Vegetation gradients in fishpond mires in relation to seasonal fluctuations in environmental factors

Sezónní kolísání faktorů prostředí a jejich souvislost s gradientem vegetace na rybničních rašeliništích

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The composition of the vegetation of fishpond mires in the Třeboň Basin (Czech Republic) was studied in relation to temporal fluctuations in certain environmental factors. The water-table depth, water pH and electrical conductivity at 49 permanent plots were measured at approximately three-week intervals from March to October 2003. Minimum, maximum, mean, median and variation in the above-mentioned environmental factors were correlated with vegetation composition. The most important environmental factors explaining the variation in vegetation were mean pH and maximum water-table level. Median conductivity increased with increase in waterlogging and eutrophication. Some seasonal trends in the dynamics of these parameters were observed. The lowest conductivity was in spring, increased continuously throughout summer and peaked in autumn. In contrast, water level decreased in summer, when evapotranspiration was greatest, and rose in autumn after heavy rainfall. The pH increased from March to June, then was stable and decreased at the end of summer. Seasonal trends were generally identical in all vegetation types. The fluctuations in the environmental factors were so considerable that they may influence the reliability of vegetation environmental analyses.

K e y w o r d s : Central Europe, electrical conductivity, fen, fluctuation, mire vegetation, water pH, water table

Introduction

Water-table fluctuations and water quality are of fundamental importance for mire vegetation (Bragazza 1997, de Mars et al. 1997, Asada 2002, Tahvanainen et al. 2002, Hájková & Hájek 2004). Water pH and electrical conductivity are the most easily measured parameters of water chemistry (Hájek & Hekera 2004). There are many studies of environmental factors and vegetation types in mountain and boreal mires (e.g. Malmer 1986, Gerdol 1995, Bragazza & Gerdol 1999, Wheeler & Proctor 2000, Økland et al. 2001, Hájek et al. 2002, Johnson & Steingraeber 2003). In contrast, data on vegetation-environment relationships are not available for Central-European lowland poor fens at fishpond margins, which have a specific water regime and whose chemical conditions are closely connected to the intensively managed fishpond ecosystem.

The mires around the fishponds in the Třeboň basin provide a good opportunity to fill this gap in mire ecology. The ponds were developed from the thirteenth century onwards from previously swampy lowlands. The littoral ecosystems of old fishponds contain reeds, tall sedges and fen vegetation. The hydrological conditions in these mires are probably more determined by man than climatic and geological factors like those in mountain or boreal mires. These mires are not purely natural, they were formed and are still influenced by man. Water-table depth in fens, for example, depends on the water regime in the adjacent fishpond, which is regulated by water gates. Numerous studies indicate that the distribution of vegetation in mires depends not only on the mean depth of the water table but also on its fluctuation (Malmer 1962, Dierschke 1969, Rybníček 1974, Asada 2002).

It has been suggested that water-table fluctuations affect root aeration and the mineral nutrition of plants (Ingram 1967). Analyses of seasonal variation in water chemistry during the growing season, using comparably sampled data sets are important for assessing the seasonal availability of nutrients in surface water (Tahvanainen et al. 2003). Most of the studies of seasonal variation in mire hydrological conditions have concentrated on ombrogenous bogs (Damman 1988, Bragazza 1993, Proctor 1994, Bragazza et al. 1998). Little is known about fluctuating environmental factors in minerogenous fens (Malmer 1962, Proctor 1995, Vitt et al. 1995, Hájková et al. 2004). It is very difficult to say to what extent the seasonal patterns found in other mires apply to climatically and geologically different regions and to those with different human impact. Hájek & Hekera (2004) report that major water chemistry variables connected with base saturation are stable and thus do not affect the reliability of vegetation-environment analyses in spring-fed fens. The extrapolation of their results to lowland fishpond mires is not, however, possible due to the completely different hydrological regime and nutrient sources in fishpond mires. The study of seasonal fluctuation in major ecological factors in mires located around fishponds is therefore needed to provide a more detailed insight into the role of seasonal fluctuations in Central-European mires in general. Although the fishpond mire vegetation has been studied extensively with respect to hydrology, there are few studies on seasonal variation (Přibáň & Jeník 2002).

The aim of our study was to characterize the vegetation of fishpond edges and reveal the seasonal patterns in major environmental factors in relation to vegetation gradients in fishpond mires.

Materials and methods

Study site

The study site is situated within the Protected landscape area, the Třeboň Basin, in the south of the Czech Republic. Six localities, fishpond Kukla (48°57'20" N, 14°53'23" E), Příbrazský fishpond (49°02'15" N, 14°56'14" E), fishpond Staré jezero (48°58'43" N, 14°53'52" E), fishpond Starý Vdovec (49°02'22" N, 14°50'12" E), fishpond Velká Lásenice (49°03'11" N, 14°57'44" E) and fishpond Vizír (48°57'43" N, 14°53'19" E) were chosen for recording temporal variations in water level and water chemistry in fens. The climate is temperate with a mean annual temperature of 7.8 °C, in the coldest month (January) of –2.2°C, and in the warmest month (July) of 17.7°C, and an average annual rainfall of 627 mm (station Třeboň).

Most of the Třeboň basin is dominated by siliceous deposits with a low concentration of electrolytes in the soil, and as a consequence poor fens are the most common type of mires. Fens around the fishponds are characterized by peat deposits of various thickness (from 10 cm to a few meters) on top of sandy deposits.

Vegetation data

In order to monitor fluctuations of environmental factors in subcontinental minerotrophic fens, 49 permanent plots were established at the six localities. The distribution of plots was intentionally not random. The plots were selected to represent all main mire vegetation types in the study area (as in Podani 1994, Somodi & Botta-Dukát 2004). Species composition was recorded during the summer of 2003 at each locality in 1 m^2 plots. The cover of both vascular plants and bryophytes was recorded using the nine-grade van der Maarel scale (1979). The height of the vegetation cover was measured and used as an indirect approximation of the productivity of the vegetation. Plant names are those used by Kubát et al. (2002), mosses by Kučera & Váňa (2003); the nomenclature of syntaxa follows Moravec et al. (1995).

Environmental factors

The water-table depth was measured manually in PVC tubes perforated throughout their length. Water pH and electrical conductivity were measured in situ using portable instruments (PH 114 CM 113, Snail Instruments, Czech Republic). At each of the 49 plots, all of the above mentioned factors were measured at approximately 20-day intervals from March to October 2003. This period corresponds to the growing season in Central Europe, when the water regime has the greatest influence on peat vegetation. The depth of peat was recorded at each sampling plot using a soil probe.

Data processing

Three related multivariate statistical techniques were used to analyse the data: two-way indicator species analysis (TWINSPAN), detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA). Each approach provides a somewhat different view of the structure of the data and when employed together these techniques can be used to complement, supplement, and evaluate other analyses (Økland 1996, Lepš & Šmilauer 2003).

Vegetation data from all stations were subjected to two-way indicator species analysis (TWINSPAN, Hill 1979) to classify the plots into groups of communities. Pseudospecies cut levels were set at 0, 5 and 25 to suit the dataset composed of percent frequency. Differences in species number in the different strata were evaluated using the Kruskal-Wallis test.

Gradient analysis was performed using DCA and CCA algorithms of the CANOCO 4.5 package (ter Braak & Šmilauer 2002). The percent frequency of the species was log-transformed and rare species were downweighted. The parameters obtained from consecutive measurements may have different significance in explaining vegetation gradients. Therefore, five statistical parameters (mean, median, minimum, maximum and standard deviation) obtained from consecutive measurement of each environmental factor, as well as the thickness of the peat layer, were used in ordinations.

The vegetation data set was subjected first to DCA, in order to assess the overall variation patterns in species composition. Ordination site scores were correlated to environmental factors using Pearson's correlation coefficient. All environmental variables were plotted onto DCA ordination diagrams as supplementary environmental data for better ecological interpretation of the axes.

Subsequently CCA was used to further examine the species-environmental relationships. Sixteen environmental variables in total were subjected to forward selection (ter Braak & Šmilauer 2002, Lepš & Šmilauer 2003) in order to determine the variables that best account for the species distribution. The marginal and conditional effects of each of these explanatory variables on species composition was then tested. The effect of the first canonical axis was tested by a permutation test (499 permutations were always used). To test the statistical significance of the second and next canonical axis partial CCA was calculated in which the first axis (or next ones) is partialled out by the covariable. Significance was again tested by permutation tests for the first canonical axis.

The seasonal trends in environmental factors and the differences in the factors among the communities (pH and conductivity also measured in open water) were investigated by Repeated measurements ANOVA. Data transformation was not required because the data were normally distributed and homogeneity of variance was assumed.

Results

Fen communities

The vegetation was classified by the third division of TWINSPAN into seven groups (Table 1). Each community is named according to the dominant or diagnostic species. The "*Utricularia* fen" (Type 1) occurs as an initial successional stage on permanently flooded sandy deposits. Syntaxonomically, this community belongs to the alliance *Sphagno-Utricularion* characteristically dominated by *Utricularia intermedia*. The shores of *Utrichlaria* pools are often occupied by a "*Rhynchospora alba* community" (Type 2) (alliance *Rhynchosporion albae*). It occurs on sandy deposits with some peat. The dominant species are *Rhynchospora alba*, *Juncus bulbosus* and *Sphagnum denticulatum*. Fens dominated by tall sedges such as *Carex lasiocarpa* and *C. rostrata* are referred to as "tall sedge communities" (Type 3) of the *Magnocarition elatae* alliance. They are found in the littoral zone of mesotrophic water. The soil is fen peat. One type of fen with a low electrolyte concentration but higher pH than poor fens was found in the study area. This "medium-rich fen" vegetation (Type 4) belongs to the alliance *Eriophorion gracilis.* Species growing there are more or less confined to rich fens: *Hamatocaulis vernicosus, Sphagnum subsecundum* and *S. contortum*. They grow together with all the common poor fen species. Such fens develop in stands saturated with mineral-rich groundwater. Species such as *Carex elata* and *C. lasiocarpa* grow together with some of the above-mentioned poor-fen and intermediate-fen species. The next three TWINSPAN columns represent poor fen vegetation belonging to the alliance *Sphagno recurvi-Caricion canescentis*. It is the most common mire vegetation in the Třeboň basin. Among the bryophytes, *Sphagnum* species play a principal role. This group was further divided into three subtypes. The first represents an intermediate type with raised-bog vegetation (Type 5). The hummock species *Calluna vulgaris* and *Oxycoccus palustris* are present here. In addition, some of the species typical for pond margins are always present, e.g. *Phragmites australis.* The species composition of the "typical poor fen" vegetation (Type 6) is quite uniform. Species such as *Carex rostrata*, *Eriophorum angustifolium, Sphagnum papilosum* or *S. fallax* often dominate. The last type (Type 7) is poor fen vegetation associated with willow cars and other wet habitats, which have an impact on species composition. The peat is slightly mineralized, as indicated by species such as *Polytrichum commune*.

Table 1. – Synoptic table of vegetation types obtained by TWINSPAN classification. The species percentage frequencies (constancies) are shown. Species are sorted according to the decreasing value in the phi coefficient. Diagnostic species for particular columns have a phi > 0.20 and are highlighted by frames. Vegetation type: *Sphagno-Utricularion* (1), *Rhynchosporion albae* (2), *Magnocaricion elatae* (3), *Eriophorion gracilis* (4), *Sphagno recurvi-Caricion canescentis* (5, 6, 7).

Vegetation type	1	2	3	4	5	6	7
Number of relevés	5	5	5	9	6	15	4
E1							
Juncus bulbosus	40	40	.	.	17	7	.
Utricularia intermedia	40	.	80	.	.	.	.
Carex lasiocarpa	80	.	100	89	33	13	75
Pinus sylvestris juv.	.	80	.	11	67	73	.
Rhynchospora alba	20	40	.	.	50	13	.
Epilobium palustre	.	.	80	.	.	.	.
Typha latifolia	.	.	40	.	.	.	.
Carex acuta	.	.	40	.	.	.	.
Galium palustre	20	.	60	44	.	.	.
Viola palustris	.	.	40	11	.	.	25
Agrostis canina	20	60	80	44	17	20	50
Lysimachia thyrsiflora	.	20	60	56	.	20	.
Lysimachia vulgaris	.	20	80	89	33	27	75
Lythrum salicaria	.	.	40	56	.	.	25
Potentilla palustris	20	.	40	100	.	20	25
Peucedanum palustre	.	.	40	89	.	7	50
Salix cinerea juv.	.	.	.	44	.	.	.
Equisetum fluviatile	.	.	.	44	.	.	25
Carex elata	.	20	40	56	.	7	25
Carex canescens	.	20	40	78	17	47	.
Carex nigra	.	20	20	44	17	7	25
Calamagrostis canescens	.	.	.	33	.	13	25
Utricularia minor	20	20	.	22	.	.	.
Carex rostrata	.	.	60	56	33	33	50
Calluna vulgaris	.	.	.	.	17	.	.
Drosera rotundifolia	20	20	.	67	83	60	25
Phragmites australis	20	.	.	11	33	20	.
Oxycoccus palustris	.	20	.	33	50	60	50
Hydrocotyle vulgaris	.	.	.	.	.	13	.
Molinia caerulea	20	20	20	.	50	47	25
Juncus filiformis	.	.	.	.	.	.	25
Eriophorum angustifolium	100	100	100	89	83	93	.
Utricularia ochroleuca	20	20	.	.	.	7	.
Lycopus europaeus	20	.	.	11	.	.	.
Frangula alnus juv.	.	.	.	11	17	.	.
E0							
Sphagnum denticulatum	.	100	.	.	33	20	.
Calliergonella cuspidata	.	.	40	22	.	.	.
Sphagnum inundatum	.	.	40	11	.	.	25
Calliergon stramineum	.	20	80	67	17	13	100
Sphagnum flexuosum	20	.	40	11	.	.	50
Sphagnum subsecundum	.	.	.	56	.	.	.
Warnstorfia exannulata	.	20	40	78	.	7	.
Aneura pinguis	.	.	.	33	.	.	.
Lophocolea bidentata	.	.	.	33	.	.	.
Sphagnum fimbriatum	.	.	.	33	.	.	50
Sphagnum palustre	20	.	20	.	100	7	100
Aulacomnium palustre	.	.	20	33	50	13	25

Sphagnum papillosum	.	.	.	.	.	53	.
Sphagnum fallax	20	40	20	11	50	80	.
Polytrichum strictum	.	.	.	.	.	27	.
Sphagnum affine	.	.	.	.	.	13	.
Polytrichum commune	.	20	.	22	33	47	75

Species present in only one column: E1: *Potentilla erecta* 3: 20, *Utricularia australis* 3: 20, *Scutellaria galericulata* 3: 20, *Cirsium palustre* 3: 20, *Cardamine amara* 4: 11, *Eriophorum vaginatum* 6: 7, *Drosera intermedia* 6: 7, *Vaccinium vitis-idaea* 6: 7, *Betula pubescens* juv. 4: 11, *Salix aurita* juv. 4: 11. E0: *Sphagnum platyphyllum* 4: 11, *Chiloscyphus polyanthos* 4: 11, *Drepanocladus aduncus* 4: 11, *Brachythecium rivulare* 4: 11, *Sphagnum magellanicum* 4: 11, *Hamatocaulis vernicosus* 4: 11, *Sphagnum contortum* 4: 11, *Sphagnum obtusum* 4: 11, *Plagiothecium denticulatum* 4: 11, *Sphagnum rubellum* 6: 7.

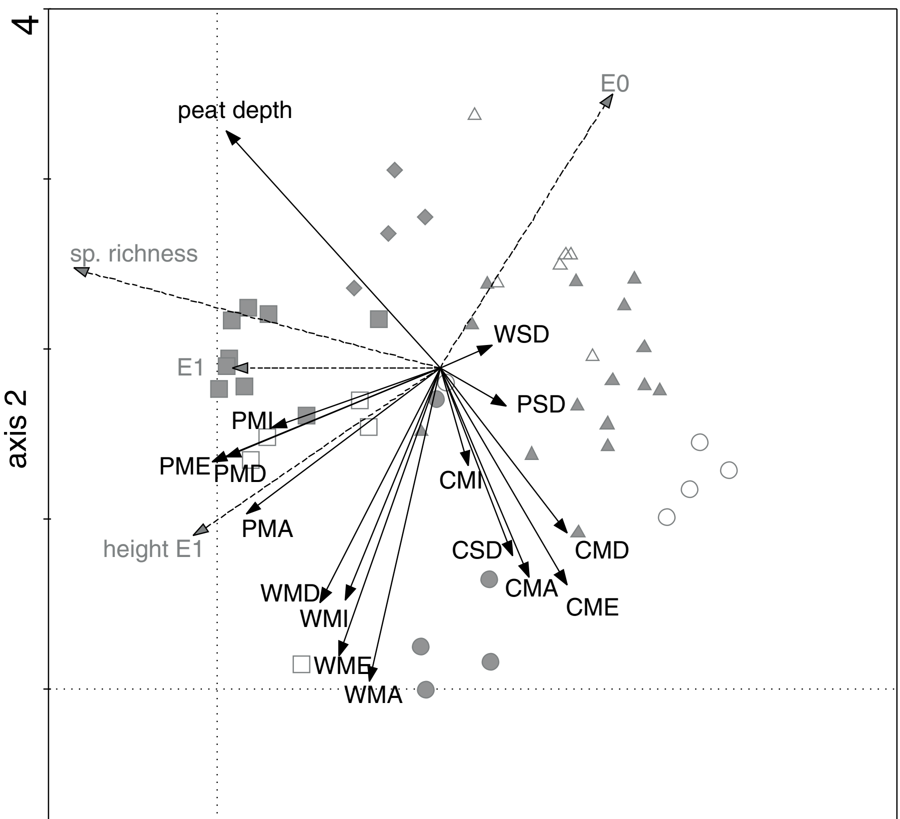

Fig. 1. – Ordination diagram of vegetation samples based on DCA with passive environmental variables. WME = mean water-table depth, WMD = median water-table depth, WMI = minimum water-table depth, WMA = maximum water-table depth, WSD = standard deviation of water-table depth, PME = mean water pH, PMD = median water pH, PMI = minimum water pH, PMA = maximum water pH, PSD = standard deviation of water pH, CME = mean electrical conductivity, CMD = median electrical conductivity, CMI = minimum electrical conductivity, CMA = maximum electrical conductivity, CSD = standard deviation of electrical conductivity, peat depth = thickness of peat layer, height E1 = height of herb layer, E0 = cover of moss layer, E1 = cover of herb layer, sp. richness = species richness. Vegetation types: □ = *Utricularia* fen, ■ = *Rhynchospora alba* community, ○ = tall sedges, ● = medium-rich fen, △ = *Sphagnum palustre* poor fen, ▲ = *Sphagnum fallax* poor fen, ◆ = *Polytrichum commune* poor fen.

The Kruskal-Wallis test showed significant differences ($P < 0.001$) in the mean species numbers among communities. The medium-rich fens are different from species-poor communities like: *Utricularia* fens, the *Rhynchospora alba* community and *Sphagnum fallax* poor fen.

Gradient analysis

The first two DCA axes are nearly equal in length (Fig. 1) and explain about 20% of the total species variability. They also correlate well with environmental data ($r_{1st\ ax.} = 0.918$; $r_{2nd\ ax.} = 0.868$). The first ordination axis is correlated significantly ($P < 0.01$) with mean pH, with species richness, height of the vegetation and herb layer cover. The second ordination axis is significantly correlated with variables related to the water regime, mainly maximum water level, and percent cover of mosses, and less markedly with mean and maximum electrical conductivity. Thickness of peat layer correlate significantly with both axes, decreasing with increasing water-table depth and increasing with increasing pH. It is negatively correlated with conductivity (Table 2).

Four canonical axes of CCA with all environmental variables were significant ($P < 0.01$), explaining about 26% (first two about 17%) of the total variability in the species data. Species-environmental correlation is similar to that in unconstrained ordination ($r_{1st\ ax.} = 0.892$, $r_{2nd\ ax.} = 0.900$). The pH parameters and thickness of peat layer were governed by both the first and second canonical axes, while conductivity and water parameters were governed by the second canonical axis.

Using the forward selection in CCA the four most important variables were selected: thickness of peat layer, maximum water level, mean pH and median conductivity (Fig. 2). They explain about 20% of the total variability in species data and a considerable part (59%) of the variance in the species-environment relations.

Temporal fluctuations in environmental factors

There were marked seasonal fluctuations in water-table depth, water pH and water electrical conductivity in the fishpond fens studied (Fig. 3). In general, seasonal trends were similar for all vegetation types. In particular, water level decreased in summer, when evapotranspiration was greatest, and rose again in autumn after rainfall. The pH increased from March to June, then was stable and then decreased at the end of summer. Electrical conductivity was low in spring, then increased continuously throughout summer and peaked in autumn.

Comparison of environmental factors among communities

Means and standard error of measured environmental parameters in the different vegetation types are shown in Table 3. Repeated measured ANOVA was significant for both, within-subject effect (seasonal fluctuation) and also between-subject effect (TWINSPAN clusters) in the case of all measured factors. According to Tukey unequal N HSD post hoc test, significant differences ($P < 0.05$) were found in pH between open pond water and all fens. Vegetation with *Rhynchospora alba* differs in conductivity from medium-rich vegetation and poor fen vegetation with *Sphagnum fallax*, which have the lowest conductivity. There were no significant differences among vegetation types in water regime according to the Tukey unequal N HSD test.

Table 2. – Correlation coefficients between environmental variables and DCA ordination scores of the sample plots along the first and the second axes. ** P < 0.01, * P < 0.05, ns – not significant.

Variable	Axis 1	Axis 2
Mean water pH (PME)	–0.40**	ns
Median water pH (PMD)	–0.36*	ns
Minimum water pH (PMI)	–0.30*	ns
Maximum water pH (PMA)	–0.35*	–0.32*
Mean electrical conductivity (CME)	ns	–0.45**
Median electrical conductivity (CMD)	ns	–0.32*
Maximum electrical conductivity (CMA)	ns	–0.41**
Standard deviation of electrical conductivity (CSD)	ns	–0.36*
Mean water-table depth (WME)	ns	–0.63**
Median water-table depth (WMD)	ns	–0.50**
Minimum water-table depth (WMI)	ns	–0.54**
Maximum water-table depth (WMA)	ns	–0.68**
Peat depth	–0.38**	0.53**
Height of herb layer	–0.40**	–0.32*
Species richness	–0.62**	0.32*
Cover of herb layer (E1)	–0.37**	ns
Cover of moss layer (E0)	ns	0.66**

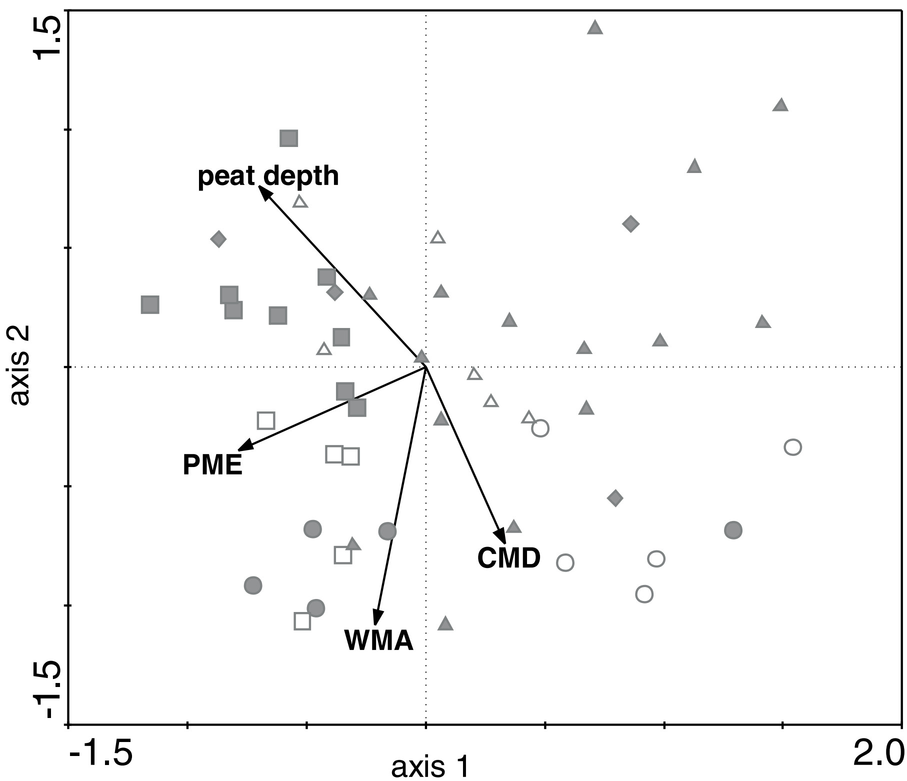

Fig. 2. – The samples-environmental variables biplot based on CCA. WMA = maximum water-table depth, PME = mean water pH, CMD = median water eletrical conductivity, peat depth = thickness of peat layer. For vegetation types symbols see Fig. 1.

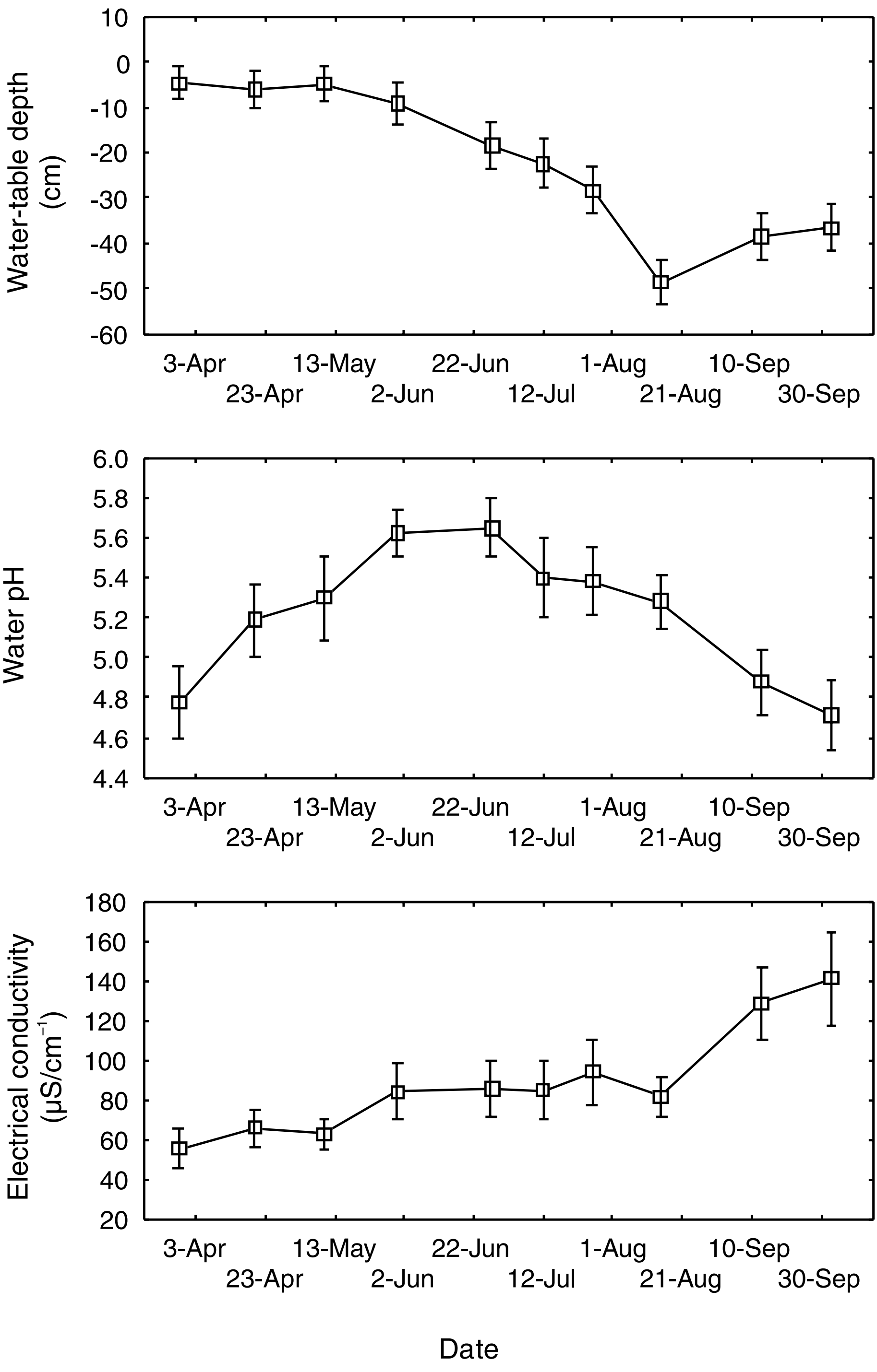

Fig. 3. – Temporal fluctuation in selected environmental variables. Vertical bars denote 0.95 confidence interval. Measurements were carried out from March to October 2003 at approximately three-week intervals.

Table 3. – Mean values (± standard error, SE) of water characteristics in the different vegetation types. Repeated measures ANOVA test revealed significant differences (P < 0.05) among vegetations types for the selected water variables. Means with the same letter do not differ significantly (Tukey HSD multiple comparison test, P > 0.05).

Vegetation type	pH		Electrical conductivity (uS/cm)		Water-table depth (cm)	
	Mean	SE	Mean	SE	Mean	SE
Utricularia fen	5.48a	0.15	118.7ab	12.4	–6.7a	5.9
Rhynchospora alba community	5.00a	0.13	125.5a	11.1	–15.2a	5.9
Tall sedges	5.36a	0.13	94.6ab	11.1	–14.3a	5.9
Medium-rich fen	5.34a	0.10	65.1b	8.8	–25.9a	4.6
Sphagnum fallax poor fen	5.28a	0.15	85.9ab	12.4	–28.9a	5.4
Sphagnum palustre poor fen	4.94a	0.09	71.1b	7.5	–28.6a	3.4
Polytrichum commune poor fen	5.14a	0.21	57.5ab	17.5	–33.0a	6.6
Open pond water	8.29b	0.29	155.2ab	24.8	–	–

Discussion

The role of environmental conditions in plant species composition

The present analysis permitted the identification of the main environmental gradients affecting the plant species composition of fishpond mires. The first two DCA axes are nearly equal in length suggesting that the whole dataset is governed by two mains gradients. The first axis corresponds to an acidity-alkalinity gradient (from medium-rich fens to poor fens). Accordingly, pH of surface water was significantly connected with this vegetation gradient. Along the second ordination axis, the vegetation of flooded fens was separated from that of the other communities, especially the drier ones (bog-fen-marsh gradient), so the second ordination axis corresponds to a water-table depth gradient. The correlation between samples and environmental variables in CCA is similar to that in unconstrained ordination. This suggests that the selected environmental variables are responsible for the variation in species composition.

Correlation between vegetation and environmental parameters permitted further clarification of the influence of the environmental factors on vegetation differentiation. The presence of tall sedge vegetation correlated with high water level, high pH and high electrical conductivity. This vegetation was also the tallest, indicating a higher nutrient availability in tall sedge communities typically located in the littoral of meso- (eu-) trophic ponds. In contrast to this, the moss cover increases in poor fen vegetation, as indicated by the presence of *Sphagnum* species. The vegetation with the highest species richness occurs in stands with the highest water pH, quite low electrical conductivity, and little eutrophication due to man. In this habitat the fluctuation in environmental factors is also very low. In contrast to this, pH, conductivity and water level fluctuate more in poor fen vegetation. A very similar result was obtained for Carpathian fens, where water level fluctuation, as well as seasonal variability in water chemistry, were larger in poor than in rich fen microhabitats (Hájková et al. 2004). The species richness is generally lower in poor than in rich fens (e.g. Hájková & Hájek 2003) due to the larger species pool of calcicole species in Central-Europe (Chytrý et al. 2003). Our results suggest another explanation for this difference in species richness – a pauperization of regional poor-fen flora due to marked fluctuations in water level, which causes extinction of some obligate fen species not adapted to changing water level. A periodical flooding by nutrient-rich pond water seems to be a major factor affecting the occurrence of rare species in poor fens.

Seasonal variation in selected environmental factors

Fluctuation in the environmental variables measured is very conspicuous in fishpond mires. For example, difference in water level from March to August is about 45 cm, difference in pH between spring, autumn and summer is about 1 pH unit, and conductivity doubled from March to October. The fluctuation in time is, in some cases, bigger than the differences among communities. The fluctuation in environmental factors is due to fluctuations in water level related to evapotranspiration and precipitation. The evapotranspiration is high in summer and as precipitation in summer 2003 were extremely low, the water level fell. It is more difficult to explain the fluctuation in pH. Many different factors influence the complex acid-base balance in mire waters, including hydrology, bedrock, soil quality, weathering rate, nutrient uptake by plants, cation and anion exchange, decomposition, redox reactions and atmospheric deposition (Shotyk 1988). The cation exchange by *Sphagnum* is an important primary source of acidity in many cases (Clymo 1987, Vitt 2000). The low pH at the beginning and end of the vegetation season may have been caused by *Sphagnum* activity. The activity of *Sphagnum* species has a large impact on the organic acidity of mire water (Tahvanainen et al. 2002). *Sphagnum* species, which are not noticeably limited by low temperatures, acidify mire water mainly in spring and autumn, when they are not limited by herb layer.

The significant autumnal increase in conductivity might be explained by decreasing water level (Baumann 1996, Hájková et al. 2004). However, in the fishpond mires studied the conductivity continued to increase even after the autumnal rains caused the water level to rise. The water in fishponds mires accumulates after rains in contrast to spring fens where the rainfall run off is accelerated and the ions are eluted. The dry and hot climate associated with the water table decrease in summer 2003 probably caused a higher biological activity in the peat resulting in the release of chemical elements into the interstitial water, which became more mobile after heavy rainfall and influenced conductivity in the sampling device (Mörnsjö 1969)

In conclusion, the vegetation of fishpond mires is particularly affected by the chemical and hydrological water conditions. These conditions are not static, but fluctuate markedly during the growing season and have a significant role in affecting vegetation types.

Conservation note

The intensive fish-production (fertilizing, fish feeding) together with inputs from the catchment area (agriculture, pollution and nutrient inputs) has caused the eutrophication of the fishponds (Pechar et al. 2002) over the last 30 years. One of the wide spread methods used in current fish farming is to retain an extremely high water table in the ponds. However, optimal hydrology for fens may not be optimal for fish breeding (Lamers et al. 2002). The nutrients in the eutrophic pond water enrich the fen areas, which are usually distant from the pond edges. Only the vegetation of *Utricularia* fens, tall-sedge fens and *Sphagnum fallax* poor fens can survive in stands influenced by eutrophic pond water. These vegetation types are more resistant to overgrowing by plant species confined to euthrophicated stands. The influence of pond water often causes tall sedges and shrubs to invade low-sedge poor fen vegetation and accelerates the succession towards more productive vegetation types.

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Souhrn

Na vybraných rybničních rašeliništích Třeboňské pánve (ČR) bylo studováno složení vegetace ve vztahu k sezónnímu kolísání faktorů prostředí. Od března do října byla v třítýdenních intervalech prováděna měření výšky vodní hladiny, pH a konduktivity na 49 trvalých plochách. Se složením vegetace byly následně korelovány minimum, maximum, průměr, medián a odchylka od průměru měřených faktorů. Nejdůležitějšími faktory vysvětlujícími variabilitu vegetace byly: průměr pH (koreluje signifikantně s 1. osou DCA), a maximální výška hladiny vody (koreluje signifikantně s 2. osou DCA). Medián konduktivity koreloval s oběma osami a zvyšoval se s rostoucím stupněm zamokření a současně vzrůstající eutrofizací stanovišť. V kolísání sledovaných parametrů byly zjištěny určité sezónní trendy. Nejnižší konduktivita byla na jaře a zvyšovala se postupně během léta, s maximem na podzim. Voda naproti tomu klesala během léta, kdy byla zvýšená evapotranspirace a začala růst až na podzim po vydatnějších deštích. Hodnota pH se zvyšovala od března do června, od konce léta pak klesala na počáteční hodnoty. Tyto sezónní trendy byly u všech vegetačních typů podobné. Kolísání měřených faktorů prostředí bylo tak výrazné, že by mohlo ovlivnit spolehlivost vegetačně-stanovištních analýz.

References

Asada T. (2002): Vegetation gradients in relation to temporal fluctuation of environmental factors in Bekanbeushi peatland. – Ecol. Res. 17: 505–518.

Baumann K. (1996): Kleinseggenriede und ihre Kontaktgesselschaften im westlichen Unterharz (Sachsen-Anhalt). – Tuxenia 16: 151–177.

Bragazza L. (1993): Seasonal changes in water chemistry in a bog on the southern Alps. – Suo 44: 87–92.

Bragazza L. (1997): *Sphagnum* niche diversification in two oligotrophic mires in the southern Alps of Italy. – Bryologist 100: 507–515.

Bragazza L., Alber R. & Gerdol R. (1998): Seasonal chemistry of pore water in hummocks and hollows in a poor mire in the southern Alps (Italy). – Wetlands 18: 320–328.

Bragazza L. & Gerdol R. (1999): Ecological gradients on some *Sphagnum* mires in the south-eastern Alps (Italy). – Appl. Veg. Sci. 2: 55–60.

Chytrý M., Tichý L. & Roleček J. (2003): Local and regional patterns of species richness in central European vegetation types along the pH/calcium gradient. – Folia Geobot. 38: 429–442.

Clymo R. S. (1987): Interactions of *Sphagnum* with water and air. – In: Hutchinson T. C. & Havas M. (eds.), Effect of atmospheric pollutants on forests, wetlands and agricultural ecosystems, p. 513–529, Springer-Verlag, Berlin.

Damman A. W. H. (1988): Spatial and seasonal changes in water chemistry and vegetation in an ombrogenous bog. – In: Verhoeven J. T. A., Heil G. W. & Werger M. J. A. (eds.), Vegetation structure in relation to carbon and nutrient economy, p. 107–119, Acad. Publ., The Hague.

de Mars H., Wassen M. J. & Olde Venrink H. (1997): Flooding and groundwater dynamics in fens in eastern Poland. – J. Veg. Sci. 8: 319–328.

Dierschke H. (1969): Groundwasser-Ganglinien einiger Pflanzengesillschaften des Holtumer Noores östlich von Bremen. – Vegetatio 17: 372–383.

Gerdol R. (1995): Community and species-performance patterns along an alpine poor-rich mire gradient. – J. Veg. Sci. 6: 175–182.

Hájek M., Hekera P. & Hájková P. (2002). Spring fen vegetation and water chemistry in the western Carpathian flysch zone. – Folia Geobot. 37: 205–224.

Hájek M. & Hekera P. (2004): Can seasonal variation in fen water chemistry influence the reliability of vegetation-environment analyses? – Preslia 76: 1–14.

Hájková P. & Hájek M. (2003): Species richness and above-ground biomass of poor and calcareous spring fens in the flysch West Carpathians, and their relationships to water and soil chemistry. – Preslia 75: 271–287.

Hájková P. & Hájek M. (2004): *Sphagnum*-mediated successional pattern in the mixed mire in the Muránska planina Mts (Western Carpathians, Slovakia). – Biologia 59: 63–72.

Hájková P, Wolf P. & Hájek M. (2004): Environmental factors and Carpathian spring fen vegetation: the importance of scale and temporal variation. – Ann. Bot. Fenn. 41: 249–262.
Hill M. O. (1979): TWINSPAN – a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes. – Ecology and Systematics, Cornell University, Ihtaca.
Ingram H. A. P. (1967): Problems of hydrology and plant distribution in mires. – J. Ecol. 55: 711–724.
Johnson J. B. & Steingraeber D. A. (2003): The vegetation and ecological gradients of calcareous mires in the South Park valley, Colorado. – Can. J. Bot. 81: 201–219.
Kubát K., Hrouda L., Chrtek J. jun., Kaplan Z., Kirschner J. & Štěpánek J. (eds.) (2002): Klíč ke květeně České republiky. – Academia, Praha.
Kučera J. & Váňa J. (2003): Check- and Red List of bryophytes of the Czech Republic (2003). – Preslia 75: 193–222.
Lamers L. P. M., Smolders A. J. P. & Roelofs J. G. M. (2002): The restoration of fen in the Netherlands. – Hydrobiologia 478: 107–130.
Lepš J. & Šmilauer P. (2003): Multivariate analysis of ecological data using CANOCO. – University Press, Cambridge, UK.
Malmer N. (1962): Studies on mire vegetation in the Archaean area of south-western Götaland (south Sweden) I. Vegetation and habitat conditions on the Akhult mire. – Opera Bot. Soc. Bot. Lund. 7:1–322.
Malmer N. (1986): Vegetation gradients in relation to environmental conditions in north-western European mires. – Can. J. Bot. 64: 375–383.
Moravec J., Balátová-Tuláčková E., Blažková D., Hadač E., Hejný S., Husák Š., Jeník J., Kolbek J., Krahulec F., Kropáč Z., Neuhäusl R., Rybníček K., Řehořek V. & Vicherek J. (1995): Rostlinná společenstva České republiky a jejich ohrožení. Ed. 2. – Severoč. Přír., Příl. 1995: 1–206.
Mörnsjö T. (1969): Studies on vegetation and development of a peatland in Scania, south Sweden. – Opera Botanica 24: 1–187.
Økland R. H. (1996): Are ordination and constrained ordination alternative or complimentary strategies in general ecological studies? – J. Veg. Sci. 7: 289–292.
Økland R. H., Økland T. & Rydgren K. (2001): A Scandinavian perspective on ecological gradients in north-west European mires: reply to Wheeler and Proctor. – J. Ecol. 89: 481–486.
Pechar L., Přikryl I. & Faina R. (2002): Hydrobiological evaluation of Třeboň fishponds since the end of the nineteenth century. – In: Květ J., Jeník J. & Soukupová L. (eds.), Freshwater wetlands and their sustainable future, Man and the biosphere series, Vol. 28, p. 31–61, UNESCO, Paris & The Panthenon Publishing Group, Lancaster.
Podani J. (1994): Multivariate data analysis in ecology and Systematics. – SPB Academic Publishing, The Hague.
Proctor M. C. F. (1994): Seasonal and short-term changes in surface-water chemistry on four English ombrogenous bogs. – J. Ecol. 82: 597–610.
Proctor M. C. F. (1995): Hydrochemistry of the raised bog and fens at Malharm Tarn National Nature Reserve, Yorkshire, UK. – In: Hughes J. M. R. & Heathwaite A. L. (eds.), Hydrology and hydrochemistry of British wetlands, p. 273–289, John Wiley & Sons, Chichester.
Přibáň K. & Jeník J. (2002): Climatic and hydrologic setting of the wet meadows. – In: Květ J., Jeník J. & Soukupová L. (eds.), Freshwater wetlands and their sustainable future, Man and the biosphere series, Vol. 28, p. 211–231, UNESCO, Paris & The Panthenon Publishing Group, Lancaster.
Rybníček K. (1974): Die Vegetation der Moore im südlichen Teil der Böhmisch-Mährischen Höhe. – Vegetace ČSSR, A6, Academia, Praha.
Shotyk W. (1988): Review of the inorganic geochemistry of peat's and peatland waters. – Earth-Science Rewiews 25: 95–176.
Somodi I. & Botta-Dukát Z. (2004): Determinants of floating island vegetation and succession in a recently flooded shallow lake, Kis-Balaton (Hungary). – Aquat. Bot. 79: 357–366.
Tahvanainen T., Sallantaus T., Heikkilä R. & Tolonen K. (2002): Spatial variation of mire surface water chemistry and vegetation in north-eastern Finland. – Ann. Bot. Fenn. 39: 235–251.
Tahvanainen T., Sallantaus T. & Heikkilä R. (2003): Seasonal variation of water chemical gradients in three boreal fens. – Ann. Bot. Fenn. 40: 345–355.
ter Braak C. J. F. & Šmilauer P. (2002): CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination Version 4.5. – Microcomputer Power, Ithaca.
van der Maarel E. (1979): Transformation of cover-abundance values in phytosociology and its effect on community similarity. – Vegetatio 39: 97–114.
Vitt D. H. (2000): Peatlands: ecosystems dominated by bryophytes. – In: Shav A. J. & Goffinet B. (eds.), Bryophyte biology, p. 312–343, Cambridge University Press, Cambridge.

Vitt D. H., Bayley S. E. & Jin T. L. (1995): Seasonal variation in water chemistry over a bog-rich fen gradient in continental western Canada. – Can. J. Fish. Aquatic Sci. 52: 587–606.
Wheeler B. D. & Proctor M. C. F. (2000): Ecological gradients, subdivisions and terminology of north-west European mires. – J. Ecol. 88: 187–203.

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