Functional types in epilithon algae communities of the Maquiné River, Rio Grande do Sul, Brazil.

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ABSTRACT: Functional types in epilithon algae communities of the Maquiné River, Rio Grande do Sul, Brazil. Functional types (FTs) are groups of organisms defined by traits and similar in their association to certain environmental variables. When FTs are used to describe communities, patterns can be more clearly related to environmental factors than when examined by species. In this paper, we explore the possibility of using functional types to describe stream benthic algae communities. For this, species composition (density) was seasonally evaluated in epilithon communities selected in six sampling stations, representing headwater, mid-catchment and downstream sites in the river. The most frequent species (26) belonging to Heterokontophyta (18), Cyanobacteria (4), Chlorophyta (3) and Rhodophyta (1) were described for growth form, cell form, attachment, cell size, resistance to disturbance, nitrogen fixation and ficobilisomes. Physical and chemical descriptors of the water were also measured. In data analysis, by using an iterative optimization algorithm implemented in software SYNCSA, a subset of traits was searched with maximum correlation to environmental variables and a subset of environmental variables was found with maximum correlation to the FT-based community gradient. FTs were defined by cluster analysis of the species using the optimal traits. Considering a longer river gradient (headwater to downstream), we identified two FTs with maximum environmental congruence to turbidity and conductivity, which were defined by cell form and resistance to disturbance. The FT characterizing the unstable, downstream zone has prism on parallelogram cell form, and medium to high disturbance resistance, represented by Nitzschia filiformis (W. Smith) Hustedt and Gyrosigma attenuatum (Kützing) Rabhenhorst. Considering a shorter river gradient, from headwater to mid-catchment zone, we identified two FTs with maximum environmental congruence to pH, conductivity and DBO_5, which were defined by cell form, attachment type and cell size.

Key-words: algae, epilithon, functional types, river and streams, periphyton, Brazil.

RESUMO: Tipos Funcionais da Comunidade de Algas Epiliticas no Rio Maquiné, Rio Grande do Sul, Brazil. Tipos funcionais (TFs) são grupos de organismos definidos por características similares e similares em sua associação a variáveis ambientais. Na descrição da comunidade por tipos funcionais, padrões podem ser mais claramente relacionados a fatores ambientais do que quando examinados por espécies. Neste trabalho, exploramos a possibilidade de utilizar tipos funcionais para descrever a comunidade de algas epiliticas. Para isto, a composição especifica (densidade) da comunidade foi sazonalmente avaliada em seis estações amostrais, representando segmentos da cabeceira, trecho médio e foz do rio. As espécies mais freqüentes (26) pertencente a Heterokontophyta (18), Cyanobacteria (4), Chlorophyta (3) e Rhodophyta (1), foram descritas pela forma de crescimento, forma celular, tipo de aderência ao substrato, tamanho celular, resistência ao distúrbio, fixação de nitrogênio e presença de ficobilinas. Descritores físicos e químicos da água foram medidos. Na análise de dados utilizando um algoritmo de otimização iterativo implementado

no software SYNCSA, foi procurado um subconjunto de características com máxima correlação com as variáveis ambientais e foi encontrado um subconjunto de variáveis ambientais com máxima correlação com gradiente da comunidade baseado em TFs. TFs foram definidos por análise de agrupamento das espécies utilizando características ótimas. Considerando todo o gradiente longitudinal do rio (cabeceiras a foz), foram identificados dois TFs com máxima congruência ambiental para turbidez e condutividade, que foram definidos pela forma celular e resistência ao distúrbio. Os TFs que caracterizaram a zona da foz foram forma celular prisma em paralelograma, e média a alta resistência a distúrbio, representadas por Nitzschia filiformis (W. Smith) Hustedt e Gyrosigma attenuatum (Kützing) Rabhenhorst. Considerando o gradiente da zona das cabeceiras ao trecho médio, foram identificados dois TFs com máxima congruência para pH, condutividade e DBO_5, definidos por forma e tamanho celular e tipo de aderência.
Palavras-chave: algas, epiliton, tipos funcionais, rio e arroios, perifiton, Brasil.

Introduction

Community analysis based on species composition has been criticized for not being able to express in terms of functional traits the relations between biotic communities and environmental conditions (Grime, 1979). Each species has combinations of traits that determine its life history and competitive ability. In this sense, there is need to describe communities by traits and not only by species composition, which will enable defining functional types that could describe in simpler terms the complexity of the ecosystem (Pillar, 1999; McIntyre et al., 1999).

A functional type (FT) is a group of organisms similar in a given set of traits and similar in their response to environmental factors and/or effects on ecosystem processes (Pillar & Sosinski, 2003). More or less equivalent concepts, under different names, have been introduced in plant ecology since long ago (Raunkier, 1934; Du Rietz, 1931). There is a link between functional types, community structure and ecosystems processes. The concept of plant functional types has been used in vegetation science as a possible mean to predict vegetation responses to changes in environmental factors, including disturbance, at global and local scale (Pillar & Orlóci, 1993; McIntyre et al., 1995; Díaz & Cabido, 1997).

A critical step in defining functional types is the choice of traits. The best traits to define functional types are those that maximize the perception of association between community and environmental variation (Pillar, 1999). Based on previous knowledge on functional relevance, a set of traits has to be selected to describe individuals or populations in communities. The analysis of the data is supported by computer algorithms to find in the initial set traits that, when used to define functional types, maximize the correlation between community composition and given environment variables (Pillar, 1999; Pillar & Sosinski, 2003). Information on potential functional traits in a large number of species and the existence of data sets of communities described by species composition would enable exploiting the association between community patterns and the environment, and between these patterns and the ecosystem functions (Schulze & Mooney, 1993).

The proposition of functional types for algae is recent. The categorization of species has been mainly based on Grime's plant life history strategy theory (Grime 1977, 1979). These categories are the competitive strategists (C), more adapted to eutrophic and undisturbed habitats; the stress-tolerant strategists (S), more adapted to oligotrophic and stable environments; and the ruderal strategists (R), more adapted to mesotrophic environment with frequent disturbance. Studies involving functional groups in algae communities have considered phytoplankton strategies associated to trophic gradients (Reynolds, 1996, 2000; Reynolds et al., 2002; Huszar & Caraco, 1998), periphyton strategies associated to nutrient supply and disturbance (McCormick 1996; Fayole et al., 1998), functional groups of marine micro and macroalgae associated to disturbance (Steneck & Dethier, 1994; Grime, 1995), and the construction of habitat matrix conceptual models (Biggs et al., 1998a; Biggs et al., 1998b). The problem has been recently examined by

Weithoff (2003), who encourages the adoption of functional concepts in the context of phytoplankton research.

It is consensus among authors that algae communities when examined by functional types can be more clearly related to environmental factors than when examined by species. Therefore, the use of functional types in the analysis of algae communities is a promising tool for environmental evaluation. In this paper we further explore this possibility by identifying functional types in epilithic algae communities and their association to water physical and chemical variables in a river in south Brazil. For that we apply an optimization algorithm (Pillar 1999; Pillar & Sosinski 2003), which was originally devised for the analysis of terrestrial plant communities.

Material and methods

Study area

The Maquiné river basin has an area of ca. 546 Km², located by the north coast of Rio Grande do Sul State, Brazil, limited by 29° 45' S to 29° 23' S and 50° 22'W to 50° 07' W (Fig. 1). It is within the limits of the Biosphere Reserve of the Atlantic Forest, characterized by remnants of tropical rain forest on the slopes and lowlands, and relatively well preserved natural grassland (Campos) and Araucaria forest on the highest altitudes (922 m) (Boldrini, 1997; Ricardo Mello, pers. comm.). The predominant geological substrate is basalt. The river sources at the higher altitudes are on wetlands and peat bogs with Sphagnum. The streams on this portion have cold water, rich on oxygen, transparent, with a rocky riverbed. There is a clear hidrogeomorphologic zoning, from the sources down to the sedimentation zone. On the latter, the river is connected to the Quadros Lake at the coastal plain of Rio Grande do Sul. The levels of nitrate and total phosphorus are low, respectively, 0.05 $mg.L^{-1}$ and 6.27 $mg.L^{-1}$ on average (Lemos & Guerra, 2002).

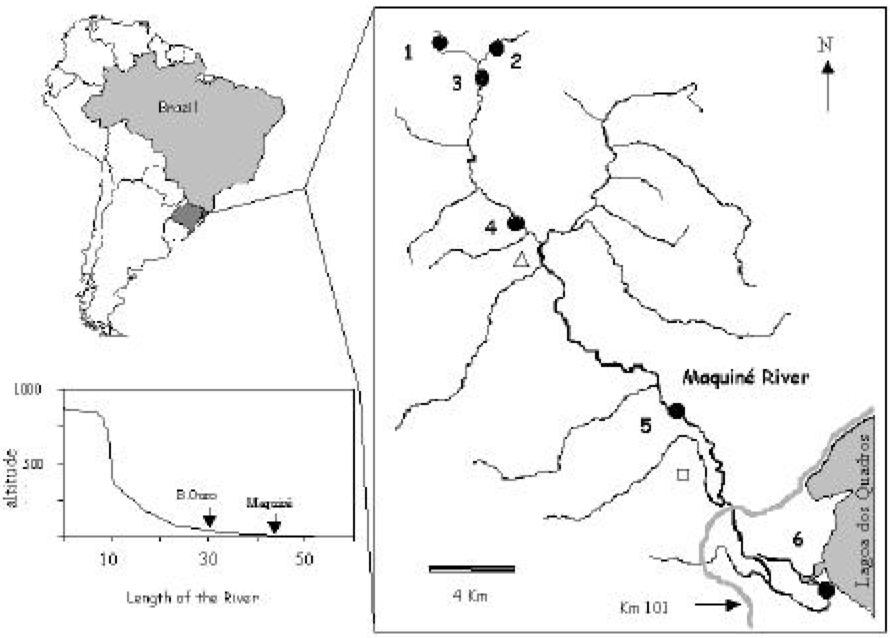

Figure 1: Geographical location of the Maquiné river watershed, RS, Brazil. The six sampling stations (black circles) and geographical references are indicated (black circles), the Maquiné city (white square), Barra do Ouro County (triangle) and the Highway – BR 101. Altitude (m); Length of river (Km).

Sampling procedure

Seasonal description of the epilithon and physical and chemical variables in the superficial water was carried out in seven low-level-water periods, between August 1999 and November 2000, at six sampling stations (station 1, 2 and 3, headwater; station 4 and 5, mid-catchments and station 6, downstream). All these except station 1 were under open canopy.

Temperature (^oC), conductivity ($\mu S.cm^{-1}$), pH, DBO_5 ($mgO_2.L^{-1}$), DQO ($mgO_2.L^{-1}$), dissolved oxygen ($mgO_2.L^{-1}$), turbidity (NTU), and velocity ($m.s^{-1}$) were measured and analyzed according to APHA (1995).

For the description of the epilithon, sampling units were selected on the surface of submersed pebbles, all oriented towards the current, with 15 to 20 cm diameter, at a depth of ca. 20 cm, near the right bank, assuming a headwater-downstream direction. At station 6 (downstream), where pebbles were absent, they were altogether artificially placed in the river ca. 30 days before the first sampling. All pebbles were basalt. On each pebble a squared surface of 25 cm^2 was delimited and the material was isolated and removed using a brush, stored in glass containers mixed with 25 ml of demineralised water and fixed with 4% formalin (Kobayasi & Mayama, 1982). At each sampling station and date, three pebbles were selected, and the collected material was taken together as a composed sampling unit with 75 cm^2, according to Lobo (1995). The material was placed on Prof. Dr. Alarich Schultz (HAS) Herbarium from the Museu de Ciências Naturais of the Fundação Zoobotânica do Rio Grande do Sul, under the numbers 103866 to 103907.

Taxonomic identification and counting

A qualitative survey of species composition was performed in advance with material collected from each sampling site. For helping the identification, slides with fresh material were prepared and examined under microscope (1000 X magnification). For diatoms, permanent slides were prepared, being the frustules cleaning performed according to Hasle & Fryxell (1970). The identification of species was based on Geitler (1932), Krammer & Lange-Bertalot (1986, 1988, 1991a, b), Simonsen (1987), Lange-Bertalot (1993), Germain (1981), Branco et al. (1996, 1997), Printz (1962).

The counting was performed in a Sedgewick Rafter chamber, with a Zeiss binocular microscope, with 450 X. Colonial, filamentous and unicellular forms were counted as individuals. Counting was done until 100 individuals of the most abundant species were found (Kozlowsky-Susuki & Bozelli, 1998). In this way, the total number of counted individuals in each chamber varied from 300 to 600. The results were expressed as density (number of individuals per cm^2) according to Wetzel & Likens (1990), modified by Schwarzbold (1992).

The determination of the dominant and abundant species was estimated using Lobo & Leighton (1986). In a sampling unit, the dominant species was the one with a relative density above 50%, and abundant species were those with a density above the mean value in the sampling unit.

Description of traits and analysis of functional types

From the total number of 74 species that were found in the survey, the ones that occurred in more than 20% of the sampling units (26 species), were described by seven morphological and fisiological traits. These were: growth form, cell form, attachment, nitrogen fixation and ficobilisomes, which are qualitative, and cell size, resistance to disturbance (physic and/or herbivory) which are quantitative. The traits and their states are in Tab. 1. All traits except nitrogen fixation and ficobilisomes were evaluated in the slides prepared with fresh material. These traits were selected for their ecological relevance suggested by previous studies (Biggs 1996, Peterson 1996, Robinson & Rushforth 1987, Reynolds 1996). The species characteristics for nitrogen fixation and ficobilisomes were described according to Cohen-Bazire & Briant (1982) and Stal (2000). The categories for the other traits were chosen based on Biggs (1996), Biggs et al. (1998a), Peterson (1996), Reynolds (1996), Dussart (1965), Germain, (1981) and Hillebrand et al. (1999).

Table I: Attributes and states used for description for the epilithon species.

Traits and references	Trait states
1. Growth form	(0) unicellular; (1) filamentous
2. Attachment Reynolds (1996); Biggs (1998a); Germain (1981)	(1) stalked; (2) mucilage pad; (3) heterotrichous; (4) prostrate; (5) mucilage tube; (6) metaphyton
3. Cellular form Hillebrand et al. (1999)	(1) elliptic prism; (2) cylinder; (3) ellipsoid; (4) cymbeloid; (5) sickle-shaped prism; (6) prism on parallelogram; (7) gomphonemoid; (8) box
4. Cell size Dussart (1965)	(1) small (nanoplankton: 20 mm); (2) medium (microplankton: 20 a 200 mm); (3) large (above 200 mm)
5. Resistance to disturbance (physical and / or herbivory) Biggs (1996, 1998a); Peterson (1996); Robinson & Rushforth (1987)	**Cell size; Attachment** (1) Low: small, medium; pad, stalked (2) Medium: medium, large; heterotrichous, tube, metaphyton (3) High: small, medium; prostrate
6. Nitrogen fixation Stal (2000)	(0) no (1) yes
7. Ficobilisomes Cohen-Bazire & Bryant (1982)	(0) no (1) yes

The identification of functional types used an optimization algorithm (Pillar & Sosinski, 2003) implemented in the computational program SYNCSA (Pillar, 2002). For this, the data was organized in three matrices: Matrix B describing the 26 species by the seven traits, matrix W describing the communities (stations x months) by the species densities; and matrix E describing the communities sites by the seven environmental variables standardized by centering and normalization. Species densities were transformed by log (x+1). The optimization algorithm identified a subset of traits, and groups of species (FTs) defined by these traits, such that a maximum congruence between community and environmental variation was revealed. Congruence was the Pearson matrix correlation $\rho(D;\Delta)$ between community chord distances (matrix D), based on FTs so defined, and environmental Euclidean distances (matrix Δ) based on the environmental variables. FTs were groups of species defined by cluster analysis (UPGMA) from Gower similarity index for the subset of traits.

In one analysis the whole river gradient (six sampling stations, 42 sampling units) was examined. In another, the more lotic (five) sampling stations (35 sampling units) were examined. For each of these analyses, the trait optimization procedure was performed iteratively. To start with, the analysis identified traits and optimal FTs by using all seven environmental variables. Then, an environmental variable subset was selected such that a maximum congruence with community variation described by FTs given by these traits; the procedure of variable subset optimization is stepwise, described in Pillar & Orlóci (1993). In the last step, traits and FTs were optimized again, just as in the first step, but now using only the optimal environmental variables.

Results

The results of the river environmental description are in Tab. II. The trait description of the species is shown in Tab. III. The optimization procedure identified two functional types (species groups) when taking into account the whole river gradient (42 sampling units). A different FT classification was found when only the lotic segment (35 sampling units) was considered (Tab. III). The FTs were such that, when community composition was described by these FTs, a maximum congruence with environmental variation was found. In the sequel we give more details on the intermediate steps followed to obtain these results.

Table II: Maximum and minimum values found in physical and chemical variables of the superficial water in six sampling stations, seven dates in a period of 16 months, Maquiné River, RS.

Variables	**Sampling stations**					
	1	**2**	**3**	**4**	**5**	**6**
Temperature (°C)	9.6 - 18	9.7 - 23	9.7 - 21.5	11 - 22	16 - 29	13 - 32
pH	5.7 - 6.3	5.5 - 6.3	6.0 - 6.6	6.4 - 7.8	6.6 - 7.8	6.7 - 7.2
Conductivity ($\mu S.cm^{-1}$)	16.7 - 22.8	16 - 22	19 - 25	22 - 28	36 - 47.4	42.2 - 61
OD ($mgO_2.L^{-1}$)	5.3 - 7.7	6.0 - 10.2	6.5 - 9.3	7.0 - 10.39	7.0 - 10.2	5.2 - 11
DBO_5 ($mgO_2.L^{-1}$)	0.4 - 3.5	0.4 - 3.5	1.0 - 3.4	1.2 - 3.5	1.5 - 4.3	2.0 - 5.5
DQO ($mgO_2.L^{-1}$)	4.0 - 10	4.0 - 9.0	4.0 - 13	4.0 - 14	4.0 - 7.7	2.75- 6.0
Turbidity (NTU)	7 - 9	4.2 - 9	7 - 9	6 - 9	6 - 9	20 - 26
Velocity ($m.s^{-1}$)	0.07 - 0.49	0.07 - 0.39	0.06 - 0.4	0.03 - 0.45	0.04 - 0.46	< 0.03
Mean depth (cm)	22	30	25	40	43	400
Altitude (m)	922	874	872	146	26	15

Table III: Species and traits used for functional types identification.

Species / Attributes	**FC**	**F**	**AD**	**TA**	**RE**	**NI**	**FI**	**42**	**35**
Achnanthidium microcephalum	0	1	1	1	3	0	0	FT 1	FT 1
Batrachospermum puiggarianum	1	2	5	3	2	0	1	FT 1	FT 2
Chamaesiphon confervicola	0	2	4	1	1	0	1	FT 1	FT 2
Cocconeis placentula	0	1	1	2	3	0	0	FT 1	FT 1
Cosmarium granatum	0	3	6	2	1	0	0	FT 1	FT 2
Cymbella helvetica	0	4	1	2	1	0	0	FT 1	FT 1
Cymbella tumida	0	4	1	2	1	0	0	FT 1	FT 1
Encyonema minutum	0	4	1	2	1	0	0	FT 1	FT 1
Encyonema perpusillum	0	4	1	2	1	0	0	FT 1	FT 1
Eunotia lunaris	0	5	6	2	1	0	0	FT 1	FT 2
Eunotia pectinalis	0	5	6	2	1	0	0	FT 1	FT 2
Fragilaria capucina	0	1	4	1	1	0	0	FT 1	FT 1
Gyrosigma attenuatum	0	6	1	2	3	0	0	FT 2	FT 1
Gomphonema clevei	0	7	2	2	1	0	0	FT 1	FT 1
Gomphonema parvulum	0	7	2	1	1	0	0	FT 1	FT 1
Homoeothrix juliana	1	2	5	3	2	0	1	FT 1	FT 2
Lyngbya corium	1	2	6	3	2	1	1	FT 1	FT 2
Heteroleibleinia kuetzingii	1	2	5	3	2	1	1	FT 1	FT 2
Microspora stagnorum	1	2	5	3	2	0	0	FT 1	FT 2
Navicula cryptocephala	0	1	1	2	1	0	0	FT 1	FT 1
Navicula imbricata	0	1	1	2	1	0	0	FT 1	FT 1
Nitzschia filiformis	0	6	3	2	2	0	0	FT 2	FT 1
Oedogonium sp	1	2	5	3	2	0	0	FT 1	FT 2
Synedra acus	0	8	4	2	1	0	0	FT 1	FT 2
Synedra rumpens	0	8	4	2	1	0	0	FT 1	FT 2
Synedra ulna	0	8	4	3	1	0	0	FT 1	FT 2

Label: FC: Growth form: (0) unicellular; (1) filamentous; F: Cellular form: (1) elliptic prism, (2) cylinder, (3) ellipsoid, (4) cymbeloid, (5) sickle-shaped prism, (6) prism on parallelogram, (7) gomphonemoid, (8) box; AD: Attachment: (1) prostrate, (2) stalked, (3) mucilage tube, (4) pad, (5) heterotrichous, (6) metaphyton (without fixation structure); TA: Cell size: (1) small, (2) medium, (3) large; RE: Resistance to disturbance (physical and / or herbivory): (1) low, (2) medium, (3) high; NI: Nitrogen fixation: (0) no (1) yes; FI: Ficobilisomes presence: (0) no, (1) yes; 42: FTs 1 and 2 (species groups) formed after analysis maximizing congruence r(D;D) between community variation based on FTs and environmental variation using all 42 sampling units along the river; 35: FTs 1 and 2 (species groups) formed after analysis maximizing congruence r(D;D) between community variation based on FTs and environmental variation using 35 sampling units (the lotic segment).

The first step in the optimization procedure, using the entire river gradient, preliminarily identified traits and FTs (not shown) determining maximum congruence with environmental variation given by the complete set of variables. The second step found that turbidity and electrical conductivity taken together produced maximum congruence with epilithic community variation given by these FTs.

A third step in the optimization procedure was applied again on the data considering now only turbidity and electrical conductivity as environmental variables. The results are in Tab. IV. The correlation (congruence) r(D;D) between community variation given by the FTs and the variation in the environmental data was maximized. The analysis revealed two optimal traits, defining two FTs. These traits were "cellular form" (cf) and "resistance to disturbance" (physical and/or herbivory) (rh) (Tab. IV, in bold), which were used to define the FTs in cluster analysis (two groups) and produced a maximum congruence r(D;D) = 0.552 considering both environmental factors. Therefore, in the analysis of the whole river gradient, cellular form and resistance to disturbance defined FTs with maximum congruence with variation in electrical conductivity and turbidity. These variables increase downstream (Tab. IV).

Table IV: Results of the optimization algorithm applied to the epilithon trait-based community data, showing the traits determining maximum congruence with turbidity and electrical conductivity (in bold). The optimal number of functional types (species groups) is also indicated. The analysis considered 42 sampling units, Maquiné River, RS, Brazil.

Congruence r (D;D)	**Groups**	**Optimal attributes**						
0.250378	8	ce						
0.552183	**2**	**ce**	**rh**					
0.450032	2	ce	ad	rh				
0.450032	2	ce	ad	ta	rh			
0.338189	18	fc	ce	ad	ta	fi		
0.338189	18	fc	ce	ad	ta	rh	fi	
0.306911	14	fc	ce	ad	ta	rh	ni	fi

Label: fc= growth form; ce= cellular form; ad= attachment; ta= cellular size; rh= resistance to disturbance (physical and / or herbivory); fi= ficobilisomes; ni= nitrogen fixation.

Functional type 1 (FT1) is a large group represented by most of the species (24) described in the sampling stations from headwaters to mid-catchment, associated to low values of turbidity and electrical conductivity. FT1 includes species with a broad range of resistance to disturbance. However, most of the species have little resistance, which are filamentous without a clear fixation structure (metaphyton) and stalked, with a medium to large cellular size. Cellular forms in FT1 were elliptic prism, cylinder, ellipsoid, cymbeloid, sickle-shaped prism and box, except prism on parallelogram.

On the other hand, FT2 characterizes the downstream site with more turbidity and electric conductivity, with prism on parallelogram cellular form and with mid to high resistance to disturbance, represented by the diatoms Nitzschia filiformis and Gyrosigma attenuatum (Tab. III). The species in FT2 have small to medium size and a firm attachment to the substrate (tube and prostrate).

The analysis of the lotic river environment (35 sampling units, sampling stations 1 to 5) indicated that the subset of variables with pH, electrical conductivity and DBO_5 gave maximum congruence with community variation. The optimization algorithm applied again on the data considering only these variables revealed three optimal attributes: cell form, attachment type and cell size, that when used to define two FTs (groups of species by cluster analysis) determined a maximum congruence of 0.387 with the environmental variables (Tab. V).

Table V: Results of the optimization algorithm applied to the epilithon trait-based community data, showing the traits determining maximum congruence with pH, electrical conductivity and DBO_5 (in bold). The optimal number of functional types (species groups) is also indicated. The analysis considered 35 sampling units (lotic segment), Maquiné River, RS.

Congruence r (D;D)	**Groups**	**Optimal attributes**						
0.125053	7	ce						
0.242103	3	ce	ad					
0.378350	**2**	**ce**	**ad**	**ta**				
0.240385	13	ce	ad	ta	ni			
0.240385	13	fc	ce	ad	ta	ni		
0.240385	13	fc	ce	ad	ta	rh	ni	
0.215471	14	fc	ce	ad	ta	rh	ni	fi

Label: fc= growth form; ce= cellular form; ad= attachment; ta= cellular size; rh= resistance to disturbance (physical and / or herbivory); fi= ficobilisomes; ni= nitrogen fixation.

The community composition matrix — with the 35 sampling units described by the two optimal FTs defined by cell form, attachment type and cell size — was submitted to ordination (Fig. 2). The ordination revealed a trend in community variation that is clearly associated to conductivity and pH. Communities at the bottom right side of the diagram are in sites with increasing values of conductivity and pH, in the transition zone between mid-catchment and downstream, characterized by FT1. Communities at the top left side of the diagram, characterized by FT2, are in sites with lower values of electrical conductivity and pH, in the headwaters zone (Fig. 2a, b, c). Although DBO_5 was a variable that contributed to maximize the congruence with communities variation described by optimum FTs, it did not show a clear association with the community pattern revealed in the ordination diagram (Fig. 2d).

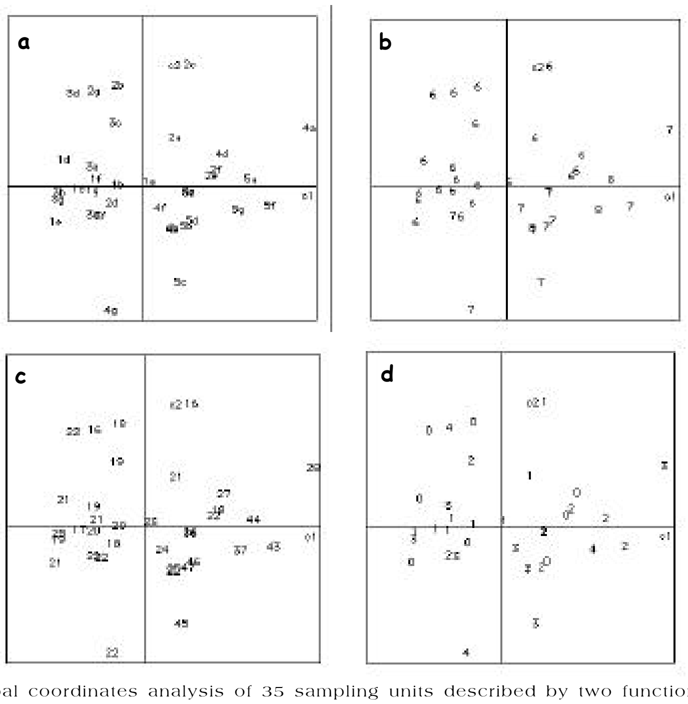

Figure 2: Principal coordinates analysis of 35 sampling units described by two functional types (FTs: c1, c2). FTs were defined by cluster analysis using three optimal traits (cellular form, attachment and cellular size), which gave maximum congruence with environmental factors (pH, conductivity and DBO_5). Ordination axes contain 61% (horizontal) and 39% (vertical) of the total variation in the data. In (a) the labels are numbers identifying the sampling units (1-5) and letters identifying the sampling month: a: August/1999; b: December/1999; c: February/2000; d: April/2000; e: May/1999; f: August/2000; g: November/2000. In (b) the same diagram identifies the sampling units by the pH, in (c) by the electric conductivity and in (d) by the DBO_5 states.

The main distinction between TF1 and TF 2 is the cell form and the attachment. FT1 is characterized by elliptic prism cell form, cymbeloid and gomphonemoid, with prostrate attachment, stalked and mucilage pad, and with small and medium size (Tab. III), represented by diatoms. FT2 is characterized by cylindrical, ellipsoid, box and prism on parallelogram cell form, attachment mucilage pad, heterotrichous and metaphyton, and all sizes classes (small, medium and large) (Tab. III), represented mainly by filamentous algae.

Discussion

The stresses caused by light deprivation and by suspension of fine sediment indicated by turbidity are likely affecting the downstream algae communities, which is the case of sampling station 6 in the Maquiné River. Heterotrophy and dormancy are metabolic strategies that might allow algae to survive extended periods of darkness. In this case, the diatom Nitzschia filiformis can develop an optional heterotrophy strategy (Tuchman, 1996). The great ability of attachment and short height are dominant adaptive characteristics in a habitat with frequent and severe enough disturbance to cause considerable phytobenthos removal. Epipsamics habitats are environmentally unstable, with high risk of frequent destruction and are characterized by low biomass algae community, dominated by prostrate forms which can only exist inside fine depressions that prevent removal (Mc Cormick, 1996). The association found between prism cellular form (Nitszchia and Eunotia) and the increase of fine sediment is corroborated in Griffith et al. (2002).

Some of the species found in our work coincide with the ones considered by Biggs et al. (1998 a, b) on its proposal for categorization of a river habitat matrix based on adaptive strategies (sensu Grime, 1979) of benthic algae, considering the supply of nutrients gradient and the level of disturbance. The presence of R strategists (ruderals) is remarkable throughout the entire Maquiné River, such as Cocconeis placentula, Encyonema minutum, Synedra ulna, Synedra rumpens, Gomphonema parvulum, and Homoeothrix. This pattern is expected, since the river systems, in general, show frequent disturbance with different intensity levels. Metaphytic species forming tangles of mucilage, characteristic at headwaters, are considered R strategists, just like prostrate diatoms, which can establish on rocks or on other algae species. We observed Chamaesiphon confervicola growing epiphytically on "Chantransia" phase of Batrachospermum. At headwater sites, we found S strategists (stress tolerant) species, typical in oligotrophic environments, such as Batrachospermum and Lyngbya sp. At mid-catchment sites we observed a group of species with a broader characteristic range, the C-S strategists (competitive and stress tolerant), such as Navicula cryptocephala and Oedogonium sp. Typical C strategists species (competitive) are expected, according to Biggs et al. (1998a), at eutrophic environments, which was not verified in the Maquiné River.

Expanded forms, with a high level of biomass, may be more competitive in more stable environments, where density-dependent interactions are more intense. Prostrate species, strongly attached, are more resistant to disturbance. However, the survival in disturbed environments is also related to the ability to colonize disturbed areas (Peterson, 1996). Since benthic algae tangles are periodically destroyed by abiotic disturbance, herbivory or senescence, both kinds of adaptations, resistance to disturbance and ability to colonize, may occur together in a given segment of the river. Considering grazing as a type of disturbance, some diatoms species are easily grazed because of the type of attachment to the substratum. For example, stalked forms, as Gomphonema may be more easily predated than horizontal forms (prostrates) as Cocconeis and Achnanthes (Robinson & Rushforth, 1987). Furthermore, it is important to consider that the proposed categories are not mutually exclusive, for the same species may present adaptations associated to multiple strategies (Mc Cormick, 1996).

It is important to note that our data refer to communities described in one river in one region, during a relatively short time span. Furthermore, only a subset of the most frequent epilithon algae species was described for the traits. In order to evaluate whether the traits and functional types that we found with highest correlation with the environmental gradients would be valid on a regional or global scale, traits and community data from similar gradients in other rivers with different species composition would be needed. However, the main objetive of this work is to show utility of the functional types approach in stream epilithon algae research.

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