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DIFFERENCES BETWEEN THE ELEMENT CONCENTRATIONS OF REED ORGANS AND THE SUBSTRATE ALONG WATER DEPTH GRADIENTS IN LAKE BALATON, HUNGARY

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A widely described phenomenon all over Europe is that reed decline begins from greater water depths – i.e. clumping is more expressed at the open water fringe while stands towards the lakeshore are homogeneous and intact. To understand the possible background processes, the present paper examined the differences between the element concentrations of reed organs (root, rhizome, stem and leaf), and the substrate (i.e. sediment or soil) along water depth gradients in Lake Balaton, Hungary. Differences between the mineral compositions of reed organs and the substrate and the impact of water depth on element concentration of samples were investigated. Relations between water depth and element concentrations of substrate and plant organs and interelement correlations in the samples were also considered.

In addition to other results, element concentrations provided indirect evidence for increasing hypoxia (anoxia) in the sediment under greater water depths possibly contributing to reed decline. Although, the greater water depth is associated with higher element concentrations in the substrate, the uptake of minerals in reed are impeded by anoxia. Towards the greater water depth, for instance, the higher N concentration of substrate was not associated with more N in leaves (even a slight decrease was observed). On the other hand, elements (e.g. Fe and S) with increasing availability in reduced state, reached high concentrations in reed leaves from greater water depth, which may also indicate the insufficient O_2 level in the rhizosphere.

Key words: flood tolerance, hypoxia, interelement correlations, *Phragmites australis*, principal component analysis, reed decline

INTRODUCTION

The effects damaging wetland habitats all over the world highlight the significance of detecting deleterious processes taking place in declining ecosystems. Plant species forming extensive associations deserve special atten-

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tion since these plants provide not only habitat and food for animals but also affect their abiotic environments significantly.

Due to its spread and complex role in aquatic ecosystems, common reed (*Phragmites australis* (Cav.) Trin. ex Steud.) is a popular object of research. Although reed decline has been detected for decades in several European lakes and there are many publications on the subject (Haslam 1989, Ostendorp 1989), in many cases even the most conspicuous phenomena have not been explained satisfactorily.

Such a phenomenon described all over Europe is that reed decline begins from the open water (i.e. from greater water depths) while stands towards the lakeshore are homogeneous and intact (Boar *et al.* 1989, Cizková-Koncalová *et al.* 1992, Picek *et al.* 2000).

Adaptations of plants to flooding have been investigated intensively (for relevant reviews, see Ernst 1990, Brändle 1991, Blom 1999). Besides the mechanical damage caused by fishes (Picek *et al.* 2000) and wave attacks (Coops *et al.* 1994), one of the main harmful effects in deeper waters is the reduction of oxygen concentration in the sediment. The latter may be aggravated by the oxygen demand of decomposing organic matter (Cizková *et al.* 1996*b*). As a consequence of decreasing oxygen concentration, nutrients are transformed to reduced state, the mineral uptake changes and some of the elements even become toxic (Ernst 1990, Yamasaki *et al.* 1992, Blom 1999). Altered microbial activity also contributes to these processes (Van der Putten 1997, Picek *et al.* 2000).

To avoid the consequences of anoxia, reed maintains a convective gas-flow from the atmosphere to the organs below the water surface and releases O_2 to the rhizosphere (Armstrong *et al.* 1992). Premature senescence, phytotoxins, insect and fungal attacks reduce this downward oxygen transport (Armstrong *et al.* 1996). In the case of insufficient O_2 supply (i.e. anoxia, ultimately) the energy demand of growth is mainly provided by anaerob fermentation (Haldemann and Brändle 1986) and flood tolerance of reed is determined by the carbohydrate level in the rhizome (Brändle 1991, Cizková-Koncalová *et al.* 1992, Cizková *et al.* 1996*a*, Van der Putten 1997). The maximum water depth that reed can still tolerate depends also on substrate conditions. *Phragmites* has an increased sensitivity to anoxia in a reductive environment (nutrient rich mud) compared with oxidising sandy substrates (Weisner and Granéli 1989). Cizková *et al.* (1996*b*) and Van der Putten (1997) suggested that reduced reed performance correlates with high organic matter content in sediment (i.e. eutrophic conditions). (However, Cizková *et al.* (1996*b*) also observed accumulated litter inside reed stands where no decline occurred.) Although eutrophication is a well investigated phenomenon, it is still questionable whether increasing nutrient availability influences the growth and existence of wetland plants and promotes decay processes in direct or indirect ways (e.g. through altered O_2

demand). Clevering (1998) considered water depth (through O_2 and CO_2-availability) as a selective force for emergent macrophytes stronger than nutrient availability.

In spite of the huge amount of studies focusing on element content of reed (for relevant review, see Dykyjová 1979, Ksenofontova 1988) only a few consider the possible correlation between water depth and mineral composition of reed (Dinka 1986, Ksenofontova 1988, Kühl and Kohl 1992, Weisner 1996). The present paper has the objective to reveal the differences between the element contents of reed organs and the sediment along water depth gradients in Lake Balaton, Hungary.

Reed decay has been observed and monitored for a long time in Lake Balaton, and investigations studying the possible reasons have provided many important results (Kovács *et al.* 1979, 1989, 1990, 1994, Dinka 1986). Since the decline of reed is detectable mostly at the northern lakeshore where water is much deeper, and clumping is more expressed at the open water fringe, this study presents characteristics in mineral concentrations correlating with that phenomenon.

MATERIAL AND METHODS

Sampling was carried out in six different reed stands at the northern and southern shores of Lake Balaton (Fig. 1) along six transects at right angles to the shore. At the northern lakeshore in the deep water (1.5–2 m) extensive reed

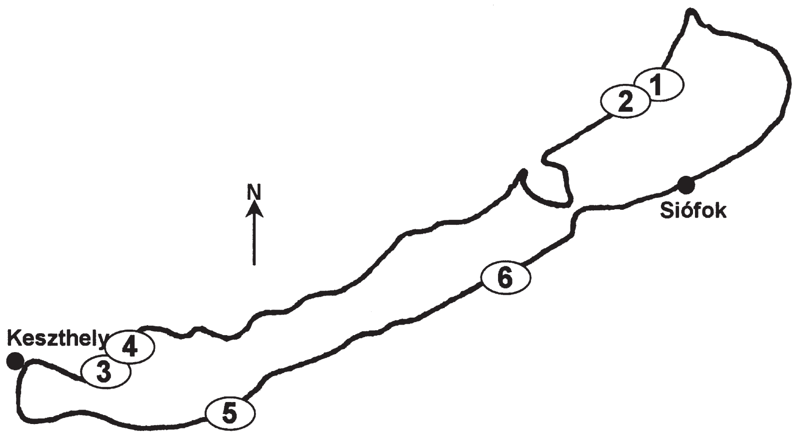

Fig. 1. Location of the six transects designated in different reed stands at Lake Balaton. Northern lakeshore: Káptalanfüred (1); Alsóőrs (2); Szigligeti-öböl–Szépkilátó (3); Szigligeti-öböl–Bece-hegy (4); southern lakeshore: Balatonfenyves (5); Balatonszárszó (6)

stands are situated which are however clumping from the open water fringe. At the southern shore in shallower water (0.5–1 m) smaller, previously retreated but nowadays expanding stands can be observed. Samples were taken in 4 zones inside each transect (Fig. 2). Zone I represents the open water fringe of reeds; zone II corresponds to the median parts of the littoral stands; zone III is situated at the boundaries of littoral and supralittoral; while zone IV takes place in supralittoral reeds (closest to the lakeshore) where the substrates are swampy meadow soils, usually. The average water depth at zones of both northern and southern shores of the lake is also shown in Figure 2.

At the 6 × 4 = 24 sites, 5 samples of substrate (i.e. sediment or soil) and reed organs (root, rhizome, stem and leaf), respectively, were collected and merged into compound samples in July 1997. After destructing reed organs in 65% HNO_3 and 30% H_2O_2 solution in heated Teflon bombs, and shaking substrate samples in 2N HNO_3 for 2 hours, the concentrations of the following elements were determined by Inductively Coupled Plasma Atomic Emission Spectrophotometer (ICP AES): Al, As, B, Ba, Ca, Cd, Co, Cr, Cu, Fe, Ga, K, Li, Mg, Mn, Mo, Na, Ni, P, Pb, Se, Si, Sr, Ti, V, and Zn. The C, N and S concentrations of samples were determined by FISONS NA 1500 C/N/S-analyser, after Dumas' method.

To evaluate (i) the differences between the nutrient concentrations of reed organs and the substrate, and (ii) the impact of water depth on element concentration of samples, standardised principal component analyses (PCA) were

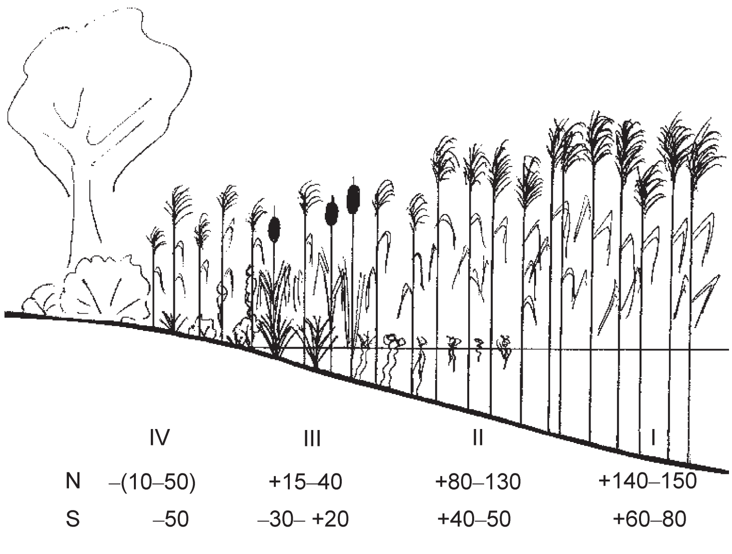

Fig. 2. Average water depth (in cm) in the four zones (I–IV) in the transects investigated at the northern (N) and southern (S) shores of Lake Balaton

performed using the SYN-TAX computer program package (Podani 1994, 1997). In case (ii), water depth data of samples were classified into successive 30 cm categories (in cm): 1: ≥120; 2: 119–90; 3: 89–60; 4: 59–30; 5: 29–1; 6: 0≥. Furthermore, correlation coefficients (Hogg and Tanis 1988) have been calculated between (iii) water depth and element concentrations of substrate and plant organs; and (iv) between element concentrations in the samples.

RESULTS

Of the elements examined, concentrations of As, Co, Ga, Li, Mo, Se, Ti and V were below the detection limit of ICP, these elements were, therefore omitted from the statistical analyses.

Differences between element concentrations of reed organs and the substrate

Figure 3 presents the result of PCA including the nutrient concentrations of reed organs and substrate. Variables (i.e. elements) are shown as vectors,

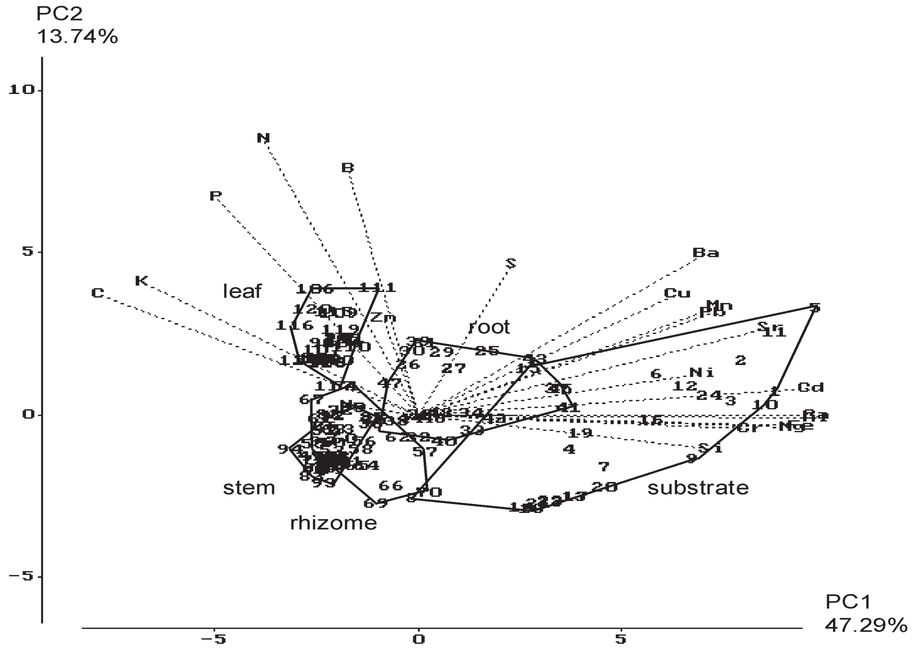

Fig. 3. PCA ordination of the nutrient concentrations of reed organs and substrate. Variables (i.e. elements) are shown as vectors, and the groups of similar objects (leaf or root samples, etc.) are enclosed by convex polygons

and the groups of similar objects (leaf or root samples, etc.) are enclosed by convex polygons. (The average element concentrations and standard deviations are shown in Table 1.) Considering the organs, stem and rhizome had the most similar mineral composition, while root is situated between the other organs and the substrate. As represented by the area of polygons (and by standard deviations in Table 1), the largest variance in the element concentrations was observed between the substrate samples, and the smallest ones between the leaf and stem samples, respectively.

Vectors directed towards the "substrate" polygon show the elements attaining the highest concentration in those samples. These elements are: Ba, Cu, Mn, Pb, Sr, Ni, Cd, Ca, Al, Cr, Mg, Fe and Si. Of the organs, root contained the highest concentrations of the nutrients mentioned above. Leaf has the greatest amount of C, K, P, N and B, while S reaches the highest concentration in the root.

Table 1
Average element concentrations (in μg/g) of the substrate and plant samples

	Substrate	Root	Leaf	Rhizome	Stem
Al	2,471±1,039	835±449	61±26	239±157	51±28
B	1.84±2.69	2.35±2.54	5.46±1.70	1.79±1.61	1.36±0.67
Ba	40.64±28.01	27.17±16.02	27.48±11.42	10.05±6.60	10.54±11.81
C	95,162±76,915	290,532±93,330	407,887±10,462	329,916±113,347	403,142±21,067
Ca	66,642±27,078	20,337±19,985	4,173±1,192	4,311±2,349	1,692±1,787
Cd	1.29±0.56	0.76±0.34	0.05±0.05	0.16±0.16	0.05±0.08
Cr	5.54±2.39	2.46±2.62	0.49±0.34	2.16±2.57	0.58±0.46
Cu	9.53±7.33	10.81±5.15	3.89±1.50	3.82±1.66	2.70±2.36
Fe	5,349±1,771	3,389±1,945	146±56	894±748	102±52
K	355±182	3,382±1,656	9,308±1,742	5,958±4,692	5,974±2,408
Mg	7,781±2,349	2,990±1,149	1625±491	1106±330	623±153
Mn	159.69±50.24	111.23±63.11	106.77±37.41	46.45±19.84	44.90±19.27
N	4,985±4,895	12,411±4,420	27,869±4,747	7,936±2,888	7,734±2,302
Na	168±119	1,122±653	242±119	905±614	561±273
Ni	10.19±4.85	7.28±5.48	3.83±3.95	4.70±5.69	2.34±1.98
P	369±117	847±358	1,567±229	748±330	761±221
Pb	11.03±11.21	6.43±3.05	1.72±1.80	2.10±0.94	2.12±3.27
S	2,824±3,830	5,026±5,328	2,084±1,519	1,980±2,852	297±430
Si	595±202	221±120	227±82	212±101	329±134
Sr	148.79±63.95	61.64±46.18	67.42±36.34	16.88±6.97	16.80±10.78
Zn	28.86±15.91	74.64±43.10	42.86±22.05	42.86±23.13	43.56±40.12

Mean±SD

Correlation between water depth and element concentrations of substrate and plant samples

Positive correlation (Table 2, above diagonal) was obtained between water depth and Ca, Cu, K, Ni, S, Si and Sr concentrations of substrate. In other words, substrate samples taken from deeper water contained higher concentrations of these elements. Of the organs, more elements correlated positively with water depth in root and leaf than in rhizome and stem. For example, greater water depth was associated with higher concentration of Ca in root and stem and that of Fe in leaf.

Sulphur accumulated in higher concentration in all organs grown on substrate containing greater amount of this element. Positive correlation was obtained between nearly all organs based on their Ca, Na and S concentrations, and between the P concentrations of root-rhizome, rhizome-stem and stem-leaf.

Negative correlation (Table 2, below diagonal) occurred in much fewer cases. Deeper water resulted, for example, in lower B concentration in substrate, K in rhizome and P in leaf. It is worth pointing out, that negative correlation was not obtained between any organs.

Differences in element concentrations of substrate and reed organs along water depth gradient

Figure 4 presents the result of PCA including the element concentrations of substrate samples. Objects classified into the same water depth categories are enclosed by convex polygons. Except for groups 5 and 6 including sub-

Table 2
Positive (above diagonal) and negative (below diagonal) correlations ($P < 0.05$) between water depth and element concentrations of substrate and plant samples

	Water depth	Substrate	Root	Rhizome	Stem	Leaf
Water depth	–	Ca, Cu, K Ni, S, Si, Sr	Ca, Ni Pb, Sr	Ni, Pb	Ca, Sr	B, Cd, Fe
Substrate	B	–	B, C, Cu P, Pb, S	B, C, Cr, N, S	Mn, S	Mn, P, Pb, S
Root		K	–	B, C, K, Mn Na, P, Pb, S Si, Zn	Ca, Fe, Mg Na, S, Si	Ca, Mg, Ni, S
Rhizome	Ba, Cu K	Cr, Mg		–	B, Ca, Cu, N, Na P, Pb, Si, Zn	B, Ca, Cu N, Na
Stem	Cr, Cu	Cd, Si			–	Ba, Ca, Cu, Fe, K, Na, P, Pb, S, Sr
Leaf	P	Na, Ni, Mg				–

strate samples taken from water depth less than 30 cm, polygons formed a series (represented by arrow from group 4 towards group 1 in Fig. 4) along the depth gradient. Mineral composition correlated with this tendency: the deeper the water where the substrates were taken from the higher the element concentrations of samples. Between samples taken from water surface less than 30 cm (polygons 5 and 6) large variances were observed.

Similar tendency was observed based on the element concentrations of leaves (Fig. 5): the greater the water depth, the higher the concentrations of some (but not all) nutrients in that organ. Elements accumulated in higher amount with deeper water are Mg, Sr, Ba, S, Ca, Si, Zn, Cd, Al and Fe. In contrast to the results observed in the substrate, nitrogen and potassium concentrations of leaves decreased slightly in sites covered by thicker water layers.

Similar divergences of mineral composition along water depth gradients were observed neither in the root, nor in the rhizome or stem.

Interelement correlations in substrate and plant samples

Many more positive interelement correlations were obtained than negative ones (Table 3). Most of these positive correlations were observed in sub-

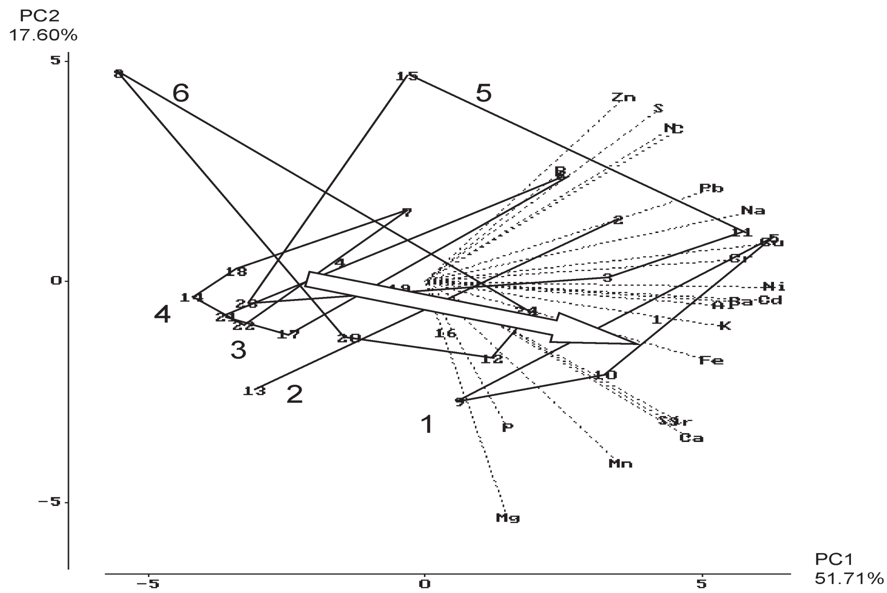

Fig. 4. PCA ordination of the element concentrations of substrate samples. Variables (i.e. elements) are shown as vectors, objects classified into the same water depth categories are enclosed by convex polygons. Water depth categories (in cm) are: 1: ≥120; 2: 119–90; 3: 89–60; 4: 59–30; 5: 29–1; 6: 0≥

strate (shown by S in Table 3), while only one negative correlation, namely between the concentrations of Mg and Zn was obtained in these samples. Positive correlations were found between the concentrations of Al-Ca and Ca-Fe in all types of samples and between K-P in all organs. Positive interelement correlations between the concentrations of Ba-Sr-Mg were also frequent. Carbon content correlated negatively with other elements in most cases: with Ca, Cd and Fe in root, rhizome and leaf. Negative correlations were observed between the concentrations of Si-Fe and Si-Mg in rhizome and between Si-N in leaf.

DISCUSSION

Differences between the mineral compositions of reed organs have been investigated by several studies. Since the content of mineral nutrients in reed depends on the developmental stage of the plant (Bayly and O'Neill 1972, Kvet 1973, Mochnacka-Lawacz 1974, Dykyjová and Hradecká 1976), and our investigations were carried out in July, that is before the element translocation

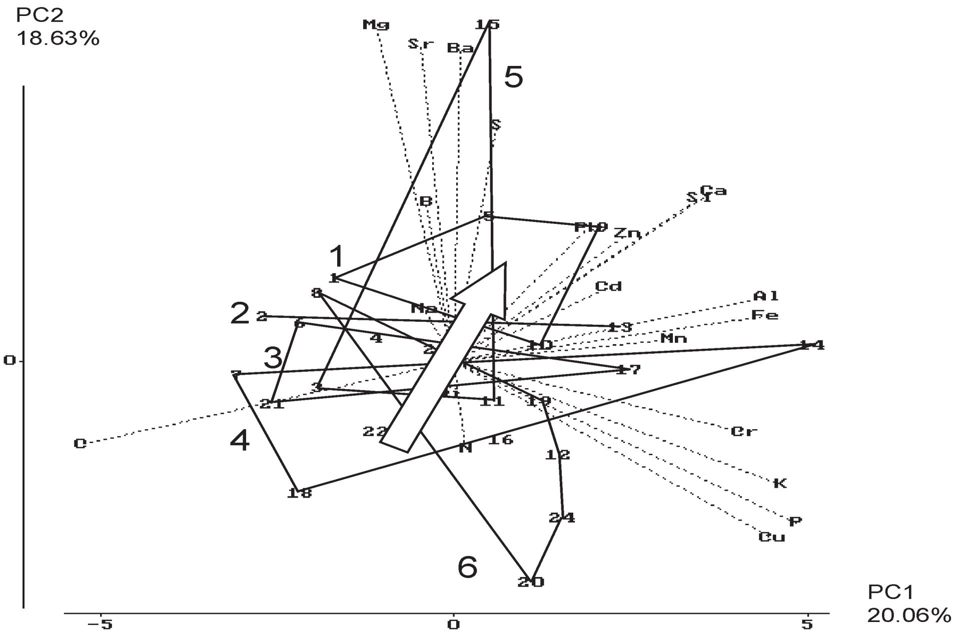

Fig. 5. PCA ordination of the element concentrations of leaf samples. Variables (i.e. elements) are shown as vectors, objects classified into the same water depth categories are enclosed by convex polygons. Water depth categories (in cm) are: 1: ≥120; 2: 119–90; 3: 89–60; 4: 59–30; 5: 29–1; 6: 0≥

Table 3
Positive (above diagonal) and negative (below diagonal) interelement correlations ($P < 0.05$) in substrate (S) and plant (root: R; rhizome: r; stem: s; leaf: L) samples

	Al	B	Ba	C	Ca	Cd	Cr	Cu	Fe	K	Mg	Mn	N	Na	Ni	P	Pb	S	Si	Sr	Zn
Al	–		SRr	S	SRLrs	SR	SRr	S	SLs	S	Rr	R		SL	SR		S	S	SL	SRrs	S
B		–	S	Rr		s		S				S	rs				Srs	SRr	s	s	S
Ba		R	–	S	SRL	SR	S	S	SR	S	Lrs	SR	S	S	Ss	R	S	Ls	Ss	SRLs	S
C	RLr		R	–		S	S	SR					SRr	S	S		S	SRr		S	S
Ca				RLr	–	SR	Sr	S	SRLrs	S	SRr	SRL		S	SRr	S	Ss		S	SRrs	
Cd				RLr		–	SRr	S	SRr	S	R	SR	S	S	S	R	Ss	S	S	SRr	S
Cr		Lr		Lr			–	SLs	Sr	SL	r	R	S	S	S	RL	SL	S	S	S	S
Cu								–	S	SL		L	S	S	S	L	S	S	S	S	SRrs
Fe		R		RLr					–	Ss	r	SR		SL	SL	R	S	S	SL	SRrs	
K				s						–		SL	s	S	S	RLrs	S	S	S	S	L
Mg								L		L	–	SRs		R	r	S		Ls	SL	SRLrs	
Mn		r		Rs			s	R				–	L		SR	SRL		s	Ss	SR	
N	L			s			r						–	S	S	Ls	SRs	SRr	s	s	S
Na		L		L								L		–	SL		SL	S	S	S	S
Ni												L			–		S	Ss	S	SRr	S
P		R						R			L					–	s	L		SR	L
Pb												r					–	S		Ss	Sr
S			R									Rr						–	s	Lr	SL
Si			r	Ls					r		r		L						–	Ss	s
Sr				R																–	
Zn	R			s							S	R		r		R					

back to the rhizome took place at the end of vegetation period (Kühl *et al.* 1997), results are compared only with papers studying the same state of reed.

In accordance with Podani *et al.* (1979), stem and rhizome had the most similar mineral composition. Considering the leaf, the highest K, P and N concentrations were determined in this organ also by Kvet (1973), Dykyjová and Hradecká (1976), Dykyjová (1979), Dinka (1986) and Mochnacka-Lawach (1974). The greatest concentrations of N and K (Dinka *et al.* 1979) and N (Ksenofontova 1988) were disclosed also in the leaf. Considering potassium, Ksenofontova (1988) determined similar concentrations of this element in all organs. At the time of sampling, most of the elements occurred in the highest concentrations in the root as compared to other plant parts. Dinka *et al.* (1979) and Suzuki *et al.* (1989) reported the same results.

Investigations on mineral composition of reed often refer to interelement relations. Based on our results, many positive but only one negative correlation were observed between the element concentrations in the substrate. Positive correlations between concentrations of Ba, Ca, Mg and Sr in reed are well known (Podani *et al.* 1979) and result from the similar chemical structure and membrane transport mechanisms of these elements. Relations of phosphorus to other elements are rather different in several studies. Our results showed positive correlations between the concentrations of P and K in all reed organs, which contradicts Podani *et al.* (1979) but confirms the findings of Nabholz and Richardson (1975) and Ksenofontova (1988).

Based on the correlation between the mineral concentrations of reed parts, no element accumulated in an organ at the expense of another. Furthermore, our results confirmed Ksenofontova's (1988) findings that a good balance exists between the P contents in the stem, leaf, panicle and rhizome. In our samples, positive correlations were observed between the P concentrations of the above organs (except for panicle, but completed with root). Sodium, calcium and sulphur also accumulated in this manner in all organs, however, the concentrations were highly different, as mentioned above.

Positive correlations between the element concentrations of substrate and reed parts were obtained in few cases indicating that despite the great amount of certain nutrients in the substrate, plants do not take up and store those elements in the organs. The reason behind – beside species-specific properties – can be the greater water depth probably causing hypoxia, as proved by both the correlation coefficients (Table 1) and PCA results (Figs 4–5). Furthermore, at Lake Balaton, particularly at the northern shore a great quantity of organic matter could be deposited in the reed stands. Therefore, the greater water depth associates frequently with thicker sediment layer making the path of oxygen flow from the atmosphere to the rhizosphere longer and causing more hypoxic conditions. However, differences between the results based on correlation coefficients and PCA's suggest that water depth may affect the mineral composition of substrate and plant organs only in specific depth intervals (>30 cm, in our case). Because of the large variance between samples taken from sites where water depth was out of that interval, correlations can remain in the background. This high variance between the element concentrations of substrate samples taken from shallower water is partly caused by geological differences of the northern and southern shores of Lake Balaton. The base rocks at the northern lakeshore are basalt, Permian red sandstone and dolomite while at the southern one are sand and loess (Majoros and Szabó 1974). The different adsorptive capacities of these rocks (lower of the latters) affect the mineral compositions of the soils developed on them.

As our results suggest, the greater water depth is associated with higher element concentrations in the substrate. (In contrast, Dinka (1986) disclosed less N and P in sediment samples taken from deeper water at Lake Balaton.) The greater amount of elements in the sediment originates from the litter of reeds growing in larger stands towards the deeper water. However, the nutrient decomposition and mineralisation processes as well as the uptake of minerals in reed are impeded by anoxia, therefore, despite the higher element concentration of the sediment in deeper water, reed can utilise only small amount of these nutrients. For the above reasons, the concentrations of certain elements in reed organs decreased towards the open water fringe of stands.

Element concentrations in reed samples taken from different water depth provided indirect evidence for increasing hypoxia (or anoxia) towards deeper water. Under aerobic conditions aquatic plants take up nitrate or ammonium at equal rates, while under anoxia the uptake of ammonium slows down and nitrate is lost rapidly (Yamasaki *et al.* 1992). Normally, in waterlogged soils, radial oxygen loss maintained by convective gas-flow can supplies sufficient oxygen for nitrifying bacteria to produce nitrate from decomposing organic material (Ernst 1990). At our sampling sites, however, towards the greater water depth the higher nitrogen concentration of substrate was not associated with more N in leaves (even a slight decrease was observed). These results may suggest the existence of insufficient O_2 level and inadequate intensity of nitrification in the rhizosphere in deeper water.

High potassium concentration in plants tolerating flooding suggests sufficient radial oxygen loss in rhizosphere, while decrease in potassium concentration may indicate sensitivity against water logging (Ernst 1990). Although substrate samples taken from deeper water at Lake Balaton contained more potassium than those from sites of shallow water, the concentration of that element decreased in leaves and rhizomes indicating that reeds at the open water fringe may not tolerate well the water depth they grow in. As Kovács *et al.* (1989) suggested, decreasing potassium level in below-ground reed organs (that is in rhizomes, in our case) may lead to "decreasing stability" of reed and contributes to a decreased tolerance against parasitic fungi and insects.

Iron availability is increased in reduced state. Due to the effective radial oxygen loss, $Fe(OH)_3$ plaques are formed on root surfaces (Peverly *et al.* 1995) preventing the waterlogged plant to absorb excessive amounts of potentially toxic Fe (Ernst 1990). Higher Fe concentration in reed leaves taken from deeper water (also presented in a previous paper: Engloner *et al.* 2000) may also indicate the insufficient O_2 level in the rhizosphere.

When radial oxygen loss from roots is not enough to oxidise the rhizosphere, sulphur as sulphide can diffuse into the waterlogged plants (Ernst 1990). At our sampling sites, towards greater water depth more sulphur was observed in reed leaves.

Since calcium concentration in leaves increased towards greater water depth and potassium decreased as mentioned above, K/Ca ratio was lower in leaves taken from deeper water. Since this ratio decreases in ageing plants (Dykyjová 1979), the difference of K/Ca ratios between plant samples taken from deep vs shallow water may reflect different degree of senescence, too.

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