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The requirements of the rare moss, *Hamatocaulis vernicosus* (Calliergonaceae, Musci), in the Czech Republic in relation to vegetation, water chemistry and management

Táňa Štechová*, Jan Kučera

Department of Botany, Faculty of Biological Sciences, University of South Bohemia, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic

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ABSTRACT

Hamatocaulis vernicosus, a rare moss, has been investigated in detail for its habitat preferences, ecology and population dynamics in the Czech Republic. At all its known sites plant species composition was described and relationships with environmental factors investigated (water table, pH, water conductivity). Experiments that included mowing and gap cutting were investigated at three sites over two years.

Hamatocaulis vernicosus had the highest cover at neutral pH (6.7–7.2) and conductivity between 100 and 250 $\mu\text{S}/\text{cm}$, although most localities had lower values. It was influenced positively by mowing only at a site with a high vascular plants cover, and gap cutting was only beneficial at sites with a low water table. The growth and vitality of *Hamatocaulis* may, therefore, be supported by suitable management especially in drier habitats.

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1. Introduction

The aim of this study was to investigate the autecology of one threatened bryophyte species. The species chosen was *Hamatocaulis vernicosus* (bryophyte nomenclature follows Kučera and Váňa (2003), that for vascular plants follow Kubát et al. (2002)), 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). In Scandinavia it is locally abundant (Söderström, 1996) but in Central Europe it is a rare species, classified in most countries as threatened (e.g., Ludwig et al., 1996; Kučera and Váňa, 2003). Because of this rarity, it has been listed in Appendix I of the Bern Convention as requiring special attention (Raeymaekers, 1990).

One of the main reasons for 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). There is limited information on the chemistry of its habitat (Janssens, 1983; Hedenäs and Kooijman, 1996; Hedenäs et al., 2003; Heras and Infante, 2000). However, it has been suggested that the genus prefers iron-rich habitats (Hedenäs and Kooijman, 1996).

The moss very rarely produces sporophytes (Smith, 1978; Hedenäs et al., 2003; Hugonnot, 2003). Clearly, spore production will be necessary for effective long-distance dispersal (Sundberg and Rydin, 2002; Sundberg, 2005), and it may be that it was more common in the past under other climatic conditions (Gunnarsson et al., 2005). Nowadays, *Hamatocaulis* is

* Corresponding author: Tel.: +420 387772303; fax: +420 387772345.

E-mail addresses: tana.stechova@bf.jcu.cz (T. Štechová), kucera@bf.jcu.cz (J. Kučera).

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almost certainly spread by gametophytic fragments, like many other peatland mosses (Poschlod and Schrag, 1990). Fragment dispersal is usually effective over short distances, unless the fragments are spread by birds or large mammals.

Wetland species such as *Hamatocaulis vernicosus* are endangered mainly because of the destruction and degradation of their habitats (Rybníček and Rybníčková, 1974). The cessation of traditional management such as extensive grazing, single-cut, late-season haymaking, and removal of mown material for bedding led to the increasing productivity and decrease of species richness (Fojt and Harding, 1995; Prach, 1996; Diemer et al., 2001). To conserve species richness, a substitution for the traditional management is necessary, and recently a range of suitable alternative management techniques have been tested in these habitats. However, the impact of these treatments on bryophytes is limited. Where it has been investigated (Moen et al., 2001), the mowing of vegetation resulted in a replacement of hummock-building species with prostrate moss species. However, Bergamini and Peintinger (2002) did not find an effect of removal of vascular plants on biomass and shoot morphology of *Calliergonella cuspidata*.

Here, we describe the observed habitat preferences of *Hamatocaulis* in the Czech Republic with respect to the water chemistry (pH, conductivity, NH_4^+ , NO_3^- , Ca^{2+} and Fe^{3+}) and its phytosociological relationships. We also performed

manipulative experiments, testing the short-term impact of mowing and measured its expansion ability into gaps created in the vegetation. There are few studies on bryophyte autecology, and we hope that this preliminary study will provide an impetus for further work in this area.

2. Material and methods

2.1. Vegetation and environmental sampling

All 28 sites where *Hamatocaulis vernicosus* was known to occur in the Czech Republic were sampled in May and June 2005 (Table 1). At each site, vegetation relevés were assessed and measurements made of the water table and a range of basic water chemistry variables (pH, conductivity). One to four relevés were recorded at each site depending on the population size of *Hamatocaulis*; at each relevé the vegetation was assessed by estimating visually the cover of all species in 4×4 m plots (58 in total).

Water pH and conductivity were measured *in situ* at four positions in each plot using portable devices (Vario pH, WTW, Germany; CM 101, Snail Instruments, Czech Republic). The water table was measured using the PVC discoloration method over the whole vegetation season (Belyea, 1999; Navrátilová and Hájek, 2005).

Table 1 – Brief description of studied sites

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

The average annual temperatures and annual precipitation are cited according to Syrový (1958).

Seven sites were chosen as representative of the major phytogeographical regions in which *Hamatocaulis* occurred in the country for a more detailed study of water chemistry (NH_4^+ , NO_3^- , Ca^{2+} , Fe^{3+}). Below-ground water samples were collected in October 2003, and June, September and October 2004. These samples were filtered and frozen within 24 h 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).

2.2. Manipulative experiments

Three sites (1–3, Table 1) with extensive *Hamatocaulis* populations were selected for manipulative experiments. Response to mowing was tested in permanent 50 × 50 cm plots ($n = 17$ at site 2; $n = 18$ at sites 1, 3), chosen to include the largest part of the population of *Hamatocaulis vernicosus* at each locality. A sketch of species distribution at each plot was drawn at a mm scale. Half of the plots were mown with a grass-hook and the biomass removed; the rest of the plots were unmown. Mowing was performed twice, in late June 2003 and late June 2004. The sketches from all plots were made again in autumn 2004 and 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 also observed in 2003 and 2004 in fourteen 15 × 15 cm gaps, 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 in both

years. At the last visit cover of *Hamatocaulis* in each gap was measured.

2.3. Data analysis

Canonical correspondence analysis (CCA) was used to evaluate the relationship between the phytosociological data and the environmental data (pH, conductivity, average water table level and its fluctuation expressed as the range between minimum and maximum values). Significance was assessed using a Monte-Carlo test with 499 permutations (Lepš and Šmilauer, 2003).

The interaction of mowing with time on populations of observed species was tested using ANOVA with repeated measurements. The relationship between water level and *Hamatocaulis* cover in gaps was investigated using multiple linear regression. ANOVA and the regression were computed using Statistica for Windows version 7.1 (StatSoft Inc, 2005).

3. Results

3.1. Vegetation, water table and chemistry at the localities

In the relevés 177 species (51 bryophytes, 126 vascular plants) were found, the most commonly associated species being listed in Table 2. The variation of vegetation composition was influenced significantly ($p = 0.002$, $F = 4.1$) by the environmental variables (Fig. 1). The first canonical axis explains 28% of the variation and is closely associated with a water chemistry gradient (pH, conductivity), whereas axis two explains 12% of the variation and appears closely associated with

Table 2 – The commonest moss and vascular plant taxa associated with *Hamatocaulis vernicosus* based on the frequency of occurrence in the vegetation samples

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

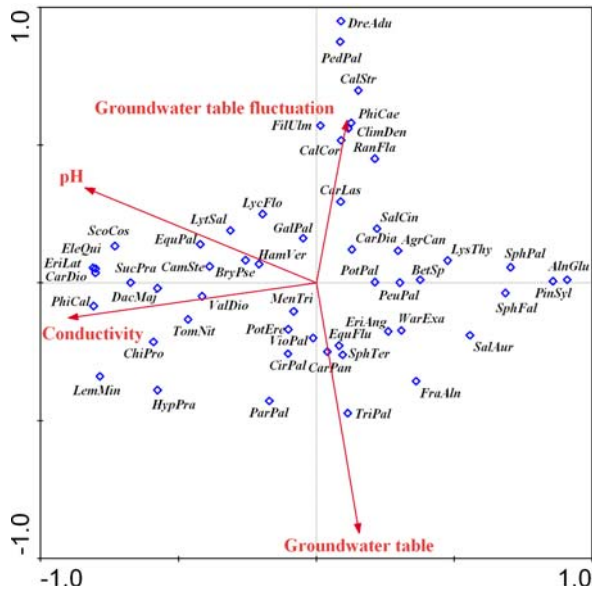


Fig. 1 – Species–environment biplot from CCA summarizing the relationship between species and the measured environmental characteristics – pH, conductivity, mean water table depth and fluctuation. Mosses: CalCor – *Calliergon cordifolium*, CamSte – *Campyllum stellatum*, ChiPro – *Chiloscyphus profundus*, 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*.

water table and its fluctuations. At the more base-rich localities (pH = ca. 7; conductivity = 100–250 $\mu\text{S}/\text{cm}$), the commonly associated mosses were *Tomentypnum nitens*, *Campyllum stellatum*, *Philonotis calcarea* and *Scorpidium cossonii*, and vascular plants included *Valeriana dioica*, *Carex dioica*, *Eriophorum latifolium* and *Eleocharis quinqueflora*. In more acid habitats (pH = 5.8–6.6, conductivity < 100 $\mu\text{S}/\text{cm}$), these were replaced by *Sphagnum fallax*, *Sphagnum subsecundum*, *Sphagnum palustre*, *Warnstorfia exannulata*, *Eriophorum angustifolium*, *Agrostis canina*, *Potentilla palustris* and seedlings of trees and shrubs,

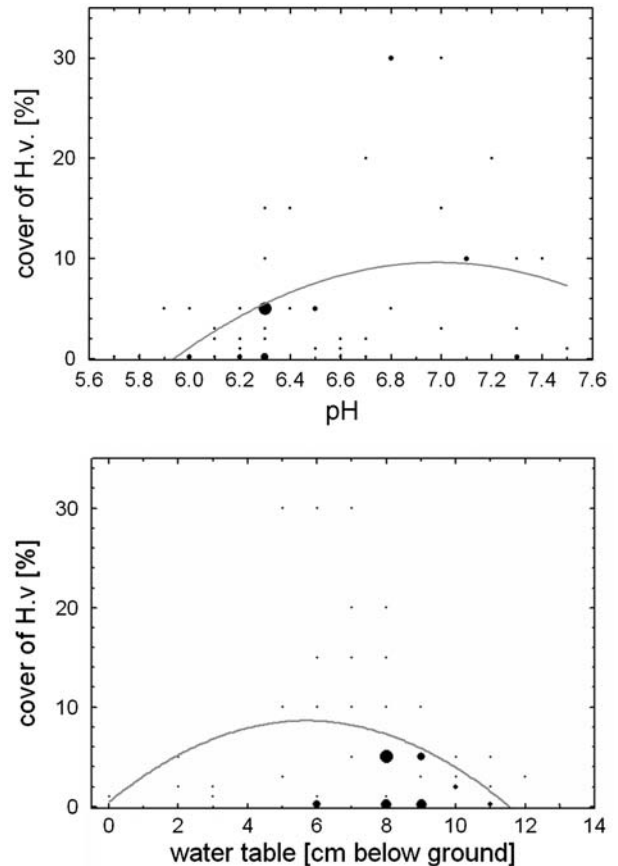


Fig. 2 – Relationship between *Hamatocaulis vernicosus* cover, pH and water table. The size of dots relates to the number of vegetation samples (range 1–5 samples).

such as *Alnus glutinosa*, *Betula* sp. div., *Pinus sylvestris* and *Salix aurita*.

Hamatocaulis cover varied between 0.05% and 30% (Fig. 2), but it exceeded 20% at only four sites. At these sites, the range of pH was between 6.7 and 7.2, conductivity was between 100 and 250 $\mu\text{S}/\text{cm}$ and the water table ranged from 5 to 7 cm below ground level. The majority of other sites were more acid (pH = 6.2–6.6) and had a lower conductivity (<100 $\mu\text{S}/\text{cm}$). The relationship between *Hamatocaulis* cover and any of these three measures (pH, conductivity, water table) was not, however, statistically significant.

The average content of NH_4^+ ranged between 0.15 and 0.3 mg/l, that of NO_3^- between 0.1 and 0.4 mg/l, and Fe^{3+} between 0.2 and 1.7 mg/l. The Ca^{2+} content varied mostly between 3 and 10 mg/l, with an exceptional range between 20 and 30 mg/l at one locality. No correlation was found between concentration of these elements and the cover of *Hamatocaulis*.

3.2. Mowing

The effect of mowing *Hamatocaulis vernicosus* (Fig. 3) 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.

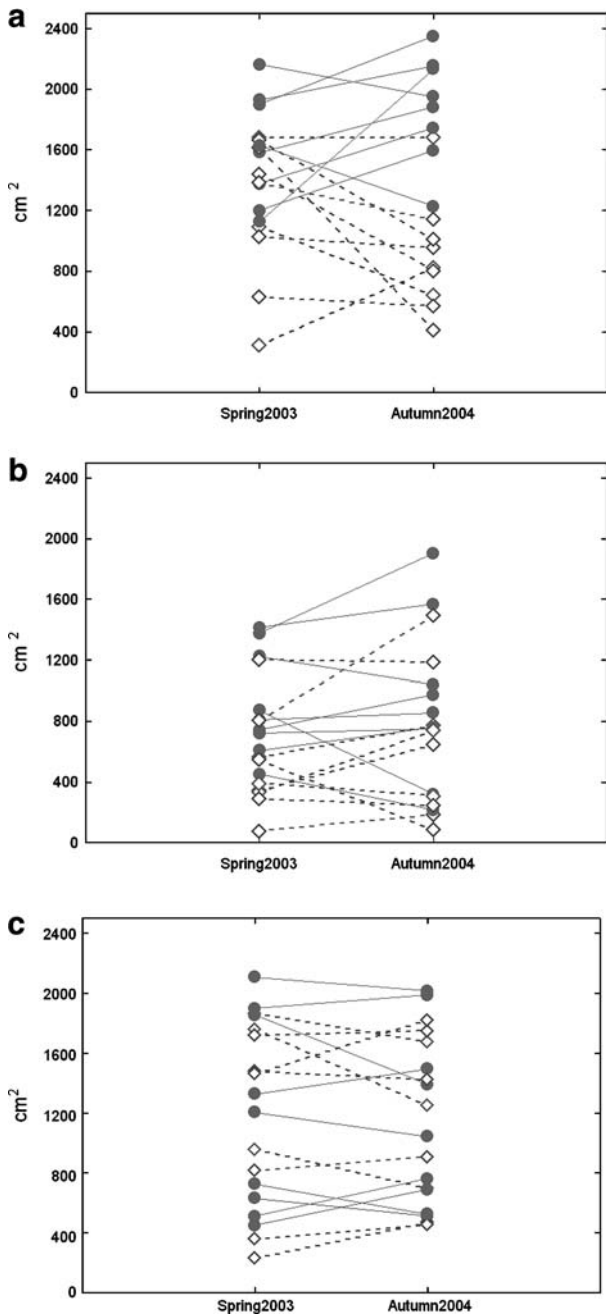


Fig. 3 – Effect of mowing *Hamatocaulis vernicosus*. Full circles show the cover of *Hamatocaulis* before and after the experiment in mown plots, empty ones represent the control plots. a – locality V Lisovech, b – locality Staré jezero, c – locality Vidlák.

3.3. Gap cutting

The expansion into gaps by *Hamatocaulis vernicosus* was dependent on gap water level ($p = 0.0005$, $F = 22.4$; Fig. 4). Shallow gaps (ca. 6–8 cm deep) with a low water level (ca. 1 cm deep) were gradually colonized by *Hamatocaulis vernicosus* and other associated mosses, most often *Calliergonella cuspidata*, *Campylium stellatum* or *Calliergon cordifolium*. In deeper gaps (ca. 10 cm) with a higher water table, *Hamatocaulis* cover was lower. No

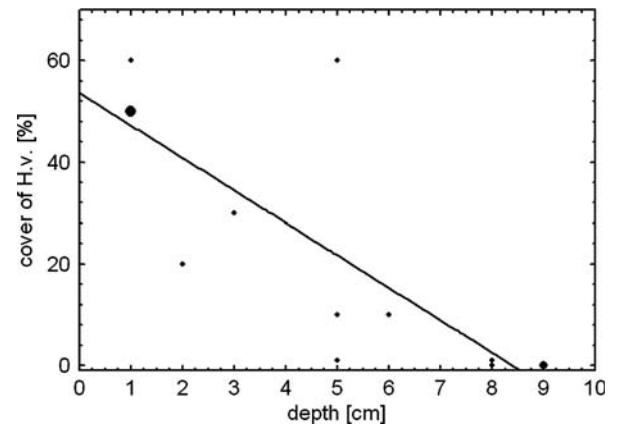


Fig. 4 – Linear regression ($p = 0.0005$, $F = 22.4$) of *Hamatocaulis vernicosus* expansion into the gaps. The size of dots relates to the frequency of observations (range 1–3 observations).

expansion was observed in gaps which were completely filled up with water (water level 8–9 cm). Similar results were observed with other associated pleurocarpous mosses.

4. Discussion

At all localities (and in 91% of vegetation samples), *Hamatocaulis vernicosus* grows with *Calliergonella cuspidata*, which accords with observations at British and German localities (Church et al., 2001; Müller and Baumann, 2004). Other regular associates include the mosses *Aulacomnium palustre*, *Straminergon stramineum* and *Bryum pseudotriquetrum* and the vascular plants *Equisetum fluviatile*, *Lysimachia vulgaris*, *Epilobium palustre*, *Potentilla erecta* and *Cirsium palustre*. The most commonly associated *Sphagnum* species were *S. teres*, *S. warnstorffii* and *S. contortum*, 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). We also found the taxonomically-related species *Scorpidium cossonii* as a common associate at sites with a high pH and conductivity, which is contrary to Swedish surveys, where *Scorpidium cossonii* rarely grows with *Hamatocaulis* (Hedenäs, 1989).

4.1. Water chemistry at the localities

The pH values at observed localities confirmed the general assumption that *Hamatocaulis* requires slightly acid to slightly base-rich conditions (Hedenäs, 1989; Vitt, 2000; Hedenäs et al., 2003; Hájková, 2005). However, Spanish data have shown *Hamatocaulis vernicosus* occurring between pH 4.5–5 (Heras and Infante, 2000), surprisingly growing alongside *Tomentypnum nitens* and *Meesia triquetra*, both species being rich-fen species. Conductivity and NH_4^+ , NO_3^- , and Ca^{2+} concentrations are consistent with values mentioned by Hedenäs and Kooijman (1996). However, our measurements for Fe concentration (mean = 0.71 mg/l) did not show any exceptional value and was much lower than the unusually high value of 2.24 mg/l

reported for the genus *Hamatocaulis* by Hedenäs and Kooijman (1996), suggesting it does not have exceptional Fe requirements.

4.2. Mowing

The differential influence of mowing on *Hamatocaulis vernicosus* appears to be correlated with vascular plant cover. At 'V Lisovech' (site 2), vascular plant cover was about 20% greater than the other two sites, where the higher water table (cf. Table 1) keeps the cover of vascular plants low.

The reasons for decline of the *Hamatocaulis* colonies with the increasing cover of vascular plants might be diverse. One of them may include a reduced solar radiation available for bryophytes through competition with the plants or their accumulating litter, litter accumulation in its own right causing nutrient concentrations to rise. Elevated nutrient concentrations have been shown to change the relative balance between moss species that are tolerant of higher nutrient concentrations and those unable to benefit from it (Malmer et al., 1992; Kooijman, 1993; Kooijman and Bakker, 1995).

4.3. Gap cutting

The ability of *Hamatocaulis* to colonize the gaps appeared to be dependent on the water table. Despite its preference for wet microsites, completely inundated gaps were never colonized. This is consistent with Janssens (1983), who describes the species not developing permanently submersed forms in contrast to, e.g., *Warnstorfia exannulata*. Consequently, gap cutting makes little sense in localities where the water table is high. The positive effect of creating gaps was noticeable in the drier sites, where the species thrived on the edges of small pools or ditches, created here (independently of our experiments) to support the growth of some vascular plants.

Hamatocaulis vernicosus was able to spread into and cover more than a half of the gaps in the course of two seasons with a horizontal growth rate of ca. 3 cm/yr. This is a slightly slower growth rate than that reported by Kooijman et al. (1994) for the related species *Scorpidium scorpioides* (3–7 cm annually). However, the latter species is substantially larger than *Hamatocaulis*; hence the relative growth rate is probably comparable. Interestingly, the *Sphagnum* species growing near the gaps never expanded into them. This may be caused by the higher pH and higher concentration of electrolytes in the hollows compared to the hummocks (Karlin and Bliss, 1984; Malmer et al., 1992), which makes the gaps unsuitable for most species of *Sphagnum*, as they prefer more acid habitats (Gorham and Janssens, 1992; Vitt, 2000).

4.4. Recommendations

We conclude that the eventual active management for *Hamatocaulis vernicosus* should take into consideration the water regime, vegetation composition and herb cover. The results of these preliminary manipulative experiments confirm that management is not necessary in all wetland habitats, being necessary only in "artificial" or man-influenced habitats such as wet meadows (Kooijman et al., 1994; Hedenäs, 2003), where the water table is unstable and cover of vascular plants high. At these localities, the growth and long-term persistence of

Hamatocaulis vernicosus can be supported by cutting small shallow gaps.

For a 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 specific research of competitive rates in *Hamatocaulis* and other moss species. Similar studies are needed for most rare bryophyte species and effective bryophyte conservation cannot be achieved until such knowledge is available.

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