Influence of substratum surface roughness on periphytic algal community structure in a shallow tropical reservoir

Influência da rugosidade do substrato sobre a estrutura da comunidade de algas perifíticas em reservatório raso tropical

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Abstract: Aim: This study aimed to evaluate the algal periphytic community structure on substrates with differing surface roughness in early and longer-term colonization; Methods: Periphyton was sampled after 30 days (June 24 to July 24, 2008) and 5 days (July 07 to July 12, 2010) substrate exposure during dry season. Plastic slides were used as artificial substrate. Treatments were smooth surface (control), low roughness, medium roughness and high roughness. Samples were collected for limnological condition and periphyton (chlorophyll-a, AFDM, algal biovolume and density, species richness and diversity) analysis; Results: Periphytic biomass, algal density and biovolume had no significant difference among treatments after 30 and 5 days colonization time. Taxonomic similarity was the lowest among treatments and the greatest difference occurred between control and treatments with roughness surface. Bacillariophyceae biovolume decreased with increasing surface roughness. Adherence forms, algal classes and species descriptors were significantly different after 5 days colonization time, especially in medium e high roughness surface. In the colonization advanced phase only species descriptors differ among treatments. Periphytic algae with pads and stalks for adherence decreased with increasing surface roughness. Conclusion: Substrate physical properties had little or no influence on periphyton biomass accumulation, total density and biovolume in this study, but algal assemblages were sensitive to changes in the microtopography. More studies are needed to increase understanding of the relation substrate-periphyton in tropical ecosystems.

Keywords: surface roughness, algae periphytic, biomass, species composition, diversity.

Resumo: Objetivos: Este estudo visou avaliar a estrutura da comunidade de algas perifíticas em substratos com diferentes graus de rugosidade na superfície na fase inicial e avançada da colonização; Métodos: O perifíton foi amostrado após 30 dias de colonização (24 junho a 24 julho/2008) e 5 dias (07-12 de julho/2010) de exposição do substrato no período seco. Lâminas de plástico foram usadas como substrato artificial. Os tratamentos foram superfície lisa (controle), baixa, média e alta rugosidade. Foram coletadas amostras para analises das variáveis físicas e químicas e do perifíton (clorofila-a, MSLC, biovolume, densidade algal, diversidade e riqueza de espécies); Resultados: A biomassa, densidade e biovolume algal não apresentaram diferença significativa entre os tratamentos na fase inicial e avançada da colonização. A similaridade na composição de espécies entre os tratamentos foi baixa e a maior diferença ocorreu entre controle e tratamentos com superfície rugosa. O biovolume de Bacillariophyceae diminui com o aumento da rugosidade na superfície. As formas de aderência, classes algais e espécies descritoras foram significativamente diferentes entre tratamentos na fase inicial da colonização, principalmente nos tratamentos de rugosidade média e alta. As espécies descritoras foram diferentes entre tratamentos somente na fase avançada da colonização. Algas perifíticas com pés e pedúnculos para aderência diminuíram com o aumento da rugosidade. As assembléias algais foram sensíveis às mudanças na microtopografia, principalmente na fase inicial da colonização; Conclusão: As propriedades físicas dos substratos apresentaram pouca ou nenhuma influência sobre o incremento de biomassa, densidade e biovolume total, mas as assembléias algais foram sensíveis às mudanças na microtopografia do substrato. Mais estudos devem ser realizados para aumentar a compreensão da relação perifíton-substrato em ecossistemas tropicais.

Palavras-chave: superfície rugosa, algas perifíticas, biomassa, composição de espécies, diversidade.

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1. Introduction

Periphyton development can be influenced by numerous abiotic and biotic factors, which act directly or indirectly on different scales (Stevenson, 1996). The substrate type can influence the periphytic community structure in the micro-environmental scale (Burkholder, 1996), because physical and chemical characteristics of the substrates often provide more than an inert surface for community (Bergey, 2005; Murdock and Dodds, 2007). In non-living substrates such as rocks, substrate chemical composition may not affect biomass accumulation and species composition (Bergey, 2008). However, the physical characteristics of the substrate, such as microtopography and orientation, may significantly affect the community structure of periphytic algal (Burkholder, 1996; Bergey, 2005; Murdock and Dodds 2007).

The topography of the microhabitat is defined by irregularities on the substrate surface (depressions, crevices and protrusions), which may influence biomass accumulation (Johnson, 1994), cell adhesion (Sekar et al., 2004) and algae susceptibility to grazing and scouring (Bergey, 1999, Bergey and Weaver, 2004). The surface irregularities can also minimize water flow action around the substrate, modifying the diffusion boundary layers (De Nicola and McIntire, 1990, Dodds and Biggs, 2002).

Algal assemblages can change substrate topography with increasing of colonization time, because algae and bacteria form a gelatinous mats. The mats may attain a thickness of a centimeter or more, completely smothering the substrata (Biggs, 1996). Thus, the substrate's physical properties can influence algal community structure, but development of the biofilm can minimize influence on the original surface. Understanding the relation between the physical properties of the substrate and algal community structure can help explain the heterogeneous nature of the periphytic community (Robson and Barmuta, 1998). In this sense, this study aims to assess the algal structure on substrates with different surface roughness in early and longer colonization time. More specifically, the study aims to answer whether algal assemblage structure change with increasing substrate roughness in a shallow tropical reservoir.

2. Material and Methods

2.1. Study area

Ninféias Reservoir (23° 80' S and 46° 37' W) is located in the PEFI, Parque Estadual das Fontes

do Ipiranga Biological Reserve (526 ha, 798 m elevation) located in São Paulo, southeastern Brazil. The reservoir's surface area is 5,433 m², volume 7,170 m³, mean depth 1.32 m, maximum depth 3.6 m and, mean theoretical residence time 7 days (Bicudo et al., 2002). Two climatic periods can be characterized over the year: a dry period with lower air temperature during autumn and winter (March-August) and a rainy period with higher temperature during spring and summer (September-February).

2.2. Experimental design

Substrates with different surface roughness were submerged to assess the influence of each substrate surface type on the periphytic algae structure. All substrates were maintained under the same conditions limnological. Periphyton was sampled after 30 days (June 24 to July 24, 2008) and 5 days (July 07 to July 12, 2010) exposure of the plastic substrate. Experiments were performed in the dry season (June and July).

The artificial substrate used for periphyton colonization was polyethylene sheets $(26 \times 76 \times 1.2 \text{ mm})$, which were easy to manipulate and chemically inert. The different degrees of surface roughness were obtained as follows: polyethylene plates were scraped in a standardized manner (15 strokes by same person) with sandpaper number 80, 60 and 40 (Blue Metal - Bosch). The treatments were designated: control, smooth surface, slides with low amount of surface roughness (sanded with sandpaper 80 grit = R1), slides with a mean amount of surface roughness (60 grit = R2), slides with a high amount of surface roughness (40 grit = R3).

Surface roughness on treatment was quantified using a portable surface roughness meter (trademark Digimess TR220 - surface roughness defined by ABNT rules NBR 6405-1985). This equipment measures the roughness by peaks and valleys height (microns) within a range of 12 mm. The roughness values were added to the total length of the plastic slide (standard 76 mm) and used in calculating the total area of colonization treatments (expressed in cm²). The roughness values ranged from 4.49-5.51 µm (mean 5.08; n = 10) in R1 treatment, 7.00-12.95 µm (mean 10.19; n = 10) in R2 treatment and 14.90-16.94 µm (mean 15.61; n = 10) in R3 treatment. Murdock and Dodds (2007) found roughness of 0.87 µm for glass, 17.1 µm for rock and 53.8 µm for brick. Thus, the roughness values created in this study are close to those described for rock.

Plastic slides from each treatment were fitted into a wooden support, forming an experimental unit. Three experimental units (n = 3) were submerged at 30 cm from the surface in the central littoral region (Zmax = 1.5m). The distance between each experimental unit was about 10 m. Fifty slides were placed sequentially (control - R1 - R2 - R3) in each experimental unit's wooden support (total 150 slides). This positioning of the slides allowed better detection of substrate roughness factor on the periphyton development. The slides containing the periphyton were collected randomly for the determination of each attribute community.

2.3. Sampling data

Periphyton sampling was performed simultaneously with the collection of water surrounding the experimental units (n = 3). The abiotic variables analyzed were the following: temperature, conductivity (Digimed), pH (pHmeter Digimed), underwater radiation (Licor LI-250A), water transparency (Secchi disc), alkalinity (Golterman and Clymo, 1971), dissolved oxygen (Golterman et al., 1978), dissolved inorganic carbon, nitrite and nitrate (Mackereth et al., 1978), soluble reactive phosphorus (SRP) and total dissolved phosphorus (TDP) (Strickland and Parsons, 1960). On the sampling day, water samples were filtered under low pressure (<0.3 atm) through Whatman GF/F membrane filters for analyses of dissolved nutrients. Unfiltered water samples were used for total nitrogen (TN) and total phosphorus (TP) determination (Valderrama, 1981) within at most 30 days from collection date. Phytoplankton chlorophyll-a analyses followed Sartory and Grobbelaar (1984).

Periphyton was collected at random sampling of polyethylene slides, and was removed from the substrate by scraping (toothbrush) and rinsing with distilled or ultrapure water. Chlorophyll-a analyses corrected for phaeophytin were carried out at most within a week from the sampling day using 90% ethanol extraction (Sartory and Grobbelaar, 1984), and dry mass and ash free dry mass techniques following APHA (1995). Quantitative determinations of algal periphyton were performed under a Zeiss Axiovert microscope (400×) according to Utermöhl (1958). Counting limit was established according to the species' rarefying curve and until reaching 100 individuals of the most common species. Biovolume ($\mu m^3 cm^{-2}$) was obtained following Hillebrand et al. (1999).

Taxonomic samplings were preserved with 4% formaldehyde water solution.

Periphytic algae were classified according to the following criteria: growth forms: unicellular, flagellate, filamentous, and colonial, forms of adherence to substrate: firmly adhered and loosely adhered. Algae with some locomotion mechanism were classified as loosely attached, and those without locomotion structure and with fixation structure were classified as firmly attached. Attached forms were further subdivided into mobile, entangled, prostrate, mucilaginous (cells enclosed by much mucilage), mucilage pad, mucilage tube or stalked forms.

Biological indexes were used as measure of the community structure (Krebs, 1999): diversity index of Shannon-Wiener (bits.ind⁻¹) and evenness. The species richness is the total number of taxa found in each sample.

2.4. Data statistical treatment

Univariate analysis was performed using the software STATISTICA 9 for Windows. Oneway ANOVA ($\alpha = 0.05$) was applied to test significant differences among treatment means (surface roughness). For the periphyton attributes (total density, total biovolume, AFDM and chlorophyll-*a*), ANOVA was performed for early and longer-term colonization time. Specific means were compared using Tukey's multiple-comparison test ($\alpha = 0.05$). Cluster analysis was calculated by Bray-Curtis index from the matrix of periphytic algae biovolume. Software PAST (Hammer et al., 2001) was used for the analysis. The matrix was made with the algae that presented more than 5% contribution to total biovolume in each treatment.

3. Results

3.1. Limnological variables

The summary of limnological variables during the study period is found in Table 1. Most limnological variables showed no significant difference between 30d and 5d, except nitrate and dissolved oxygen concentration (p > 0.01).

3.2. Periphyton

Chlorophyll-*a*, AFDM, density and total biovolume showed no significant difference between treatments in both colonization times (Figure 1). Despite the absence of significant differences, the total density was 23.7% lower on rough surfaces

Table 1. Mean values and standard deviation (n = 3) of water variables in each study period (30 days = 30d; 5 days = 5d).

Variables	30d	5d
Water temperature (°C)	18.1 ± 0.1	18.4 ± 0.5
Underwater radiation (µmol.S ⁻¹ .cm ²)	142.2 ± 40.3	188.8 ± 45.6
Water transparency (m)	1.2 ± 0.1	1.0 ± 0.1
Alkalinity (mEq.L ⁻¹)	0.22 ± 0.001	0.20 ± 0.001
Electrical conductivity (µS.cm ⁻¹)	53.5 ± 2.2	55.1 ± 0.06
Dissolved oxygen (mg.L ⁻¹)	5.6 ± 0.2	7.4 ± 0.7
Free Carbon Dioxide (mg.L ⁻¹)	9.0 ± 0.4	7.0 ± 0.2
Hydrogen potential	6.2 ± 0.1	6.4 ± 0.2
Total phosphorus (µg.L⁻¹)	6.9 ± 2.4	8.1 ± 0.7
Total Nitrogen (µg.L ⁻¹)	1034.7 ± 106.8	1012.5 ± 140.8
N-NH ₄ (µg.L ⁻¹)	132.3 ± 23.4	118.8 ± 11.8
N-NO ₂ (µg.L ⁻¹)	7.3 ± 0.3	8.7 ± 0.3
N-NO ₃ (µg.L ⁻¹)	589.2 ± 135.6	245.7 ± 17.5
PDT (µg.L ^{_1})	<4	<4
P-PO ₄ (µg.L ⁻¹)	<4	<4



Figure 1. Chlorophyll-a, AFDM, density and algal biovolume (n = 3; \pm SD) in surface roughness treatment (C= control; R₁ = low roughness; R₂ = medium roughness; R₃ = high roughness) after 30 and 5 days colonization time.

than on smooth (control) after 30 days colonization time.

During the study period, 89 taxa were identified. The most abundant algal class was Chlorophyceae with 41 species and Zygnemaphyceae was represented with 20 taxa. *Cosmarium* (9) and *Scenedesmus* (11) were the genera with more species. There were no species exclusive to each treatment.

Species richness, diversity and evenness values did not differ significantly between treatments with surface roughness and control (smooth) (Table 2). The presence of smooth or rough surface had no significant influence on the biological indices.

Algal class biovolume was not significantly different between treatments after 30 days colonization time (Figure 2). In 5 days colonization time, the multiple comparison test showed that Bacillariophyceae biovolume decreased significantly in treatments R2 and R3 (F = 37.68; p = 0.0002). The biovolume of this class was 2.7 times higher in control than in treatment R3. The biovolume of Chrysophyceae (F = 57.15; p = 0.021) and

Table 2. Diversity, species richness and evenness (n = 3; ± SD) of periphytic algae community on different substrates after 30 days (30d) and 5 days (5d) colonization time (C = control; R_1 = low roughness; R_2 = medium roughness; R_3 = high roughness).

	Diversity		Richness		Evenness	
	30d	5d	30d	5d	30d	5d
Control	3.5(±0,31)	3.5(±0,10)	64(±5,77)	26(±0,58)	0.58(±0.041)	0.74(±0.01)
R1	3.8(±0,18)	3.7(±0,32)	61(±2,08)	30(±6,08)	0.64(±0.022)	0.75(±0.21)
R2	3.9(±0,08)	3.7(±0,33)	61(±2,08)	27(±4,58)	0.67(±0.010)	0.78(±0.02)
R2	3.7(±0,23)	3.6(±0,18)	60(±2,64)	31(±2,51)	0.63(±0.041)	0.73(±0.02)



Figure 2. Relative biovolume (n = 3) of periphytic algal classes in roughness treatment (C = control; R_1 = low roughness; R_2 = medium roughness; R_3 = high roughness) after 30 and 5 days colonization time.

Zygnemaphyceae (F = 44.45; p = 0.040) showed significant differences in only R3 control and treatment.

Diatoms *Eunotia flexuosa* (Brébisson) Kützing (24-27%) and *Frustulia crassinervia* (Brébisson) Lange-Bertalot and Krammer (22-26%) were the main species descriptors in control after 5 and 30 days colonization time.

Compared to the control, *Eunotia flexuosa* decreased significantly from 53% to 77% with increasing surface roughness in longer colonization time (Figure 3; F = 12.27; p = 0.002). *Gomphonema gracile* biovolume was also reduced (40-86%) significantly in the treatments with rough surface as compared to control. In this colonization time, *F. crassinervia* was abundant species in all treatments (19-31%). *F. crassinervia* was co-abundant with *Oscillatoria pulcherrima* Azevedo and Sant'Anna (11%) and *Gloeocystis vesiculosus* Nägeli (11%) and *Eunotia flexuosa* (11%) in R1 treatment, with *Eunotia flexuosa* (10%) in R2 treatment and with *Pseudanabaena galeata* Böcher (11%) in R3 treatment.

In 5 days colonization time, *Eunotia flexuosa* and *Frustulia crassinervia* were the main descriptors in the control (24%, 13%, respectively) and R1 treatment (26%, 12%, respectively) (Figure 3). The main descriptors in R2 treatment were *Chromulina elegans* Doflein (16%), *Chlamydomonas epibiotica* G.M. Smith (15%), *Trachelomonas volvocina* var. *volvocina* (13%) and *Frustulia crassinervia* (12%). However, main descriptors in the R3 treatment was *Cosmarium margaritatum* (Lundell) Roy and Bisset var. *margaritatum* f. *minor* (Boldt) West and West (31%), *Peridinium umbonatum Stein* (8%) and *Chromulina elegans* (13%).

The life forms of periphytic algae altered the representation in the treatments with rough surface, but the changes were not significant (Figure 4). Unicellular forms were dominant in all treatments (>50%), except in treatments R2 and R3 after 5 days colonization time. Flagellate biovolume increased 51.8% and 45.5% contribution in the R2 and R3 treatment, respectively, after 5 days colonization time.

The adherence forms responded to changes in the substrate surface, but the modifications were



■ R3 ■ R2 ■ R1 □ Control

Figure 3. Biovolume of descriptor species (>5% of total biovolume; n = 3) in surface roughness treatment (C = control; R_1 = low roughness; R_2 = medium roughness; R_3 = high roughness) after 30 and 5 days colonization time.

more evident and significant only after 5 days colonization time (Figure 4). Firmly attached algae were dominant after 30 days colonization time (>50%) in all treatments. Despite the lack of significant difference, the relative biovolume of loosely attached forms showed a slight increase in rough surfaces (10-15%). Algae firmly attached to the substrate increased significantly in treatments with rough surface after 5 days colonization time (F = 5.0.84; p = 0.013).

Compared to control, there was significant reduction in the contribution of algae with

pads for fixation after 30 days colonization time (R1 = 55%; R2 = 60%; R3 = 78%; F = 14.92; p = 0.002). The biovolume of these algae were also significantly reduced by treatments R2 and R3 after 5 days colonization time (F = 5.583; p = 0.023). The biovolume of other forms of fixation was not significantly different in both colonization times.

Cluster analysis showed that the taxonomic similarity of periphytic algae community was high (<70%) on different surfaces (Figure 5) after 30 and 5 days colonization time. In both colonization times, the species composition was different



Figure 4. Relative biovolume (n = 3) of growth forms, size classes, adherence forms and adherence type of periphytic algae in surface roughness treatment (C = control; R_1 = low roughness; R_2 = medium roughness; R_3 = high roughness) after 30 and 5 days colonization time.

between control and treatments with rough surface at the level of 20-30%. The species composition in treatments R1 and R3 had a difference in level of 20% after 30 and 5 days colonization time. While species composition in the R2 treatment was more similar to R3 treatment after 30 days colonization time, and with treatment R1 in the 5 days after colonization time. Periphytic algal community presented high similarity in treatments with rough surface, showing that surface roughness does not strongly influence species composition.

4. Discussion

In this study, the smooth or rough substrate surface showed little or no influence on the periphyton biomass increment in shallow tropical reservoir, regardless of colonization time. On the other hand, algal assemblages were more sensitive to increased surface roughness, especially after 5 days colonization time. The influence of substrate topography on the periphytic community structure was well demonstrated in lotic ecosystems (Bergey, 2005; Murdock and Dodds, 2007). In tropical



Figure 5. Cluster analysis of periphytic algae biovolume in surface roughness treatment (C = control; R_1 = low roughness; R_2 = medium roughness; R_3 = high roughness) after 30 and 5 days colonization time.

streams, Branco et al. (2010) have found increased macroalgae abundance with increasing surface roughness. However, the substrate type was not the primary factor controlling the periphytic algae structure in tropical floodplain (Rodrigues and Bicudo, 2001).

The resources availability (light and nutrients) is considered the most important factor in determining the periphytic algae structure (Vadeboncoeur and Steinman, 2002), while the substrate type can be a secondary factor (e.g. Rodrigues and Bicudo, 2001). In this study, periphyton in different treatments was developed in the same limnological condition, thereby resource availability was similar for all treatments. In relation to colonization time, the limnological condition in the 5d and 30d were quite similar, especially phosphorus availability. This element is important because it was identified as a limiting nutrient for the periphyton growth in the Ninféias Reservoir (e.g. Fermino et al., 2011).

Surface roughness can promote organic matter accumulation due to the presence of crevices (Johnson, 1994). Studies have shown that stones roughness may protect sufficient algae to augment their recovery in streams following disturbance (Bergey, 2005). However, in this study there was no significant positive response from biomass and total biovolume to roughness after 30 and 5 days colonization time. Probably, the substrate surface roughness influence on biomass increment can be less important for phycoperiphyton in reservoir than lotic system.

Contrast to the response of biomass, algal assemblages were more sensitive to the surface's

physical changes after 30 and 5 days colonization time. This fact was evidenced by low similarity of species composition between the control (smooth surface) and treatments with rough surface. According to Bergey (2005), the topography of the substrate can create a heterogeneous microhabitat where algae with specific adaptive strategies are selected.

Despite the high contribution of Frustulia crassinervia in all treatments after 30 days colonization time, community structure between treatments was differentiated by co-abundant species. Frustulia crassinervia is adheres to the substrate by secreting mucilage canal raphe and may form mucilage tubes (Round et al., 1990). Moreover, others species that produce enough mucilage were found in greater biovolume on rough surfaces (R1, R2, R3) than smooth surface (control), such as Gloeocystis vesiculosus, Eutetramorus globusus and Cosmarium margaritatum var. minor. These colonial Chlorococcales have a broad firm envelope; specifically Gloeocystis can form concentric layers of mucilage (Shubert, 2003). In general, desmids are known for their high capacity to secrete copious mucilage (Domozych and Domozych, 2008). Therefore, surface roughness does not significantly change community physiognomy at longerterm colonization phase (30d), but favored the development of species-rich mucilage.

Adherence forms, algal classes and species descriptors were significantly different after 5 days colonization time, especially in treatments R2 and R3. The algal assemblage was also sensitive to substrate surface roughness in this phase. However, the structural attributes differences were more evident and significant in the early phase than in advanced. Studies showed the increase in biofilm thickness could reduce the external influence on the community and act directly on the photosynthetic properties of the community (Allison, 2003; Sekar et al., 2004, Dodds et al., 1999). Probably, the increased biofilm thickness with the advance of colonization time may have minimized the influence of the substrate surface roughness.

During early colonization (5 days), the smooth surfaces and low surface roughness (R1 treatment) showed dominance of unicellular algae with adhesion to the substrate by mucilage tubes, stalks and pads as Frustulia crassinervia, Gomphonema gracile e Eunotia flexuosa respectively. In contrast, roughness favored the increase of flagellated algae, which are loosely attached and mobile (R2 treatment) or surrounded by mucilage (R3 treatment). Among the mucilaginous forms, Zygnemaphyceae was the most important, particularly Cosmarium. This genus can even move by gliding through the large secretion of mucilage (Domozych and Domozych, 2008). The flagellated Chromulina elegans and Chlamydomonas epibiotica have been most successful on the surfaces with high surface roughness (R2 and R3 treatments). Both species are r-strategists and have adaptive strategies for rapid colonization of nude substrates (Happey-Wood, 1988). Moreover, the flagellum presence confers the ability of efficient resource use in the periphyton matrix (Happey-Wood, 1988).

The substrate's physical properties can determine the type of algal adherence, which may have influence on nutrient assimilation, susceptibility to grazing, scour resistance and dissection (Sekar et al., 2004). Clearly, the rough surface is not favored by species with adherence by pads and stalks, such as diatoms Eunotia flexuosa and Gomphonema gracile, in the early and longer colonization time. E. flexuosa rosette shapes attached apically by small mucilaginous pads and G. gracile by mucilaginous stalks (Hoagland et al., 1982). Another structural feature observed in the rough surface was the increased participation of algae loosely attached to the substrate, that is, without setting structure specifies. In lotic ecosystem, the higher proportion of algae firmly adhered to surface roughness can suggest the community resistance to scouring (Murdock and Dodds, 2007). The physical properties can have effects on resistance and resilience of the algal community in the face of environmental perturbations (Bergey, 1999, 2005). Presently, this relationship is probably not important in lentic ecosystem.

5. Conclusions

The physical properties of the substrate had little or no influence on periphyton biomass accumulation, total density and biovolume in the Ninféias Reservoir. On the other hand, algal assemblages were sensitive to changes in the microtopography, especially in the early colonization when the thickness of the matrix is still small. Thus, the results indicated that smooth or rough surface may not be the primary determinant factor of the algal periphytic community organization. However, the physical properties of the substrate should not be disregarded, especially species composition. To Murdock and Dodds (2007) substrate physical properties should not be ignored in the sampling design, especially when comparing sites using different substrates. As the structural variability of the periphytic community is enormous, we recommend that experimental studies are performed with many repetitions so that we can make generalizations about the relationship between substrate and periphyton in tropical ecosystems.

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