

RELATIONSHIPS BETWEEN ENVIRONMENTAL FACTORS AND VEGETATION IN NUTRIENT-ENRICHED FENS AT FISHPOND MARGINS

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Abstract: Vegetation-environment relationships were investigated in fens of the Třeboň basin (Czech Republic), which are enriched by nutrients and calcium from intensively managed and limed fishponds to test the hypothesis of altered gradient structure after long-term nutrient enrichment in fens. Water-table depth, pH, conductivity, N-NH₄⁺, N-NO₃⁻, PO₄³⁻, total P, SO₄²⁻, K⁺, Ca²⁺, Mg²⁺ and Fe were measured four times in 30 vegetation plots of 16 m² during the 2004 vegetation season. Both constrained and unconstrained ordination (DCA, CCA) were used to relate environmental factors to the species composition of the vegetation. The relationships among particular factors were revealed using PCA. Four fen vegetation types obtained by TWINSpan classification were compared with measured factors using repeated measures ANOVA. Vegetation types differed significantly in water-table depth, water pH and Ca²⁺, Mg²⁺, K⁺, and N-NO₃⁻ content. The concentration of major nutrients fluctuated noticeably during vegetation season and displayed large variation within vegetation types. Temporarily the concentration of different nutrients reached extremely high values. However, high nutrient supply has not altered the gradient structure of the vegetation. Water pH and water-table depths were found to be two major determinants of species variation in fishpond-margin fens, as in the majority of other environments studied throughout the Northern Hemisphere. Species richness of both vascular plants and bryophytes was partly explained by pH. However, the extent of variation in total mineral richness and potassium concentration were the next two most important variables determining bryophyte species richness. Water in flooded poor-fen vegetation, directly affected by water from limed fishponds, had calcium and magnesium concentration similar to fishpond water. The calcium concentrations of about 20 mg l⁻¹ in typical poor-fen vegetation have no analogy in the ecological literature. High phosphorus level presumably buffers the effect of calcium by enhancing bryophyte biomass depositing superfluous calcium. In conclusion, extremely high long-term nutrient supply to fishpond-margin fens have not altered gradient structure, but shifted chemical limits of plant communities.

Keywords: Central Europe, Fluctuation, Třeboň, Vegetation, Water level and chemistry, Wetlands

Nomenclature: KUBÁT et al. (2002), KUČERA & VÁŇA (2003)

INTRODUCTION

A long tradition of exploring vegetation-environmental relationships in mires started decades ago in Scandinavia (e.g. DU RIETZ 1949, SJÖRS 1952). The research continues in several parts of the world. Many studies agree that base richness and water regime are the

major determinants controlling floristic variation in mires (e.g. TAHVANAINEN et al. 2002, JOHNSON & STEINGRAEBER 2003, HÁJKOVÁ & HÁJEK 2004, NEKOLA 2004). The disaccord occurs when the role of nutrient availability is considered. WHEELER & PROCTOR (2000) in their review paper, stressed the fertility gradient, which is connected to nutrient availability, while ØKLAND et al. (2001) did not find any support for this gradient within Fennoscandian mires. The majority of Fennoscandian studies, indeed, refer to the pristine regions in the boreal zone and in the mountains. The Central- and western-European mires, however, have often survived as islands in agricultural and strongly eutrophicated landscape (KOERSELMAN et al. 1990, PAULISSEN et al. 2004) and serve as refugia for many threatened plants and animals. Some recent studies in mire ecology suggest that increasing input of available nutrients could alter the chemical limits of plant communities. Poor *Sphagnum*-fens could be developed under more calcareous conditions, for example (KOOIJMAN & KANNE 1993, GUNNARSSON et al. 2000, HÁJEK et al. 2002, HÁJKOVÁ & HÁJEK 2003, PAULISSEN et al. 2004). Another consequence of enhanced nutrient supply is the proportion of ubiquitous species increasing to the detriment of mire specialist (FOJT & HARDING 1995, PAULI et al. 2002). In this study, we will test the hypothesis of altered gradient structure after long-term nutrient enrichment. As there are some indices that high nutrient supply can induce a change from rich-fen to poor-fen vegetation, we will test whether even long-term and intense nutrient supply is strong enough to suppress base richness as the major environmental determinant of variation in species composition of fens.

Base richness seems to be the major control of vegetation variation and species richness in mires (e.g. CHYTRÝ et al. 2003, SCHUSTER & DIEKMAN 2003, HÁJKOVÁ & HÁJEK 2003, TAHVANAINEN 2004). However, the next important factor for variation in species richness at the local scale is its relationship with productivity and the species richness-productivity patterns are influenced by the kind of nutrient limitation (OLDE VENTERINK et al. 2003). OLDE VENTERINK et al. (2001) have found that in fens a similar share of variation in species density was explained by biomass the same way as by environmental factors not related to biomass; they also have found density of threatened species increasing with decreasing P availability even within low-productive fens. CHAPIN et al. (2004) showed that nutrient effects on above-ground net primary production differ between base-rich and acidic mires as well as among principal functional groups. Moreover, several studies reported the change of species-rich fens towards species-poor *Sphagnum*-dominated fens probably caused by raised nutrient supply under unchanged calcium concentration (HEDENÅS & KOOIJMAN 1996a, GUNNARSSON et al. 2000, BELTMAN et al. 2001, HÁJEK et al. 2002). There is therefore a presumption that such a variable influence of nutrient enrichment to species-richness and productivity patterns could eliminate the role of pH in determining plant species richness under extremely high nutrient input.

The next major objective of this study will be testing the presumably synergistic effect of base saturation, nutrient enrichment and fluctuation in environmental variables to the floristic diversity of fen vegetation in an agricultural landscape. In spite of high nutrient and calcium supply to extensively managed fishponds, there are some remnants of regionally exceptional vegetation full of rare, threatened and relic plants in adjacent fens (NAVRÁTILOVÁ & NAVRÁTIL 2005a) suggesting that these fens are somehow buffered against negative

influence of eutrophicated pond water. The large fluctuation of environmental factors found in fishpond-margin mires (NAVRÁTILOVÁ & NAVRÁTIL 2005b) could be a key to understanding this phenomenon. Many studies in mire ecology have shown that the extent of the variation in environmental factors would become a separate factor in itself, more important than mean or median value (DIERSCHKE 1969, RYBNÍČEK 1974, WIERDA et al. 1997, ASADA 2002, HÁJKOVÁ et al. 2004). For example, the fluctuation of water level causes that vegetation, bottom layer especially, is under direct influence of eutrophicated water only during a part of the year. The important issue we have to know if we want to assess the effect of high nutrient supply to fen vegetation is whether fluctuation of water chemistry variables is synchronized with water level fluctuation. We therefore hypothesize that multidimensional analysis of all environmental factors will explain recent vegetation patterns better than single factors.

The mires at fishpond margins in the Třeboň basin (southern Bohemia, Czech Republic) whose chemical conditions are closely connected to the intensively managed and fertilized fishpond ecosystem (LAZAR 1978, PECHAR et al. 2002) represent a unique model habitat to test the hypotheses about altered gradient structure of fen vegetation subjected to long-term nutrient enrichment.

MATERIALS AND METHODS

Study sites

Minerotrophic mires around the fishponds of the Třeboň Basin region, in the southern part of the Czech Republic, offer a good opportunity to study the above-mentioned relationships. The 15 most representative and accessible fens were chosen for this study (Fig. 1). The climate is temperate with a mean annual temperature of 7.8 °C, the mean annual temperature of the coldest month (January) of -2.2 °C, the mean annual temperature of the warmest month (July) of 17.7 °C and average annual precipitation of 627 mm (VESECKÝ 1961). Geological substrate of the Třeboň basin is quite uniform. Siliceous cretaceous and tertiary sandstones and sandy deposits overlying granite bedrock dominate the bedrock. Some of the aquifers are rich in Fe and/or alkaline ions. Arterial water springs and/or inflow from surrounding areas and/or pond water as well as precipitation saturate the mires. In most cases, the water has low electrolyte concentration relative to non-siliceous bedrock except for sites influenced mainly by pond water and spring areas. However, properties of water sources are not well known because of the mixed influence of these four sources on all sites. The mires have been affected by human activities such as peat mining, fish farming and agriculture. Poor fens are the most common ones among mire vegetation types, rich fens are rarer and are often located in spring areas.

Vegetation data

Plots were selected subjectively after a thorough investigation of all fen vegetation types (during 2002–2003) to maximize variation in vegetation and environmental conditions in the Třeboň basin. Thirty plots on 15 localities (Fig. 1) were selected; numbers of plots in one locality vary by largeness and diversity of the locality. In most cases there is one plot of one

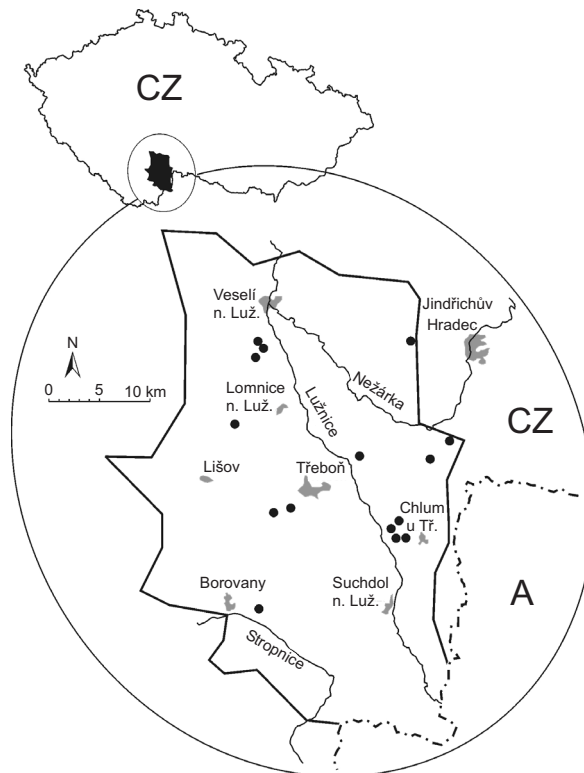


Fig. 1. Location of the study sites.

vegetation type from one locality, except for large and diverse localities. Selected plots thus represent all main mire vegetation types in the study area (for method see also SOMODI & BOTTA-DUKÁT 2004). Species composition was recorded in 2004, during the summer when the vegetation is in optimum. The plot size was always 4×4 m. The cover of both vascular plants and bryophytes was recorded using the nine-grade scale (VAN DER MAAREL 1979). The height of the vegetation cover was measured to indirectly approximate the productivity of the vegetation.

Environmental factors

The water-table depth was measured manually in PVC tubes perforated throughout their length. PVC tubes were placed in the central part of each of the 30 sampling plots. The water was always pumped out of the PVC tubes and allowed to refill before sampling. Water pH and conductivity, both standardized at 20°C , were measured in situ using portable instruments (PH 114, CM 113, Snail Instruments, Czech Republic). Conductivity caused by H^+ ions in acid waters was subtracted (SJÖRS 1952). Water samples were collected from the same permanent plots (PVC tubes). Water was placed in plastic bottles and transported to the laboratory within two to twelve hours. The contact of sampled water with air was short in all cases. Prior to further analyses, water samples were filtered through a $1.2 \mu\text{m}$ filter.

Water samples were collected also from the pond neighbouring each site. The pond sampling sites were selected in open water nearest to each fen and were marked with a bamboo stake. The variation of water level in the pond was measured with respect to these stakes. Pond water samples were collected near the water surface.

Anions were analyzed after chemical reaction spectrophotometrically with FIA (Tecator, Sweden) flow analyzer. The principle of determination of N-NH_4^+ (ammonia nitrogen) is that the aqueous sample containing ammonium ions is injected into a carrier stream, which is merged with a sodium hydroxide stream. In the resulting alkaline stream gaseous ammonium is formed that may diffuse through a gas permeable membrane into an indicator stream. This indicator stream comprises a mixture of acid-base indicators, HI, where I denotes the indicator anions. The ammonia gas reacts with HI and the anion concentration of the indicators will increase. The resulting colour shift can be measured photometrically. N-NO_3^- (nitrate) was firstly reduced to nitrite passing the sample through a copperized cadmium reductor. The nitrite reacts with sulphanilamide in an acidic solution to form a diazo compound. The diazotized product is the coupled with N-(1-naphtyl)-ethylenediamine dihydrochloride. The intensity of the formed azo dye, which is proportional to the sum of the nitrate and nitrite originally present in the sample, is measured at 540 nm; orthophosphate (PO_4^{3-}) was determined after reaction with ammonium molybdate to form the heteropoly molybdophosphoric acid, which is reduced in a second step to phosphomolybdenum blue by stannous chloride in a sulphuric acid medium. The intensive blue colour of the formed heteropoly compound is measured at 690 nm; total phosphorus was determined identically as orthophosphates after the mineralization by HClO_4 , and hydrolysis of not dissolved pyrophosphates in a high temperature; SO_4^{2-} were determined by method of methyl-thymol blue in alkaline solution. Cations were determined by atomic sorbefacient spectrophotometry with SctrAA 640 (Varian Techtron, Australia) by flame method. K^+ , Mg^{2+} and total Fe in the flame of acetylene-air, Ca^{2+} in the flame of N_2O -acetylene. Detecting limits for anion determination were $10 \mu\text{g l}^{-1}$ ($20 \mu\text{g l}^{-1}$ for total P), and for cations were 0.01 ppm for K^+ , Mg^{2+} and total Fe, and 0.02 ppm for Ca^{2+} . The laboratory used has interlaboratory calibration tests ASLAB.

Because previous studies showed noticeable fluctuation of major nutrient concentrations in fens (VITT *et al.* 1995, TAHVANAINEN *et al.* 2003, HÁJEK & HEKERA 2004), water chemistry was sampled four times a year from April to September 2004 in all plots. This period corresponds to the growing season in Central Europe when the water regime has the greatest influence on peat vegetation. The first set of measurements was conducted at the beginning of the growing season (11th April), second and third during the growing season (1st June, 5th August) and fourth at the end of growing season (28th September).

Statistical analysis

Three related multivariate statistical techniques were used to analyze vegetation data: two-way indicator species analysis (TWINSPAN), detrended correspondence analysis (DCA), and canonical correspondence analysis (CCA). Each approach provides a somewhat different view of data structure and when employed together the techniques can be used to complement, supplement, and evaluate the other analyses (ØKLAND 1996, LEPSŠ & ŠMILAUER

Table 1. Four vegetation types classified by the second division of TWINSpan. Species with considerable fidelity (phi coefficient above 25) were selected as a diagnostic species.

No.	Name	Dominant species	Diagnostic species	Average number of species per plots	s.e.	No. of plots
1	Flooded fen	<i>Sphagnum denticulatum</i> , <i>S. palustre</i>	<i>Utricularia intermedia</i> , <i>Carex elata</i> , <i>Juncus bulbosus</i> , <i>Lycopus europaeus</i> , <i>Sphagnum denticulatum</i>	10	2	5
2	Poor fen	<i>Sphagnum fallax</i> , <i>S. papillosum</i>	<i>Utricularia ochroleuca</i> , <i>Polytrichum commune</i> , <i>Sphagnum fallax</i> , <i>S. papillosum</i>	10	2	10
3	Medium-rich fen	<i>Calliergonella cuspidata</i> , <i>Sphagnum flexuosum</i> , <i>S. teres</i>	<i>Agrostis canina</i> , <i>Carex chordorrhiza</i> , <i>C. nigra</i> , <i>Equisetum fluviatile</i> , <i>Lysimachia thyrsoiflora</i> , <i>Menyanthes trifoliata</i> , <i>Drepanocladus exannulatus</i> , <i>D. vernicosus</i> , <i>Sphagnum platyphyllum</i> , <i>S. teres</i> , etc.	21	2	12
4	Rich fen	<i>Sphagnum palustre</i>	<i>Carex davalliana</i> , <i>C. dioica</i> , <i>Parnassia palustris</i> , <i>Potentilla erecta</i> , <i>Rhynchospora alba</i> , <i>Trichophorum alpinum</i> , <i>Utricularia minor</i> , <i>Aneura pinguis</i> , <i>Drepanocladus cossonii</i> , <i>Homalothecium nitens</i> , <i>Sphagnum contortum</i> , <i>S. subnitens</i> , <i>S. warnstorffii</i> , etc.	38	3	3

2003). Vegetation data were classified using TWINSpan – a polythetic divisive classification method that uses two-way indicator species analysis (HILL 1979). Pseudospecies cut levels were set at 0, 5 and 25% to suit the dataset composed of percent frequency. We used classification at the level of four groups (Table 1). Differences of species number of the vegetation types were evaluated by Kruskal-Wallis test. The concentration of species occurrences in vegetation type (fidelity) was calculated by phi coefficient (CHYTRÝ et al. 2002) to show the species that characterize particular vegetation types.

Gradients in species composition of the vegetation in relation to the environment were assessed using detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) algorithms of the CANOCO 4.5 package (TER BRAAK & ŠMILAUER 2002). The percentage frequency of the species was log-transformed and rare species were downweighted.

The vegetation data set was subjected first to DCA in order to assess the overall variation patterns in species composition independent from environmental factors measured. Ordination site scores were correlated to means, medians, minimum, maximum and coefficient of variation of all measured environmental factors using Kendall tau. Medians and coefficients of variation of all environmental variables were plotted onto DCA ordination diagrams as supplementary environmental data for better ecological interpretation of the axes.

The same analysis was performed separately for bryophyte subset and for vascular plant subset.

Subsequently we used CCA to test the ability of each measured factor to explain variation in species composition of the vegetation and to find the measured factors explaining maximum variation in species data under minimum number of variables involved into constrain ordination model (so-called forward selection procedure, see TER BRAAK & ŠMILAUER 2002, LEPŠ & ŠMILAUER 2003). The parameters obtained from consecutive measurements may have different significance in explaining vegetation gradients. Therefore, five statistical parameters (mean, median, minimum, maximum, and coefficient of variation) obtained from consecutive measurement of each environmental factor were used in the analyses. The effect of the first canonical axis was tested by permutation test (499 permutations were always used). To test the statistical significance of the second canonical axis we calculated partial CCA where the first axis was partialled out by using it as a covariable. Significance was again tested by the permutation test. The factors were stepwise added into the model with a threshold of $P < 0.05$ to entry.

Principal components analysis (PCA) was used for indirect ordination of environmental data with an objective to find main gradients in the water chemistry of all studied sites and to test whether sites similar in environmental conditions as a whole harbour the same vegetation type. In addition to environmental variables from 30 fens, environmental data from 10 fishponds were subjected to analysis to find out how the chemistry of pond water is similar to the chemistry of each vegetation types. Four values obtained from repeated measurement of each environmental variable were used. The values of measured environmental variables were log-transformed to approximate normal distributions. However, the water-level data from fishponds were excluded. The values of each environmental variable were standardized to mean 0 and variance 1 in PCA analysis. Medians and coefficients of variation of environmental variables related to 1st and 2nd axes were plotted onto PCA ordination diagrams as supplementary environmental data, instead of species display, for better clarity of the diagram. Correlations between water chemistry of four fen types and fishpond water were tested by Pearson correlation coefficient.

The seasonal trends in fluctuation of environmental factors and the differences in measured factors among communities and fishpond water, respectively, were investigated using repeated measures analysis of variance (RMANOVA). The relationships between species richness (dependent variable) and means, medians, minima, maxima and coefficients of variation of measured environmental factors, cover of each individual vegetation layer and height of herb layer were evaluated by stepwise multiple linear regression using forward variable selection with a threshold of $P < 0.05$ to entry. The relationships between each of these environmental variables and species richness were correlated using Kendall tau correlation coefficient.

RESULTS

Gradient analysis

The first two DCA axes were nearly equal in length (Fig. 2) and together explained about 21% of the total species variability (Table 2). They also correlated very well with

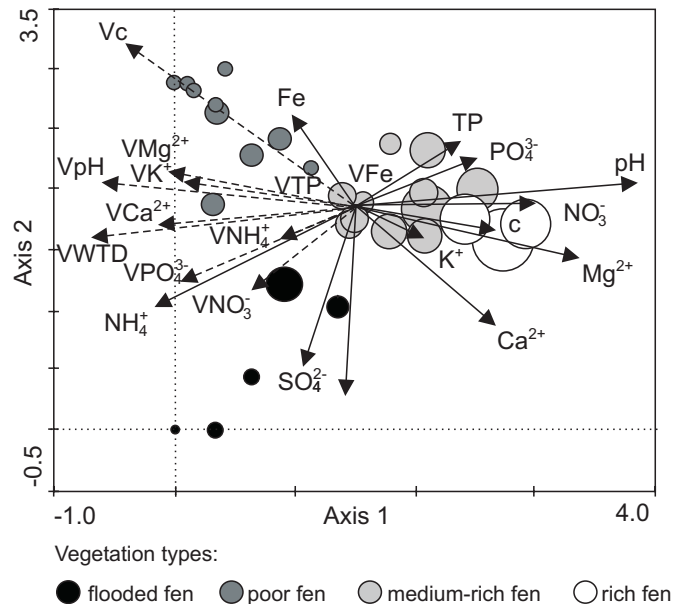


Fig. 2. DCA simple ordination plot of samples with the environmental variables passively projected onto the ordination. The size of the symbols corresponds to species richness (number of species in relevé). Species scores along the first and second DCA axes are in Appendix. (WTD – water-table depth, TP – total phosphorus, c – conductivity, “V” before symbol of variable is coefficient of variation).

environmental data; species-environment correlations (see TER BRAAK & ŠMILAUER 1998, LEPSŠ & ŠMILAUER 2003) along first two axes are high ($r_{1\text{st ax.}} = 0.963$; $r_{2\text{nd ax.}} = 0.846$).

The first ordination axis was correlated significantly with pH (mean, median, minimum and variation), Ca^{2+} (minimum and variation), variation of Mg^{2+} , variation of conductivity, variation of water-table depth and NH_4^+ (median). The second ordination axis was significantly correlated with water level (median), conductivity (minimum and variation), Ca^{2+} (mean, median and minimum), Mg^{2+} (min), and Fe (mean and median) (Table 3). We can generalize that not only pH but also all measured variation in environmental variables were negatively correlated with the first DCA axis. Along the first axis rich fens were clearly separated from poor fens (poor-rich gradient). Along the second axis the poor fens were divided into flooded ones and non-flooded ones. The general pattern remained the same in the DCA of bryophyte subset. In DCA of the vascular plant subset, the gradient of base richness was not so clear. The poor fens were in the middle of the gradient and were surrounded by the other vegetation types. This pattern can be partly explained by the broader ecological amplitude of the majority of vascular plants relative to bryophytes.

CCA was applied to test the hypothesis about the influence of base richness and water level on the species composition of the vegetation. The variables that most effectively and significantly explained the species composition of the plant communities were minimum pH, maximum water table, maximum K^+ and minimum PO_4^{3-} (Fig. 3). Together they explained about 25% of the total variability. The first two canonical axes captured most of the variation of the species data (about 18%). The results of the permutation test showed that both the first

Table 2. Summary of detrended correspondence analysis (DCA), partial detrended correspondence analysis of vascular plants (DCAv), of mosses (DCAm), canonical correspondence analysis (CCA) of 30 fen types, and principal component analysis (PCA) of 30 fen types and 10 ponds.

	Axis	DCA	DCAv	DCAm	CCA	PCA
Eigenvalue	1	0.464	0.448	0.815	0.356	0.319
	2	0.326	0.282	0.537	0.303	0.162
	3	0.191	0.162	0.380	0.147	0.089
	4	0.013	0.098	0.185	0.106	0.065
	Total inertia	3.712	3.101	5.399	3.712	
Length of gradient	1	2.919	2.798	5.879		
	2	2.990	2.750	4.767		
	3	2.587	2.425	4.735		
	4	1.800	1.521	2.898		
Species environment correlation	1	0.963	0.825	0.965	0.911	0.985
	2	0.846	0.923	0.943	0.881	0.979
	3	0.834	0.976	0.979	0.874	0.977
	4	0.982	0.951	0.800	0.823	0.939
Cumulative percentage variance Species data	1	12.5	14.5	15.1	9.6	31.9
	2	21.3	23.6	25.0	17.8	48.1
	3	26.4	28.8	32.1	21.7	57.0
	4	29.9	31.9	35.5	24.6	63.5
Species-environmental relations	1	13.9	11.3	15.8	39.0	35.6
	2	21.2	21.4	26.3	72.2	53.4
	3	0.0	0.0	0.0	88.3	63.2
	4	0.0	0.0	0.0	100.0	69.8

and second axes are significant ($P < 0.01$), demonstrating that the relationship between the species occurrences and the environmental variables was highly significant. Eigenvalues of the first two axes in CCA are only slightly smaller than those in DCA, and species-environmental correlations in CCA for the first two axes are high ($r_{1\text{st ax.}} = 0.911$, $r_{2\text{nd ax.}} = 0.881$). This indicates that the variables included in CCA really captured much of the variation in the species data. These findings were supported by similar ordination patterns in DCA and CCA. Rich fens and moderately rich fens were divided from poor fen according to pH values. Flooded fens were not clearly separated in CCA from non-flooded poor fens, indicating that maximum water level cannot solely explain the clear floristic differences among them.

The first two axes in PCA of water-chemistry factors explain the most of the variability in the environmental data (48%). The first axis represented the pH and conductivity of water and concentrations of major cations (Ca^{2+} , Mg^{2+} , K^+), SO_4^{2-} , and NO_3^- , the second axis the concentrations of NH_4^+ , PO_4^{3-} , total P (Fig. 4). The pond sites were separated from other fen sites. However, the constituent fen types were not clearly separated. The poor-rich gradient was only slightly outlined. The rich-fen samples were close to fishpond ones in the diagram although they occurred on springs that are not influenced by pond water. This is evidently caused by high values of pH, Ca^{2+} , K^+ and conductivity (Table 4).

Table 3. Kendall tau correlation coefficients between environmental variables and ordination axes of DCA (see Fig. 2). Significance levels: * – $P < 0.05$, ** – $P < 0.01$, *** – $P < 0.001$, n.s. – not significant.

Environmental variable	DCA (Total data set)		DCA (Vascular plants)		DCA (Mosses)	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Mean water table depth	n.s.	n.s.	n.s.	n.s.	n.s.	-0.34**
Median water table depth	n.s.	-0.26*	n.s.	n.s.	n.s.	-0.38**
Maximum water table depth	n.s.	n.s.	-0.35**	n.s.	n.s.	-0.28*
Variation of water table depth	-0.34**	n.s.	n.s.	n.s.	0.27*	n.s.
Mean pH	0.47***	n.s.	n.s.	n.s.	-0.43***	n.s.
Median pH	0.44***	n.s.	n.s.	n.s.	-0.36**	n.s.
Minimum pH	0.44***	n.s.	n.s.	n.s.	-0.44***	n.s.
Variation of pH	-0.38**	n.s.	n.s.	n.s.	0.47***	n.s.
Median conductivity	n.s.	n.s.	n.s.	n.s.	n.s.	-0.28*
Minimum conductivity	n.s.	-0.27*	n.s.	n.s.	-0.31*	-0.36**
Variation of conductivity	-0.31**	0.36*	n.s.	n.s.	0.41**	0.37**
Mean Ca ²⁺	n.s.	-0.28*	n.s.	n.s.	n.s.	-0.27*
Median Ca ²⁺	n.s.	-0.27*	n.s.	n.s.	-0.26*	-0.29*
Minimum Ca ²⁺	0.38**	-0.29*	n.s.	n.s.	-0.38**	-0.27*
Variation of Ca ²⁺	-0.27*	n.s.	n.s.	n.s.	0.27*	n.s.
Median Mg ²⁺	n.s.	n.s.	n.s.	n.s.	-0.26*	-0.29*
Minimum Mg ²⁺	n.s.	-0.26*	n.s.	n.s.	-0.31*	-0.31*
Variation of Mg ²⁺	-0.28*	n.s.	n.s.	n.s.	0.30*	n.s.
Mean Fe	n.s.	0.31*	n.s.	n.s.	n.s.	n.s.
Median Fe	n.s.	0.33*	n.s.	n.s.	n.s.	n.s.
Mean NH ₄ ⁺	n.s.	n.s.	n.s.	-0.27*	n.s.	n.s.
Median NH ₄ ⁺	-0.26*	n.s.	n.s.	-0.33*	n.s.	n.s.
Maximum NH ₄ ⁺	n.s.	n.s.	-0.26*	-0.27*	n.s.	n.s.
Minimum NO ₃ ⁻	n.s.	n.s.	0.36**	n.s.	n.s.	n.s.
Minimum of total P	n.s.	n.s.	-0.27*	n.s.	n.s.	n.s.
Maximum of total P	n.s.	n.s.	-0.31*	n.s.	n.s.	n.s.
SO ₄ ²⁻ content	n.s.	n.s.	n.s.	n.s.	n.s.	-0.27*

Temporal fluctuation of environmental factors

There are marked seasonal trends in fluctuations of the measured parameters. Fluctuation was more considerable in flooded- and poor fens than in rich- and moderately rich fens (Fig. 5). For example, water level amplitude was about 20 cm in poor fens, but only about 5 cm in rich fens. In 2003, the same pattern was found in fluctuation of pH and conductivity (NAVRÁTILOVÁ & NAVRÁTIL 2005b). General trends could be detected in fluctuation of water level, pH, conductivity, Ca²⁺, Mg²⁺. Water table depth decreased in summer when evapotranspiration was higher and rose in autumn after rainfalls. The pH increased from spring to summer and decreased at the end of vegetation season. The lowest conductivity occurred in the spring, increased continuously throughout summer; and reached highest values in autumn. The trends in fluctuation of main cations are similar to the trend in conductivity. The anion concentrations fluctuate noticeably during vegetation season. In contrast to other measured factors, the anions (except NO₃⁻) showed no significant difference among the four defined vegetation types. In addition, there were considerable differences even within vegetation types. Further, the fluctuation of anions within vegetation types is, in some cases, bigger than the differences among vegetation types.

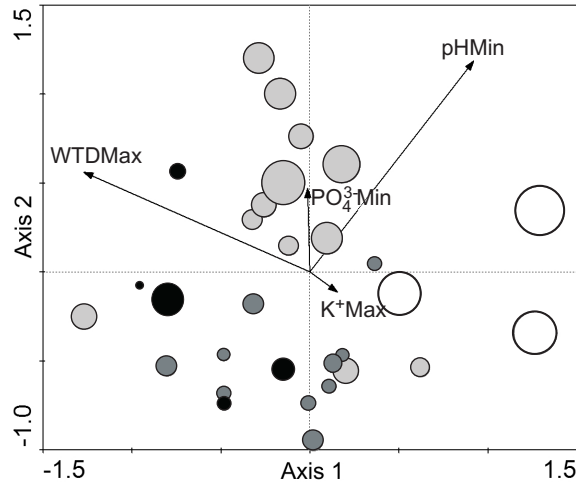


Fig. 3. Position of vegetation types according to four water parameters selected by forward selection algorithm in CCA (for legend see Fig. 2).

Comparison of environmental factors across vegetation types

The means and standard errors of environmental parameters in the four vegetation types are shown in Table 4. Between-subject (TWINSpan clusters) effect of RMANOVA was significant for water-table depth, water pH, Ca^{2+} , Mg^{2+} , K^{+} and NO_3^- . Within-subject effect (seasonal fluctuation) of RMANOVA was significant for water-table depth, water pH, conductivity, Ca^{2+} , Mg^{2+} , Fe, and NO_3^- . In some cases, the anion concentrations reached extremely high levels that have not been found in unpolluted fens (see Table 5 and Discussion).

Relationships between species richness and environmental factors

In a multiple linear regression, species richness of vascular plants correlated positively with minimum pH and negatively with both maximum water table and total percentage cover of the vegetation (Table 6). Total species richness mirrored this trend as it was governed by the richer taxonomical group, vascular plants. Fluctuation of K^{+} , however, accounted for a substantial part in species richness variation of bryophytes, followed by ammonium concentration, water-table depth and total vegetation cover. To test whether the effect of fluctuation of K^{+} and ammonium concentration could be only correlative of base saturation (fluctuation of K^{+} and ammonium increased towards poor fens), we eliminated these variables from the model and repeated the multiple regression. The variance of bryophyte species richness explained by the included factors did not change markedly, but the factors involved in the model have changed. The extent of seasonal variation in conductivity, i.e., variation in mineral richness, became the major predictor. When it was further eliminated, the explained variance was reduced by 25%. Further, when both variations in conductivity and maximum K^{+} concentration were eliminated, the explained variance was reduced even by 50%. Hence, bryophyte species richness is controlled mostly by the extent of fluctuation of environmental

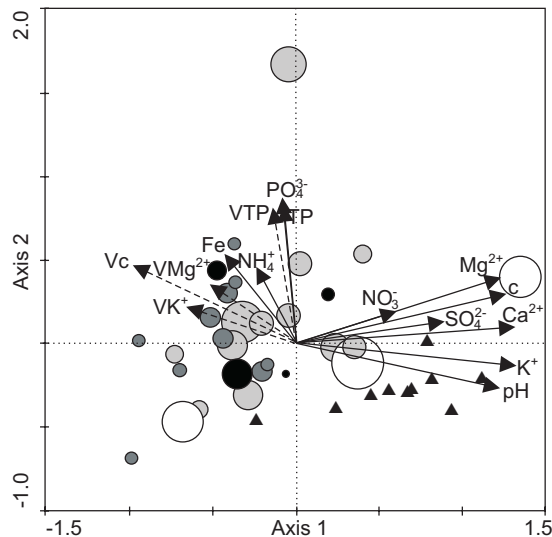


Fig. 4. PCA ordination of environmental variables. Ordination plot of samples with passively projected medians and coefficients of variation of all environmental variables (\blacktriangle – pond water; for other legend see Fig. 2).

factors in fishpond-margin fens. The Kendall tau correlations (Table 7) as well as scatter-plots (Fig. 6) confirm this fact. The water chemistry of fishpond water was similar to that of flooded- and poor fens. The rich-fen water chemistry was quite different (Table 8).

The Kruskal-Wallis test showed significant differences ($P < 0.001$) in the mean number of species among vegetation types. According to multiple comparisons of mean ranks of all groups, flooded fens are different from rich fens, and poor fens are different from moderately rich and rich-fen communities.

DISCUSSION

High nutrient levels in fishpond-margin fens

The nutrient levels found in fens at fishpond margins were extremely high, as expected. In some cases the concentration of major nutrients exceeded those measured directly in free pond water (Table 3). This is probably due to nutrient accumulation in fishpond sediments. In contrast to water in open fishpond, nutrients remain in upper parts of fen soil, from where they are released into soil water during water-level drawdown and decomposition of peat layer.

Comparison of water chemistry data published from other European and Northern-American fens show that unequalled values of N and P are attained in moderately rich fens. Fishpond-margin moderately rich fens had ammonium concentrations reaching temporarily up to 23.4 mg l^{-1} . The extensive study of habitats of wetland *Amblystegiaceae* at a wide geographic range in Sweden (HEDENÄS & KOIJMAN 1996b) presents the highest ammonium concentrations of about 6 mg l^{-1} . By analogy, one of the highest ammonium values reported from Northern-American fens are those of ANDERSON & DAVIS (1997) who have found a maximum 2.28 mg l^{-1} of ammonium. Comparably high ammonium concentrations were found only from poor fens of other fishpond-margin mire in the central part of Czech

Table 4. Descriptive statistics of water chemical variables. Mean and standard error were calculated by repeated measures ANOVA from four repeated measurements on 40 plots for each vegetation type (see Table 1)/pond water. The statistical significance of the tests of between subject effect (TWINSPAN clusters)/within subject effect (time) are in parentheses; * – significant at $P < 0.05$ and n.s. – not significant. (WTD – water table depth, c – conductivity, TP – Total P).

Fen type/fishpond	WTD (**/*) (cm)	pH (**/*)	c (n.s./*) ($\mu\text{S cm}^{-1}$)	Ca ²⁺ (**/*) (mg l^{-1})	Mg ²⁺ (**/*) (mg l^{-1})	K ⁺ (*n.s.) (mg l^{-1})
Flooded fen	0 ± 5	4.74 ± 0.29	111 ± 31	19.63 ± 4.53	4.12 ± 1.10	1.94 ± 0.63
Poor fen	-12 ± 4	4.67 ± 0.21	89 ± 22	8.62 ± 3.20	2.21 ± 0.78	1.52 ± 0.45
Medium-rich fen	-3 ± 3	5.22 ± 0.19	112 ± 20	15.16 ± 3.05	3.36 ± 0.74	1.83 ± 0.43
Rich fen	-8 ± 7	5.58 ± 0.37	167 ± 40	23.67 ± 5.85	7.59 ± 1.42	3.00 ± 0.82
Pond water	-23 ± 4	7.23 ± 0.21	165 ± 22	22.73 ± 3.20	4.79 ± 0.78	3.48 ± 0.45

Fen type/fishpond	NH ₄ ⁺ (n.s./n.s.) (mg l^{-1})	NO ₃ ⁻ (**/*) (mg l^{-1})	PO ₄ ³⁻ (n.s./n.s.) (mg l^{-1})	TP (n.s./n.s.) (mg l^{-1})	Fe (n.s./*) (mg l^{-1})	SO ₄ ²⁻ (n.s.) (mg l^{-1})
Flooded fen	0.39 ± 0.25	0.18 ± 1.00	0.02 ± 0.06	0.07 ± 0.12	9.14 ± 4.77	41.46 ± 7.11
Poor fen	0.24 ± 0.17	0.08 ± 0.71	0.04 ± 0.04	0.11 ± 0.09	12.58 ± 3.37	27.48 ± 5.03
Medium-rich fen	0.52 ± 0.16	0.12 ± 0.64	0.09 ± 0.04	0.21 ± 0.08	9.12 ± 3.22	32.26 ± 4.59
Rich fen	0.04 ± 0.32	5.38 ± 1.29	0.01 ± 0.08	0.05 ± 0.16	3.77 ± 6.16	29.21 ± 9.18
Pond water	0.19 ± 0.18	0.28 ± 0.74	0.01 ± 0.04	0.07 ± 0.09	0.79 ± 3.37	38.63 ± 5.03

Table 5. Minima and maxima of nutrient concentrations in water.

Fen type/ fishpond	NH ₄ ⁺ (mg l^{-1})		NO ₃ ⁻ (mg l^{-1})		PO ₄ ³⁻ (mg l^{-1})		Total P (mg l^{-1})		K ⁺ (mg l^{-1})	
	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
Flooded fen	0.01	1.68	0.00	2.41	0.00	0.12	0.03	0.31	0.34	6.53
Poor fen	0.00	1.69	0.00	0.89	0.00	0.37	0.04	0.92	0.06	5.27
Medium-rich fen	0.00	13.44	0.00	0.97	0.00	1.39	0.03	4.83	0.12	5.12
Rich fen	0.00	0.07	0.01	23.41	0.00	0.03	0.03	0.07	0.78	7.79
Pond water	0.00	2.23	0.00	4.29	0.00	0.12	0.03	0.21	0.79	12.27

Republic (NEUHÄUSL 1975) and from one dried-up poor fen meadow in the Western Carpathians (POULÍČKOVÁ et al. 2003). In our study, nitrate concentration was highest in base-rich spring-fed fens. The same pattern is often reported (e.g. PERSSON 1962, TAHVANAINEN et al. 2002, HÁJEK & HEKERA 2004, HEDENÄS & KOOIJMAN 2004), but the maxima of nitrate concentration found in this study, above 20 mg l^{-1} , are several fold larger than in the studies cited above. Moreover, we detected lower, but still rather high values of nitrates in flooded poor fens (up to 2.4 mg l^{-1}) that obviously copy the values found in open fishponds. Phosphate and total phosphorus concentrations were higher in fishpond-margin moderately rich fens than in naturally “eutrophic” lacustrine marshes and fens (cf. BAYLEY & MEWHORT 2004) and are comparable only with polluted fens of Netherlands (BOOTSMA & WASSEN 1996) and with poor fens colonized by *Juncus effusus* in Germany (BERTRAM 1988). However, in rich fens, maximum phosphorus concentrations were low and did not

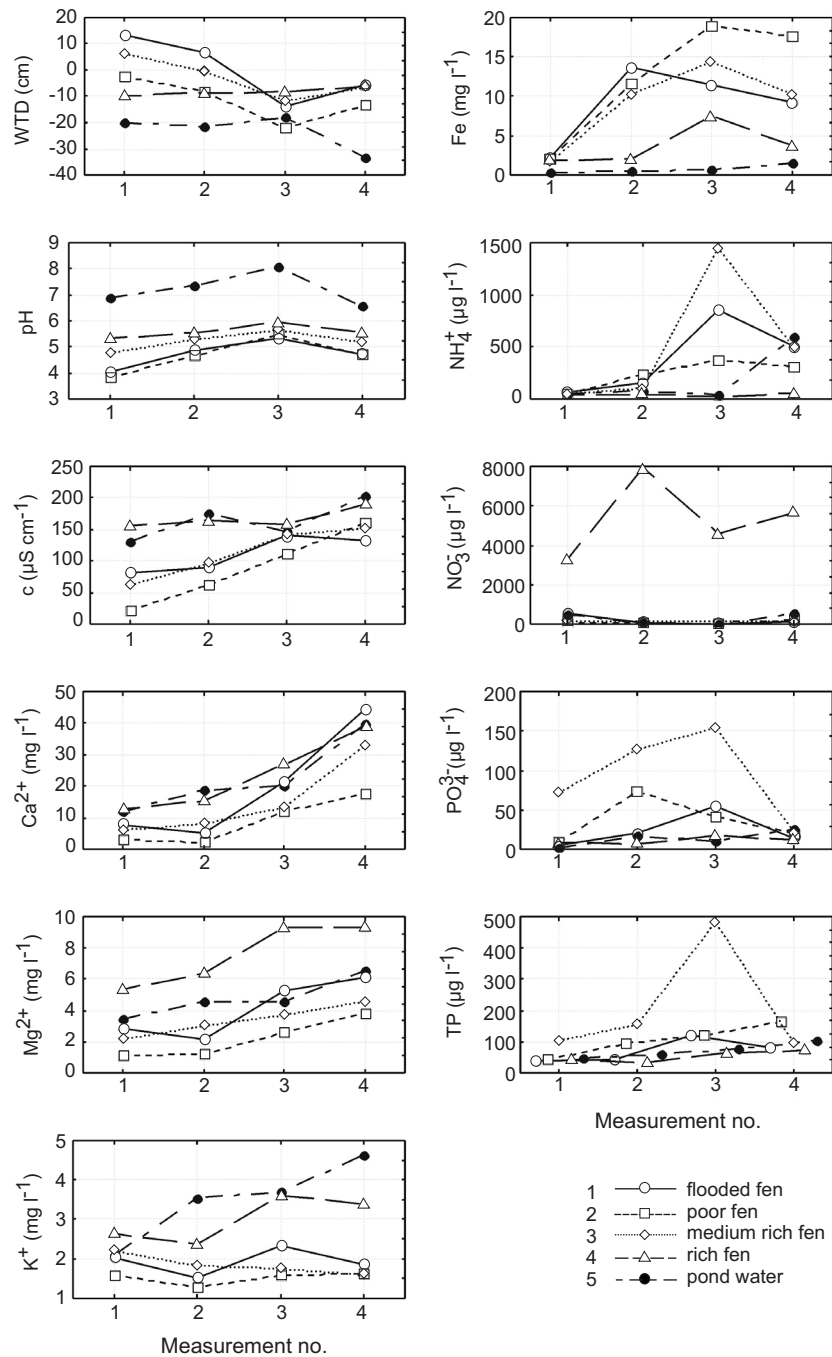


Fig. 5. Seasonal fluctuation of environmental factors for four fens types (see Table 1) and pond water. Factors were measured four times from April to September 2004 on 30 permanent plots and 10 adjacent fishponds (WTD – water-table level, c – conductivity).

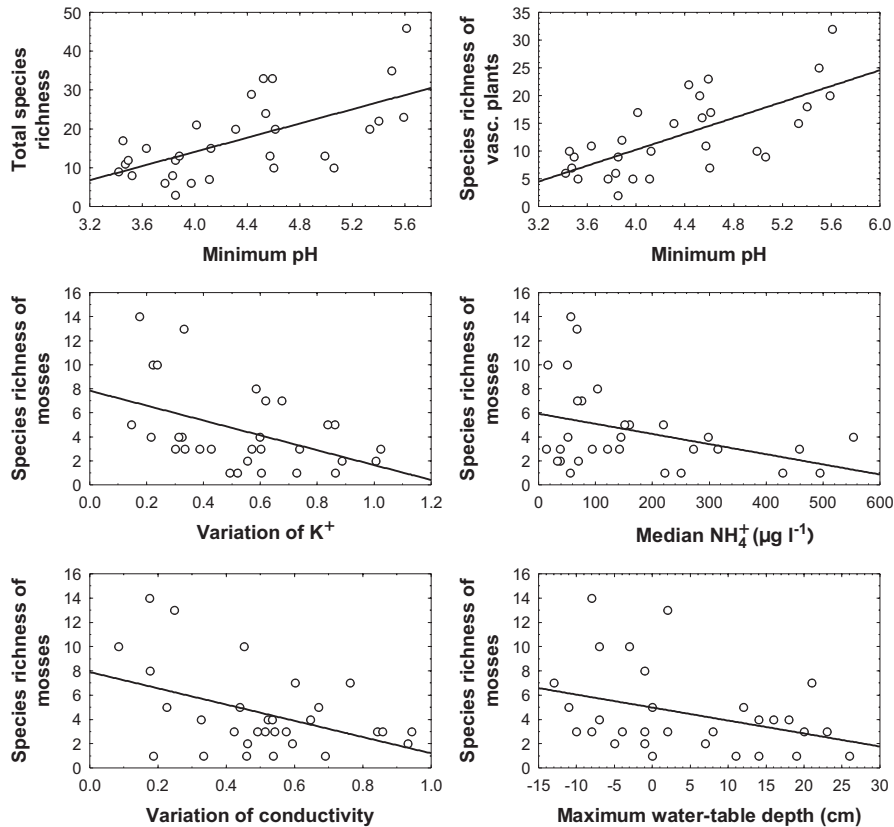


Fig. 6. Scatter-plots of main environmental variables selected by multiple regressions versus species richness. Line means linear regression between variables.

reach maximum concentrations reported from fens in literature (SLOBODDA 1979, VITT et al. 1995, BOOTSMA & WASSEN 1996, HEDENÄS & KOOLJMAN 1996b, HÁJEK et al. 2002, TAHVANAINEN 2004). The different hydrology of rich fen remnants, which are mostly fed by springwater, is probably the reason. The low P level possibly maintains rich-fen vegetation even in N-enriched conditions. This hypothesis has support in ecological literature. Nutrient, especially phosphorus supply seemed to compensate for the intolerance to high mineral levels in poor-fen species *S. fallax* that populate rich fens in Netherlands (KOOLJMAN & KANNE 1993). By analogy, LIMPENS et al. (2003) found that the expansion of *S. fallax* at the high deposition bog sites was limited by phosphorus. The expansion of *Sphagnum flexuosum* and *S. fallax* into rich fens results in acidification and consequent change into poor-fen vegetation (BELTMAN et al. 2001, HÁJKOVÁ & HÁJEK 2003). All other vegetation types have high levels of dissolved P similar to that found in open fishpond. The fishpond-to-fen connection is evident in these cases. High phosphorus supply is presumably responsible for development of poor fens even under high Ca²⁺ levels about 20 mg l⁻¹ (see also HÁJEK et al. 2002) as is further suggested by the correlation between fishpond- and poor-fen water chemistry (Table 8).

Table 6. Result of stepwise multiple regression of species richness on environmental factors. For scatter-plots see Fig. 6. (WTDMax – maximum of water-table depth; VK⁺ – variation of K⁺; cover E₁ – cover of herb layer; Vc – variation of conductivity; *T* – test value of the hypothesis that the intercept is equal to 0; Adjusted *R*² – coefficient of multiple determination).

	Regression coefficient	s.e.	Stand. regression coefficient	<i>T</i>	Sig.	Adjusted <i>R</i> ² (cumulative)
Total species richness						
pHMin	10.917	1.795	0.744	6.081	0.000	0.366
WTDMax	-0.476	0.119	-0.541	-4.011	0.000	0.488
cover total	-0.273	0.098	-0.369	-2.785	0.010	0.591
Species richness of vascular plants						
pHMin	8.201	1.251	0.791	6.556	0.000	0.460
WTDMax	-0.277	0.083	-0.445	-3.349	0.002	0.543
cover total	-0.152	0.068	-0.291	-2.226	0.035	0.602
Species richness of mosses						
VK ⁺	-5.382	1.429	-0.392	-3.767	0.001	0.175
NH ₄ ⁺ Median	-0.010	0.002	-0.435	-4.034	0.000	0.300
cover E ₁	0.083	0.018	0.513	4.540	0.000	0.401
WTDMax	-0.181	0.037	-0.600	-4.926	0.000	0.562
cover total	-0.097	0.029	-0.385	-3.351	0.003	0.689
Species richness of mosses, coefficient of variance of K ⁺ and cover total were eliminated from the model						
Vc	-9.125	2.048	-0.600	-4.457	0.000	0.165
WTDMax	-0.148	0.037	-0.493	-4.046	0.000	0.374
pHMedian	1.983	0.755	0.326	2.626	0.015	0.476
K ⁺ Max	-1.033	0.305	-0.504	-3.386	0.002	0.550
Ca ²⁺ Mean	0.107	0.042	0.342	2.520	0.019	0.630

A disaccord between potassium concentrations in fishpond water (high) and in fen water (lower) was found. Potassium concentrations measured in the fens were within the ranges reported for unpolluted spring-fed fens (HÁJEK et al. 2002, TAHVANAINEN 2004). Maximum potassium concentrations, however, correlated with the cover of vascular plants. This corresponds to the relationship between K⁺ concentration and productivity found by WASEN et al. (1990). The pattern suggests K-limitation of the study fens; plants take up all potassium when its concentration increases.

Apart from extreme nutrient supply to fishpond-margin fens, the major patterns in species richness and species composition do not differ from pristine fens to such an extent as could be expected. The major gradients in both species composition and species richness more or less correspond to those most often reported in literature (WHEELER & PROCTOR 2000, ØKLAND et al. 2001, HÁJKOVÁ & HÁJEK 2003, 2004, TAHVANAINEN 2004).

Species richness

Water pH accounted for the principal part of variation in vascular plant species richness. Due to high seasonal fluctuation of pH, the minimum pH was a better predictor than mean or maximum pH. The temporarily high pH values that occurred in poor fens in summer were

Table 7. Kendall tau correlation coefficients between total species richness, species richness of mosses and species richness of vascular plants versus significant environmental variables. Significance levels: * – $P < 0.05$, ** – $P < 0.01$, *** – $P < 0.001$, n.s. – not significant.

	Species richness	Species richness of vascular plants	Species richness of mosses
Maximum water-table depth	n.s.	n.s.	-0.25*
Variation of water-table depth	n.s.	-0.26**	n.s.
Mean pH	0.41**	0.44***	0.26*
Median pH	0.38**	0.40**	0.27*
Minimum pH	0.42**	0.47**	n.s.
Variation of pH	-0.38**	-0.42**	-0.26*
Variation of conductivity	-0.33**	-0.32*	n.s.
Minimum Ca ²⁺	0.34**	0.34**	0.30*
Variation of Ca ²⁺	-0.26*	-0.26*	n.s.
Variation of Mg ²⁺	-0.26*	-0.27*	n.s.
Variation of K ⁺	n.s.	n.s.	-0.32*
Median NO ₃ ⁻	n.s.	n.s.	0.28*
Variation of PO ₄ ³⁻	-0.26*	n.s.	n.s.
Variation of total P	n.s.	n.s.	-0.33*

probably caused by increased microbial activity and algae photosynthesis (for another example see MUÑOZ et al. 2003). The correlation between pH and vascular plant species richness has been repeatedly confirmed in mires (SCHUSTER & DIEKMAN 2003, CHYTRÝ et al. 2003, TAHVANAINEN 2004) and it seems to be valid across various scales (HÁJKOVÁ & HÁJEK 2003, 2004). The modern calcicole/calcifuge disparity in species pool that resulted from historical processes (PÄRTEL 2002, EWALD 2003) is one possible explanation, but the ecophysiological causes cannot be omitted (TYLER 2003). The second independent predictor, maximum water level, decreases species richness due to high concentration of toxic iron (SNOWDEN & WHEELER 1993), inducing anoxia and hindered seedling establishment. The pattern in bryophyte species richness found in nutrient-rich fishpond-margin fens seems to be caused primarily by local ecological factors. The major predictor of bryophyte species richness is the extent of conductivity variation. There are probably only a few bryophyte species that overcome widely fluctuating mineral richness. Independently of this pattern, increasing potassium concentration correlated negatively with species richness, probably due to the acceleration of the growth of dominant species. Maximum water level and base saturation also significantly contributed to the model. However, when conductivity variation and maximum K⁺ were excluded from the multiple regression, the explained variation declined by 50%. These results suggest that the historical explanation of the correlation between species richness and pH/calcium gradient as suggested by PÄRTEL (2002) cannot be extrapolated to bryophytes. A similar lack of relationship between bryophytes species density and pH was found also by HÁJKOVÁ & HÁJEK (2004).

Water level and nutrients

The role of water-level dynamics in nutrient-enriched fens is complex. At the landscape scale, the high correlation between water level and vegetation gradient is partly caused by

Table 8. Pearson correlation coefficients between water chemistry of each vegetation type and fishpond water. Significance levels: ** – $P < 0.01$, *** – $P < 0.001$, n.s. – not significant.

Fen type/fishpond	Flooded fen	Poor fen	Medium-rich fen	Rich fen	Pond water
Flooded fen	1.00	0.79***	0.86***	n.s.	0.59***
Poor fen	0.79***	1.00	0.79***	n.s.	0.58***
Medium-rich fen	0.86***	0.79***	1.00	n.s.	n.s.
Rich fen	n.s.	n.s.	n.s.	1.00	0.39**
Pond water	0.59***	0.58***	n.s.	0.39**	1.00

covariation with pH. In contrast to rich fens, poor acidic fens occur often in habitats with fluctuating water table. Rich-fen vegetation is strongly confined to water level not falling below ca. 20–30 cm (KOPECKÝ 1960, FLINTROP 1994, HÁJKOVÁ et al. 2004). In our study, however, only fluctuation in water level correlated with poor-rich gradient, while mean water level controls the second, independent gradient in species composition. It separated *Utricularia*- and tall-sedge fens. Maximum water level did not correlate significantly with the two major gradients, but its effect on vegetation variation was revealed by CCA (see also WIERDA et al. 1997, HÁJKOVÁ & HÁJEK 2004). Its major effect lies in lowering species richness (Table 6).

The importance of the fluctuation of water level in buffering the effect of nutrient-rich fishpond water can be assessed by numerous indices. High ammonium levels in fen water, sometimes higher than those measured directly in fishponds, are most likely caused by peat decomposition that takes place when water level decreases. The high water level can therefore disable the nutrient release. However, when the water level rises above the peat layer, the nutrient-enriched fishpond water gets directly into the moss layer. The P-rich fishpond water makes the dominance of acidifying *Sphagnum flexuosum* possible even in calcium-rich fens. The true rich-fen vegetation can survive only at spring outflows away from direct influence of fishpond water, as is indicated by low P-level. The overflowing of rich fens by fishpond water would probably cause their change into poor fens. Currently, fishpond-margin rich fens do not significantly differ from poor fens in calcium nor in pH, but in phosphate concentrations. The mean calcium concentration in flooded poor fens with *Sphagnum denticulatum* is nearly 20 mg l⁻¹, much higher than reported in literature (but see HÁJEK et al. 2002). Such a high calcium concentration in poor fens can be explained only by increased tolerance of *Sphagnum* to calcium under high nutrient (N, P, K) levels (KOOIJMAN & KANNE 1993, HÁJEK et al. 2002).

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APPENDIX

Species scores along the first and second DCA axes. Second column shows the vegetation type (1– flooded fen, 2 – poor fen, 3 – medium-rich fen, 4 – rich fen; see Table 1) to which the species reaches considerable fidelity (phi coefficient above 20).

Species	Vegetation type	DCA1 score	DCA2 score
<i>Sphagnum denticulatum</i>	1	-0.802	-0.950
<i>Sphagnum fallax</i>	2	-0.759	3.906
<i>Sphagnum papillosum</i>	2	-0.690	3.634
<i>Utricularia ochroleuca</i>	2	-0.424	2.512
<i>Carex limosa</i>	-	-0.374	3.234
<i>Phragmites australis</i>	-	-0.021	1.835
<i>Betula pubescens</i>	2	0.163	4.297
<i>Polytrichum commune</i>	2,4	0.320	2.806
<i>Utricularia intermedia</i>	1	0.360	-0.405
<i>Juncus bulbosus</i>	1,4	0.539	-0.269
<i>Eriophorum angustifolium</i>	2	0.550	0.880
<i>Iris pseudacorus</i>	1	0.702	1.432
<i>Nymphaea candida</i>	1	0.738	0.556
<i>Carex rostrata</i>	2	0.767	3.139
<i>Lycopus europaeus</i>	1	0.806	0.456
<i>Oxycoccus palustris</i>	4	0.845	2.272
<i>Carex lasiocarpa</i>	1	0.932	0.830
<i>Carex elata</i>	1	0.982	1.324
<i>Sphagnum cuspidatum</i>	-	0.984	2.919
<i>Lysimachia thyrsiflora</i>	3	1.059	1.802
<i>Picea abies</i>	3	1.062	3.056
<i>Juncus filiformis</i>	-	1.175	3.637
<i>Sphagnum flexuosum</i>	-	1.204	1.355
<i>Calamagrostis canescens</i>	-	1.215	2.007
<i>Bidens cernuus</i>	3	1.262	1.301
<i>Utricularia australis</i>	3	1.262	1.301
<i>Sphagnum inundatum</i>	3	1.314	1.858
<i>Juncus effusus</i>	3	1.371	2.835
<i>Drosera rotundifolia</i>	4	1.386	2.609
<i>Agrostis canina</i>	3	1.443	0.957
<i>Lythrum salicaria</i>	3	1.493	1.928
<i>Carex canescens</i>	3	1.505	2.197
<i>Lysimachia vulgaris</i>	3	1.581	1.656
<i>Carex nigra</i>	3	1.870	2.908
<i>Epilobium palustre</i>	3	1.911	2.114
<i>Rhynchospora alba</i>	4	1.914	0.405
<i>Peucedanum palustre</i>	3	1.954	1.977
<i>Pinus sylvestris</i>	4	1.964	2.376
<i>Typha angustifolia</i>	3	2.008	2.531
<i>Eleocharis palustris</i> agg.	3	2.036	0.834
<i>Glyceria fluitans</i>	3	2.036	0.834
<i>Phalaris arundinacea</i>	3	2.036	0.834
<i>Ranunculus flammula</i>	3	2.036	0.834
<i>Scutellaria galericulata</i>	3	2.036	0.834
<i>Sparganium emersum</i>	3	2.036	0.834
<i>Carex chordorrhiza</i>	3	2.122	2.871

Species	Vegetation type	DCA1 score	DCA2 score
<i>Galium palustre</i>	3	2.218	1.623
<i>Sphagnum subsecundum</i>	-	2.225	2.515
<i>Warnstorfia exannulata</i>	3	2.252	2.051
<i>Potentilla palustris</i>	3	2.275	2.330
<i>Calliergon stramineum</i>	3	2.539	1.915
<i>Molinia caerulea</i>	4	2.576	2.384
<i>Equisetum fluviatile</i>	3,4	2.589	2.403
<i>Frangula alnus</i>	3	2.591	1.904
<i>Hamatocaulis vernicosus</i>	3	2.669	1.025
<i>Helodium blandowii</i>	3	2.732	2.012
<i>Sphagnum platyphyllum</i>	3	2.756	1.386
<i>Carex diandra</i>	3	2.793	2.977
<i>Sphagnum majus</i>	3	2.793	2.977
<i>Betula pendula</i>	-	2.827	2.184
<i>Calamagrostis epigejos</i>	3	2.829	1.025
<i>Sphagnum fimbriatum</i>	3	2.846	1.258
<i>Calliergonella cuspidata</i>	4	2.855	1.266
<i>Brachythecium rivulare</i>	3	2.858	1.613
<i>Carex acuta</i>	3	2.858	1.613
<i>Chiloscyphus polyanthos</i>	3	2.858	1.613
<i>Drepanocladus aduncus</i>	3	2.858	1.613
<i>Lophocolea bidentata</i>	3	2.874	0.902
<i>Menyanthes trifoliata</i>	3	2.897	2.859
<i>Salix cinerea</i>	3	2.913	1.856
<i>Sphagnum palustre</i>	3,4	2.918	0.964
<i>Drosera intermedia</i>	1,4	2.958	0.688
<i>Sphagnum teres</i>	3	3.018	2.628
<i>Utricularia minor</i>	4	3.067	2.225
<i>Alnus glutinosa</i>	4	3.177	2.631
<i>Polytrichum strictum</i>	4	3.232	1.806
<i>Carex echinata</i>	4	3.248	2.706
<i>Juncus alpinoarticulatus</i>	4	3.296	1.028
<i>Viola palustris</i>	4	3.310	1.529
<i>Aulacomnium palustre</i>	4	3.316	1.678
<i>Carex dioica</i>	4	3.350	1.315
<i>Eriophorum gracile</i>	4	3.350	1.315
<i>Hydrocotyle vulgaris</i>	4	3.350	1.315
<i>Calluna vulgaris</i>	4	3.354	1.896
<i>Nardus stricta</i>	3	3.358	2.410
<i>Sphagnum contortum</i>	4	3.400	1.362
<i>Aneura pinguis</i>	4	3.407	1.368
<i>Holcus lanatus</i>	4	3.604	1.855
<i>Potentilla erecta</i>	4	3.635	1.785
<i>Sphagnum warnstorffii</i>	4	3.654	1.663
<i>Succisa pratensis</i>	4	3.660	1.713
<i>Drosera anglica</i>	4	3.765	1.454
<i>Cirsium palustre</i>	4	3.810	1.798
<i>Juncus articulatus</i>	4	3.820	1.727
<i>Carex panicea</i>	4	3.832	1.523
<i>Angelica sylvestris</i>	4	3.850	1.238
<i>Briza media</i>	4	3.850	1.238

Species	Vegetation type	DCA1 score	DCA2 score
<i>Carex demissa</i>	4	3.850	1.238
<i>Carex flava</i>	4	3.850	1.238
<i>Eriophorum latifolium</i>	4	3.850	1.238
<i>Fissidens adianthoides</i>	4	3.850	1.238
<i>Philonotis fontana</i>	4	3.850	1.238
<i>Pinguicula vulgaris</i>	4	3.850	1.238
<i>Rhytidiadelphus squarrosus</i>	4	3.850	1.238
<i>Salix aurita</i>	4	3.850	1.238
<i>Scirpus sylvaticus</i>	4	3.850	1.238
<i>Sphagnum subnitens</i>	4	3.850	1.238
<i>Tomenthypnum nitens</i>	4	3.850	1.238
<i>Bryum pseudotriquetrum</i>	4	3.919	1.461
<i>Carex pulicaris</i>	4	3.919	1.461
<i>Parnassia palustris</i>	4	3.933	1.511
<i>Galium uliginosum</i>	4	3.953	1.576
<i>Scorpidium cossonii</i>	4	3.953	1.576
<i>Trichophorum alpinum</i>	4	3.976	1.659
<i>Campylium stellatum</i>	4	4.055	1.933
<i>Carex davalliana</i>	4	4.055	1.933
<i>Equisetum sylvaticum</i>	4	4.055	1.933
<i>Linum catharticum</i>	4	4.055	1.933