



Relationship among carnivorous macrophyte *Utricularia foliosa* L. and species composition and life forms of periphytic algae community

Relação entre macrófita carnívora *Utricularia foliosa* L. e a composição de espécies e formas de vida da comunidade de algas perifíticas

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Abstract: Aim: Present study evaluated the life forms and taxonomic structure of the periphytic algae community on *Utricularia foliosa* L. (modified leaf and stem) and artificial substrate during the four seasons in a tropical shallow reservoir. **Methods:** We evaluated the periphyton on natural and artificial substrate in order to evaluate the influence of substrate type on the taxonomic structure of algal community. Monospecific stands of *U. foliosa* were selected. Water and periphyton sampling were performed within *U. foliosa* stands in the autumn (April/2010), winter (July/2010), spring (November/2010) and summer (February/2011). Nylon thread was used as the artificial substrate. The community structure was evaluated through life forms, species richness, diversity and species composition. **Results:** Species diversity was significantly different only among seasons. The life forms and species richness were different between substrate types and seasons. Entangled filamentous algae had higher biovolume in the periphyton on artificial substrate and unicellular flagellated algae had higher biovolume on natural substrate. Species composition changed among the seasons and species descriptors differed among substrates types. Species-level taxonomic classification responded clearly to the substrate type. **Conclusions:** We concluded that the taxonomic structure and life forms of periphytic algae on artificial substrate poorly represented the natural periphyton on *U. foliosa*. The type of substrate strongly influenced the periphyton–*Utricularia* relationship.

Keywords: life forms; artificial and natural substrates; species composition; shallow reservoir.

Resumo: Objetivo: O presente estudo avaliou as formas de vida e a estrutura taxonômica da comunidade de algas perifíticas sobre *Utricularia foliosa* L. (folha modificada e caule) e substrato artificial durante quatro estações em um reservatório tropical raso. **Métodos:** Nós comparamos o perifiton sobre substrato natural e artificial para avaliar a influência do tipo de substrato sobre a estrutura taxonômica da comunidade de algas. Bancos mono específicos de *U. foliosa* foram selecionados. Amostras de água e perifiton foram coletadas no interior dos bancos de *U. foliosa* no outono (abril/2010), inverno (julho/2010), primavera (novembro/2010) e verão (fevereiro/2011). Fio de náilon foi usado como substrato artificial. Com base no biovolume algal, a estrutura da comunidade foi avaliada através das formas de vida, riqueza de espécies, diversidade e composição de espécies. **Resultados:** Diversidade de espécies foi significativamente diferente apenas entre as estações do ano. As formas de vida e riqueza de espécies diferiram entre os tipos de substrato e estações. Algas



filamentosas emaranhadas apresentaram maior biovolume no perifíton em substrato artificial e algas unicelulares flageladas tiveram maior biovolume em substrato natural. A composição de espécies mudou entre as estações e as espécies descritoras diferiu entre os tipos de substrato. A classificação taxonômica a nível de espécie respondeu claramente ao tipo de substrato. **Conclusões:** Nós concluímos que estrutura taxonômica e formas de vida das algas perifíticas sobre substrato artificial teve baixa representatividade do perifíton sobre *U. foliosa*. O tipo de substrato influenciou fortemente a relação perifíton-*Utricularia*.

Palavras-chave: formas de vida; substrato artificial e natural; composição de espécies; reservatório raso.

1. Introduction

Aquatic macrophytes play a significant role in the functioning and structure of biological communities of lacustrine ecosystems (Thomaz & Cunha, 2010). Submerged macrophytes are frequently covered by periphytic algae and the association between macrophytes and periphyton suggests the existence of ecological interactions (Jones et al., 2000; Olsen et al., 2015). Many authors have discussed the effect of aquatic macrophytes on the periphytic algae, but conclusions have been controversial. Studies have suggested the existence of a positive interaction between macrophytes and periphyton, mainly because macrophytes may be a source of nutrients for the periphyton (Burkholder, 1996). Conversely, some species of macrophytes can release allelopathic compounds which inhibit periphyton growth (Erhard & Gross, 2006). Another possibility is the existence of neutral interactions, in which the macrophyte is simply an area for colonization and the nutrient supply to the periphyton is insignificant (Burkholder, 1996). Thus, studies that address the periphyton-macrophyte relationship can contribute to the understanding of periphyton ecology.

Considering that the dynamics of periphytic algae communities differ between morphoclimatic regions, the periphyton-substrate relationship can show specific characteristics in tropical regions. Studies have shown the influence of substrate type on periphyton biomass accrual and nutrient status in temperate and tropical ecosystems (e.g. Kiss et al., 2003; Guariento et al., 2009); however, others have reported that environmental factors, such as nutrient availability and hydrodynamic regime, may be more important in determining community structure (Rodrigues & Bicudo, 2001; Diaz-Olarte et al., 2007). In habitat scale, macrophyte influence can be more important than environmental conditions (Tarkowska-Kukuryk & Mieczan, 2012; Grutters et al., 2017). Macrophyte life form and architecture seems to play a significant role in determining the periphyton structure (Jones et al., 2000; Biolo et al., 2015; Fernandes et al., 2016).

When considering nutrient availability, nutrient supply can be negligible for periphyton on *Potamogeton richardsonii* (Cattaneo & Kalff, 1979), but *P. illinoensis* seems to act as an extra source of nutrients for the periphyton (Burkholder & Wetzel, 1990). Since the classical study by Cattaneo & Amireault (1992), there has been a discussion about whether periphyton on artificial substrate is representative or not of natural communities, mainly in relation to the indication of water quality. The relationship between periphyton and macrophyte also has several gaps in knowledge, for example, whether macrophyte have a strong influence on species composition in the periphytic algae community in tropical ecosystems.

The carnivorous macrophyte *Utricularia foliosa* L. obtains its nutrient supply, mainly nitrogen, from carnivory activities realized by the leaves which have been modified into bladders (Guisande et al., 2007). Studies have indicated a mutual interaction between *Utricularia* and periphyton grazers (Jones et al., 1999; Sirová et al., 2009), which may have improved overall periphyton nutrient status. According to Jones et al. (1999), the periphyton which adhered to the bladders would help with prey attraction, permitting more successful predation. For Sirová et al. (2009), besides being attractive, periphyton could also serve as a source of nutrients for macrophytes. Santos et al. (2013) showed that the microenvironmental conditions of *U. foliosa* had a positive influence on biomass accumulation and nutrient content in the periphyton and was a determining factor for the presence of the descriptor species in the periphytic algae community.

Considering substrate can drive changes in the periphyton (Vadeboncoeur et al., 2006; Santos et al., 2013) and macrophyte-periphyton relationship may change seasonally (Cattaneo & Kalff, 1978), we evaluated the taxonomic structure and life forms in the periphytic algae community on the stem and leaves of the *Utricularia foliosa* and on the artificial substrate in four seasons. Our hypothesis is that *U. foliosa* could significantly influence the periphytic algae community structure,

mainly changing the species composition and life forms. In addition, we analyzed the periphyton on modified leaf to investigate whether the taxonomic structure would be different on another part of the plant, particularly where particle digestion occurs. This study contributes to the knowledge of the relationship between the periphyton and *Utricularia foliosa*, which is widely distributed in shallow aquatic ecosystems (Walker, 2004).

2. Materials and Methods

2.1. Study area

The study was realized in the Ninfeias reservoir, a small (area 5433.0 m²), shallow (Z_{mean} 1.3 m) and mesotrophic reservoir with a mean residence time of 7.2 days (Bicudo et al., 2002). The reservoir is located in the Parque Estadual das Fontes do Ipiranga (23°38'18.95" S and 46°37'16.3" W). The littoral region has an abundant macrophyte flora, highlighting *Nymphaea* spp. and *U. foliosa* Linnaeus as the most abundant species.

Periphyton and water samples were collected within *Utricularia foliosa* L. stands in autumn (April/2010), winter (July/2010), spring (November/2010), and summer (February/2011). According to Santos et al. (2013), plots were numbered and randomly selected (n = 3). Sampling sites had distance of 10 m from one another to minimize differences in environmental conditions.

2.2. Experimental design

Periphyton and water samples were collected within *Utricularia foliosa* L. stands in autumn (April/2010), winter (July/2010), spring (November/2010), and summer (February/2011).

Utricularia foliosa L. stands were divided into 1 m² plots for determination of the sampling sites. Plots were numbered, and three plots were randomly selected (n = 3). Sampling sites had distance of 10 m from one another to minimize differences between environmental conditions. The experimental design was described in detail in Santos et al. (2013). Sampling sites had distance of 10 m from one another to minimize differences between environmental conditions.

In each macrophyte stand, the artificial substrate, a nylon thread (1 mm diam.), was horizontally fixed in the central part of the macrophyte stand and positioned as close as possible to the macrophyte. The artificial substrate exposure time for periphyton colonization was 30 days at sampling sites. This exposure time was chosen because periphytic biomass accumulation is high at this colonization time in the studied reservoir (Casartelli et al., 2016), allowing a better comparison with the periphyton on artificial substrate and *Utricularia*. The stem and modified leaves of *U. foliosa* L were sampled. Young and senescent plants were excluded from the study, so only mature periphyton was sampled. Periphyton was removed from the artificial and natural substrates by gentle scraping with a brush and distilled water jets. For more details see Santos et al. (2013). It is emphasized that both artificial and natural substrates were submitted to the same limnological conditions (Table 1).

2.3. Periphyton attributes

Algal quantifications were accomplished using a Zeiss Axiovert microscope and followed Utermöhl (1958), and sedimentation time in chamber

Table 1. Mean values and standard deviation (n = 3) of limnological variables in *Utricularia foliosa* stands (see Santos et al., 2013).

	Autumn	Winter	Spring	Summer
Temperature (°C)	22.0	18.0 ± 0.2	21.6 ± 0.4	24.9
Conductivity (µS.cm ⁻¹)	57.0 ± 0.6	57.4 ± 2.0	54.5 ± 1.5	47.3 ± 0.5
pH	6.1 ± 0.02	6.0 ± 0.1	6.5 ± 0.03	6.0 ± 0.1
Subaquatic radiation (µmol.s ⁻¹ .m ⁻²)	119.3 ± 43.3	328.2 ± 194.2	698.8 ± 130.6	76.6 ± 19.7
Light penetration (%)	71.3 ± 13.5	65.5 ± 7.9	73.6 ± 8.4	80.0 ± 13.3
Alkalinity (mEq.L ⁻¹)	0.2	0.2	0.3	0.3
Dissolved oxygen (mg.L ⁻¹)	4.0 ± 0.4	4.7 ± 0.7	4.0 ± 0.2	3.2 ± 0.4
Free CO ₂ (mg.L ⁻¹)	17.6 ± 0.7	27.5 ± 3.9	30.0 ± 4.3	30.3 ± 5.1
DIN (µg.L ⁻¹)	1305.4 ± 26.3	661.3 ± 49.3	162.1 ± 6.5	698.4 ± 60.7
Total nitrogen (µg.L ⁻¹)	2163.5 ± 47.9	1119.4 ± 48.1	359.9 ± 91.6	1400.2 ± 69.7
P-PO ₄ (µg.L ⁻¹)	<4.0	<4.0	<4.0	<4.0
Total phosphorus (µg.L ⁻¹)	21.5 ± 19.9	9.8 ± 1.8	9.0 ± 1.5	14.4 ± 0.7
N:P molar ratio	226.3 ± 33.8	146.4 ± 10.9	35.9 ± 1.4	154.6 ± 13.4
Suspended particulate matter (mg.L ⁻¹)	11.2 ± 6.2	4.4 ± 0.8	4.4 ± 1.0	3.8
Plant coverage (%)	14.0 ± 11.0	20.7 ± 4.9	67.7 ± 40.7	92.0 ± 7.2

following Lund et al. (1958). Counting limit was established through the species rarefying curve and until reaching 100 individuals of the most common species. Periphytic algae density was estimated according to Ferragut et al. (2013). Biovolume was calculated by multiplying each species' density by its average volume ($\mu\text{m}^3 \cdot \text{cm}^{-2}$). Most algal biovolume was obtained from Fonseca et al. (2014).

In order to refine the adaptive strategies, the algae were classified into the following life forms, including form of adherence, based on literature (Biggs et al., 1998; Graham & Wilcox, 2000): colonial/cenobial, colonial flagellated, colonial non-flagellated, entangled filamentous, fixed filamentous, free filamentous, unicellular with mucilaginous disk, unicellular flagellated, unicellular immobile, unicellular mucilaginous, and unicellular mobile without flagella. Life forms considered abundant were those whose biovolume was higher than 20% of total biovolume. Forms of adherence to substrate were classified in firmly adhered and loosely adhered (Goldsborough & Robinson, 1996). Algae with some locomotion mechanism were classified as loosely attached, and those without locomotion structure and with fixation structure were classified as firmly attached.

Species richness was defined as the number of species per sample. Simpson diversity index (1-D) was calculated using species biovolume matrix of the periphytic algae (Magurran, 2004).

2.4. Statistical analysis

Two-way ANOVA was used to determine the influence of seasonality and substrate type on periphytic algae life forms, species richness and diversity ($\alpha = 0.05$). The data were logarithmized to meet the assumptions of the analysis. The comparison of means was performed using Tukey and Student Newman Keuls (SNK; < 0.05). These analyses were performed using the SigmaPlot 11.0.

To detect the species composition similarity of periphyton between substrate types was performed Hierarchical Cluster Analysis, which was carried based on the algal biovolume using Bray-Curtis index and Unweighted pair-group average (UPGMA). The permutational multivariate analysis of variance (Two-way PERMANOVA) was used to compare assemblage composition in the periphyton among substrate types and seasons based on biovolume. This analysis was executed using Bray-Curtis index and 9999 permutations. Cluster analysis and PERMANOVA were executed in the PAST 3.14 (Hammer et al., 2001).

We used Principal Coordinates Analysis (PCoA) to reduce the dimensionality of species data and identify the species with the highest association with the type of substrate. The species matrix was elaborated with species that contributed with $\geq 3\%$ of the total biovolume of sample. PCoA was performed with covariance matrix, Bray-Curtis distance measure and, data transformed by variation amplitude (ranging: $[(x-x_{\min}) / (x_{\max}-x_{\min})]$). Monte Carlo randomization test was performed, and axes interpreted were those with $P < 0.05$. Data were transformed with software FITOPAC (Shepherd, 1996) and multivariate analysis was performed in PC-ORD 6.0 (McCune & Mefford, 2011).

3. Results

The species richness in the periphytic algae had significant difference among seasons and substrates (ANOVA: $P < 0.001$), with higher values in the modified leaf and the other substrates (Tukey: $P < 0.005$; 1A). Species diversity was high in all substrates and seasons (>0.7), except during the spring (Figure 1B), but the statistical difference was detected only among seasons (ANOVA: $P = 0.03$). The highest values were found in summer.

Species composition similarity in the cluster analysis between periphyton on three substrate types showed two groups at the level of 25% similarity: artificial and natural (stem and modified leaves) substrates (Figure 2). The greater similarity was detected between stem and modified leaves in autumn and summer (50% and 55%, respectively).

Life forms biovolume of periphytic algae on artificial and natural substrates changed among seasons (Figure 3). Biovolume of entangled filamentous and unicellular flagellated algae had statistical difference only between substrates (ANOVA: $P < 0.03$). Algae entangled filamentous had higher biovolume on artificial (0.1%-54.7%), while the unicellular flagellated algae had higher biovolume on natural substrate (1.8%-45.5%). Biovolume of unicellular mucilaginous and unicellular mobile algae without flagella showed statistical difference among seasons and substrates and interaction between seasonality and substrate was significant (ANOVA: $P < 0.03$). These life forms had the highest biovolume on the natural substrates.

The relative biovolume of the algae firmly adhered to the periphyton on the artificial substrate varied from 15.0 to 45.1%, stem from 12.5 to 23.5% and leaf from 12.6 to 21.5%. Therefore, the periphyton on *U. foliosa* was predominantly loosely adhered.

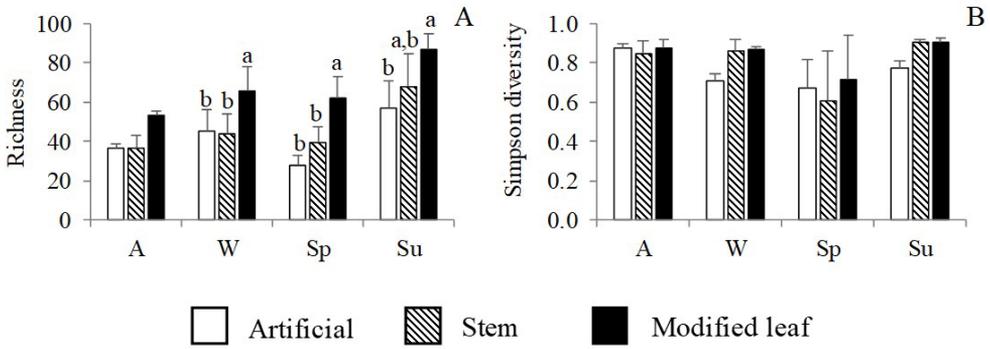


Figure 1. Species richness (A) and Simpson diversity (B) ($n = 3$, \pm SD) of periphytic algae on artificial substrate, stem and modified leaves of *Utricularia foliosa* during the four seasons (A Autumn, W winter, Sp spring, Su summer). Attribute with different letters are statistically significantly different.

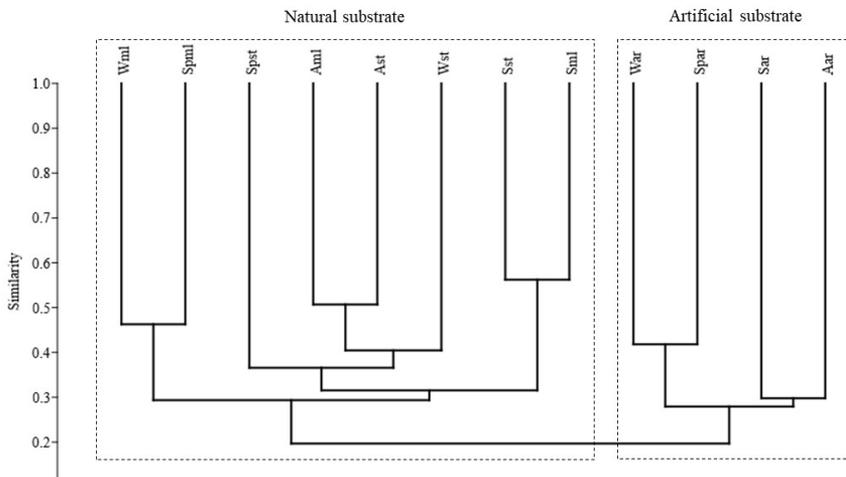


Figure 2. Bray-Curtis similarity index of biovolume of 106 species of the periphytic algal community on artificial and natural substrates (stem and modified leaves) during seasons. Abbreviations of sample units: first letter refer to season (A autumn, W winter, Sp Spring, S summer) and the other letters to substrate (art-artificial, st-stem, ml-modified leaves).

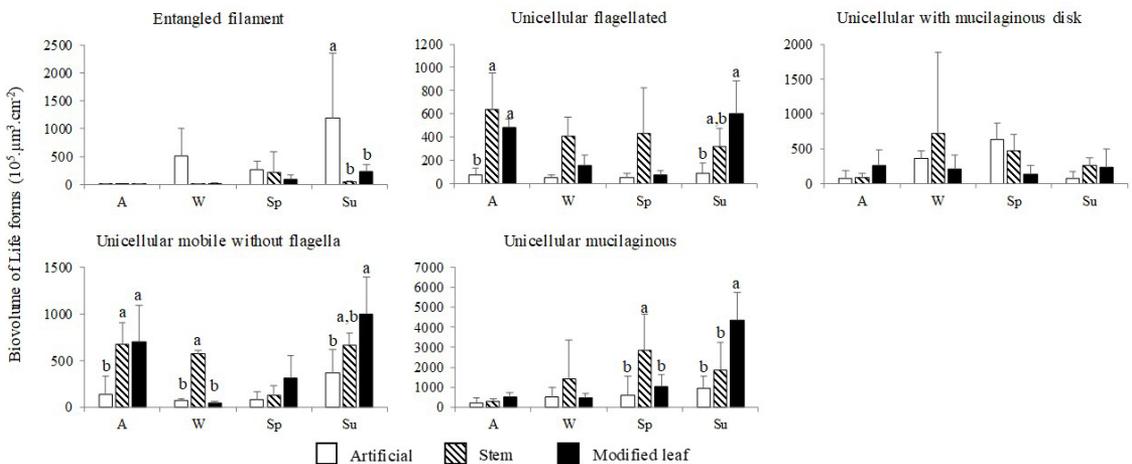


Figure 3. Biovolume of life forms ($n = 3$, \pm SD) on artificial substrate, stem and modified leaves of *Utricularia foliosa* in seasons (A Autumn, W winter, Sp spring, Su summer). Attribute with different letters are statistically significantly different (SNK: $\alpha = 0.05$).

PCoA explained 43% of biological data variability in the first two ordination axes (Figure 4), only axis 1 was considered significant at the randomization test (Monte Carlo: $P < 0.001$). Stem and modified leaves units were showed high correlation with high biovolume of *Chlamydomonas epibiotica* Ettl, *Chlamydomonas planctogloea* Skuja, *Chromulina elegans* Doflein, *Cosmarium botrytis* Meneghini ex Ralfs, *Cryptomonas erosa* Ehrenberg, *Pinnularia divergens* W. Smith, *Scenedesmus acutus* Meyen, *Scenedesmus westii* (Smith) Chodat,

Stauroneis phoenicenteron (Nitzsch) Ehrenberg (Pearson correlation: $r = 0.6$). Artificial substrate units correlated with high biovolume of the *Bulbochaete* spp. and *Eunotia sudetica* Otto Müller (Pearson correlation: $r = -0.55$).

Two-way PERMANOVA showed that taxonomic structure of periphytic algae presented significant difference between substrates and seasons ($P < 0.001$). It was observed a significant interaction between seasonality and substrate factors ($P = 0.005$).

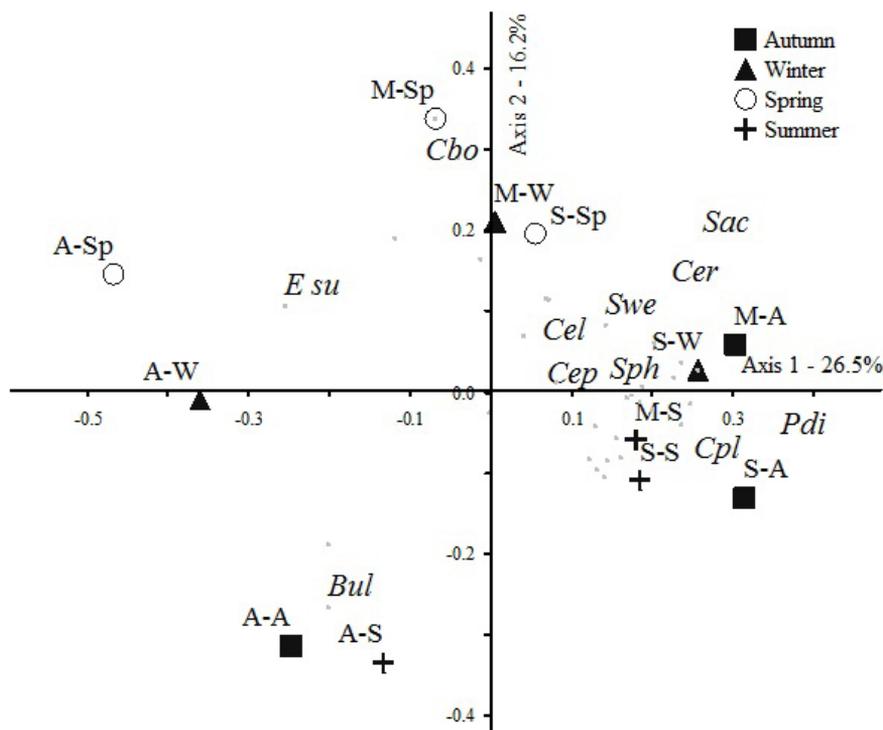


Figure 4. PCoA of periphytic algae biovolume (31 species; $\geq 3\%$ total biovolume) on artificial and natural (stem and modified leaves) substrates in four seasons. Abbreviations: Sample units: first letter refer to substrate type (A, artificial; S, stem; M, modified leaves) and second to seasons (A-Autumn, W-Winter, Sp-Spring, S-Summer). Pearson correlation between species biovolume and scores of axes 1 and 2 and respective codes are shown in Table 2.

Table 2. Pearson correlation of periphytic algae biovolume (r) with axes 1 and 2 of PCoA and respective codes and the type of association with each substrate.

Taxa	Codes	Axis 1	Axis 2	Association
<i>Bulbochaete</i> spp.	Bul	-0.365	-0.615	artificial
<i>Chlamydomonas epibiotica</i> Smith	Cep	0.676	-0.051	natural
<i>Chlamydomonas planctogloea</i> Skuja	Cpl	0.639	-0.099	natural
<i>Chromulina elegans</i> Doflein	Cel	0.772	0.031	natural
<i>Cosmarium botrytis</i> Meneghini ex Ralfs	Cbo	-0.072	0.631	natural
<i>Cryptomonas erosa</i> Ehrenberg	Cer	0.606	0.060	natural
<i>Eunotia sudetica</i> Otto Müller	Esu	-0.557	0.290	artificial
<i>Pinnularia divergens</i> W. Smith	Pdi	0.613	-0.143	natural
<i>Scenedesmus acutus</i> Meyen	Sac	0.627	0.121	natural
<i>Scenedesmus westii</i> (Smith) Chodat	Swe	0.666	0.494	natural
<i>Stauroneis phoenicenteron</i> (Nitzsch) Ehrenberg	Sph	0.618	-0.056	natural

4. Discussion

In a previous study, seasonal variation of limnological conditions was considered a determinant for the periphyton-*Utricularia* relationships, either intensifying or minimizing macrophyte influence on the periphyton (Santos et al., 2013). Our results showed that life forms, richness, diversity and species composition of periphytic algae were influenced by substrate type and seasonality, and the strong interaction between factors was observed. Despite the expected seasonal variation in the taxonomic structure of periphytic algal community, the type of substrate was shown to play a significant role in species composition, as well as the predominant life form. Therefore, similarly to the nutrient status, biomass and descriptor species (Santos et al., 2013), the species composition and life forms were influenced by substrate type, but the differences were only significant in the spring and summer. Therefore, seasonality influenced changes in the species composition and degree of similarity between the types of substrate.

Differences in periphyton species richness showed the existence of different microenvironmental conditions among substrates, which was probably due to carnivory occurrences on modified leaves (nutrient availability). In addition, differences in microtopography of the substrates types may have influenced on species richness and composition, as observed in some studies (e.g. Bergey, 1999; Schneck & Melo, 2012). At microscale, the periphytic matrix plays a significant role in nutrient availability, since it acts as a trap for the nutrients due to its polyanionic character (Lock et al., 1984; Burkholder, 1996). Therefore, physical and chemical aspects of the substrate types may explain the differences in species richness, as well as in the other attributes analyzed in the periphyton.

Regarding life forms, entangled filamentous algae presented high biovolume in the periphyton on artificial substrates, especially during the winter and summer. This life form presents efficient transport of nutrients between cells, mainly phosphorous (Cattaneo, 1987; Horner et al., 1990), which is a rather advantageous strategy in an inert substrate and an environment with low P availability in water. In contrast, we found the unicellular flagellated algae had higher biovolume on natural substrate, stem and modified leaves, indicating that microenvironmental conditions were favorable for algae with the ability to efficiently exploit the environment. Another form with motility, unicellular mobile algae without flagella,

was also predominant, having adopted an adaptive strategy on natural substrate, especially on the modified leaves. Thus, the algae in the periphyton on the natural substrate had the ability to position itself strategically in the matrix, allowing the use of resources available from the substrate and water column. Unicellular mucilaginous algae had high biovolume in the periphyton on artificial and natural substrates during the period with high macrophyte coverage (spring and summer), when high shading occurs. Besides the significant role played in the adhesion of the algae on substrate, the mucilage excretion may also be an adaptation to low light conditions (Brook & Williamson, 1988; Domozych et al., 2007). Therefore, our results suggest that the most of adhesion strategies of the periphytic algae were associated with the type of substrate and were strongly influenced by seasonality.

Regarding the species with the highest biovolumes ($\geq 3\%$ total biovolume) in the periphyton, we found nine species with high association with *U. foliosa*, particularly *Scenedesmus westii*, *Chlamydomonas epibiotica*, *Chlamydomonas planctogloea* and *Chromulina elegans*. These results revealed the high contribution of flagellate forms (except for *Scenedesmus*) in the periphyton, showing the predominance of loosely adhered species to the natural substrate. Only two algae species were more associated with artificial substrate (*Eunotia sudetica* and *Bulbochaete* spp.). *Bulbochaete* spp. adheres firmly to the substrate via rhizoids (Wehr & Sheath, 2003) and was one of the filamentous more abundant in the periphyton on artificial substrate. Our findings showed that the species-level taxonomic classification of the periphytic algae community responded primarily to type of substrates. Studies evidenced high similarity between the diatom community on natural and artificial substrates (e.g. Lane et al., 2003), while other studies reported that representativeness was dependent on the type of natural substrate (Townsend & Gell, 2005) or had low representativeness (e.g. Barbiero, 2000). Mutinová et al. (2016) reported that host plants may not always provide a neutral substrate for microalgal epiphyton and, consequently, biomonitoring surveys should account for variations relating to this factor.

Considering that the set of species available within the *U. foliosa* stand was the same for the colonization of all substrates, our results showed the importance of the macrophyte characteristics for periphyton species composition.

Our results showed the existence of differences between microenvironmental conditions in the artificial substrate, stem and modified leaves, such as microtopography and nutrient availability. We concluded that the taxonomic structure and life forms of periphytic algae on artificial substrate poorly represented the natural periphyton on *U. foliosa*.

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