

NITROGEN AND PHOSPHORUS RESORPTION IN TWO WETLAND MACROPHYTES

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Abstract

Nitrogen (N) and phosphorus (P) resorption efficiency (RE) and, resorption proficiency (RP) and functional strategies in *Schoenoplectus lacustris* subsp. *tabernaemontani* and *Typha latifolia* occurring in Cernek Lake and Uzun Lake with different nutrient status situated in Bafra town in Central Black Sea Region of Turkey was investigated. Mass-based N and P concentrations during summer (from June to September) in both species were rather higher than those of British, European and American wetland species. However, both N- and P-limitations were found in both species during the sampling period. It has been found that transitional strategy between CS and C strategies (C/CS) was common for the two species, whilst *T. latifolia* individuals in Cernek Lake exhibited CS strategy. N resorption was incomplete in Cernek and Uzun Lakes in both species. P resorption was complete in Uzun Lake for both species, whereas P resorption was intermediate in Cernek Lake, but more proficient for *T. latifolia*. Both PRE and PRP in *T. latifolia* individuals in Cernek Lake were higher than those in *Schoenoplectus lacustris* subsp. *tabernaemontani* individuals and this shows that CS species has an efficient internal cycling of P.

Introduction

It has long been known that nitrogen (N) and phosphorous (P) are critical components of plant nutrition and these two elements most commonly limit plant growth in both terrestrial and aquatic ecosystems (Chapin, 1980; Ratnam *et al.*, 2008; Jabeen & Ahmad, 2012). It has been reported that leaf photosynthetic capacity is closely linked to changes in the nitrogen allocation patterns (Zheng *et al.*, 2012). N and P are also one of the main factors which limit plant growth in many wetlands (Bilgin *et al.*, 2003; Güsewell, 2005a). In nutrient-limited ecosystems plant species use nutrients more efficiently to reduce nutrient loss (Berendse & Aerts, 1987; May & Killingbeck, 1992; Grime, 2002; Kutbay *et al.*, 2003).

Foliar resorption is a strategy for effective use of nutrients and it increases the control of an individual plant over the nutrient resources and it allows the plant to reutilize them (Mayor & Roda, 1992; Minoletti & Boerner 1994; Yasumura *et al.*, 2005; Yuan *et al.*, 2005). N and P are largely withdrawn from senescent leaves before leaf abscission (van Heerwaarden *et al.*, 2003). From a biological perspective, an important advantage of measuring resorption as proficiency rather than efficiency is a more unequivocal measure (Killingbeck, 2004).

Foliar resorption has been defined in 2 ways as resorption efficiency (RE) and resorption proficiency (RP) (Killingbeck, 1996; Killingbeck, 2004). RE is meant as the ratio of the resorbed amounts of nutrient losses during the leaf senescence to its prior amount deposited in the leaves (Killingbeck, 1996; Ozbucak *et al.*, 2008). RP is the content of a nutrient in senesced leaves and is not subject to temporal variation in nutrient content in green leaves and timing of sampling (Lajtha, 1987; Zotz, 2004; Kobe *et al.*, 2005).

Foliar resorption enables that the plant is less subject to external nutrient availability and this is a significant mechanism for aquatic plants like terrestrial plants.

Wetland plants have short-lived leaves and resorption efficiency plays a greater role than life span for their nutrient conservation (Aerts & Chapin, 2000; Güsewell, 2005a). Morphological and regenerative traits of wetland plant communities were shown to possess characteristic tissue nutrient signatures consistent with their preferred growing conditions and the type of nutrient limitation faced (Willby *et al.*, 2001). Grime (2002) proposed some strategies to explain the adaptation of plants against competition, stress and disturbance. Grime's model distinguishes further intermediate secondary strategies (CS: competitive stress-tolerant, CR: competitive ruderal, SR: Stress-tolerant ruderal, CSR: Competitive stress-tolerant ruderal) that may have evolved in habitats where no single factor predominated (Greulich & Bornette, 1999) and these strategies can be used to explain the differences with respect to foliar resorption patterns (Cakir *et al.*, 2010).

Wetlands are very important ecosystems due to their high productivity. However, natural wetlands have been declined day by day throughout the world. So foliar resorption strategies of wetland plants are of crucial importance (Gill *et al.*, 2012; Saeed *et al.*, 2013). The aim of this study was to define monthly changes of nitrogen (N) and phosphorus (P), and to determine N and P resorption efficiency (RE) and, resorption proficiency (RP) in two co-occurring species (*Schoenoplectus lacustris* subsp. *tabernaemontani* and *Typha latifolia*) in Cernek Lake and Uzun Lake near Bafra town in Central Black Sea Region. Cernek and Uzun Lake had different nutrient status and N and P were more limited in Cernek Lake (Bilgin *et al.*, 2003). Our second aim was to determine the probable relationships among RE, RP and leaf N and P concentrations. The studied species were also classified according to Grime's CSR strategies to determine the interaction between nutrient-limitation and nutrient use strategies.

Material and Methods

Study area: The study area is located in Kızılırmak Delta situating in northern and northeast part of Bafra town (Central Black Sea Region). Kızılırmak Delta has been formed as a result of alluvial processes and one of the most important deltas in Turkey. This study was carried out in Cernek and Uzun Lake which covers a 369 ha and 294 ha area, respectively. The studied lakes were formed as a result of longshore sediment drift. Cernek and Uzun Lakes are separated from the Black Sea with a sand bed and by a 0.5-2 km wide set, respectively (Fig. 1; Baris *et al.*, 2005). Cernek Lake is less productive with respect to N and P concentrations as compared to Uzun Lake (Bilgin *et al.*, 2003; Yasar, 1994; Oktener, 2004).

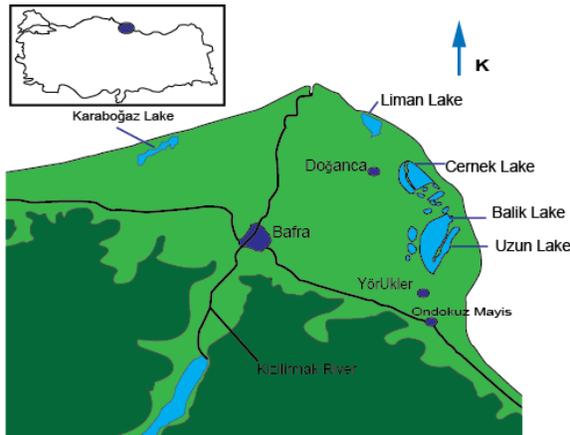


Fig. 1. Map of the study area (retrieved and arranged from Baris *et al.*, 2005).

Mean annual temperature and mean annual precipitation in the study area are 13.7°C and 806.4 mm, respectively. Mean maximum (July) and minimum (February) temperatures are 33.8°C and -2.8°C respectively. Mean annual humidity is 79.81% and according to this data semi-humid Mediterranean climate is seen in the study area. Precipitation regime is Central Mediterranean (Turkish Ministry of Agriculture 2002).

Sampling and chemical analysis: *Typha latifolia* belongs to *Typhaceae* and this family includes aquatic or semi-terrestrial perennial herbs occurring in watersides, lakes, ditches and canals. *Schoenoplectus lacustris* subsp. *tabernaemontani* is a 3 m in height, rhizomatous perennial belonging to *Cyperaceae* and occurring on alluvial flats, near streams, shallow lakes and lagoons (Davis, 1984; Davis, 1985).

This study was carried out between June 2005-October 2005. Transects, each of 9 m long, were laid at the points where both species co-occurred in both lakes. Whole leaf samples of *T. latifolia* were used to obtain reliable data of whole-plant level (Vernescu *et al.*, 2005). Photosynthesizing shoots of *S. lacustris* subsp. *tabernaemontani* were used because all leaves are reduced to bladeless sheaths (Davis, 1984; Rejmankova, 2005). At least 7 individuals from each species were

evaluated in each sampling period. Five to 6 leaves and photosynthesizing shoot samples of each species were selected along the transects in each sampling period.

Leaf and shoot samples were dried at 70°C to constant weight and powdered in a mill. After that, N and P concentrations were determined by using standard methods (Allen *et al.*, 1986). Canopy height, dry matter content, flowering period, the onset of flowering, lateral spreading, dry leaf weight, and specific leaf area were used to find Grime's strategies for the studied species (Hodgson *et al.*, 1999; Cakir *et al.*, 2010).

N and P resorption efficiency (NRE and PRE) was calculated as $[(NG-NS) / NG] \times 100$, where NG and NS are either N or P concentrations in mature green-leaf (G) and senescent leaf (S), respectively (Cakir *et al.*, 2010). N resorption proficiency (NRP) and P resorption proficiency (PRP) are the highest N and P concentrations in senescence leaves, respectively. NRE, PRE, NRP and PRP were expressed as $mg\ g^{-1}$ because no losses of mass occurred during senescence for wetland plants (Rejmankova, 2005).

Statistical analysis: Repeated measures of ANOVA (RMANOVA) and multivariate general linear models were used for the evaluation of N and P concentrations, N/P ratio, NRE, PRE, NRP and PRP (SPSS Inc. 1999). Nutrient concentrations were selected as dependent variables, while localities and months were selected as independent (fixed) variables. Pearson correlation coefficients between leaf traits and RE and RP, respectively were also calculated. Tukey's honestly significant difference (HSD) test was used to rank means following RMANOVA.

Results

T. latifolia individuals in Cernek Lake exhibited CS strategy. However, *S. lacustris* subsp. *tabernaemontani* individuals in Cernek and Uzun Lake and *T. latifolia* individuals in Uzun Lakes belonged to transitional strategy between CS and C strategies (C/CS).

N and P concentrations changed significantly during growth period regarding both species and localities. No significant differences were found between the species and localities in terms of N concentration. N/P ratio were not significantly changed with respect to localities, growth period and species. Locality *month interaction was significant except for N/P ratio and P concentration. N and P concentrations were significantly different with respect to locality *species interaction. However, only N concentration was significantly different with respect to month *species interaction. Locality *month *species interaction was significant in terms of all of the studied parameters (Table 1).

Some significant differences were also found with respect to RE like nutrient concentrations. The studied species were significantly different with respect to NRE. However, no significant differences were found between Cernek and Uzun Lakes regarding NRE. Locality *species interaction was significant except for NRE (Table 2).

Table 1. The evaluation of nitrogen and phosphorus concentrations and N/P ratio by repeated measures of ANOVA (RMANOVA).

Source	Dependent variable	F-value	Sig.
Locality	P mg/g	19.850	0.001**
	N mg/g	0.310	0.579NS
	N/P	1.195	0.278NS
Month	P mg/g	26.959	0.001**
	N mg/g	135.761	0.001**
	N/P	0.816	0.518NS
Species	P mg/g	17.470	0.001**
	N mg/g	3.441	0.067NS
	N/P	0.932	0.337NS
Locality * Month	P mg/g	0.931	0.450NS
	N mg/g	12.031	0.001**
	N/P	2.242	0.072NS
Locality * Species	P mg/g	25.065	0.001**
	N mg/g	12.422	0.001**
	N/P	1.093	0.299NS
Month * Species	P mg/g	2.486	0.050NS
	N mg/g	9.828	0.001**
	N/P	2.514	0.048*
Locality * Month * Species	P mg/g	6.147	0.001**
	N mg/g	5.949	0.001**
	N/P	3.207	0.017**

NS: Not significant * <0.05 ** <0.01 **Table 2. The evaluation of NRE, PRE, NRP and PRP by repeated measures of ANOVA (RMANOVA).**

Source	Dependent Variable	F-value	Significance
Species	NRE	5.771	0.029*
	PRE	0.224	0.642NS
	NRP mg/g	3763.600	0.001**
	PRP mg/g	126.943	0.001**
Locality	NRE	4.363	0.053NS
	PRE	0.071	0.919NS
	NRP mg/g	10.000	0.006**
	PRP mg/g	14.033	0.002**
Locality * Species	NRE	0.034	0.855NS
	PRE	15.272	0.001**
	NRP mg/g	10.000	0.006**
	PRP mg/g	11.973	0.003**

NS: Not significant * <0.05 ** <0.01

NRE was higher in *T. latifolia* in Cernek Lake, while it was higher in *S. lacustris* subsp. *Tabernaemontani* from Uzun Lake. The same holds true for PRE in both species. PRE in *T. latifolia* individuals in Cernek Lake was higher than the individuals in Uzun Lake. However, the opposite trend was found for *S. lacustris* subsp. *tabernaemontani* (Table 3).

There were significant correlations between green leaf N concentration and NRE in both species in Cernek Lake. Statistically significant and negative correlations were found between senescent leaf N and P concentrations and NRE and PRE, although some of them were not significant in *S. lacustris* subsp. *tabernaemontani* individuals in Uzun Lake. The correlations between green leaf N concentrations and NRP in both species were not significant. However, PRP was significantly and

negatively correlated with green leaf P concentration in Cernek Lake. Similarly, senescent leaf N and P concentrations were negatively correlated with NRE and PRE, respectively and these correlations were usually significant except for *S. lacustris* subsp. *tabernaemontani* in Uzun Lake. There was a significant correlation between N/P ratio and NRE in *S. lacustris* subsp. *tabernaemontani* in Cernek Lake. However, the other correlations between N/P ratio and NRE were not statistically significant. Negative correlations were found between N/P ratio and PRE in *S. lacustris* subsp. *tabernaemontani* in Cernek Lake and Uzun Lake. Both positive and negative correlations were found among green leaf N/P ratio and NRP and PRP, respectively. Similarly, both positive and negative correlations were found among senescence leaf N/P ratio and RE and RP, respectively (Table 4).

Table 3. Resorption efficiency (RE) and resorption proficiency (RP).

	Cerneke lake		Uzun lake	
	NRE (%)	NRP (mg/g)	NRE (%)	NRP (mg/g)
<i>T. latifolia</i>	76.90 ± 8.07	22.40 ± 2.50	70.71 ± 3.46	12.32 ± 1.12
<i>S. lacustris</i> subsp. <i>tabernaemontani</i>	75.24 ± 1.55	11.21 ± 0.03	76.20 ± 1.72	11.20 ± 0.03
	Cerneke lake		Uzun lake	
	PRE (%)	PRP (mg/g)	PRE (%)	PRP (mg/g)
<i>T. latifolia</i>	80.33 ± 3.04	0.58 ± 0.05	62.00 ± 7.70	0.42 ± 0.03
<i>S. lacustris</i> subsp. <i>tabernaemontani</i>	53.00 ± 7.86	0.62 ± 0.05	66.66 ± 7.45	0.30 ± 0.03

Table 4. Pearson correlations among leaf nutrient concentrations and RE and RP.

	<i>T. latifolia</i>		<i>S. lacustris</i> subsp. <i>tabernaemontani</i>	
	Cerneke lake	Uzun lake	Cerneke lake	Uzun lake
Green leaf N concentration-Green leaf P concentration	0.770*	-0.220NS	0.721*	-0.578NS
Green leaf N concentration-Green leaf P concentration	-0.055NS	-0.039NS	0.500NS	0.210NS
Green leaf N concentration-NRE	0.660*	0.760*	0.998**	0.995**
Green leaf P concentration-PRE	-0.700*	0.380NS	0.424NS	0.976**
Green leaf N concentration-NRP	-0.300NS	-0.610NS	-0.167NS	-0.170NS
Green leaf P concentration-PRP	-0.919**	-0.220NS	-0.645*	-0.490NS
Senescent leaf N concentration-NRE	-0.907**	-0.980**	-0.167NS	-0.080NS
Senescent leaf P concentration-PRE	-0.922**	-0.813*	-0.704*	-0.560NS
Green leaf N/P-NRE	0.140NS	0.450NS	0.645*	0.120NS
Green leaf N/P-PRE	0.550NS	0.330NS	-0.686*	-0.976**
Green leaf N/P-NRP	-0.390NS	-0.390NS	-0.780*	0.976**
Green leaf N/P-PRP	-0.790*	-0.430NS	0.050NS	0.660*
Senescence leaf N/P-NRE	-0.710*	0.180NS	-0.662*	0.200NS
Senescence leaf N/P-PRE	0.873**	0.963**	0.741*	-0.560NS
Senescence leaf N/P-NRP	0.410NS	-0.250NS	0.662*	0.560NS
Senescence leaf N/P-PRP	-0.881**	-0.919**	-0.933**	-0.980**

NS: Not significant * <0.05 ** <0.01

The highest N concentrations were found in June and July in Uzun Lake and Cerneke Lake, respectively, in *T. latifolia*. N concentration was found to be decreased during September (Fig. 2). N-limitation was observed during the sampling period except for June for *S. lacustris* subsp. *tabernaemontani* in Cerneke Lake, while N-limitation was found in June, September and, October for *S. lacustris* subsp. *tabernaemontani* in Uzun Lake. P-limitation was only found in June for *S. lacustris* subsp. *tabernaemontani* in Cerneke Lake, whereas P-limitation was found from July to August in Uzun Lake. P concentrations of *T. latifolia* in Cerneke Lake were higher as compared to those in Uzun Lake and the highest P concentrations were found in June in both lakes (Fig. 3).

The opposite trend was found in *S. lacustris* subsp. *tabernaemontani* with respect to N concentrations and the highest N concentrations were found in June and July in Cerneke and Uzun Lakes, respectively (Fig. 4). P concentrations of *S. lacustris* subsp. *tabernaemontani* in Uzun Lake were higher from June to August, whereas P concentrations were increased in Cerneke Lake from August to October (Fig. 5). The highest N/P ratio was found in August and September, respectively in *T. latifolia* in Uzun and Cerneke Lake. However, the highest N/P ratio was found in June and July in Cerneke Lake and Uzun Lake, respectively in *S. lacustris* subsp. *tabernaemontani* (Figs. 6 and 7).

Discussion

There were significant differences among populations with respect to macronutrient concentrations (Gilani *et al.*, 2011). Mass-based N and P concentrations especially from June to September in both species were rather high as compared to British, European and American wetland species (Rejmankova, 2005; Güsewell, 2004). This may be indicate luxury consumption of N and P for both species in Cerneke and Uzun Lakes (Svengsouk, 2001). Koerselman and Meuleman (1996) recommended an N/P ratio <14 was regarded as indicative of N limitation and the N/P ratio >16 as indicating P limitation in wetland plants (Willby *et al.*, 2001). Both N- and P-limitations were found in the two species during the sampling period. Both species exhibited CS or C/SC transient strategies. CS species represented the dominant functional type of wetland vegetation. It has been reported that a higher incidence of infers N-limitation in CS plants (Grime, 2002; Willby *et al.*, 2001). N-limitation was observed from June to August in *T. latifolia* which exhibit CS strategy in Cerneke Lake. However, N-limitation was found during the sampling period except for August in *T. latifolia* in Uzun Lake. P-limitation was found in September and October for *T. latifolia* in Cerneke Lake. However, P-limitation was only found in August for the in Uzun Lake in *T. latifolia*.

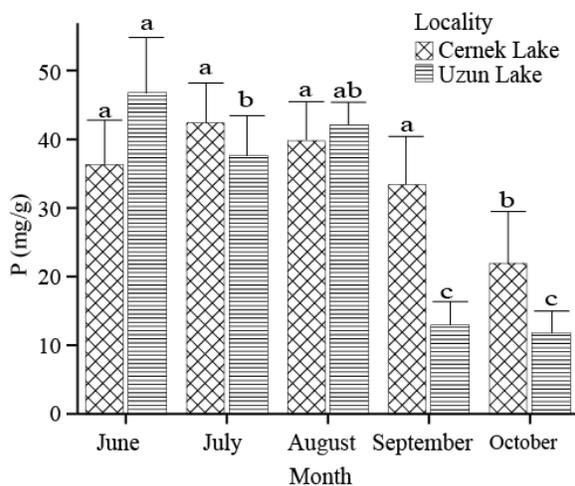


Fig. 2. N(mg/g) concentrations in *T. latifolia* individuals during the study period.

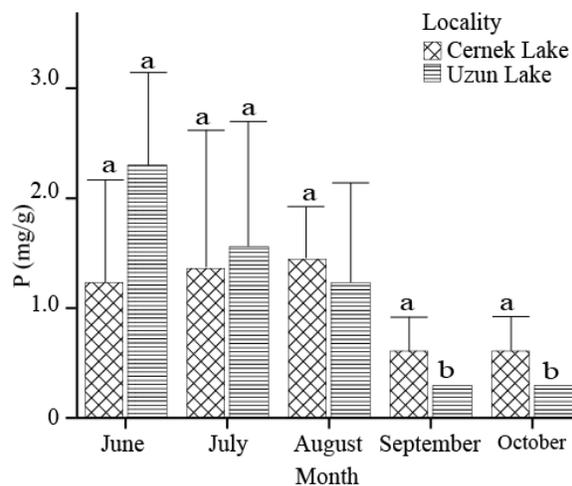


Fig. 5. P (mg/g) concentrations in *S. lacustris* subsp. *tabernaemontani* individuals during the study period.

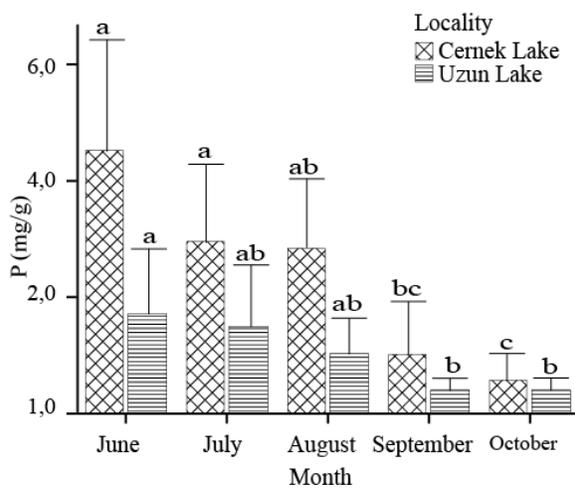


Fig. 3. P (mg/g) concentrations in *T. latifolia* individuals during the study period.

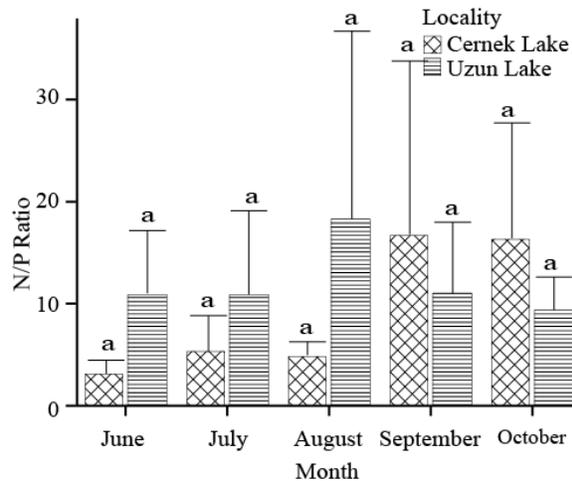


Fig. 6. N/P ratio in *T. latifolia* individuals during the study period.

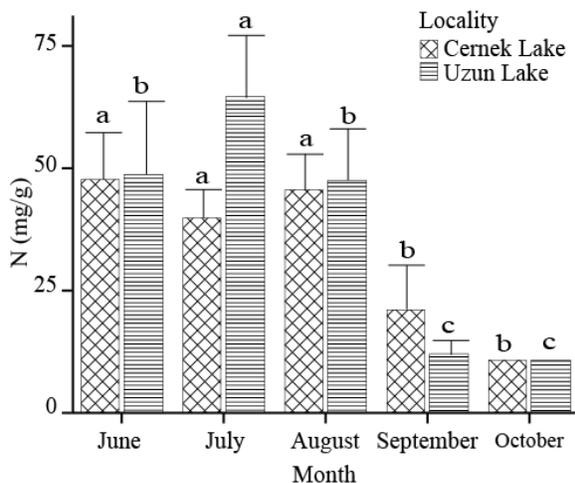


Fig. 4. N(mg/g) concentrations in *S. lacustris* subsp. *tabernaemontani* individuals during the study period.

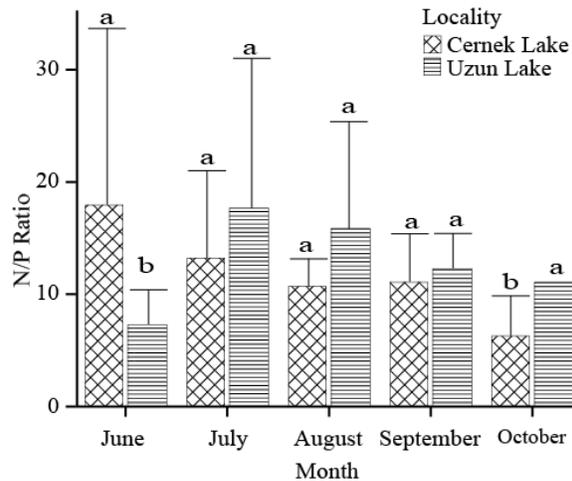


Fig. 7. N/P ratio in *S. lacustris* subsp. *tabernaemontani* individuals during the study period.

N/P ratios of CS species were found to be 12.8 and 16.2, respectively, in British and European wetlands (Güsewell, 2004). Mean N/P ratio of *T. latifolia* in Cernek and Uzun Lake from June to July was lower than that of British and Europe wetland species. Similarly, mean N/P ratios of *T. latifolia* in Cernek Lake in August and *S. lacustris* subsp. *tabernaemontani* in Uzun Lake in June were also lower than those of British and Europe wetland species.

Green leaf N concentration and NRE were positively correlated in both species in Cernek and Uzun Lakes. Rejmánková & Snyder (2008) reported a positive correlation between NRE and N in green leaf tissue in *Typha* and they stated *Typha* individuals resorbed N tightly and used it to support new growth. Our data show that *S. lacustris* subsp. *tabernaemontani* individuals also resorbed N tightly because positive correlations were found between green leaf N concentration and NRE in Cernek Lake and Uzun Lake.

Negative correlations were found between green leaf P concentrations and PRP in *T. latifolia* and *S. lacustris* subsp. *tabernaemontani* individuals in Cernek Lake. This may be explained on the basis of NRP and PRP decreases with increasing nutrient concentrations in green leaves (Kobe *et al.*, 2005). NRE and PRE overlap in plants independently and, NRP and PRP are aligned for the co-occurring species (Ławniczak, 2011).

Ratnam *et al.*, (2008) stated that N/P ratio is a poor predictor of RE. No significant correlations were found between N/P ratio and NRE except for *S. lacustris* subsp. *tabernaemontani* individuals in Cernek Lake. Both positive and negative correlations were found among green and senescent leaf N/P ratio, and NRP and PRP, respectively. It can be inferred that the interaction between N/P ratio and foliar resorption may be controversial.

Statistically significant and negative correlations were found between senescent leaf N and P concentrations and NRE and PRE. These negative correlations showed that N and P were considerably resorbed in both species (Güsewell, 2005b; Bertiller *et al.*, 2006).

Killingbeck (1996) stated that if N and P concentrations in senescent leaves are below 7 mg g⁻¹ and 0.5 mg/g⁻¹, respectively, resorption of N and P is highly proficient (Norris & Reich, 2009; Kılıc *et al.*, 2010). According to these threshold values N resorption was incomplete in Cernek and Uzun Lakes in both species. P resorption was complete in Uzun Lake for both species, whereas P resorption was intermediate in Cernek Lake, but more proficient for *T. latifolia* individuals (Kutbay & Ok, 2003). We conclude that P resorption was incomplete in macrophytes in P-deficient habitats according to the benchmark levels (Killingbeck 1996). Ławniczak (2011) was found similar results for macrophytes.

Güsewell (2005b) reported NRE values of wetland plants that ranged from 0-87%. Rejmánková (2005) found that NRE values in *Typha* species and graminoids were 50.8 and 43.9, respectively. NRE values were within the ranges reported by Güsewell (2005b), whereas higher

than those of threshold values reported by Rejmánková (2005). Güsewell (2005b) also reported that PRE values for wetland plants ranged from 30-96% (Zotz, 2004). PRE values in the present study were similar to those reported for the other wetland plants. However, PRE values in *T. latifolia* individuals in Cernek Lake were rather higher compared to benchmark levels. According to Rejmánková (2005) the values for *Typha* species and graminoids were 69.6 and 62.8, respectively. However, PRE values in Uzun Lake in both species were similar to the values reported by Rejmánková (2005). PRE values of *S. lacustris* subsp. *tabernaemontani* individuals in Cernek Lake were lower than the threshold values.

Plant species may be different from each other with respect to resorption strategies in habitats with different nutrient status (Lin *et al.*, 2009; Wood *et al.*, 2010; Huang *et al.*, 2012). Aerts & Chapin (2000) stated that P-resorption is more important in P-limited habitats as compared to N-limited habitats. *T. latifolia* individuals were more successfully adapted to P-limited habitats than any other individuals of wetland species (Svengsouk, 2001). Severe P-limitation occurred in Cernek Lake (Bilgin *et al.*, 2003) and P is normally the most limiting nutrient in wetlands (Anderson & Lockaby, 2011). Both PRE and PRP were found to be higher in *T. latifolia* individuals in Cernek Lake. *T. latifolia* individuals in Cernek Lake exhibited CS strategy and CS species has an efficient internal cycling of P (Güsewell, 2004). Rejmánková & Snyder (2008) stated that *Typha* has a high capacity for mobilizing P that accumulates in its tissues for growth.

Our results demonstrated that high RP (lower nutrient concentration in senescent leaves) provides adaptation to unproductive habitats and optimal use of N and P for wetland species (Zahoor *et al.*, 2012). Highly proficient NRE was found in *S. lacustris* subsp. *tabernaemontani* individuals in both lakes. Both species show P-limitation during growth period. Anderson & Lockaby (2011) stated that only N/P ratios can be an inconclusive indicator of nutrient limitation and other evidence (high PRE and complete PRP) supported P-limitation. *T. latifolia* used P efficiently especially in P-limited habitats because *T. latifolia* individuals had high PRE and biochemically complete PRP in Cernek Lake.

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