Nitrogen and phosphorus resorption efficiency, and N : P ratios in natural populations of *Typha domingensis* Pers. in a coastal tropical lagoon

Eficiência de reabsorção de nitrogênio e fósforo, e razões N : P em populações naturais de *Typha domingensis* Pers. em uma lagoa costeira tropical

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Abstract: Aim: We studied nitrogen (N) and phosphorus (P) resorption patterns in *Typha domingensis* Pers. in a tropical coastal lagoon during different seasons of throughout one year. **Methods:** Resorption of N and P is uttered as resorption efficiency (NRE and PRE, respectively), which may be used as an indicator of a nutrient limitation. Higher resorption efficiency values might indicate limitation of a certain element for the growth of aquatic macrophytes. **Results:** N was inferred to be less limiting than P for the growth of *T. domingensis* in Campelo Lagoon, since N content varied less than P content and resorption efficiency of N was lower than that of P and, concomitantly, low resorption efficiency of this element. However, *T. domingensis* of Campelo Lagoon frequently utilized P that was already present in its tissues, contributing to the longer residence time of this element in system. Green leaves of *T. domingensis* showed N : P ratio, ranging 49-96, corroborating the inference of P limitation. **Conclusions:** N : P ratio and resorption efficiency indicate P limitation by *T. domingensis* in Campelo Lagoon.

Keywords: wetland, aquatic macrophyte, senescing leaves, nutrients.

Resumo: Objetivo: Estudamos padrões de reabsorção de nitrogênio (N) e fósforo (P) em *Typha domingensis* Pers. em uma lagoa costeira tropical durante diferentes estações do ano. **Métodos:** Reabsorção de N e P é dito como a eficiência de reabsorção (NRE e PRE, respectivamente), o que pode ser utilizado como um indicador de limitação nutricional. Os maiores valores de eficiência de reabsorção podem indicar limitação de um determinado elemento para o crescimento de macrófitas aquáticas. **Resultados:** N demonstrou ser menos limitante que P para o crescimento de *T. domingensis* na lagoa do Campelo, já que a eficiência de reabsorção de N variou menos do que o de P e, concomitantemente, baixa eficiência de reabsorção desse elemento. No entanto, *T. domingensis* da lagoa do Campelo freqüentemente utiliza P, que já estava presente em seus tecidos, contribuindo para o maior tempo de residência deste elemento no sistema. As folhas verdes de *T. domingensis* apresentaram a razão N : P, variando de 49-96, corroborando a inferência de limitação P. **Conclusões:** Razão N : P e eficiência de reabsorção indicam a limitação de P por *T. domingensis* na lagoa do Campelo.

Palavras-chave: áreas alagáveis, macrófitas aquáticas, folhas senescentes, nutrientes.

1. Introduction

Lagoons are commonly shallow aquatic ecosystems with expressive occurrence of aquatic macrophytes (McGlathery et al., 2007). These plants provide habitat and organic matter for diverse ecological processes (Thomaz and Cunha, 2010). Aquatic macrophytes influence ecological recycling during transference of nutrients from sediment and/or water to plant (e.g. plant nutrient uptake) and from plant to water environment (e.g. grazing, plant exudation and mineralization) (Ziegler and Benner, 1999; Nunes et al., 2007; Bakker et al., 2013).

Plants possess mechanisms by which essential nutrients are assimilated, translocated and accumulated (Marschner, 1995). Nutrient uptake is initial process to plant development. Other processes are translocation and resorption that decrease the assimilation of nutrients from environment (Aerts, 1996). Translocation is the transfer of elements, especially compounds of C, from leaves to other plant structures (De Deyn et al., 2012). Resorption is the move of nutrients from senescing tissues to organs with intense metabolic activity, as growing ones, and to storage tissues (Killingbeck, 1996).

Nutrient-poor plant groups, mostly those deficient in N and P, regularly attain these elements by resorption from senescent plant tissues (Aerts et al., 2007). This process is a strategy utilized by plants to retain nutrients internally and to avoid losses (Nordell and Karlsson, 1995; Escudero and Mediavilla, 2003), increasing nutrient use efficiency (Bridgham et al., 1995) and competitive advantage in low-nutrient environments (Aerts and Chapin, 2000), despite it is in all environments (Rejmánková, 2005). Thus, plant growth is determined not only by nutrients acquired from substrates, but also by nutrients reused by the plants.

Norby et al. (2000) verified that the link involving nutrient levels (N and P) in living and senescent parts depends on the resorption capacity of the plants. The quality of debris produced by aquatic macrophytes is affected by the nutrient resorption, which so affects decomposition route in the environment (Debusk and Reddy, 2005). So, obtaining conception about resorption forms and their causes by quantifying resorption efficiency is important for considerate plant growth in ecosystem (Nambiar and Fife, 1991; Covelo et al., 2008). Aspects controlling resorption remain weakly understood (Norris and Reich, 2008).

One method utilized to study internal translocation of N and P is the N : P ratio in plant individual parts (Eckstein and Karlsson, 2001; Güsewell, 2004). Such ratios may also be used as indicators of N and P limitation in the environment. The N : P ratio is utilized because, it is without difficulty obtained and can be compared with other studies (Güsewell and Koerselman, 2002; Zhang et al., 2008). N : P ratios have been used to explain ecological changes and to manage these communities (Matson et al., 1999; Cárdenas and Campo, 2007; Kozovits et al., 2007).

Resorption efficiency in aquatic macrophytes is poorly known compared to that of terrestrial plants. Therefore, the aims of this study were (1) to determine N and P concentrations and N : P ratios in green and senescing leaves of *T. domingensis* and (2) to examine N and P resorption efficiency of this emergent aquatic macrophyte growing in Campelo Lagoon.

2. Material and Methods

Campelo Lagoon is located in Campos dos Goytacazes and São Francisco de Itabapoana municipalities of Rio de Janeiro State, between the latitudes of 21° 38' and 21° 42' S and the longitudes of 41° 08' and 41° 12' W (Figure 1). The origin of this coastal lagoon, which is geologically founded upon quaternary fluvial marine sedimentary deposits, is attributed to the formation processes of the Paraiba do Sul River delta. It is considered to be a typical continental sand plain lagoon. Its catchment area is mainly used for pasture and monoculture of sugarcane. Along its entire marginal area it is possible to observe the existence of dense colonization of the aquatic macrophyte *T. domingensis* Pers. Other macrophytes are found around the lagoon as *Bacopa arenaria* (J.A. Schmidt) Loefgr. & Edwall., *Justicia laevilinguis* (Nees ex Mart.) Lindau. and *Mimosa nigra* Hub., *Cyperus giganteus* Vahl., *Eichhornia crassipes* (Martius) Solms-Laubach., *Eleocharis acutangula* (Roxb.) Schult., *Nymphoides indica* (L.) O. Kuntze. and *Schoenoplectus californicus* (C.A. Mey.) Soják.; and *Salvinia auriculata* Aubl., in the deep littoral zone. The submersed macrophytes in the lagoon are *Ceratophyllum demersum* L., *Egeria densa* Planch., *Najas marina* L., *Cabomba caroliniana* A. Gray. and *Utricularia foliosa* L.

Campelo Lagoon lies in a region that presents tropical climate with annual average rainfall of 1,000 mm and average temperatures between 20 and 30 °C (FIDERJ, 1978). The highest rainfall incidence occurs from November to January, decreasing in February and increasing again in

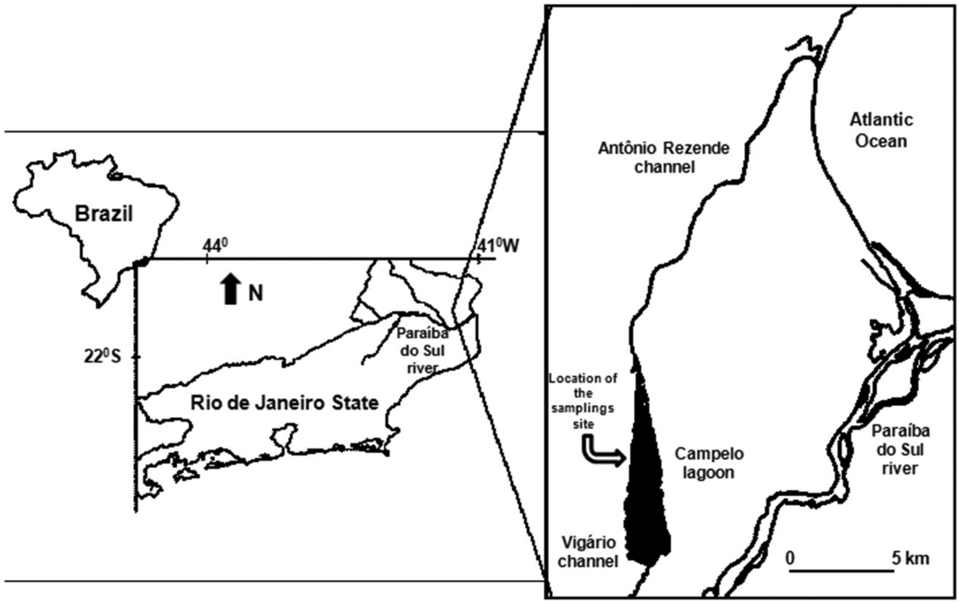

Figure 1. Study area and location of the sampling site in the Campelo Lagoon.

March and April. The local soil is sandy and poor in nutrients (podzol hydromorphic) (CIDE, 1997). Sampling was carried out every season from September 2004 to September 2005 in the littoral zone of Campelo Lagoon. Five quadrats of 0.25 m^2 were sampled during each season in the lagoon (Spring – 09/30/04, 10/14/04, 10/26/04, 11/11/04 and 11/29/04; Summer – 12/21/04, 01/14/05, 01/28/05, 02/14/05 and 03/02/05; Autumn – 03/30/05, 04/15/05, 04/29/05, 05/13/05 and 06/15/05; Winter – 06/30/05, 07/15/05, 08/02/05, 08/16/05 and 08/31/05). Harvested samples of *T. domingensis* were separated into completely green and senescent (< 60% green color, light brown, still attached to shoot base) leaves. In the laboratory, plant samples were washed under running water and dried in a stove at 80 °C for 72 hours. The plant samples were powdered and stored in hermetically sealed bottles. Aliquots were removed in order to determine N and P concentrations. N was determined through Perkin Elmer 2400 (CHNS/O) elemental analyzer, and P, after acid digestion, was determined through spectrophotometric reading of colored complex at 885 nm (Delgado et al., 1994) in triplicate.

N resorption efficiency (NRE) and P resorption efficiency (PRE) were calculated according to Killingbeck's proposal (1996):

$$RE\ (\%) = 100 \times (1 - [\text{nutrient}]_{\text{senescing}} / [\text{nutrient}]_{\text{green}}),$$

where RE is the nutrient (N or P) resorption efficiency, $[\text{nutrient}]_{\text{green}}$ is the N or P concentration of green leaves, and $[\text{nutrient}]_{\text{senescing}}$ is the N or P concentration of senescing leaves.

For both leaves, nutrient concentrations and ratios were analyzed by Kruskal-Wallis test, and the differences between seasons were verified by Dunn's Multiple Comparison test. Pearson correlations were used to assess the relationships between the various parameters. A significance level of $p < 0.05$ was used in all tests.

3. Results

Mean N concentrations (± SD) in cattail tissue during the study period were 33.04 ± 2.15 mg DW g^{-1} for green leaves and 30.54 ± 2.01 mg DW g^{-1} for senescing leaves. Statistically significant differences were observed between green and senescing leaves ($p < 0.05$) (Table 1). Mean P concentrations (±SD) were 1.07 ± 0.18 mg DW g^{-1} for green leaves and 0.34 mg DW g^{-1} (varying from 0.18 to 0.91 mg DW g^{-1}) for senescing leaves. N : P ratios differed significantly ($p < 0.05$) (Table 1) among green and senescing leaves. NRE and PRE ($p > 0.05$) not differed significantly among seasons. The mean value of NRE was 7% (varying from 4 to 12%), while PRE values were about 9 times as high (68%, varying from 58 to 74%) (Figure 2). In this study, N, P and N : P were positively correlated between green and senescing leaves; however, they did not differ significantly ($p > 0.05$). Variation in the N : P ratio was primarily determined by variation in P concentration, because the N concentration of

Table 1. N and P mean content (mg DW g^{-1}) and N : P in the different leaves of the aquatic macrophyte *T. domingensis* in four different seasons (Spring, Summer, Autumn and Winter) and Mean Annual. The standard deviation is in parenthesis. Identical letters indicate groups of means with no statistically significant differences at the 95 % confidence level.

Leaves	Nutrient	Seasons				Mean Annual
		Spring	Summer	Autumn	Winter	
Green	N *	31.96 (1.35) b	31.50 (0.79) b	33.24 (2.20) ab	35.46 (1.68) a	**33.04 (2.15)**
	P *	0.95 (0.14) b	1.02 (0.08) ab	1.06 (0.23) ab	1.26 (0.10) a	**1.07 (0.18)**
	N : P ^{ns}	75.29 (9.99)	68.81 (5.11)	72.37 (17.90)	62.68 (5.91)	**69.79 (11.16)**
Senescing	N *	28.14 (1.92) b	30.34 (1.01) ab	31.16 (1.11) a	32.52 (0.73) a	**30.54 (2.01)**
	P ^{ns}	0.30 (0.04)	0.27 (0.07)	0.46 (0.27)	0.34 (0.05)	**0.34 (0.15)**
	N : P ^{ns}	207.83 (25.27)	265.46 (72.61)	181.62 (72.92)	214.65 (30.89)	**217.39 (59.46)**

- ns: not significant. - * Significant at $p < 0.05$.

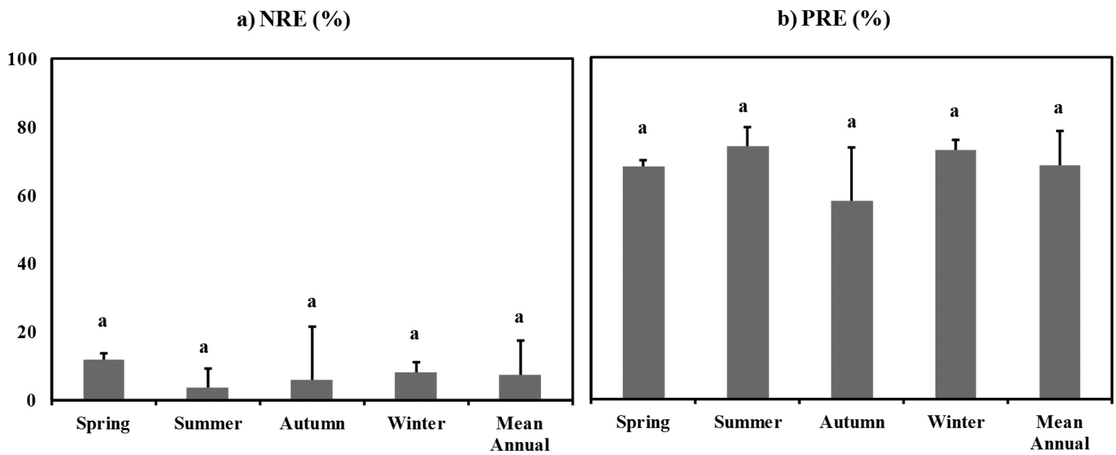

Figure 2. Fluctuation a) NRE and b) PRE for leaves of *T. domingensis* in four different seasons (Spring, Summer, Autumn and Winter) and Mean Annual. The bar indicates standard deviation. Identical letters indicate groups of means with no statistically significant differences at the 95% confidence level.

T. domingensis was relatively stable. The correlation among these variables was negative, but statistically significant only for P ($p < 0.05$). Relationships of N, P and the N : P ratio of green leaves with NRE and PRE presented positive correlations. The N : P ratio of senescent leaves was positively correlated with PRE ($r = 0.8$; $p < 0.01$).

4. Discussion

N presented a pattern possibly related to greater availability of this element in the sediment. Nutrient availability patterns in flooded areas were often limited by P (Bedford et al., 1999). The study presents a short-term, making it difficult to form generalizations, but it suggests limitation by P in the littoral area of Campelo Lagoon. These results are supported by other studies in wetlands worldwide (Lorenzen et al., 2001; Miao, 2004; Zotz, 2004). The low resorption efficiency of N strongly suggests that this nutrient was primarily taken up from the sediment of Campelo Lagoon.

Temporal variation patterns and the range of variation in N and P concentration in *T. domingensis* leaf tissues in Campelo Lagoon suggest that environmental factors affect nutrient resorption. These aquatic macrophytes occasionally deplete nutrients in their habitats, probably impeding invasion by competitors (Johnson and Rejmánková, 2005; Richardson et al., 2008a). Nutrient concentrations in green tissues of *T. domingensis* from Campelo Lagoon were similar to those described in similar tropical wetlands occupied by emergent aquatic macrophytes: 34 mg DW g^{-1} for N and 2 mg DW g^{-1} for P (Ennabili et al., 1998; Miao et al., 2000). In wetlands, as in other flooded habitats, environments that are poor in nutrients are generally dominated by species that have low nutrient concentrations in their leaves; as nutrient availability increases, these species are replaced by plants with higher nutrient concentrations in their leaves (Richardson et al., 2008a). Grasses usually dominate sediments poor in P, because of their lofty resorption efficiency (Güsewell, 2005a). On the other hand, large stands of *T. domingensis*, which generally colonizes areas that are rich in nutrients, were observed in Campelo Lagoon.

Estimate of the nutrient contents of green and senescing leaves is a sensitive method to determine nutrient availability (Miao, 2004). This relationship may be more resourceful than resorption efficiency. In addition, these differences between green and senescing leaves might be an indicator of reduce nutritional (Güsewell, 2004; Bertiller et al., 2005). Apparently, the small variation in N content involving green and senescing leaves might be result of N availability in the sediment of Campelo Lagoon. Changes in P content of green and senescing leaves reflect variation in P availability in the environment. The capacity of plants to regulate the use of nutrients in low concentrations has been found in several studies (Drenovsky and Richards, 2006; Richardson et al., 2008b). N concentrations in living tissues of *T. domingensis* in Campelo Lagoon indicate that this element is not limiting. This fact may be related to the historical development and specific characteristics of the environment that may influence the resorption of this element. Yuan et al. (2005) have indicated that some plants are more competent in resorption of N than other species that are less able to adjust to their environment. From this fact, it has been speculated that *T. domingensis* in Campelo Lagoon is adapted to environments poorer in P; therefore, resorption of this nutrient is expected to be high. Even if the nutrient content is higher in the sediment, resorption seems to be more effective for rapid growth of plants that have strong nutritional demands (Güsewell, 2005b).

The criteria for limiting nutrients proposed by Koerselman and Meuleman (1996) suggest that a plant tissues N : P between N limitation – N : P < 14 and P limitation – N : P > 16. Based on these criteria, the N : P ratios observed in *T. domingensis* tissues during seasons of this study indicate strong limitation by P.

The data presented herein suggest a connection between resorption and indicators of P limitation expressed by *T. domingensis* in Campelo Lagoon. High N availability and low P across the study period may cause an imbalance of these nutrients in *T. domingensis* tissues, can affecting the growth and reproduction processes in Campelo Lagoon. N availability varied less than P availability; NRE was lower than PRE. Nutrient resorption seems to be flexible, and the observed data suggest that *T. domingensis* is adapted to develop in environments limited by P. In addition, this study indicates a need for a better understanding of the factors that control the resorption efficiency and retention of nutrients in senescing parts of *T. domingensis* in Campelo Lagoon. Change in the resorption of nutrients is important for nutrient cycling in Campelo Lagoon.

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