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Peak-season and off-season distribution of mineral nutrients in littoral vegetation of an ancient shallow reservoir

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Abstract Differences between peak-season and off-season dry mass, organic matter mass, and both concentrations and pools (standing stocks) of ash, N, P, K, Ca, Mg and Na were investigated in the rhizosphere soil, and live and dead aboveground plant biomass at 14 sites hosting 4 plant community types in the littoral zone of a eutrophic ancient shallow reservoir of about 5 km^2 area, the Rožmberk fishpond (S. Bohemia, CZ). Comparisons between the peak-season and off-season data and several stoichiometric relations calculated from them provided an insight into the mineral nutrient economy of the examined types of the fishpond littoral vegetation. It is rooted in relatively nutrient-poor sandy soil, but differently enriched with nutrients contained in either the percolating fishpond water, or that of springs located at the landward edge of the littoral zone. The degree of eutrophication of our sampling sites and their vegetation thus seem to be positively correlated with the degree of contact of the plants´ rhizosphere with the nutrient-richer fishpond or spring water.

Keywords Littoral wetlands · Nutrient pools · Nutrient resorption · Plant communities · Rhizosphere · Stoichiometry

Introduction

Autotrophic plants, thanks to their uptake of mineral nutrients and other elements or compounds from the soil and water, the nutrient use for metabolic and growth processes as well as nutrient storage in their tissues, are the main drivers of the anabolic (anti-entropy) phases of biogeochemical flows and cycles in most ecosystems of the Earth (see, e.g., Gopal & Masing, 1990; Dykyjová & Úlehlová, 1998; Vymazal, 2017). On the other hand, heterotrophic organisms, such as most bacteria, fungi and animals, are the main drivers of the catabolic or degradation phases of these flows and cycles. Wetland ecosystems of various types are no exception from this general rule. In this paper, our attention was concentrated on the mineral nutrient budgets in the vegetation and mutual soil–plant nutrient transfers in four wetland plant community types typical of the littoral zones of many

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Central European standing water bodies. For these assessments, we made use of data on mineral nutrient concentrations and standing stocks and size estimates of the soil–plant nutrient transfers published earlier by Květ & Ostrý (1988), who partly used the data on soil analyses published by Ostrý & Zákravský (1988). They studied stands of four wetland plant community types as defined by Hroudová et al., (1988), located in different sub-zones of the littoral zone of a single Central European shallow standing water body, a large fishpond, which has become eutrophic in the course of the last 100 years. This trophy increase has resulted from a rapid increase of the intensity of pond management for fish (mainly common carp, *Cyprinus carpio* L.) rearing (Hejný et al., 2002; Pechar et al., 2002).

The purpose of the investigations described in this paper was to test the following three hypotheses: (1) Habitat sets of the four community types studied differ in nutrient supply to the vegetation and in the size of organic matter pools in the rhizosphere, reflecting the distances of the sites of each plant community type from the shoreline (both into and from the water). (2) Aboveground biomass of the four community types contains different pools (standing stocks) of mineral nutrients; differences also exist in the efficiency of late-season nutrient resorption from above- to belowground plant parts (estimated from differences between the summer and fall nutrient standing stocks in aboveground live or dead plant biomass). (3) Given the clear effect of hydrology on biomass production (see, for example, Hrivnák, 2005), we expect that soil moisture content will affect plant nutrient standing stocks.

Methods

Study Site

Mineral nutrient contents and standing stocks were measured in aboveground plant structures and the rhizosphere soil in 14 sites of four different plant community types in the littoral zone of the Rožmberk fishpond, a sixteenth century shallow reservoir (mean depth = 1.5 m) situated in the Třeboň Basin Biosphere Reserve (BR) and Protected Landscape Area (PLA), South Bohemia, Czech Republic (Fig. 1). The pond was formed by damming the Lužnice River, a tributary to the Vltava River, which is the main Bohemian tributary to the Labe/Elbe River, which flows into the North Sea. Rožmberk pond, the largest fishpond in the Czech Republic with an area of about 5 km^2, was designed and is still used for fish rearing and flood control (Hejný et al., 2002). In addition, it also receives treated municipal wastewater from the nearby town of Třeboň. The pond was also the repository of treated sewage from a now-defunct pig farm, a practice that ended in 2008. The pig sewage contained large amounts of suspended solids. This nutrient input, along with the intensive practices of maintaining a dense fish stock by the addition of manure

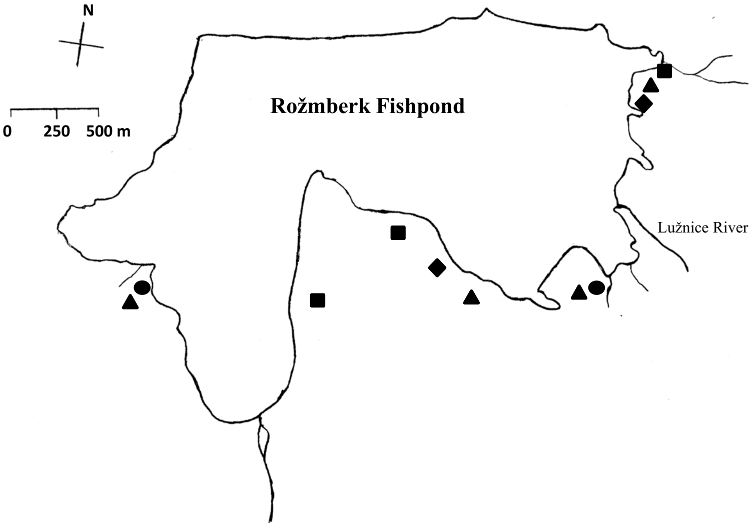

Fig. 1 Map showing the location of the studied littoral plant stands along the Rožmberk fishpond. Studied communities: *Phragmites australis* (diamonds); *Carex acuta* (triangles); *Calamagrostis canescens* (squares); *Glyceria maxima* (circles). Drawing based on Hroudová et al., (1988)

and grain as fish feed, led to the pond becoming very eutrophic in its certain parts, especially along its western shore (Fig. 1).

The four studied community types were dominated (and thus named) by the following species (numbers of sites in brackets): *Phragmites australis* (Cav.)Steud. *(3). Carex acuta* L. *(5), Calamagrostis canescens* (Weber)Roth *(3)* and *Glyceria maxima* (Hartman)Holmberg *(3)*. These sites were selected to represent the ranges of habitats colonized by each of these plant community types. Plant nomenclature follows Kaplan (2019). For more detailed soil and vegetation characteristics of the 14 sites selected for our investigations, see Hroudová et al., (1988). Briefly, the *Phragmites australis* and *Glyceria maxima* community types are closest to open water, followed by the *Carex acuta* community in the middle and the *Calamagrostis canescens* community being most landward. The *Phragmites australis* type can grow in nutrient-rich organic to nutrient-poor sandy substrates over a wide range of water depths (up to 1.2 m; Hroudová et al., 1988), forming dense stands. The *Glyceria maxima* community also grows mostly on nutrient-rich, muddy substrates in habitats protected from wave disturbance. The *Carex acuta* community can tolerate a wide range of hydrologic and nutrient conditions, being tolerant of long-term flooding as well as fluctuating water levels and growing in meso-to-eutrophic habitats. *Calamagrostis canescens* prefers relatively drier wetland habitats often associated with shrubs and alder carrs (Hroudová et al., 1988).

Sample collection

The harvest method was used to estimate the aboveground biomass of each community at each site. Either live summer (peak season) or dead fall (off-season) biomass was harvested from four replicate square plots (0.25 m^2) in the *Phragmites*, *Glyceria* or *Calamagrostis* communities, and from four replicate 0.5 m^2 rectangular plots in the *Carex*-dominated community. Live-plant samples (summer, collected between June 28–July 6, 1982) were divided into species and then dried at 85 °C to estimate the dry weight (DW) of each of them. This period was selected for the live aboveground plant biomass sampling because, under Central European climatic conditions, it is this time of year that the plant stands selected for our study exhibit the highest nutrient standing stocks, each calculated as the product of the respective nutrient concentration in live aboveground stand biomass and the amount of this biomass. It is also usually the time of maximum plant biomass for this region (see, e.g., Květ 1971, 1973 and Dykyjová & Úlehlová 1978 for *Phragmites australis*; Dykyjová 1983 for *Carex acuta* and *Calamagrostis canescens* and Westlake 1966 and Dykyjová & Úlehlová 1978 for *Glyceria maxima).*

Litter samples were actually collected in early spring (May–June) 1983 because of the inability of collecting litter in November 1982 due to heavy snowfall and subsequent flooding. It was assumed that the amount of litter collected is a slight underestimation due to the high probability of low rates of decomposition under the snow cover over the winter. The collected litter was also dried at 85 °C and weighed to determine its DW.

Soil blocks (16 × 16 cm) were taken from the upper 20–30 cm of the soil profile, which was assumed to equal the greatest proportion of the rhizosphere (rooting zone, estimate of about 90% of the roots). Sampling occurred six times in the year at each site, with the seasonal samples averaged to develop soil characteristics for each site. Peak- and off-season nutrient contents and nutrient pools were determined from the June 28 and November 17, 1982, sampling dates. The nutrient pools were calculated by transposing the data to a 1.0 m^2 surface area (individual nutrient concentration × soil bulk density for a volume below the square meter ground area; Květ and Ostrý 1988).

NO_3^-, total nitrogen (TN), total phosphorus (TP), Ca, K, Na and Mg were measured in both the plant and soil samples, while NH_4^+, orthophosphate (PO_4) and carbon were measured only in the rhizosphere soil samples. Chemical analyses of the plant material corresponded with methods recommended by the Czechoslovak Ministry of Agriculture at that time (Koppová et al., 1955). NO_3^- was measured using an ion-selective electrode, TN by the Kjeldahl method, TP colorimetrically using the molybdenum blue technique, flame photometry was used to estimate Ca, K and Na, while Mg content was determined complexometrically. The ash content of the plant material was determined by ignition at 450 °C, which was then used to calculate plant organic matter by subtracting the ash content from the dry mass of the samples.

Rhizosphere soil nutrient contents were estimated as described by Ostrý & Zákravský (1988). Briefly, pH was determined electrometrically in H_2O and KCl, NH_4^+ colorimetrically, TN using the Kjeldahl method, PO_4 colorimetrically, Ca, Mg, K and Na by both flame and absorption spectrophotometry, and soil organic matter (SOM) as oxidizable C (by $K_2Cr_2O_7$). Volumetric soil moisture content (SWC) was determined from the last sampling (November 16, 1982) using the methods described by Klika et al (1954). For the other soil parameters, the seasonal values were averaged to develop the soil characteristics for each site.

All nutrient contents were first estimated as dry weight percentages and then extrapolated to standing stocks (g m^{-2}). Stoichiometric ratios were determined on a mol mol^{-1} basis.

Data analyses

Two of the original sites (a *Carex* and *Glyceria* site each) studied in 1982 were omitted from this analysis, because they were not located in the littoral zone of the fishpond, but in adjacent wet meadows. In addition, one of the *Phragmites*-dominated communities was omitted from the dataset, because this one site was found to be an outlier with very different soil and plant characteristics. Therefore, eleven sites were analyzed: *Phragmites australis* (2). *Carex acuta* (4), *Calamagrostis canescens* (3) and *Glyceria maxima* (2). Differences between the four community types were analyzed using principal components analysis (PCA) with the plant and soil rhizosphere nutrient standing stocks as the explanatory variables. Monte Carlo tests (replicates = 999) were run to determine significant differences. Pearson correlations were calculated to determine which particular explanatory variables were significantly related to particular axes. The multivariate analyses were run using PC-ORD v 6 (McCune & Mefford 2011).

One-way ANOVAs were run to determine the significance of between-community differences in soil pH and SWC. In addition, ANOVAs were also conducted to test between-community differences in N and P resorption efficiencies (RE). The REs were calculated as the differences between the N and P standing stocks in the summer and fall (litter) aboveground plant structures ($RE = Summer_{nutr} - Fall_{nutr}/Summer_{nutr}$). The data were natural log-transformed in order to meet assumptions about normality and homogeneity of variance. The ANOVAs were run using SYSTAT v 11.

Results

Nutrient contents

Average plant and rhizosphere nutrient contents for each community type are given in Tables 1 and 2. The soils of all four community types were acidic, with pH_{H2O} ranging from 3.65 in the *Glyceria*-dominated community to 5.25 in the *Calamagrostis*-dominated community (Table 1). This difference was not statistically significant [$F_{3,7} = 1.57$, $P = 0.28$] even though there was almost an order of magnitude difference. The *Calamagrostis*-dominated habitats were not only less acidic, but drier than those of the other communities, however, again, the difference was not significantly different [$F_{3,\ 7} = 2.34$, $P = 0.16$]. The soils of the *Calamagrostis*-dominated community were significantly more mineral (significantly higher bulk density) and poorer in nutrients, especially TN, Ca and Na, than those of the other community types (Table 1a).

Nutrient contents in the rhizosphere soil, when expressed on a meter square basis (standing stocks), usually showed significant differences between the community types or the seasons (Table 1b). For example, the soil in the *Glyceria* community was significantly richer in TN, PO_4, Ca and Mg, while the *Calamagrostis* community soils had the highest K, Na and SOM levels. Significant seasonal differences were seen for TN, PO_4, K and Na (Table 1b).

Aboveground plant nutrient percentages did not differ significantly at the time of peak biomass in July (Table 2). However, the communities had significantly different nutrient contents in the off-season, with the *Glyceria* community having the highest nutrient contents followed by either the *Carex* or *Phragmites* community, while the *Calamagrostis* community typically had the lowest nutrient contents. For the off-season samples, only K and the ash content did not differ between the community types.

Table 1 Mean (±1 SD) rhizosphere a) nutrient contents (ppm) and b) nutrient pools (g m^{-2}) for the four wetland plant community types. Acronyms: community—Phraus = *Phragmites australis*; Caracu = *Carex acuta*; Calcan = *Calamagrostis canescens*; Glymax = *Glyceria maxima*. Nutrients—TN = total nitrogen; SOM = soil organic matter; SWC = volumetric soil water content, as proportion. Statistical analyses in rows: small letters signify between-community differences; capital letters represent between-season differences

(a)

Community/nutrients	Phraus	Caracu	Calcan	Glymax
NH_4	374.00 ± 155.56	201.00 ± 120.05	130.67 ± 42.25	271.00 ± 219.20
NO_3	25.50 ± 21.36	7.70 ± 3.94	4.80 ± 1.25	6.50 ± 3.54
TN	30,415.00 ± 11,730.90a	19,295.00 ± 4598.24ab	9606.67 ± 4269.77b	29,470.00 ± 3167.84a
PO_4	33.50 ± 28.99	23.25 ± 6.02	16.67 ± 5.51	62.00 ± 42.43
Ca	8237.50 ± 1856.16a	5456.25 ± 899.62ab	2541.67 ± 945.49b	9800.00 ± 3323.40a
K	1627.50 ± 350.02	998.75 ± 297.02	995.00 ± 196.79	1185.00 ± 84.85
Na	1005.00 ± 63.64a	627.50 ± 29.86bc	541.67 ± 38.19c	932.50 ± 293.45ab
Mg	825.00 ± 537.40	553.50 ± 174.66	281.67 ± 123.93	1085.00 ± 685.89
SOM	1,095,850.00 ± 362,109.38a	554,700.00 ± 168,174.87ab	392,300.00 ± 106,632.50b	687,300.00 ± 49,638.90ab
Bulk density, g cm^{-3}	9.36 ± 1.88b	24.04 ± 6.01ab	80.85 ± 42.99a	26.80 ± 1.82ab
pH	4.44 ± 0.23	4.38 ± 0.37	4.97 ± 0.41	4.18 ± 0.76
SWC	0.82 ± 0.25	0.83 ± 0.10	0.62 ± 0.13	0.91 ± 0.03

Community	Phraus		Caracu		Calcan		Glymax	
(b)								
Community/nutrients	Peak season	Off-season	Peak season	Off-season	Peak season	Off-season	Peak season	Off-season
NH_4	4.06 ± 3.76	8.18 ± 5.83	4.56 ± 2.09	4.92 ± 2.01	3.61 ± 2.68	9.44 ± 2.21	10.77 ± 3.58	10.12 ± 8.82
NO_3	0.11 ± 0.08	0.45 ± 0.30	0.22 ± 0.09	0.20 ± 0.08	0.09 ± 0.03	0.34 ± 0.11	0.49 ± 0.17	0.24 ± 0.16
TN	279.14 ± 125.08b	314.42 ± 237.90	320.80 ± 161.02b	483.04 ± 38.41	319.63 ± 120.81ab	543.63 ± 22.27	666.52 ± 51.57a	1075.93 ± 41.58
PO_4	1.87 ± 3.01bA	1.62 ± 1.98 B	0.22 ± 0.05abA	0.60 ± 0.08 B	0.57 ± 0.23 abA	1.45 ± 0.77 B	0.52 ± 0.07 aA	2.28 ± 1.69 B
Ca	76.05 ± 61.46b	87.80 ± 29.45	122.76 ± 71.88b	160.69 ± 76.28	91.61 ± 46.40b	154.91 ± 25.95	320.90 ± 68.68a	364.76 ± 112.93
K	29.96 ± 30.45	60.70 ± 68.91	16.14 ± 7.44	27.50 ± 6.65	38.54 ± 19.40	78.99 ± 33.98	33.10 ± 19.96	42.06 ± 1.09
Na	19.54 ± 18.51	33.15 ± 34.71	11.78 ± 7.14	18.06 ± 5.75	28.32 ± 17.33	48.84 ± 28.42	20.56 ± 1.55	34.56 ± 12.76
Mg	10.82 ± 8.63b	8.79 ± 3.90	12.64 ± 8.22ab	17.28 ± 11.70	12.67 ± 6.15ab	16.81 ± 3.87	31.18 ± 14.12a	41.46 ± 26.17
SOM	16,670.30 ± 14,816.21b	10,754.07 ± 9101.42	15,470.73 ± 6905.86ab	13,390.70 ± 1780.19	38,781.13 ± 23,980.32a	26,973.80 ± 9645.34	15,034.35 ± 2609.72ab	24,931.90 ± 168.57

Table 2 Nutrient contents and standing stocks (g m^{-2}) in aboveground plant structures in the (a) peak (summer) and (b) off-season periods in four plant community types in the Třeboň Basin Biosphere Reserve (TBBR) studied in 1982–83. Nutrient content units given with each factor in the summer period. Acronyms: community—Phraus = *Phragmites australis*; Caracu = *Carex acuta*; Calcan = *Calamagrostis canescens*; Glymax = *Glyceria maxima*. Nutrients—TN = total nitrogen. Statistical analyses in rows: small letters signify overall between-community differences. Seasonal differences marked in Factor column: ** < 0.01; *** < 0.001

(a)

Community/factor	Phraus		Caracu		Calcan		Glymax	
	Content	g m^{-2}	Content	g m^{-2}	Content	g m^{-2}	Content	g m^{-2}
Biomass ***	–	662.20±75.10a	–	540.75±241.34b	–	307.37±74.64b	–	918.95±192.54a
NO_3 (mg*kg^{-1}) ***	213.35±75.73	1.10±1.17ab	137.27±82.15	0.53±0.21b	164.39±89.98	0.21±0.09b	180.80±180.04	1.84±2.00a
TN (g*kg^{-1}) ***	32.86±16.36	11.26±5.63ab	31.84±28.73	9.23±3.25b	50.41±29.49	4.96±1.35c	17.76±1.68	16.48±4.96a
PO_4 (g*kg^{-1}) ***	2.86±0.97	1.21±0.50ab	3.28±3.09	0.89±0.24b	3.78±2.26	0.40±0.18c	2.78±0.19	2.84±0.06a
Ca (g*kg^{-1}) **	7.25±7.82	1.58±0.50b	6.29±7.29	1.45±0.54b	8.91±5.99	0.73±0.12c	4.21±0.44	3.82±0.40a
K (g*kg^{-1}) ***	27.48±22.80	7.52±0.86ab	25.31±20.22	7.53±2.46ab	47.12±31.53	3.89±0.18b	19.11±6.79	18.22±9.92a
Na (g*kg^{-1}) **	0.92±0.67	0.38±0.08a	0.47±0.52	0.12±0.05b	0.66±0.37	0.06±0.01b	0.70±0.66	0.58±0.48a
Mg (g*kg^{-1}) ***	3.94±3.39	0.99±0.16a	3.82±4.78	0.83±0.33a	5.23±3.50	0.44±0.10b	1.10±0.61	0.96±0.35a
Ash (g*kg^{-1}) ***	94.70±64.91	33.98±1.31a	97.92±82.26	26.12±6.83b	150.43±81.14	15.08±5.34b	78.71±1.44	72.19±13.83a

(b)

Community/factor	Phraus		Caracu		Calcan		Glymax	
	Content	g m^{-2}	Content	g m^{-2}	Content	g m^{-2}	Content	g m^{-2}
biomass	–	456.00±147.22	–	195.22±45.91	–	191.43±29.54	–	391.55±128.76
NO_3	26.88±3.49	0.14±0.05	31.28±4.66	0.08±0.04	26.84±2.29	0.06±0.02	56.28±0.12	0.38±0.13
TN	9.24±2.99	4.68±2.38	11.29±1.48	2.20±0.65	6.15±1.21	1.16±0.12	12.05±3.04	4.54±0.38
PO_4	0.52±0.29	0.27±0.18	0.80±0.22	0.16±0.07	0.40±0.19	0.07±0.04	1.48±0.23	0.56±0.11
Ca	1.73±0.47	0.97±0.26	3.64±0.74	0.72±0.29	2.63±0.23	0.50±0.08	4.71±0.08	1.84±0.59
K	0.97±0.01	0.68±0.20	2.85±0.57	0.58±0.26	1.62±0.32	0.31±0.06	3.03±2.90	1.38±1.54
Na	0.56±0.38	0.29±0.23	0.22±0.04	0.04±0.01	0.20±0.04	0.04±0.01	0.56±0.22	0.24±0.16
Mg	0.74±0.05	0.38±0.03	1.46±0.26	0.29±0.10	0.75±0.06	0.14±0.02	1.48±0.08	0.59±0.23
Ash	50.26±12.01	20.83±3.64	45.78±7.92	8.79±1.80	76.85±13.07	15.12±6.38	65.88±13.07	25.06±3.51

Table 3 Aboveground and rhizosphere stoichiometric molar ratios (mean ± 1 SD) from summer and fall 1982 for the four plant communities. Community acronyms: Phraus = *Phragmites australis*; Caracu = *Carex acuta*; Calcan = *Calamagrostis canescens*; Glymax = *Glyceria maxima*. Statistical analyses in rows: small letters signify between-community differences; capital letters represent between-season differences

Community/nutrients	Phraus		Caracu		Calcan		Glymax	
	Peak season	Off-season	Peak season	Off-season	Peak season	Off-season	Peak season	Off-season
N/P Above	23.67 ± 6.26 aA	38.50 ± 7.75 aB	22.55 ± 2.73 aA	32.44 ± 5.73 aB	29.34 ± 7.87 aA	44.50 ± 26.89 aB	12.89 ± 4.15 bA	17.94 ± 1.87 bB
Rhizo	1596.38 ± 6348.25	1724.24 ± 1762.80	3506.70 ± 2033.18	1807.84 ± 351.38	1272.24 ± 152.41	1059.20 ± 676.74	2844.85 ± 167.62	1464.55 ± 1128.34
N/K Above	4.21 ± 1.15 A	22.03 ± 11.43 B	3.41 ± 0.41 A	11.22 ± 2.12 B	3.55 ± 0.87 A	10.63 ± 0.92 B	2.72 ± 0.72 A	23.64 ± 25.21 B
Rhizo	41.42 ± 23.84	37.75 ± 38.73	61.10 ± 35.65	52.11 ± 17.17	25.02 ± 6.76	21.83 ± 9.64	70.28 ± 46.72	71.45 ± 4.61
P/K Above	0.18 ± 0.06 A	0.62 ± 0.37 B	0.15 ± 0.01 A	0.35 ± 0.09 B	0.13 ± 0.06 A	0.29 ± 0.12 B	0.23 ± 0.13 A	1.23 ± 1.28 B
Rhizo	0.05 ± 0.05	0.03 ± 0.02	0.02 ± 0.01	0.03 ± 0.01	0.02 ± 0.01	0.02 ± 0.01	0.02 ± 0.02	0.07 ± 0.05
P/Ca Above	1.10 ± 0.53 abA	0.40 ± 0.15 abB	0.83 ± 0.17 abA	0.28 ± 0.03 abB	0.70 ± 0.24 bA	0.18 ± 0.09 bB	0.97 ± 0.12 aA	0.40 ± 0.05 aB
Rhizo	0.04 ± 0.06	0.04 ± 0.05	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01
Ca/Mg Above	1.05 ± 0.34 bA	1.53 ± 0.21 abB	1.08 ± 0.08 bA	1.50 ± 0.20 abB	1.02 ± 0.11 bA	2.12 ± 0.14 aB	2.65 ± 1.22 aA	1.92 ± 0.13 abB
Rhizo	4.16 ± 0.39	6.46 ± 2.61	6.06 ± 1.46	6.24 ± 1.61	4.44 ± 0.60	5.65 ± 0.60	6.62 ± 1.66	6.02 ± 2.15

The *Glyceria*- and *Phragmites*-dominated communities produced significantly greater biomass, being larger in summer than in the off-season. This resulted in significant between community type differences in aboveground nutrient standing stocks (Table 2). As would be expected, the aboveground nutrient stocks were significantly greater in July at the time of peak biomass, with the exceptions of Ca and Na, which were higher in summer, but not significantly.

The significant seasonal effects in aboveground nutrient standing stocks were reflected in the changes in stoichiometric ratios between the seasons (Table 3). The N/P, N/K and P/Ca ratios showed the greater loss of P and K relative to N in plant material in the off-season when the aboveground structures had senesced, while the significant seasonal effect on the P/K ratio showed the even faster removal of K. The communities were usually P limited, as expressed by the N/P ratio, except for the *Glyceria* community, thereby producing a significant community effect for this ratio (Table 3).

The C, N and Ca contents tended to be larger in the aboveground plant compartment. The soil contained much larger amounts of the other nutrients (PO_4, K, Na, Mg). This relationship held for both seasons, with the exception of Ca, which was equally distributed between the two compartments in the off-season.

Multivariate analyses

The PCA clearly differentiated the communities in terms of plant and rhizosphere nutrient standing stocks (Fig. 2). The first three axes explained 73.37% of the variability in the data and were all significant (Monte Carlo test, $P < 0.001$). Plant standing stocks were the main factors separating the communities along axis 1, explaining 37.45% of the variation in the data. The *Glyceria maxima* and *Phragmites australis* communities had the highest standing stocks for all nutrients in summer, being far greater than for the other community types as well as compared to the off-season stocks. The *Calamagrostis canescens* and *Glyceria maxima* communities separated from the other community types along axis 2 (explained variation = 23.04%) in relation to rhizosphere nutrient contents, especially K, Na, inorganic N ($NO_3 + NH_4$) and PO_4. The *Calamagrostis canescens* community then separated from the other community types along axis 3 (variation explained = 12.88%) due to the drier

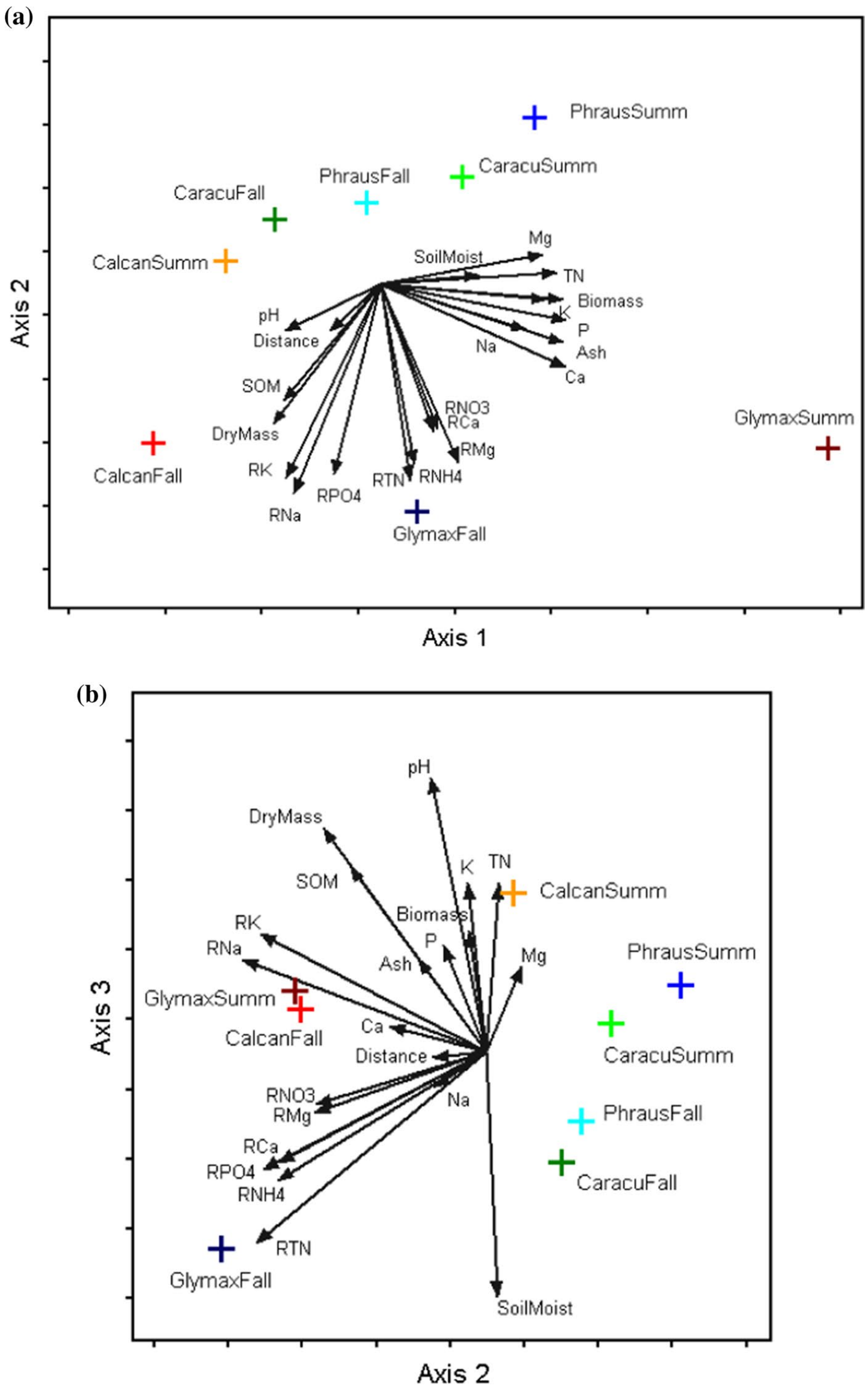

Fig. 2 Principal components analysis (PCA) showing centroids of the community types in relation to the plant and rhizosphere soil factors. A) Axes 1 and 2; B) axes 2 and 3. Percent variance explained: Axis 1 = 37.37; axis 2 = 23.04; axis 3 = 12.88. Community types: Phraus = *Phragmites australis*; Caracu = *Carex acuta*; Calcan = *Calamagrostis canescens*; Glymax = *Glyceria maxima*. Seasons: Summ = summer, peak season; fall = off-season. Factors: TN = total nitrogen; SOM = soil organic matter; SoilMoist = soil moisture content; distance = distance of stand to open water. Rhizosphere soil factors designated with R

(lower SWC) and less acidic characteristics of this habitat.

Resorption efficiencies

Data of the summer and off-season N and P standing stocks in the plant communities were used to

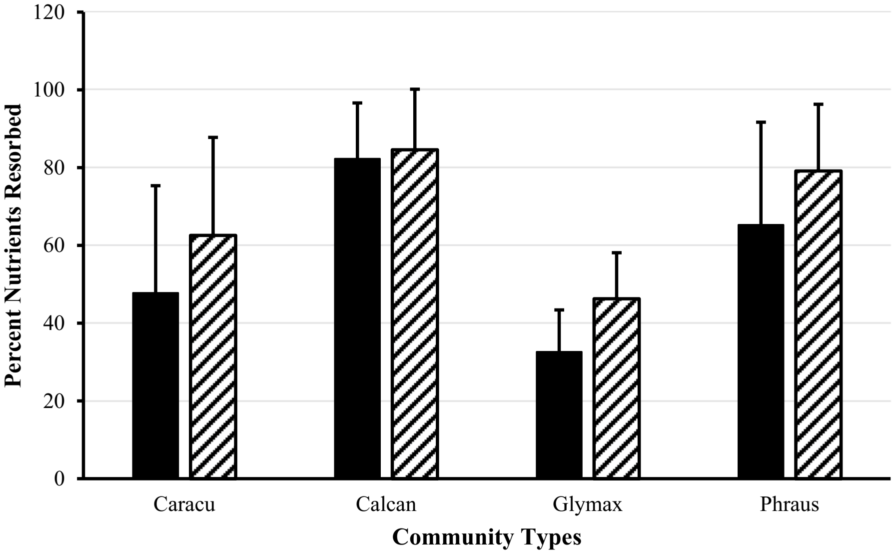

Fig. 3 Mean (± 1 SD) nitrogen and phosphorus resorption efficiencies (RE_N, RE_P, respectively) for the four studied fishpond littoral plant communities. Bars: RE_N = black; RE_P = crossed hatch. Community acronyms: Phraus = *Phragmites australis*; Caracu = *Carex acuta*; Calcan = *Calamagrostis canescens*; Glymax = *Glyceria maxima*

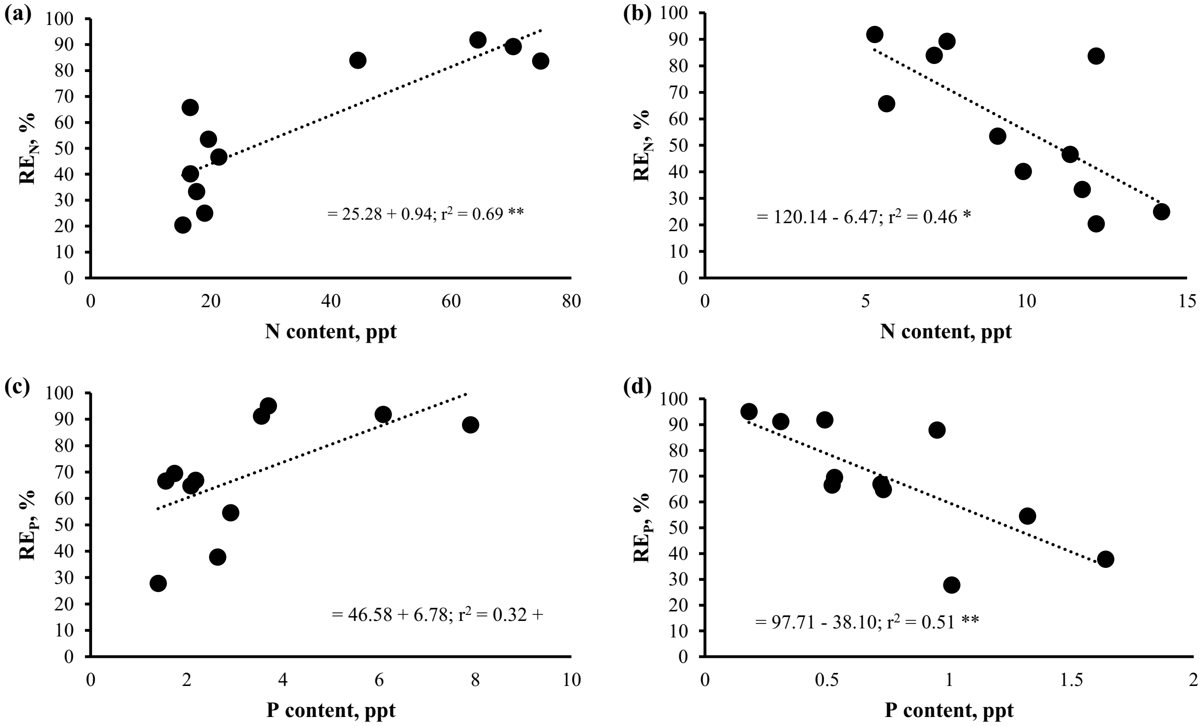

Fig. 4 Relationships between N or P contents ($g{*}kg^{-1}$) in aboveground plant structures to the respective resorption efficiency (RE_N, RE_P). **a** N content in peak season to RE_N; **b** N content in off season to RE_N; **c** *P* content in peak season to RE_P; **b** P content in off season to RE_P. *P* values: + < 0.10; * < 0.05; ** < 0.01

determine nutrient resorption efficiencies (RE_N and RE_P, respectively). The *Calamagrostis canescens* community retained the greatest amount of both nutrients (greatest reduction between summer and off-season contents), followed in order by the *Phragmites australis*, *Carex acuta* and *Glyceria maxima* communities (Fig. 3). While there were clear trends, the between-community differences were not significant ($P > 0.10$).

RE_N and RE_P were plotted against their respective peak and off-season nutrient contents ($g*kg^{-1}$) to determine whether there were any potential relationships (Fig. 4a–d). Significant relationships were found for RE_N and the peak (positive) and off-season (negative) TN contents (Fig. 4a, b), while there was a significant relationship only between RE_P and the off-season P contents (Fig. 4d). The peak season P content had a weakly positive relationship with RE_P (Fig. 4c).

Discussion

There is great interaction between plant and soil nutrient contents, with these two components forming a tightly coupled system (Pugnaire et al., 2019). Soil nutrient supply can greatly influence plant species composition and production (Willby et al., 2001). The resulting effect on plant tissue nutrient contents and stoichiometry is then connected to ecosystem functions, such as litter decomposition and nutrient fluxes (Allen & Gillooly 2009; Yu et al., 2020). These effects are observed not only across environmental gradients, but also when affected by human activities. Here, we presented a historic record of plant and soil nutrient contents, which developed in a particular management context, thereby providing a baseline for comparing how these changing conditions may affect the mineral nutrient economy of these wetland plant communities.

The range of the various nutrient percentages and standing stocks were similar to those found in other wetland plant communities in South Moravia or Bohemia (Květ 1973, 1975, and Dykyjová & Květ, 1982, respectively) as well as in more spatially-distant regions (Willby et al., 2001; Lou et al., 2012; Yu et al., 2020). The N and P contents ($g*kg^{-1}$) in our four plant communities ranged from 16.1 to 19.8 and 1.3 to 3.2, respectively, which are on the low end of the range found for riparian wetlands in China (Yu et al., 2020) and nutrient-rich wetlands in Poland (Ławniczak, 2011), but similar to those found for depressional wetlands in the same country (Lou et al., 2012) or in a range of herbaceous wetlands in the UK (Willby et al., 2001). The exception was our *Glyceria*-dominated community, which had significantly greater P and Ca contents, which appears to be characteristic of this community compared to the other three.

Similar to other studies (Aerts & Chapin, 2000), we predicted that the habitat conditions would significantly differ between the four studied community types (hypothesis one). The habitats of the four studied wetland plant communities differed from each other, with the *Glyceria maxima* community growing on nutrient-richer substrates while, on the other end, the *Calamagrostis canescens* community type was found on more mineral, nutrient-poorer soils. The nutrient content of the habitats showed some trends, but did not differ statistically, due to the small number of sites. The *Calamagrostis*-dominated sites did have greater SOM, but the organic layer was much thinner (top 15 cm of the soil profile) than for the other community types, in which the organic layers were up to 60 cm thick (Ostrý & Zákravský, 1988). The *Glyceria*- and *Phragmites*-dominated community soils had greater TN and Ca pools compared to the *Calamagrostis* soils. This latter community type is often found in areas closer to the upland edges of wetlands or in shrub-dominated depressions (Hroudová et al., 1988). Therefore, these results only partially support the first hypothesis, showing the need to have a larger number of sites for each community type.

Contrary to the second hypothesis, the plant nutrient contents did not differ between the community types. However, because of the significantly greater amounts of biomass in the *Glyceria*- and *Phragmites*-dominated communities, there were significant differences in plant nutrient standing stocks. As would be expected, the plant nutrient pools differed seasonally due to resorption, with significant reductions in all plant nutrient pools, with the exception of Ca, and a concomitant increase in the soil pools in the off-season samples. The autumnal shift in nutrients from the plants to the soil is also noted by the changes in the respective stoichiometric ratios. These show a large decrease in the off-season P and K contents in the plant tissues, represented by significantly increased N/P and N/K ratios, with similarly significant decreases of these ratios for the soil pools. The significant change in the P/K ratio in the plant tissues indicates that a larger shift occurred in K than for P. The greater loss of K compared to P seen in our study was also found for *Typha latifolia* L. (Květ 1975) and *P. australis* (Květ 1973) stands in South Moravia, with most of the loss of both nutrients being due to large reductions in leaf and stem contents, as also found by Ławniczak (2011). Overall, the stoichiometric ratios indicate that these wetland communities are N-limited, except for the *Glyceria*-dominated community, which was either P limited or co-limited by both N and P (Güsewell et al., 2003; Koerselman & Meuleman, 1996).

Although N and P resorption efficiencies did not statistically differ due to the large variation in the data resulting from the small number of study sites, there were clear trends, with the *Calamagrostis canescens* and *Phragmites australis* communities being more efficient in storing N, and to a lesser degree P, than the *Carex acuta* or *Glyceria maxima* communities. The range of RE_N and RE_P (32.6–82.3% and 42.3–84.6%, respectively) in our study is similar to the range of average global resorption values (Vergutz et al., 2012), but higher than for nutrient-rich wetlands (Ławniczak, 2011). This is not surprising since our sites had lower sediment nutrient contents compared to those in Poland. Resorption efficiencies would be expected to be greater in nutrient-poorer conditions, but there is still great uncertainty concerning this matter (Aerts, 1996; Kobe et al., 2005; Ławniczak, 2011). However, such comparisons must be made cautiously, since the off-season nutrient contents were determined from plant structures that had senesced several months previously. Therefore, it is possible that the resorption values in our study are inflated.

We found significant relationships between the resorption efficiencies and their respective nutrient contents. However, both RE_N and RE_P showed asymptotic relationships with the respective nutrient contents in peak season plant structures (Fig. 4a, c), with threshold concentrations of ~ 30 $g*kg^{-1}$ for N and 3.2 $g*kg^{-1}$ for P. The higher resorption efficiencies with higher N or P contents are similar to other wetland studies (Güsewell, 2005), but contrary to others (Kobe et al., 2005; Ławniczak, 2011). Therefore, our results support the view that resorption efficiency may not be completely related to external nutrient supply (Killingbeck, 1996; Aerts, 1996).

Neither soil water content (SWC) nor distance from open water was significantly related to the aboveground nutrient contents, contrary to hypothesis three. This may be due to the source of the nutrients. In many cases, wetlands receive nutrient additions from the surrounding terrestrial areas (Mitsch & Gosselink, 2000). However, the studied habitats are part of different sub-zones of the littoral zone of a large fishpond (Straškraba, 1968). According to Wetzel´s (1983) terminology, the two most waterward sub-zones of concern are the eulittoral and infralittoral sub-zones. Along the shores of the Rožmberk fishpond, they are characterized by a relatively thick (up to about 0.4 m) organic sediment of the förna or dy types along the leeward shores, while no or only a thin (up to 0.05 m) layer of both fine organic and mineral gyttja-like mud particles has been deposited along the windward shores (accumulation and erosion zones according to Husák & Hejný, 1978). The differently thick topsoil of the landward and only rarely flooded supralittoral and epilittoral sub-zones (Wetzel, 1983) can be classified as a limnic fen (Neuhäusl, 1966), which is an organo-mineral soil formed in acidic fens (pH usually between 3.5 and 5.5). The subsoil of the entire littoral zone consists of an up to several meters thick clay or sandy clay layer (Dykyjová & Úlehlová, 1978; Hejný et al., 2002; Hroudová & Zákravský, 2002; Prach, 2002). There was a great intensification of fishpond management in the former Czechoslovakia beginning in the 1950s, which has continued to the present, resulting in large degradation of the water quality (Hejný et al., 1981). It is likely that the studied littoral habitats receive more nutrients from the eutrophic fishpond waters than from terrestrial sources (Pechar et al., 2002).

Conclusions

The results of our study partly supported as well as contradicted our initial hypotheses:

1. Hypothesis 1 (habitats differ in sediment nutrient supply) was only partly supported, with the *Glyceria*-dominated community type having significantly greater TN, Ca and Na contents compared to the *Calamagrostis*-dominated habitat. However, other nutrients as well as pH and soil water content (SWC), while showing trends, did not differ significantly between the community types. This lack of significant differences is likely

due to the large inherent variation of the dominant plant species;

2. The data mostly supported hypothesis 2 (aboveground plant nutrient stocks and nutrient resorption efficiencies differ between community types). The *Glyceria* and *Phragmites* communities produced significantly more biomass than the *Carex* or *Calamagrostis* communities, which led to significant differences in aboveground nutrient standing stocks. However, between-community type differences in nutrient contents were not significant. N and P resorption efficiencies showed trends, but did not differ significantly between the community types.
3. No significant relationship was found between SWC and the plant nutrient stocks, thereby contradicting hypothesis 3. The lack of any significant relationship is, again, likely due to the large variability of the dominant species as well as the small number of sample sites.

It is clear that similar future studies need to include more sample sites than those included in this study. Even with that limitation, it is apparent that changes in ecological conditions lead to changing plant community structure, with certain community types being replaced by others. Such knowledge would mandate the wise management of littoral wetlands so that they can adequately provide the functions which contribute to a healthy ecological system.

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Author contributions JK, IO, PZ and ZH developed, conducted and ran the original experiment on which the manuscript is based. KE analyzed the data. KE and JK wrote the manuscript. All authors read and approved the manuscript.

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Data availability All data analyzed during this study are from Hroudová (1988) and are included in this manuscript. Data may be obtained upon request from the corresponding author. No genetic material was used or analyzed as part of this study.

Declarations

Research involving human participants or animals Testing of humans or other animals was not part of this study.

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