous reviewers for critical comments on the manuscript.

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