Original Research

Nitrogen, Phosphorus, and Potassium Resorption Efficiency and Proficiency of Four Emergent Macrophytes from Nutrient-Rich Wetlands

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Abstract

This study examined the nutrient dynamics of nitrogen (N), phosphorus (P), and potassium (K) resorption from senescing leaves in four hydrophytes. Differences in N, P, and K concentrations of green leaves during the vegetation season were studied to test the influence of plant strategy on nutrient resorption efficiency. Live leaves were tagged at defined canopy heights and collected in the period from March to August. Senescent leaves were collected in September. All tissue samples were analyzed for N, P, and K concentrations. Significant differences in N resorption and N utilization among the four macrophytes were observed. Particularly high values of N concentrations were detected in *Phragmites australis* in comparison with other species. However, these differences were not observed with respect to P and K resorption efficiencies and proficiencies. Nitrogen and phosphorus resorption efficiency was lowest in *Glyceria maxima* (22.0%) and highest in *Phragmites australis* (49.9%), indicating that minor proportions of these nutrients were translocated to the rhizomes during senescence. The analyses of changes in nutrient concentrations in green leaves during the vegetation season suggest that wetland species with different nutrient strategy uptakes can show similar final nutrient concentrations in plant tissue. In the present study, macrophytes were characterized by high leaf N concentrations, higher litter N concentrations, and lower values of NRE, which documents the high productivity of these plants and their importance in primary production in wetlands.

Keywords: leaf nutrient status, senescence, nutrient conservation, resorption efficiency

Introduction

Nitrogen (N) and phosphorus (P) resorption during leaf senescence plays an important role in the nutrient cycling in most terrestrial and wetland plants [1-3]. Before abscission, approximately 50% of the leaf N is withdrawn from senescing leaves to be resorbed in growing parts or stored in plant tissue until the next growing season for further plant growth [3]. Therefore, resorption reduces the need for the uptake of nutrients from the environment, and the next year plants are partly independent of current nutrient concentrations in the soil. This process has important consequences in plant species competition, plant fitness, nutrient uptake, and productivity, particularly for plants growing in nutrient-poor environments [4, 5].

The percentage of the nutrient pool withdrawn from the foliage before leaf senescence indicates the ability of a plant to resorb nutrients and is called nutrient resorption efficiency. Nitrogen, phosphorus, and potassium resorption efficiencies (NRE, PRE, and KRE, respectively) are calculated

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by measuring the nutrient concentrations of mature and senescing leaves. Nutrient resorption from senescing leaves may also be quantified by nutrient resorption proficiency (NRP), which can be expressed as nutrient concentrations in senescent leaves [3]. NRP is influenced by external factors such as wind, frost, nutrient and water availability, timing of abscission, and shade [1, 6, 7]. These factors may cause changes in nutrient resorption between studied years.

Variations in NRE were also observed among species and life forms [8, 9]. Proportions between N resorption in plants may range from 5% up to 80% in natural conditions [1]. In addition, interspecific resorption plasticity was observed in controlled experiments as well as between the same species growing in different habitats [5]. Moreover, this relationship between nutrient availability and nutrient retention is not always clear. In some studies, a significant correlation between N concentrations and NRE was detected [9]. However, Cartaxana and Catarino [10] showed that the efficiency of the nitrogen resorption process may be related to plant species rather than to nitrogen concentrations in plant tissues or nitrogen availability in the soil.

Species from N-poor habitats showed particularly high NRE, indicating an adaptive plant strategy for growth in infertile habitats [1, 9]. On the other hand, high NRE was also observed in perennial plants, which did not show a strong response to changes in N supply [1, 2]. High variation in nitrogen and phosphorus resorption efficiencies may reflect the capability of plants to conserve N or P, but it cannot be used to explain the distribution of life forms over habitats differing in soil fertility [9].

Likewise, nutrient resorption proficiency is often used to describe the level of nutrient reduction during senescence and to express the amount of N and P that becomes available for decomposition after leaf shedding [3]. Values of NRP and phosphorus resorption proficiency (PRP) change with nutrient availability in the soil; therefore, these indices may reflect the effect of increased nutrient availability in the soil. In natural habitats, species that grow in nutrient-rich sites have higher foliar concentrations of a particular nutrient in comparison to nutrient-poor sites [8]. Also, studies carried out in controlled conditions [11, 12] showed that increased N concentrations in plant tissues due to N fertilization caused lower resorption proficiencies. Phosphorus resorption proficiencies also strongly depend on nutrient availability in soil. They are higher in species with a long life span characterized by high nutrient resorption efficiency to reduce nutrient loss [1]. Little attention was paid to K resorption efficiency and proficiency. Potassium ions play an important role and can limit plant growth.

In the present study, differences in N, P, and K concentrations of green leaves during the vegetation season were studied to test the influence of plant strategy on nutrient resorption efficiency. Variations in N, P, and K resorption proficiencies between wetland species were tested in the littoral zone of a polymictic lake.

Materials and Methods

Study Area and Species

The study was carried out in the littoral zone of Lake Niepruszewskie, located in central-western Poland (52º22.700' N, 16º37.200' E). The lake is situated in the Samica Stęszewska River basin and functions as a major sub-basin of the river basin area. This is a very elongated, postglacial lake of 253 ha and average depth of 3.1 m, with a well-developed littoral zone. Water quality in the lake is characterized by high concentrations of phosphorus and intensive algal blooms [13]. The water level in the lake is regulated at its outlet by a weir. Maximum water level of 76.90 m a.s.l. occurred during winter months, and the minimum of 76.4 m a.s.l. during summer. During the 2008 vegetation season, the water level varied from 76.3 to 77.0 m a.s.l.

Lake Niepruszewskie is situated in the central Wielkopolska climatic region [14], which belongs to the continental climate of moderate temperature zone, with mean monthly air temperatures ranging from -0.4ºC in January to 18.5ºC in July, and an annual mean temperature of 8.8ºC. During the 2008 vegetation season, temperatures varied from 5.0ºC in March to 20.1ºC in July, with average annual temperature of 10.2ºC. Mean annual precipitation was 496 mm, comparable to the average annual precipitation in the Wielkopolska region [14].

The dominant vegetation in the littoral zone of Lake Niepruszewskie belongs to the physiological alliances *Phragmitetum australis*, *Typhetum angustifoliae*, *Caricetum acutiformis*, and *Glycerietum maximae* [13, 15]. Plants selected for the study were the dominant wetland species of the major stands or communities in this zone. Four emergent macrophytes were selected: *Phragmites australis* (Cav.) Trin. ex Steud. (common reed), *Typha angustifolia* L. (lesser reedmace), *Carex acutiformis* L. (lesser pond sedge), and *Glyceria maxima* (C. Hartm.) Holmb. (reed sweet grass).

Glyceria maxima preferred sites with high K and N concentrations in sediments compared to other species (Table 1). The lowest N concentrations were observed at sites with *Typha angustifolia*. *Carex acutiformis* and *Phragmitetum australis* preferred quite similar habitat conditions with respect to nutrient concentrations in sediments [16].

Field Procedure

Sampling sites were selected in 28 different parts of the naturally developed littoral zone of Lake Niepruszewskie. Each sampling site consisted of four replicates. The aboveground biomass of littoral vegetation of each community type was harvested at ground level from three randomly placed subplots (each 50 x 50 cm). Green leaves were collected monthly throughout the vegetation season (from April to September) to observe changes of leaf tissue nutrients. To calculate nutrient resorption efficiency, green leaves were collected in July and August, senescent leaves in September.

Table 1. Nutrient concentrations in sediments with four macrophytes in peak standing stock in 2008.

	N	P	K	$N\text{-}NH_4$	$N\text{-}NO_3$
	mg·g^{-1} sediment			mg·100 g^{-1} sediment	
	Carex acutiformis				
Mean	4.08	2.13	6.22	1.10	0.26
SD	1.23	0.67	1.78	0.84	0.04
	Glyceria maxima				
Mean	7.08	2.11	14.03	1.49	0.68
SD	0.78	0.13	4.69	0.16	0.49
	Phragmites australis				
Mean	3.14	3.24	7.72	1.04	0.24
SD	2.30	1.73	2.20	1.06	0.25
	Typha angustifolia				
Mean	0.43	2.03	5.92	0.79	0.24
SD	0.10	0.31	2.12	0.66	0.16

Laboratory Procedure

Plant samples were sorted according to species into living and dead fractions, dried for 48 h at 70ºC and weighed. For further nutrient determinations, the plant material of dominant helophytes was digested using the Kjeldahl procedure [17]. N and P concentrations of the diluted digested material were determined colorimetrically on a Srecord 40, and K concentration with flame emission spectroscopy, on a Sherwood Model 425.

Calculations

Nitrogen, phosphorus, and potassium resorption efficiencies (RE) were calculated on the basis of each nutrient concentration in green (C_g) and senescing (C_s) leaves [3]:

$$RE(\%) = ((C_g - C_s)/C_g)\cdot 100\%$$

Nitrogen, P, and K concentrations in senescing leaves were used directly as indicators of nutrient resorption proficiencies (NRP, PRP, KRP, respectively) [3].

Statistical Analyses

All statistical analyses were performed using Statistica (StatSoft, Poland) software. The data were transformed (square root or logarithmic) to assess the homogeneity of variance. Differences among species in nutrient concentrations, nutrient resorption efficiencies and nutrient resorption proficiencies, as well as significances of the differences between the nutrient concentrations within the vegetation season were tested with analyses of variance (repeat measurements ANOVA) and a posteriori Tukey's test. Linear correlations between nutrient concentrations in mature or senescing leaves and nutrient resorption efficiency were quantified and tested with Pearson's correlation coefficients.

Results

Significant two-way interactions between the effects of month and species were found for N, P, and K concentrations in green leaves between all species during the vegetation season. At the beginning of the vegetation season, significantly high N concentrations were observed in fast-growing *Glyceria maxima* and *Phragmites australis* (Fig. 1a). In the maximum standing stock (August), differences between species almost disappeared. Only reeds were characterized by significantly higher N concentrations in comparison to other studied species. A similar pattern was observed with respect to P and K concentrations (Table 2). The differences observed in P and K concentrations between species at the beginning of the vegetation season disappeared with plant growth (Fig. 1b, c). Overall, the biggest differences occurred between *Carex acutiformis*, which showed low nutrient concentrations, and remaining species. In September, significant decreases of nutrient concentrations were recorded, except in *C. acutiformis*, which indicated translocation of nutrients to the belowground biomass.

Nitrogen concentrations in green leaves in the maximum standing stock in four macrophytes ranged from 0.76% to 2.17%. The mean lowest concentrations were found in *Typha angustifolia* (1.22%), the mean highest N concentrations were measured in *Phragmites australis* (1.51%), and they were significantly higher in comparison to other species (Fig. 2a). Significant differences of N con-

Table 2. Results of the two-way ANOVA tests of the effects of the time and differences between species on nitrogen, phosphorus, and potassium concentrations.

Source	df	N (%)		P (%)		K (%)	
		F	Sig.	F	Sig.	F	Sig.
Species	3	19.19	0.000***	14.12	0.000***	10.79	0.000***
Month	6	107.31	0.000***	133.51	0.000***	61.49	0.000***
Species × Month	16	9.211	0.000***	5.21	0.000***	2.66	0.001**

*Data are F-ratios and significance levels given as *** $p<0.001$; ** $p<0.01$; * $p<0.05$; ns – $p\geq0.05$.

centrations between live and senescent tissue among different species indicate differences of nitrogen resorption efficiencies (NRE) (Table 3). NRE was lowest in *Glyceria maxima* (22.0%) and highest in *Phragmites australis* (49.9%) (Fig. 1d).

Nitrogen concentrations in senescent leaves ranged from 0.45% in *P. australis* to 1.37% in *T. angustifolia*, with an average of 0.80% (Fig. 1a). Significant differences in N concentrations in senescent leaves among species were not detected (Table 3). Levels of N and P in senescing leaves were significantly correlated ($r=0.68$, $p<0.05$).

Phosphorus and potassium concentrations in green and senescent leaves did not differ significantly between plant species in the maximum standing stock (Fig. 1b, c, Table 3). However, significant differences occurred between nutrient concentrations in live and senescent tissues. Average tissue P ranged from 0.08% to 0.10% and from 0.02 to 0.1% in senescent leaves. Average K concentrations varied from 0.80% in *P. australis* to 0.97% in green parts of *G. maxima*. The biggest variations were observed in senescent leaves. The lowest concentrations were measured in *P. australis* tissues and the highest in *G. maxima* (Fig. 2). A similar pattern was observed with respect to potassium resorption efficiency (KRE); the lowest KRE occurred in *P. australis* (47.5%), the highest in *G. maxima* (65.63%) (Table 3, Fig. 2f). However, these differences were not significant. Phosphorus content in senescent tissues indicated that phosphorus resorption efficiency (PRP) did not differ among the studied species. The lowest values were observed in *P. australis* and the highest in *C. acutiformis,* and *G. maxima* (Fig. 2e).

NRE and nutrient concentrations in green and senescent leaves were plotted against each other to examine potential relationships among these parameters. Significant linear concentrations between NRE and N concentrations in green (positive) and senescent (negative) leaves were found (Fig. 3a, b). A significant negative correlation between leaf levels of PRE and P concentrations in senescent leaves was detected (Fig. 3 d). Correlations between KRE and K concentrations in live and senescing leaves were significant but weaker than those observed for N and P.

Discussion

Nitrogen concentrations in live tissues of *Phragmites australis* and *Typha angustifolia* averaged 0.8-0.9%. This value is comparable to those given for forbs and graminoids by Aerts and Chapin [1], and for sedges given by Aerts et al. [18] and Güsewell [19], which were in the range of 0.5-2.1% and 0.4-2.8%, respectively. The highest N concentrations were measured in *Phragmites australis* and *Glyceria maxima* at the beginning of the vegetation season, although in the standing stock, N concentrations in the four helophytes did not differ significantly among *Glyceria maxima*, *Typha angustifolia,* and *Carex acutiformis*. Significantly higher N

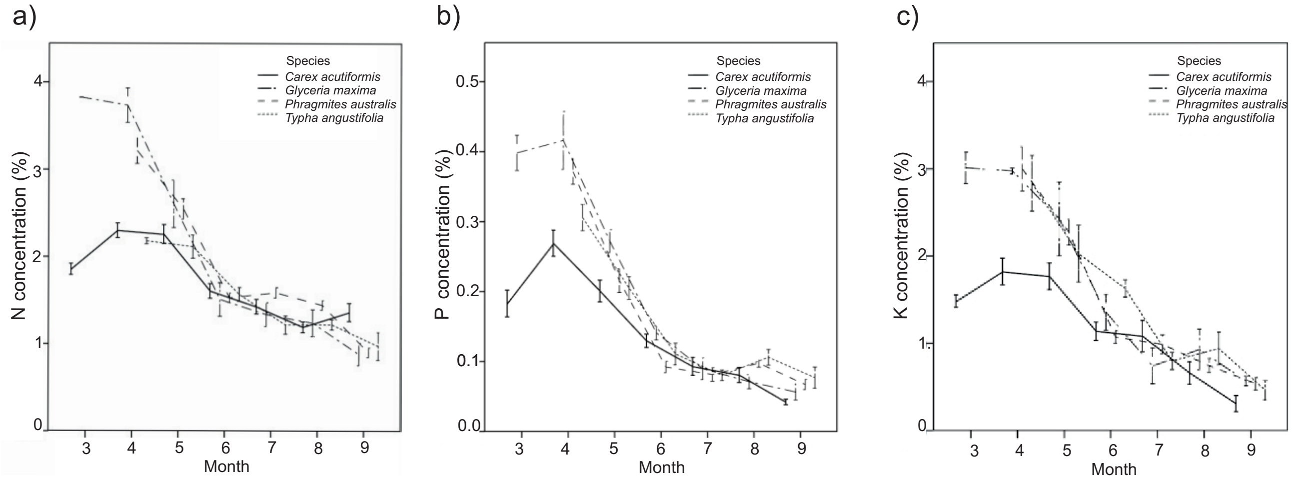

Fig. 1. Changes of a) N, b) P, and c) K concentrations in green leaves of four macrophytes during vegetation season.

Table 3. Results of the one- or two-way ANOVA testing differences for nitrogen, phosphorus, and potassium concentrations and nutrient resorption efficiency* among species and leaf types (green and senescing).

Source	df	N (%)		P (%)		K (%)	
		F	Sig.	F	Sig.	F	Sig.
Species	3	1.39	0.248 ns	1.31	0.273 ns	1.28	0.284 ns
Leaves	1	63.40	**0.000*** **	18.01	**0.000*** **	38.46	**0.000*** **
Species × Leaves	3	3.72	0.013*	0.27	0.848 ns	1.52	0.213 ns
		NRE		PRE		KRE	
Species	3	9.16	**0.000*** **	1.06	0.371 ns	0.57	0.636 ns

*K concentrations, NRE, PRE, KRE were square-rooted transformed. Data are F-ratios and significance levels given as ***p < 0.001; ** p<0.01; * p<0.05; ns – p≥0.05.

concentrations were observed only in *Phragmites australis* in comparison with other studied species. This suggests that, in uniform and fertile habitats, foliage nutrients do not differ between studied species. However, nutrient concentrations can change as a response to a stressing factor, which may be individual and differ among these species [20].

A pattern similar to N also applies to P and K concentrations in plant tissues. At the beginning of the vegetation season, changes between species were significant; however, they disappeared with the passage of time. These results confirm a study by Tylová et al. [21], who detected similar patterns of responses of *P. australis* and *G. maxima* to high nutrient availabilities. They reported a similar increase of biomass production, extension of vegetative growth, and translocation of N into belowground parts in both species [21]. Likewise, differences in growth strategy and sensitivity to high nutrient availability of *Phragmites* and *Glyceria* have been described in many studies [20-22].

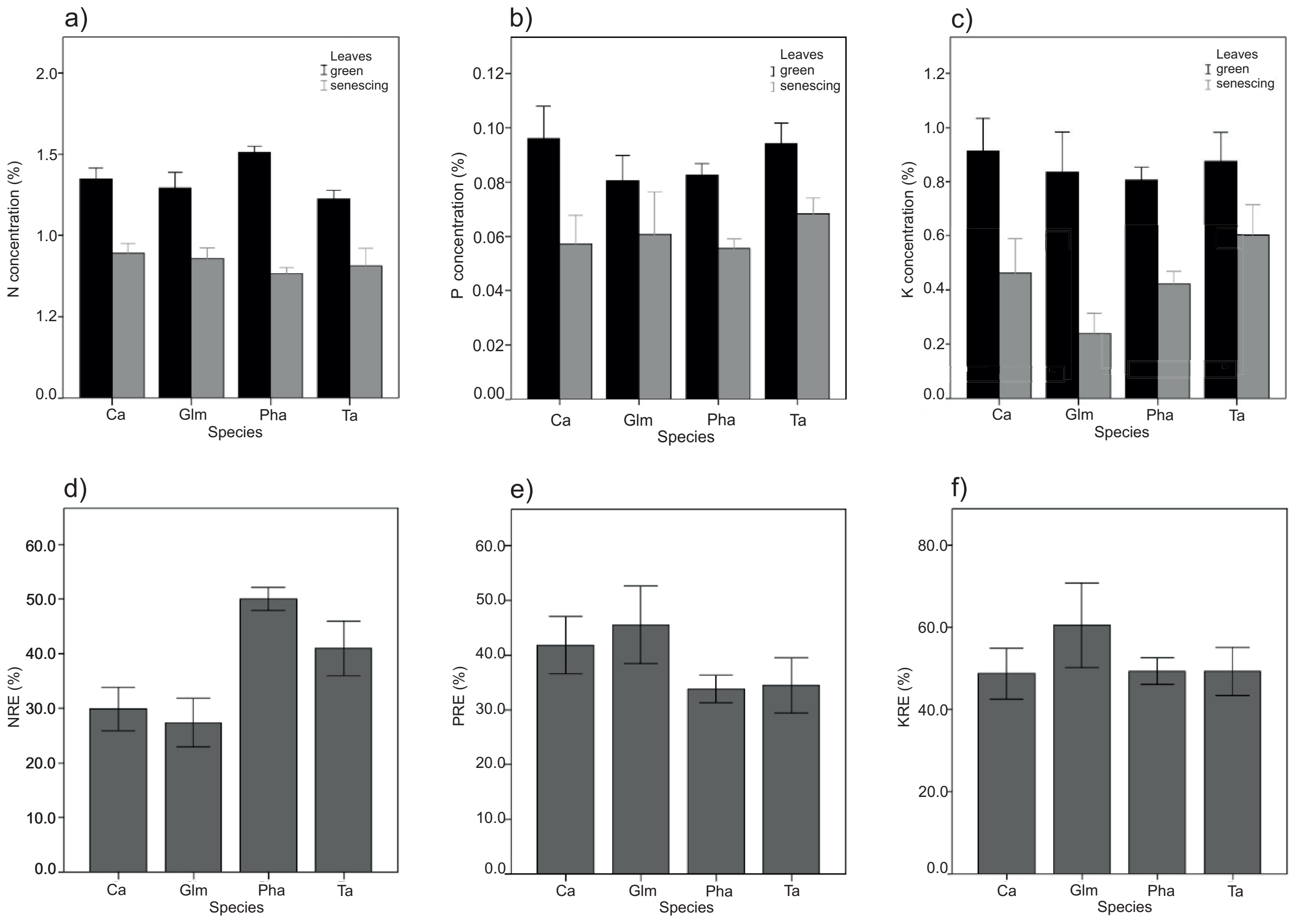

Fig. 2. Nitrogen (a), phosphorus (b), and potassium (c) concentrations in green and senescing leaves of four macrophytes in peak standing stock, and nitrogen (d), phosphorus (e), and potassium (f) resorption efficiency (NRE, PRE, PRE, respectively) of four macrophytes.
Abbreviations: Ca – *Carex acutiformis*, Glm – *Glyceria maxima*, Pha – *Phragmites australis*, Ta – *Typha angustifolia*

In this study, nutrient translocations to the belowground biomass were observed in September. Nitrogen resorption efficiencies varied among species, ranging from 22% to 50%. This results are lower than those reported by Wright and Westoby [23] for Australian trees and shrubs, and by Güsewell [19] for wetland graminoids. Nutrient resorption was mainly studied for woody plants, although less attention was dedicated to herbaceous plants [1, 2] and emergent macrophytes [25]. NRE values of emergent macrophytes, investigated in the littoral zone of this polymictic lake, were rather low in comparison with other studies [8, 9]. High proportions of dead leaves observed in investigated species is typical for nutrient-rich sites, where species are always characterized by a high proportion of senescing and green leaves [25].

A lot of attention has been paid to nitrogen resorption efficiencies at the expense of studies on P and K translocation. Phosphorus plays an important role in plant growth and is one of the components of key molecules such as nucleic acids, phospholipids, and ATP, and is also involved in controlling key enzyme reactions and regulation of metabolism [26], while K is an important element in osmoregulation, enzyme activation and carbohydrate translocation [27]. Furthermore, K might influence N concentrations in leaves, photosynthetic activity and water use efficiency [27]. Potassium monovalent cations are characterized by higher susceptibility to leaching loss than organically bound nutrients such as N or P [6, 28]. Phosphorus resorption efficiency in the studied species fluctuated around 38%, which is typical for plants from rich environments. Species characteristic for strongly P-limited sites have higher PRE, which fluctuated around 80% [19, 24, 29]. Variations within species in PRE were much larger than in NRE, which was also confirmed by Aerts and Chapin [1].

Many investigations have been carried out on resorption patterns of different nutrients in order to recognize mechanisms and relationships between them. However, a high degree of inter nutrient independence has been suggested by the absence of significant correlations between N and P resorption efficiencies [11]. Nevertheless, relationships between N and P concentrations in senescing leaves were observed by Killingbeck [3]. In the current study, levels of N and P in senescing leaves were significantly correlated. This suggests that although mobilization and transport of N and P overlap in plants independently, the reduction of both nutrients according to Killingbeck [3] in leaves during senescence (resorption proficiency) is aligned for the species which grow in the same habitats. On the other hand, Feller et al. [29] reported a positive relationship between increasing P availability and N economy leading to an increase in NRE, which may suggest that N resorption may be incomplete under P deficiency.

Relationships between nutrient resorption efficiencies and nutrient concentrations in green leaves have often been demonstrated for trees [7, 23], but for graminoids these correlations were not always observed [19]. In this study, a significant positive correlation between NRE and N status in green leaves was found and it was consistent with other

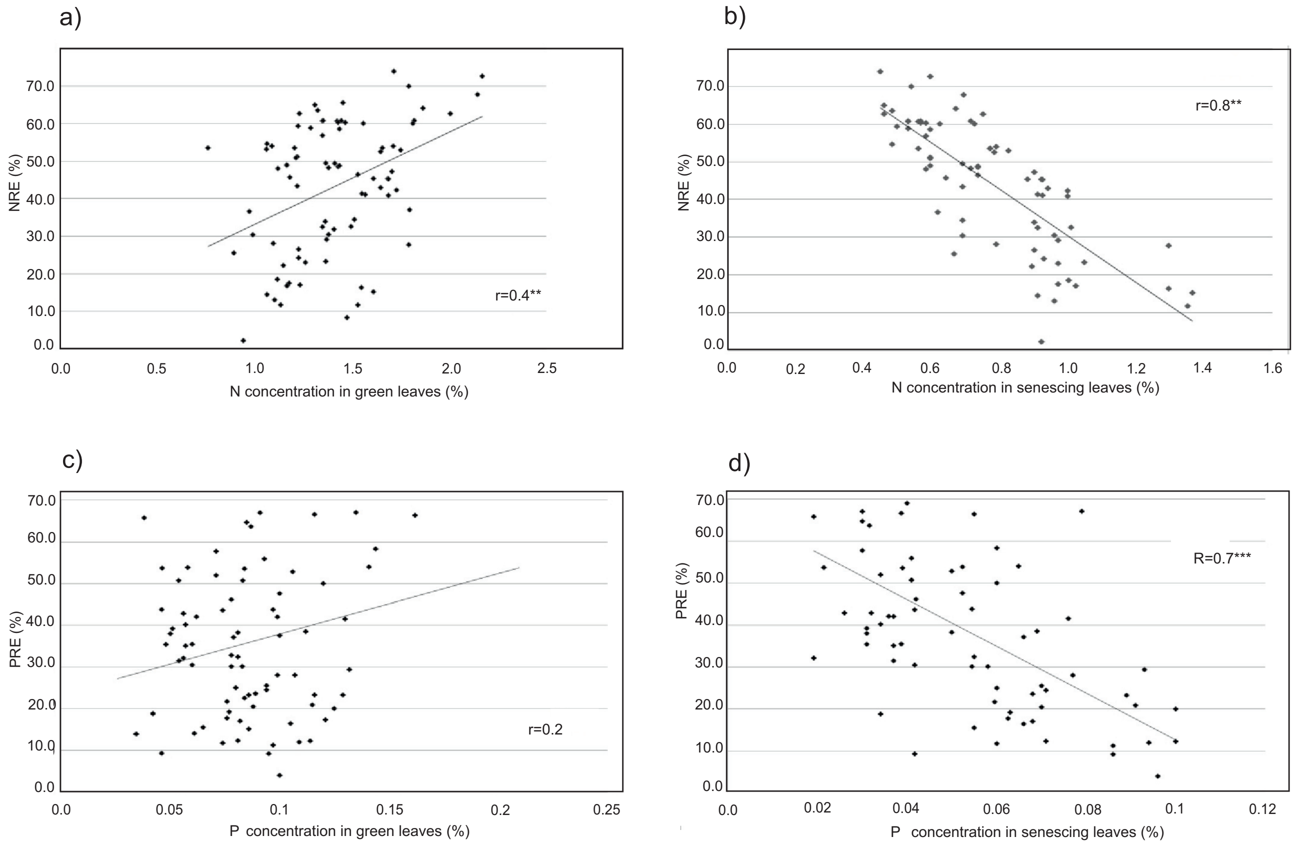

Fig. 3. Relationships between a) N concentrations in green leaves and NRE, b) N concentrations in senescing leaves and NRE, c) P concentrations in green leaves and PRE, and d) P concentrations in senescing leaves and PRE.

studies [4, 9, 24]. Moreover, correlations between NRE and N concentrations are not always observed [2], which could be explained by nitrogen solubilization activity [10, 30].

A relationship between PRE and P concentrations in senescing leaves was significant but much weaker than that observed between NRE and N concentrations in the studied macrophytes. No such correlations were detected in green leaves between KRE and K levels. Moreover, nutrient concentrations in plant tissues need not necessarily reflect high nutrient resorption efficiencies, as could be expected. A decrease of PRE was observed in species growing in P-rich sites or after P fertilization [6, 19, 24]. However, even extremely high P concentrations did not always cause a downregulation of PRE. In controlled conditions, strong reductions of PRE in five sedges were noted when P concentrations in green leaves were higher than 2 $mg \cdot g^{-1}$. In contrast, in a Dutch fen relatively high PREs were observed with high foliar P concentrations (3-4 $mg \cdot g^{-1}$) [25]. Using a global database, Kobe et al. [31] found that resorption efficiency generally declined with increasing leaf nutrient status, within and among species. These results support the current study, in which correlations between nutrient resorption efficiencies and foliar nutrient concentrations were observed. However, no correlation was detected between KRE and K concentrations in green leaves, suggesting intensive leaching loss during senescence [32].

The analysis of nutrient concentrations in the studied macrophytes indicated that emergent macrophytes did not differ significantly in their abilities to reduce N or P and K in senescing leaves. In this study, nitrogen resorption proficiencies were comparable and varied between 0.45 and 1.34% N in different species, among which according to Killingbeck [3] *T. angustifolia* could be considered as a high N-proficient plant (>1% N in senescing leaves). These results are comparable to N concentrations in dead leaves of graminoids [25], and are much higher than biochemical lower limits for N and P in senescing leaves (0.3% N and 0.01% P) reported by Killingbeck [3] and Aerts and Chapin [1].

Aerts et al. [18] and van Heerwaarden et al. [8] showed that species from N-limited sites reach complete resorption in comparison with those from unlimited nutrient sites. In eutrophic conditions, resorption efficiency of *Phragmites australis* ranged from 0% to 50% [33, 34], and Tylová et al. [21] reported that it could reach even 60% in conditions after the early frost. The current studies were performed in a nutrient-rich lake, suggesting that the tested species did not complete their resorption. These results confirm studies of Kühl and Kohl [35] and Lippert et al. [36], who observed delayed translocation of N into belowground organs, and high N concentrations in mature leaves of emergent macrophytes even at the beginning of the winter time. Also, Kobe et al. [31] observed in wetland graminoids high nutrient concentrations in senescing leaves, which indicated that plants grown under eutrophic conditions exhibited less efficient N conservation.

Differences between N and P concentrations in plant tissues are caused not only by nutrient translocation to the rhizome, but also by leaching during rain events or following dew formation and microbial activities [37]. Phosphorus is physically more mobile than N in plant tissues and may be easily leached from plant material. However, the correlation between N and P concentrations for all data combined were highly correlated ($r=0.842$, $p<0.0001$), indicating that resorption rather than leaching was the overriding mechanism leading to the observed N and P concentrations in the present studies.

Applications

Emergent macrophytes play an important role in the nutrient cycle in lake ecosystems through high uptake of nutrients and high capacity to store nutrients in the plant structures. This make it possible to use reeds for nutrient removal from the lake ecosystem with the aim of improving water quality in lakes. The most efficient way to achieve this target is to mow emergent macrophytes before leaves reach senescence and nutrients are translocated to other plant parts. In general, the studied macrophytes were characterized by high leaf N concentrations, comparable to N resorption efficiency, higher litter N concentrations and lower values of NRE in comparison with other species, for example evergreens [1] or species from P-limited sites [25]. These leaf traits are the main determinants of high plant productivity [20, 38] and make plants more adaptable to environmental changes than other species [1, 39]. In addition, this kind of species is characterized by a high ability to replace other plant species with increasing soil nutrient availability that is observed in many eutrophic lakes.

Conclusions

In this study, significant differences in N resorption and N utilization among four emergent macrophytes, growing in the nutrient-rich littoral zone, were observed. Particularly high values were detected in *Phragmites australis* in comparison with other tested species. However, these differences were not observed with respect to phosphorus and potassium resorption efficiencies and proficiencies. The performed analyses of changes in nutrient concentrations found in green leaves during the vegetation season suggest that wetland species having a different strategy of nutrient uptake in eutrophic conditions can show similar final nutrient concentrations in plant tissue. In the present study, macrophytes were characterized by high leaf N concentrations, higher litter N concentrations and lower values of NRE, which determine the high productivity of these plants and their importance in primary production in wetlands.

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