Nitrogen:phosphorus ratio as the main ecological determinant of the differences in the species composition of brown-moss rich fens in north-eastern Poland

Poměr dusíku a fosforu jako hlavní ekologické vysvětlení rozdílů v druhovém složení minerálně bohatých mechových slatinišť severovýchodního Polska

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Dedicated to Kamil Rybníček and Eliška Rybníčková on the occasion of their 80th birthdays

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The species composition of 22 mires (brown-moss rich fens) was surveyed in north-eastern Poland, located in continental boreo-nemoral Europe. Detailed analyses of the water chemistry, biomass N, P, and K content, productivity and water level were made. Two floristically different types of rich-fen vegetation occur in this area, one with numerous *Caricetalia davallianae* (calcicole) species such as *Scorpidium cossonii*, *Campylium stellatum*, *Carex lepidocarpa* and *Eriophorum latifolium* (Cd fens) and the other with a few *Caricetalia davallianae* species and mainly *Hamatocaulis vernicosus*, *Marchantia polymorpha*, *Plagiomnium ellipticum*, *Carex diandra* and *C. rostrata* (non-Cd fens). In these two rich-fen types surface water chemistry and water levels were similar, but the Cd fens characteristically had higher pHs and lower PO_4^{3-} concentrations. N and P availability revealed by the N:P ratio is the ecological factor that best accounts for the differences in species composition of the two rich-fen types: the non-Cd fens are N-limited while the Cd-fens are usually P-limited. Moreover, the Cd fens differ from the non-Cd fens in a higher productivity of the bryophyte layer. In the case of P and K concentrations, there is a correlation between that in vascular plants and bryophytes, while N concentrations are not correlated. We believe that in the case of low productive ecosystems the use of the broad "nutrient availability gradient" should be replaced by a (from) N-(to) P-limitation gradient with N:P ratio as a useful measure. Natural N-limited, low-productive rich fens and their ecological conditions can be a phenomenon typical of continental-eastern temperate European areas, which have been poorly surveyed and need further research.

K e y w o r d s: bryophytes, calcicole species, *Caricetalia davallianae*, continental fens, extremely rich fens, N:P ratio, nutrient availability, productivity, surface water chemistry

Introduction

Nutrient availability is considered to be one of the most important ecological gradients determining floristic variation within mire vegetation, along with the poor-rich gradient and water-level gradient (Wheeler & Proctor 2000, Hájek et al. 2006). Nutrient-rich habitats are often highly productive but species-poor, while ecosystems with limited nutrient availability support low-productive, species-rich plant communities (Wheeler & Shaw 1991, Wassen & Olde Venterink 2006). N:P ratio in vascular plant biomass is a generally accepted (although criticized, e.g. Güsewell et al. 2003) tool for assessing the factor limiting a particular patch of vegetation (Wassen et al. 1995, Koerselman & Meuleman 1996, Olde Venterink et al. 2003). It influences not only the productivity and species richness (Olde Venterink et al. 2003) and the presence of endangered species (Wassen et al. 2005), but also the species composition is different in N- to P-limited vegetation (Verhoeven & Schmitz 1991, Bedford et al. 1999).

Drainage for agricultural purposes and use of fertilizers has resulted in the eutrophication of mire ecosystems (Grootjans et al. 1986, Verhoeven & Schmitz 1991, Kooijman 1992, Succow & Joosten 2001). In addition, anthropogenic N-deposition accelerates the eutrophication processes (van Duren & Pegtel 2000, Paulissen et al. 2004) and can result in a shift from N- to P-limitation (Wassen et al. 2005, Phuyal et al. 2008, Elser et al. 2009). The supply of nitrogen from the air in the Netherlands (50 kg N ha^{-1}·year^{-1}) is from five to ten fold greater than in Poland (5–10 kg N ha^{-1}·year^{-1}), especially in the poorly developed north-eastern rural part of the country (Verhoeven et al. 1996).

The classification of mire (including rich-fen) vegetation has been a matter of ongoing discussion since Koch's (1926) contribution, as presented in Rybníček's (1985) survey of classification approaches in Europe. The brown moss-sedge vegetation of extremely rich fens is usually attributed to the *Caricetalia davallianae* order (= *Tofieldietalia*), usually within the *Caricion davallianae* alliance (Braun-Blanquet 1949, Oberdorfer 1992, Matuszkiewicz 2008, Hájek & Hájková 2011), the majority of the characteristic species of these syntaxa are also "rich fen indicators" sensu Du Rietz (1949). It is suggested that P-limitation is essential for development of species-rich *Caricion davallianae* vegetation (Boeye et al. 1997), which is usually attributed to immobilization of P due to calcium precipitation (Boyer & Wheeler 1989).

There are some data on moss-sedge rich fens with a low percentage of calcicole rich-fen specialists/*Caricetalia davallianae* species in the eastern part of Europe. These fens are usually dominated by *Carex rostrata* or *C. diandra* and are characterized by a significant cover of grasses. The data on these fens include "*Drepanocladus*-reichen Kraut-Gras-Assoziationen" and "*Camptothecium*-reichen Kraut-Gras-Assoziationen" in the vicinity of Moscow (Katz 1929), "*Hypneto-Caricetum* der Quellmoore" and *Rumicetum acetosae* in spring fens in former East Prussia (Steffen 1931), *Festuco rubrae-Caricetum rostratae* in north-eastern Poland (Sokołowski 1986–1987), *Sphagno-Caricetum rostratae* (with hardly any *Sphagnum*) and *Caricetum diandrae* in north-western Poland (Wołejko 2000), *Caricetum limoso-diandrae caricetosum rostratae* in the Biebrza valley (Pałczyński 1975) and vegetation with *Menyanthes trifoliata*, *C. rostrata*, *Hamatocaulis vernicosus*, *Tomentypnum nitens* and *Festuca rubra* in the Rospuda valley (Jabłońska et al. 2011). Similar vegetation, with a variety of endangered plants (e.g. *Saxifraga hirculus* and *Stellaria crassifolia* – Pawlikowski 2010) and species of snails (Schenková et al. 2011) is

recorded in a number of non-disturbed, (predominantly) soligenous rich fens in the Lithu-anian Lake District (north-easternmost Poland). The surface waters in these plant commu-nities are reported to have relatively high P concentrations (Pawlikowski 2008) and at least some of them were co-limited by P and N (Fujita et al. 2010).

The aim of this paper is to answer the following questions: (i) Which ecological factors (including surface water chemistry, water level and N, P, K availability) determine the spe-cies composition in extremely rich fens in north-eastern Poland, especially those with a low percentage of the fen-indicating *Caricetalia davallianae* species? (ii) How does N, P-availability influence the species composition and productivity of vascular plants and bryophytes, respectively? (iii) Are the N, P and K contents of vascular plants similar to those in bryophytes?

Material and methods

Study area

In north-eastern Poland there are features characteristic of a post-glacial landscape. This area is situated in the northern part of the nemoral forest zone (boreo-nemoral transitional zone). The climate is under strong continental influence. The average annual temperature over the period 1971–2000 was 6.3°C, 1991–2000 6.8 °C and 2001–2005 6.9 °C and the average precipitation 591, 575 and 601 mm per year, respectively (Anonymous 2011; data from the Suwałki meteorological station).

Sampling procedure

In 2011, a total of 50 plots were located at random in 22 extremely rich fens (Fig. 1) with vegetation dominated or codominated by carpets of brown-moss (in order to exclude a micro-topography gradient from the analysis, i.e. not to include hummock or hollow vegetation and plots undergoing rapid succession). In each plot a 9 m^2 (3 × 3 m) relevé using a 7-grade Braun-Blanquet scale (Westhoff & van der Maarel 1978) method was undertaken. In the centre of each relevé area, two litres of surface water were collected from the moss layer, half of which was preserved by adding 1 mL H$_2$SO$_4$ per 1 L of sam-ple. The pH and EC of the water was analysed using a portable device. At the end of July, from an area of 0.25 m^2, living (green) parts of vascular plants and bryophytes were col-lected (using scissors) separately and placed in paper bags to dry out. The water level was measured in previously dug pits twice during 2011 (in July and September). Names of vas-cular plants and mosses follow Mirek et al. (2002) and Hill et al. (2006), respectively.

Analysis of water chemistry

After transporting the samples to the laboratory, Ca^{2+}, Na$^+$ and K$^+$ concentrations were determined using a flame spectrophotometer, Mg^{2+} concentrations an atomic absorption spectrophotometer, Cl$^-$ by the argentometric method, chemical oxygen demand (COD) as consumption of KMnO$_4$ in an acid medium and carbonate hardness by titration with 0.01 N HCl using methyl orange as an indicator. The following were measured spectro-photometrically: total Fe (using the rhodanate method), dissolved SiO$_2$ (molybdate
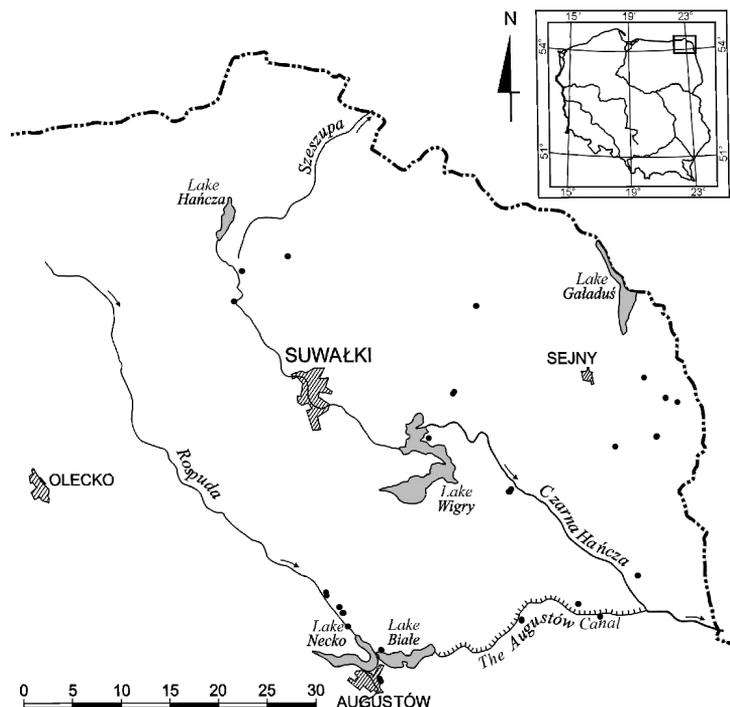
Fig. 1. – Map of north-eastern most Poland with the locations of the rich fens surveyed.

method), PO_4 (molybdate method), NO_3^- (using phenoldisulphonic acid), NH_4^+ (Nessler's method), SO_4^{3-} (barium chloride) and colour (based on the platinum-cobalt scale). Total Fe, PO_4^{3-}, NO_3^-, NH_4^+ and COD-$KMnO_4$ were determined using the preserved water. Concentrations of K^+ and Na^+ were determined in 100 mL solutions extracted with 2 mL HCl (1+1). In strongly coloured samples, the colour was reduced using aluminium hydroxide. These determinations were made following the methods described by Hermanowicz & Dojlido (1999).

Biomass analyses

Dried biomass was used as a measure of productivity. A few grams of dry matter removed at random from each sample were ground into a powder, which was used for N, P and K determinations. The percentage of nitrogen was determined using a CHNS analyser NA 2500 series, CE Instruments, ThermoQuest Italia S.p.A. and conventional standards. The methods of determining phosphorus and potassium were those described by Ostrowska et al. (1991) for plant dry matter. 1.000±0.001 g of plant dry matter was mineralized in quartz bowls for four hours at a temperature of 450°C. The ash was then dissolved in hot 10% hydrochloric acid and dried for an hour at 110°C to precipitate silica and then dissolved again in acid. The resulting solution was filtered and quantitatively transferred into 50 cm^3 flasks filled with distilled water before it was used to determine the phosphorus and potassium contents. Phosphorus was determined using the colorimetric molybdate method with

photorex. Prior to this analysis the solution obtained by mineralization was diluted 100 times. The phosphate concentrations were determined using a spectrophotometer HACH DR/4000 and calculated in terms of the percentage of phosphorus in the dry plant material. Potassium content was determined directly using the solution and flame photometry (photometer JENWAY PFP7), and calculated in terms of the percentage of potassium in dry matter.

Ratios of the nutrient contents, expressed in terms of the percentages of the elements in dry matter, were calculated and a limitation model for each sample identified using the critical values for vascular plants proposed by Wassen et al. (2005). N:P ratio values below 13.5 indicate N-limitation, between 13.5 and 16 N and P co-limitation and above 16 P-limitation, while N:K ratio above 2.1 and K:P ratio below 3.4 were assumed to indicate K (co)limitation.

Data processing

The relevés were classified using the modified TWINSPAN algorithm (Roleček et al. 2009) implemented in JUICE software (Tichý 2002; pseudo-species cut levels of species percentage cover 0, 5, 25; see Roleček 2005, Dítě et al. 2006). The differences in the species composition and relations between the different types of vegetation and surface water chemistry were revealed using detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) (CANOCO for Windows Version 4.0; Ter Braak & Šmilauer 2002). The Mann-Whitney U test (Zar 1999) was used to determine significant differences between the different types of vegetation. The number of calcicole species in the relevés was calculated using Ellenberg's R value ≥ 7 (Ellenberg & Leuschner 2010) and the number of *Caricetalia davallianae* species by using the Polish national list by Matuszkiewicz (2008).

Results

The TWINSPAN analysis divided the dataset into two groups: (i) one with numerous species of *Caricetalia davallianae* (hereinafter referred to as "Cd fens") with *Scorpidium cossonii* dominant in the moss layer and (ii) one with a low percentage of species of *Caricetalia davallianae* and *Hamatocaulis vernicosus* ("non-Cd fens"; Table 1). In addition to the presence of plants associated with the *Scheuchzerio-Caricetea nigrae* class, the Cd fens are best distinguished by the presence of *Caricetalia davallianae*-specialists (e.g. *Carex lepidocarpa*, *Campylium stellatum*, *Eleocharis quinqueflora* and *Eriophorum latifolium*). Among the other species there are some wetland generalists (*Scutellaria galericulata*, *Peucedanum palustre*, *Lycopus europaeus*) and particular bryophytes (e.g. *Philonotis fontana* and *Aneura pinguis*). In contrast, non-Cd phytocoenoses are characterized by a lower percentage of species of the class *Scheuchzerio-Caricetea nigrae* (the most frequent are *Eriophorum angustifolium*, *Menyanthes trifoliata*, *Carex diandra* and *C. limosa*) and a few *Caricetalia davallianae*-specialists (mainly *Carex dioica* and orchids). They are best distinguished by the presence of numerous tall species of sedge– and reed-bed communities (e.g. *Carex rostrata*, *Typha latifolia*, *Cicuta virosa*, *Ranunculus lingua*), meadow plants (e.g. *Rumex acetosa*, *Lychnis flos-cuculi*) and a distinct set of bryophytes (including *Marchantia polymorpha* and *Plagiomnium ellipticum*).

Table 1. – Synoptic table of 50 relevés (after TWINSPAN classification) listing the diagnostic species, species with a high frequency (> 30%) and *Caricetalia davallianae* species (according to Matuszkiewicz 2008; indicated by an asterisk). Fidelity values (phi coefficient) are listed for species that differ significantly based on the Fisher's exact test (P < 0.05) and frequency values (%) are given in superscripts. Shrubs and trees are not included. For both types of fens, n = 25.

Vegetation type	non-Cd fens	Cd fens
Diagnostic species of non-Cd fens:		
Hamatocaulis vernicosus	88.6^{100}	$\_^{12}$
Marchantia polymorpha	68.6^{64}	$\_^{.}$
Agrostis stolonifera	50.0^{88}	$\_^{40}$
Plagiomnium ellipticum	50.0^{40}	$\_^{.}$
Carex rostrata	46.8^{96}	$\_^{56}$
Carex diandra	44.6^{80}	$\_^{36}$
Stellaria palustris	43.6^{32}	$\_^{.}$
Epilobium palustre	40.8^{80}	$\_^{40}$
Rumex acetosa	40.3^{28}	$\_^{.}$
Typha latifolia	40.0^{36}	$\_^{4}$
Cardamine pratensis	37.5^{92}	$\_^{60}$
Lychnis flos-cuculi	36.9^{24}	$\_^{.}$
Cicuta virosa	36.4^{32}	$\_^{4}$
Ranunculus lingua	30.6^{44}	$\_^{16}$
Calliergon giganteum	28.8^{76}	$\_^{48}$
Diagnostic species of the Cd fens:		
*Scorpidium cossonii**	$\_^{4}$	96.1^{100}
*Carex lepidocarpa**	$\_^{.}$	96.1^{96}
*Campylium stellatum**	$\_^{.}$	78.3^{76}
Carex panicea	$\_^{.}$	62.4^{56}
*Eleocharis quinqueflora**	$\_^{8}$	61.8^{68}
Juncus articulatus	$\_^{8}$	51.4^{56}
Scutellaria galericulata	$\_^{.}$	43.6^{32}
*Epipactis palustris**	$\_^{44}$	41.7^{84}
*Eriophorum latifolium**	$\_^{.}$	40.3^{28}
Drosera anglica	$\_^{8}$	37.5^{40}
Cirsium palustre	$\_^{4}$	36.4^{32}
Peucedanum palustre	$\_^{16}$	34.3^{48}
Mentha ×verticillata	$\_^{.}$	33.3^{20}
Pedicularis palustris	$\_^{.}$	33.3^{20}
Philonotis fontana	$\_^{.}$	33.3^{20}
Phragmites australis	$\_^{4}$	32.7^{28}
*Liparis loeselii**	$\_^{12}$	31.9^{40}
Aneura pinguis	$\_^{4}$	28.8^{24}
Lycopus europaeus	$\_^{12}$	28.1^{36}
Eupatorium cannabinum	$\_^{12}$	28.1^{36}
Species with a high frequency not listed above:		
Bryum pseudotriquetrum	$\_^{80}$	$\_^{84}$
Eriophorum angustifolium	$\_^{92}$	$\_^{80}$
Menyanthes trifoliata	$\_^{80}$	$\_^{80}$
Calliergonella cuspidata	$\_^{80}$	$\_^{68}$
Carex limosa	$\_^{64}$	$\_^{80}$
Galium palustre	$\_^{80}$	$\_^{60}$
Equisetum fluviatile	$\_^{56}$	$\_^{52}$
Drosera rotundifolia	$\_^{36}$	$\_^{36}$
Utricularia minor	$\_^{44}$	$\_^{36}$
Triglochin palustre	$\_^{32}$	$\_^{48}$
Lysimachia thyrsiflora	$\_^{32}$	$\_^{32}$

Galium uliginosum	_28	_48
Caltha palustris	_32	_28
Lysimachia vulgaris	_28	_32
Carex lasiocarpa	_24	_48
Caricetalia davallianae species not listed above:		
*Carex dioica**	_16	_24
*Parnassia palustris**	_8	_24
*Scorpidium scorpioides**	_4	_20
*Pinguicula vulgaris**	_.	_4

The floristic difference between the two types of vegetation is clearly confirmed by DCA ordination (Fig. 2). On the left of the first ordination axis there are almost only non-Cd, N-limited samples, while on the right there are the Cd, P- and N-limited samples as well as N-P co-limited samples, although P-limited samples dominate. In addition, P-limited fens differ floristically from the majority of N-limited fens. In the Cd fens the bryophyte biomass is higher than the vascular plant biomass, while in the non-Cd fens the biomass of both layers is comparable. Moreover, the Cd fens differ from the non-Cd fens by a higher biomass of bryophytes (Fig. 3). Primary productivity of vascular plants is negatively correlated with the N:P ratio (Fig. 4).

The analyses of surface water chemistry revealed that it is very similar in the Cd and non-Cd fens (Fig. 3). Only the pH and carbonate hardness indicate that the Cd fens are slightly more alkaline (pH median value = 7.07) than the non-Cd fens (pH median value =
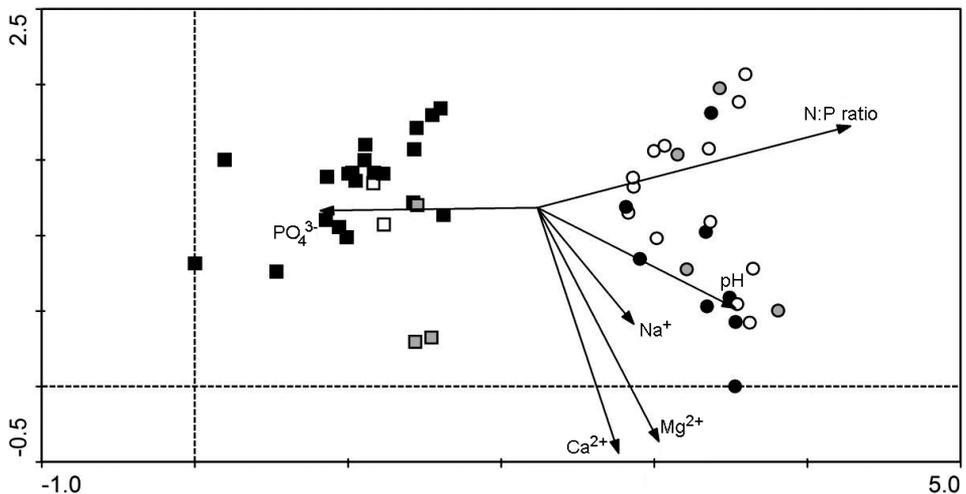

Fig. 2. – DCA ordination plot of 50 relevés (eigenvalues: $\lambda_1 = 0.61$; $\lambda_2 = 0.23$) along with passively projected explanatory variables, which were significant in the CCA (based on the forward selection procedure and Monte Carlo permutations). The non-Cd fens are indicated by squares, Cd fens by circles. Black colour indicates N-limitation, grey N-P co-limitation, white P-limitation (using critical values of Wassen et al. 2005).
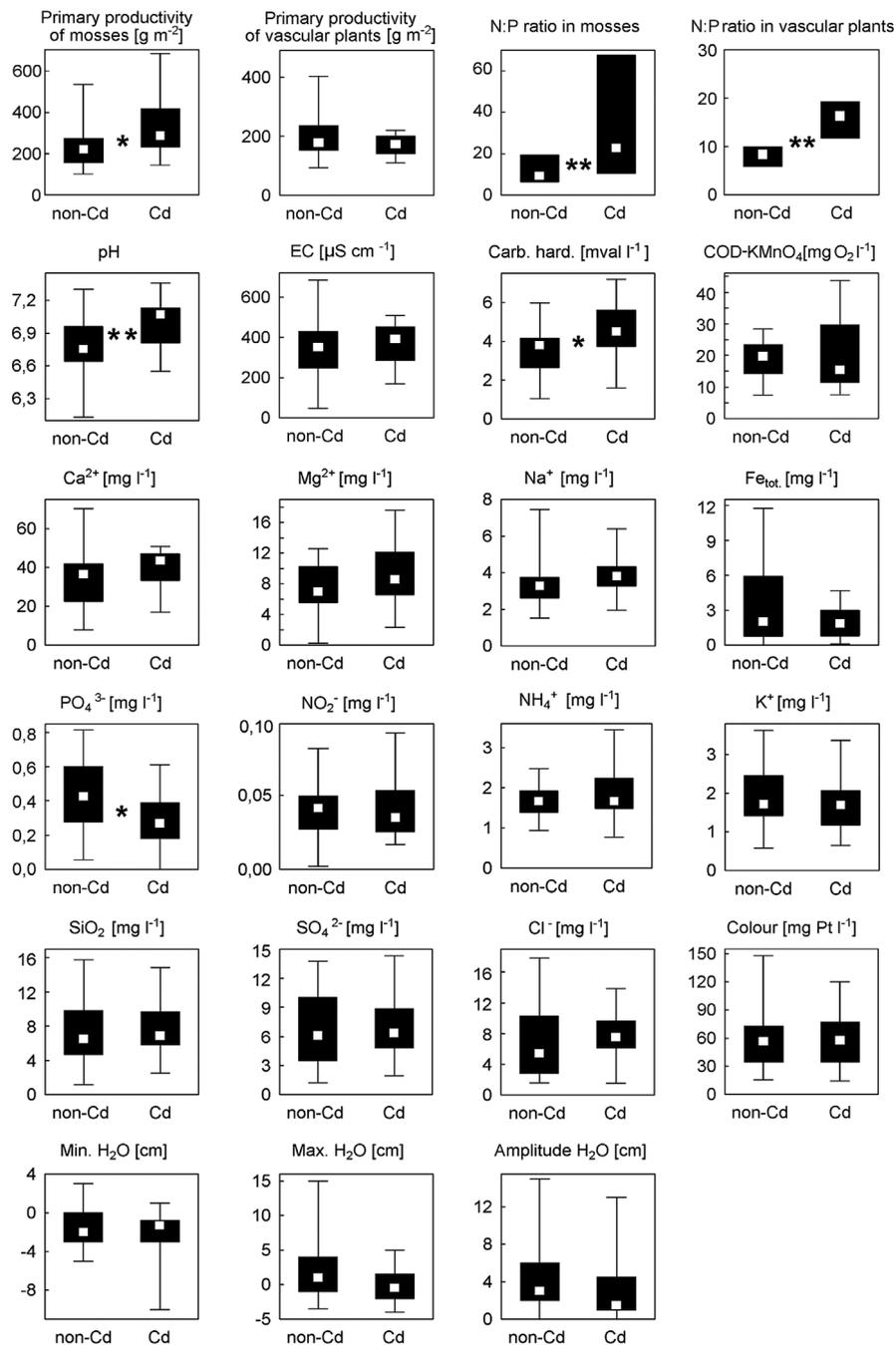
Fig. 3. – Differentiation of non-Cd fens and Cd-fens in terms of above-ground biomass, N:P ratios in bryophytes and vascular plants, surface water chemistry and water level. Black boxes indicate 25–75% interquartile ranges of values and white boxes the medians. Significant differences (Mann-Whitney U test) are indicated by asterisks: * ($P < 0.05$) and ** ($P < 0.01$). Single outlying values are not shown on graphs in the case of COD-KMnO$_4$, Fe$_{tot}$, PO$_4^3$, NO$_3^-$, SO$_4^{2-}$ and Cl$^-$.
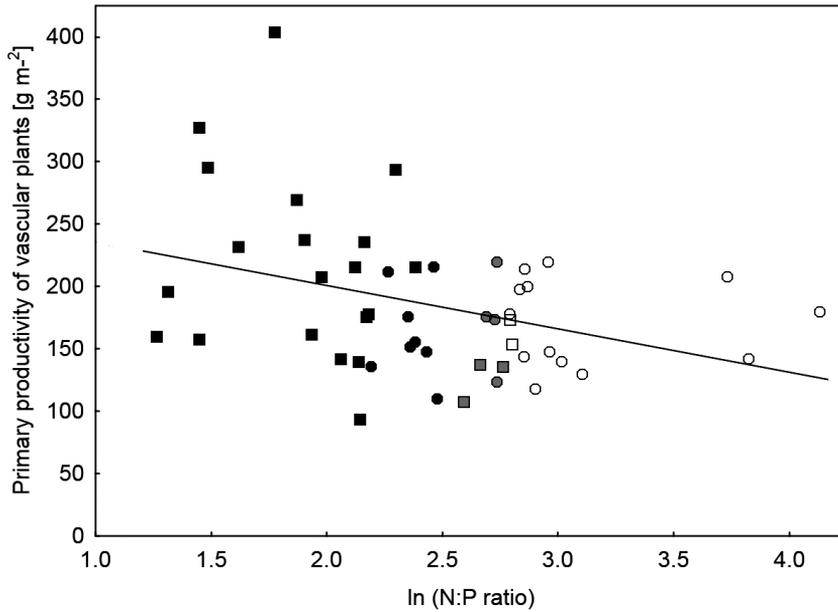
Fig. 4. – Above-ground biomass vs N:P ratios for vascular plants of non-Cd fens (squares) and Cd fens (circles). N:P ratio was calculated from percentages of the elements in dry matter. Black colour indicates N-limitation, grey N-P co-limitation, and white P-limitation (using critical values of Wassen et al. 2005); P = 0.0109, r^2 = 0.1274.
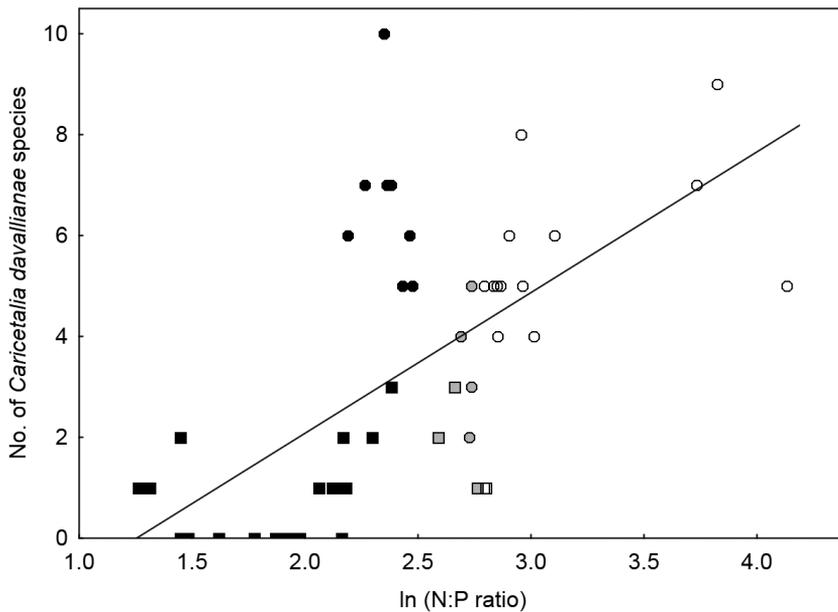

Fig. 5. – Number of *Caricetalia davallianae* specialists (according to Matuszkiewicz 2008) vs N:P ratios in above-ground biomass of vascular plants; P < 0.0001, r^2 = 0.3801. For explanations see Fig. 4.
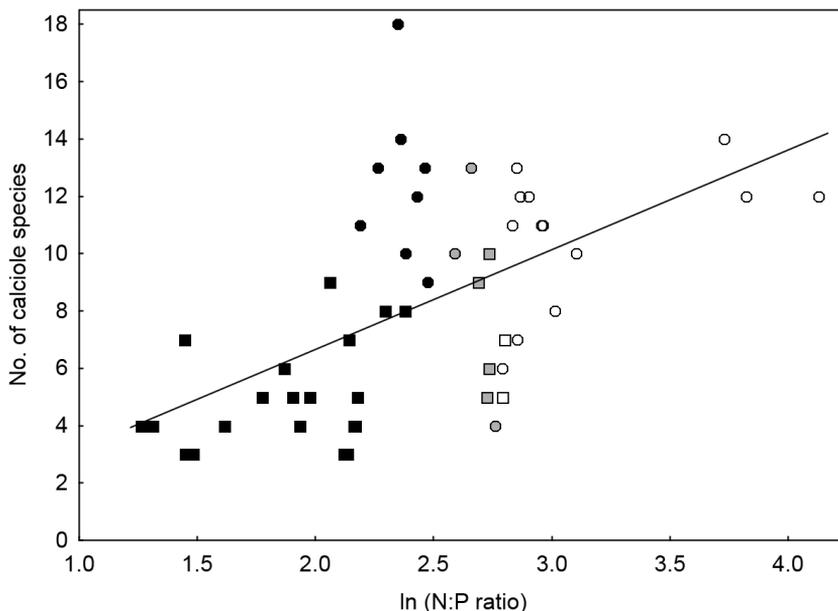
Fig. 6. – Number of calciole species (with Ellenberg's R value ≥ 7) vs N:P ratios in above-ground biomass of vascular plants; P < 0.0001, r^2 = 0.3173. For explanations see Fig. 4.

6.75). In addition, the Cd-fens have a lower (although largely overlapping) PO_4^{3-} concentrations (0.00–1.28 mg·L^{-1}) than the non-Cd fens (0.06–2.88 mg·L^{-1}). Orthophosphate and iron concentrations are correlated (y = –0.2093+8.7418x; P < 0.0001; r^2 = 0.6599). The CCA analysis (eigenvalues: λ_1 = 0.42; λ_2 = 0.19) revealed that the significant variables (based on the forward selection procedure and Monte Carlo permutations) were N:P ratio, PO_4^{3-}, Ca^{2+}, Mg^{2+} and Na^+ concentrations as well as pH. N:P ratios and higher pH values, typical of the Cd fens, are positively correlated with the first ordination axis, while higher PO_4^{3-} concentrations are negatively correlated with this axis. The N:P ratio is the main ecological factor explaining the floristic differences between the non-Cd and Cd fens. Cd fens tend to develop under more mineral-rich conditions (excluding Fe; Fig. 3) than the non-Cd fens, but there is also an independent and weak gradient of Ca^{2+}, Mg^{2+} and Na^+ concentrations related to the second axis. The ordination (Fig. 2) and the comparison of N:P ratios of the Cd-fens and non Cd-fens (Fig. 3) indicate a higher N:P ratio (and subsequently frequent P-limitation) in the Cd fens, while the non-Cd fens have lower N:P ratios when both vascular plants and bryophytes are compared.

The number of both *Caricetalia davallianae* species (Fig. 5) and calciole species (Fig. 6) is positively correlated with the N:P ratio. In addition, the pH values are weakly correlated with the number of calciole species (y = –20.8975+4.2375x; P = 0.0288; r^2 = 0.0957). Phosphorus and potassium contents of the vascular plants reflect those in bryophytes but this is not the case for nitrogen. Nevertheless, there is a non-linear correlation between the N:P ratio in vascular plants and bryophytes (Fig. 7).
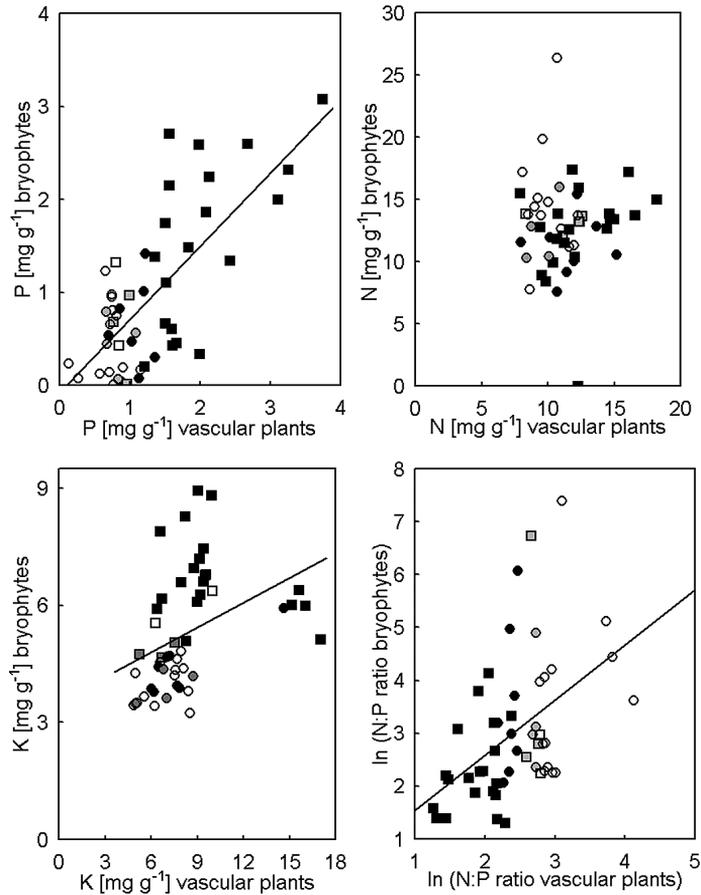
Fig. 7. – P, N, K concentrations and N:P ratios in bryophytes vs P, N, K concentrations and N:P ratios in vascular plants; $P < 0.0001$, $r^2 = 0.5256$; $P = 0.7740$, $r^2 = 0.0017$; $P = 0.0037$, $r^2 = 0.1627$; $P = 0.0006$, $r^2 = 0.2202$, respectively. For explanations see Fig. 4.

Discussion

Type of limitation and critical N:P ratios

Our data confirm the conclusions of many authors (e.g. Olde Venterink et al. 2003, Øien 2004, Wassen et al. 2005, Rozbrojová & Hájek 2008) that species composition is determined by (among other ecological factors) the type of limitation, which is reflected in the N:P ratio. In north-eastern Poland the N:P ratio seems to be the main ecological factor explaining differences in the species composition of Cd- and non-Cd fens, as there are very few other differences in the chemistry of the surface waters of these two types of rich fen. However, it is clear that there can be a discrepancy between species composition and type of limitation in both Cd and non-Cd fens; in particular some Cd fens are N-limited according to

the values proposed by both Wassen et al. (2005) and Olde Venterink et al. (2003). One explanation for this incompatibility is that the reaction of plants to increased N-availability can be delayed (Güsewell et al. 2002) and vegetation can undergo dynamic succession after changes in the habitat (Verhoeven & Schmitz 1991). It should be pointed out that the critical values proposed for N- or P-limited sites are a subject of discussion (Boeye et al. 1997, Güsewell et al. 2003, Olde Venterink et al. 2003, Güsewell 2004) and the analytical methods used for determining N (Kjeldahl's vs elemental analysis) and P (various modifications of the molybdate method vs inductively coupled plasma technique) and the preparation of samples can influence the stoichiometry results and hinder the comparisons. Thus it seems more reasonable to speak about "trends" rather than absolute types of limitation. We did not discuss the K content of biomass since the presented results confirm that primary productivity in natural, non-drained and unmanaged fens is seldom limited by potassium due to the constant input of K with groundwater and lack of hay removal, which would result in the export of potassium (van Duren & Pegtel 2000, Olde Venterink et al. 2003).

Why are there few calcicole and Caricetalia davallianae species in some alkaline, extremely rich fens?

Although Cd fens are distinguished by slightly more alkaline conditions than non-Cd fens, both Cd- and non-Cd fens develop under mineral rich conditions typical of (rich) fens (Vitt 2000, Wheeler & Proctor 2000). Although *Caricetalia davallianae* vegetation occurs where P is the limiting nutrient, e.g. in England (Boyer & Wheeler 1989), the Netherlands and Belgium (Verhoeven & Schmitz 1991, Boeye et al. 1997), similar fens occur that are N-limited. Rozbrojová & Hájek (2008) report P-limitation only in extremely calcium-rich, calcareous tufa-forming fens, while N:P ratios in some peat-forming *Caricion davallianae* extremely rich fens indicate N-limitation. Øien (2004) reveals no clear limitation in boreal rich-fen vegetation of the *Caricion atrofuscae* alliance (*Caricetalia davallianae* order).

In our dataset the trend towards P-limitation in *Caricetalia davallianae* vegetation seems to be clear and the occurrence of both calcicole and *Caricetalia davallianae* species is positively correlated with the N:P ratio (and increasing P-limitation). Surprisingly, there seems to be no significant influence of pH on the presence of the above species. This suggests that the species we consider to be calcicole may only be species adapted to low P-availability. Critchley et al. (2002) concluded that calcicole steppe species occur under low nutrient conditions, especially low P-availability.

It should be pointed out that among both *Caricetalia davallianae* and calcicole species that can persist in the largely N-limited, non-Cd fens, there are hardly any mosses or sedges (except for *Carex dioica*), while orchids do not seem to be affected by this type of limitation. Øien (2004) reports an indifferent reaction of *C. dioica* to the different types of limitation. It seems that the orchids in question (*Epipactis palustris*, *Liparis loeselii* and *Dactylorhiza incarnata*) are rather indifferent to both P- and N-limitation, which may be due to their mycorrhizal relations (Rasmussen 2002). This contrasts with the results of Hejcman et al. (2010), who observed a decline in abundance of other species of orchid after P-enrichment, while they were not affected by application of N-fertilizers at P-limited sites. Bryophytes (at least the specialists of the *Caricetalia davallianae* order) seem to have a competitive advantage under P- rather than N-limitation, as their productivity in Cd fens is higher.

N-limitation in the non-Cd fens in north-eastern Poland corresponds with the significantly higher PO_4^{3-} concentrations in their surface waters, which confirms the nutrient limitation of Cd- and non-Cd fens differs and that there is higher content of P in vegetation with few calcicole rich-fen species. The question is why there is a higher availability of P in habitats with non-Cd vegetation. The link between P-availability in rich fens and their geochemical properties is well studied (Richardson & Marshall 1986). High calcium content and, subsequently, calcium precipitation should contribute to low P-availability (Boyer & Wheeler 1989). However the difference in P-availability in Cd and non-Cd fens is difficult to explain on this basis since the calcium contents of both types of fen overlap.

More recent papers focus mostly on the relations between P precipitation, Fe availability and redox potential (van Dijk et al. 2004, Zak et al. 2004, 2010, Geurts et al. 2008). However, these studies are mainly of altered (drained fen meadows) or restored ecosystems and the mechanisms controlling P-availability in natural, peat-forming fens are poorly studied. Fe-related P precipitation is reported to decrease P-availability in many mires (e.g. Verhoeven & Schmitz 1991, Wassen & Barendregt 1992, van Duren & Pegtel 2000, Zak et al. 2004) but does not seem to be relevant in our rich fens since in them the concentrations of PO_4^{3-} and Fe_{tot} are positively correlated. In addition, the surface waters in the non-Cd fens, that are richer in PO_4^{3-} than in the Cd fens, are often characterized by higher Fe concentrations. Zak et al. (2004) report the lack of a correlation between P availability and Fe:P ratios (the opposite of the pattern in our results) but suggest that the Fe-driven immobilization of P is favoured by high pH which may be important in case of the Cd fens. In the non-Cd fens the pH values are significantly lower (although largely overlapping), which, along with greater fluctuations in water level, could contribute to the increased release of phosphorus. Iron can be toxic to some *Caricetalia davallianae/*calcicole plants, as is the case for many wetland species (Snowden & Wheeler 1993).

Long-lasting N-deposition, an important factor influencing the N:P ratio in the biomass of many western-European fens and the shift from N- to P-limitation (Olde Venterink et al. 2003, Tessier & Raynal 2003, Wassen et al. 2005, Phuyal et al. 2008) can most probably be neglected in the case of our data from the fens in north-eastern Poland, where human-influenced atmospheric deposition is much lower (Verhoeven et al. 1996, Paulissen et al. 2004).

Rich fens with few Caricetalia davallianae species and the main ecological gradients

Our results are in accordance with studies suggesting that primary productivity of vascular plants decreases with decrease in P-availability (e.g. Olde Venterink et al. 2003). This relationship seems to exist even within very low-productive rich fens. However, in both Cd and non-Cd fens the productivity of the vegetation is low in terms of the productivity limits defined by Olde Venterink et al. (2003) and Wassen et al. (2005). Since non-Cd vegetation is largely N-limited, in their case the low productivity should be attributed to low N-availability. In contrast, the low productivity of Cd fens is driven usually by low P-availability. Therefore, we suggest that the gradient between high productive tall-sedge and low productive small-sedge communities (e.g. Boyer & Wheeler 1989, Wheeler & Proctor 2000) is irrelevant when dealing with low-productive, brown-moss rich-fen phytocoenoses. We suggest that the above mentioned gradient does not exist in the latter type of vegetation and should be replaced by a N-to-P limitation gradient, which can be defined in terms of the biomass N:P ratio.

The pH values recorded in the non-Cd fens are well within the limits of those recorded for extremely rich *Caricion davallianae* fens in central Europe (Hájek et al. 2006). Nevertheless, while the Cd fens we studied meet this criterion, many of the north-eastern Polish non-Cd fen phytocoenoses cannot be assigned to extremely rich fens since "calcicole plant species" are usually scarce and sometimes even lacking. As Hájek's et al. (2006) classification covers the floristic variation within central-European fens we conclude that the species composition in continental-eastern European rich fens does not fit within that scheme.

There is an urgent need to obtain reliable data from other eastern European areas (Belarus, European temperate Russia) in order to verify the north-eastern Polish pattern on a broader geographical scale. Detailed floristic data of Katz (1929) from the surroundings of Moscow confirm the presence of extremely rich fens with few *Caricetalia davallianae* species in that area. When comparing the pH values with those recorded in corresponding Scandinavian vegetation sensu Sjörs (1950), both Cd and non-Cd fens fit well within "transitional rich fens". Scandinavian data (e.g. Nordhagen 1936, Du Rietz 1949, Sjörs 1950, Dierßen 1982, Øien 2004) show that the *Caricetalia davallianae* species are a constant component of rich-fen vegetation in the boreal part of Europe. On the basis of our results and data from eastern-continental Europe (e.g. Katz 1929, Steffen 1931), the most distinctive feature of non-Cd extremely rich fens in the above area is the permanent and usually abundant presence of numerous eutrophic wet-meadow plants, such as *Agrostis stolonifera* and species typical of the *Calthion* (but not *Molinion*) alliance, such as *Lychnis flos-cuculi* and *Rumex acetosa*. Such vegetation could be natural fen meadows, which is in agreement with Hájek et al. (2006), who define "fen grasslands" by "the high abundance of nutrient-requiring grasses and herbaceous plants rather than purely by fen origin and management". Such natural, peat forming (e.g. Jabłońska et al. 2011) fen meadows developing in rich fens in eastern-continental Europe could be considered as a source of species for anthropogenic wet meadows of the *Calthion* alliance, which are also reported to be N-limited (van de Riet et al. 2010).

It should be noted that our results largely confirm the bipartite division of rich fens in Alberta in continental-western Canada (Slack et al. 1980, Vitt & Chee 1989, 1990). The similarity is striking, especially when considering the bryophytes. These authors distinguish between "extreme-rich fens", with e.g. *Scorpidium* spp. and *Campylium stellatum*, and "moderate-rich fens", with e.g. *Hamatocaulis vernicosus*, *Plagiomnium ellipticum* and *Carex diandra* among the most typical species. Extreme-rich fens differ from moderate-rich fens in more alkaline conditions (mean pH of 7.3 vs 6.7). There is a tendency towards higher N and lower P concentrations in the surface waters of the former type, while the latter type shows the opposite pattern. The continental rich fens with few *Caricetalia davallianae* species in the herbaceous plant layer both in Alberta and Poland do not fit the classification schemes and poor-rich gradient concepts for either boreal (e.g. Du Rietz 1949, Sjörs 1950) or central Europe (Hájek et al. 2006).

Syntaxonomical position of the extremely rich fens in north-eastern Poland

The crucial role of (rich-) fen indicators in Cd fens indicates they should be included in the *Caricetalia davallianae* order. They represent various associations, including *Caricetum paniceo-lepidocarpae* (Braun 1968, Kwiatkowski 1999), *Campylio stellati-Caricetum lasiocarpae* (Hájek & Hájková 2011) and *Campylio stellati-Trichophoretum alpini*

(Rybníček 1974, Pałczyński 1975, Hájek & Hájková 2011). The majority of non-Cd fens can be assigned to the *Caricetum diandrae* association (Wołejko 2000, Matuszkiewicz 2008). The presence of a few *Caricetalia davallianae* species seems to rule out their inclusion among other extremely rich-fen communities of that order.

Much more unclear is the affiliation of non-Cd phytocoenoses to higher rank syntaxa. The *Caricetum diandrae* association is usually assigned to the *Caricion lasiocarpae* alliance. However, in the case of rich-fen vegetation this is ecologically and floristically inconsistent and is criticized because the *Caricion lasiocarpae* alliance would then embrace both poor fens and rich fens even within one plant association (e.g. Duvigneaud 1949, Rybníček 1985, Críodáin & Doyle 1994, Koska & Timmermann 2004). It should be noted that non-Cd phytocoenoses are distinguished by an abundant presence of species primarily connected with tall-sedge (including the dominant *Carex rostrata*), reed-bed and meadow communities, while typical fen species (of the *Scheuchzerio-Caricetea nigrae* class) have, with few exceptions (*Menyanthes trifoliata*, *Eriophorum angustifolium*, *Carex diandra*, *C. limosa*), a less important role. The non-Cd phytocoenoses show some affinities with the *Sphagno warnstorfii-Tomentypnion nitentis* alliance (*Caricetalia davallianae* order), although, among others, they lack calcitolerant *Sphagnum* species, which is a basic feature of that syntaxon (Hájek & Hájková 2011). Therefore, the syntaxonomic position of the *Carex diandra* and *C. rostrata*-dominated rich fens with few *Caricetalia davallianae* species needs large-scale revision. However, we believe they should remain within the *Scheuchzerio-Caricetea nigrae* class, forming a core of higher rank syntaxa, outside the *Caricetalia davallianae* order.

Hamatocaulis vernicosus vs Scorpidium cossonii

Our results are in agreement with the existing data on the habitat requirements of the two main dominant species in Cd and non-Cd fens, *S. cossonii* and *H. vernicosus*, respectively. The former usually occurs at more alkaline sites than the latter (e.g. Rybníček 1974, Vitt & Chee 1990, Dierßen 2001, Hedenäs 2003, Štechová et al. 2008). We confirm that *H. vernicosus* did not seem to occur at P-limited sites (Rozbrojová & Hájek 2008), although in central Europe both species are often found growing together in *Caricetalia davallianae* communities (Rybníček 1974, Štechová et al. 2008, Hájek & Hájková 2011), which in north-eastern Poland is rarely true in the case of *S. cossonii* and *H. vernicosus*.

Are N, P, K contents of vascular plants and bryophytes correlated?

Our results confirm that one cannot assess the type of limitation by calculating the N:P ratio for bryophytes and applying the critical values developed for vascular plants (see Olde Venterink et al. 2003, Wassen et al. 2005). As Jiroušek et al. (2011) report for *Sphagnum,* a threshold value between P- and N-limitation of 30, different critical values for the N:P ratio should be used when assessing the type of limitation for bryophytes. In contrast to the results of Niinemets & Kull (2005), who report a linear correlation between N, P concentrations and N:P ratios in vascular plants and bryophytes in calcareous wooded meadows in Estonia, we revealed only a linear correlation with P (and K), non-linear correlation with N:P ratios and lack of correlation in the case of N in these two layers of vegetation. The above phenomenon seems to suggest that bryophytes and vascular plants respond differently to nutrient availability (Verhoeven & Schmitz 1991, Niinemets & Kull 2005, Rydin & Jeglum 2006).

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Souhrn

Autoři této studie zkoumali na 22 lokalitách v severovýchodním Polsku druhové složení minerálně bohatých mechových slatinišť. Zároveň detailně analyzovali chemismus vody, koncentraci dusíku, fosforu a draslíku v biomase mechorostů a cévnatých rostlin a hladinu vody. Zjistili, že se v území vyskytují dva kontrastní typy studované vegetace. První se vyznačuje velkým zastoupením kalcikolních slatiništních specialistů, kteří jsou vázáni na porosty řádu *Caricetalia davallianae*, například *Scorpidium cossonii*, *Campylium stellatum*, *Carex lepidocarpa* a *Eriophorum latifolium*. Druhý typ obsahuje málo druhů řádu *Caricetalia davallianae* a převažují zde druhy *Hamatocaulis vernicosus*, *Marchantia polymorpha*, *Plagiomnium ellipticum*, *Carex diandra* a *C. rostrata*. Měřený chemismus vody a hydrologické podmínky prostředí se mezi těmito dvěma typy příliš nelišily. První typ blízký řádu *Caricetalia davallianae* však měl o něco vyšší pH (medián 7.07 oproti 6.75 ve druhém typu) a nižší koncentrace fosforu (maximální hodnoty 1,28 mg l^{-1} oproti 2,88 mg l^{-1} ve druhém typu). Tyto rozdíly však nepostačují pro vysvětlení tak výrazných rozdílů v druhovém složení. Jako faktor, který nejlépe vysvětlil pozorovanou variabilitu studované vegetace, se ukázal typ živinové limitace, zjištěný pomocí N:P poměru v biomase rostlin. Produktivita prvního společenstva (*Caricetalia davallianae*) se ukázala být ve většině případů limitována fosforem, zatímco produktivita druhého společenstva byla limitována dusíkem. Určitý rozdíl se ukázal i v množství nadzemní biomasy mechového patra, které bylo vyšší v prvním společenstvu (*Caricetalia davallianae*). Koncentrace fosforu a draslíku (ale ne dusíku) v biomase cévnatých rostlin a mechorostů vzájemně korelovaly. Obecný gradient přístupnosti živin je tedy v případě málo produktivních ekosystémů příliš široký na to, aby detailně postihl variabilitu v druhovém složení. Gradient míry limitace fosforem, který lze odhalit pomocí N:P poměru v nadzemní biomase, se ukázal jako užitečnější. Přirozeně dusíkem limitovaná minerálně bohatá slatiniště by mohla být fenoménem typickým pro kontinentálně laděnou část východní Evropy, kde byly ekologické podmínky minerálně bohatých slatinišť dosud málo zkoumány.

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