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Ecological study of the moss *Hamatocaulis vernicosus*

Ph.D. Thesis

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Annotation

The thesis is focused on the endangered wetland moss *Hamatocaulis vernicosus*. The studies included vegetation and chemical characteristics of the species' habitats and long-term reaction to management and other environmental factors, comparison of ecological requirements of *H. vernicosus* and two related species, differences of habitat preferences among some European regions (Bohemian Massif, Western Carpathians, Southern Europe) and among parts of the Czech Republic. Recent and historical distribution of the species was compared, including the quantification of all recent populations.

Declaration [In Czech]

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List of papers authors' contribution

Paper I Štechová T. & Kučera J. (2007): The requirements of the rare moss, *Hamatocaulis vernicosus* (Calliergonaceae, Musci), in the Czech Republic in relation to vegetation, water chemistry and management. – Biological Conservation 135: 443–449.

Paper II Štechová T., Kučera J. & Šmilauer P. (2012): Factors affecting population size and vitality of *Hamatocaulis vernicosus* (Mitt.) Hedenäs (Calliergonaceae, Musci). – Wetlands Ecology and Management 20: 329–339.

Paper III Štechová T., Hájek M., Hájková P. & Navrátilová J. (2008): Comparison of habitat requirements of the mosses *Hamatocaulis vernicosus*, *Scorpidium cossonii* and *Warnstorfia exannulata* in different parts of temperate Europe. – Preslia 80: 399–410.

Paper IV Štechová T., Holá E., Manukjanová A. & Mikulášková E. (2010): Distribution and habitat requirements of the moss *Hamatocaulis vernicosus* (Mitt.) Hedenäs in the Bohemian Forest. – Silva Gabreta. 16: 1–11.

Paper V Štechová T., Štech M. & Kučera J. (2012): The distribution of *Hamatocaulis vernicosus* (Mitt.) Hedenäs (Calliergonaceae, Bryophyta) in the Czech Republic. Bryonora 49: 5–16.

The following table shows the major contributions of authors to the original articles.

	I	II	III	IV	V
Original idea	TS, JK	TS	MH, TS	TS	TS, JK
Field work	TS	TS	TS, MH, PH, JN	TS, EH, AM, EM	TS, MS, JK
Revision of herbaria	-	-	-	-	TS
Chemical analyses	TS	TS	-	TS, AM	-
Data analyses	TS	PS	MH	TS	TS
Manuscript preparation	TS, JK	TS, JK	TS, MH, PH	TS	TS, JK, MS

AM = Alžběta Manukjanová, EH = Eva Holá, EM = Eva Mikulášková, JK = Jan Kučera, JN = Jana Navrátilová, MH = Michal Hájek, MS = Milan Štech, PH = Petra Hájková, PS = Petr Šmilauer, TS = Táňa Štechová

Contents

Introduction

Bryophytes are important components of mire ecosystems. With often a high coverage, the bryophyte layer accounts for a large part of the biomass, not only in bogs dominated by *Sphagnum* spp., but also in rich fens (Sjörs 1950, Clymo 1983, Kooijman 1992, Hájková & Hájek 2003, Hájková & Hájek 2004, Vitt & Wieder 2008). Bryophytes lack the root system and in nearly all mire species there is hardly any internal transport system. Mineral nutrients are taken up directly through the leaves, which are one cell layer thin and usually lack a protecting cuticle (Proctor 1982). The direct contact with the surrounding water, in the absence of roots and rhizomes exploring the soil compartment more substantially, may result in higher sensitivity to changes in the environment compared to vascular plants (Bates & Farmer 1992, Bergamini et al. 2009). Bryophytes play an indicator role of the present state of the habitat, as demonstrated for the rich fens by Juutinen (2011). After a change of environmental conditions, loss of rich fen bryophytes is more rapid than that of the phanerogams (Mälson et al. 2008), hence the changes in bryophyte layer may precede overall changes in the phanerogam vegetation (Bates & Farmer 1992).

Rich fen bryophytes were therefore subject to many studies in last years. In most cases, the studies employed the fen bryophytes as a whole. This can be illustrated in several papers dealing with the species composition of bryophytes in various vegetation types and contrasting site conditions (van Baaren et al. 1987, Hájková & Hájek 2004, Hájková et al. 2004, Hájek et al. 2006). Other studies describe in detail the reaction of bryophytes to various site conditions in terms of chemical composition (Aerts et al. 2001, Bergamini & Peintinger 2002, Bragazza et al. 2003, 2004, Drexler et al. 2003, Paulissen et al. 2005, Kooijman & Paulissen 2006). Attention was paid to the loss of peatland bryophytes' diversity on human-affected sites (Bergamini et al. 2001, Bergamini et al. 2009), and to the possibilities of their protection and restoration of an appropriate management (Barry et al. 2008, Hájková et al. 2009). Nevertheless, the results of the studies dealing with a proper treatment for a particular species are not always applicable to all target species at the locality, as the reaction to management may differ e.g. in case of hummock and pool-inhabiting species in a bog (Moen et al. 2001).

There have been only few studies investigating the ecological requirements of individual bryophyte species – and not only rich fen species. Habitat requirements and competition abilities were studied in the threatened species *Scorpidium scorpioides* (Kooijman 1992, 1993, Kooijman et al. 1994, Kooijman & Bakker 1994, 1995, Kooijman & Westhoff 1995). Another study dealt with the rare peat moss Sphagnum molle (Hekilla & Lindholm 1998). Other studies dealing with the rare peatland species rather have a regional character, describing the situation at individual sites.

This thesis attempts at elucidating the problems of retreat and protection of the most sensitive peatland bryophytes on the model species *Hamatocaulis vernicosus*, which typically represents rare and threatened fen species. It is a widely distributed but rarely common Holarctic bryophyte, occurring most frequently in the boreal zone (Hedenäs 1989). It belongs to a group of taxa restricted to formerly glaciated and periglacial areas (Janssens 1983), being thus e.g. in Scandinavia locally relatively abundant (Hedenäs 1993, Söderström 1996), however even there the number of localities decreases (Juutinen 2011). In other parts of the Europe, it is a rarer species, classified in most countries as threatened to some extent (e.g. Sérgio et al. 1994, Ludwig et al. 1996; Erzberger & Papp 2004, Kučera & Váňa, 2005). It has been recommended to a special attention within the whole European Union, attaining even the official listing in the Bern Convention (Council Directive 92/43/EEC 1992). The rarity of *H. vernicosus* is probably based on the reported specific habitat requirements (Hedenäs 1999). According to Hedenäs and Hugonnot (Hedenäs 1989, Hedenäs 2003, Hugonnot 2003), *H. vernicosus* occurs at continually wet fens and spring sites, often at peaty lake shores in northern and Western Europe. It prefers mineral-rich sites; pH at the localities in northern Europe ranges between 5.7 – 7.8 and between 5.4 – 7.3 in the Alps (Hedenäs et al. 2003), North American sites have been reported to span pH values between 5 – 8 (Janssens 1983). Conductivity at the Swedish localities was reported between 16 and 396 µS/cm (Hedenäs 2003). Basic chemical characteristics at the sites of occurrence in Central Europe are summarized in **Paper I, III** and **IV**, those from southern Europe were published in Paper III. Everywhere, the species avoids localities with high calcium content (Hedenäs 1989, Hedenäs & Kooijman 1996, Hedenäs et al. 2003), while it prefers higher concentration of iron ions (Hedenäs & Kooijman 1996), which was confirmed at the Central European localities (**Paper II**).

The most common accompanying species of *H. vernicosus* are the mosses *Calliergonella cuspidata, Campylium stellatum, Calliergon giganteum, Sphagnum teres*, and *S. contortum*, and the vascular plants *Carex nigra*, *C. diandra, C. rostrata, Menyanthes trifoliata* a *Potentilla palustris* (**Paper I** and **III**). The frequency of accompanying species can slightly vary in individual regions, similarly to the chemical characteristics of the sites (**Paper III and IV**).

The study of ecological requirements of *H. vernicosus* may be obscured by the fact that the morphologically defined species has been shown to be represented by two genetically different lineages, which might be regarded as cryptic species (Hedenäs & Eldenäs 2007). One of the lineages is widespread in Europe, and was also sampled from several localities in Minnesota (United States). The other lineage occurs only south of the boreal zone in Europe, and was in addition sampled from single localities in Peru and northernmost Asiatic Russian Federation. According to the authors of the study, both cryptic species do not differ in their ecological requirements. This finding was however tested only with respect to the preference for basic chemical composition of water (pH and conductivity), and needs to be studied in more detail.

During the last decades, many fen moss species lost their natural habitat and have become rare (Kooijman 1992, Güsewell et al. 1998, Vasander et al. 2003). The area of unimpaired fens decreased markedly and habitats suitable for surviving of *H. vernicosus* and other sensitive mosses is often only refuge of fen surrounding agriculture land, ruderal vegetation or shrubland communities. These small refuges are predominantly in the immediate vicinity of springs or wet depressions, often artificially dug trenches or pools (Štechová & Štech 2009, **Paper V**). Therefore, *H. vernicosus* populations underwent a substantial reduction. Of the nearly 150 historically known localities in the Czech Republic, the species nowadays survived at only one-third (**Paper V**). In the changed conditions, only a subtle fraction of the original population often survives. The reasons for the decrease of populations are various. Many localities have been completely destroyed and converted to agricultural or forest production land (Růžička 1987, 1989). Other localities have not been totally destroyed but the site conditions were changed in the way that the species could not survive anymore. A common cause of adverse alteration of site conditions has been the sinking of underground water level. Drainage of the fens may alter the peat chemistry, such as the decrease of pH and leakage of cations (Naucke et al. 1993). Biological attributes change and the dominant species expand (Graf et al. 2010). These processes can be enhanced by cessation of the management (mowing and grazing), resulting in nutrient content increase and promoting secondary succession towards tall forb and shrubland communities (van Belle et al. 2006). In such disturbed habitats, competitive rates between vascular plants and bryophytes and between bryophytes mutually are changed considerably. In habitats with lower pH, calcifuge *Sphagnum* species expand and suppress rich fen bryophytes (Kooijman & Bakker 1994, Grootjans et al. 1996). Reaction of *H. vernicosus* to the lowered pH and higher Sphagnum competition is similar to that of other rich fen mosses – smaller and less vital populations at localities with the high cover of Sphagna (**Paper I, II** and **IV**).

For conservation of *H. vernicosus* and other rare fen bryophytes, re-establishing of the management is necessary at many sites. High cover of the herb layer is a key negative factor influencing the populations of the target species (**Paper II**). Therefore a regular mowing is necessary at localities with the dense vegetation cover. At localities, where the herb layer expansion is blocked by the high level of underground water, no mowing is necessary (**Paper I**). Even there, however, occasional removal of establishing woods is essential (**Paper IV**). At drier sites, hollowing shallow gaps in the proximity of rare bryophytes is beneficial, as this promotes the creation of sufficiently wet open space with low competition pressure, where the sensitive targets species may expand (**Paper I**). However, the traditional management (mowing or grazing) is not always sufficient for the long-term protection of endangered species, and hydrological restoration is often necessary (Mälson et al. 2008, Bergamini et al. 2009).

Aims of the study:

1. Vegetation and chemical characteristics of the *H. vernicosus* localities in the Czech Republic; comparison of sites in the different parts of the Czech Republic (**Papers I, II, IV**).
2. Comparison of the ecological requirement of *H. vernicosus* with the ecological requirement of potential competitors - related species (*Scorpidium cossonii, Warnstorfia exannulata*) (**Paper III**).
3. Comparison of Czech localities with sites in different parts of Europe (Western Carpathian, Southern Europe) (**Paper III**).
4. Reaction of *H. vernicosus* to management at localities (**Papers I, II**).
5. Long-term reaction of *H. vernicosus* to different environmental factors (**Paper II**).
6. Comparison of the recent and historical distribution of *H. vernicosus* in the Czech Republic, quantitative characteristics of all recent populations (**Paper V**).

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Paper I

Biological Conservation 135: 443-449, 2007

Vegetation, water chemistry and management at the localities of *Hamatocaulis vernicosus* (Mitt.) Hedenäs (*Calliergonaceae*, Musci) in the Czech Republic

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Abstract

Hamatocaulis vernicosus has been revised in detail for its habitat preferences, ecology and population dynamic at all recent localities in the Czech Republic. The sites were surveyed for belowground water level, pH and conductivity of water, and the phytosociological relationships were analysed upon the evaluation of vegetation relevés. Seven localities in different parts of the Czech Republic were selected for a more detailed analysis of water chemistry – NH_4^+, NO_3^-, Ca^{2+} and Fe^{3+} and three localities were selected for manipulative experiments that included mowing and gap cutting during two years.

Hamatocaulis vernicosus had the highest cover at neutral pH (6.7 – 7.2) and conductivity between100 and 250 µS/cm, although most localities had lower values. No correlation was found between the cover of *Hamatocaulis* and the concentrations of NH_4^+ (range 0.15 – 0.30 mg/l), NO_3^- (0.1 – 0.4 mg/l), Ca^{2+} (3 – 10 mg/l), or Fe^{3+} (0.2 – 1.7 mg/l).

Populations of *Hamatocaulis vernicosus* were positively influenced by mowing only at a site with a high cover of vascular plants, and gap cutting was only beneficent at sites with lower water table. The growth and vitality of *Hamatocaulis* can thus be supported by suitable management especially in drier habitats.

Key words: fens, water table, mowing, gap cutting, vegetation

Introduction

Hamatocaulis vernicosus [1] is a widely distributed but rarely common Holarctic species, occurring most frequently in the boreal zone (Hedenäs, 1989). It belongs to a group of taxa restricted to formerly glaciated and periglacial areas (Janssens, 1983), being thus e.g. in Scandinavia locally relatively abundant (Hedenäs, 1993, Söderström, 1996) but in Central Europe it is a rarer species, classified in most countries as threatened to some extent (e.g. Ludwig et al., 1996; Kučera and Váňa, 2003). Due to its general rarity, it has been recommended to a special attention within the whole European Union, being listed in Appendix I of the Bern Convention (Raeymaekers, 1990).

One of the main reasons of the rarity of *Hamatocaulis vernicosus* is its specific habitat requirements (Hedenäs, 1999). It occurs in mineral-rich but usually not particularly calcium-rich habitats, typically in moderately rich fens with local flushes (Hedenäs, 1989, Hugonnot, 2003). The available information about the habitat chemistry (Janssens, 1983; Hedenäs and Kooijman, 1996; Hedenäs et al., 2003; Heras and Infante, 2000) is however sparse and often without the indication of representativeness of the data. Hedenäs and Kooijman (1996) noted that the genus prefers iron-rich habitats, reporting the highest value among a group of wetland genera of *Amblystegiaceae* s.l.

Typical associated moss species of *Hamatocaulis vernicosus* include e.g. *Calliergonella cuspidata, Straminergon stramineum, Tomentypnum nitens, Sphagnum teres, S. contortum* and *S. flexuosum* (Church et al., 2001; Hájková and Hájek, 2004; Müller and Baumann, 2004). Among less common associates, Müller and Baumann (2004) noticed *Sphagnum angustifolium* in Germany. Dominant associated vascular plants include *Carex lasiocarpa, C. echinata, C. nigra, Pedicularis palustris, Drosera rotundifolia* and *Parnassia palustris* (Heras and Infante, 2000; Müller and Baumann, 2004; Hájek et al., 2005); Hedenäs (1989) noted the rare *Saxifraga hirculus* as an associated species in Scandinavia.

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[1] The nomenclature of bryophytes follows Kučera and Váňa (2003), that of vascular plants follows Kubát et al. (2002).

There is not much information about the propagation of the species. The moss very rarely produces sporophytes (Smith, 1996; Hedenäs et al., 2003; Hugonnot, 2003) but spore production, which is obviously necessary for effective dispersal among sites (Sundberg and Rydin, 2002; Sundberg, 2005) could more common in the past under other climatic conditions (Gunnarsson et al., 2005), considering its recent broad distribution. Nowadays, *Hamatocaulis* is probably mostly spread by gametophytic fragments, similarly as many other peatland mosses (Poschlod and Schrag, 1990). This ensures dispersal at only short distances within a site, unless the occasional spreading by birds or large mammals occurs.

Wetland species are endangered mainly because of destruction and degradation of their habitats (Rybníček and Rybníčková, 1974). The cessation of traditional management, that included mostly extensive grazing, single late-season haymaking and removal of the mown material for bedding, led to the decrease of species richness and changes in community productivity (Fojt and Harding, 1995; Prach, 1996; Diemer et al., 2001). To conserve the species richness, a substitution of the traditional management is necessary therefore many recent studies investigated the possibilities of suitable alternative management in these habitats. However, only a small part of these studies is investigated in mosses.

Moen et al. (2001) studied influence of mowing on species composition in wetland habitats. According to their results, hummock building species were replaced by prostrate moss species at mown plots. Bergamini and Peintinger (2002) did not find out effect of removal of vascular plants on biomass and shoot morphology of *Calliergonella cuspidata*. Vanderpoorten et al. (2004) found out, that in calcareous grasslands the mowing influences the continuity and composition of moss layer.

In this paper, we tried to describe the habitat preferences of *Hamatocaulis* with respect to the water chemistry (pH, conductivity, NH_4^+, NO_3^-, Ca^{2+} and Fe^{3+}) and its phytosociological relationships in the main vegetation types of mires in the Czech Republic. For a better understanding of its ecology and conservation in Central Europe, we performed manipulative experiments, including the short-term impact of mowing and expansion ability into created gaps in the vegetation.

Material and Methods

Vegetation and environmental data sampling

Vegetation relevés, water table and basic water chemistry (pH, conductivity) were analyzed at all localities of *Hamatocaulis vernicosus* in the Czech Republic, known to the authors in spring 2005 (Table 1, Fig. 1). One to four relevés (in relation to population size of *Hamatocaulis*) were analysed in plots 4 × 4 m using the visual percentage cover estimate of all present species. In total, 58 plots were sampled during May and June 2005, when the probability of finding all present species is relatively high. The altitude of the localities was taken into account when choosing the sampling date.

Water pH and conductivity were measured *in situ* using portable devices (Vario pH, WTW, Germany; CM 101, Snail Instruments, Czech Republic). Measurements were made at four spots in *Hamatocaulis* patches in each of the 58 sampling plots. Belowground water table was measured using the PVC discoloration method during the whole vegetation season (Belyea, 1999; Navrátilová and Hájek, 2005).

Seven localities were chosen to be representative of the major phytogeographical regions of *Hamatocaulis* occurrence in the country (Fig. 1) for a more detailed study of water chemistry (NH_4^+, NO_3^-, Ca^{2+}, Fe^{3+}). Belowground water samples were collected in October 2003 and in June, September and October 2004. The samples were filtered over a glass filter and frozen within 24 hours for later analysis. NH_4^+ and NO_3^- were determined colorimetrically by flow injection analysis (FIAstar 5012 analyzer, Sweden), Ca^{2+} and Fe^{3+} concentration was analysed spectrophotometrically (SpectrAA 640, Australia).

Manipulative experiments

Three localities (sites 1 – 3, Table 1, Fig. 1) with more extensive populations of *Hamatocaulis* were selected for manipulative experiments. The reaction to mowing was tested on 17 (site 2) or 18 (sites 1 and 3) permanently fixed plots of 50 × 50 cm. The plots were chosen to include the largest part of the population of *Hamatocaulis vernicosus* at the localities and the reaction was evaluated by the changes in species' cover. A sketch of species distribution with per cent estimate of observed species was drawn from every plot to a millimetre paper. Half of the plots were mown (including woody seedlings) with a grass-hook and the rest of the plots were kept unmown. The biomass was removed from the mown plots. The mowing was performed twice, in late June 2003 and late June 2004. The sketches from all plots were made again in autumn 2004. The changes in cover were evaluated from the sketches using the Scion Image program (Scion Corporation, 2000).

The ability of *Hamatocaulis* to expand into created gaps was observed during two years in 14 gaps measuring 15 × 15 cm, dug in each of the three localities. Each gap was cut close to an extant *Hamatocaulis* colony. The gap depth was dependent on the turf thickness and varied between 6 and 14 cm. The water level in gaps was measured in June and October of both years. In course of the last visit, per cent cover of *Hamatocaulis* in each gap was noted for later evaluation.

Data analysis

To evaluate the phytosociological relevés, the data matrices with species data were subjected to canonical correspondence analysis (CCA) with the measured readings (pH, conductivity, average water table level and its fluctuation expressed as the range between minimum and maximum value) as explanatory variables. Partial Monte Carlo permutation test was used to assess the usefulness of each explanatory variable used in the ordination model (Lepš and Šmilauer, 2003).

The interaction of mowing and time impact on populations of observed species was tested using ANOVA in BACI design. The dependence of cover of *Hamatocaulis* in gaps on water level was tested using the multiple linear regression. The data were analysed in the Statistica for Windows package ver. 7.1 (StatSoft Inc., 2005).

Table 1 Brief description of studied sites. The average annual temperatures and annual precipitation are cited according to Syrový (1958). The first number of the site size corresponds to the area of the whole nature reserve (where applicable), the number in parentheses is the estimate of the biotope area with suitable conditions for *Hamatocaulis vernicosus*.

Number	Locality	elevation (m a.s.l.)	average annual temp. [°C]	annual precipitation [mm]	size of the biotope [ha]	number of vegetation samples	average cover of vascular plants [%]	water level [cm below ground ± SD]
1	Staré jezero	440	8	625	10	4	60	3.0±2.7
2	V Lisovech	650	6	750	3	4	80	8.2±3.3
3	Vidlák	280	8	675	10	4	55	4.4±3.5
4	Břehyně - Pecopala	275	8	625	2	2	55	5.3±8.5
5	Matenský rybník	525	8	675	2	2	80	4.5±3.4
6	Ruda	415	8	625	10	2	50	2.0±2.0
7	Kaliště	655	6	750	4	0	70	–
8	Bažiny	620	7	850	1	1	70	3.3±1.5
9	Červený rybník	300	8	625	0.5	2	55	7.5±3.2
10	Dolejší rybník	450	8	575	3	4	55	3.8±5.4
11	Chvojnov	605	7	675	4	1	50	4.0±2.0
12	Hůrky	500	8	525	1	1	70	5.3±4.2
13	Jezdovické rašeliniště	575	7	675	0.5	1	75	3.3±3.1
14	Louky u Černého lesa	570	7	750	3	1	60	4.7±1.5
15	Na Klátově	485	7	675	0.27	1	60	5.7±1.5
16	Na Oklice	660	7	675	10	3	70	4.6±2.8
17	Novozámecký rybník	255	8	625	4	1	60	2.0±1.0
18	Nový rybník u Rohozné	560	7	750	0.5	2	55	5.7±2.9
19	Odměny u rybníka Svět	435	8	750	0.5	2	55	1.2±3.7
20	Prameny Klíčavy	430	8	525	0.5	2	60	3.2±1.2
21	Rašeliniště u Suchdola	625	7	675	2	2	70	1.3±1.5
22	Ratajské rybníky	590	7	750	0.5	2	45	10.8±4.8
23	Řeka	555	6	850	10	4	50	6.3±3.1
24	Řežabinec	370	8	575	0.5	2	55	2.7±2.5
25	Skalské rašeliniště	700	6	850	5	2	60	2.3±1.8
26	Strádovka	580	7	750	0.5	1	60	2.0±3.6
27	Šimanovské rašeliniště	605	7	675	4	3	55	2.4±2.7
28	Zhůřská pláň	1000	5	1100	0.5	1	80	6.0±2.0

Results

Vegetation, water table and chemistry at the localities

177 species (51 bryophytes and 126 vascular plants) were noted in 57 vegetation samples. The most commonly associated species are listed in Table 2. The variation of vegetation composition was significantly ($p = 0.002$, $F = 4.1$) influenced by the environmental conditions (Fig. 2). The first canonical axis, explaining 28.1% of the data variability, is closely fitted by the gradient of the basic water chemistry – pH and conductivity; water table level and its fluctuation fit the second canonical axis, which explains 12.2% of the variability in the data set. At more base rich localities (pH about 7 and conductivity between 100 and 250 µS/cm), the associated mosses were mainly *Tomentypnum nitens, Campylium stellatum*, *Philonotis calcarea* and *Scorpidium cossonii,* and the vascular plants included *Valeriana dioica*, *Carex dioica*, *Eriophorum latifolium* and *Eleocharis quinqueflora. Sphagnum fallax, S. subsecundum, S. palustre* and *Warnstorfia exannulata* were common associated mosses in more acid habitats (pH between 5.8 and 6.6 and conductivity below 100 µS/cm), as were *Eriophorum angustifolium, Agrostis canina, Potentilla palustris* and seedlings of trees and shrubs, such as *Alnus glutinosa, Betula* sp. div., *Pinus sylvestris* and *Salix aurita*.

The cover of *Hamatocaulis* in vegetation samples varied between 0.05% and 30% (Fig. 3) but only at four localities the cover was 20% and more. At such localities, the pH values ranged from 6.7 to 7.2, the conductivity from 100 to 250 µS/cm and the water table from 5 to 7 cm below ground. The majority of studied localities exhibited nevertheless somewhat more acid pH (between 6.2 and 6.6) and lower conductivity (below 100 µS/cm). The relation of *Hamatocaulis* cover on pH, conductivity and water table was however not statistically significant.

The concentrations of NH_4^+, NO_3^-, Ca^{2+}, Fe^{3+} at the localities are shown in Fig. 4. No correlation was found between NH_4^+, NO_3^-, Ca^{2+}, Fe^{3+} concentration and the cover of *Hamatocaulis* in vegetation relevés.

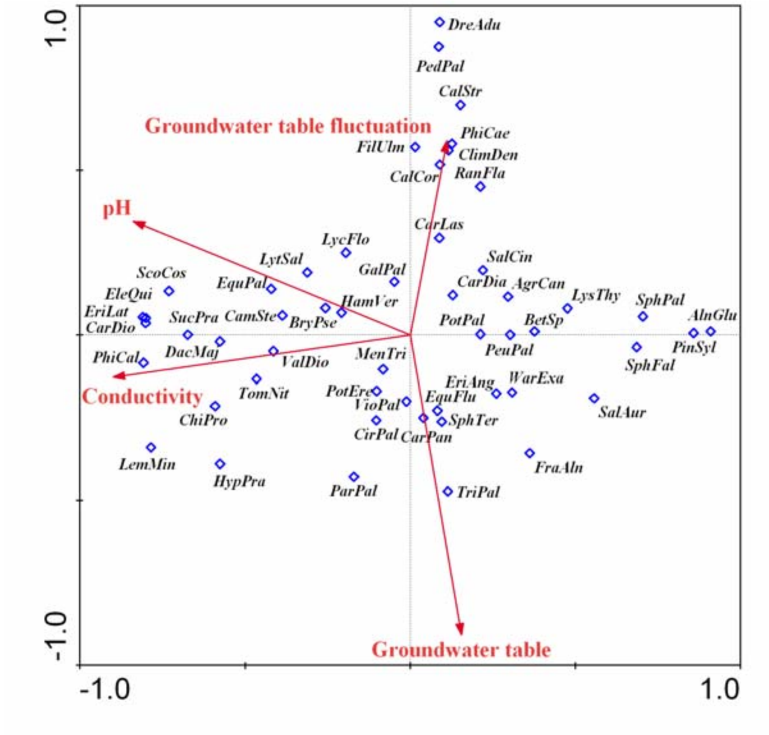

Fig. 1 Species-environment biplot from CCA summarizing preferences of mosses and vascular plants in principal environmental characteristics – pH, conductivity, water table (average values) and fluctuation (range between the minimum and maximum value). Monte Carlo Permutation Test of significance of first canonical axis p=0.002. Eigen-values of the first two axes explain 28.1 and 12.2 % of the variability in species data.

Mosses: *CalCor – Calliergon cordifolium, CamSte – Campylium stellatum, ChiPro – Chiloscyphus profundus, CliDen – Climacium dendroides, DreAdu – Drepanocladus aduncus, HamVer – Hamatocaulis vernicosus, HypPra – Hypnum pratense, PhiCae – Philonotis caespitosa, PhiCal – P. calcarea, ScoCos – Scorpidium cossonii, SphFal – Sphagnum fallax, SphPal – S. palustre, SphTer – S. teres, TomNit – Tomentypnum nitens, WarExa – Warnstorfia exannulata*

Vascular plants: *AgrCan – Agrostis canina, AlnGlu – Alnus glutinosa, BetSp – Betula sp., CalStr – Calamagrostis stricta, CarDio – Carex dioica, CarLas – C. lasiocarpa, CarPan – C. panicea, CirPal – Cirsium palustre, DacMaj – Dactylorhiza majalis, EquPal – Equisetum palustre, EleQui – Eleocharis quinqueflora, EriAng – Eriophorum angustifolium, EriLat – E. latifolium, FilUlm – Filipendula ulmaria, GalPal – Galium palustre, LemMin – Lemna minor, LycFlo – Lychnis flos-cuculi, LysThy – Lysimachia thyrsiflora, LytSal – Lythrum salicaria, MenTri – Menyanthes trifoliata, ParPal – Parnassia palustris, PedPal – Pedicularis palustris, PeuPal – Peucedanum palustre, PinSyl – Pinus sylvestris, PotEre – Potentilla erecta, PotPal – P. palustris, RanFla – Ranunculus flammula, SalAur – Salix aurita, SalCin – S. cinerea, SucPra – Succisa pratensis, TriPal – Triglochin palustre, ValDio – Valeriana dioica, VioPal – Viola palustris*

Table 2 The most commonly associated moss and vascular plants species with *Hamatocaulis vernicosus* according to the frequency of occurrence in the vegetation samples.

Mosses		***Vascular plants***	
Associated species	**% samples**	**Associated species**	**% samples**
Calliergonella cuspidata	91	*Carex nigra*	72
Aulacomnium palustre	61	*Equisetum fluviatile*	70
Bryum pseudotriquetrum	60	*Carex rostrata*	67
Sphagnum teres	60	*Potentilla palustris*	65
Straminergon stramineum	56	*Galium uliginosum*	61
Campylium stellatum	44	*Menyanthes trifoliata*	61
Sphagnum warnstorfii	30	*Lysimachia vulgaris*	60
Warnstorfia exannulata	30	*Agrostis canina*	58
Sphagnum fallax	28	*Carex diandra*	54
Tomentypnum nitens	28	*Galium palustre*	51
Amblystegium radicale	25	*Valeriana dioica*	51
Calliergon giganteum	25	*Epilobium palustre*	49
Calliergon cordifolium	23	*Salix cinerea*	47
Sphagnum contortum	23	*Viola palustris*	47
Climacium dendroides	21	*Carex panicea*	46
Scorpidium cossonii	21	*Eriophorum angustifolium*	42
Drepanocladus polygamus	18	*Potentilla erecta*	42
Hypnum pratense	16	*Cirsium palustre*	40
Aneura pinguis	12	*Carex lasiocarpa*	39
Sphagnum fimbriatum	12	*Peucedanum palustre*	37
Sphagnum flexuosum	12	*Betula sp.*	33
Sphagnum palustre	12	*Equisetum palustre*	33

Mowing

The impact of mowing on populations of *Hamatocaulis vernicosus* is shown in Fig. 5. The influence of mowing was significant only at the locality 'V Lisovech' ($p = 0.0213$, $F = 6.6$), where the cover of *Hamatocaulis vernicosus* increased in mown plots and decreased rapidly in control plots in majority of cases. The cover of vascular plants at the locality was between 80 and 90% (Table 1). The populations at the other two localities did not show any clear tendency across the plots.

Gap cutting

The expansion into gaps by *Hamatocaulis vernicosus* was dependent on gap water level ($p = 0.0005$, $F=22.4$; Fig. 6). Shallow gaps (ca 6 – 8 cm deep) with a low water level (about 1 cm high) were gradually colonized by *Hamatocaulis vernicosus* and other associated mosses, most often *Calliergonella cuspidata*, *Campylium stellatum* or *Calliergon cordifolium*. In deeper gaps (about 10 cm) with higher water level, the cover of *Hamatocaulis* was lower. No expansion of the species was observed in gaps, which were completely filled up with water (water level 8 – 9 cm). Similar outcomes were observed in other associated pleurocarpous mosses – none of the mentioned species differed from *Hamatocaulis* in expansion ability.

Discussion and Conclusions

Vegetation in relation to Hamatocaulis vernicosus

At all localities (and in 91% of vegetation samples), *Hamatocaulis vernicosus* grows together with *Calliergonella cuspidata*. This is in accordance with the observations at British and German localities (Church et al., 2001; Müller and Bauman, 2004), being obviously caused by the large tolerance of *Calliergonella cuspidata* to a great amplitude abiotic factors (Hájková, 2005). Other regularly associated moss (*Aulacomnium palustre, Straminergon stramineum* and *Bryum pseudotriquetrum*) and vascular plant species (*Equisetum fluviatile, Lysimachia vulgaris, Epilobium palustre*, *Potentilla erecta* and *Cirsium palustre*) also belong to the euryecious wetland plants. The most commonly associated *Sphagnum* species at the Czech localities were *S. teres*, *S. warnstorfii* and *S. contortum*, which are all known to be relatively calcitolerant species and *S. fallax*, which thrives in a wide range of chemical and hydrological conditions (Daniels and Eddy, 1990; Hájková and Hájek, 2004). Another commonly associated species, which occurs at all more base-rich localities, is *Campylium stellatum*. In contrast, Müller and Bauman (2004) recorded this species only in a few samples in German localities. A similar case is that of *Calliergon giganteum*, *C. cordifolium*, *Carex rostrata* and *C. lasiocarpa*, which we noted relatively often but were found only in one or a few samples in Germany and *C. diandra* did not occur at all. On the other hand, *Sphagnum angustifolium*, mentioned by Müller and Bauman (2004) or

Philonotis fontana in Britain (Church et al., 2001) were not found here or only at one locality.

At our localities with a higher pH and conductivity, a common associated moss is the taxonomically related species *Scorpidium cossonii*. Contrary to the Swedish localities, where *Scorpidium cossonii* grows with *Hamatocaulis* very rarely (Hedenäs, 1989), we could observe an immediate competition between *Hamatocaulis* and *Scorpidium cossonii* at two most base-rich localities.

Water chemistry at the localities

The pH readings at observed localities corresponded to the general assumption that the species requires slightly acid to slightly basic habitats (e.g. Hedenäs, 1989; Vitt, 2000), agreeing well with other studies (Hedenäs et al., 2003; Hájková, 2005). As far as we know, contrasting data were only provided by Heras and Infante (2000), whose pH readings from Spanish wetlands with *Hamatocaulis vernicosus* ranged between 4.5 – 5. The recorded associated rich-fen species that included *Tomentypnum nitens* or *Meesia triquetra* however suggest that the readings might have been wrong.

The conductivity values and average values of NH_4^+ and NO_3^- concentration correspond to literature records as well (Janssens, 1983; Hedenäs, 2003; Hájková, 2005; Hedenäs and Kooijman, 1996).

Regarding Ca^{2+} concentration, Hedenäs et al. (2003) underline that the species mostly does not grow in particularly calcium-rich habitats, based a.o. on measurements ranging between 2.5 and 56.8 mg/l Hedenäs (2003). However, according to Vitt (2000), Ca^{2+} concentrations 20 mg/l and more are considered to be characteristic for extremely rich fens. Janssens (1983) also reported a wide range of Ca^{2+} concentration (8 – 97 mg/l) in North American localities and maintained that *Hamatocaulis vernicosus* often grew in shaded habitats on calcareous substrata. Our values did not reach 10 mg/l except the locality Vidlák (20 mg/l), confirming thus our habitats of *Hamatocaulis vernicosus* being relatively poor in calcium.

Little information has been known about the iron concentration. Hedenäs and Kooijman (1996) reported an unusually high value of 2.24 mg/l for the genus *Hamatocaulis*, while for the other genera the values ranged between 0.59 and 1.65 mg/l. Our measurements (the average of 0.71 mg/l) did not show any exceptional value.

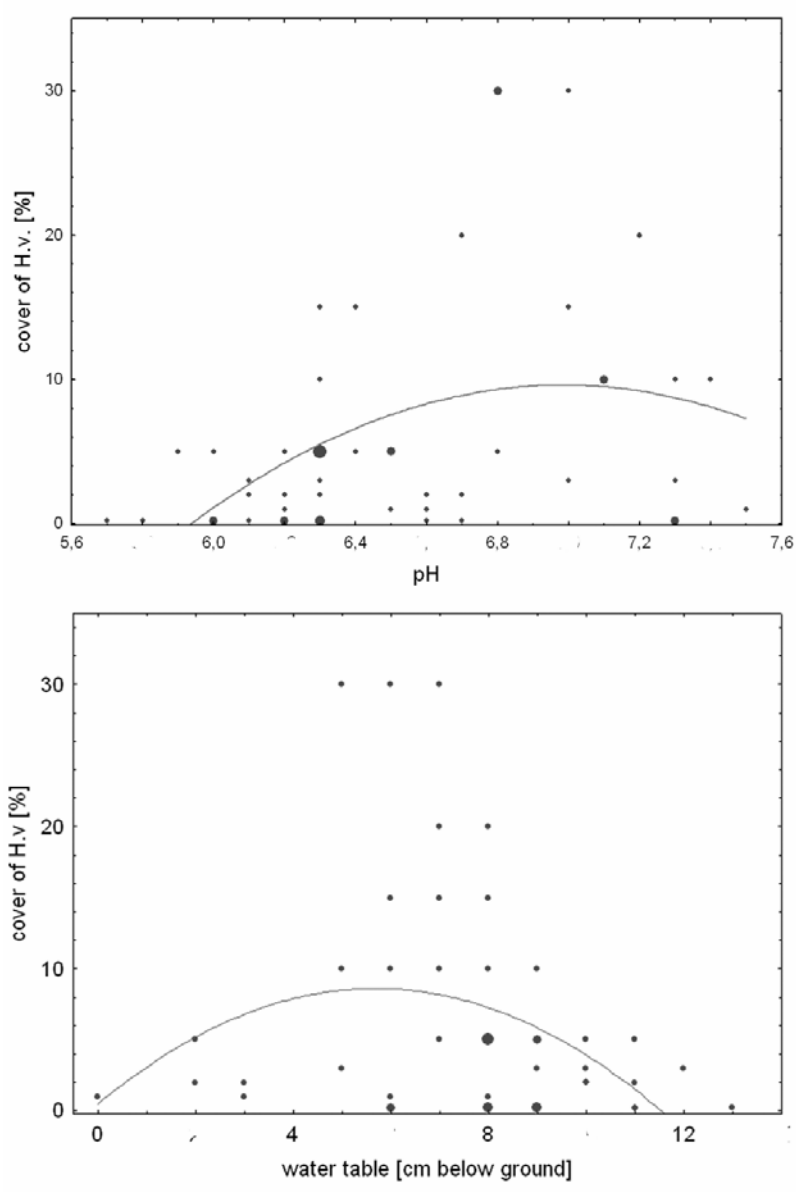

Fig. 2 Dependence of *Hamatocaulis vernicosus* cover on pH and water table. The size of dots relates to the number of vegetation samples (range 1 – 5 samples).

Mowing

The different influence of mowing on populations of Hamatocaulis vernicosus at the localities seems to be correlated with the cover of vascular plants. At ‘V Lisovech’, the vegetation cover is about 20% higher than at ‘Vidlák’ and ‘Staré jezero’. The lower cover at the latter two localities is correlated with the higher level of the water table (cf. Table 1), which keeps the cover of vascular plants naturally low.

The reasons for decline of Hamatocaulis colonies with the increasing cover of vascular plants might be diverse. One of them may include the lower solar radiation available for bryophytes. Another possible explanation for bryophyte decrease may be the litter accumulation, causing the nutrient concentration to rise. The change in the competitive rates between mosses, which are more tolerant to higher nutrient concentration and those, which are unable to benefit from it (cf. Malmer et al., 1992; Kooijman and Bakker, 1993) may cause the decline of species intolerant to eutrophication.

At locality ‘V Lisovech’, where the influence of mowing was evident, the initial cover at some of the mown plots was higher than in the control plots, as the choice of mown plots could not completely accidental because of limited population size of the species at the locality. Based on the field experience, it is nevertheless safe to assume that all initial micropopulations were in favourable conditions for the growth of Hamatocaulis vernicosus; hence the decrease of population cover in control plots was not the reflection of adverse environmental conditions.

Gap cutting

The ability of *Hamatocaulis* to colonize the gaps was found to be dependent on the water level. Despite its preference of wet microsites, the completely inundated gap has never been colonized. This is consistent with the opinion of Janssens (1983), who states that the species does not develop permanently submersed forms in contrast to e.g. *Warnstorfia exannulata*. Consequently, excavating gaps makes little sense in localities, where the water table is high. The positive effect of creating gaps in relatively drier sites was also observed at localities, where the species thrived on the edges of small pools or ditches, created here (independently on our experiments) to support the growth of some vascular plants.

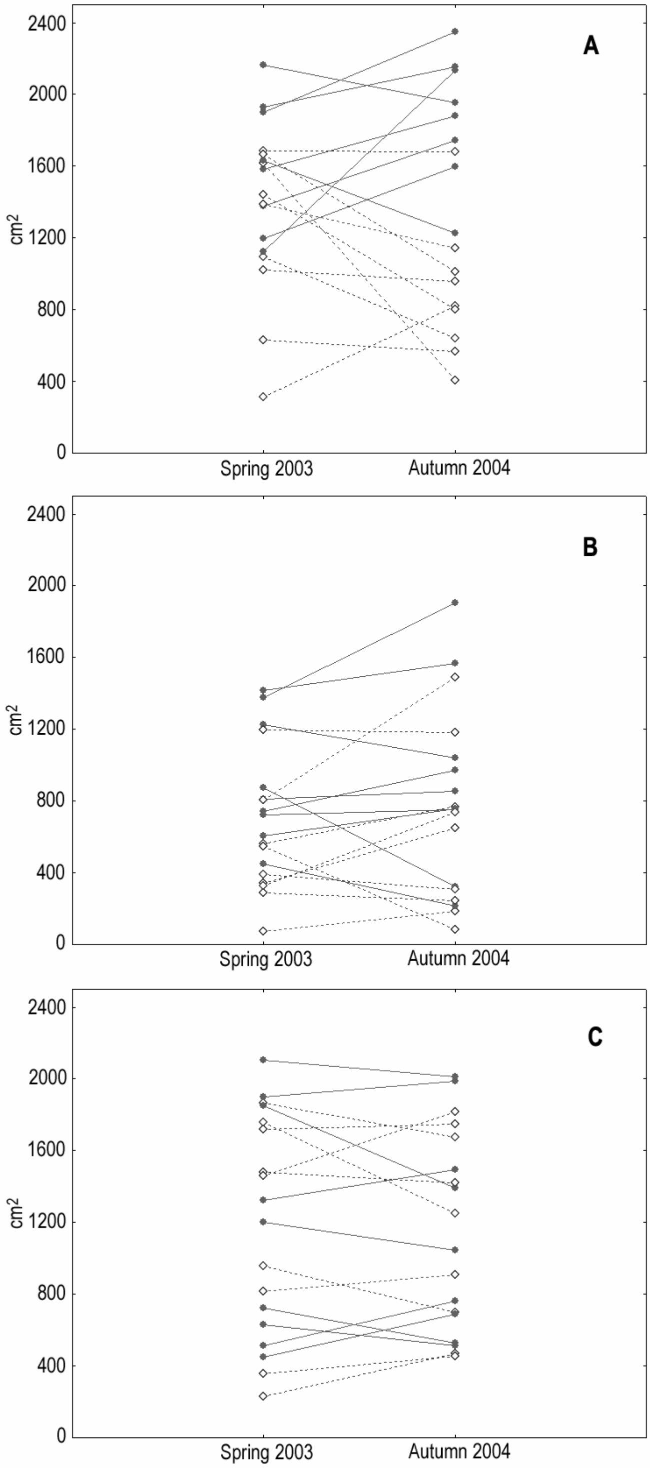

Fig. 3 Effect of mowing on populations of *Hamatocaulis vernicosus*. Full circles show the cover of *Hamatocaulis* before and after the experiment in mown plots, empty ones represent the control plots. A – locality V Lisovech, B – locality Staré jezero, C – locality Vidlák.

Hamatocaulis vernicosus was able to grow over more than a half of the gaps in course of two vegetation seasons, i.e. spreading at about 3 cm/yr. This seems to be a slower linear growth than that of the related species *Scorpidium scorpioides* (3 – 7 cm annually), reported by Kooijman et al. (1994). However, the latter species is substantially larger than *Hamatocaulis*; hence the relative growth is probably comparable. Interestingly, the *Sphagnum* species growing near the gaps never expanded into them. It may be caused by the pH that in the lower parts of bogs or fens may be higher than in the hummock (Karlin and Bliss, 1984; Malmer et al., 1992), unsuitable for most of *Sphagnum* species, preferring more acid habitats (Gorham and Janssens, 1992; Vitt, 2000).

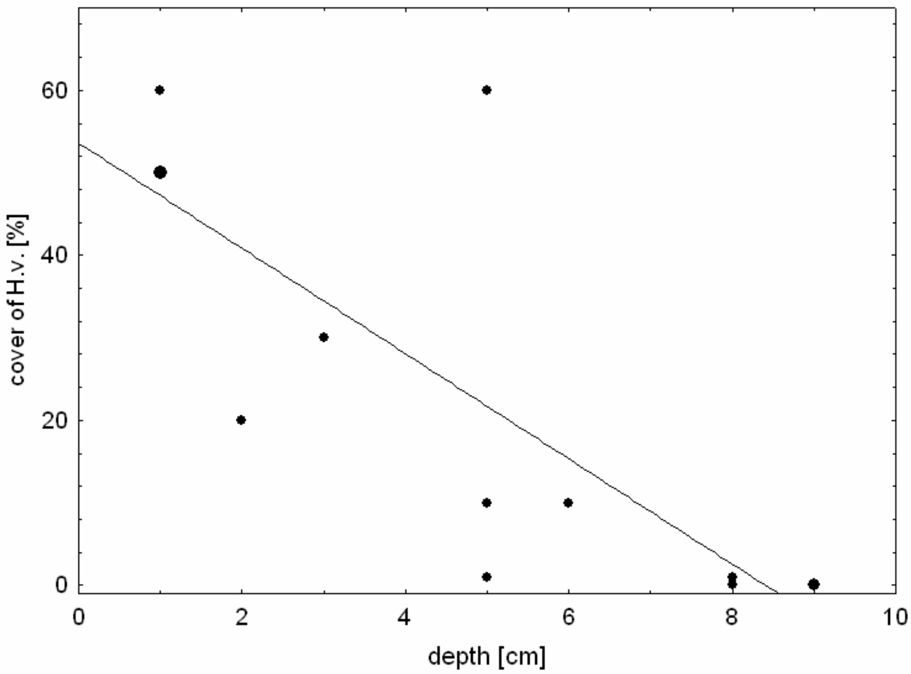

Fig. 4. Linear regression (p = 0.0005, F=22.4) of *Hamatocaulis vernicosus* expansion into the gaps. The size of dots relates to the frequency of observations (range 1 – 3 observations)

Recommendations

We can conclude that the eventual active management should take into consideration the water regime, vegetation composition and herb cover at each locality. The results of manipulative experiments confirm that the management is not necessary in all kinds of wetland habitats, being only indispensable especially at "artificial" or man-influenced habitats like wet meadows (see

Kooijman et al., 1994; Hedenäs, 2003), where water level is unstable and cover of vascular plants high. At these localities, the growth of *Hamatocaulis vernicosus* can be supported by cutting small shallow gaps.

For more exact prediction of reaction of *Hamatocaulis* populations to management, more detailed investigation of variation in growth rates of *Hamatocaulis* in different habitats is necessary, as well as a specific research of competitive rates *Hamatocaulis* and other moss species.

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Factors affecting population size and vitality of *Hamatocaulis vernicosus* (Mitt.) Hedenäs (Calliergonaceae, Musci)

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Abstract
Hamatocaulis vernicosus, a rare moss species, was monitored in 33 fens in the Czech Republic for five to six years. Population size, vitality and trends of population development were recorded. Water chemistry, water level fluctuation, vegetation type and cover, as well as mowing regime were assessed and the effect of these potential predictors on the species populations was examined. Populations of *H. vernicosus* were affected mainly by the density of vascular plants – the species thrived best in habitats with sparse herb and abundant “brown moss” cover. Other important factors included water table fluctuation and water concentration of iron. Populations were more vital and prospered better in sites with a stable water table and more iron-rich conditions. Dependence of population parameters on other measured characteristics of water chemistry was not detected.

Key words: bryophytes, fens, management, pH, water chemistry

Introduction

Bryophytes are important components of mire ecosystems. Due to the degradation of peatlands during the last decades, many moss species have been rapidly decreasing and their existence has been threatened (Kooijman 1992;

Mälson & Rydin 2007; Štechová and Štech 2007). Species of rich fens have been among the most severely threatened due to general rarity as well as the specific dynamics of this habitat (Hájek et al. 2006; Vitt and Wieder 2008). Additionally, from the Central European perspective, they have been at risk due to their occurrence in densely populated and heavily exploited landscapes.

Hamatocaulis vernicosus (Calliergonaceae) is a typical representative of threatened rich fen mosses. Due to its general rarity in Europe, it has been recommended for special attention within the European Union, being listed in Appendix II of the Bern Convention (Council Directive 92/43/EEC 1992). The coherence of *H. vernicosus* from a phylogenetic species perspective was challenged recently after molecular markers pointed toward the existence of two separate lineages (Hedenäs and Eldenäs 2007). Both of these occurred in Central Europe (as of this writing confirmed in Switzerland and Austria); it was suggested that they be interpreted as cryptic species.

H. vernicosus occurs in Central Europe predominantly in rich and moderately rich fens of the alliance *Sphagno warnstorfiani-Tomenthypnion*. Less often it is able to grow in extremely rich fens of the alliance *Caricion davallianae* and very rarely in the poorer communities of *Caricion fuscae* (Hájek et al. 2006). Site conditions of *H. vernicosus* were studied earlier by Hedenäs and Kooijman (1996), who reported mean values for the concentration of chemical components at localities in Sweden. Interestingly, the representatives of the two phylogenetic lineages were not shown to have significantly different ecological requirements (Hedenäs and Eldenäs 2007). It may be inferred that the earlier reported narrow niche of *H. vernicosus* can thus largely be applied to both cryptic taxa.

Information on the sites of *H. vernicosus* in the Czech Republic has been revised since 2001 within the framework of the NATURA 2000 project; their most recent occurrences have been monitored since 2003. In our previous study (Štechová and Kučera 2007), we investigated several key aspects of *H. vernicosus* ecology – the vegetation composition at its localities, detailed chemistry of water samples in a limited selection of seven localities and the effect of management represented by experimental mowing at three localities. Our attempt at testing the influence of water chemistry on the dynamics of populations in the Czech Republic did not reveal any dependence.

Building on the above information, we designed an experiment with broader-scaled monitoring that spanned 33 sites, representing about 65% of the recently identified locations of *H. vernicosus* in the Czech Republic. Monitoring included detailed water chemistry and underground water table recording at fixed plots. In addition, we noted the vegetation composition, the dynamics of *H. vernicosus* populations and the type of management applied by the owners or conservation authorities over the course of five to six years.

We asked two questions:

1. What is the influence of water chemistry and water level on population size, vitality and dynamics?
2. How do habitat type, density of vegetation cover and intensity of management affect species populations?

Material and Methods

Field sampling and laboratory analyses

Data were sampled at 33 localities of *H. vernicosus* in the Czech Republic in the years 2005 – 2010 (at 3 localities, data were sampled only in the years 2006 – 2010 – see Table 1). The sampled localities were all identified as of autumn 2006, when the water samples for analyses were collected (with the exception of three sites that were not visited due to their difficult accessibility). The studied sites were situated across most of the areas with natural fen occurrence in the Czech Republic at the altitudes between 250 and 960 m. The average annual temperature at these sites was reported to be in the range 5 – 8°C and annual precipitation in the range 550 – 1100 mm (Tolasz 2007).

One permanent plot (4 × 4 m) was fixed at each site. It was located to include the largest part of the population of *H. vernicosus* at each locality. The sites were visited twice a year, though in a few cases only once. The timing of visits was planned to ensure an approximately identical degree of vegetation development in the course of the whole vegetation season. This meant May and June for spring visits, autumn visits in September and October, depending on the altitude. Only the first visits in the first year, during which we recorded the vegetation samples, occurred in early summer (June and July) to ensure the recording of most of the vascular plant species. The vegetation samples enabled the analysis of the bryophyte, herb and shrub cover.

During most of the visits, we measured pH and conductivity; however, some readings were missing, particularly the conductivity readings in 2007 and 2008, caused by device failures. Both chemical characteristics were measured in situ at three points in each plot using a portable device (Vario pH, WTW, Germany; Snail Instruments, Czech Republic). Underground water was sampled for detailed analyses of water chemistry (NH_4^+, NO_3^-, PO_4^{3-}, Ca^{2+}, Fe); these were collected directly in the *H. vernicosus* patches in 2006 in late summer to early autumn (September/October), when the chemical gradients are more stable (Tahvanainen et al. 2003).

The samples were filtered over a glass filter and frozen within 24 h for later analysis. NH_4^+, NO_3^- and PO_4^{3-} were determined colorimetrically by flow injection analysis (FIA Lachat QC8500 – Lachat Instruments, USA), total N (LiquiTOC), Ca^{2+} and Fe concentrations were analyzed spectrophotometrically (SpectrAA 640, Australia). The water table (minimum and maximum) was measured mostly over the course of the whole vegetation season using the PVC discoloration method (Belyea 1999; Navrátilová and Hájek 2005). In each permanent plot, a vegetation relevé was recorded in June or July with respect to the altitude of the site by making a visual estimate of the cover of all species.

Management intensity applied by the owners or conservation authorities at the localities was estimated on a three-grade scale: 0 – no management, 1 – sporadic mowing once every two or three years, 2 – regular yearly mowing. No management was recorded at 9 sites (fens, fishpond margins and springs), sporadic management at 6 sites (fen meadows, fishpond margins and springs) and regular management at 18 sites (fens, fen meadows and springs) – see Table 1. Fen meadows without management, fens with sporadic management and fishpond margins with regular yearly mowing where *H. vernicosus* occurs were unknown in the Czech Republic. Mowing was mostly done using brush cutters. All sites which were recently regularly mown shared a similar management history from the mid-20th century. They were gradually abandoned until late 1990s or early 2000s. Then management was resumed, albeit no longer for agricultural but rather for conservation purposes, with brush-cutters replacing mowers.

The habitats were classified into four groups. These were: fishpond margins (fens developed along the banks of fishponds, which were affected by pond water), springs (habitats with flowing spring water), fen meadows (drier habitats with peat thickness less than 1 m) and fens (wetter habitats with peat thickness greater than 1 m).

Three characteristics of *H. vernicosus* populations were evaluated at each locality: population size, vitality and trend of population development.

Population size was estimated on a five degree scale. 1 – less than 100 stems, 2 – no more than 0.25 m2, 3 – 0.25–1 m2, 4 – 1–5 m2 and 5 – more than 5 m2.

Vitality was recorded on each visit during four- to six-year observations. It was assessed on a three degree scale: 1 – the majority of stems faded, partially rotten or very thin and lean, 2 – most stems with normal vitality, green, faded and rotten stems rare, 3 – all stems vital and sturdy. The vitality of the moss was a quite variable characteristic, which often fluctuated widely between visits, probably depending on the actual water table depth and herb shading. As no notable increase or decrease in vitality was evident at any site, we assessed the vitality of the population as the mean value of all observations.

The trend of population development was recorded every year and was evaluated on the basis of changes of population size between the visits. This characteristic was estimated by using sketch micromaps of populations or their parts (according to population sizes). We used a three degree scale: 1 – the population size decreasing, 2 – the population size not changing (change within ca 10%), 3 – the population size increasing. The definitive value of this characteristic was the mean value of all observations.

Data analysis

Variables representing the concentration of ions and conductivity values were log-transformed.

The effects of considered factors, listed in Table 2, on the three recorded population characteristics were modelled by a general linear model. Final models were selected based on their parsimony, measured by the AIC statistic (Akaike, 1974). This approach usually provided a more liberal selection of predictors (Chambers and Hastie 1992) and was also difficult to compare with studies, where parametric approaches to model selection were adopted. We have therefore re-evaluated the individual term of the models selected with AIC using parametric analysis of variance and F statistic. Statistical analyses were performed using the R program, version 2.8 (R Development Core Team, 2008).

Table 1. Description of studied sites

	Population size	Vitality	Trend of population development	Observation period [years]	Coordinates [WGS 84]	pH	Conductivity [uS.cm^{-1}]	Fe [mg.l^{-1}]	Ca [mg.l^{-1}]	NH_4 [ug.l^{-1}]	NO_3 [ug.l^{-1}]	PO_4 [mg.l^{-1}]	Altitude [m a.s.l.]	Average water table [cm]	Water fluctuation [cm]	Management intentisty	moss cover [%]	herb cover [%]	shrub cover [%]	Sphagnum cover [%]	Habitat type
Bažiny	2	2.4	2.3	6	N50°17'47" E016°17'59"	6.4	152	0.26	22.1	145	66.4	12.5	620	-3	6	2	60	70	0	20	Spring
Červený rybník	5	3	2	6	N50°44'07" E014°33'10"	6.8	193	2.07	13.6	15.7	33.4	21	300	-10	7	0	90	50	5	25	fishpond margin
Dolejší rybník	3	1.7	1.5	6	N49°25'57" E013°49'17"	5.7	508	3.35	37.8	78.3	43.4	7.59	450	-11	30	1	60	60	0	2	fishpond margin
Hrádecká bahna	3	2.1	1.7	6	N49°42'47" E013°39'32"	7.0	185	0.82	19.6	9.98	74.2	11.5	400	-8	10	2	90	90	0	50	fen meadow
Hůrky	3	2.2	1.7	6	N49°53'45" E013°11'01"	6.1	67	1.13	6.28	16.9	79.4	7.71	550	-5	4	0	60	60	2	50	Spring
Chvojnov	2	3	3	6	N49°24'26’’ E15°25'09’’	6.3	102	0.95	14.2	19.4	53.2	13.8	605	-6	4	2	60	50	0	25	Fen
Jezdovické rašeliniště	1	1.4	1.2	6	N49°19'25" E015°27'42"	6.3	265	0.43	22.6	33.1	52.6	9.97	575	-2	5	2	40	75	0	20	Spring
Kaliště	1	1.1	1.4	6	N49°19'25" E015°27'42"	6.5	123	1.94	11	53.5	49.1	9.08	655	-7	2	2	80	80	0	65	fen meadow
Klatov	3	2.9	2.8	6	N49°08'15" E015°27'08"	7.0	301	0.1	31	245	105	16.6	485	-6	5	2	80	60	0	0	Spring
Křemelná 2	5	3	3	5	N49°10'13" E013°19'58"	6.6	45	0.42	4.2	161	143	18.3	960	-2	1	0	90	40	0	60	Spring
Louky u Č. lesa	3	2.7	3	6	N49°35'09" E015°56'34"	6.2	148	0.91	18.4	11.2	30.7	11.6	570	-5	3	2	60	60	0	30	Fen
Louky v Jeníkově	2	3	3	5	N49°44'18" E015°57'52"	6.3	209	1.27	9.45	61	44	22	630	-8	3	2	60	80	0	25	fen meadow
Matenský rybník	2	1.6	1.2	6	N49°09'04" E014°55'51"	6.2	192	5.82	9.0	257	37.7	66.6	525	-10	15	2	60	80	0	5	fen meadow
Na Oklice	4	2.6	1.7	6	N49°24'15" E015°23'40"	6.5	77	54.1	16.7	147	51.2	11.7	660	-9	5	1	80	70	0	20	Spring
Nad Svitákem	1	1.2	1.3	6	N49°23'48" E015°24'17"	6.7	177	0.55	16.6	4.79	69.8	12.2	630	-2	2	0	10	90	5	10	fishpond margin
Novozámecký rybník	2	3	2	6	N50°36'45" E014°35'07"	7.2	230	1.17	32.7	1	33	8.53	255	-2	2	2	70	60	0	0	fen meadow
Nový rybník u Rohozné	4	1.9	1.3	6	N49°48'13" E015°49'11"	6.3	153	3.61	12.2	391	45.4	12.8	560	-8	9	1	40	60	3	2	fishpond margin
Odměny u rybníka Svět	2	1.8	2	6	N48°59'31" E014°43'33"	5.9	51	1.17	4.46	19.2	84.3	10.8	435	-2	20	0	80	60	5	80	Fen
Podtrosecká údolí	5	2.5	2.3	6	N50°31'28" E015°13'02"	7.0	241	1.97	41.3	7.3	56.7	9.48	280	-3	10	2	50	60	0	0	Fen
Prameny Klíčavy	3	2.7	3	6	N50°08'45" E013°49'43"	6.7	227	0.4	25	4.17	72.1	16	430	-5	2	2	70	60	0	40	Spring
Rašeliniště u Suchdola	3	2	2.3	6	N49°07'55" E015°14'18"	6.1	151	1.07	47.9	204	68	7.55	625	-5	3	2	90	70	0	40	Spring
Ratajské rybníky	3	1.7	1.5	6	N49°46'09" E015°56'02"	6.8	219	0.08	14.9	39.3	45	29.2	590	-11	19	1	60	50	0	1	fishpond margin

	Population size	Vitality	Trend of population development	Observation period [years]	Coordinates [WGS 84]	pH	Conductivity [uS.cm^{-1}]	Fe [mg.l^{-1}]	Ca [mg.l^{-1}]	NH_4 [ug.l^{-1}]	NO_3 [ug.l^{-1}]	PO_4 [mg.l^{-1}]	Altitude [m a.s.l.]	Average water table [cm]	Water fluctuation [cm]	Management intentisty	moss cover [%]	herb cover [%]	shrub cover [%]	Sphagnum cover [%]	Habitat type
Ruda jih	3	3	2.8	6	N49°08'43" E014°41'26"	6.6	166	2.99	14.6	917	108	18.1	415	-7	4	0	50	50	0	35	Fen
Ruda sever	2	1.3	1.8	6	N49°09'05" E014°41'21"	6.3	173	1.14	14.7	300	75.1	10.6	415	-6	7	0	40	45	0	20	Fen
Řeka	5	3	3	6	N49°39'59" E015°51'10"	7.1	247	0.52	46.4	165	48.8	11.3	555	-6	8	2	80	50	0	0	Spring
Řežabinec	3	1.8	2	6	N49°15'04" E014°04'58"	6.3	129	1.90	9.5	42.1	29.1	19.1	370	-4	5	2	80	60	0	60	fen meadow
Staré jezero	4	2.3	2.3	6	N48°58'45" E014°53'51"	5.3	60	13.4	12.4	349	152	13.7	440	-6	6	0	60	60	1	40	Fen
Strádovka	2	1.9	2.3	6	N49°48'33" E015°48'12"	6.5	98	2.39	15.1	26.1	44.7	9.36	580	-10	21	0	35	60	0	10	fishpond margin
Šimanovské rašeliniště	2	1.5	1.5	6	N49°27'01" E015°26'48"	6.4	108	1.33	17.9	15	43.8	9.52	605	-4	4	2	70	50	0	30	Spring
V Lisovech	4	2.3	1.6	6	N49°14'49" E015°16'44"	5.7	104	0.33	11.9	29.4	61.1	14.2	650	-6	6	1	70	60	1	40	fen meadow
V Rájích	2	3	2	5	N48°59'11" E014°42'31"	6.5	205	0.06	39.3	44.7	390	31.6	445	-7	5	2	70	50	0	15	Spring
Velká Kuš	2	1.8	2	5	N49°23'39" E013°47'41"	6.3	208	6.53	13.1	351	62	36	482	-17	5	1	80	80	0	0	fen meadow
Zlámanec	2	2.7	2.8	6	N49°42'19" E015°55'56"	6.0	147	3.07	16.2	143	41.8	46.5	620	-6	3	2	60	70	0	35	fen meadow

Results

According to the fitted models, the size of *H. vernicosus* populations is negatively affected by herb and *Sphagnum* cover, yet positively affected by increasing iron concentration and density of bryophyte and shrub cover (Table 3, Fig. 1). However, the effects of bryophyte, *Sphagnum* and shrub cover are not significant in the parametric test.

The vitality of populations is positively correlated with the density of moss layer, whereas it is negatively correlated with the herb and *Sphagnum* cover and the degree of water level fluctuation (Table 3, Fig. 1). The trend of population development seems to be negatively correlated with the density of herb cover, water table fluctuation and density of shrub cover, which is positively correlated with population size (Table 3, Fig. 1). The effect of shrub cover was, however, not significant in the parametric tests.

Except for the iron content, which positively affected population size, no significant influence of chemical composition of water on *H. vernicosus* populations was shown.

Table 2. Median and quartile range of all analyzed site characteristics. Predictors selected on the basis of AIC statistics in one of the considered models are shown in bold. Shrub cover had nonzero value only at seven localities (ranging from 1-5% cover), its average value is 0.67%.

	median	**lower quartile**	**upper quartile**
pH	6.3	6.2	6.8
conductivity [µS/cm]	139	87	180
Fe [mg/l]	1.17	0.52	2.39
Ca^{2+} [mg/l]	15.10	12.20	22.61
NH_4^+ [µg/l]	44.7	16.9	165
NO_3^- [µg/l]	53.2	43.8	74.2
PO_4^{3-} [µg/l]	12.5	10.0	18.3
altitude [a.s.l.]	555	435	620
average water table [cm under stem apex]	-6	-7	-4
water fluctuation [cm]	5	3	8
bryophyte cover [%]	60	60	80
herb cover [%]	60	50	70
shrub cover [%]	0	0	0
***Sphagnum* cover [%]**	25	5	40

Table 3. Summary of the linear models fitted for the three parameters of H. vernicosus populations. Full model selected based on AIC value is shown, the presented F statistic values and type I error estimates (p) only supplement the parsimony-based results. The order of selected predictors represents the order of their selection into model, based on the AIC statistics.

Population size

predictor	regression coefficient	$F_{1,27}$	p
herb cover	-0.0376	7.19	0.012
Fe	+0.5394	3.82	0.061
bryophyte cover	+0.0249	2.66	0.115
***Sphagnum* cover**	-0.0165	2.64	0.116
shrub cover	+0.1590	1.99	0.170

Population vitality

predictor	regression coefficient	$F_{1,28}$	p
herb cover	-0.0179	7.05	0.013
water table fluctuation	-0.0348	5.87	0.022
bryophyte cover	+0.0126	3.05	0.092
***Sphagnum* cover**	-0.0086	3.55	0.070

Trend of population development

predictor	regression coefficient	$F_{1,29}$	p
herb cover	-0.0166	4.59	0.041
water table fluctuation	-0.0295	4.70	0.038
shrub cover	-0.0917	2.13	0.156

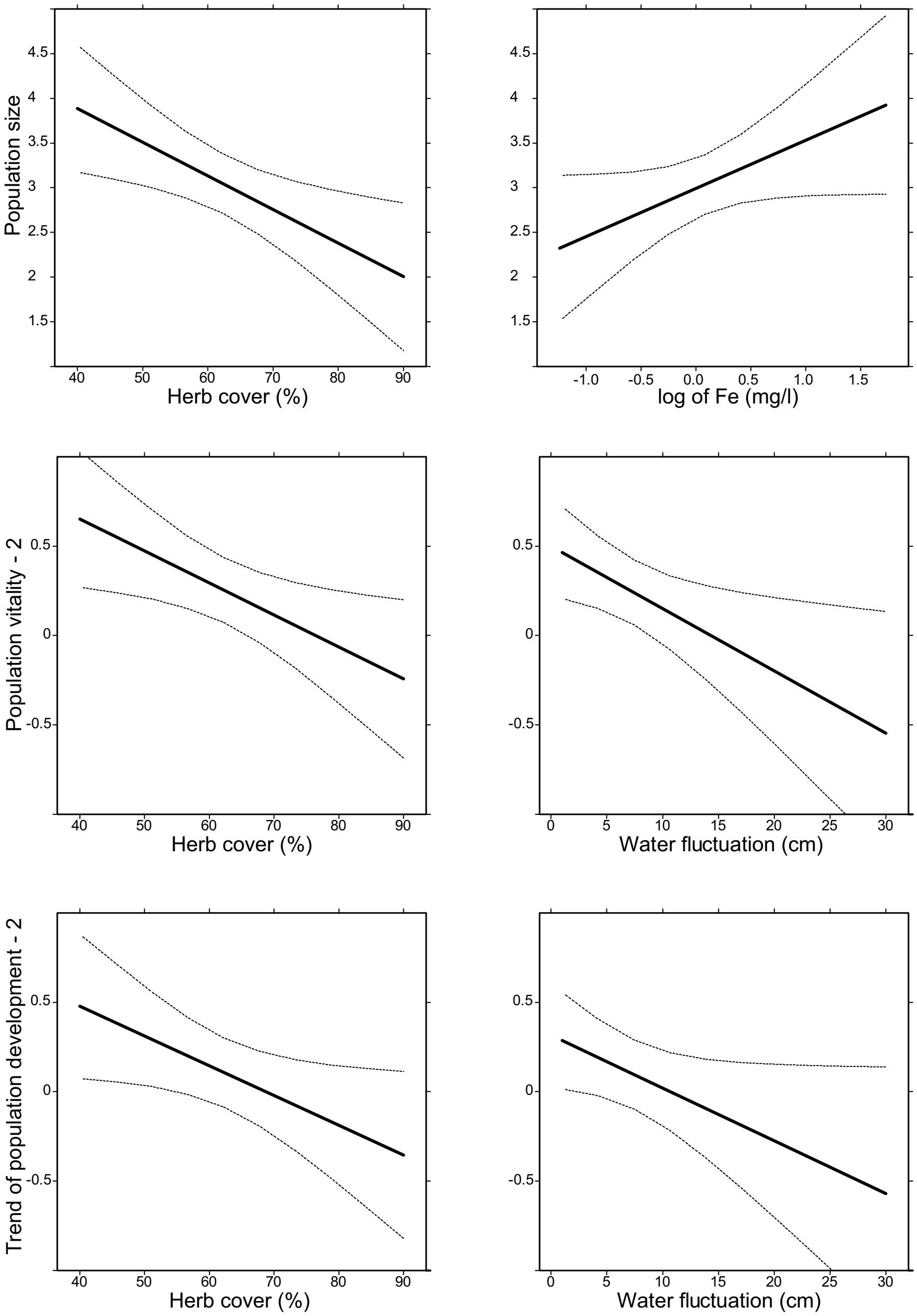

Fig. 1. Visual presentation of the partial effects of significant predictors from the three regression models summarized in Table 3. Dashed lines delineate 95% confidence regions (or intervals, in the case of categorical predictor). In the first row, the effects on population size are presented, and the effects on the average population vitality and on the population size increase are shown, respectively, in the second and third row.

Discussion

According to our results, herb cover is the most important factor negatively affecting all three measured characteristics, which included the size of *H. vernicosus* populations, their vitality and population development trend. Generally, the moss layer is held down by a high cover of vascular plants (Hájková et al. 2009), but each species reacts differently to this factor. Herb cover sensitively responds to the intensity of management at *H. vernicosus* localities. Hence regular mowing is necessary at localities where the water table does not keep the cover of vascular plants low (Štechová and Kučera 2007). No correlation between the management intensity and vascular plant cover in this study could be found given the existence of few localities where the water table is high and herb cover sparse despite the absence of management. Moreover, the mowing is often not sufficient to keep aboveground vascular plant biomass low in the case of increased eutrophication and decreased water level (Bergamini et al. 2009).

No correlation was detected between the phosphate content and herb layer cover, contrary to the positive correlation in most other studies (e.g. Venterink et al. 2009, Gerdol et al. 2010). The interactions between phosphate content and other factors enhancing or suppressing the herb layer (management intensity, water table fluctuation) might be too complicated to render the positive effect of phosphate on herb layer. Also, the single phosphate determination might not have been sufficient for revealing the existing trends due to the possible variance in the readings. Moreover, the phosphate content available to the plants might have differed considerably from the total content measured, as argued by Kooijman and Hedenäs (2009).

A probably misleading effect was the significant positive correlation between population size of *H. vernicosus* and the cover of shrubs. The species preferred open-canopy microsites (Bauer et al. 2007), which was also confirmed in our other studies. The trend of *H. vernicosus* population development was negatively affected by the cover of higher shrubs (Table 3). The shrub cover was recorded at only 7 of 33 localities (Table 1). A significant positive effect from shrubs on the population size was likely caused by the unusual situation at the "Červený rybník" site, where *H. vernicosus* grew in very favourable conditions (permanently wet, sparse herb cover); its population was large, and it had not yet responded to the recent gradual expansion of *Salix* *cinerea* shrubs. The positive effect of shrubs was not significant in the parametric test.

A cover of *Sphagna*, which were the most serious bryophyte competitors for other fen mosses (Paulissen et al. 2004), had a negative effect on population size and vitality. Habitats dominated by *Sphagna* were generally less suitable for *H. vernicosus* (and other brown mosses) due to adverse chemical conditions (Hájek et al. 2006), as well as the direct competition for space, light, and possibly nutrients. Plants of *Sphagnum* benefitted from their more robust constitution and higher growth rate, as evidenced already by Kooijman (1993). *H. vernicosus* stems growing among *Sphagna* were thin and lean probably due to lack of light.

Another advantage for *Sphagnum* species was their ability to acidify habitats, handicapping the more calcicole species. During natural succession with associated acidification, rich fen bryophytes were replaced by calcium-tolerant *Sphagna*, and then by *Sphagna* with an optimal occurrence in mineral-poor fens or bogs (Glime et al. 1992, Bragazza and Gerold 1999). In our study, pH and mineral richness were not selected as significant factors affecting *H. vernicosus* populations. However, higher *Sphagnum* cover and lower pH were significantly correlated.

Water table fluctuation also had a significant impact on the vitality of the target species and the trend of its development in our study. The best vitality was recorded in fen and spring habitats, where the water table was high and relatively stable. The moss was found to be less vital at fishpond margins, where water conditions were very unstable (cf. Navrátilová and Navrátil 2005; Štechová and Štech 2009), as the water table fluctuated according to the water table of the managed fishpond. The worst vitality was generally recorded in populations from majority of fen meadows, where the moss often suffered from the lack of water, caused by frequent artificial drainage.

The reduction of *H. vernicosus* populations was recorded at majority of sites with high water table fluctuation. That was expected at localities where the water level repeatedly decreases deep below the surface – this situation often has led to the extinction of many rich fen bryophytes (Mälson et al. 2008). However, population reduction was observed also at several localities where the water table was often a few centimetres above the surface during the vegetation season and mosses were inundated. This negative effect confirmed that the studied moss does not tolerate long-term inundation, as noted already by Janssens (1983).

The positive correlation of the iron content with population size was very interesting for us, as it contradicted the results from our previous studies (Štechová and Kučera 2007; Štechová et al. 2010). On the other hand, this result was supported by earlier data from Hedenäs and Kooijman (1996), who stated that *H. vernicosus* preferred iron-rich habitats. Different iron contents at the same localities can be caused by different sampling times, because it was known that iron concentrations fluctuate widely in time (Hájek and Hekera 2004). This could have influenced our previous study, for which most samples were taken in spring, when the chemical gradients were believed to be quite variable and weakly definable (Tahvanainen et al. 2003). The positive iron effect on *H. vernicosus* population size may be explained by the lower uptake of Ca ions in conditions of higher iron content (cf. Zohlen and Tyler 2000), disadvantaging the competing calcicolous moss species (e.g. *Scorpidium cossonii*, *Campylium stellatum*, *Palustriella commutata*).

We found no statistically significant effect from nutrient concentrations on *H. vernicosus* populations. This was a surprising result because an increase in nutrients together with a decrease in the water table has been considered one of the main factors causing the retreat of many fen bryophytes (e.g. Kooijman and Bakker 1995; Paulissen et al. 2004, 2005, Bergamini et al. 2009). We must consider the possibility that the nutrient content in the water did not always correspond to the amount of nutrients available to the mosses. Especially in the more calcareous fens, net N and P mineralization was found to be relatively low by Kooijman and Hedenäs (2009). Therefore the simple measuring of nutrient content in the surrounding water might have been insufficient for true detection of a nutrient influence on the studied species.

The nutrient contents in our study were quite variable within the monitored plots. The average NH_4^+ content from 33 localities in this study was roughly half of that measured in our previous study (about 220 µg/l in samples from seven localities, Štechová and Kučera 2007), although all seven sites from the last study were included in this study, too. This discrepancy can be explained by a high seasonal variation in water chemistry (Tahvanainen et al. 2003), because the sampling term was different in this and the last study. The average value reported by Hedenäs and Kooijman (1996) from the Swedish sites was even higher (350 µg/l). Likewise the average NO_3^- content about 70 µg/l was almost half of that of the previous study, whereas the Swedish average was 90 µg/l. Concentrations of PO_4^{3-} were not analysed in our previous study, but according to the results of this study the average content was about 20 µg/l, which was the same value as that reported by the Swedish sites.

We must of course acknowledge that a part of the unexplained variability might relate to the possible occurrence of two recently discovered phylogenetic lineages (Hedenäs and Eldenäs 2007) with non-identical realized niches in the investigated area. However, that study proved that no difference exists in habitat preferences between the two cryptic species as represented by the basic factors of water chemistry (pH and conductivity). This seems to indicate that our results might be applied irrespective of the precise genetic identity of the studied populations, at present only identifiable by genetic barcoding.

We conclude that the population size and the vitality of *H. vernicosus* are affected mainly by the density of vascular plant cover. A higher cover of *Sphagna* also has a negative effect on population performance. Water conditions are very important for the vitality of the moss and the development of its populations; the species thrives best in habitats with a relatively stable water table. Another important factor affecting *H. vernicosus* populations is the content of Fe ions, as the populations prosper better in iron-rich conditions. Based on this research, population characteristics do not appear to be dependent upon nutrient contents. Future studies should probably consider the identity of the studied populations within the recognized cryptic species.

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Paper III

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Comparison of habitat requirements of the mosses *Hamatocaulis vernicosus*, *Scorpidium cossonii* and *Warnstorfia exannulata* in different parts of temperate Europe

Porovnání stanovištních nároků mechů *Hamatocaulis vernicosus*, *Scorpidium cossonii* a *Warnstorfia exannulata* v různých částech temperátní Evropy

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Abstract

Habitat affinities of the red-listed and EU Habitat Directive moss species *Hamatocaulis vernicosus* and the more widely distributed allied species *Scorpidium cossonii* and *Warnstorfia exannulata* were analysed. Ecological preferences of these fen mosses, with respect to water pH, water conductivity, Ellenberg's moisture and nutrient indicator values, were compared in three different European locations (Bohemian Massif, the West Carpathians and Bulgaria) using logistic regressions fitted by means of Huisman-Olff-Fresco models. Inter-specific co-occurrences of the species were also investigated. *Warnstorfia exannulata* preferred slightly acid conditions, about pH 5.6 at all the locations studied. Ecological behaviour of *S. cossonii* was very similar at all the locations, where it occupied base-rich habitats (pH > 7). The pH optimum of *H. vernicosus*, occupying habitats in the middle part of the base richness gradient, varied between locations from 6.0 in Bulgaria to 6.7–7.0 in the West Carpathians and Bohemian Massif. Niche diversification followed the gradient in Ellenberg nutrient indicator values and was similar at all the locations. In the Bohemian Massif and Bulgaria, the occurrence of *W. exannulata* was further associated with a relatively high moisture indicated by the Ellenberg indicator value. The results obtained from the Huisman-Olff-Fresco models accord with the results of inter-specific co-occurrences. Moreover, the latter method revealed a link between *H. vernicosus* and the occurrence of disjunctly occurring boreal sedges, suggesting the relic nature of *H. vernicosus* habitats at these locations.

Keywords: brown mosses, bryophyte, *Drepanocladus*, fen, HOF modelling, mineral richness, mire, niche diversification, water pH

Introduction

Hamatocaulis vernicosus is a red-listed moss species throughout most of Europe and particularly in the Central European region, attaining even the official listing of the Bern Convention (Council Directive 92/43/EEC 1992). An increasing focus on *Hamatocaulis vernicosus* because of its protected status by EU Habitat Directive in network Natura 2000 led to a more detailed exploration of its habitat requirements in Europe. The species occurs in fens, where it can dominate together with the closely related species *Scorpidium cossonii* and *Warnstorfia exannulata*, and other brown mosses (Bergamini et al 2001, Hájek et al. 2006). All three species are similar with respect to growth type but their niche diversification is less known than that of other important mire genera such as *Sphagnum* (e.g., Daniels & Eddy 1990, Bragazza 1997, Hájková & Hájek 2004, 2007) or *Philonotis* (Hájková et al. 2007). Even though a clear ecological separation of these species along a pH gradient is reported for the boreal zone (Janssens 1983, Hedenäs & Kooijman 1996), they often grow together in Central Europe (Štechová & Kučera 2007). In other parts of Europe, little is known about the habitat affinities of these three important fen species.

Previous studies on the habitat preferences of the three species studied (Janssens 1983, Hedenäs & Kooijman 1996, Hedenäs 2003) have mostly been done in the boreal and boreoatlantic zone, where their habitat preferences were compared by means of ranges and medians of environmental factors measured in tufts of these mosses. The objective of our study is to model the realized niches of the species in terms of complete environmental gradients. We use field data from SE Europe (Bulgarian mountains), where these species have not been previously investigated and data from two contrasting Central-European locations (the Bohemian Massif and the West Carpathians), for which only incomplete information is available (Hájková 2005, Štechová & Kučera 2007). In the West Carpathians, calcareous fens are the most frequent mire habitat (Hájek et al. 2007). Acidic fens are more common at the two other locations, especially in the cold mountains in Bulgaria (Hájková & Hájek 2007).

In this paper, we address the question how the realized niches of these species differ in areas where both the commonness of particular habitats and the relative frequency of the species differ. According to the evolutionary species pool hypothesis (e.g., Pither & Aarssen 2005, Hájek et al. 2007), ecological optima and amplitudes of species differ due to differences in the incidences of acidic and base-rich habitats, and according to the theory of competitive release (e.g., Coudun & Gégout 2005), species should occupy a different or have a wide realized niche, when there are fewer competitors. Finally, the results of species response curve modelling is compared with inter-specific co-occurrences of these species.

Materials and Methods

Study area

These species were studied in the Bohemian Massif in the Czech Republic (BM), the West Carpathians in Slovakia, Czech Republic and Poland (WC) and the Bulgarian mountain ranges (BG). In BM, the localities are predominantly in the Třeboňská pánev basin and Českomoravská vrchovina highland (cf. Štechová et al. 2007), where there is an abundance of natural mires and springs. A few of the localities are scattered over the entire BM, which includes a major part of the Czech Republic, except for the easternmost part. The geological bedrock of BM is formed predominantly of metamorphosed schists (phyllite, mica schist, gneiss, amphibolite) permeated by granites. In WC (Slovakia, Poland, Czech Republic), most of the samples originate from the flysch bedrock, where geological strata (bed) of sandstone and claystone alternate and differ both in chemistry and proportion of sandstone and claystone. However, data for other bedrocks such as limestone or granite are also included in the study. In BG, mires were investigated in mountains where mires naturally occur (e.g., Rhodopes, Rila, Pirin, Stara Planina, Vitosha, Osogovska Mt, Sredna Gora Mts). Granite, gneiss, granodiorite, sandstone, claystone, siltstone, metamorphosed shale, marble and limestone form the bedrock at particular study regions. All the study sites are located within the temperate climate zone. BM has a more oceanic climate compared to the other two locations, with mean annual temperatures mostly between 4 and 8 °C, and precipitation sum mostly between 600 and 900 mm per year (Tolasz 2007). In WC, mean annual temperatures at the study sites were between 3 and 7.5 °C in most cases (mean for all sites 5.2 °C) and precipitation sums mostly between 750 and 1100 mm (mean for all sites 940 mm). The climate in BG is continental, only locally influenced by the Mediterranean. Climatic data are not available for the majority of the study sites. The rate of evaporation at high temperatures at altitudes up to ca 1000 m a.s.l. (mean annual temperature 10 °C or more, precipitation sum about 600–700 mm) is not suitable for the development of *Sphagnum* mires (Hájková & Hájek 2007). The altitudinal belt of ca 1300–1800 m a.s.l. corresponds to the Central European beech and spruce vegetation belts and contains most types of mire, except for subalpine and alpine mires. The climate of the subalpine and alpine zones in the Bulgarian high-mountains (mostly above 1800 m a.s.l.) is cold and humid. The mean annual precipitation on the highest peaks varies around 1000 mm and the mean annual temperature around –2 °C (Lieth et al. 1999). Of the species studied, only *W. exannulata* was found in the (sub)alpine wetlands.

Field data sampling

Samples of vegetation were collected from springs and mires in BM, WC and BG in grow-ing periods in 2001–2005. At lower altitudes, most samples were collected between the end of May and beginning of July, but in the high mountains between the end of June and September. For the numbers of the samples collected in each area see Table 1. All vegetation-plot and environmental data from mires were included in the analysis, regardless of whether they contained the target species (see Vetaas 2000, Hájková et al. 2007 for the advantages of this method). An area of 16 m^2 was sampled in most cases; plots that were obviously heterogeneous in terms of superficial structure, vegetation type or physical-chemical properties of the water were avoided.

Cover of all species was estimated using the nine-grade Braun-Blanquet scale (van der Maarel 1979).

Water conductivity and pH, both standardized at 20°C, were measured in situ using portable instruments. Water conductivity (ln-transformed) accurately reflects the mineral richness (Ca+Mg) of the groundwater, especially in spring-fed mires (Sjörs & Gunnarson 2002; Hájek & Hekera 2004). Conductivity due to H^+ ions was subtracted for acidic waters with a $pH < 5.5$ (Sjörs 1952). Both these physical-chemical factors (pH, conductivity) are relatively stable over time compared to other factors such as iron or phosphorus concentrations, and separate major fen types throughout the season (Vitt et al. 1995, Tahvanainen et al. 2003, Hájek & Hekera 2004, Hájek et al. 2005). In spring fens, the measurements were of the water surrounding the mosses. When the water level was several centimetres below the surface, a small shallow pit was dug and water allowed to clarify before measurement. On the basis of the composition in the vegetation samples, the Ellenberg indicator values for moisture and nutrients were calculated as unweighted means of all vascular plant species present in vegetation plots.

Table 1. Frequencies of the moss species in the samples collected in particular regions.

Region/species	Total	*Hamatocaulis vernicosus*	*Scorpidium cossonii*	*Warnstorfia exannulata*
Bohemian Massif	478	76 (15.9%)	42 (8.8%)	76 (15.9%)
West Carpathian	676	29 (4.3%)	220 (32.5%)	60 (8.9%)
Bulgarian Mts	483	24 (4.9 %)	6 (1.2%)	146 (30.2%)

Hedenäs & Kooijman (1996) stressed the importance of the concentration of iron in water in determining the distribution of *H. vernicosus*. In our study the iron content was not measured because of constraints on time and financial support. Iron concentration fluctuates widely in time (e.g., Hájek & Hekera 2004) and it is impossible to monitor it in such an extensive study. However, results from the Czech Republic show that the occurrence of *H. vernicosus* is not obligately associated with high iron content (Štechová & Kučera 2007).

The nomenclature follows Kubát et al. (2002) and Kučera & Váňa (2003). Nomenclature of S European vascular plants not in Kubát et al. (2002) follows Andreev et al. (1992).

Data analysis

For all the species at each location, the probability of their occurrence was analysed with respect to pH, ln-transformed conductivity and Ellenberg indicator values using a logistic regression fitted using Huisman-Olff-Frescomodels (HOF; Huisman et al. 1993). HOF is a hierarchical set of five species response models, which increase in complexity: model I – flat with no response, II –monotonously increasing or decreasing, III– monotonously increasing or decreasing with a 'plateau', IV – symmetric unimodal and V – asymmetric unimodal response. For these models, four parameters were estimated, which was done using a non-linear maximum likelihood estimation procedure (Oksanen & Minchin 2002). This routine was run externally from the JUICE program (Tichý 2002) using a procedure developed by David Zelený and Lubomír Tichý and available at http://botanika.bf.jcu.cz/david/hof.php. Ten outlying conductivity values for salt-rich travertine fens (2000–10,000 $\mu S.cm^{-1}$) were not included in the analysis as they strongly influenced the shapes of the species response curves. Only one sample from these high-conductivity fens contained some plants of one of the study species (*S. cossonii*). For each species the response optimum, defined as that part of the gradient where the predicted probability of occurrence was highest, and the response interval (i.e., ecological amplitude), defined as the distance between parts of the gradient where the predicted probability of occurrence reached more than half of that of the maximum predicted probability of occurrence, were determined.

At each location, the vascular plants and bryophytes that had similar habitat requirements to the target species were determined by calculating the inter-specific associations of the species. The phi-coefficient has was used as a measure of species fidelity (Chytrý et al. 2002).

Results

Frequency of target species

The number of samples containing particular target species differs across locations (Table 1). The highest frequency of *Hamatocaulis vernicosus* was recorded in BM, while that of *Scorpidium cossonii* was highest in WC, where this species occurred in one third of the samples. In contrast, the frequency of *S. cossonii* in the Bulgarian samples was very low; this species was recorded only in six samples at three recently discovered localities. *Warnstorfia exannulata* occurred most frequently in the Bulgarian mountains, especially above the timberline.

Habitat requirements of target species

Response curves of the species to pH, conductivity, Ellenberg moisture and nutrient indicator values showed a high level of niche differentiation within the species group, which is consistent across regions (Fig. 1, Table 2). While ecological requirements clearly differed among the species within each region, the species optima and amplitudes were shifted between regions in several cases.

Diversification of the realized niches along the pH gradient of the species studied was clear. *Warnstorfia exannulata* preferred slightly acid conditions, about pH 5.6 at all the locations studied. *Scorpidium cossonii* represented the other extreme, with a monotonic response curve peaking at the alkaline end of the gradient at all locations. Its optimum revealed by the HOF method corresponded to the maximum pH value in the data set. The position of realized niche of *Hamatocaulis vernicosus* was intermediate. Response optimum of *H. vernicosus* on the pH gradient varied in the different areas, from pH 6.0 in Bulgaria, which is close to the optimum of *W. exannulata*, to pH 6.7–7.0 in WC and BM, which is close to the optimum of *S. cossonii*. The patterns in species niche diversification with respect to conductivity (Fig. 1) were similar to those with respect to pH, with the exception of Bulgarian data set in which the realized niche of *H. vernicosus* was better differentiated from that of *S. cossonii* than at the two other locations studied.

The species realized niches differed not only in terms of pH and conductivity, but also in terms of Ellenberg's moisture and nutrients (Fig. 1). *Warnstorfia exannulata* occurred in wetter habitats than the other two species at both the BG and BM localities, but not in WC. *Hamatocaulis vernicosus* and *S. cossonii* had roughly the same moisture demands. *Warnstorfia exannulata* was tolerant of a wide range of Ellenberg's nutrients at all locations, but its optimum shifted towards less mineral-and more nutrient-rich habitats in WC.

The optimum of *S. cossonii* was in nutrient-poorer habitats that of *H. vernicosus*.

Inter-specific co-occurrences

Association of other bryophyte species with particular target species confirmed the ecological requirements indicated by the environmental variables (Table 3). The species composition of the vegetation harbouring target species varied according to the species and region. Of the potential competitors of *H. vernicosus*, *Calliergonella cuspidata* wasstrongly associated with this species in both BM and BG mires. As regards *Sphagnum* species, the vegetation affinities of *H. vernicosus* were similar to those of *Sphagnum teres* in BM and that of *S. contortum* in BG. In WC, this species was not strongly associated with any *Sphagnum* species. At all three regions, *H. vernicosus* was positively associated with vascular plant species with a boreal and boreo-continental distribution, which are considered to be glacial relicts in Central and SE Europe, namely *Menyanthes trifoliata* (BM, WC), *Carex diandra* (BM), *C. lasiocarpa* (WC), *C. chordorrhiza* (WC), *C. dioica* (WC) and *C. buxbaumii* s.s. (BG). In Bulgaria, *H. vernicosus* was strongly positively associated also with grass and herb species typical of managed fen grasslands in SE Europe (e.g., *Holcus lanatus*, *Myosotis sicula*, *Oenanthe banatica*).

Species, which were strongly associated with *Scorpidium cossonii*, represent mostly a geographically rather uniform group of strongly calcium-tolerant species of low-productive habitats (*Campylium stellatum*, *Eriophorum latifolium*, *Carex panicea* and *Eleocharis quinqueflora*). Although the species associated with *W. exannulata* variedconsiderably among the regions studied, they were mostly species typical of poor and moderately rich fens, which lack calcium-tolerant species (e.g., *Carex canescens*, *Juncus filiformis*, *Lysimachia thyrsiflora*, *Potentilla palustris*, *Sphagnum flexuosum* and *S. subsecundum*). In WC and BG, the species of sub-alpine springs (e.g., *Carex lachenalii*, *Philonotis seriata*, *Primula farinosa* subsp. *exigua*, *Sphagnum platyphyllum*, *Swertia perennis*, *Warnstorfia sarmentosa*) also showed a positive association with *W. exannulata*.

Table 2. Optima and amplitudes(in parentheses)of habitat parameters of the mosses obtained by using the HOF models. Cond – conductivity; Moist – Ellenberg moisture; Nutr – Ellenberg nutrients. Conductivity optimum and amplitude were calculated from ln-transformed values. Optima are presented as untransformed values, whereas amplitudes are presented on a ln-scale (*). Ellenberg indicator values were calculated as unweighted mean from all vascular plant species present in the vegetation plot.

	Bohemian Massif				Western Carpathians				Bulgaria Mountains			
	pH	Cond	Moist	Nutr	pH	Cond	Moist	Nutr	pH	Cond	Moist	Nutr
Hamatocaulis vernicosus	7.03	6.60	8.06	3.45	6.68	5.35	8.32	3.17	5.98	4.63	7.63	3.45
	(1.94)	(2.36)	(0.96)	(1.42)	(0.72)	(1.61)	(0.79)	(1.42)	(1.18)	(1.07)	(0.91)	(1.41)
Scorpidium cossonii	8.23	6.60	8.35	2.42	8.20	5.97	8.08	2.51	8.30	6.90	6.00	2.97
	(1.17)	(1.02)	(1.52)	(0.92)	(2.26)	(3.74)	(1.57)	(1.44)	(0.53)	(0.58)	(12.00)	(0.74)
Warnstorfia exannulata	5.60	4.66	9.31	3.26	5.69	3.36	7.65	6.20	5.61	1.79	9.12	2.33
	(2.81)	(2.89)	(1.00)	(2.10)	(1.42)	(2.04)	(3.70)	(2.54)	(1.70)	(2.61)	(1.96)	(2.58)

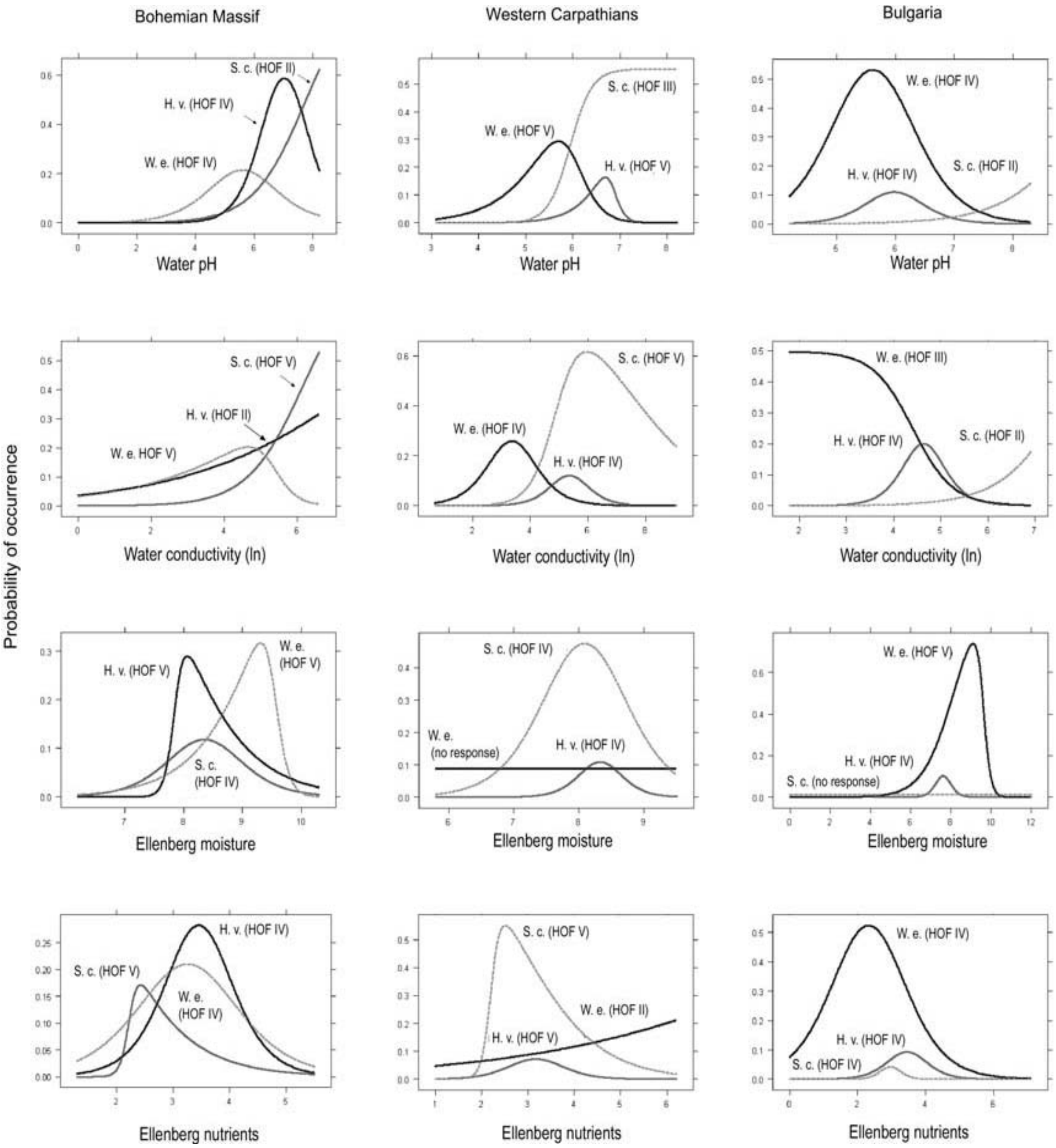

Fig. 1. – Species response curves, in terms of water pH, water conductivity (ln-transformed), and Ellenberg moisture and nutrient indicator values obtained by using logistic regression and HOF models, for the different regions studied. H.v. – *Hamatocaulis vernicosus*, S.c. – *Scorpidium cossonii*, W.e. – *Warnstorfia exannulata*.

Table 3. Species which are positively associated with the moss species in particular regions. The number in parenthesis is the value of phi-coefficient indicating the strength of the inter-specific association between the species studied and other species in the data set.

Species studied	**Czech Republic**	**Western-Carpathian**	**Bulgaria**
Hamatocaulis vernicosus	*Calliergonella cuspidata (56.63)*	*Carex lasiocarpa (41.37)*	*Sphagnum contortum (34.06)*
	Bryum pseudotriquetrum (56.43)	*Tomentypnum nitens (29.54)*	*Calliergonella cuspidata (33.58)*
	Equisetum fluviatile (55.32)	*Salix pentandra (29.2)*	*Philonotis cespitosa (33.51)*
	Menyanthes trifoliata (43.26)	*Galium uliginosum (28.03)*	*Myosotis sicula (30.91)*
	Carex diandra (41.71)	*Carex chordorrhiza (25.66)*	*Holcus lanatus (29.52)*
	Campylium stellatum (41.64)	*Menyanthes trifoliata (24.56)*	*Galium palustre (28.68)*
	Sphagnum teres (38.41)	*Valeriana simplicifolia (23.06)*	*Carex buxbaumii s.s. (28.2)*
	Valeriana dioica (35.33)	*Riccardia multifida (21.35)*	*Plagiomnium affine agg. (27.37)*
	Drepanocladu polygamus (31.48)	*Carex dioica (18.82)*	*Veronica scutellata (27.22)*
	Calliergon giganteum (31.21)	*Crepis paludosa (18.27)*	*Oenanthe banatica (25.11)*
Scorpidium cossonii	*Campylium stellatum (58.77)*	*Campylium stellatum (58.52)*	*Carex lepidocarpa (32.6)*
	Eriophorum latifolium (47.87)	*Eleocharis quinqueflora (54.18)*	*Dactylorhiza incarnata (32.49)*
	Carex panicea (45.97)	*Carex davalliana (53.42)*	*Eleocharis quinqueflora (30.98)*
	Parnassia palustris (43.55)	*Pinguicula vulgaris (52.69)*	*Eleocharis uniglumis (29.21)*
	Fissidens adianthoides (43.53)	*Eriophorum latifolium (49.96)*	*Epilobium parviflorum (26.6)*
	Juncus alpinoarticuslatus (41.36)	*Bryum pseudotriquetrum (49.47)*	*Blysmus compressus (24.61)*
	Eleocharis quinqueflora (39.59)	*Parnassia palustris (45.44)*	*Linum catharticum (24.12)*
	Trichophorum alpinum (37.99)	*Primula farinosa (43.68)*	*Carex panicea (22.23)*
	Carex demissa (36.84)	*Carex panicea (42.84)*	*Ononis arvensis (22.23)*
	Linum catharticum (36.80)	*Equisetum palustre (41.08)*	*Philonotis calcarea (22.17)*
Warnstorfia exannulata	*Sphagnum subsecundum (30.08)*	*Sphagnum subnitens (27.59)*	*Carex nigra (43.33)*
	Campylium polygamum (27.67)	*Lotus pedunculatus (27.29)*	*Sphagnum platyphyllum (32.40)*
	Carex elata (24.90)	*Sphagnum contortum (27.05)*	*Primula farinosa s. exigua (32.39)*
	Potentilla palustris (22.98)	*Viola palustris (26.58)*	*Sphagnum subsecundum (32.33)*
	Calliergon giganteum (21.77)	*Juncus bulbosus (24.66)*	*Scapania irrigua (31.70)*
	Lysimachia thyrsiflora (21.41)	*Carex demissa (23.11)*	*Nardus stricta (31.54)*
	Sphagnum obtusum (18.51)	*Sphagnum flexuosum (22.87)*	*Philonotis seriata (30.61)*
	Sphagnum fimbriatum (17.75)	*Carex canescens (21.71)*	*Pinguicula balcanica (30.32)*
	Calamagrostis canescens (17.59)	*Sphagnum squarrosum (21.55)*	*Warnstorfia sarmentosa (26.11)*
	Peucedanum palustre (17.42)	*Drosera rotundifolia (20.77)*	*Juncus filiformis (25.76)*

Discussion

Niche diversification

Comparison of species response curves, response optima and amplitudes with respect to pH and conductivity showed that our working hypothesis of different optima for a species indifferentregionsholdsonlyfor *H.vernicosus*, which occupies the middle of both the pH and conductivity gradients. Ecological behaviour of two other species (*W. exannulata*, *S. cossonii*) was very similar at all the locations. In Bulgaria, *H. vernicosus* occupied slightly acidic habitats and showed a wider ecological amplitude with respect to pH. A possible explanation for this is the ecotypic adaptation of local populations caused by differences in the histories of the localities, i.e. distribution of refugia with respect to substrate acidity (Hájková et al. 2008). Pleniglacial refugia for mire flora are found mostly on crystalline bedrocks in Bulgaria and are rather acidic for that reason. On the other hand, the refugia in the West Carpathians are often alkaline (Hájek et al. 2007, Horsák et al. 2007). A shift in ecological optimum towards acidic conditions is recorded for other bryophytes in Bulgaria, especially *Sphagnum warnstorfii*, *S. teres* (Hájková & Hájek 2007) and *Aulacomnium palustre* (Hájková et al. 2008). However, a change in competitive regimes can contribute to a wider realized niche as shown by *H. vernicosus* in Bulgaria, where *S. cossonii* is ex-tremely rare and *W. exannulata* is confined to the highest altitudes. This pattern can be re-garded as a sign of competitive release, i.e. extension of the species ecological amplitude in the absence of a potential competitor (Coudun & Gégout 2005). We assume there is a potential for competition between the species studied at the landscape level due to niche overlap between *H. vernicosus* and the other two species (Štechová & Kučera 2007). Al-though bryophytes can tolerate low resource levels, they compete intensely with each other. There is abundant evidence from community structure and transplantation experi-ments that competitive hierarchies among bryophytes exist, with well-adapted species su-perior to widespread ones in specific environments (see Rydin 1997 for review). At some of the localities studied, many small fens are dominated by one species (*S. cossonii*, *H. vernicosus*, *W. exannulata*) and the other two species are absent, even when habitat condi-tions appear to be favourable. On the other hand, the mosses studied often grew together not only in the vegetation plot, but also in mixed clumps at other localities (e.g., Třeboňská pánev basin in the Bohemian Massif). Future research should focus on addressing ques-tions under which conditions competitive exclusion occurs within the group of species studied.

Comparison of our results with those published on the habitat preferences of the spe-cies studied is not straightforward, because the latter are mostly presented in terms of the minimum, maximum and mean/median values of particular measurements. These values may reflect differences in the commonness of particular habitats among regions and possi-ble stochastic occurrences of the species in sub-optimal conditions, even when the species are in fact ecologically similar at all the locations (e.g., Hájková et al. 2007). All our mea-surements of pH and conductivity in the habitats of *H. vernicosus* fall within the range re-ported from Scandinavia (pH 5.4–7.8 and conductivity 16–396 μS.cm^{-1}; Hedenäs 2003). Mean values reported from Scandinavia (Hedenäs & Kooijman 1996, Hedenäs & Eldenäs 2007) are close to the optima of *H. vernicosus* in Bulgaria.

Concerning *W. exannulata*, the optimal pH value was similar at all locations and varied only between 5.6 and 5.7. However, the realized niche of this species is wide as it can toler-atehigherpHlevels.Awiderealizednicheof *W.exannulata* was reported long ago, e.g. by Limpricht (1904), who described many varieties of this species (Limpricht 1904). Like-wise, the controversial reports on the ecological requirement of *W. exannulata* in modern ecological literature may reflect the wide realized niche of this species. Results originating from different geographical location or climatic conditions (Jannsens 1983, Ilyashuk 2002, Szankowski & Klosowski 2004) indicate acidophilous behaviour of this species, while the study of Hedenäs (2003) characterized *W. exannulata* as a species typical of in-termediate mineral-rich environments.

Niche diversification in this group of species along the base saturation gradient coin-cides partially with nutrient availability, approximated by the Ellenberg indicator values of the co-occurring vascular plants. *Scorpidium cossonii* performed optimally in nutrient-poorer habitats than *H. vernicosus* in all three locations. The former species occurs frequently in base-richest tufa-forming fens, which are very poor in phosphorus, whereas the latter prefers extremely rich fens that are not phosphorus-limited (Rozbrojová & Hájek 2008). In the Bohemian Massif, many fens harbouring *H. vernicosus* occur at fishpond margins that are eutrophicated by pond water rich in phosphorus. In contrast, *S. cossonii* is, even in the same mire complex, confined to spring fens that are fed by groundwater poor in phosphates and ammonium (Navrátilová et al. 2006).

Other aspects of **Hamatocaulis vernicosus** *distribution*

The next factor that shapes the distribution of this study group of species is the relic char-acter of the *H. vernicosus* localities, which is indicated by the frequent co-occurrence of boreal sedges. This is supported by the fact that *H. vernicosus* is common in the regions where there are relic mires, but absent where the mires are young. This species was ex-tremely rare, and currently is extinct at the Beskydy Mts (NW margin of the Carpathians), where mires developed after extensive deforestation during the largest Walachian coloni-zation, which occurred 600–700 years ago (Rybníčková et al. 2005), but rather common in the neighbouring Orava region where fens have a long history (e.g., Rybníček & Rybníčková 2003, Horsák et al. 2007). Recent colonization of new areas is not assumed, because the dispersal ability of *H. vernicosus* is very poor in Central and SE Europe. During our study, sporophytes were observed only a few times in field and only once in herbaria.

Besides relic species, *H. vernicosus* often co-occurs with the ubiquitous wetland spe-cies *Calliergonella cuspidata* (see also Church et al. 2001 and Müller & Bauman 2004), which is competitively stronger than fen moss specialists when the nutrient supply is increased (Kooijman 1993) and can benefit also from the increased shading that results from the enhanced growth of vascular plants (e.g., van der Hoeven et al. 1993). As the distribution of rare species of bryophytes is often a product of a trade-off between the probability of colonizing new habitats and the establishment in the presence of competitors (Hutsemekers et al. 2008), the low dispersal ability of *H. vernicosus* combined with frequent co-occurrence with competitively superior species seems to be the crucial factors determining its rarity and threatened status in Central and S Europe. Further conservation monitoring should therefore focus on the inter-specific interactions between *H. vernicosus* and its potential competitors at localities with different nutrient inputs.

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Souhrn

Článek se zabývá studiem ekologických nároků a mezidruhových vazeb tří blízce příbuzných bokoplodých slatiništních mechů v odlišných částech Evropy (Český masiv, Západní Karpaty a Bulharsko). Největší pozornost je věnována druhu *Hamatocaulis vernicosus*, který je považován za celoevropsky ohrožený mech a je sledován v rámci programu Natura 2000. Dalšími studovanými druhy jsou *Scorpidium cossonii* a *Warnstorfia exannulata*, které podobně jako první druh často tvoří dominantu v různých typech rašeliništních biotopů a představují tak jeho potenciální kompetitory. Ve srovnání s podobnými studiemi ze severní Evropy jsme k posouzení diverzifikace nik mezi sledovanými druhy použili křivky druhových odpovědí na gradienty prostředí (HOF modely), kde do analýzy vstupují i údaje ze slatinišť, kde se zájmové druhy nevyskytují.

Srovnání mezi regiony ukázalo, že *Hamatocaulis vernicosus* má větší zastoupení než *Scorpidium cossonii* ve fytocenologických snímcích pocházejících z oblasti Českého masivu a Bulharska, zatímco *Scorpidium cossonii* se nejčastěji vyskytuje ve snímcích ze Západních Karpat. *Warnstorfia exannulata* je dosti častá v Českém masivu a v Bulharsku, kde je však vázána jen na nejvyšší polohy.

Na základě výsledků HOF modelů lze říci, že *Warnstorfia exannulata* má ve všech studovaných oblastech širokou realizovanou niku, preferuje však spíše kyselá stanoviště s pH kolem 5.6, zatímco *Scorpidium cossonii* vyhledává biotopy s nejvyšším obsahem bází (pH vyšší než 7). Optimální pH pro výskyt druhu *Hamatocaulis vernicosus* se pohybuje v rozmezí 6 až 7 v závislosti na

regionu. Tento posun ve stanovištních nárocích lze vysvětlit jak lokální adaptací místních populací na různé úrovně pH v závislosti na historické četnosti jednotlivých biotopů v krajině, tak i kompetičními vztahy měnícími se s četností jednotlivých druhů. Srovnání dále ukázalo, že *Warnstorfia exannulata* roste spíše na stanovištích s vyšší hladinou podzemní vody a má větší toleranci vůči zvýšené-mu obsahu živin. Produktivita stanoviště se podílí i na diverzifikaci nik druhů *Hamatocaulis vernicosus* a *Scorpidium cossonii*. Výsledky HOF modelů byly potvrzeny i stanovením druhů s vysokou mírou věrnosti (fidelity) ke studovaným druhům. Tato analýza navíc ukázala vazbu druhu *Hamatocaulis vernicosus* na biotopy s výskytem boreálních druhů ostřic, které jsou ve studovaných oblastech považovány za reliktní. Zjištěné výsledky mohou pomoci při výběru lokalit ohroženého druhu *Hamatocaulis vernicosus* tak, aby se druh chránil v prostředí, na které je v daném území dobře adaptován.

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Paper IV

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Distribution and habitat requirements of the moss *Hamatocaulis vernicosus* (Mitt.) Hedenäs in the Bohemian Forest

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Abstract

The species *Hamatocaulis vernicosus* is a fen moss, which is endangered and protected in Europe. Recent-ly we have known 9 localities of this species in the Bohemian Forest. Vegetation relevés and detailed water chemistry were investigated at all localities and subsequently compared with data on *H. vernicosus* from different parts of the Czech Republic. The studied species grows in similar vegetation types in all of the Czech localities, including the Bohemian Forest. However, in the Bohemian Forest sites, chemical composition of water differs markedly, particularly in Ca, Mg and NO_3^- contents.

Key words: bryophytes, Czech Republic, fens, Šumava Mts., vegetation, water chemistry

Introduction

Hamatocaulis vernicosus is a red-list moss species throughout most of Europe, attaining even the official listing of the Bern Convention (COUNCIL DIRECTIVE 92/43/EEC 1992). An increased focus on *Hamatocaulis vernicosus* because of its protection under the EU Habitat Directive led to a more detailed exploration of its habitat requirements in Europe (e.g., HUGONNOT 2003, MÜLLER & BAUMANN 2004).

The species prefers mineral rich habitats with a high groundwater table. However, sometimes it occurs also at fishpond margins, where it is able to survive even slight eutrophication by nutrient-rich pond water, or in fen meadows, where abundance and vitality of the moss decrease due to a lack of water (HEDENÄS 1989, NAVRÁTILOVÁ et al. 2006, ŠTECHOVÁ & KUČERA 2007, ŠTECHOVÁ et al. 2008).

In the Czech Republic, 50 recent localities of *H. vernicosus* are known. The localities occur predominantly in the Třeboňská Pánev basin and Českomoravská Vrchovina highland, where natural conditions favour abundant mire and spring occurrences. The Bohemian Forest (Šumava Mts.) is also very rich in mires, but until 2003, only two records of *Ham-tocaulis vernicosus* were known from this region. VELENOVSKÝ (1894) mentioned the occur-rence of the species in the vicinity of Železná Ruda and Hůrka. Since 2003, more intense bryofloristic research has started and the moss was found in different parts of the Bohemian Forest as well (HOLÁ & JAKŠIČOVÁ 2004, MIKULÁŠKOVÁ 2007, ŠTECHOVÁ et al. 2007). Currently, the species is known from nine localities in the Bohemian Forest. These localities differ from localities in other parts of the Czech Republic not only by a markedly higher altitude, but also by the different composition of the vegetation at some sites. Hence we decided to study the vegetation relationships of *Hamatocaulis vernicosus* and groundwater chemistry at its localities in the Bohemian Forest. We asked the following specific questions:

1 What is the distribution of *H. vernicosus* in the Bohemian Forest and how big are the populations at the different localities?

2 Under which water chemistry does the species occur?

3 Which species do grow together with *H. vernicosus*?

4 Are *H. vernicosus* populations endangered? What kind of management is most suitable for the long term conservation of the *H. vernicosus* populations?

Material and methods

In the summers 2005–2008, vegetation at nine localities of *Hamatocaulis vernicosus* in the Bohemian Forest was assessed in the same way as the other localities of this moss in the Czech Republic (ŠTECHOVÁ & KUČERA 2007, ŠTECHOVÁ & ŠTECH, 2009). In each locality, vegetation was analysed in one plot of 4×4 m. The plots were placed to cover the largest part of *H. vernicosus* populations. At the sites, where populations of *H. vernicosus* were small, the 4×4 m plots were rather large for bryological investigation and the large plot size can be responsible for the large variation in the species composition. However, the same sizes were used for all sites to obtain comparable results of investigation. Percentage cover of all vascular plants and bryophytes was visually estimated.

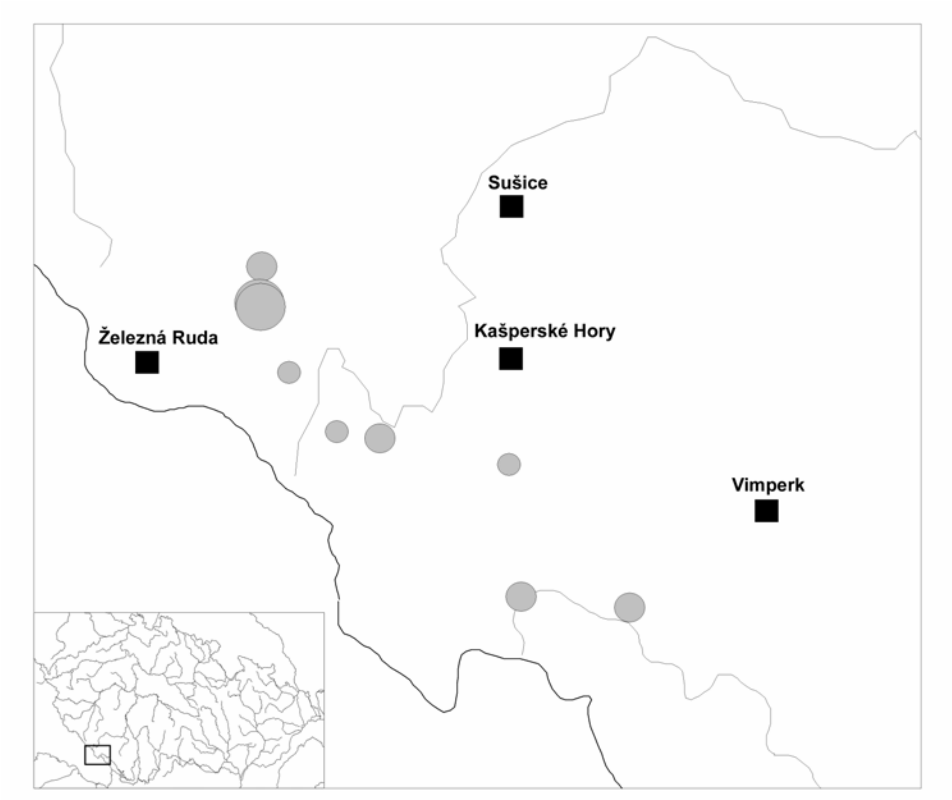

Fig. 1 Map of the studied localities. The symbol size corresponds to population size of the species at localities.

Because the chemistry is more stable in autumn (TAHVANAINEN et al. 2003), all water samples for detailed analyses of water chemistry were collected at one day in November (2008). The samples (one sample per plot; each sample was mixed from three parts that ware collected at points in the immediate vicinity of the studied moss) were filtered over a glass filter and frozen within 24 hours for later analyses. NH_4^+, NO_3^- and PO_4^{3-} were determined colorimetrically by flow injection analysis (FIA Lachat QC8500 – Lachat Instruments, USA), total N (LiquiTOC), Ca^{2+}, Fe, Mg^{2+}, Na^{+} and K^{+} concentration was analyzed spectrophotometrically (SpectrAA 640, Australia). Water pH was measured *in situ* using a portable device (Vario pH, WTW, Germany). The measurements were conducted directly in free spring water circumfluent the studied mosses. When the water level was several centimetres below the surface, the small shallow pit was dug and spring water was allowed to clarify before measurement. Measurements were made at three spots in *Hamatocaulis* patches within each of the sampling plots.

Differences between water chemistry of localities in the Bohemian Forest and 19 sites in other parts of the Czech Republic (ŠTECHOVÁ & KUČERA 2007, ŠTECHOVÁ & MANUKJANOVÁ, unpubl.) were tested by non-parametric Mann Whitney U-tests in the Statistica for Windows package ver. 8 (STATSOFT INC. 2007).

The nomenclature of bryophytes follows KUČERA & VÁŇA (2005), the nomenclature of vascular plants follows KUBÁT et al. (2002).

Results and Discussion

Distribution of Hamatocaulis vernicosus *in the Bohemian Forest*

We found *Hamatocaulis vernicosus* at nine localities in the Bohemian Forest (Table 1, Fig. 1). All sites belong to large complexes (usually tens of hectares) of peaty habitats in various stages of succession. Three localities are located in the surrounding of the former village of Zhůří NE of Železná Ruda, three other localities occur around the village of Prášily and the other localities are situated close to the villages Horská Kvilda, Kvilda, and Borová Lada. Compared with localities in other parts of the Czech Republic (e.g., ŠTECHOVÁ & ŠTECH, 2009), most of the populations of *H. vernicosus* are rather small. At the locality "Slunečná near Prášily", the population of *H. vernicosus* comprises only of about ten stems. The moss grows here in a narrow moist ditch directly among *Sphagnum teres* and *S. flexuosum*. Populations of *H. vernicosus* are small also at the "Zhůří near Horská Kvilda" and "Jezerní Potok" localities; about one hundred stems were found at each site. At the two latter localities, no intense competition with *Sphagnum* species is presumed, as *H. vernicosus* grows mainly among *Warnstorfia exannulata* and *Calliergonella cuspidata*. At the "Kvilda", "Velký Bor" and "Zhůřská Pláň" localities, the populations of *H.*

vernicosus are larger, and the moss grows in rather compact clumps with size of about 500 cm2. The population at the "Chalupská Slať" mire has approximately the same size as at the previous three localities, but pattern of the moss growth is more similar to the first three localities: the stems were dispersed in a wet stretch of about 5 m among *Sphagnum flexuosum* and *S. teres*. At the "Zhůří near Křemelná 1 and 2" localities, the species grows in mosaic with *Sphagnum* species (most often *S. flexuosum, S. contortum*, and *S. warnstorfii*) and other brown mosses (*Calliergonella cuspidata*, *Calliergon giganteum*, *Campylium stellatum*, or *Scorpidium cossonii*). Its absolute cover is a few square metres. This population belongs to the largest populations of *H. vernicosus* in the Czech Republic.

Table 1. Geographic information on the localities of *Hamatocaulis vernicosus* in the Bohemian Forest. Co-ordinates measured by GPS (WGS 84; accuracy approximately 5 m).

Locality	Zonation of national park	Altitude (m)	Co-ordinates	Cadastral unit
Chalupská slať	I. zone NP	960	N49°00'09" E013°39'44"	Svinná Lada
Jezerní potok near Cetlova Hůrka	I. zone NP	860	N49°08'01" E013°21'30"	Prášily
Kvilda	II. zone NP	1060	N49°00'31" E013°33'55"	Kvilda
Slunečná near Prášily	II. zone NP	898	N49°06'02" E013°24'03"	Prášily
Velký Bor	II. zone NP	855	N49°05'49" E013°26'22"	Prášily
Zhůří near Horská Kvilda	II. zone NP	1124	N49°04'55" E013°33'17"	Zhůří near Horská Kvilda
Zhůří near Křemelná 1	II. zone NP	898	N49°10'21" E013°19'54"	Zhůří
Zhůří near Křemelná 2	II. zone NP	910	N49°10'13" E013°19'58"	Zhůří
Zhůřská pláň, PR	NP	1000	N49°11'34" E013°20'02"	Zhůří

With respect to both great fen commonness in the Bohemian Forest and limited knowledge of their bryoflora, we can not exclude new findings of *H. vernicosus* at other localities in future. Therefore, thorough exploration of this area would be very desirable.

Chemistry at the localities

Water chemistry at *H. vernicosus* localities in the Bohemian Forest (Table 2) differs significantly from that at other Czech localities in Ca^{2+} content ($U = 12$, $p = 0.0003$), Mg^{2+} content ($U = 6$, $p = 0.0001$), and NO_3^- content ($U = 41$, $p =$

0.03). Calcium, magnesium and nitrate concentrations are obviously lower at the Bohemian Forest sites. Analogous, but not statistically significant pattern was found also for iron and potassium (Table 3, Fig. 2). It is interesting that for some of the water chemistry measurements (pH, Na^+, total N, NH_4^+, and NO_3^-), variation in the Bohemian Forest (9 localities) was larger than in other sites of the Czech Republic (19 localities).

Table 2. Chemical composition of the water at nine localities with occurrences of *Hamatocaulis vernicosus* in the Bohemian Forest.

Locality	pH	Ca $mg.l^{-1}$	Na $mg.l^{-1}$	K $mg.l^{-1}$	Mg $mg.l^{-1}$	Fe $mg.l^{-1}$	N-NH4 $ug.l^{-1}$	N-NO3 $ug.l^{-1}$	total N $mg.l^{-1}$	P-PO4 $ug.l^{-1}$
Chalupská slať	6.20	4.16	50.92	1.60	1.54	0.55	9.02	34.64	0.90	9.11
Jezerní potok	5.40	3.22	6.36	0.41	0.76	0.50	42.05	37.61	0.90	8.57
Kvilda	5.70	2.20	5.29	0.26	0.71	0.48	14.46	25.26	0.68	8.57
Slunečná near Prášily	6.10	1.97	1.74	2.99	0.37	0.22	28.26	23.45	0.93	16.91
Velký Bor	6.10	2.85	4.26	0.68	0.70	0.53	85.61	94.07	1.33	10.19
Zhůří near Horská Kvilda	5.60	2.71	6.75	7.04	1.10	0.16	738.63	15.88	1.60	14.49
Zhůří near Křemelná 1	6.30	3.31	6.36	0.36	0.91	0.34	41.69	22.30	0.74	14.76
Zhůří near Křemelná 2	7.00	3.16	6.52	0.35	0.91	0.28	17.00	44.19	0.55	11.26
Zhůřská pláň, PR	6.70	6.49	8.27	3.42	1.08	0.43	274.00	45.84	2.29	12.61

In the Bohemian Forest, the average pH values (6.1) are very similar to the average values previously found in other parts of the Czech Republic (6.2; ŠTECHOVÁ & KUČERA 2007, ŠTECHOVÁ & ŠTECH, 2009), and in Scandinavia (6.3; HEDENÄS & KOOIJMAN 1996). All of our pH measurements fall within the range reported from Scandinavia (5.4–7.8; HEDENÄS 2003). It is likely that pH of the habitats plays some role in shaping the population size of *H. vernicosus*. In more acid conditions, abundance of *Sphagnum* spp. is very high and spatial competition between *Sphagnum* spp. and *H. vernicosus* as well as other mosses of neutral habitats is presumed to be very strong with advantages for the *Sphagnum* species (cf. KOOIJMAN & BAKKER 1994, 1995). The highest pH we measured was about 7 at “Zhůří near Křemelná 2”, where the population size is comparable to the three largest populations of the species in the Czech Republic. Interestingly, sites of these largest populations also have pH ~7 (ŠTECHOVÁ & KUČERA 2007, ŠTECHOVÁ & ŠTECH in prep.).

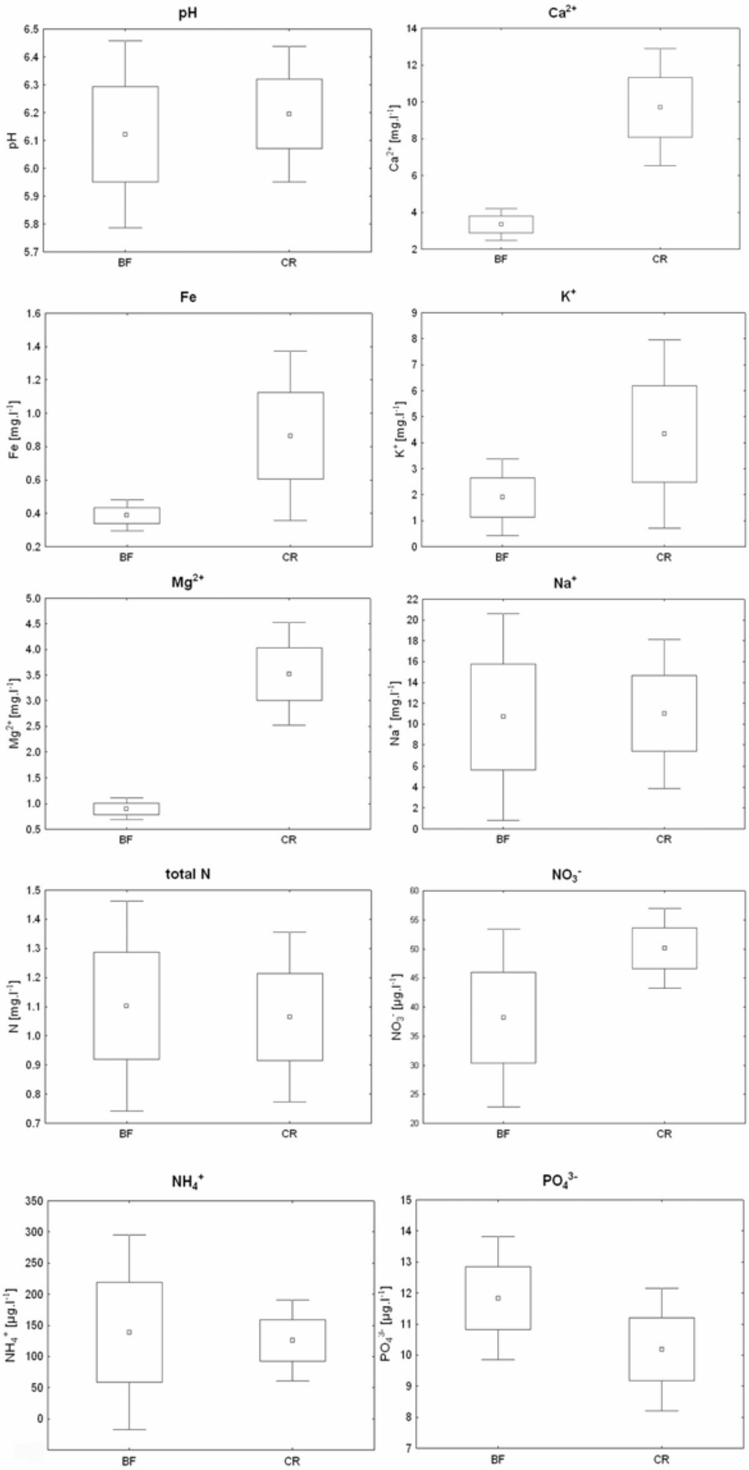

Fig. 2 Comparison of water chemistry at localities in the Bohemian Forest (n = 9) and other parts of the Czech Republic (n = 19).

On the other hand, Ca^{2+} content, which is also one of the most crucial factors influencing species composition of fen vegetation (e.g., TAHVANAINEN 2004), is very low at the localities in the Bohemian Forest, ranging between 2 and 6.5 $mg.l^{-1}$. At all other Czech localities of

H. vernicosus, Ca^{2+} content was not lower than 3.5 $mg.l^{-1}$ and its mean value was about 10 $mg.l^{-1}$ (ŠTECHOVÁ & KUČERA 2007, ŠTECHOVÁ & MANUKJANOVÁ, unpubl.), which is analogous to Scandinavian localities of the species, where the lowest reported value is 2.5 $mg.l^{-1}$ (HEDENÄS 2003), and the mean value is about 14.8 $mg.l^{-1}$ (HEDENÄS & KOOIJMAN 1996).

Contents of Fe was slightly lower (mean values 0.39 $mg.l^{-1}$) than at other Czech localities (mean content about 0.8 $mg.l^{-1}$; ŠTECHOVÁ & KUČERA 2007), and considerably lower than at localities in Scandinavia, where mean Fe content was 2.24 $mg.l^{-1}$ (HEDENÄS & KOOIJMAN 1996) and the lowest measured value was 0.41 $mg.l^{-1}$ (HEDENÄS 2003). Our results thus disagree with an opinion of HEDENÄS & KOOIJMAN (1996), who argue that high iron concentration is an important factor in determining the distribution of *H. vernicosus* (cf. ŠTECHOVÁ et al. 2008).

Mean content of K^{+} is 1.9 $mg.l^{-1}$ in the Bohemian Forest, whereas it is 4.3 $mg.l^{-1}$ at other parts of the Czech Republic and 1.25 $mg.l^{-1}$ in Scandinavia (HEDENÄS & KOOIJMAN 1996). Mean Mg^{2+} concentration is significantly lower in the Bohemian Forest (0.8 $mg.l^{-1}$) than in other parts of the Czech Republic (3.5 $mg.l^{-1}$). In Scandinavia, mean Mg^{2+} concentration is 2.5 $mg.l^{-1}$ (HEDENÄS & KOOIJMAN 1996). Mean Na^{+} content (10.7 $mg.l^{-1}$) is higher than at Scandinavian localities (4 $mg.l^{-1}$; HEDENÄS & KOOIJMAN 1996) and it does not differ from other Czech localities (ŠTECHOVÁ & MANUKJANOVÁ, unpubl.).

Content of NO_3^{-} was significantly lower in the Bohemian Forest (38 $\mu g.l^{-1}$) than at other Czech localities (50 $\mu g.l^{-1}$). Mean value reported from Scandinavia is much higher (90 $\mu g.l^{-1}$; HEDENÄS & KOOIJMAN 1996).

Other nutrient contents (total N, NH_4^+, and PO_4^{3-}) do not differ from other Czech localities (ŠTECHOVÁ & KUČERA 2007, ŠTECHOVÁ & MANUKJANOVÁ, unpubl.). However, NH_4^+ and $PO_4$are lower comparing to localities in Scandinavia, where the NH_4^+ mean concentration is 350 µg.l^{-1} and the mean PO_4^{3-} concentration is 20 µg.l^{-1}. (HEDENÄS & KOOIJMAN 1996).

Table 3. Mean values and standard errors of the chemistry at localities in the Bohemian Forest Mts. and in other parts of the Czech Republic. The last column contains the p-values of the Mann Whitney U-tests.

	Bohemian Forest Mts.		Czech Republic		p-level of
	mean	std. err.	mean	std. err.	M-W U-test
pH	6.10	0.17	6.24	0.11	0.5884
Ca (mg.l^{-1})	3.34	0.45	9.71	1.62	0.0003
Na (mg.l^{-1})	10.72	5.06	11.01	3.64	0.2378
K (mg.l^{-1})	1.90	0.76	4.33	1.85	0.1155
Mg (mg.l^{-1})	0.90	0.11	3.52	0.51	0.0001
Fe (mg.l^{-1})	0.39	0.05	0.87	0.26	0.4312
NH_4 (ug.l^{-1})	122.09	88.49	125.65	33.17	0.3016
NO_3 (ug.l^{-1})	38.14	7.79	50.09	3.48	0.0304
PO_4 (mg.l^{-1})	11.83	1.01	10.19	1.01	0.4030
N (ug.l^{-1})	1.10	0.18	1.06	0.15	0.6228

Species composition at the localities

86 species (28 bryophytes and 58 vascular plants) were noted within the nine vegetation samples. Although the species composition at the localities of *H. vernicosus* varied considerably among the studied localities, the associated species were mostly species of moderately rich fens, at most of the localities without presence of any calcium indicators. The most commonly associated species (Table 4) were similar to species associated with *H. vernicosus* in other parts of the Czech Republic (ŠTECHOVÁ & KUČERA 2007, ŠTECHOVÁ et al. 2008).

Fairly atypical species composition was found at Chalupská Slať, where *H. vernicosus* grew together with *Sphagnum magellanicum*, *Andromeda polifolia*, *Calluna vulgaris*, and *Eriophorum vaginatum*, which are rather diagnostic species of submontane and montane raised bogs (CHYTRÝ & TICHÝ 2003). However, chemical composition of groundwater at this locality is very similar to other localities and therefore we suppose that some local springs in the immediate vicinity of the *H. vernicosus* patches are more basic.

Table 4. Vascular plants and bryophytes most commonly associated with *Hamatocaulis vernicosus* according to the frequency of occurrence in the vegetation samples.

Vascular plants		**Mosses**	
Associated species	**% samples**	**Associated species**	**% samples**
Potentilla erecta	9	*Sphagnum warnstorfii*	9
Carex rostrata	8	*Sphagnum teres*	8
Cirsium palustre	8	*Aneura pinguis*	5
Equisetum fluviatile	8	*Calliergonella cuspidata*	5
Valeriana dioica	8	*Campylium stellatum*	4
Viola palustris	8	*Sphagnum contortum*	4
Carex panicea	7	*Warnstorfia exannulata*	4
Galium uliginosum	7	*Aulacomnium palustre*	3
Tephroseris crispa	7	*Bryum pseudotriquetrum*	3
Agrostis canina	6	*Scorpidium cossonii*	3
Carex echinata	6	*Sphagnum flexuosum*	3
Carex nigra	6	*Straminergon stramineum*	3
Crepis paludosa	6	*Calliergon cordifolium*	2
Eriophorum angustifolium	6	*Calliergon giganteum*	2
Caltha palustris	5	*Chylosciphus polyanthos*	2
Equisetum sylvaticum	5	*Philonotis fontana*	2
Oxycoccus palustris	5		
Salix aurita	5		
Betula sp.	4		
Cardamine pratensis	4		
Luzula campestris	4		
Pinguicula vulgaris	4		

Conservation recommendation for localities

At the monitored plots of the Bohemian Forest fens, *H. vernicosus* seems to not be endangered by water deficiency and groundwater table decrease, or eutrophication, and will prosper as long as site hydrology is not actively disturbed. However, neither hydrology distur bances nor eutrophication are presumed due to localization of the sites in I and II zones of the Šumava National Park. It contrasts to most of the localities in other parts of the Czech Republic, where the sites have often been drained and which are surrounded by intensively managed agricultural land (ŠTECHOVÁ & ŠTECH, 2009).

Until the mid-20th century, the fens were managed regularly. Today, the sites are not managed except the locality "Zhůří 1", where occasional grazing is made. Due to the high water table at all localities, succession of shrubs and trees has not been very intense, and abandoned areas have remained at least partially without woods. The high water table helps to keep low cover of herbs as well, so the management of regular annual mowing is not necessary. However, preventive occasional cutting of self-seeding shrubs, mowing or grazing once every few years is useful at all localities to prevent . The large populations at the "Zhůří near Křemelná 1 and 2" localities seem to be stable (these populations have been monitored since 2005 and 2006, respectively), forming specific vegetation units. Very small populations ("Jezerní potok", "Slunečná near Prášily", and "Zhůří near Horská Kvilda") are endangered not only by competition with *Sphagnum* species, but also by accidental disturbances. Due to rare sporophytes production of *H. vernicosus* (ŠTECHOVÁ et al. 2008), it can be assumed that these very small populations are remnants of formerly larger populations and they have not originated by a recent colonization. For the protection of *H. vernicosus* populations at these sites, manual removing of surrounding *Sphagnum* species would be beneficial, as it would facilitate the growth of the species in free space without competitors (cf. ŠTECHOVÁ & KUČERA 2007).

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Appendix 1. List of phytosociological samples. Plant covers are listed in percents. Sampled area is 16 m^2. Exact localization of the samples can be found in Table 1.

	Chalupská slať	Jezerní potok	Zhůří near Křemelná 1	Zhůří near Křemelná 2	Kvilda	Slunečná near Prášily	Velký Bor	Zhůrské pláně	Zhůří near Horská Kvilda
E	90	70	90	95	60	95	80	85	95
E0	80	50	80	90	50	90	70	60	80
E1	50	50	70	40	40	80	50	80	80
E2									1
E2									
Betula sp.									1
E1								80	
Acer pseudoplatanus		0.05							
Agrostis canina	0.2	1		1	0.2		1	0.2	
Andromeda polyfolia	1								
Amthoxanthum odoratum								0.2	0.2
Angelica sylvestris				0.2		0.2			
Betula sp.	3					5	3		5
Bistorta major			0.2		0.2				
Briza media				0.2		0.2	0.2		
Calamagrostis epigejos									0.2
Calamagrostis villosa				0.2					
Caltha palustris			5	0.2		1		3	0.2
Caluna vulgaris	2								
Cardamine pratensis	0.2		0.2					0.2	0.05
Carex canescens			3			1	5		
Carex demissa				0.2					
Carex echinata		5		3	0.2	3	5		25
Carex flava						5			1
Carex nigra	15		10	3		1		5	10
Carex ovalis								0.2	
Carex panicea	1	20	5		1		0.2	5	5
Carex rostrata	20	10	25	3	25	30	3		5
Cirsium heterophyllum				0.2					
Cirsium palustre	0.2	0.2			0.2	0.2	1		0.2
Crepis paludosa			1		5	5	3	40	10
Dactylorhiza fuchsii						0.2			0.2

	Chalupská slať	Jezerní potok	Zhůří near Křemelná 1	Zhůří near Křemelná 2	Kvilda	Slunečná near Prášily	Velký Bor	Zhůrské pláně	Zhůří near Horská Kvilda
Dactylorhiza majalis			0.2		0.2			1	
Drosera rotundifolia			0.2	1			0.2		
Epilobium palustre				0.2			0.2	0.2	
Equisetum sylvaticum		1	0.2	3		0.2		0.2	
Equisetum fluviatile	0.2		0.2	3	0.2	0.2	0.2	3	1
Eriophorum angustifolium		5		3	15		40	0.2	3
Eriophorum vaginatum	5			3					
Festuca rubra				1					
Filipendula ulmaria		0.2						10	
Galium uliginosum	0.2	0.2	0.2		0.2		0.2	0.2	1
Geum rivale			0.2						
Chaerophyllum hirsutum								15	0.2
Juncus alpinoarticulatus				1					
Juncus articulatus				5		2			
Juncus effusus		0.2		3					3
Luzula campestris	0.2		1	0.2				0.2	
Lychnis flos-cuculi			3						
Melampyrum pratense	0.2								
Molinia caerulea		5							
Myosotis palustris agg.			1						0.05
Nardus stricta				5		3			2
Oxycoccus palustris	10		0.2	5		10			1
Pedicularis palustris			0.2	1		5			
Picea abies						0.2			
Pinquicula vulgaris				0.2			0.2		
Pinus sylvestris	0.2								
Potentilla erecta	1	1	0.2	5	5	5	3	1	5
Pyrola sp.									0.2
Ranunculus acer						0.2			0.2
Ranunculus auricomus								0.2	
Rumex acetosa								0.2	
Rumex sp.			0.2						
Salix aurita	3	15	10				0.2		5
Salix cinerea						0.2			
Tephroseris crispa	0.2	2	15			5	0.2	2	3

	Chalupská slať	Jezerní potok	Zhůří near Křemelná 1	Zhůří near Křemelná 2	Kvilda	Slunečná near Prášily	Velký Bor	Zhůrské pláně	Zhůří near Horská Kvilda
Trientalis europea				0.2					
Vaccinium uliginosum	0.2								
Valeriana dioica	0.2	1	1	3		5	1	0.2	2
Vicia craca						0.2			
Viola palustris	0.2	1	0.2	1	1		1	0.2	1
Willemetia stipitata				2					
E0								60	
Aneura pinguis		0.2			0.2		0.2	0.2	0.2
Aulacomnium palustre	1						0.5		5
Bryum pseudotriquetrum		0.2					3	0.2	
Calliergon cordifolium			1			0.2			
Calliergon giganteum				10				0.2	
Calliergonella cuspidata					3	3	1	3	60
Campylium stellatum		1	1	10			0.2		
Climacium dendroides								3	
Hamatocaulius vernicosus	0.2	0.2	15	5	0.2	0.05	2	0.2	0.2
Chylosciphus polyanthos								0.2	0.2
Pellia sp.								0.2	
Philonotis fontana		0.2	2						
Polytrichum commune				0.2					
Polytrichum strictum				3					
Rhitidiadelphus squarrosus									0.2
Riccardia multifida		0.2					0.2		0.2
Scorpidium cossonii			5	1			1		
Sphagnum contortum		3	15	1			3		
Sphagnum denticulatum					2				
Sphagnum fallax		10							
Sphagnum flexuosum	30			60		40			
Sphagnum magelanicum	1								
Sphagnum squarrosum								3	
Sphagnum subsecundum	1								
Sphagnum teres	40	40	3		10	10	20	25	5
Sphagnum warnstorfii	5	2	35	0.2	30	40	40	25	10
Straminergon stramineum	0.2		1		1				
Warnstorfia exannulata		3			5		1		0.2

Paper V

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The distribution of *Hamatocaulis vernicosus* (Mitt.) Hedenäs (Calliergonaceae, Bryophyta) in the Czech Republic

Rozšíření druhu *Hamatocaulis vernicosus* (Calliergonaceae, Bryophyta) v České republice

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Abstract

The historical and recent distribution of *Hamatocaulis vernicosus*, a species of Annex II of the Habitats Directive, was studied on the basis of herbarium specimens, a review of published literature and the authors' own survey of potentially suitable biotopes. The species has been recorded recently at 54 localities, while its occurrence was not verified at 75 historical localities supported by specimens, and at 14 unsupported localities. Population size ranges from a few stems to tens of square metres; most of the populations are considered to be adversely affected by various negative factors including unstable water regime, eutrophication, lack of appropriate management, expansion of woodland and other successional changes.

Keywords: *Hamatocaulis vernicosus,* distribution, fens, Natura 2000, threatened

Introduction

Hamatocaulis vernicosus (Mitt.) Hedenäs is a species that mostly occurs in rich and moderately rich fens with a relatively stable water regime (Štechová et al. 2012). In Central Europe, it mostly grows in plant communities of the alliance *Sphagno warnstorfiani-Tomenthypnion*, more rarely in the alliance *Caricion* *davallianae* and seldom in *Caricion fuscae* (Hájek et al. 2006). Negative changes in water regime, shifts in the chemical conditions towards acidification and the long-term absence of suitable management has caused the number of localities of *H. vernicosus* to decrease rapidly over the last century. The species has thus become relatively rare and vulnerable not only in the Czech Republic (listed as Vulnerable in the current Red List, Kučera & Váňa 2005) but in the whole of Europe. The overall decrease of populations in Europe prompted its listing in the Bern Convention and monitoring within the Natura 2000 network.

Data on the current distribution, population size and biology of *H. vernicosus* in the Czech Republic have been accumulated rapidly over the last decade. While there were less than ten recent observations of the species in the country as of 2000, the request for surveillance within the Natura 2000 framework triggered a revision of historical localities, which led to the discovery of several new sites and initiated long-term monitoring of existing localities. These surveys occurred particularly in the Českomoravská vrchovina highlands and South Bohemia (Kučera 2001, 2002), North and Northeast Bohemia (Buryová 2001, Pohlová 2001), and the Šumperk region (Zmrhalová 2001, Hradílek & Zmrhalová 2003). Štechová & Kučera (2007) published the results of a study of vegetation composition and basic chemistry at 28 localities, as known in 2005. The detailed chemistry and effect of different abiotic factors on *H. vernicosus* populations were subsequently studied at 33 sites (Štechová et al. 2012). Other studies were focused at regional level. Štechová et al. (2007) described localities in Western Bohemia and the Bohemian Forest, Štechová & Štech (2008) compared the historical and recent status of localities in the Českomoravská vrchovina highlands, and Štechová et al. (2010) compared localities in the Bohemian Forest with localities in other parts of the Czech Republic. New occurrences have continued to be recorded every year (significant additions were for instance presented by Lysák, 2010) but it can be expected that the rate of new discoveries will now substantially decelerate, as most of the potentially suitable biotopes in the country have already been visited. This study thus aims at summarizing the historical and recent distribution of *H. vernicosus*, and assesses population size and threat status at extant localities in the Czech Republic.

Material and Methods

The summary of distribution is based on a review of the literature, revision of herbarium specimens, verification of historical localities, and targeted searches in potentially promising sites. Loan requests were made to Czech herbaria containing more than 200 bryophytes specimens (the list of bryophytes specimen numbers was published on the website of the Moravian Museum Brno, but the list is not currently available). Requests were made not just for *Hamatocaulis vernicosus*, but also for the related species *Scorpidium cossonii, S. revolvens* and *Warnstorfia exannulata*, because of commonly incorrect determinations. Material was obtained from the following herbaria: BRA, BRNM, BRNU, CB, CBFS, CHOM, HR, LI, LIT, MJ, MP, OLM, OP, PL, PR, PRC, SAV, SLO and the private herbarium of J. Váňa. Foreign herbaria were not consulted except for major ones in Slovakia and the herbarium in Linz, as there was no indication in the literature of the existence of specimens that would not have been present as duplicates in the studied herbaria.

Historical localities have been searched for the occurrence of *Hamatocaulis vernicosus* since 2001. Simultaneously, we began a series of visits to localities where the composition of the vegetation appeared suitable for the occurrence of the species, based on literature sources and personal information from local experts. We have particularly targeted localities with the known occurrence of fen mosses commonly associated with *H. vernicosus* (*Meesia triquetra, Paludella squarrosa, Scorpidium scorpioides, Calliergon giganteum*), calcitolerant Sphagna (*S. warnstorfii, S. teres, S. contortum*), or the vascular plants that are often associated with *H. vernicosus* at its known localities (e.g. *Carex diandra, C. lasiocarpa, C. davalliana, Eriophorum latifolium, Menyanthes trifoliata, Parnassia palustris*).

Monitoring of populations with respect to changes in population size, vitality, and vegetation composition was initiated following the respective discoveries at all the recent localities. The localities were initially monitored every year, thereafter every two years. All localities regarded as recent were visited in 2010 or 2011 except for the locality Volákův kopec, visited in 2011 by T. Peterka.

Results

On the basis of our revision of herbarium specimens and exploration of potential biotopes, we were able to prove 129 sites of recent or historical occurrence. 14 localities reported in the literature remained unsupported by a herbarium specimen. There are recent occurrences of *H. vernicosus* at 54 localities (Fig. 1). The altitudinal range of recent localities spans some 900 metres between 255 and 1125 m a.s.l., though historically *H. vernicosus* occurred at both lower (180 m a.s.l.) and higher (1300 m a.s.l.) altitudes (Fig. 2). The extent of the recent populations is very variable, ranging from only a few shoots to about 30 m^2 (Table 1, Fig. 3).

A list of the historical and recent localities follows. The localities are arranged according to the regional phytogeographic classification of the Czech Republic – Skalický (1988).

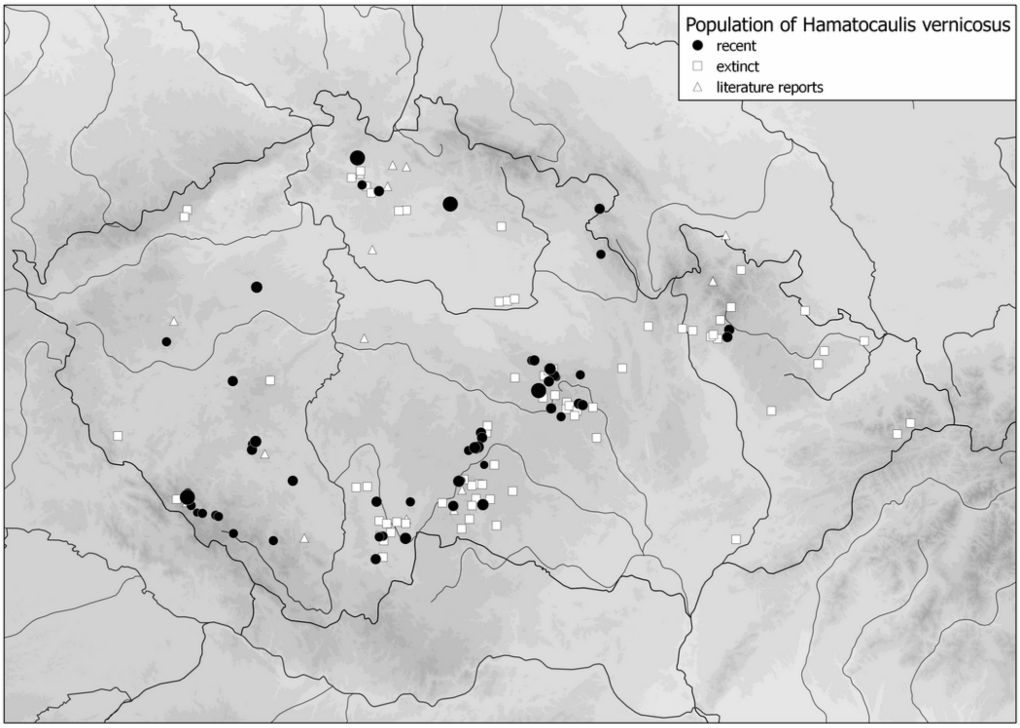

Fig. 1 Map of distribution of *Hamatocaulis vernicosus* in the Czech Republic. Symbol size corresponds to the category of population size of the species as tabulated in Fig. 3.

Historical and recent localities supported by specimens (the recent localities are underlined):

15c. Pardubické Polabí – Soprčský rybník: Froněk, 1942 (sub *Hypnum intermedium*, MP!) – Přelouč, Neratov: Froněk, 1948 (MP!) – Lázně Bohdaneč: Froněk, 8 collections between 1942 and 1956 (partim sub *Drepanocladus intermedius*, MP!). **18b. Dolnomoravský úval** – Bzenec: Podpěra, 1906 (BRNM!, CB!, PR!). **25a. Krušnohorské podhůří** – Lideň: Ditrich, 1929 (CHOM!; Diettrich 1931) – Třetí Dolský mlýn: Váňa, 1961 (priv. herb. Váňa!; Váňa 1966). **31a. Plzeňská pahorkatina vlastní** – Ždánov: Kresl, 1935 (PL!) – Hůrky: Vondráček, 1956 (sub *Drepanocladus intermedius*, BRA!, PL!, PR!), Štechová, 2005 (CBFS!; Štechová & Kučera 2007, Štechová et al. 2007). **32. Křivoklátsko** – Prameny Klíčavy: Jakšičová, 2004 (CBFS; Holá & Jakšičová 2004, Štechová & Kučera 2007). **35a Holoubkovské Podbrdsko** – Hrádecká bahna: Štechová, 2006 (CBFS!; Štechová et al. 2007). **36a. Blatensko** – Dolejší rybník: Velenovský, (PRC!; Velenovský 1897), Stuchlý, 1958 (PRC!), Váňa, 1958 (BRNM!), Skalický, 1984 (PRC!), Jakšičová, 2002 (CBFS!; Štechová & Kučera 2007) – Smyslov: Štechová, 2007 (CBFS!) – Velká Kuš: Štechová, 2006 (CBFS!; Štechová 2006). **37g. Libínské Předšumaví** – Křišťanovický rybník: Štechová 2011 (CBFS!). **37m. Vyšebrodsko** – Vyšší Brod-Horní mlýn: Schiffner, 1896 (BRNM!), Schiffner 1902 (BRNM!, CB!, OP!, priv. herb. Váňa). **38. Budějovická pánev** – Řežabinec: Ježek, 1954 (BRNM!), Kučera, 2001 (CBFS!; Štechová & Kučera 2007) – Vodňany, Malá Outrata Hejný, 1947 (PRC!). **39. Třeboňská pánev** – Třeboň: Weidmann, 1887 (PR!; Weidmann 1895) – Lomnice n. Lužnicí: Velenovský, 1894 (PRC!), Weidmann, 1895 (Weidmann 1895), Pirola, 1971 (sub *Drepanocladus intermedius,* CB!) – Borkovice: Velenovský, 1896 (PRC!; Velenovský 1897), Velenovský 1899, (PRC!), Ježek 1952 (BRNM!) – Zálší: Štěpán, 1909 (CB!) – Chlum u Třeboně: Kalenský, 1910 (BRNM!) – Mažice: Pilous, 1941 (PR!) – Rožmberk: Ježek, 1943 (BRNM!, PR!) – Domanín: Ježek, 1950 (sub *Drepanocladus intermedius*, PL!) – Třeboň, Vimperky: Ježek, 1950 (BRNM!, sub *Drepanocladus intermedius*, CB!) – Přeseka, Velký Tisý: Stuchlý, 1959 (PRC!, priv. herb. Váňa) – Stará Hlína, Hodějov: Ježek, 1951 (BRNM!, PR!) – Švarcenberk: Ježek, 1951 (BRNM!) – Jílovice: Ježek, 1952 (BRNM!) – Pístina: Ježek, 1954 (BRNM!) – V Rájích: Albrecht & Ševčík (Albrecht & Ševčík 1982), Štechová, 2006 (CBFS!) – Odměny u rybníka Svět: Kučera, 2001 (CBFS!; Štechová & Kučera 2007), Štechová, 2009 (Štechová et al. 2010b) – Ruda u Horusic: Albrecht (Albrecht 1985), Kučera, 2001, 2002 (CBFS!; Štechová & Kučera 2007) – Staré jezero: Kučera, 2002 (CBFS!; Kučera et al. 2002), Štechová, 2003 (CBFS! Štechová & Kučera 2007), Navrátilová (Navrátilová & Navrátil 2005) – Brouskův mlýn: Štechová, 2005 (CBFS!). **51. Polomené hory** – Novozámecký rybník: Velenovský, 1901 (PRC!), Němcová, 1997, 1998 (LIT!), Kučera, 2001 (CBFS!; Štechová & Kučera 2007), Váňa, 2001 (priv. herb. Váňa!). **52. Ralsko-Bezdězská tabule** – Břehyně: Schiffner, 1886 (Schiffner & Schmidt 1886), Kučera, 2001 (CBFS!), Váňa, 2001 (priv. herb. Váňa!), Štechová, 2004 (CBFS!; Štechová & Kučera 2007) – Páterov: Podpěra, 1897 (PR!) – Doksy: (Velenovský 1897), Vilhelm, 1901 (sub *Hypnum intermedium* BRNM!, PR!) – Staré Splavy, Sluneční dvůr: Müller, 2000 (DR, Anonymus 2000). **53a. Českolipská kotlina** – Žízníkov: Watzel (Watzel 1874), Schiffner, 1884 (OP!; Schiffner & Schmidt 1886), Váňa, 1959 (priv. herb. Váňa) – Peklo – Zahrádky: Schiffner, 1885 (CHOM!, OP!; Schiffner &

Schmidt 1886) – Červený rybník u Pihele: Váňa, 2001 (priv. herb. Váňa!), Štechová, 2003 (CBFS!; Štechová & Kučera 2007). **55d. Trosecká pahorkatina** – Podtrosecká údolí: Balátová – Tuláčková, 1967 (Balátová-Tuláčková 1968), Štechová, 2003 (CBFS! Štechová & Kučera 2007). **57a. Bělohradsko** – Lázně Bělohrad: Pilous, 1955 (sub *Drepanocladus revolvens*, LIT!). **58g. Sudetské mezihoří, Broumovské stěny** – Řeřišný: Kučera, 2006 (CBFS!; Kučera 2006). **59. Orlické hory** – Bažiny: Jakšičová, 2004 (CBFS!; Jakšičová 2004), Štechová, 2005 (Štechová & Kučera 2007). **63. Českomoravské mezihoří** – Svitavy: Kalmus, 1889 (BRNM!, OP!, PR!) – Výprachtice, Halda: Tušla, 1957 (sub *Drepanocladus intermedius*, PL!). **66. Hornosázavská pahorkatina** – Chotěboř: Bayer, (PR!). **67. Českomoravská vrchovina** – Jindřichov: Roemer, (PR!), Slavonice, Šatlava: Podpěra, 1907 (sub *Drepanocladus exannulatus* PR!) – Dalečín: Podpěra, 1909 (PR!) – Jabloňov, Věžná: Šmarda, 1942 (sub Drepanocladus revolvens, BRNM!) – Nové Město na Moravě, Olešná, Velký Mitov: Šmarda, 1943 (sub *Drepanocladus revolvens*, BRNM!) – Telč – Borovná, ryb. Šilhan: Šmarda, 1944 (sub *Drepanocladus aduncus*, BRNM!) – Lidéřovice: Růžička, 1962 (MJ!; Růžička & Novotný 2006) – Střížovice – Vlčice: Růžička, 1962 (MJ!; Růžička & Novotný 2006) – Řečice: Růžička, 1962 (MJ!; Růžička & Novotný 2006) – Popice: Pospíšil, 1974 (BRNM!) – Ořechov: Pospíšil, 1974 (BRNM!) – Telč, Studnice: Doležal, 1976 (BRA!, MJ!; Růžička 1987) – Rašeliniště Loučky: Rybníček, (Rybníček 1974), Doležal, 1976 (sub *Drepanocladus exannulatus,* BRA!) – Skorkov – Muksín: Doležal, 1976 (BRA!, BRNM!, MJ!) – Zvolenovice: Růžička, 1976 (sub *Drepanocladus revolvens*, BRNM!, BRA!, MJ!) – Chvojnov: Doležal, 1976 (partim sub *Drepanocladus revolvens*, BRA!, MJ!; Růžička 1989), Kučera, 1996 (CBFS!; Soldán 1996), Kučera, 2002 (CBFS!; Štechová & Kučera 2007), Štechová, 2005 (Štechová & Štech 2009) – Nad Svitákem: Růžička, 1982 (MJ!; Růžička 1989), Kučera, 2002 (CBFS!), Štechová, 2006 (Štechová & Štech 2009) – Šimanovské rašeliniště: Růžička, 1982 (MJ!, OLM!), Kučera, 2002 (CBFS!; Štechová & Kučera 2007), Štechová, 2006 (CBFS!; Štechová & Štech 2009), Novotný, 2009 (BRNM!; Štechová et al. 2010b) – Na Oklice: Růžička, 1983 (MJ!, OP!; Růžička 1989), Plášek, 1992 (OP!), Kučera, 2002 (CBFS!), Štechová, 2004, 2005 (CBFS!; Štechová & Kučera 2007, Štechová & Štech 2009) – Jezdovické rašeliniště: Kučera, 2002 (CBFS!; Štechová & Kučera 2007), Štechová, 2005 (Štechová & Štech 2009) – Matenský rybník: 2002 Kučera, (CBFS!), Štechová, 2003 (CBFS!; Štechová & Kučera 2007), Navrátilová (Navrátilová & Navrátil 2005) – Na Klátově: Hofhanzlová & Ekrt, 2004 (CBFS!; Hofhanzlová et al. 2005), Štechová, 2005 (Štechová & Kučera 2007, Štechová & Štech 2009) – Branišov: Lysák, 2009 (CBFS!) – Ve Sklenářích: Lysák, 2010 (CBFS!). **69b. Sečská vrchovina** – Studnice: Kalenský, 1891 (MP!) – Hlinsko: Kalenský, 1891 (MP!) – Pláňavy: Kalenský, 1898 (MP!) – Ratajské rybníky: Zmrhalová, 1990 (OLM!), Buryová, 2003 (DUKE; Kučera et al. 2003), Štechová, 2005 (Štechová & Kučera 2007, Štechová & Štech 2009), Gutzerová, 2009 (Štechová et al. 2010b) – Nový rybník u Rohozné: Buryová, 2003 (DUKE), Štechová, 2005 (Štechová & Kučera 2007, Štechová & Štech 2009), Marková & Mikulášková, 2009 (priv. herb. Marková, priv. herb. Mikulášková; Marková et al. 2009) – Strádovka: Buryová, 2003 (DUKE), Štechová, 2005 (Štechová & Kučera 2007, Štechová & Štech 2009). **72. Zábřežsko-uničovský úval** – Šumperk, Angerwiesen: Paul, 1901 (PR!), 1904 (BRNM!; Hruby 1914). **73b. Hanušovická vrchovina** – Třemešek – Jestřábí potok: Schenk 1908

(OLM!, PR!; Podpěra 1908) – Bohutín: Balátová, 1966 (BRNM!). **74b. Opavská pahorkatina** – Hlučín – Zábřeh: Duda, 1951 (sub *Drepanocladus intermedius* OP!; Duda 1994) Šmarda, 1951 (sub *Drepanocladus revolvens*, BRNM!; Šmarda 1953), Pospíšil, 1955 (OLM!, sub *Drepanocladus aduncus*, BRNM!), Pospíšil, 1964 (sub *Drepanocladus uncinatus*, BRNM!) – Úvalno Duda, 1951 (PR!, sub *Drepanocladus revolvens*, PL). **75. Jesenické podhůří** – Mladoňov: Schenk, 1908 (sub *Drepanocladus cossonii*, PR!) – Jakubčovice: Duda, 1951 (OP!) – Březová: Duda, 1957 (PR!) – Ranošov: Duda, 1963 (OLM!, OP!) – Skalské rašeliniště: Hradílek, 2003 (BRNM!; Hradílek et al. 2010), Štechová, 2005 (Štechová & Kučera 2007), Hradílek, 2009 (Štechová et al. 2010b). **87. Brdy** – Obecnice – Třemošná: anonymous 1861 (PR!). **88.a Královský hvozd** – Železná Ruda: Velenovský, 1894 (PRC!; Velenovský 1987). **88.b Šumavské pláně** Zhůřská pláň: Holá, 2004 (CBFS!; Holá & Jakšičová 2004), Štechová, 2005 (Štechová & Kučera 2007, Štechová et al. 2007), Štechová, 2008 (Štechová et al. 2010) – Zhůří u Křemelné: Holá, 2005 (Holá 2006), Štechová, 2005 (Štechová et al. 2007), Štechová, 2008 (Štechová et al. 2010) – Kvilda: Mikulášková, 2006 (priv. herb. Mikulášková!; Mikulášková 2007), Štechová, 2007 (Štechová et al. 2007), Štechová, 2008 (Štechová et al. 2010) – Zhůří u Horské Kvildy: Mikulášková, 2006 (priv. herb. Mikálášková!; Mikulášková 2007), Štechová, 2007 (Štechová et al. 2007), Štechová, 2008 (Štechová et al. 2010) – Prášily, Slunečná: Holá, 2007 (CBFS!), Štechová, 2008 (Štechová et al. 2010) – Velký Bor: Holá, 2007 (CBFS!), Štechová, 2008 (Štechová et al. 2010) – Jezerní potok: Mikulášková, 2008 (priv. herb. Mikulášková), Štechová, 2008 (Štechová et al. 2010) – Chalupská slať: Mikulášková, 2008 (priv. herb. Mikulášková), Štechová, 2008 (Štechová et al. 2010). **90. Jihlavské vrchy** – Doupě – Řídelov (NR Bažantka): Šmarda, 1944 (sub *Drepanocladus revolvens,* BRNM!), Rybníček (Rybníček 1974) – Horní Dubenky: Šmarda, 1959 (sub *Drepanocladus exannulatus*, BRNM!) – Řásná, ryb. Smrkovský: Doležal, 1976 (BRA!, BRNM!, MJ!; Růžička 1987) – Rašeliniště u Suchdola: Rybníček (Rybníček 1974), Kučera, 2005 (CBFS!; Štechová 2005); Štechová, 2006 (Štechová & Kučera 2007, Štechová & Štech 2009), Štechová, 2009 (Štechová et al. 2010b) – Rašeliniště Kaliště: Lorber, 1978 (MJ!), Kučera, 2002 (CBFS!), Štechová, 2006 (Štechová & Štech 2009) – V Lisovech: Růžička 1982 (MJ!; Růžička & Novotný 2006), Růžička & Čech, 2001 (sub *Drepanocladus revolvens* MJ!; Řepka et al. 2001), Kučera, 2002 (CBFS!), Štechová, 2003 (Štechová & Kučera 2007), Brom, 2005 (BRNM!), Štechová, 2005 (Štechová & Štech 2009). **91 Žďárské vrchy** – Žďár n. Sázavou, Ryznanka: Šmarda, 1942 (sub *Drepanocladus uncinatus,* BRNM!) – Nové Město na Moravě, Zubří: Šmarda, 1942 (sub *Drepanocladus revolvens,* BRNM!) – Řeka: Šmarda, 1943 (sub *Drepanocladus revolvens,* BRNM!), Kučera, Buryová & Marková, 2003 (CBFS!, DUKE, priv. herb. Marková; Kučera et al. 2003), Štechová, 2005 (CBFS!; Štechová & Kučera 2007, Štechová & Štech 2009) – Nové Město na Moravě, Rokytno: Šmarda, 1943 (sub *Drepanocladus revolvens,* BRNM!) – Nové Město na Moravě, Ochozy: Šmarda, 1948 (sub *Drepanocladus revolvens,* PR!) – Cikháj: Růžička, 1967 (MJ!; Růžička & Novotný 2006) – Velké Dářko: Stuchlý, 1961 (PRC!), Novotný, 1985 (BRNM!) – Louky u Černého lesa: Novotný, 1986 (BRNM!; Novotný & Kubešová 2003), Štechová, 2005 (Štechová & Kučera 2007, Štechová & Štech), Kubešová & Novotný, 2009 (Štechová et al. 2010b) – Zlámanec: Kučera, 2003 (CBFS!; Kučera et al. 2003), Štechová, 2005 (Štechová & Štech 2009) – Louky v Jeníkově: Štechová, 2006 (CBFS!;

Štechová & Štech 2009) – Borová u Poličky: Peterka & Hájek, 2008 (priv. herb. Peterka) – Šafranice: Lysák, 2009 (CBFS!) – Odranec: Lysák, 2009 (CBFS! Štechová et al. 2010b) – Panská: Lysák, 2009 (CBFS!) – Roženecké Paseky: Lysák & Štech, (CBFS!) – Voláků̊v kopec: Peterka, 2011 (CBFS!). **97. Hrubý Jeseník** – Rejvíz: Matouschek (Matouschek 1904), Podpěra, 1904 (PR!), Šmarda, 1947 (sub *Drepanocladus revolvens* OP!, BRNM!), Pilous, 1954 (PR!) – Na Skřítku: Schenk, 1911 (PR!), 1917 (BRNM!; Podpěra 1913, 1921), Šmarda (Šmarda 1952), Váňa, 1962 (priv. herb. Váňa) – Velká kotlina: Matouschek (Matouschek 1901), Laus (Laus 1910), Schenk, 1932 (SLO!) – Pstruží potok: Hájková & Hájek, 2009 (priv. herb. Hájková; Hájková 2009). **99a. Radhošťské Beskydy** – Staré Hamry: Beňa, 1902 (PR!) – Visalaje: Podpěra, 1941 (sub *Drepanocladus exannulatus*, PR!).

Literature reports unsupported by specimens:

12. Dolní Pojizeří – Košátky (Sitenský 1886). **28e. Žlutická pahorkatina** – Manětín (Bauer 1893). **36a. Blatensko** – Čekanice (Velenovský 1897). **37i. Chvalšinské předšumaví** – Lhenice, Koubovský rybník (Albrecht 1983). **52. Ralsko-Bezdězská tabule** – Kuřivody (Sitenský 1886). – Lázně Kundratice (Watzel 1874). **53a. Českolipská kotlina** – Okřešice (Schiffner & Schmidt 1886). **53b. Ploučnické Podještědí** – Stráž p. Ralskem, Dubnice (Schiffner & Schmidt 1886). **64b. Jevanská plošina** – Struhařov (Dědeček 1881). **67. Českomoravská vrchovina** – Stráž n. Nežárkou (Weidmann 1895). – Kunžak, Mosty (Rybníček 1974). **74a. Vidnavsko-osoblažská pahorkatina** – Vidnava (Vicherek 1958, Duda & Pilous 1959). **88b Šumavské pláně** – Stará Hůrka (Weidmann 1895). **90. Jihlavské vrchy** – Horní Pole (Rybníček 1974). **97. Hrubý Jeseník** – Prameny Hučivé Desné (Hruby 1914).

Erroneous records:

15b. Hradecké Polabí – Opočno, Broumarské slatiny *Štechová* 2008 (CBFS!; Štechová & Štech 2008) = *Scorpidium cossonii*. **69b. Sečská vrchovina** – Dědová, Bahna: *Lysák & Gutzerová* 2007 (priv. herb. Gutzerová!; Gutzerová 2009) = *Hypnum pratense*. **85. Krušné hory** – Boží Dar, Pod Špičákem: Váňa 1965 (priv. herb. Váňa!; Váňa 1967) = *Scorpidium cossonii.*

Potential localities of* H. vernicosus *visited with negative results:

6. Džbán Na Novém rybníce, V Bahnách. **11a. Všetatské Polabí** Hrabanovská černava. **12. Dolní Pojizeří** Polabská černava. **13a. Rožďalovická tabule** Louky u rybníka Proudnice, Žehuňský rybník. **15b. Hradecké Polabí** Zbytka. **22. Halštrovská vrchovina** Lužní potok, Ztracený rybník. **26. Český les** Mechové údolí, Milov, Prameniště Kateřinského potoka. **28d. Toužimská vrchovina** Rašeliniště u Polínek. **30b. Rakovnická kotlina** Červená louka. **31a. Plzeňská pahorkatina vlastní** Bejkovna, Dlouhá louka, Louka u Šnajberského rybníka, Luňáky. **35d. Březnické Podbrdsko** Malý Kosatín. **36a. Blatensko** Kovašínské louky, Zaboří. **36b. Horažďovicko** Mečichov. **37e. Volyňské Předšumaví** Chalupy u Stach, Nad Zavírkou. **37g. Libínské Předšumaví** Pod Sviňovicemi. **37h. Prachatické předšumaví** Kralovické louky. **37p. Novohradské podhůří** Klenský rybník, Zámek. **39. Třeboňská pánev** Člunek, Dvořiště, Hliníř, Horusická blata, Krvavý a Kačležský rybník, Lhota u Dynína, Rašeliniště Hovízna, Ruda u Kojákovic, Žemlička. **41. Střední Povltaví** Jezero u Dědovic. **42a. Sedlčansko-milevská pahorkatina** Dehetník. **42b. Táborsko-vlašimská pahorkatina** Jesení. **51. Polomené hory** Ráj. **52. Ralsko-bezdězská tabule** Baronský rybník, Hradčanské rybníky, Shnilé louky, Swamp**. 61c. Chvojenská plošina** Pětinoha. **67. Českomoravská vrchovina** Blanko, Horní Lesák, Hrádeček, Hrachoviště, Hruškovec, Luží u Lovětína, Opatovské zákopy, Rybník Hraničník u N. Bystřice, Rybník Šalamoun u N. Bystřice, U Milíčovska, U potoků, Urbánkův palouk, Vílanecké rašeliniště. **69b. Sečská vrchovina** Bahna, Buchtovka, Rašeliniště u Filipova, Zubří. **84b. Jablunkovské mezihoří** Vřesová stráň. **88b. Šumavské pláně** Kvilda (springs 1 km S of Kvilda), Pasecká slať, Ždárek. **88d. Boubínsko-stožecká hornatina** Pravětínská lada. **88g. Hornovltavská kotlina** Kotlina pod Pláničským rybníkem, Račínská prameniště. **89. Novohradské hory** Prameniště Pohořského potoka. **90. Jihlavské vrchy** Bor, Zhejral. **91. Žďárské vrchy** Javorek, Olšina u Skleného, Pernovka, Pod Kamenným vrchem, Sklenské louky, Staviště, U Bezděkova, U Tučkovy hájenky. **95a. Český hřeben** Hraniční louka, Kačenčina zahrádka, Pod Zakletým, Rašeliniště pod Předním vrchem, Velká louka.

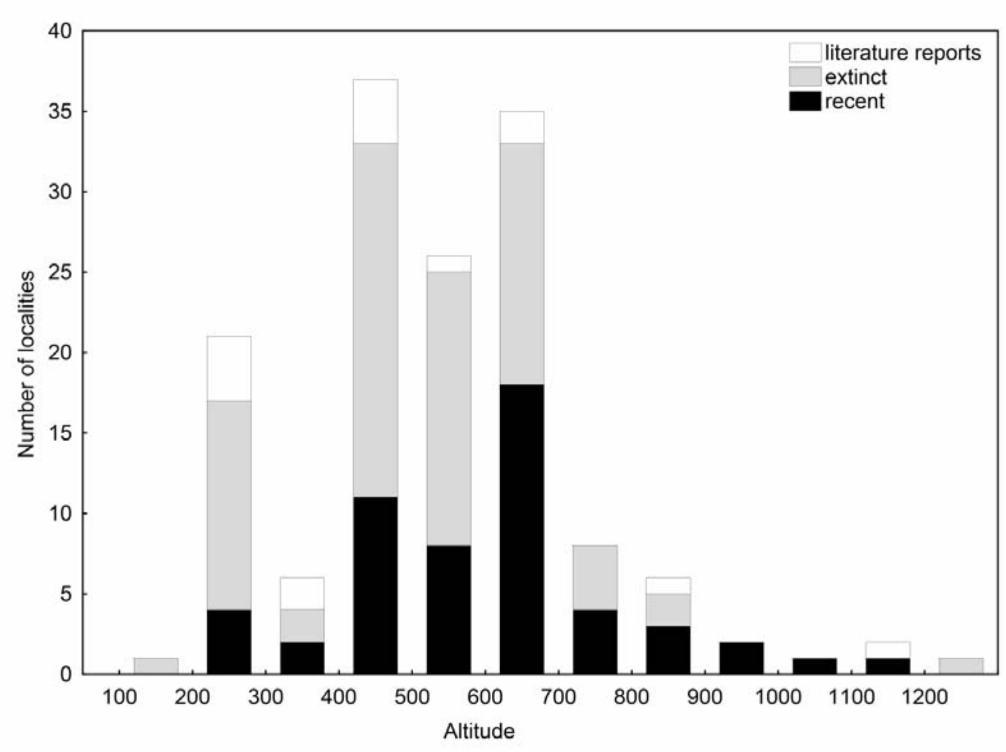

Fig. 2 Altitude of historical and recent localities.

Table 1. Brief description of recent localities

Locality	Localization	GPS coordinate [WGS 84]	Altitude [m a.s.l.]	Population size [m2]	Endangered	Reasons of threat
Bažiny	spring 800 m NW Rovenské Šediviny	50.296389°N, 16.299722°E	620	0.1	no	
Borová u Poličky	fen meadow 200 m W Borová	49.742889°N, 16.152944°E	630	0.03	yes	too intensive mowing and low water table
Branišov	fen meadow 850 m NNE Branišov	49.473639°N, 15.438667°E	640	0.5	yes	eutrophication
Brouskův mlýn	fen meadow 1.1 km NNE Třebeč	48.883222°N, 14.682417°E	450	2	yes	low water table
Břehyně - Pecopala	fen 1.4 km NE and 2 km ENE gamekeeper´s lodge Břehyně	50.584539°N, 14.706881°E 50.581017°N, 14.718989°E	270	2	yes	expansion of *Phragmites australis* and water table fluctuation
Červený rybník u Pihele	peat pond margin 500 NE Pihel	50.735278°N, 14.552897°E	290	20	yes	successional changes as a result of lack of management
Dolejší rybník	fen 800 m SE Tchořovice	49.432919°N, 13.821322°E	450	3	yes	eutrophication, water table fluctuation and by expansion of *Typha latifolia*
Hrádecká bahna	fen meadow E Hrádek	49.713233°N, 13.658972°E	400	0.3	yes	low water table and expansion of *Phragmites australis*
Hůrky	spring 1.5 km N Hůrky	49.8979°N, 13.182372°E	550	0.03	yes	woodland expansion
Chalupská slať	fen 800 m NE Svinná Lada	49.001951°N, 13.660761°E	960	0.2	yes	woodland expansion
Chvojnov	fen 1 km WSW Dušejov	49.407222°N, 15.419167°E	605	8	yes	expansion of *Phragmites australis*
Jezdovické rašeliniště	fen 1.5 km W Jezdovice	49.323611°N, 15.461667°E	675	20 stems	yes	shade of surrounding trees
Jezerní potok u C. Hůrky	spring 1 km SW Cetlova Hůrka	49.133519°N, 13.357932°E	860	0.1	yes	woodland expansion
Křišťanovický rybník	fen meadow 500 m N Křišťanovice	48.969361°N, 13.951107°E	795	0.01	yes	successional changes as a result of lack of management
Kvilda	spring 1.3 km SW Kvilda	49.008631°N, 13.565169 °E	1060	0.06	no	
Louky u Černého lesa	fen 700 m N Zelená hora	49.586108°N, 15.942917°E	570	1	no	
Louky v Jeníkově	fen meadow 600 m SE Jeníkov	49.738542°N, 15.964531°E	630	1	yes	eutrophication
Matenský rybník	fen meadow 1.1 km NW Matná	49.151139°N; 14.931031°E	520	0.02	yes	low water table
Na Klátově	spring 700 m SE Myslůvka	49.137708°N, 15.452425°E	485	2	yes	eutrophication
Na Oklice	fen 1 km N Milíčov	49.404217°N, 15.394517°E	660	7	yes	expansion of *Phragmites australis*

Locality	Localization	GPS coordinate [WGS 84]	Altitude [m a.s.l.]	Population size [m2]	Endangered	Reasons of threat
Nad Svitákem	fen 700 m E Milíčov	49.396667°N, 15.404722°E	630	0.02	yes	woodland expansion
Novozámecký rybník	fen meadow N Jestřebí	50.6125°N, 14.5853°E	255	0.1	yes	woodland expansion
Nový rybník u Rohozné	peat pond margin 500 m ESE Rohozná	49.803683°N, 15.81985°E	555	8	yes	water table fluctuation and woodland expansion
Odměny u rybníka Svět	fen 1 km NE Spolský mlýn	48.992033°N, 14.725981°E	435	0.02	yes	woodland expansion
Odranec	spring 600 m SSE Odranec	49.608572°N, 16.141557°	740	1	no	
Panská	spring 700 m SE Roženecké Paseky	49.601944°N, 16.168822°E	720	1	yes	eutrophication and woodland expansion
Podtrosecká údolí	fen 900 m ENE Bohuslav	50.524328°N, 15.217447°E	280	25	yes	expansion of *Phragmites australis*
Prameny Klíčavy	spring 400 m EW railway station Řevničov	50.145861°N, 13.828825°E	430	3	no	
Pstruží potok	fen 1.5 km SW Stará Ves	49.950278°N, 17.220556°E	675	3	no	
Rašeliniště Kaliště	fen SE railway station Jihlávka	49.250346°N, 15.296565°E	655	20 stems	yes	low water table and expansion of *Phragmites australis*
Rašeliniště u Suchdola	fen NW Suchdol	49.132028°N, 15.238453°E	625	2	yes	eutrophication
Ratajské rybníky	peat pond margin 700 m NE Hlinsko and spring 650 m NE Hlinsko	49.769364°N, 15.933906°E 49.768303°N, 15.932761°E	585	2	yes	water table fluctuation
Roženecké Paseky	spring NW Roženecké Paseky	49.606917°N, 16.165083°E	650	0.05	yes	woodland expansion
Ruda	fen 300 m W and 550 m SSW station Ruda	49.151589°N, 14.689161°E 49.145317°N, 14.690775°E	415	1.5	yes	woodland expansion
Řeka	spring 500 m NNW Hluboká	49.666597°N, 15.852992°E	555	30	no	
Řeřišný	fen meadow 800 m NE Machov	50.504363°N, 16.29206°E	480	0.1	no	
Řežabinec	fen meadow 1 km SSE Lhota u Kestřan	49.251214°N; 14.083072°E	370	0.3	yes	expansion of *Calamagrostis canescens*
Skalské rašeliniště	fen 850 m N Horní Město	49.918194°N, 17.211386°E	685	4	yes	expansion of *Phragmites australis*
Slunečná u Prášil	spring 1.5 km ESE Prášily	49.100207°N, 13.399124°E	885	50 stems	yes	woodland expansion
Smyslov	fen meadow 1.5 km NE Pole	49.419489°N, 13.802408°E	460	2	yes	eutrophication and low water table

Locality	Localization	GPS coordinate [WGS 84]	Altitude [m a.s.l.]	Population size [m2]	Endangered	Reasons of threat
Staré jezero	fen 300 m W U Kanclíře	48.979306°N, 14.897444°E	440	6	yes	woodland expansion
Strádovka	eat pond margin 700 m NW Rohozná	49.809397°N, 15.803394°E	580	0.04	yes	low water table and successional changes as a result of lack of management
Šafranice	fen 1.1 km SE Veselíčk	49.548°N, 16.013558°E	615	0.05	yes	expansion of *Phragmites australis*
Šimanovské rašeliniště	fen 500 m S Šimanov	49.450397°N, 15.446708°E	605	1.5	yes	expansion of *Calamagrostis epigejos*
V Lisovech	fen 1.2 km NW railway station Jihlávka	49.24705°N, 15.278983°E	650	6	yes	expansion of *Phragmites australis* and *Typha latifolia*
V Rájích	spring 400 m SW Spolský mlýn	48.986375°N, 14.708678°E	440	0.03	yes	expansion of *Phragmites australis*
Ve Sklenářích	spring 1.5 km NW Nový Rychnov	49.391751°N, 15.34933°E	650	0.05	yes	successional changes as a result of lack of management
Velká Kuš	fen 1 km ENE Lnářský Málkov	49.3943°N, 13.794869°E	480	0.1	yes	eutrophication and expansion of *Typha latifolia*
Velký Bor u Prášil	spring 1.1 km SE former Velký Bor	49.096584°N, 13.43773°E	860	0.1	no	
Zhůří u Horské Kvildy	spring 500m W Zhůří	49.082111°N, 13.554589°E	1125	1	yes	woodland expansion
Zhůří u Křemelné	two springs 600 and 800 m S chapel in former Zhůří	49.172391°N, 13.331285°E 49.170361°N, 13.332856°E	900	20	no	
Zhůřská pláň	fen meadow 700 m NNW Hadí vrch	49.192669°N, 13.334139°E	1000	0.04	yes	successional changes as a result of lack of management
Zlámanec	fen meadow 700 m SSW Vortová	49.705311°N, 15.932294°E	620	1.5	no	

Discussion

Hamatocaulis vernicosus was widely scattered in the Czech Republic in the past, restricted to fen habitats, which predominantly occurred in the lower and middle altitudes of the South and North Bohemian basins (Třeboňská and Českobudějovická pánev, Českolipská kotlina), Českomoravská vrchovina highland, and in the foothills of Hrubý and Nízký Jeseník Mts. In these areas, the substrate and hydrological and geomorphological conditions are best suited to the occurrence of rich fens. This overall distribution pattern has changed somewhat in more recent times. With respect to altitudinal range (Fig. 2), we were able document the retreat of the species from lower altitudes between 200 – 300 m a.s.l., while the centre of distribution remained at moderate altitudes, despite the dramatic decline of *H. vernicosus* in absolute numbers from localities in the Českomoravská vrchovina highland. The altitudinal distribution seemingly extended into higher altitudes to judge from recent, previously unrecorded, finds of several upland occurrences in the Bohemian Forest (Štechová et al. 2010). The shift in the altitudinal distribution can however hardly be attributed to the shift in competition rates as a result of climate warming but rather, unequal human impact occurred at lower and higher altitudes in the Central European landscape. Although the date and causes of the loss of *H. vernicosus* sites are diverse and often unclear, they commonly follow a similar scenario in individual regions. In most regions, drainage and conversion to agricultural land have been the primary causes of the destruction of localities. At first this affected the most fertile and warmer regions (the basin of the Labe River, southern Moravia); here the process was already documented in the course of the 19th century, and the highest percentage of decline in localities is evident in these regions, (Fig. 2). In other regions, the process continued rather slowly in the first half of the 20th century, while the major destructive changes occurred as recently as in the 1980s, as documented for many localities in the Českomoravská vrchovina highland by Růžička (1987, 1989). At many localities, the extinction of *H. vernicosus* was not directly caused by conversion to agricultural land. Rather the sites experienced slower succession changes following the cessation of the mowing, which promoted the secondary succession towards tall forb and shrubland communities (Štechová & Kučera 2007). Different competition rates might sometimes have been connected to the increased nutrient content in water sources, which was particularly the case along ponds with intensive fish production, for instance in the Třeboň basin (Štechová et al. 2012).

Another interesting reason for the decline of some populations is the slow acidification of peatland biotopes in the higher mountains. This seems to have occurred in the Hrubý Jeseník Mts., at the localities Na Skřítku and Rejvíz, which are still considered to be valuable mires. However, the conditions are nowadays more acid than at most other localities, and this acidification is thought to have occurred over the last fifty years (Zmrhalová 2001). The occurrence of *H. vernicosus* is still a possibility in the Velká Kotlina, where e.g. *Pseudocalliergon trifarium* still occurs, although the species was not found during a recent intensive bryological survey of this locality (Kučera et al. 2009).

Since 2001, we have not recorded a single loss in the occurrence of *H. vernicosus*. However, a number of sites in which the species occurs have been seriously degraded by several adverse factors, which are reflected in a reduction in population size. Nevertheless, the overall occurrence of *H. vernicosus* in the Czech Republic is not immediately endangered if current conditions at its localities, including active conservation management, remain unchanged.

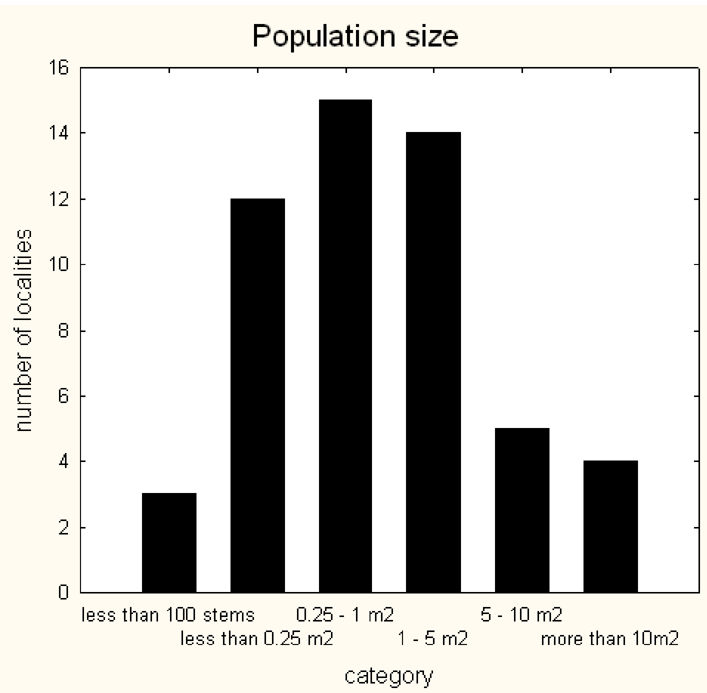

Fig. 3 Number of localities according to population size categories.

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Shrnutí

Hamatocaulis vernicosus je pleurokarpní mech rostoucí v rašelinných a slatinných biotopech. V posledním desetiletí je mu věnována zvýšená pozornost, protože byl zařazen mezi evropsky významné druhy. Byla provedena kompletní revize herbářových položek a literárních zdrojů, historické lokality byly posléze ověřovány. Bylo navštíveno i dalších cca 100 rašelinišť s vegetačním složením podobným lokalitám, na nichž studovaný druh roste, a na řadě z nich se podařilo jeho výskyt potvrdit.

Celkově bylo nalezeno 129 lokalit doložených herbářovou položkou. Dalších 14 lokalit bylo zjištěno pouze na základě literárních zdrojů. 54 lokalit se podařilo recentně (v r. 2010 a 2011) ověřit. Druh je široce rozšířen téměř po celé ČR, centrem jeho výskytu je Českomoravská vrchovina, Třeboňsko a Šumava. Velikost populací se pohybuje od několika lodyžek do desítek čtverečních metrů. *H. vernicosus* není v ČR bezprostředně ohrožen, největším nebezpečím pro jeho výskyt jsou pomalé sukcesní změny, které na lokalitách probíhají v důsledku dřívějších zásahů do vodního režimu, změn chemismu nebo absence vhodného managementu.

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Conclusions

Hamatocaulis vernicosus grows in the mineral-rich habitats, it has the highest cover at neutral pH (6.7 – 7.2) and conductivity between100 and 250 µS/cm, although most localities had lower values. The vegetation composition at *H. vernicosus* sites is variable according to pH and water table gradient. No noticeable difference between localities in different regions was found within the Czech Republic. However, the optimal conditions of the species are shifted towards more acid conditions (pH about 6) at localities in the southern Europe. No correlation was found between *H. vernicosus* population prosperity and the nutrient concentration; however, the populations are more extensive in iron richer conditions.

The main factor affecting *H. vernicosus* populations is the density of vascular plant cover – the species thrived best in habitats with sparse herbs and abundant "brown mosses". Therefore, at localities with the high vascular plants cover, regular mowing is necessary. The species prefers habitats with the stable high water table. At sites with lower water table, its growth and vitality can be supported by shallow gap cutting.

In the Czech Republic, the species has been recorded at 54 localities, while its occurrence was not verified at 89 historical localities. Population size at recent localities ranges from a few stems to tens of square metres; most of the populations are considered to be adversely affected by various negative factors. Nevertheless, the overall occurrence of *H. vernicosus* in the Czech Republic is not immediately endangered if current conditions at its localities, including the active conservation management, remain unchanged.

Perspectives

A number of questions remains open even after the completion of the above presented papers. First of all, it is necessary to address the questions related to the existence of differentiated phylogenetic lineages within *Hamatocaulis vernicosus*, which were suggested to represent cryptic species by Hedenäs & Eldenäs (2007). Before looking for the differences in ecological preferences of the two cryptic taxa, it might be worth to examine in detail the microspeciation processes within *H. vernicosus* s.l. (and other closely related taxa) in the global perspective, which would help to assess the biological status of the discovered lineages.

Further questions are from a major part connected with the practical protection of a species at the locality. One such aspect is the vegetative reproduction and regeneration from stem fragments and the survival rate of young regenerating plants in various conditions. This topic is being studied in the framework of another dissertation at the Department of Botany. Detailed knowledge of these issues could substantially help in planning the active conservation measures at localities with small and unstable population of the target species. It particularly applies to the chances of the species to expand into other parts of the locality, estimating the consequences of the direct impact of the mowing technique to the species, or the use of the direct disturbation of the turf for spreading to the neighbouring micro-localities. Another aspect of conservation importance is the competition study between the target species and other bryophytes in various chemical and moisture conditions. The knowledge would facilitate the realization of specific treatments (excavating the gaps, removal of competitive species) at individual localities, where *H. vernicosus* is threatened.

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