

Faculty of Biological Sciences
University of South Bohemia



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

Rigorózní práce

Táňa Štechová
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Anotation:

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.

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České Budějovice 18. 12. 2006

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Táňa Štechová

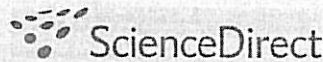
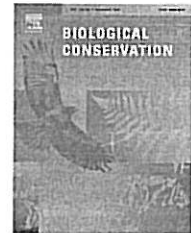
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2 The requirements of the rare moss, *Hamatocaulis* 3 *vernicosus* (Calliergonaceae, Musci), in the Czech Republic 4 in relation to vegetation, water chemistry and management

5 Tárna Štechová*, Jan Kučera

6 Department of Botany, Faculty of Biological Sciences, University of South Bohemia, Branišovská 31, CZ-370 05 České
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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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39 1. Introduction

40 The aim of this study was to investigate the autecology of one
41 threatened bryophyte species. The species chosen was *Hama-*
42 *tocaulis vernicosus* (bryophyte nomenclature follows Kučera
43 and Várna (2003), that for vascular plants follow Kubát et al.
44 (2002)), a widely distributed but rarely common holarctic spe-
45 cies, occurring most frequently in the boreal zone (Hedenäs,
46 1989). It belongs to a group of taxa restricted to formerly gla-
47 ciated and periglacial areas (Janssens, 1983). In Scandinavia it
48 is locally abundant (Söderström, 1996) but in Central Europe it
49 is a rare species, classified in most countries as threatened
50 (e.g., Ludwig et al., 1996; Kučera and Várna, 2003). Because of
51 this rarity, it has been listed in Appendix I of the Bern Conven-
52 tion as requiring special attention (Raeymaekers, 1990).

53 One of the main reasons for the rarity of *Hamatocaulis ver-*
54 *nicosus* 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 produc-
tion 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 almost certainly spread by gametophytic fragments, like
many other peatland mosses (Poschlod and Schrag, 1990).

* Corresponding author: Tel.: +420387772303; fax: +420387772345.

E-mail addresses: tana.stechova@bf.jcu.cz (T. Štechová), kucera@bf.jcu.cz (J. Kučera).
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- 71 Fragment dispersal is usually effective over short distances,
72 unless the fragments are spread by birds or large mammals.
73 Wetland species such as *Hamatocaulis vernicosus* are
74 endangered mainly because of the destruction and degrada-
75 tion of their habitats (Rybníček and Rybníčková, 1974). The
76 cessation of traditional management such as extensive graz-
77 ing, single-cut, late-season haymaking, and removal of mown
78 material for bedding led to the increasing productivity and
79 decrease of species richness (Fojt and Harding, 1995; Prach,
80 1996; Diemer et al., 2001). To conserve species richness, a
81 substitution for the traditional management is necessary,
82 and recently a range of suitable alternative management
83 techniques have been tested in these habitats. However, the
84 impact of these treatments on bryophytes is limited. Where
85 it has been investigated (Moen et al., 2001), the mowing of
86 vegetation resulted in a replacement of hummock-building
87 species with prostrate moss species. However, Bergamini
88 and Peintinger (2002) did not find an effect of removal of vas-
89 cular plants on biomass and shoot morphology of *Calliergo-*
90 *nella cuspidata*.
- 91 Here, we describe the observed habitat preferences of
92 *Hamatocaulis* in the Czech Republic with respect to the
93 water chemistry (pH, conductivity, NH_4^+ , NO_3^- , Ca^{2+} and
94 Fe^{3+}) and its phytosociological relationships. We also per-
95 formed manipulative experiments, testing the short-term
96 impact of mowing and measured its expansion ability into
97 gaps created in the vegetation. There are few studies on
98 bryophyte autecology, and we hope that this preliminary
99 study will provide an impetus for further work in this
100 area.
-
- 101 **2. Material and methods**
- 102 **2.1. Vegetation and environmental sampling**
- 103 All 28 sites where *Hamatocaulis vernicosus* was known to occur
104 in the Czech Republic were sampled in May and June 2005 (Ta-
105 ble 1). At each site, vegetation relevés were assessed and mea-
106 surements made of the water table and a range of basic water
107 chemistry variables (pH, conductivity). One to four relevés
108 were recorded at each site depending on the population size
109 of *Hamatocaulis*; at each relevé the vegetation was assessed
110 by estimating visually the cover of all species in 4×4 m plots
111 (58 in total).
- 112 Water pH and conductivity were measured *in situ* at four
113 positions in each plot using portable devices (Vario pH,
114 WTW, Germany; CM 101, Snail Instruments, Czech Republic).
115 The water table was measured using the PVC discoloration
116 method over the whole vegetation season (Belyea, 1999;
117 Navrátilová and Hájek, 2005).
- 118 Seven sites were chosen as representative of the major
119 phytogeographical regions in which *Hamatocaulis* occurred
120 in the country for a more detailed study of water chemistry
121 (NH_4^+ , NO_3^- , Ca^{2+} , Fe^{3+}). Below-ground water samples were col-
122 lected in October 2003, and June, September and October
123 2004. These samples were filtered and frozen within 24 h for
124 later analysis. NH_4^+ and NO_3^- were determined colorimetrically
125 by flow injection analysis (FIAstar 5012 analyzer, Sweden);
- Ca^{2+} and Fe^{3+} concentration was analysed spectrophotometri- 126
cally (SpectrAA 640, Australia). 127
- 2.2. Manipulative experiments** 128
- Three sites (1–3, Table 1) with extensive *Hamatocaulis* popula- 129
tions were selected for manipulative experiments. Response 130
to mowing was tested in permanent 50×50 cm plots ($n = 17$ 131
at site 2; $n = 18$ at sites 1, 3), chosen to include the largest 132
part of the population of *Hamatocaulis vernicosus* at each 133
locality. A sketch of species distribution at each plot was 134
drawn at a mm scale. Half of the plots were mown with a 135
grass-hook and the biomass removed; the rest of the plots 136
were unmown. Mowing was performed twice, in late June 137
2003 and late June 2004. The sketches from all plots were 138
made again in autumn 2004 and changes in cover were eval- 139
uated from the sketches using the Scion Image program 140
(Scion Corporation, 2000). 141
- The ability of *Hamatocaulis* to expand into created gaps was 142
also observed in 2003 and 2004 in fourteen 15×15 cm gaps, 143
dug in each of the three localities. Each gap was cut close to 144
an extant *Hamatocaulis* colony. The gap depth was dependent 145
on the turf thickness and varied between 6 and 14 cm. The 146
water level in gaps was measured in June and October in both 147
years. At the last visit cover of *Hamatocaulis* in each gap was 148
measured. 149
- 2.3. Data analysis** 150
- Canonical correspondence analysis (CCA) was used to evalu- 151
ate the relationship between the phytosociological data and 152
the environmental data (pH, conductivity, average water table 153
level and its fluctuation expressed as the range between min- 154
imum and maximum values). Significance was assessed 155
using a Monte-Carlo test with 499 permutations (Lepš and 156
Šmilauer, 2003). 157
- The interaction of mowing with time on populations of 158
observed species was tested using ANOVA with repeated 159
measurements. The relationship between water level and 160
Hamatocaulis cover in gaps was investigated using multiple 161
linear regression. ANOVA and the regression were com- 162
puted using Statistica for Windows version 7.1 (StatSoft 163
Inc, 2005). 164
-
- 3. Results** 165
- 3.1. Vegetation, water table and chemistry at the localities** 166
- In the relevés 177 species (51 bryophytes, 126 vascular plants) 167
were found, the most commonly associated species being 168
listed in Table 2. The variation of vegetation composition 169
was influenced significantly ($p = 0.002$, $F = 4.1$) by the environ- 170
mental variables (Fig. 1). The first canonical axis explains 28% 171
of the variation and is closely associated with a water chem- 172
istry gradient (pH, conductivity), whereas axis two explains 173
12% of the variation and appears closely associated with 174
water table and its fluctuations. At the more base-rich local- 175
ities (pH = ca. 7; conductivity = 100–250 $\mu\text{S}/\text{cm}$), the commonly 176
associated mosses were *Tomentypnum nitens*, *Campylium stella-* 177

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 ± 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	Vídlák	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	Zhůrská pláň	1000	5	1100	0.5	1	80	6.0 ± 2.0

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

178 tum, *Philonotis calcarea* and *Scorpidium cossonii*, and vascular
179 plants included *Valeriana dioica*, *Carex dioica*, *Eriophorum latifo-*
180 *lium* and *Eleocharis quinqueflora*. In more acid habitats
181 (pH = 5.8–6.6, conductivity < 100 µS/cm), these were replaced
182 by *Sphagnum fallax*, *Sphagnum subsecundum*, *Sphagnum palus-*
183 *tre*, *Warnstorfia exannulata*, *Eriophorum angustifolium*, *Agrostis*
184 *canina*, *Potentilla palustris* and seedlings of trees and shrubs,
185 such as *Alnus glutinosa*, *Betula* sp. div., *Pinus sylvestris* and *Salix*
186 *aurita*.

187 *Hamatocaulis* cover varied between 0.05% and 30% (Fig. 2),
188 but it exceeded 20% at only four sites. At these sites, the range
189 of pH was between 6.7 and 7.2, conductivity was between 100
190 and 250 µS/cm and the water table ranged from 5 to 7 cm be-
191 low ground level. The majority of other sites were more acid
192 (pH = 6.2–6.6) and had a lower conductivity (<100 µS/cm).
193 The relationship between *Hamatocaulis* cover and any of these
194 three measures (pH, conductivity, water table) was not, how-
195 ever, statistically significant.

196 The average content of NH₄⁺ ranged between 0.15 and
197 0.3 mg/l, that of NO₃⁻ between 0.1 and 0.4 mg/l, and Fe³⁺ be-
198 tween 0.2 and 1.7 mg/l. The Ca²⁺ content varied mostly be-
199 tween 3 and 10 mg/l, with an exceptional range between 20
200 and 30 mg/l at one locality. No correlation was found between
201 concentration of these elements and the cover of
202 *Hamatocaulis*.

3.2. Mowing

The effect of mowing *Hamatocaulis vernicosus* (Fig. 3) was sig-
nificant 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.

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). Shal-
low 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 cuspi-*
data, *Campylium stellatum* or *Calliergon cordifolium*. In deeper
gaps (ca. 10 cm) with a higher water table, *Hamatocaulis* cover
was lower. No 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), *Hamato-*
caulis vernicosus grows with *Calliergonella cuspidata*, which ac-

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

223 cords with observations at British and German localities
 224 (Church et al., 2001; Müller and Baumann, 2004). Other regular
 225 associates include the mosses *Aulacomnium palustre*,
 226 *Straminergon stramineum* and *Bryum pseudotriquetrum* and the
 227 vascular plants *Equisetum fluviatile*, *Lysimachia vulgaris*, *Epilo-*
 228 *bium palustre*, *Potentilla erecta* and *Cirsium palustre*. The most
 229 commonly associated *Sphagnum* species were *S. teres*, *S.*
 230 *warnstorffii* and *S. contortum*, all known to be relatively calcitol-
 231 erant species, and *S. fallax* which thrives in a wide range of
 232 chemical and hydrological conditions (Daniels and Eddy,
 233 1990; Hájková and Hájek, 2004). We also found the taxonom-
 234 ically-related species *Scorpidium cossonii* as a common associ-
 235 ate at sites with a high pH and conductivity, which is
 236 contrary to Swedish surveys, where *Scorpidium cossonii* rarely
 237 grows with *Hamatocaulis* (Hedenäs, 1989).

238 4.1. Water chemistry at the localities

239 The pH values at observed localities confirmed the general
 240 assumption that *Hamatocaulis* requires slightly acid to slightly
 241 base-rich conditions (Hedenäs, 1989; Vitt, 2000; Hedenäs et al.,
 242 2003; Hájková, 2005). However, Spanish data have shown *Ham-*
 243 *atocaulis vernicosus* occurring between pH 4.5–5 (Heras and In-
 244 fante, 2000), surprisingly growing alongside *Tomentypnum*
 245 *nitens* and *Meesia triquetra*, both species being rich-fen species.
 246 Conductivity and NH_4^+ , NO_3^- , and Ca^{2+} concentrations are con-
 247 sistent with values mentioned by Hedenäs and Kooijman
 248 (1996). However, our measurements for Fe concentration
 249 (mean = 0.71 mg/l) did not show any exceptional value and
 250 was much lower than the unusually high value of 2.24 mg/l re-
 251 ported for the genus *Hamatocaulis* by Hedenäs and Kooijman
 252 (1996), suggesting it does not have exceptional Fe requirements.

4.2. Mowing

The differential influence of mowing on *Hamatocaulis vernico-*
sus 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. Ta-
 ble 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 caus-
 ing nutrient concentrations to rise. Elevated nutrient concen-
 trations 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 con-
 trast 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

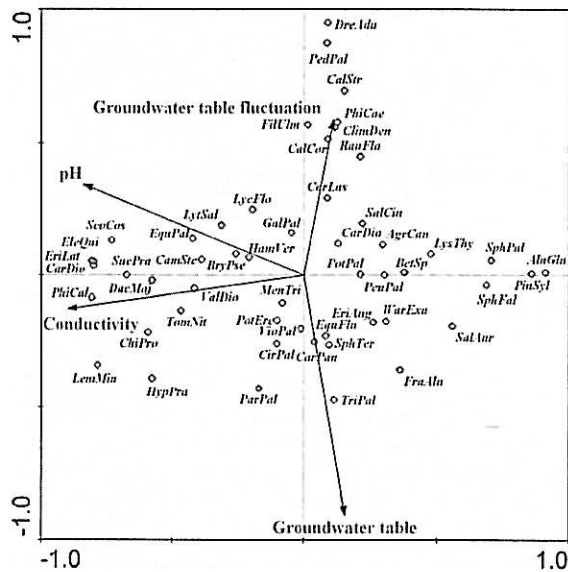


Fig. 1 – Species–environment biplot from CCA summarizing the relationship between species and the measured environmental characteristics – pH, conductivity, mean water table depth and fluctuation. Mosses: CalCor – Calliargon cordifolium, CamSte – Campylium stellatum, ChiPro – Chiloscypus profundus, CliDen – Climacium dendroides, DreAdu – Drepanocladus aduncus, HamVer – Hamatocaulis vernicosus, HypPra – Hypnum pratense, PhiCae – Pilonotis 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 thyrsoiflora, 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.

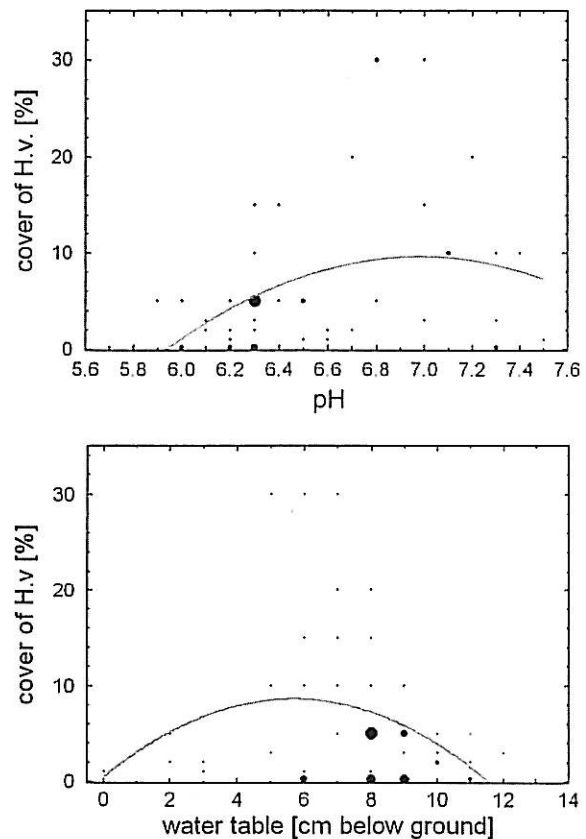


Fig. 2 – Relationship between Hamatocaulis vernicosus cover, pH and water table. The size of dots relates to the number of vegetation samples (range 1–5 samples).

283 a horizontal growth rate of ca. 3 cm/yr. This is a slightly
 284 slower growth rate than that reported by Kooijman et al.
 285 (1994) for the related species *Scorpidium scorpioides* (3–7 cm
 286 annually). However, the latter species is substantially larger
 287 than *Hamatocaulis*; hence the relative growth rate is probably
 288 comparable. Interestingly, the *Sphagnum* species growing near
 289 the gaps never expanded into them. This may be caused by
 290 the higher pH and higher concentration of electrolytes in
 291 the hollows compared to the hummocks (Karlin and Bliss,
 292 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). 293
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4.4. Recommendations 295

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. 296
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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. 307
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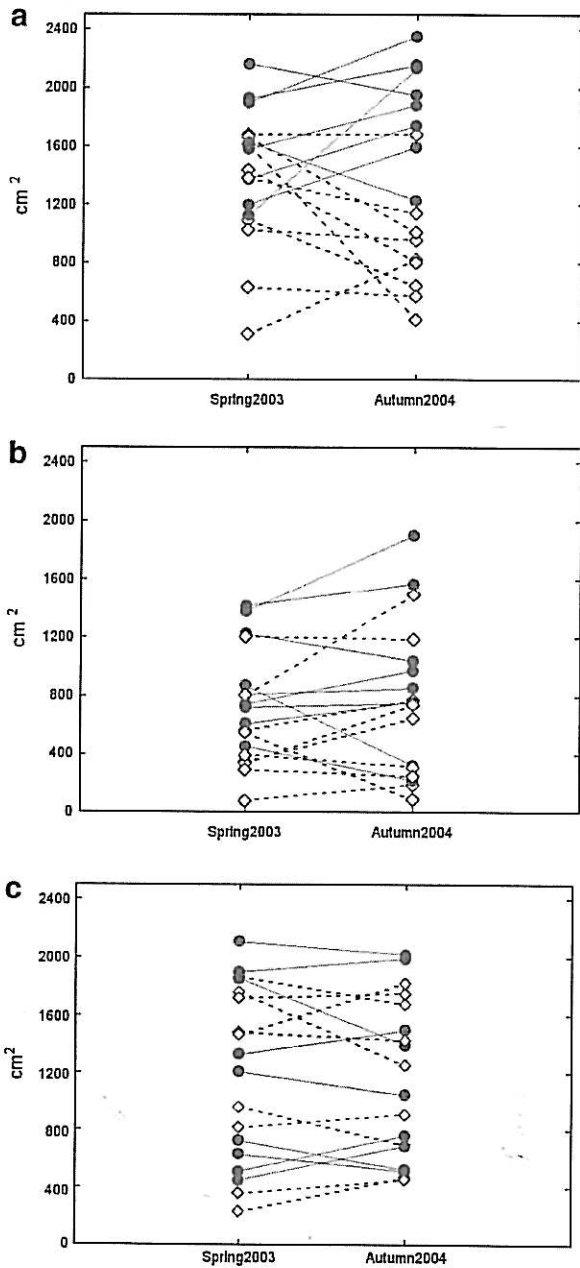


Fig. 3 – Effect of mowing *Hamatocaulis vernicosus*. Full circles show the cover of *Hamatocaulis* before and after the experiment in mown plots, empty ones represent the control plots. a – locality V Lisovech, b – locality Staré jezero, c – locality Vidlák.

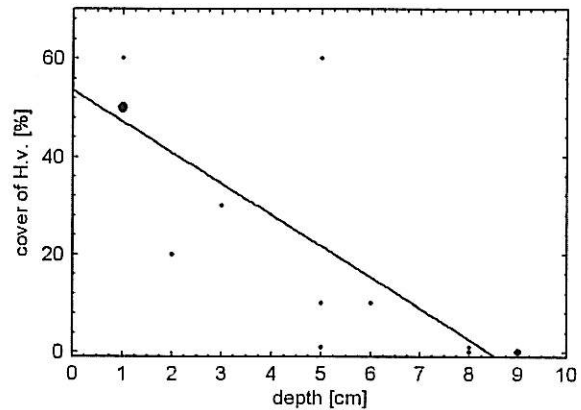


Fig. 4 – Linear regression ($p = 0.0005$, $F = 22.4$) of *Hamatocaulis vernicosus* expansion into the gaps. The size of dots relates to the frequency of observations (range 1–3 observations).

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