Substrate-mediated direct and indirect effects on periphytic biomass and nutrient content in a tropical coastal lagoon, Rio de Janeiro, Brazil.

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ABSTRACT: Substrate-mediated direct and indirect effects on periphytic biomass and nutrient content in a tropical coastal lagoon, Rio de Janeiro, Brazil. A short scale field experiment was conducted to determine the individual and interactive effects of developmental time and substrates on periphytic biomass, total phosphorus (P) and total nitrogen (N) content in a tropical, humic coastal lagoon characterized by dense stands of aquatic macrophytes. The experiment was conducted at Cabiúnas lagoon (Northern Rio de Janeiro, Brazil) and performed during 30 days using three different substrates, two natural (green and senescent leaves of Typha domingensis Pers.) and one artificial (plastic ribbons). Periphyton biomass accrual was higher in senescent leaves of Typha and was a function of biofilm age in all substrates. Periphyton nutrient amount significantly increased throughout the experiment, however when expressed per unit of biomass or as percetange of dry weight, periphyton nutrient content decreased throughout the time. Periphyton biomass on senescent leaves presented lower P and N concentrations per unit of biomass. In general, natural substrates negatively affected periphytic nutrient content. We conclude that substrate-mediated process not associated to nutrient release could enhance periphytic biomass accrual with potential implications for periphyton bulk stoichiometry.
Key-words: Periphyton, aquatic macrophytes, Typha domingensis, nutrient content, nutrient stoichiometry.

RESUMO: Efeitos diretos e indiretos mediados pelo substrato na biomassa e no conteúdo nutricional perifítico em uma lagoa costeira tropical, Rio de Janeiro, Brasil. Um experimento de campo de curta escala foi realizado para se determinar os efeitos individuais e interativos de diferentes tempos de desenvolvimento da biomassa, conteúdo de fósforo e nitrogênio de comunidades perifíticas de uma lagoa costeira tropical húmica, caracterizada por densos estandes de macrófitas aquáticas. O experimento foi conduzido na Lagoa Cabiúnas (Nordeste do Rio de Janeiro, Brasil) durante 30 dias utilizando três diferentes substratos, dois naturais (folhas jovens e senescentes de Typha domingensis Pers.) e um artificial (tiras de plástico). A biomassa perifítica foi significativamente maior nas folhas senescentes de Typha e foi uma função da idade do biofilme em todos os substratos. A quantidade de nutrientes do perifíton aumentou ao longo do tempo, no entanto quando expresso por unidade de biomassa ou como porcentagem de peso seco, o conteúdo de nutrientes perifítico diminuiu no decorrer do experimento. A biomassa perifítica que crescia em folhas senescentes de Typha apresentou um menor conteúdo de P e N em relação aos demais substratos. Em geral, o substrato natural afetou negativamente o conteúdo de nutrientes perifítico. Nós concluímos que processos mediados pelo substrato que não estejam relacionados à liberação de nutrientes possam favorecer o desenvolvimento da biomassa perifítica com potenciais implicações para sua estequiometria.
Palavras-chave: Perifíton, macrófitas aquáticas, Typha domingensis, conteúdo nutricional, estequiometria.

Introduction

Periphyton is generally dominated by photosynthetic organism which may be unicellular, colonial or filamentous species from a variety of pro- and eukaryotic phyla. Nonetheless, the periphyton assemblage represents a complex community with heterotrophic bacteria, fungi, protozoa and

small metazoa (meiofauna), as well as autotrophic components in close spatial proximity. With regard to nutrient limitation, only recently periphyton communities become a subject of investigation (Stevenson et al., 1996). Not much is know about nutrient status (surplus of N or P) of benthic communities in lakes and its coupling with total standing biomass. If no other factors are interfering, an increase of available nutrients is supposed to cause an increase in the internal nutrient content of the algae, followed by an increase in productivity and an increase in algal biomass (Kahlert & Pettersson, 2002).

Nutrient sources for benthic algal community include the overlying water, nutrient release by the substrate, and internal nutrient recycling (Mulholland 1996). The nutrient absorption from the overlying water is, especially in lakes, often restricted by "boundary layer constraints" caused by quiescent water through which solutes can travel only by slow diffusion (Burkholder, 1996). Therefore, substrate as nutrient source assumes a greater importance in lake ecosystems, although the scientific background on this subject presents many controversies (Cattaneo & Kalff, 1979; Wetzel, 1983; Morin, 1986; Fairchild & Everett 1988; Putz, 1997). The importance of substrates as nutrient supply to attached organisms is rarely addressed (Vandeboncoeur et al., 2001). Previous studies showed that attached algae could obtain nutrients from macrophytes (Moeller et al., 1988; Wetzel, 1996) and sediments (Hagerthey & Kerfoot, 1998), improving the nutrient status of attached algae (Kahlert, 2001). However, the importance of substrates as nutrient sources might change with some aspects of the environment. Lake trophy should be negatively correlated with substrate importance (Kahlert, 2001), although such statement may be not a rule (see Hansson, 1992; Havens et al., 1996; Vadenboncoeur et al., 2001).

In coastal lagoons, the high perimeter:volume ratio and the shallowness provides favorable conditions for the development of a large littoral region (Kjerfve, 1994). Macrophyte species, which segregate along the littoral-zone slope, continuously provide new substrata for periphyton colonization (Wetzel, 1990; Schindler & Scheuerell, 2002). However, periphyton ecology in tropical coastal aquatic ecosystems is markedly absent, and is necessary for a complete picture of the ecosystem functioning, since they can be dominant primary producers in these systems (Wetzel, 1983). Some studies carried out in Brazilian coastal lagoons provided valuable information about periphytic biomass accrual and the effects of artificial and natural substrates to periphytic composition and nutrient content (Fernandes & Esteves, 1996; Fernandes, 1997). These studies pointed out that ambient nutrient availability was major source of variation for periphytic properties and no clear effect between substrates were detected, except for community composition. However, these studies were conducted in an eutrophic system where the relative importance of substrates as nutrient source is expected to be low (Kahlert, 2001).

A field experiment was used to evaluate the importance of different substrates (artificial and natural) to periphytic properties with special emphasis on substrate role as nutrient source to attached organisms. The aim of this study was to give an overview of the variation, in a short time scale, of biomass and nutrient status of periphyton communities in an oligotrophic tropical humic coastal lagoon.

Materials and Methods

Study Area

This study was carried out in Cabiúnas Lagoon, located at Restinga de Jurubatiba National Park, Rio de Janeiro - Brazil (22° 15' S, 41° 40' W). Cabiúnas is a pristine coastal lagoon surrounded by a natural 'restinga' ecosystem which is characterized by coarse-sand soil and bushy vegetation. Its highly permeable watershed and dentritic morphometry favor a great input of terrestrial dissolved organic matter into the lagoon (Farjalla & Esteves 2002). It has a surface area of 0.35 km² and a mean depth of 2.5 m. It is a freshwater waterbody and the water is classified as humic and slightly acidic (pH 6.3) with an average temperature of 23.6 °C and mean concentrations of dissolved phosphorus less than 1.0 mM. The littoral zone supports dense stands of an emergent macrophyte Typha domingensis Pers..

Experimental Design

Plastic ribbons and the emerged part of green and senescent leaves of T. domingensis, randomly selected, were

chosen as substrates for periphyton growth. Senescent leaves were chosen because senescent shoots or leaves of most emergent aquatic macrophytes start to decay without detachment, resulting in the presence of large crops of dead standing plant detritus during much of the year (Newell, 1993), and therefore, a highly available substrate for periphyton colonization in the Cabiúnas lagoon. Emergent parts of macrophyte leaves were cut (detached) at the water surface level, to avoid previous periphyton colonization.

Detached leaves and plastic ribbons of 20-cm length were attached to wooden structures to keep them in a horizontal position, parallel to the water surface. Previous analyses showed that such wooden structures do not leach organic matter into the water which could influence the outcome of this study (data not showed). Although plant leaves are naturally positioned in a vertical orientation, we chose the horizontal position to keep light evenly distributed along the length of the leaves, thereby decreasing variability due to depth-light attenuation. The wooden structures were buried in the sediment and the substrates were kept at a depth of ca. 0.3 m in an open area close to a stand of T. domingensis (time zero for periphyton colonization) . Secchi disk depth was 2.0 m in this area and water column depth was ca. 2.5 m. This study was carried out for 30 days (February 6 – March 8, 2003).

The experiment started with several replicates, and the sampling was carried out by just taking some of the pool of replicates every sampling day. The substrates colonized were collected in triplicates after 4, 15 and 30 days of incubation. The leaves and the ribbons were cut and transferred into under water chambers so that changes in periphyton were minor.

Limnological variables as temperature, conductivity (multi-functional probe YSI-30), depth, pH (Analion-2000) and dissolved oxygen (portable oxymeter YSI-95) were measured every sampling day. Water samples were also collected for analysis of dissolved organic carbon (using a Carbon Analyzer TOC 5000 Shimadzu), total nitrogen (Mackereth et al., 1978) and phosphorus (APHA, 1989) concentrations.

In the laboratory periphyton from the upper face of leaves and ribbons were scraped with a razor blade and filtered through a GF/F Whatman filter (0.75 mm pore size) for chlorophyll-a (CHLa) and ash free dry weight (AFDW – a indicative of periphytic biomass) analysis. CHLa was determined by extraction with boiling ethanol and spectrophotometer measurements. AFDW was determined after drying the GF/F filter at 70° C for dry weight determination and later ashed at 500° C during 1h for ash determination. Periphyton samples were scraped in triplicates to determine phosphorus (P) (Mackereth et al., 1978) and nitrogen (N) content (APHA, 1989). Total nitrogen was measured after persulfate oxidation and nitrate reduction in a cadmium column with post nitrite determination in a flow injection analyzer and total phosphorus was measured with the ammonium-molybdate method after persulfate oxidation. Leaf and ribbon areas were also determined.

Differences in the measured parameters in relation to exposure time and type of substrates were compared using bi-factorial ANOVA followed by a Tukey HSD test. Independent factors comprised substrates (n = 3) and time (n = 3). Log-transformed variables were used throughout to reduce the observed heterogeneity in the variance.

All the statistical analyses were performed using the statistical program STATISTICA 6.0.

Results

The limnological variables in the sampling site during the study period are presented in Table I. The range of the results was very short, which indicates a very low variation in the water conditions throughout the experiment.

AFDW significantly increased with exposure time in all substrates (ANOVA, $p < 0.05$). Senescent leaves presented a significant increase from day 4 to day 15 (Tukey, $p < 0.05$ - 3 fold) and from day 15 to day 30, while green leaves and plastic presented a significant increase in periphytic AFDW only after 30 days of incubation (Tukey, $p < 0.05$ - Fig. 1 A). CHLa content presented a significant increase in both artificial and green- leaf substrates from day 4 to day 15 (Tukey, $p < 0.05$), but this increase was not observed from day 15 to day 30. CHLa content in senescent leaves presented a different pattern with

significantly higher value than the other substrates on day 4 (Tukey, $p < 0.05$) , and maintenance of this value throughout the experiment period (Fig. 1 B)

Table I: Range of water parameters in the sampling site during the present study (Days 1-30).

Abiotic parameters	**Range**
Water temperature (° C)	28.0 - 29.1
Secchi disc trasparency (m)	1.10 - 1.20
Depth (m)	2.20 - 2.23
Total P (mmol/L)	0.83 - 0.9
Total N (mmol/L)	66.07 - 78.99
Dissolved organic Carbon (mg/L)	23.5 - 23.9
Conductivity at 25°C (mS/cm)	558 - 563

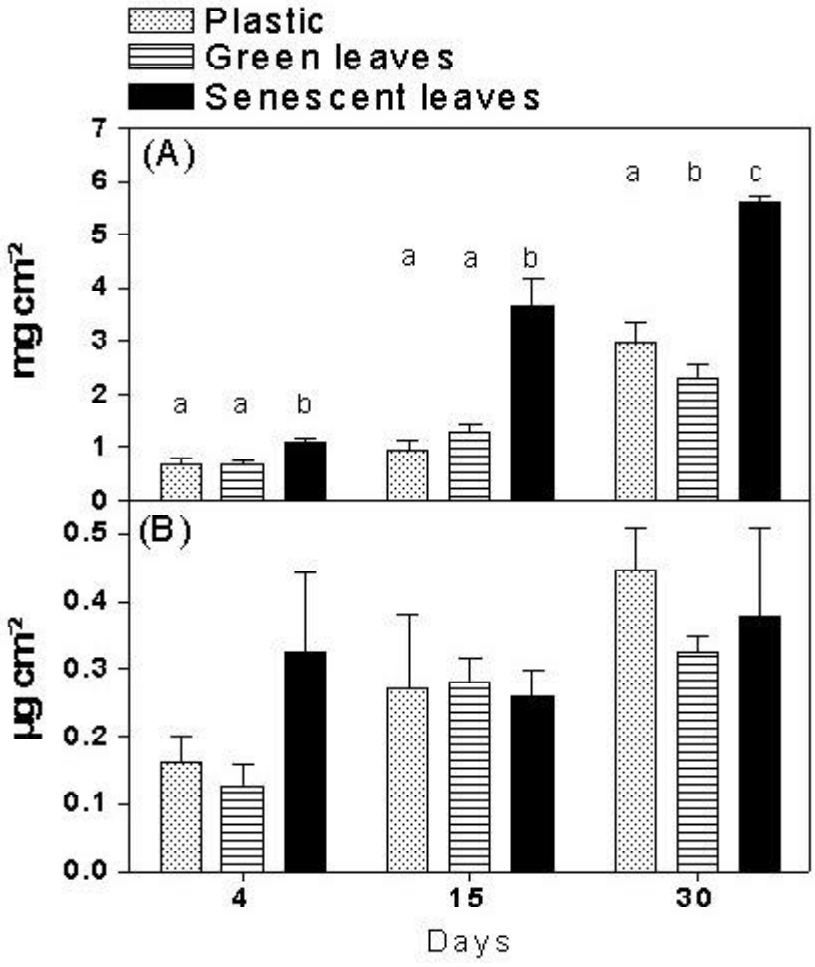

Figure 1: Ash Free Dry Weight (A); and Chlorophyll-a (B) on plastic substrate, green and senescent leaves of T. domingensis throughout the study period. Different letters above graph bars represents significant difference among substrate type within each sampling day. Each bar represents the mean ± SD. (No significant difference was observed for Chlorophyll-a measurements within each sampling day).

N and P concentrations per unit area (nutrient amount) increased significantly as a result of exposure time (ANOVA, $p < 0.05$ - Fig. 2 A and B). N increase was significant from day 4 to day 15, (Tukey, $p < 0.05$ - 3 to 4 fold) while from day 15 to day 30 no significant differences were observed. The increase in P was gradual in all substrates. The value on day 30 was significantly higher than that on day 15 which was significantly higher than the one on day 4 (Tukey, $p < 0.05$). There was no significant difference for P and N amount among substrates, except for the lower N content in green leaves on day 15 (Tukey, $p < 0.05$). Concentration of N and P per unit dry weight (nutrient content) showed a significant decrease in all substrates with exposure time (ANOVA, $p < 0.05$ - Fig. 3 A and B). Same pattern observed when expressed as mass percentage of dry weight (Fig. 4 A and B). P content was significantly lower in the periphyton from senescent leaves (Tukey, $P < 0.05$), same pattern observed for N content, however just for the day 30 (Tukey, $p > 0.05$).

Periphytic AFDW:CHLa ratio was significantly higher on senescent leaves of Typha (Tukey, $p < 0.05$) except on day 4 (Fig. 5). This result highlights the substrate effect on the contribution of autotrophic and heterotrophic components to periphytic biomass.

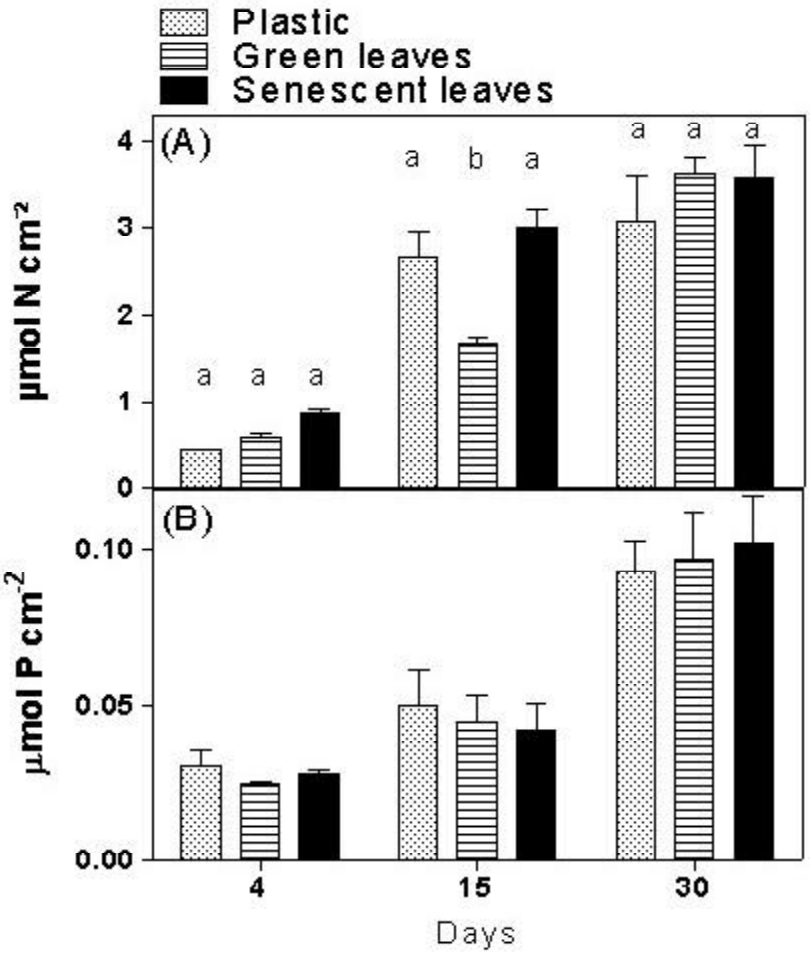

Figure 2: Nitrogen (A) and phosphorus (B) content of periphyton on plastic substrate, green and senescent leaves of T. domingensis throughout the study period. Different letters above graph bars represents significant difference among substrate type within each sampling day. Each bar represents the mean ± SD. (No significant difference was observed for phosphorus measurements within each sampling day).

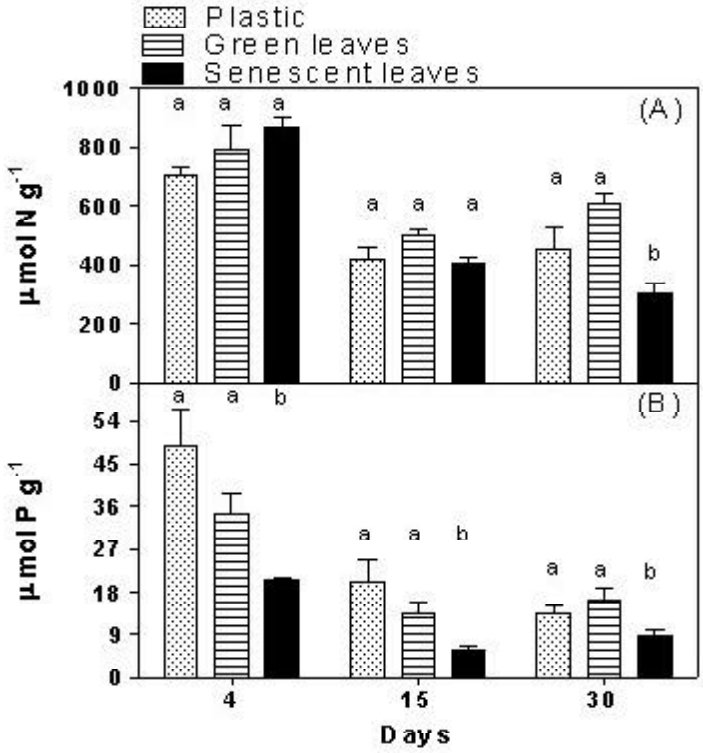

Figure 3: Nitrogen (A) and phosphorus (B) content per unit of dry weight of periphyton on plastic substrate, green and senescent leaves of T. domingensis throughout the study period. Different letters above graph bars represents significant difference among substrate type within each sampling day. Each bar represents the mean ± SD.

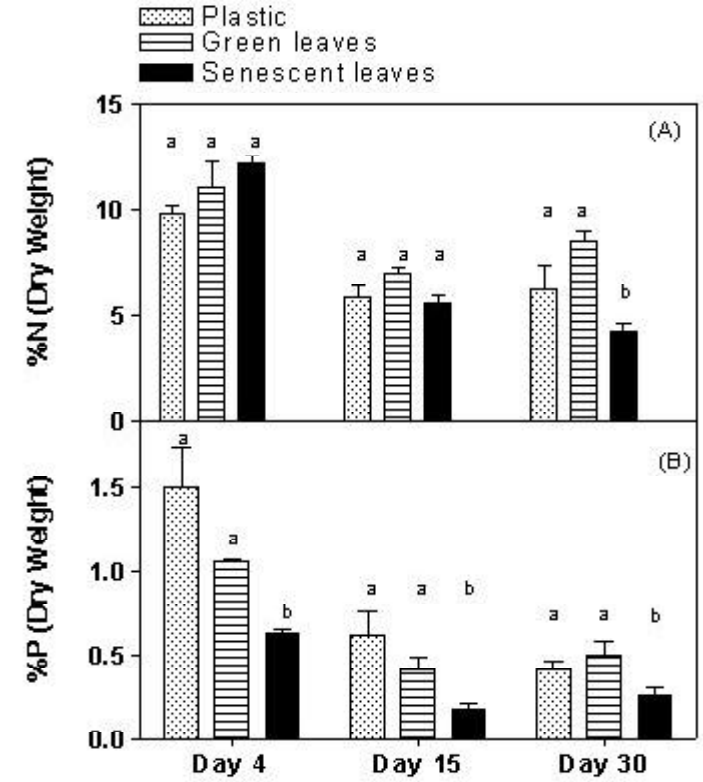

Figure 4: Percentage of nitrogen (A) and phosphorus (B) mass content of periphytic dry weight on plastic substrate, green and senescent leaves of T. domingensis throughout the study period. Different letters above graph bars represents significant difference among substrate type within each sampling day. Each bar represents the mean ± SD.

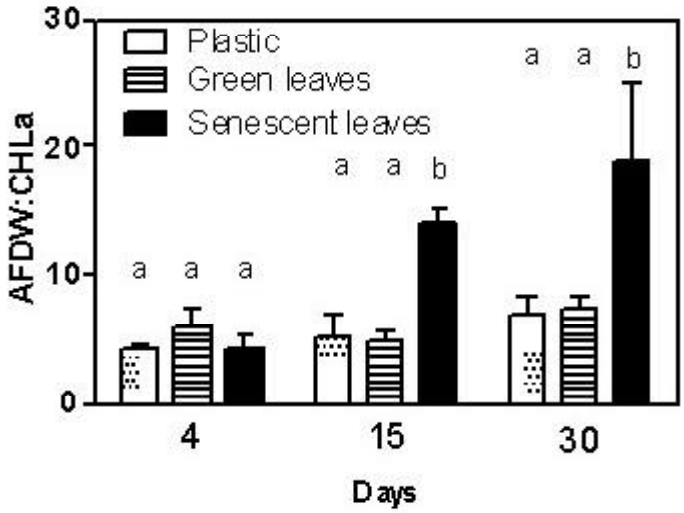

Figure 5: Proportion of periphytic ash free dry weight (AFDW) to CHLa on plastic substrate, green and senescent leaves of T. domingensis throughout the study period. Different letters above graph bars represents significant difference among substrate type within each sampling day. Each bar represents the mean ± SD.

Discussion

We observed a significant effect of time and substrate, especially for senescent leaves, on periphytic AFDW and nutrient content, and these results reinforces the importance of the substrate to periphyton features. Previous studies have already shown the positive effect of natural substrates on periphyton biomass (Morin, 1986; Putz 1997), but our findings are particularly interesting regarding periphytic nutrient content. Periphyton on senescent leaves presented higher biomass but lower P and N content (Fig. 3 and 4). These results suggest that natural substrates can enhance periphytic biomass not just through nutrient improvement, which may have potential implications for periphyton stoichiometry.

AFDW increased in all substrates with exposure time, which confirms that periphyton biomass is a function of the biofilm age (Christenson & Characklis, 1990). In this study no significant difference in periphytic biomass was found between green leaves and the artificial substrate, although significant differences were found when these substrates were compared to senescent leaves. Higher periphytic biomass is expected in natural substrates because they can benefit from the nutrients released through substrate decomposition and leaching, especially in oligotrophic systems (Kahlert & Pettersson, 2002). However, periphytic nutrient content on senescent leaves presented the lower P content among substrates, even when compared to the artificial one. Farjalla et. al (2000) showed that Typha domingensis has a very low decomposition rate when compared to other macrophyte species. Possibly, the release of nutrients through Typha decomposition was too low to have pronounced effects on periphyton elemental composition (N and P content). Carignan & Kalff (1982) have shown that for example Myriophyllum is unimportant as a P source for the attached algae, only 3.4–9% of algal P is derived from the plant host. This result suggests that other factors, not just nutrient improvement, might positively affect periphyton nutrient content. Some authors pointed out the importance of surface texture of macrophyte leaves enhancing periphyton development (Morin, 1986; Dudley & D'Antonio, 1991). Senescent leaves of Typha have a quite wrinkled surface that may facilitate the colonization by auto- and/or heterotrophic organisms, which may explain the highest periphyton AFDW in this substrate. In addition, Mann & Wetzel (1996) showed that senescent culms of Typha latifolia (same macrophyte genus used in this experiment) released more dissolved organic carbon than young culms during the decomposition processes. Hence, the release of organic compounds may stimulate the periphytic heterotrophic compartment and may contribute to explain the highest periphytic biomass in senescent leaves. On

the other hand, Gallardo-Williams et al. (2002) isolated several compounds from aqueous extracts and leachates of Typha domingensis, among them, various phenolic acids. Many allelopathic interactions in aquatic systems occur as surface-associations, either in benthic communities or between photoautotrophs and their epiphytes (Gross 2003), preventing or decreasing periphyton colonization. Although allelopathic effects on epiphytic density and productivity cannot be excluded, we cannot assure allelopathy as a mechanistic factor determining differences between the substrates used in this experiment. The release of allelopathic compounds were observed for both green (Gallardo-Williams et al., 2002) and senescent (Maie et al., 2006) Typha leaves and the periphytic community on the plastic substrate never achieved higher AFDW than those found on natural substrates. Further studies are necessary to evaluate the quantitative and qualitative differences in the release of allelopathic substances of young and senescent Typha leaves and their consequences on periphyton colonization.

An efficient internal nutrient recycling in periphyton communities is expected, due to 'a close aggregation of algal and heterotrophic microbial components' in the community, and this recycling has been shown to be a substantial source of nutrients to the biofilm (McCormick et al., 1998). Stelzer & Lamberti (2001) pointed out that preferential mineralization of nutrients, such as nitrogen and phosphorus in relation to carbon, can promote a reduction in nutrients per unit of dry weight and consequently in C:N:P ratios along the sucessional stages of the periphytic community, supporting the reduction in periphyitic P and N content along our experiment. Nutrient recycling within the community should be higher as higher the community biomass (Mullohand 1996), more nutrients must be mineralized to sustain a greater biomass, and thus the lower periphytic nutrient content to the total biomass on senescent leaves could be explained by its higher internal activity. Benthic organisms should be able to satisfy their nutrient demand mainly by uptake from lake water when the amount of nutrients on the overlying water is high. Since oligotrophic lakes usually present low nutrient concentrations, internal loading is expected to play the major role. In addition even when overlying water concentrations are high, the boundary layer prevents fast nutrient uptake (Borchardt, 1996). Changes on periphytic autotrophic:heterotrophic ratio could also influence periphyton stoichiometry. Frost et al. (2005) pointed out that low prevalence of algal cells is likely to be directly linked to the production of mucilage and other organic material of bacterial and/or algal origin, with important consequences to periphyton stoichiometry. They concluded that total periphytic C:P ratios are highly sensitive to changes in algal cellular C:P ratios and therefore, periphyton stoichiometry should be governed by the algal contribution to periphytic biomass. In addition, the proportions of N and P are different in the biomass of bacteria and algae (Fagerbakke et al. 1996; Kahlert 1998). In fact, the periphytic AFDW:CHLa ratio was significantly higher in senescent leaves, and thus differences in the total biomass and the imbalance of periphytic autotrophs to heterotrophs among substrates could indirectly affect periphyton nutrient content. These results may have crucial implications for ecosystems functioning especially concerned with benthic thophic relationships. Physiological models (Sterner, 1997) predict that, above critical levels of food C:P, herbivores have reduced growth efficiency (growth as a fraction of carbon ingestion) as a consequence of maintaining their homeostasis in C:P. Thus, periphyton may be a more nutritious food source in early stages of development (lower C:N and C:P ratios) and a less nutritious food when growing on senescent detritus of Typha.

In conclusion, our study evidences that Typha plant detritus can positively affect periphyton biomass compared to an artificial (inert) substrate. Although our experiment lacks in its ability to provide mechanist explanations for the differences observed for periphytic biomass among substrates, changes in periphytic biomass were probably influenced by the release of labile compounds by the substrates and substrate physical texture. Our results also evidenced that periphyton nutrient content was indirectly affected by the substrate. Enhancing periphytic biomass through mechanisms not related to nutrient release, senescent leaves could alter periphytic internal nutrient recycling rates and its proportions of autotrophic and heterotrophic

components, which can influence its bulk nutrient content. These results are particularly important because indirect substrate-mediated negative effects on periphytic nutrient content are seldom addressed in ecological studies and may have crucial implications to periphytic stoichiometry and hence to ecosystem functioning, specially in shallow lakes where periphyton constitutes as a major component to whole ecosystem biomass. Further investigations should be focused in provide mechanistic explanations of the influence of the substrates on periphyton dynamics and its consequences to other components of the system as well as the substrate diversity on whole lake periphyton standing stock.

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