



## Distribution of plant communities, ecological strategy types and diversity along a moisture gradient

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**Keywords:** Biodiversity, Marsh, Plant functional types, Vegetation, Wet meadow.

**Abstract:** The influence of water regime on the zonation of wetland communities, distribution patterns of plant species, ecological strategies and biodiversity, was studied in this work. Vegetation of the herbaceous wetland was sampled along a transect, in accordance with the standard central European method. Water level was also measured. The changes in plant species composition, plant functional types (ecological strategies, life forms) and diversity were studied. Classification of vegetation relevés enabled the definition of five grassland communities. The same pattern remained in DCA ordination also when the species matrix was replaced with a matrix of ecological strategies. Relevés were always segregated into distinct plant communities and distributed along the moisture gradient in the same way. Biodiversity is strongly negatively correlated with moisture—it is decreasing with decreasing ground level. Plant ecological strategy types (C-S-R) change significantly along the transect as well. In communities thriving on the driest sites (*Trisetum-Centaureetum*), there are three times more C- than C-S-strategists, while in the wettest sites (*Caricetum elatae*) C-S-strategists predominate over C-strategists by almost two times. At the same time R- and C-R-strategists, as well as therophytes, which are present in drier sites almost disappear in the wettest sites. We show that the moisture gradient essentially influences the distribution pattern of plant communities, species diversity, and manifestation of certain ecological strategy types.

**Abbreviations:** DCA—Detrended Correspondence Analysis, C-S-R—Competitors-Stress tolerators-Ruderals (strategy types), WPGMA—Weighted Pair Group Method with Averaging, Ce—*Caricetum elatae*, Cv—*Caricetum vulpinae*, AJ—*Agrostio-Juncetum conglomerati*, SD—*Succisello-Deschampsietum cespitosae*, TC—*Trisetum-Centaureetum*.

**Nomenclature:** Ehrendorfer (1973) for taxa, Ellmauer and Mucina (1993); Balátová-Tulácková et al. (1993); Zelnik (2005b, 2007) for syntaxa.

### Introduction

Ecological gradients and diversity of wetlands have been the object of several studies throughout Europe for several years (Wassen et al. 2002, Hájek and Hájková 2004, Bottadukát et al. 2005, Zelnik 2005b, 2005c, Hájková et al. 2006), since the threat to the biodiversity of these ecosystems is still increasing (Joyce and Wade 1998, Zelnik 2005a). A decrease in biodiversity of wet meadows due to intensified agricultural use has been pointed out by several authors (Joyce and Wade 1998, Joyce 2001, McCrea et al. 2001) stressing that loss of species and/or diversity threatens ecosystem functioning and sustainability (Hobbie et al. 1994, Tilman et al. 1996).

Water regime is one of the most important factors determining plant species composition, properties and distribution of wetland vegetation (Brose and Tielbörger 2005, Kluse and Allen-Diaz 2005, Zhou et al. 2006). The correlation between water regime, composition and distribution of herbaceous wetland plant communities has been proved many times (e.g., Wassen et al. 2002, Hudon et al. 2005, Urban 2005). The zonation of the alluvial meadow plant communities ap-

peared to be regulated by varying the water regime or moisture gradient (Selinger-Looten et al. 1999, Dwire et al. 2004, van Eck et al. 2005).

In wetlands the water regime, which is expressed by different parameters (see Wassen et al. 2002), is strongly correlated with elevation of the ground surface (or depth of water level) (Urban 2005). Selinger-Looten et al. (1999) reported that the distribution of plant communities is explained by the extent of the floods and soil texture. The coarsest sediments constitute the alluvial levee, which drains fast and is the most elevated. On silty deposits, more hygrophilic meadows are found, but in the lowest sites on the waterproof clayey sediments, mostly wetland species are found. For simplification, following Urban (2005) the water regime in the broad sense could be presented with an easily measured elevation gradient.

It is well-known that moisture and/or elevational gradient are reflected in the variation of plant ecological strategies of wetland plant communities (Dwire et al. 2004). Plants may adopt a certain reproductive mode combined with various degrees of competitive strength and stress tolerance that con-

tribute to their success under specific environmental conditions (Körner 1994). Kluse and Allen-Diaz (2005) discovered the primary importance of edaphic conditions (e.g., moisture gradient) in meadows, which determine the competitiveness between individual species and influence plant distributions. In the wettest sites, stress tolerating species dominate, but in moist meadow communities, competition plays a greater role in determining species composition (Grime 1979, 2001, Keddy 1992, Dwire et al. 2004).

Functional grouping of components of vegetation reduces the complexity, which enables the comparison of higher levels such as vegetation types (Körner 1994). Distributions of functional groups are predictable along resource gradients (Hobbie et al. 1994). The system of CSR plant strategies (Grime 1979, 2001) is the most appropriate way of providing a functional interpretation of plant communities, as was evidenced by Pierce et al. (2005), Caccianiga et al. (2006), and Pierce et al. (2007).

Grime's (1973, 2001) 'humped-backed' model demonstrates that the highest biodiversity and species richness are apparent with moderate stress, with the lowest diversities at low and high levels of stress. Many authors (Grime 1973, Wassen et al. 2002, Dwire et al. 2004) found higher species richness in the vegetation types in the elevated, drier parts of the floodplain. The characteristic of the studied area is impermeable ground and finely articulated microrelief, which causes small-scale variety in water regime and vegetation. We hypothesise that a gradient in moisture (elevation above the water table) is correlated with vegetation distribution, community composition, species diversity and plant ecological strategies, in a wetland consisting of marsh and wet-meadow ecosystems.

The aims of our study were:

- to analyse the influence of moisture gradient on the distribution patterns in vegetation in a wetland area, considering variation of vegetation and plant species composition, and
- to measure the correlation of the distribution of plant ecological strategy types and species diversity with the moisture gradient.

## Material and methods

### *Study site*

The studied wetland is located in SE Slovenia, near the town of Krško (N 45°53'50'', E 15°25'20'', and ca. 153 m a.s.l.), on the alluvial deposits of the Senuša brook (tributary of the Krka river) and older Pleistocene clayey deposits. This site is surrounded by extensive swamps, which form the woody landscape of the Krakovo forest, so the vegetation of this area is very diverse and still well preserved, as intensive land-use has never been possible here. The wetland vegetation of this area is very specific, since many new plant communities have been described here (Zelnik 2005c). This area

is also important as many endangered plant species grow there and it is an important stepping-stone on migratory routes (Zelnik 2005a). This area has the continental climate of southeast Slovenia with mean annual temperature of 10°C and mean annual precipitation of 1100 mm. It belongs to the sub-Pannonian phytogeographic area.

### *Vegetation sampling and hydrology measurements*

Vegetation was investigated according to the standard Central European method (Braun-Blanquet 1964, Westhoff and van der Maarel 1973). The cover-abundance values were transformed according to van der Maarel (1979). Sampling was done between May and July in 2001 and 2002. The vegetation was analysed on a 120 m long transect which was set along the elevational and/or moisture gradient and consists of 24 plots. The elevation of the ground surface of the specific plots was measured as the water depth in the period of the highest water level. The elevation of the non-flooded plots was measured with the transparent tube. This elevation was used as an indicator of soil moisture. We used plots of the size of 4 m × 4 m, as recommended by Chytrý and Otýpková (2003), and/or Podani and Csontos (2006) for the studies on grassland vegetation. Investigated plots were arrayed along a transect within the 5 m × 5 m grid, where the additional 1 m distance served as a buffer zone. The upper end of this transect was never under the impact of surface water, while the lower end was flooded for about two months within the growth season. The fluctuation of the water table was studied during the growth season (March-October). The fieldwork was done in 2001 and 2002. There were six gauges to measure the fluctuation.

### *Data analysis*

Similarity analyses of the relevés were carried out using the computer program SYN-TAX 2000 (Podani 2001); a hierarchical classification method (WPGMA) was performed. Dissimilarity of relevés was measured with the Similarity ratio complement. Clusters of relevés were classified into syntaxa according to Ellmauer and Mucina (1993), Balátová-Tuláčková et al. (1993), as well as local studies (Zelnik 2005b, 2007).

The ordination of the relevés was performed with DCA, to avoid arch effect and highlight the studied gradient, using the program CANOCO 4.02 (ter Braak and Šmilauer 2002). Since the ecological functions of the communities are better described by plant functional types than floristic composition (Whittaker 1975, Pillar 1999) we describe the vegetation according to plant functional traits following (Klotz et al. 2002). Two data sets were used (see Feoli and Scimone 1984, Díaz and Cabido 1997, Čarni et al. 2005), first the species matrix (120 taxa × 24 sample plots) and second the plant functional traits matrix obtained by multiplying the relevé matrix by the matrix of plant ecological strategies. The plant strategies have been defined using the BIOLFLOR database (Klotz and Kühn in Klotz et al. 2002, pp. 197-201) that considers Grime's classification (Grime 1979, 2001). We also

used categories C-R, C-S and C-S-R representing combinations of the competitor (C), stress-tolerant (S) and ruderal (R) strategies. Both data sets were analysed by means of DCA.

We measured two aspects of biodiversity of the individual sites ( $\alpha$ -diversity), as suggested by Whittaker (1972): species richness ( $N$ ) or diversity as the number of species in a sample of standard size, and diversity measured by the most widely used Shannon-Wiener's index ( $H'$ ). The calculation of Shannon-Wiener's diversity index and the average cover values (Barkman's TCV) was made with the programme JUICE 5.1 (Tichý 2002). Biodiversity between the communities and/or adjacent plots along the transect ( $\beta$ -diversity), was measured with Whittaker's index, which is most effective (Magurran 2004), and calculated with the programme JUICE 5.1 (Tichý 2002). Mean  $\beta$ -diversity (between communities) and confidence intervals were calculated by bootstrap sampling (499 samples). Relations between species diversity, functional types and elevational gradient were calculated using the software STATISTICA 6.0. For regression analysis, linear models were applied.

## Results

### Zonation of plant communities

Five vegetation units were detected on the basis of relevé clustering, using the hierarchical classification method. Individual clusters were classified into five associations from different orders and classes according to their floristic composition: *Trisetum-Centaureetum*, *Succisello-Deschampsietum*, *Agrostio-Juncetum*, *Caricetum vulpinae*, *Caricetum elatae*.

*Trisetum-Centaureetum macroptili* Zelnik 2007 is classified into the order *Arrhenatheretalia*. It thrives on least wet sites where the soil has the coarsest texture and is most permeable to water, and they are somewhat raised above the surrounding ground as well. These meadows are also fertilized every two years at most. The association was further divided into two subassociations: *Trisetum-Centaureetum avenulosum pubescentis*, which cannot withstand flooding at all and *T.-C.*

*potentilletosum repentis*, which thrives on wetter sites and tolerates short-term floods.

*Succisello inflexae-Deschampsietum caespitosae* was classified into the order *Molinietalia* and thrives on soils with a heavier texture, with high silt and clay content. This community can tolerate several weeks of flooding.

*Agrostio-Juncetum conglomerati* from the order *Molinietalia* thrives in hollows and depressions where rainwater collected from adjacent areas can stagnate on the surface for several weeks. Those soils are mostly amphigleyic - upper layers are impermeable to water.

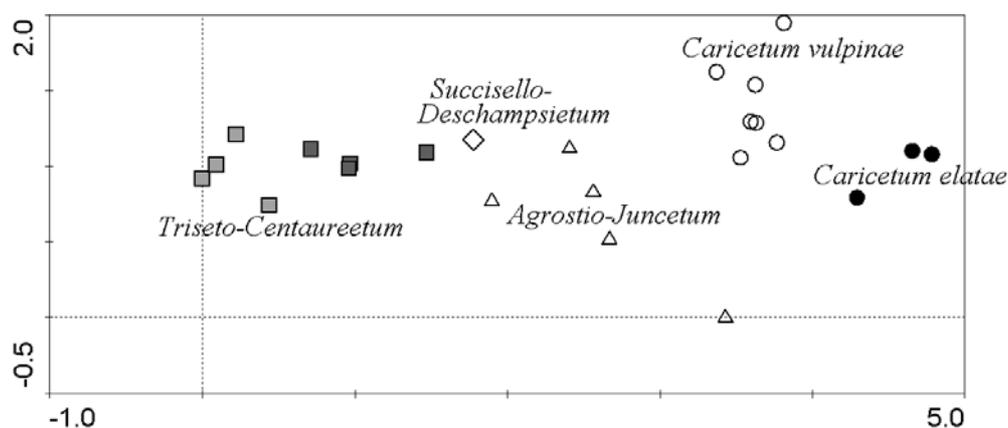
*Caricetum vulpinae* is a marsh community, so it occupies wetter sites than the previous one. It is classified into the order *Phragmitetalia* and class *Phragmiti-Magnocaricetea*. Subassociation *succiselletosum inflexae* was described within the research area, as *Succisella inflexa* dominates in these stands.

*Caricetum elatae* is also classified into the order *Phragmitetalia*. It occupies the wettest sites, which frequently drain not earlier than in June. Few other species besides the characteristic ones occupy these extreme conditions.

The distribution of vegetation relevés in DCA ordination (Fig. 1) enables clear separation of the communities defined by the classification method, moreover their distribution follows the vegetation zonation along the transect and/or moisture gradient in the field. The relevés are segregated into five distinguished groups (communities) along the first axis, which represents the moisture gradient. At the left-hand side of the diagram (Fig. 1), the relevés of the mesic community *Trisetum-Centaureetum* are displayed. The marsh community *Caricetum elatae* thrives on the lowest and wettest sites of the transect and these relevés are located on the right side of the diagram.

### Species distribution

Vegetation relevés in the DCA ordination are segregated into more or less distinctive groups according to plant species



**Figure 1.** DCA ordination of relevés (species data). Eigenvalues of the first two axes are 0.69 and 0.15.

**Table 1.** Average cover synoptic table for specific associations in the studied wetland. Species with average cover value (Barkman's TCV) greater than 2% are displayed only. The plant strategy of the species is also indicated.

Community	TC	SD	AJ	Cv	Ce	strategy type
No. of relevés	8	1	5	7	3	
Average cover	2.6	4.6	3.8	4.8	7.9	
Average nonzero cover	3.9	4.6	5.1	6	8.6	
Presences per plot	45	45	32	17	9.7	
<b>Characteristic species:</b>						
<i>Centaurea jacea macroptilon</i>	39.2	.	0.8	.	.	C
<i>Holcus lanatus</i>	33.6	2	1.2	.	.	C
<i>Calamagrostis epigejos</i>	21	.	.	.	.	C
<i>Anthoxanthum odoratum</i>	15.4	2	0.8	.	.	CSR
<i>Betonica officinalis</i>	12.8	.	.	.	.	C
<i>Deschampsia cespitosa</i>	.	88	1	.	.	C
<i>Poa pratensis</i>	10.8	13	2.6	.	.	C
<i>Agrostis canina</i>	1.2	13	80	5.4	.	CSR
<i>Potentilla reptans</i>	0.9	3	22.2	0.3	.	CSR
<i>Gratiola officinalis</i>	0.4	2	16.6	0.9	.	CSR
<i>Juncus conglomeratus</i>	1.5	3	16	4.7	.	C
<i>Festuca pratensis</i>	5	3	14.8	.	.	C
<i>Succisella inflexa</i>	0.5	3	4	67.3	2	CS
<i>Carex vulpina</i>	0.5	2	2	25.1	.	CSR
<i>Ranunculus repens</i>	1.4	2	16	21.6	2.3	CSR
<i>Iris pseudacorus</i>	.	.	0.8	14	1	CS
<i>Carex elata</i>	.	.	.	0.6	88	CS
<b>Common species:</b>						
<i>Festuca rubra agg.</i>	8.2	.	.	.	.	C
<i>Trisetum flavescens</i>	4.4	.	.	.	.	CSR
<i>Cruciata glabra</i>	3.5	.	.	.	.	CSR
<i>Leontodon hispidus</i>	2.4	.	.	.	.	CSR
<i>Galium verum</i>	3.8	2	.	.	.	CS
<i>Potentilla erecta</i>	2.1	2	.	.	.	CSR
<i>Rumex acetosa</i>	2.1	2	.	.	.	C
<i>Carex pallescens</i>	2.1	2	.	.	.	CSR
<i>Ranunculus acris</i>	6.4	2	3.4	.	.	C
<i>Plantago lanceolata</i>	2.4	2	0.8	.	.	CSR
<i>Lathyrus pratensis</i>	1.9	3	.	.	.	C
<i>Carex tomentosa</i>	0.8	3	.	.	.	CSR
<i>Filipendula ulmaria</i>	0.2	3	0.8	.	0.7	C
<i>Leucanthemum vulgare agg.</i>	4.2	2	3.4	.	.	C
<i>Carex hirta</i>	1.2	2	6.8	0.9	.	C
<i>Trifolium patens</i>	1.8	2	4.2	.	.	CR
<i>Juncus effusus</i>	0.2	2	1.4	7	2	C
<i>Galium palustre</i>	1	2	2.2	2.4	2	CS
<i>Peucedanum palustre</i>	.	.	.	0.6	6	CS
<b>Other species:</b>						
<i>Briza media</i>	1.8	.	.	.	.	CSR
<i>Centaurea jacea agg.</i>	1.4	.	.	.	.	C
<i>Cerastium holosteoides</i>	1.5	.	.	.	.	CR
<i>Cynosurus cristatus</i>	1.4	.	.	.	.	CSR
<i>Daucus carota</i>	1.4	.	.	.	.	CR
<i>Galium mollugo agg.</i>	1.4	.	.	.	.	C
<i>Luzula campestris agg.</i>	1.6	.	.	.	.	CSR
<i>Veronica chamaedrys</i>	1.8	.	.	.	.	CSR
<i>Carex spicata</i>	0.5	2	.	.	.	CS
<i>Dactylis glomerata</i>	1.1	2	.	.	.	C
<i>Veronica serpyllifolia</i>	0.5	2	.	.	.	CSR
<i>Salix cinerea</i>	.	2	.	.	.	C
<i>Sonchus species</i>	.	2	.	.	.	C
<i>Ajuga reptans</i>	2	2	0.4	.	.	CSR
<i>Angelica sylvestris</i>	0.2	2	0.4	.	.	C
<i>Carex leporina</i>	0.8	2	1.2	.	.	CSR
<i>Stellaria graminea</i>	1.5	2	0.8	.	.	CS
<i>Taraxacum officinale</i>	0.5	2	1.2	.	.	CSR
<i>Valeriana officinalis</i>	0.2	2	0.8	.	.	C
<i>Poa trivialis</i>	0.5	2	1.8	.	.	CSR
<i>Trifolium pratense</i>	2	.	1.2	.	.	C
<i>Cardamine pratensis agg.</i>	0.2	2	1.6	1.7	.	CSR
<i>Carex panicea</i>	0.5	2	2	0.7	.	CSR
<i>Centaurea carniolica</i>	2	2	0.4	0.3	.	C
<i>Lychnis flos-cuculi</i>	1.5	2	2	1.4	.	CSR
<i>Prunella vulgaris</i>	2	2	0.4	0.3	.	CSR
<i>Lysimachia nummularia</i>	1	.	1.4	0.4	.	CSR
<i>Lythrum salicaria</i>	0.5	2	1.6	2	2	CS
<i>Rumex crispus</i>	1.9	2	1.2	1.9	0.7	C
<i>Lycopus europaeus</i>	0.2	.	1.2	0.3	1.3	CS
<i>Fritillaria meleagris</i>	.	.	1.2	0.3	.	CSR
<i>Lotus tenuis</i>	.	.	1.4	0.3	.	CS
<i>Mentha aquatica</i>	.	.	1.2	0.6	.	CS
<i>Ranunculus flammula</i>	.	.	1.6	1.6	.	CSR
<i>Veronica scutellata</i>	.	.	.	1.4	.	CS

data (Fig. 1), corresponding to the plant communities along the transect. The first gradient length is 4.78 SD, which indicates the unimodal distribution of the species data, as does the eigenvalue  $> 0.4$  (ter Braak and Verdonschot 1995). The first axis represents the moisture gradient and enables the clearest separation of the relevés into specific communities according to the tolerance of the species for the flood duration.

At the left-hand side of the diagram (Fig. 1), there are relevés with species which can withstand only short-term flood (few days) or no flood at all (Table 1, col. TC). These stands consist mainly of nonwetland mesophytic species (*Centaurea jacea* ssp. *macroptilon*, *Holcus lanatus*, *Calamagrostis epigejos*), and of the characters of the order *Arrhenatheretalia* (e.g., *Trisetum flavescens*, *Poa pratensis*). Species that can tolerate several weeks long flood periods (*Deschampsia cespitosa*, *Agrostis canina*, *Gratiola officinalis*, *Juncus conglomeratus*, *Succisella inflexa*, *Potentilla reptans*, *Ranunculus repens*) are characteristic of wet meadows of the *Molinietalia* order (Table 1, cols SD & AJ). Their position is in the middle of the diagram (Fig. 1), as well as along the moisture gradient. Marsh species (*Carex elata*, *C. vulpina*, *Iris pseudacorus*) dominate on the lowest sites of the transect (Table 1, cols Cv & Ce).

#### Ecological strategy types and life forms

The DCA ordination (Fig. 2) enabled clear separation of the sites. The distribution pattern of different ecological strategists enables the same separation of the sites, as with the original species data (Fig. 1). Strong correlation of ecological strategists and moisture gradient was also calculated with regression analysis (Fig. 3). The proportion of C-strategists is strongly negatively correlated with moisture, but positively with elevation ( $r = 0.739$ ; Fig. 3a). Additionally, the proportion of C-R-strategists is also negatively correlated with moisture and positively with elevation ( $r = 0.850$ ; Fig. 3d). By contrast, C-S-strategists are positively correlated with the moisture gradient and negatively with elevation ( $r = -0.833$ ; Fig. 3c), since their abundance was much higher in non-elevated sites. The indifferent C-S-R-strategists showed almost no correlation with the moisture gradient ( $r = 0.418$ ; Fig. 3b). Their relatively high share along most of the transect is presented in Table 2.

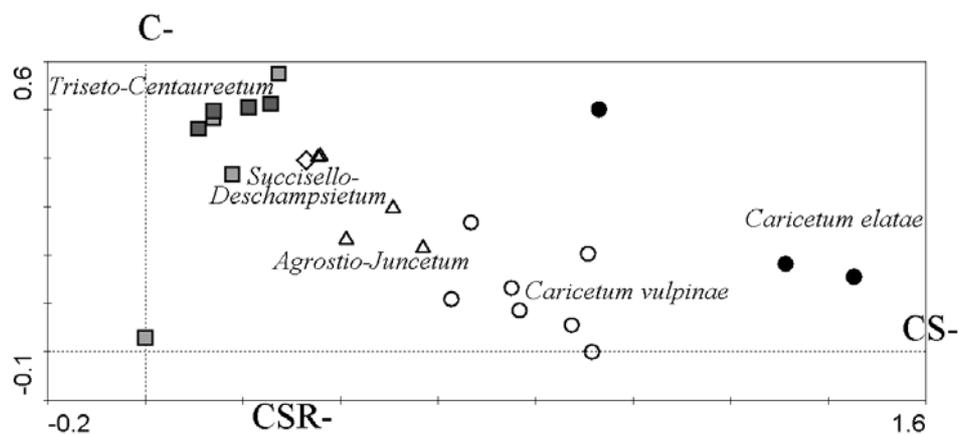
The moisture gradient represents the first axis again (Fig. 2). On the left side there are relevés that consist mainly of the species of the mesic meadows, where C-strategists are more successful (Fig. 3). The relevés of wet meadow communities are located in the middle, since these stands consist of an equalized mixture of different strategists (C-S-R, C, C-S) (Table 2). Marsh species dominate on the lowest and wettest sites of the transect and are mostly C-S-strategists (Fig. 3). These relevés are located on the right part of the diagram (Fig. 2).

In the case of life forms such separation was not effective, since the share of the most frequent life form i.e. hemi-cryptophytes, does not correlate with the moisture gradient ( $r$

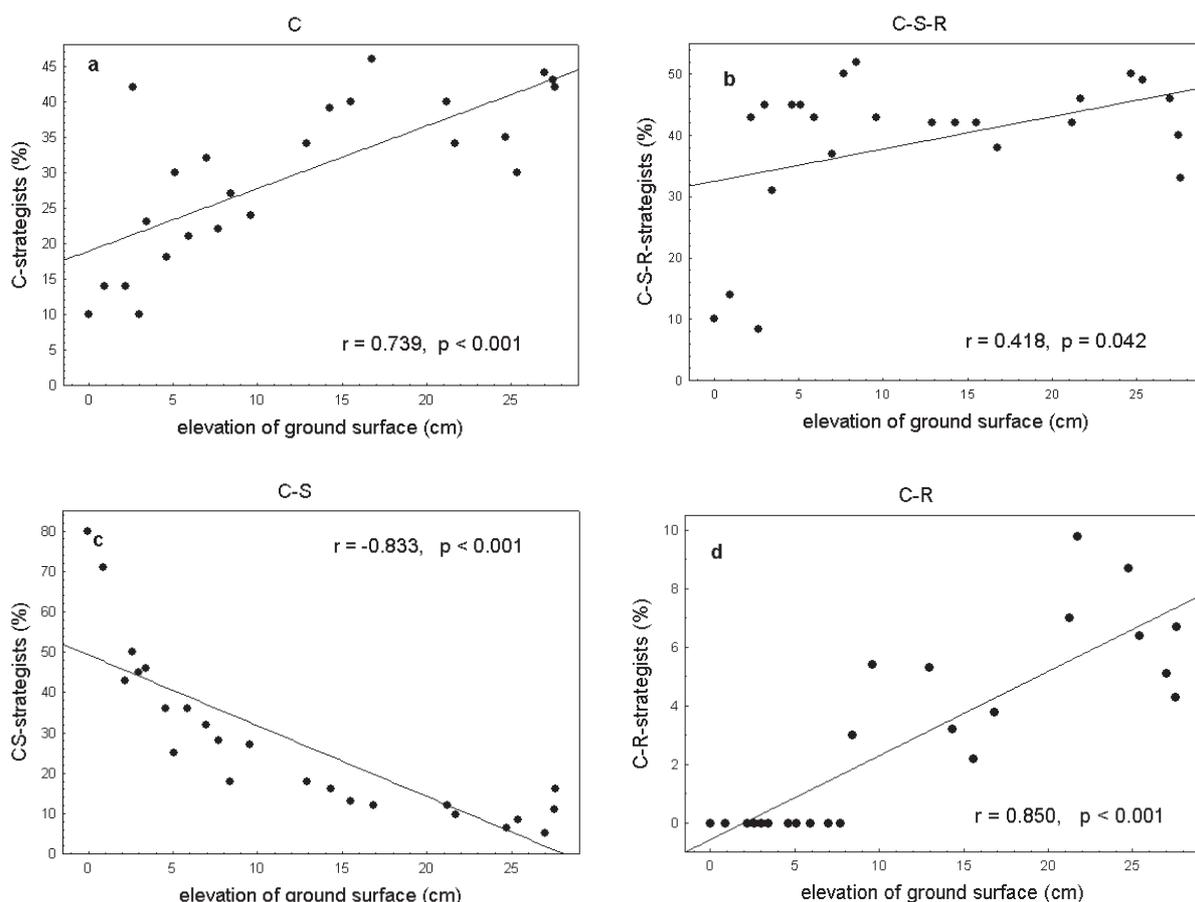
= 0.179). Correlation was very highly significant ( $p < 0.001$ ) in the case of therophytes ( $r = 0.795$ ) and chamaephytes ( $r = 0.832$ ), but these two groups have only a low proportion in the relevés and are often missing.

*Species diversity*

Both  $\alpha$ -diversity indices strongly correlate with the elevational or moisture gradient. The correlation was very strong in case of species richness (Fig. 5a) ( $r = 0.890$ ,  $p <$



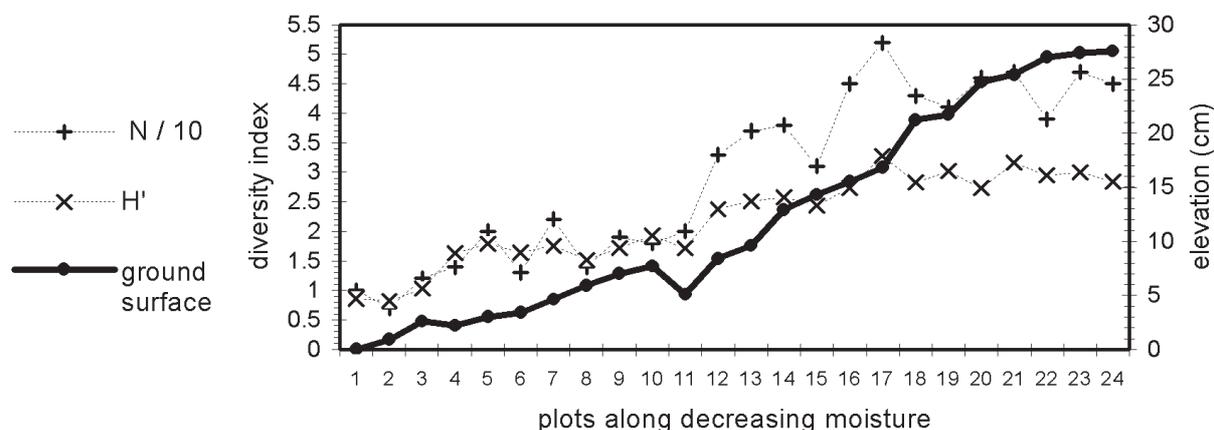
**Figure 2.** DCA ordination of sites according to plant primary ecological strategies. Eigenvalues of the first two axes are 0.14 and 0.02. Cumulative percentage variance of the data for the first two axes was 65.2 and 72.3%, respectively.



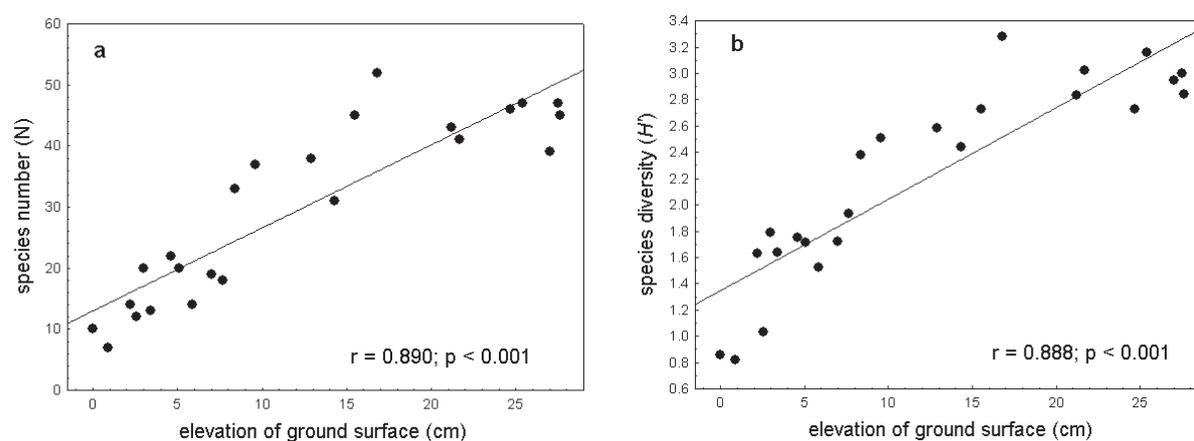
**Figure 3.** Relation between the proportion of ecological strategy types (C-S-R) in relevés and the increasing moisture as the stress factor. Each of the patterns was fitted with a linear regression model.

**Table 2.** The share (%) of C-S-R-strategies in 24 relevés along the transect. The discontinuities more or less overlap with communities (shaded numbers = 20% or over, numbers in bold = 40% or over).

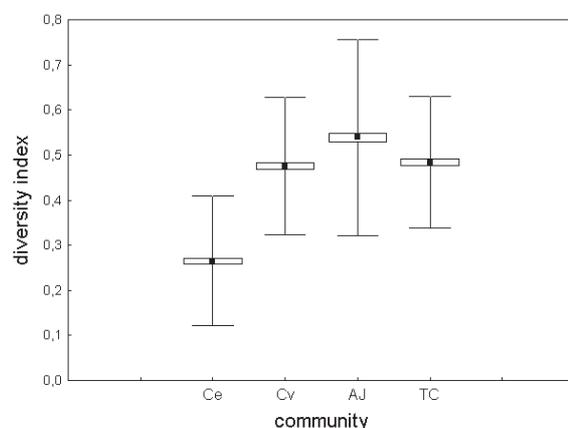
strategy type	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
C-S	<b>80</b>	<b>71</b>	<b>50</b>	43	45	46	36	36	32	28	25	18	27	18	16	13	12	12	10	7	9	5	11	16
C-S-R	10	14	8	43	45	31	45	43	37	<b>50</b>	45	<b>52</b>	43	42	42	42	38	42	46	<b>50</b>	49	46	40	33
C	10	14	<b>42</b>	14	10	23	18	21	32	22	30	27	24	34	39	40	46	40	34	35	30	44	43	42
C-R												3	5	5	3	2	4	7	10	9	6	5	4.3	7
R																					6		2.1	



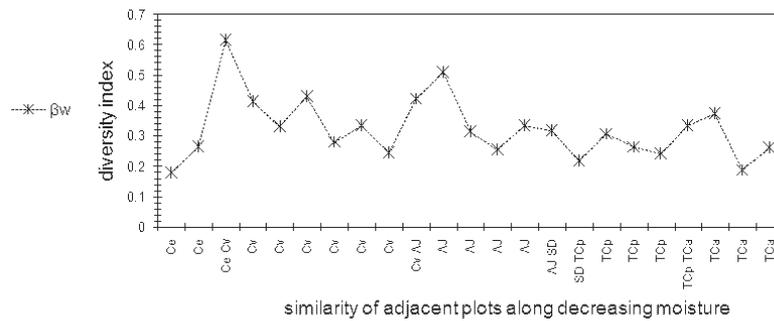
**Figure 4.** Relation of plant species diversity ( $\alpha$ ) and elevation of the ground surface (moisture gradient).



**Figure 5.** The behaviour of species number (a) and species diversity (b) along the ground surface elevation and moisture gradient respectively. Each of the patterns was fitted with a linear regression model.



**Figure 6.** Mean, standard error (box) and standard deviation (whiskers) of  $\beta$ -diversity of the communities presenting similarity/dissimilarity between the communities calculated as Whittaker's diversity index.



**Figure 7.** Change of similarity/dissimilarity between adjacent plots along the transect, presented as Whittaker's  $\beta$ -diversity index (Ce—*Caricetum elatae*, Cv—*Caricetum vulpinae*, AJ—*Agrostio-Juncetum conglomerati*, SD—*Succisello-Deschampsietum caespitosae*, TCP—*Trisetum-Centaureetum potentilletosum*, TCa—*Trisetum-Centaureetum avenuletosum*).

0.001), as well as in case of species diversity (Fig. 5b) ( $r = 0.888$ ,  $p < 0.001$ ). Species richness is the highest in the elevated parts of the floodplain (e.g., *Trisetum-Centaureetum*). Plant species diversity decreases with decreasing elevation (Figs 4-5) and increasing moisture gradient, respectively.

Average  $\beta$ -diversity is the highest in the wet meadow community *Agrostio-Juncetum conglomerati* ( $\beta_w = 0,54$ ), which is in the middle of the studied gradient (Fig. 6). The  $\beta$ -diversity between the adjacent plots along the transect (dissimilarity) reaches the highest values on the transitions between the communities (Fig. 7). In both cases, the community *Succisello-Deschampsietum caespitosae* is an exception since one relevé was recorded in this transect only, and this community is defined by the dominance of *Deschampsia caespitosa*.

## Discussion

### *Distribution of the plant communities and species*

The crucial role of the water regime for shaping the distribution and species composition of herbaceous wetland communities had been discovered by many authors (e.g., Wassen et al. 2002, Dwire et al. 2004, Brose and Tielbörger 2005, Urban 2005), and we have demonstrated that the moisture gradient also governs species richness, diversity and plant ecological strategies. The first ordination axis in all presented ordinations (Figs. 1, 2) corresponds to the moisture gradient.

We found five plant communities ordered along the moisture gradient, and their distribution is in accordance with Balátová-Tuláčková et al. (1993), Zelnik (2005c). They correspond to three different orders, classified in the same way as in Selinger-Looten et al. (1999).

The distribution of plant species is explained by the extent of the floods and type of the deposits (Selinger-Looten et al. 1999, van Eck et al. 2005). Mesophilic plant species dominate on the highest sites, which drain rapidly. They form the community *Trisetum-Centaureetum*. More hygrophilic species, characteristic for the wet meadows, thrive in the middle parts of the gradient, which are still relatively quickly

drained. These species form the communities *Succisello-Deschampsietum* and *Agrostio-Juncetum*. Species which favour water saturated soils are typical of the lowest areas. These wetland species form two marsh communities *Caricetum vulpinae* and *Caricetum elatae*.

### *Distribution of plant functional types*

A clear distribution pattern of plant ecological strategies was discovered along the moisture gradient. Individual communities occur according to their tolerance for flooding as the stress factor. The studied ecological strategy types and life forms efficiently enable the comparison of vegetation types, which is also evidence that certain ecosystem functions are independent of taxonomic composition (Körner 1994). CSR-classification together with multivariate analysis provide a robust explanation of why species composition changes along environmental gradients (Caccianiga et al. 2006).

Marsh communities occur on the lowest sites and are often flooded, and marsh species are tolerant of seasonal flooding since they are mostly C-S-strategists (Grime 2001). C-S-strategists are generally robust perennial strong competitors of the sites with at least one environmental factor in maximum or minimum (Klotz and Kühn 2002). These species are typical stress-tolerant competitors (Grime 2001, Klotz and Kühn 2002). They differ from C-strategists in their capacity for lateral vegetative spread (rhizomes, expanding tussocks), lower maximum potential relative growth rates, larger lifespan of leaves (evergreens), pronounced peak in shoot biomass in the summer (Grime 2001).

Wet and moist meadow communities are composed of a greater diversity of species (Figs. 4, 5), plant strategists (Fig. 3, Table 2) and life forms, which are generally less tolerant of waterlogged conditions. In these communities, competition and other biotic interactions play a greater role in determining species composition and vegetation structure (Grime 1979, 2001, Keddy 1992, Dwire et al. 2004).

Wet meadow communities consist of a mixture of different strategists (C-S-R, C, C-S). Temporary floods within the growth season eliminate some of the more competitive meso-

philic species, and enable this coexistence. The share of C-S-strategists is increasing towards the wetter sites where the competitors (C) are not able to survive longer flood periods that cause anoxic conditions, and stress facilitates tolerating species (Balátová-Tuláčeková 1968).

The relevés of the moist meadows consist mainly of the non-wetland species. There C-strategists are more successful and the presence of C-R- and R-strategists is also characteristic.

### Species diversity

Quite a high number of the plant species was recorded along a relatively short distance (120 m). The high number of taxa in wetlands is a result of small-scale species richness (Hudon et al. 2005), which is a result of ecological gradients (Grime 1979, 2001). In this case, moisture was found as a very important gradient for explaining species richness, which is also in agreement with Grime (1973) and Schaffers (2002).

Species richness is the highest in the communities of the elevated parts of the floodplain (e.g., *Trisetum-Centaureetum*) and decreases with the decreasing elevation of the soil surface (Figs. 4, 5). This correlation was very highly significant in case of plant species richness, as well as in case of plant species diversity. Both parameters were at least three times lower than in the most elevated sites (Figs. 4, 5). Species richness is the lowest on sites where unfavourable conditions exclude all but a few highly specialized species (Grime 2001) and seems to be a function of flood duration (Wassen et al. 2002, Dwire et al. 2004).

We noticed that floods stem from rain- and run-off water (Zelnik 2005c), which is nutrient-poor, and facilitates nutrient leaching. This makes the ecosystem more oligotrophic (Zelnik 2005b,c), which generally enables higher species diversity, since the conditions on very nutrient-poor sites almost never allow the dominance of a small number of highly competitive species (Grime 2001). At large scales, productivity is mostly positively correlated with diversity, but the relationship is often neutral or negative at smaller scales, such as among field sampling plots (Grime 1973, Harrison et al. 2006) as was revealed in our research.

Very low water-permeability of these mineral soils and consequent clear differences in water levels have generated relatively sharp borders between contact communities, as is reflected in higher values of  $\beta$ -diversity for the adjacent plots of two different communities along the transect. This characteristic enables thriving of so diverse vegetation types on such a small place (small-scale pattern), as can be seen from high values of  $\beta$ -diversity between the studied communities.

### Conclusion

We found that the moisture gradient has created a specific distribution of plant communities and caused structural and functional differences in the vegetation, since the corre-

lation with the moisture gradient was confirmed on the level of species composition, functional types (ecological strategies, life forms) and biodiversity.

The moisture gradient determines the competitiveness between individual species and dominance of species tolerant of floods in the wettest sites, and the change to dominance of competitors in mesic sites was already recorded by (Grime 1979, 2001, Keddy 1992, Dwire et al. 2004). Greater species richness was mirrored by greater functional diversity, as was also found by Pierce et al. (2007).

**Acknowledgements.** We thank Mr. A. McConell-Duff for correcting and reviewing the English text. This research was financially supported by the Ministry of Higher Education, Science and Technology.

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Received September 8, 2007  
 Revised January 17, 2008  
 Accepted February 2, 2008