Habitat variability and classification of *Utricularia* communities: comparison of peat depressions in Slovakia and the Třeboň basin

Variabilita biotopů a klasifikace společenstev s bublinatkami (*Utricularia*): srovnání rašelinných depresí na Slovensku a v Třeboňské pánvi

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Dítě D., Navrátilová J., Hájek M., Valachovič M. & Pukajová D. (2006): Habitat variability and classification of *Utricularia* communities: comparison of peat depressions in Slovakia and the Třeboň basin. – Preslia 78: 331–343.

Vegetation with species of *Utricularia* and that dominated by *Eleocharis quinqueflora*, which occupy the same habitats. was studied in minerotrophic mires and oligotrophic wetlands associated with ponds. Relative to water and soil chemistry, the communities of *Utricularia ochroleuca* s.l. and *U. intermedia* occurred in mineral-poor and those of *U. minor* and *U. australis* in mineral-rich conditions. Rare stands with *U. vulgaris* occurred in conditions that were intermediate in mineral richness. Four communities belonging to the class *Isoëto-Littorelletea* were distinguished. Vegetation without bladderworts and dominated by *E. quinqueflora* occurs in calcareous fens and belongs to the class *Scheuchzerio-Caricetea fuscae* (the *Caricion davallianae* alliance). Vegetation with *U. intermedia* is characterized by high vascular plant cover and belongs to the class *Scheuchzerio-Caricetea fuscae*. *Utricularia ochroleuca* s.l. prefers open, acidic and waterlogged depressions in peat, whereas *U. intermedia* grows mostly in the shade under vegetation canopy. In this study, *U. minor* and *U. australis* have been found mainly in the more alkaline and mineral-rich habitats, and both species also tolerated extremely high mineral richness.

Keywords: fens, *Isoëto-Littorelletea,* mire, syntaxonomy, water pH, wetland vegetation, Třeboň basin, West Carpathians

Introduction

Over the last two decades, national vegetation surveys have been published for Austria, Slovakia, the Netherlands, United Kingdom and other countries. Currently, there is great interest in preparing a comprehensive vegetation survey for Europe (Rodwell et al. 2002). However, national and Pan-European classification systems differ due to differences in the respective phytosociological traditions, spatial distribution of vegetation units and often also absence of data. The existence of a feedback provides a comparison and stimulates new research. In many cases, a detailed investigation of ecological characteristics is needed in order to understand the underlying mechanisms determining the vegetation pattern observed in a landscape. The bladderwort vegetation occurring in depressions in peat is a good example. The variability in relation to the environment of this vegetation have been poorly studied.

The classification of bladderwort vegetation is ambiguous and depends on the authors. Rybníček (1984) associated plant communities harbouring bladderworts with minerotrophic mires (the *Scheuchzerio-Caricetea fuscae* class), whereas other authors (Müller & Görs 1960, Mucina 1997, Valachovič 2001, Rodwell et al. 2002) considered them to be part of the *Isoëto-Littorelletea* class and others a separate class *Utricularietea intermedio-minoris* (Braun 1970, Pott 1992, Dierssen 1996). The vegetation is markedly dependent on water reaction and mineral richness. The alliance *Sphagno-Utricularion* originally included vegetation in all habitats with bladderworts, from dystrophic peat bogs to calcium-rich alkaline fens. Later, ecological differences were used to separate the alliance *Scorpidio-Utricularion*, which is made up of alkaline and calcium-rich types, but this was not accepted in some vegetation surveys (Braun 1968, Dierssen 1996). This is partly due to the equivocal delimitation of this vegetation to communities of the *Scheuchzerio-Caricetea fuscae* class.

The habitat preferences of bladderwort species and communities, namely water pH and conductivity, have been studied, especially in Germany by e.g. Pietsch (1977), Dierssen & Dierssen (1984) and Dierssen (1996), and in Poland (Kosiba 2004). Adamec & Lev (2002) present ecological data on *Utricularia ochroleuca* and *U. intermedia* in the Czech Republic.

Species-poor communities dominated by bladderworts (*Utricularia* sp. div.) are rare in Central Europe, with the exception of *U. australis* eutrophic marsh and fishpond communities. In the former Czechoslovakia, all habitats were exposed to threat of drainage and eutrophication as were the majority of potentially diagnostic taxa. Published Slovak data are scarce and are only for species-rich vegetation of fen type. The majority of the relevés were originally classified as the *Eleocharitetum pauciflorae* association. As the published relevés were from rather large plots, they gave no indication of the diversity on the medium scale. In the Czech Republic, only a few relevant relevés are stored in the Czech National Phytosociological Database (Chytrý & Rafajová 2003) and they are mostly from non-fen depression communities (e.g. *Sparganietum minimi*).

The goal of this study was to present original data on both the species composition and ecology of mire bladderwort vegetation in Slovakia and the Třeboň basin, the centre of distribution of these habitats in the Czech Republic. This paper presents an analysis conducted with the aim of verifying the position of mire bladderwort communities in a classification system. The second aim of the paper is to elucidate the ecological demands of bladderwort vegetation and individual taxa using detailed field measurements of ecological conditions.

Material and methods

Study areas

The investigation was conducted in the Slovak and Czech Republics. Relevés were made over the entire distribution of *U. minor* in Slovakia. The study area covers northern Slovakia (Inter-Carpathian basins, Orava region) and one locality in the Poľana Mts. The dry summer in 2003 prevented the confirmation of all finds of *U. minor* in Slovakia, but some new localities, not listed in the Flora of Slovakia (Šípošová & Oťahelová 1997) were found (see Electronic Appendix 1). The depressions populated by *Eleocharis quinqueflora* though lacking bladderworts, were also sampled to shed more light on the differentiation between *Caricion davallianae* and typical bladderwort vegetation. For this, a few of the relevés originated from regions outside the area described above. The altitudes of the localities ranged between 450 and 885 m a.s.l., with an average of 620 m.

The Czech sites were located in the Třeboň basin, S Bohemia. The sites were in the littorals of mezo- to eutrophic fishponds on sandy soil or peat of various depths, from 5 cm to several meters. The altitude of these localities ranged between 415 and 470 m a.s.l., with an average of 438 m. For further information on the study sites see Electronic Appendix 1.

Vegetation sampling

Vegetation with five *Utricularia* species was studied: (1) *U. minor*, (2) *U. ochroleuca* s.l. (incl. *U. stygia*), (3) *U. intermedia*, (4) *U. australis* and (5) *U. vulgaris.* Additionally, patches dominated by *Eleocharis quinqueflora*, but with an identical structure and water regime, were sampled in Slovak fens. In total, 76 relevés (36 from Slovakia and 40 from the Třeboň basin) were obtained.

Species composition was recorded during the summer of 2002–2003 from plots of 1–16 m^2. Relevés of different sizes were used in two independent analyses (see below). The cover of both vascular plants and bryophytes was recorded using a nine-grade scale (Barkman et al. 1964, van der Maarel 1979). In Slovakia, the habitats studied often occurred in conspicuous depressions of irregular shape, which are sharply delimited from surrounding rich-fen vegetation. In such cases, the choice of the vegetation plot proved difficult. Water is the factor, which is necessary for the optimal development of floating bladderwort communities. The depth of the water varied from 1 to 50 cm. The sampling areas were restricted to where shallow water evidently persisted for a long time. Only submerged plants or plants growing in open water were recorded. Nevertheless, small areas of shallow water with undulating terrain allow the development of tussocks with sedges and other vascular plants that were also recorded in the relevés.

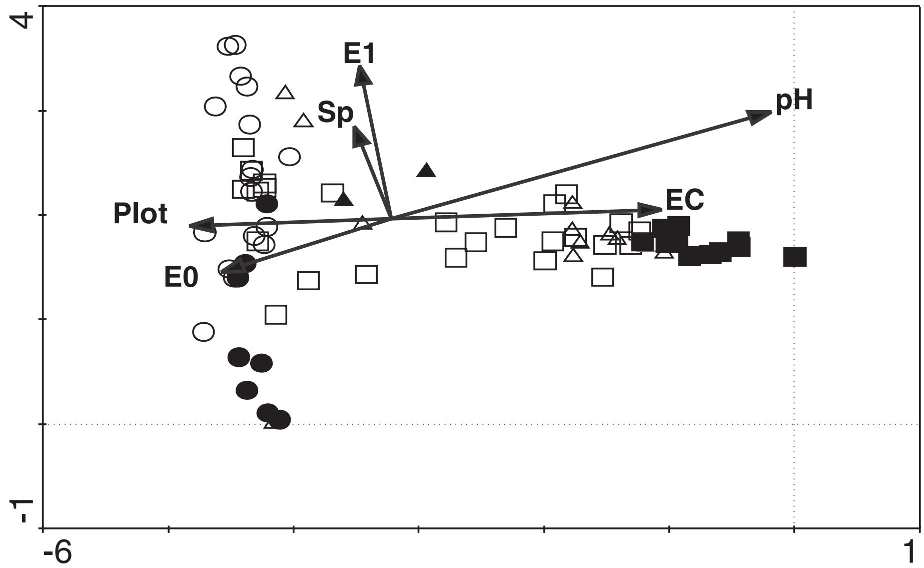
Nomenclature for bryophytes follows Kučera & Váňa (2003), for vascular plants Kubát et al. (2002) and for syntaxa Valachovič (2001).

Environmental data sampling

Water conductivity and pH, both standardized at 20 °C, were measured directly in the field using portable instruments (CyperScan PC 300 or CM 101 & PH 119, Snail Instruments). These rather stable factors in fens (Hájek & Hekera 2004) correlate best with fen vegetation composition and all other water chemistry parameters (Hájek et al. 2002, Sjörs & Gunnarson 2002). Conductivity due to H^+ ions in acid water (pH < 5.5) was subtracted (Sjörs 1952). When measurements were taken more than once, the values were averaged.

Data processing

The first step in the data processing was the numerical classification of all relevés by TWINSPAN (Hill 1979). Three pseudospecies cut levels (0%, 5% and 25% of cover) and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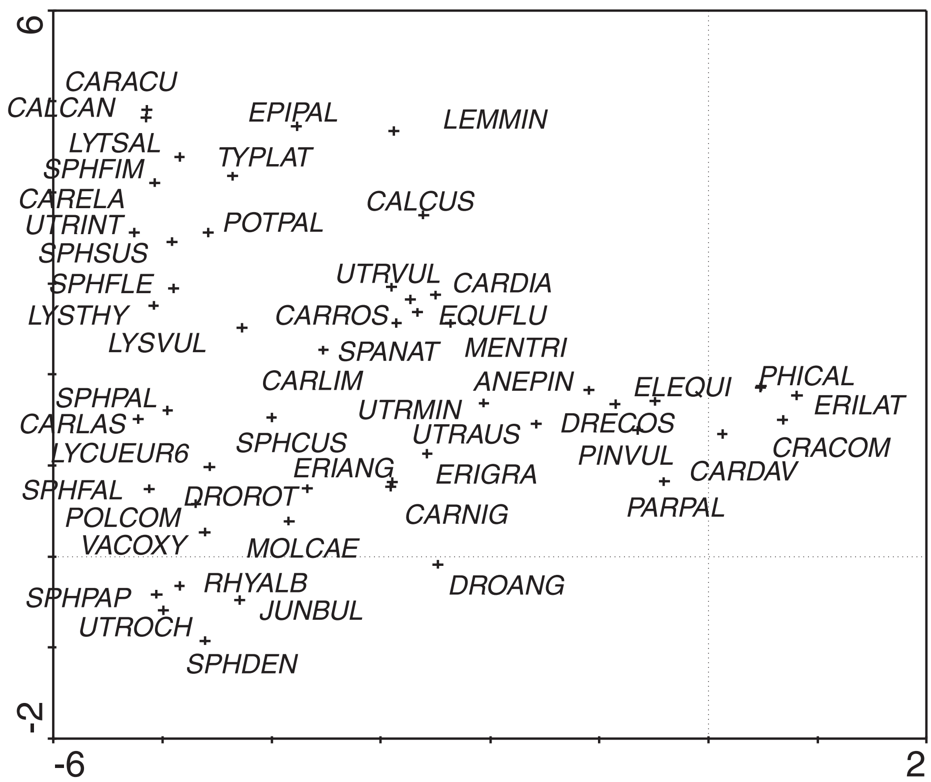
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CARDIA
SPHFLE
LYSTHY
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EQUFLU
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MENTRI
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ANEPIN
ELEQUI
PHICAL
SPHPAL
ERILAT
CARLAS
UTRMIN
DRECOS
UTRAUS
SPHCUS
CRACOM
LYCUEUR6
PINVUL
ERIANG
ERIGRA
CARDAV
SPHFAL
DROROT
CARNIG
PARPAL
POLCOM
VACOXY
MOLCAE
RHYALB
DROANG
SPHPAP
JUNBUL
UTROCH
SPHDEN

three divisions were applied. Two allied groups with minute, ecologically not interpretable differences were merged into one. The JUICE software (Tichý 2002) was used to select the diagnostic species by calculating the phi-coefficients (Chytrý et al. 2002) and for preparing the resulting phytosociological table. Phi-coefficients were standardized for relevé size for all groups. The species in the table were sorted according to their fidelity to the vegetation type and those with positive fidelity and, simultaneously, a probability of random occurrence in the vegetation type of lower than 0.1% determined by Fisher's exact test (see Chytrý et al. 2002), were regarded as diagnostic.

Further, the entire data set with log-transformed cover values was subjected to detrended correspondence analysis (DCA) with down-weighting of rare species, using CANOCO software (ter Braak & Šmilauer 1998). Supplementary variables (pH, conductivity, cover of layers, plot size and number of species) were plotted onto the resulting DCA ordination diagram for a better ecological interpretation of the axes. In the next step, the data set was divided into Slovak (calcium-rich) and Czech (calcium-poor) subsets and the analyses repeated.

Since the recommended plot size for the *Isoëto-Littorelletea* class is under 4 m^2 (Chytrý & Otýpková 2003), the control data set was separately subjected to DCA. It consisted of only 26 relevés of smaller plot size (1–3 m^2). In order to verify the marked differentiation of Czech relevés along the second axis (see Results), the data from the Třeboň basin were replaced by new data from the same areas collected from permanent plots of 1 m^2 and long-term means of environmental variables (10 measurements, see Navrátilová & Navrátil 2005).

To analyse the differences among bladderwort species, the data set was divided according to presence (dominance) of particular bladderwort species. The measured factors associated with the resulting groups of samples were compared by using Tukey Honestly post-hoc test for unequal *n* in one-way ANOVA.

◀ Fig. 1. – DCA ordination of of the entire data set of vegetation samples (76 relevés) with the environmental variables passively projected onto the ordination: EC = electrical conductivity; E0 = cover of the moss layer; E1 = cover of the herb layer; Plot = plot size; Sp = number of species. The presence of species in samples is indicated by using different symbols: ■ *Eleocharis quinqueflora*, □ *Utricularia minor*, ○ *Utricularia intermedia*, ● *Utricularia ochroleuca*, ▲ *Utricularia vulgaris*, △ *Utricularia australis*. Ordination of samples (A), classified according to presence/dominance of particular bladdewort species or *Eleocharis quinqueflora*; (B) ordination of species: ANEPIN = *Aneura pinguis*, CALCAN = *Calamagrostis canescens*, CALCUS = *Calliergonella cuspidata*, CARACU = *Carex acuta*, CARDAV = *Carex davalliana*, CARDIA = *Carex diandra*, CARELA = *Carex elata*, CARLAS = *Carex lasiocarpa*, CARLIM = *Carex limosa*, CARNIG = *Carex nigra*, CARROS = *Carex rostrata*, CRACOM = *Cratoneuron commutatum*, DRECOS = *Drepanocladus cossonii*, DROANG = *Drosera anglica*, DROROT = *Drosera rotundifolia*, ELEQUI = *Eleocharis quinqueflora*, EPIPAL = *Epilobium palustre*, EQUFLU = *Equisetum fluviatile*, ERIANG = *Eriophorum angustifolium*, ERIGRA = *Eriophorum gracile*, ERILAT = *Eriophorum latifolium*, JUNBUL = *Juncus bulbosus*, LEMMIN = *Lemna minor*, LYCEUR = *Lycopus europaeus*, LYSTHY = *Lysimachia thyrsiflora*, LYSVUL = *Lysimachia vulgaris*, LYTSAL = *Lythrum salicaria*, MENTRI = *Menyanthes trifoliata*, MOLCAE = *Molinia caerulea*, PARPAL = *Parnassia palustris*, PHICAL = *Philonotis calcarea*, PINVUL = *Pinguicula vulgaris*, POLCOM = *Polytrichum commune*, POTPAL = *Potentilla palustris*, RHYALB = *Rhynchospora alba*, SPANAT = *Sparganium natans*, SPHCUS = *Sphagnum cuspidatum*, SPHDEN = *Sphagnum denticulatum*, SPHFAL = *Sphagnum fallax*, SPHFIM = *Sphagnum fimbriatum*, SPHFLE = *Sphagnum flexuosum*, SPHPAL = *Sphagnum palustre*, SPHPAP = *Sphagnum papillosum*, SPHSUB = *Sphagnum subsecundum*, TYPLAT = *Typha latifolia*, UTIAUS = *Utricularia australis*, UTIRINT = *Utricularia intermedia*, UTIMIN = *Utricularia minor*, UTROCH = *Utricularia ochroleuca* s.l., UTRVUL = *Utricularia vulgaris*, VACOXY = *Vaccinium oxycoccos*.

Results

Classification

The TWINSPAN classification of 76 relevés clearly showed that each bladdewort species is a character species of some of the relevé groups defined by total species composition, except for *U. vulgaris* (Table 1). The vegetation type with *Eleocharis quingueflora* that lacks bladdewort species, traditionally classified as *Eleocharitetum pauciflorae* association (*Caricion davallianae*), was clearly separated from all bladdewort communities, even those with *Eleocharis quinqueflora*. Also emerging from this analysis is the occurrence of two ecologically different groups, acidophilous plant communities partly corresponding to the alliance *Sphagno-Utricularion* (groups 5–6) and two basiphilous communities clearly corresponding to the alliance *Scorpidio-Utricularion* (groups 2–3). Presence of tall-sedges, reed beds and helophytes in the *U. intermedia* communities is due to presence of deeper water.

Ordination of the entire data set

The ordination diagram (Fig. 1) shows the detailed separation of calcium-rich alkaline and calcium-poor acidic habitats according to pH and conductivity. The relevés from the Třeboň basin, mostly with *U. intermedia* and *U. ochroleuca* s.l., are separated from the Slovak relevés and unlike them are differentiated along the second axis. The *Eleocharis quinqueflora* communities are on the right of the major base-richness gradient. The community with *U. minor* has its optimum in the central part of this poor-rich gradient and tolerates both acid conditions in the Třeboň basin and alkaline conditions in Slovakia. The first axis explains twice as much of the variation in species data (13.1%) as the second (6.6%). The second axis shows the gradient within acidic fens from communities with *U. ochroleuca* s.l. to those with *U. intermedia*. The species tolerating long-term inundation have their optima in the upper part of this axis (*Carex acuta, C. elata, Lemna minor, Riccia fluitans, Typha latifolia*), which suggests that the second major gradient is connected with the water regime. The species that need a seasonal decrease in the level of water table to the soil surface (e.g. *Rhynchospora alba, Juncus bulbosus* and *Sphagnum denticulatum*) are placed at the bottom of this axis. The factor that best correlates with the second axis is the cover of the herb layer, which increases towards the flooded part of the gradient.

Ordination of the two data subsets and of the control data set

A separate analysis based on material from Slovakia explicitly distinguished relevés with *Utricularia* species from those free of bladderworts and dominated by *Eleocharis quinqueflora* (Fig. 2). The two where *U. vulgaris* was found are the most acid. The first

▶ Table 1. – Synoptic table of bladdewort communities with standardized phi-coefficients (first number) and percentage constancies (second number). The species with a positive standardized fidelity and a probability of less than 0.1% of occuring at random in a particular vegetation type (determined by using Fisher's exact test) are regarded as diagnostic for that vegetation type (values shown in bold). The *Salix* juveniles are omitted. The high-rank syntaxa are indicated on the uppermost line: Cd – *Caricion davallianae*, ScU – *Scorpidio-Utriculation*, SpU – *Sphagno-Utricularion* and ? means unclear syntaxonomical position. See Electronic Appendix 1 (http://www.ibot.cas.cz/preslia) for a full phytosociological table, geographical position and coordinates of the relevés, and header data.

High-rank syntaxon	Cd	ScU	ScU	?	?	SpU
Group no.	1	2	3	4	5	6
No. of relevés	10	9	12	5	32	8
Species with a positive fidelity to the vegetation types						
Eleocharitetum quinqueflorae:						
Bryum pseudotriquetrum	**87/90**	– / .	– /17	– / .	– / .	– / .
Eleocharis quinqueflora	**82/100**	– /56	– /67	– / .	– / .	– / .
Potentilla erecta	**71/70**	– /11	– / .	– / .	– / .	– / .
Equisetum palustre	**70/80**	– /22	– /42	– / .	– / .	– / .
Briza media	**65/60**	– / .	– / .	– / .	– / .	– / .
Cirsium palustre	**63/60**	– /11	– / .	– / .	– / .	– / .
Philonotis calcarea	**58/50**	– / .	– / .	– / .	– / .	– / .
Palustriella commutata	**58/50**	– / .	– / .	– / .	– / .	– / .
Parnassia palustris	**51/50**	– / .	– /17	– / .	– / .	– /12
Prunella vulgaris	**51/40**	– / .	– / .	– / .	– / .	– / .
Base-rich peat depressions:						
Scorpidium cossonii	– /80	**62/89**	**68/92**	– / .	– / .	– / .
Utricularia australis basiphilous community:						
Utricularia australis	– / .	**73/78**	– / .	– / .	– / 9	– /12
Triglochin palustris	– /70	**66/89**	– /75	– / .	– / .	– / .
Scorpidio-Utricularietum minoris:						
Utricularia minor	– / .	– / .	**80/100**	– /60	– /34	– / .
Juncus articulatus	– /60	– /44	**58/75**	– / .	– / 3	– / .
Triglochin maritimum	– / .	– / .	**51/42**	– / .	– / .	– / .
Carex viridula	– / .	– / .	**45/33**	– / .	– / .	– / .
Sphagnum contortum-Utricularia sp. div. community:						
Sphagnum contortum	– / .	– / .	– /25	**77/80**	– / .	– / .
Sparganium natans	– / .	– / .	– / .	**65/60**	– / .	– / .
Utricularia intermedia community:						
Potentilla palustris	– / .	– / .	– / .	– /40	**72/75**	– / .
Straminergon stramineum	– / .	– / .	– / 8	– /.	**64/62**	– / .
Agrostis canina	– / .	– / .	– / .	– / .	**64/69**	– /38
Lysimachia vulgaris	– /10	– / .	– / .	– /20	**59/69**	– /38
Peucedanum palustre	– / .	– / .	– / .	– / .	**57/53**	– /12
Utricularia intermedia	– / .	– / .	– / .	– / .	**54/50**	– /12
Warnstorfia exannulata	– / .	– / .	– / .	– / .	**54/50**	– /12
Sphagnum palustre	– / .	– / .	– / .	– /20	**54/53**	– /12
Carex lasiocarpa	– / .	– / .	– / .	– / .	**49/44**	– /12
Carex elata	– / .	– / .	– / .	– / .	**48/38**	– / .
Carex canescens	– / .	– / .	– / .	– /20	**47/41**	– / .
Lysimachia thyrsiflora	– / .	– / .	– / .	– / .	**47/41**	– /12
Aulacomnium palustre	– / .	– / .	– / 8	– / .	**43/41**	– /12
Calamagrostis canescens	– / .	– / .	– / .	– / .	**43/31**	– / .
Sphagnum flexuosum	– / .	– / .	– / .	– / .	**41/28**	– / .
Sphagnum inundatum	– / .	– / .	– / .	– / .	**38/25**	– / .
Sphagno-Utricularietum ochroleucae						
Sphagnum denticulatum	– / .	– / .	– / .	– / .	– / 3	**76/75**
Utricularia ochroleuca	– / .	– / .	– / .	– / .	– / 6	**74/75**
Sphagnum papillosum	– / .	– / .	– / .	– /20	– / 6	**62/62**
Juncus bulbosus	– / .	– / .	– / .	– / .	– /12	**60/62**
Rhynchospora alba	– / .	– / .	– / .	– / .	– /16	**58/62**
Other bladdewort species:						
Utricularia vulgaris	– / .	– / .	– / .	– /**40**	– / .	– / .
Other species with a minimum frequency 50% in some column:						
Eriophorum angustifolium	– /**50**	– /**56**	– /**67**	– /**100**	– /**88**	– /**75**
Carex rostrata	– /30	– /**89**	– /**58**	– /**100**	– /**78**	– /12
Carex lepidocarpa	– /**50**	– /22	– /42	– / .	– / .	– / .
Carex panicea	– /**60**	– /22	– /**50**	– /40	– / .	– / .
Campylium stellatum	– /30	– /**67**	– /**58**	– /40	– / .	– / .
Menyanthes trifoliate	– /20	– / .	– /**50** – / .	– /16	– / .	
Carex nigra	– /20	– /11	– / 8	– /**60**	– /34	– /38
Drosera rotundifolia	– / .	– / .	– /25	– /40	– /**56**	– /**50**
Vaccinium oxycoccos	– / .	– / .	– / 8	– / .	– /28	– /**62**
Molinia caerulea	– /10	– / .	– / 8	– / .	– /31	– /**62**

axis accounts for 13.6% of the variability and corresponds to the pH gradient. The role of conductivity, i.e. mineral richness, is suppressed; the second axis which is corelated with conductivity accounts for only 6.9% of the variability in species data.

The DCA analysis of the data from the Třeboň basin showed that the gradient from *Utricularia ochroleuca* s.l. floating fens through typical fen vegetation to tall sedge with *U. intermedia* is the most important in this subset (Fig. 3). The first axis explains approximately twice as much of the variation in species data (14.6%) as the second (7.5%) and correlates best with water pH ($r = 0.803$, $P < 0.01$). This trend was obscured in the analysis of the entire data set. Cover of the herb layer also increases along the gradient towards tall sedge with *U. intermedia*. The DCA analysis of the control data set (Fig. 4) revealed a similar distribution pattern of plant communities and environmental variables. The first axis accounts for 16.1% of the variation in species data and the second only 7%. The pH gradient along the first axis is much stronger than for the analyses using all 76 relevés. It is indirect confirmation that both small and large plots can be used if the habitats are homogeneous.

Habitat and vegetation affinity of particular species

The post-hoc test confirmed that there were significant differences ($p < 0.05$) in water pH (Fig. 5A) and conductivity (Fig. 5B) among the habitats populated by various bladderwort species. The most acid sites were occupied by *U. ochroleuca* s.l., followed by *U. intermedia* along the base-richness gradient. Other bladderwort species (*U. minor, U. australis*) were recorded at pH of about 6–7. The most alkaline habitats (pH 7.0–7.5) were mostly free of bladderworts and dominated by *Eleocharis quinqueflora*. A similar pattern was detected for conductivity, which reflects total mineral richness of water and is often positively correlated with pH. However, the highest mean mineral richness was found only in *Utricularia australis* habitats. *U. minor* was found in extremely mineral-rich, nearly subhalophytic conditions in two cases. Values of chemical factors important for *U. vulgaris* cannot be properly evaluated due to poor data: this species was recorded only in two plots. *Utricularia vulgaris* is common in lowland waterbodies like euthropic lakes with macrophyte vegetation.

Discussion

Classification of bladderwort communities in Slovakia

The analysis of the gradient from poor acidic to rich alkaline fens confirmed that significant ecological differences exist between bladderwort communities and indicated the vegetation should be classified into two units, in particular the two alliances *Sphagno-Utricularion* and *Scorpidio-Utricularion* as in Pietsch (1965), not one alliance with two sub-alliances (cf. Braun 1968). However, all Slovak relevés should be classified in *Scorpidio-Utricularion* but for the two relevés with *U. vulgaris*, which are from slightly acidic habitats and tend to the alliance *Sphagno-Utricularion.* It is important to remember that the moss *Scorpidium scorpidioides*, which gave the alliance its name has only one confirmed locality in Slovakia (Migra & Šoltés 1998) and is replaced in the structure of the community by the ecologically vicarious *Drepanocladus cossonii* (syn. *Scorpidium cossonii*). Bladderwort communities and *Caricion davallianae* vegetation are not clearly delimited in Slovakia because of the common existence of transitional relevés. *Eleocharis*

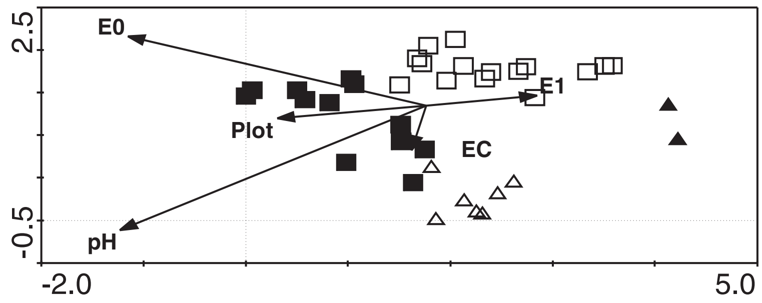

Fig. 2. – DCA ordination of vegetation samples from Slovakia with the environmental variables passively projected onto the ordination (36 relevés; EC = electrical conductivity; E0 = cover of the moss layer; E1 = cover of the herb layer, Plot = plot size). For symbols see Fig 1.

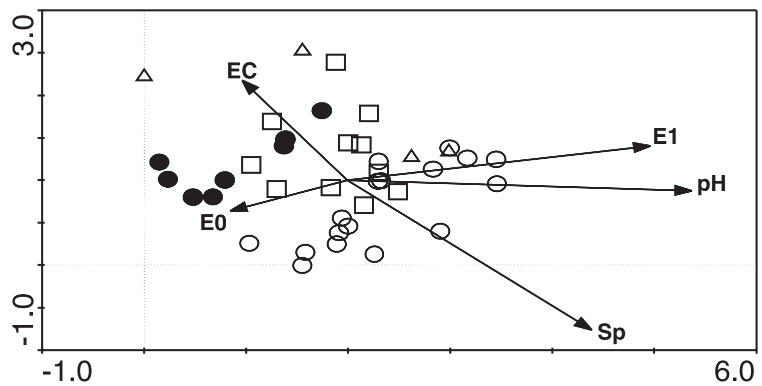

Fig. 3. – DCA ordination of vegetation samples from the Třeboň basin with the environmental variables passively projected onto the ordination (40 relevés; EC = electrical conductivity; E0 = cover of the moss layer; E1 = cover of the herb layer; Sp = number of species). For symbols see Fig 1.

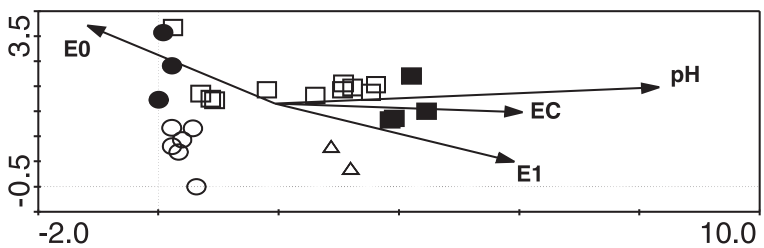

Fig. 4. – DCA ordination of the control data set (26 relevés of plots under 3 m^2) with the environmental variables passively projected onto the ordination (EC = electrical conductivity; E0 = cover of the moss layer; E1 = cover of the herb layer). For symbols see Fig 1.

quinqueflora grows together with some bladderwort species and also forms pure stands of the *Eleocharitetum pauciflorae* association. In contrast to bladdewort communities, there is a high presence and dominance of vascular plants in calcareous *Caricion davallianae* fens. In shallow, permanently irrigated water-bodies the rich-fen species (e.g. *Blysmus*

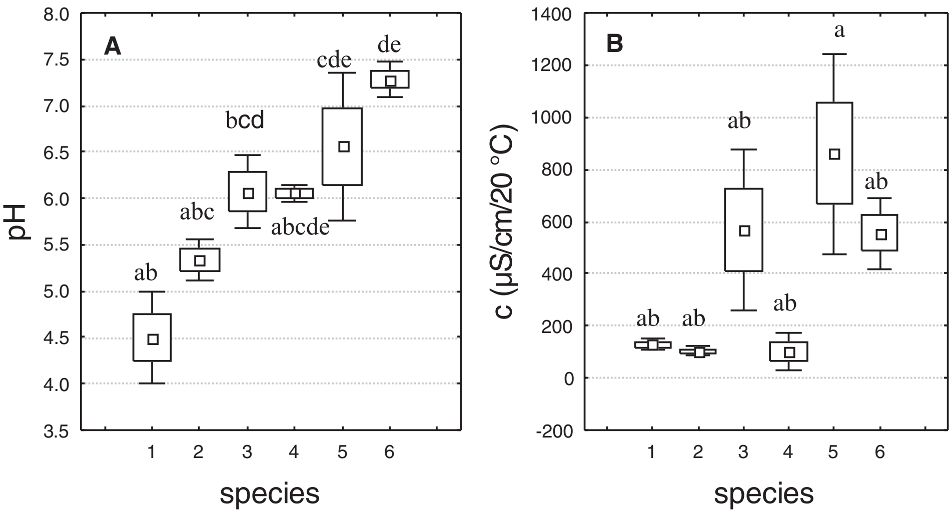

Fig. 5. – Box and whisker plots of the pH (A) and conductivity (B) values of the vegetation types distinguished according to presence of particular bladdewort species or *Eleocharis quinqueflora*. The means are indicated by the square boxes, the size of which indicates S.E. The letters above the boxes indicate the results of Unequal N HSD post-hoc test ($P < 0.05$). The same letter indicates that these pecies are not significantly different: 1 = *Utricularia ochroleuca* s.l., 2 = *U. intermedia*, 3 = *U. minor*, 4 = *U. vulgaris*, 5 = *U. australis*, 6 = *Eleocharis quinqueflora*.

compressus, *Carex hostiana*, *Primula farinosa*, *Schoenus ferrugineus* and *Triglochin maritime*) are very rare even though there is a high concentration of calcium in the water. Probably the temperature of the water is the main factor, preventing the occurrence of these species. On hot summer days small water pools warm up and the oxygen content of the water falls. This probably eliminates those vascular plant species that need highly oxygenated water (see also Hájková & Hájek 2004) and direct root contact with a lime substratum. The combination of: shallow pools (5–20 cm), lime-rich, nutrient- and oxygen poor and rather warm water are the optimal conditions for the growth of bladderworts, especially *U. minor*, in rich fens. The competing species are cryptogams (*Chara* sp. div., *Sphagnum* sp. div., *Drepanocladus* s.l. sp. div.) and vascular plants are rare.

Classification of bladderwort communities in the Czech Republic

Two associations of bladderwort vegetation (*Sphagno-Utricularietum intermediae, Scorpidio-Utricularietum minoris*) are reported from the Czech Republic (Moravec 1983). In the Třeboň basin, these two associations do not form separate and clearly differentiated groups. Nevertheless, some relevés with *U. minor* were of slightly alkaline habitats similar to those of the Slovak rich fens. Other bladdewort communities were dividied into (i) floating fens with *U. ochroleuca* s.l. and (ii) flooded fens with *Caricion lasiocarpae* species. The relevés from floating fens with *U. ochroleuca* s.l. and some species of mineral poor habitats were clearly differentiated according to both species composition and habitat quality. This group corresponds with the association *Sphagno-Utricularietum ochroleuceae*, reported by Spalek (2002) from Poland. This vegetation type is recorded here for the first time in the Czech Republic. This association occurred in the poorest part of fens where the water level fluctuates around the moss layer. In spring, these habitats are covered by a few centimeters of water and in summer the water stagnates at the ground level. The herb layer is extremely sparse. This association represents an initial successional stage, which can change to the communities of the *Rhynchosporion albae* alliance, which occupy the drier parts of the same fens. These two vegetation types often form a spatial-temporal mosaic. The second vegetation type with *Utricularia* species found in the Třeboň basin includes many species of tall sedges and of poor- and moderately-rich fens. *Utricularia intermedia* is the diagnostic species of this group, but reaches only 50% frequency. This bladdewort species occurs in tall-sedge vegetation (*Peucedano-Caricetum lasiocarpae*, *Caricetum rostratae*, *Caricetum elatae*, *Caricetum gracilis*) in moist and the more nutrient-rich parts of the gradient represented by the second DCA axis of the entire data set, or in typical fen vegetation of *Scheuchzerio-Caricetea fuscae* (central section of the 2nd axis). *Utricularia minor* reaches a frequency of 34% in this vegetation type and occurs in nutrient- and mineral-rich fens.

Ecological differentiation of bladderwort communities

These results accord with the contention that *U. ochroleuca* s.l. occurs on wet peaty soils where the water level is at the surface and can tolerate full sunlight, whereas *U. intermedia* can only grow submerged or sheltered from direct sunlight under a canopy of vegetation (Adamec & Lev 2002, Schlosser 2003). Indeed, both the cover of vascular plants and presence of water macrophytes increased in the trend towards *U. intermedia* stands in this study. Further, the gradient from *U. ochroleuca* s.l. to *U. intermedia* stands can be explained in terms of nutrient availability, as is evident from the presence of more nutrient-demanding species in the *U. intermedia* vegetation. It accords well with reports of Adamec & Lev (2002) and Kosiba (2004) who found that the concentration of ammonium in *U. ochroleuca* s.l. stands is significantly lower that in *U. intermedia* stands. The high nutrient availability results in higher vascular plant productivity and a denser canopy; the insolation of the bottom layer decreases.

Water pH is the next factor segregating *U. ochroleuca* s.l. and *U. intermedia* stands in this study areas; it increases in the trend towards *U. intermedia* vegetation. However, this feature seems to be only of regional validity and is probably mediated by the water regime. Adamec & Lev (2002) as well as Kosiba (2004) found a quite opposite pattern. They report a higher pH in *U. ochroleuca* s.l. habitats. Dierssen & Dierssen (1984), by analogy, report the occurrence of *U. ochroleuca* s.l. communities in fens with a pH of about 6.2 and conductivity of about 133 μS/cm, with a seasonal increase in pH to 7.5 in the dry period in October. In North America, Cooper (1996) found *U. ochroleuca* s.l. even in calcareous alkaline fens with a pH of above 7.5.

In this study, *U. minor* and *U. australis* have more alkaline and more mineral-rich optima and tolerate extremely high mineral richness, especially compared to *U. ochroleuca* and *U. intermedia*. A similar result is reported by Kosiba (2004) for Poland. Not even this difference seems to be generally valid. According to Dierssen (1996), *U. minor* prefers more acidic water (pH = 4.6–6.0), whereas *U. intermedia* grows better at neutral pHs (5.6–7.0, cf. Dierssen 1996). This disagreement may be due to the absence of *U. intermedia* in Slovakia and the generally more acidic conditions in the Třeboň basin. Anyway, it is a general fact that *U. minor* can grow in water with a pH ranging from 4.5 to 9.0 (Pietsch 1977). *Utricularia minor* populations that prefer alkaline habitats above pH 7.0 occur in Slovakia (this study), but for example also in Bulgarian submontane fens (Hájková et al., unpublished data). Here, ecologically different populations grow in extremely mineral-poor subalpine fens of the *Primulo exiguae-Caricetum echinatae* association with a median pH value below 6 and a conductivity values of about 30 µS/cm (Hájková et al. 2005).

See http://www.ibot.cas.cz/preslia for Electronic Appendix 1.

Acknowledgements

We thank A. Dobošová, Z. Kuderavá, P. Hájková and M. Horsák for their help with collecting samples in Slovakia, and especially R. Šoltés, P. Hájková and S. Kubešová for determining some bryophyte specimens. Two anonymous reviewers are acknowledged for valuable comments to the first draft of the manuscript. Tony Dixon kindly improved our English. The postgraduate students and staff of the Department of Botany, Masaryk University, Brno, are acknowledged for constructive comments on the presentation of our results at a postgraduate seminar. The research in Slovakia was financially supported by the long-term programme Plant communities of Slovakia (M.V., D.D., D.P.; VEGA grants no. 2/4105/98 and 1/7452/20) and partly by a grant project GAČR 206/02/0568 (M.H.). In the Czech Republic (J.N.), the study was supported by grants nos. FRVS G553/2004, MSM0021622416, and AV0Z60050516.

Souhrn

Předmětem studia byla vegetace s dominancí bublinatek (*Utricularia* sp. div.) na depresích minerotrofních rašelinišť a na rybničních mokřadech a příbuzná vegetace s *Eleocharis quinqueflora* osidlující stejné biotopy. V závislosti na pH vody a půdy, minerální bohatosti a obsahu živin na stanovišti se druhové složení vegetace zkoumaných biotopů mění od minerálně chudých společenstev s *Utricularia ochroleuca* s.l. and *U. intermedia* po minerálně bohatá společenstva s *U. minor* a *U. australis.* Stanoviště s *U. vulgaris* jsou na studovaných biotopech vzácná a leží ve střední části popisovaného gradientu. Čtyři z rozlišených společenstev patří ke třídě *Isoeto-Littoreletea*. Vegetační typ bez bublinatek s dominancí *Eleocharis quinqueflora* patří mezi vápnitá slatiniště třídy *Scheuchzerio-Caricetea fuscae* (svaz *Caricion davallianae*). Vegetace s *U. intermedia* je charakteristická velkou pokryvností bylinného patra a patří rovněž ke třídě *Scheuchzerio-Caricetea fuscae. U. ochroleuca* s.l. upřednostňuje otevřené kyselé rašelinné deprese, zatímco *U. intermedia* roste zejména pod vegetačním zápojem. Druhy *U. minor* a *U. australis* mají v našem studovaném území optima posunuta k bazičtějším a minerálně bohatším stanovištím, oba druhy tolerují i extrémně velkou minerální bohatost.

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Received 15 November 2004
Revision received 1 October 2005
Accepted 25 January 2006