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Microhabitat and plant structure of Characeae (Chlorophyta) populations in streams from São Paulo State, southeastern Brazil

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Abstract – Microhabitat distribution was investigated in five populations of Characeae (two of *Chara guairensis*, two of *Nitella subglomerata* and one of *Nitella* sp.) to determine the distributional patterns, the morphometric and reproductive adaptations to varying environmental conditions and niche width on a scale of few centimeters. Variations in physical variables revealed some general trends of microhabitat distribution for the Characeae populations studied, with occurrence under the following conditions: slow and narrow current velocities; substrata predominantly composed of small particle size (sand-clay) ; variable and generally low depths. In terms of morphological adaptations, we found some general patterns: plants with longer whorl branchlets also had longer internodes in all populations studied, whereas longer plants had also thicker axis. The former were generally associated with higher biomass (percent cover). Few correlations of morphological characters were observed with environmental variables (e.g. plant length with irradiance: negative in two populations and positive in one population). Despite the general patterns of occurrence mentioned above, our results also indicated that each population differed in its responses to environmental variables and had particular morphological and reproductive adaptations. The Characean populations occurred under a narrower range of microhabitat conditions than other macroalgae from lotic habitats, particularly lower current velocity (6.7-9.8 cm s^{-1}) and a more specific substratum type (sand-clay). Niche width values (0.60-0.99) of the Characeae populations studied indicate a high degree of habitat specialization and are among the highest yet found in lotic macroalgae. The relatively narrow variations in microhabitat conditions and high niche widths here reported for Characean populations, suggest a lower tolerance to variations in current velocity, depth, irradiance and substratum type. These characteristics probably explain the relatively restricted distribution of Characeae species in streams of São Paulo State with low frequency of records in most regions.

***Chara* / Characeae / current velocity / freshwater green algae / microhabitat / *Nitella* / plant structure / stream**

Résumé – La distribution en fonction des microhabitats a été étudiée dans cinq populations de Characées (deux de *Chara guairensis*, deux de *Nitella subglomerata* et une de *Nitella* sp.) dans le but de déterminer la structure des distributions, les adaptations morphologiques et reproductrices aux variations des conditions écologiques et les largeurs de niche sur une échelle de quelques centimètres. Les variations des caractéristiques physiques mettent en évidence quelques tendances générales de la distribution des populations de Characées dans les microhabitats en fonction des conditions suivantes : courant lent, substrat composé en majeure partie de petites particules (argile sableuse), profondeur

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variable et généralement faible. Les adaptations morphologiques généralement observées sont les suivantes : les plantes avec des phylloïdes plus longs ont aussi des entre-nœuds plus longs dans toutes les populations étudiées tandis que les plantes les plus longues ont aussi les axes les plus épais. Les premières sont en général associées à des biomasses plus importantes (pourcentage de recouvrement). Il a été observé quelques corrélations de caractères morphologiques avec des variables écologiques (longueur des plantes avec éclairement dans trois populations). En dépit de ces tendances générales, nos résultats indiquent aussi que chaque population répond différemment aux variables écologiques et montre des adaptations morphologiques et reproductrices particulières. Les populations de Characées apparaissent dans une gamme de microhabitats plus étroite que celle des autres macroalgues des milieux lotiques, notamment en ce qui concerne la vitesse du courant (6,7-9,8 cm s^{-1}) et le type de substrat (argile sableuse). Les valeurs de largeur de niche (0,60-0,99) des populations étudiées indiquent un haut degré de spécialisation et sont parmi les plus hautes observées chez les macroalgues lotiques. Les variations relativement faibles des conditions de microhabitats et les hautes valeurs de largeur de niche de ces populations de Characées suggèrent une tolérance faible aux variations de la vitesse du courant, de la profondeur, de l'éclairement et du type de substrat. Ces caractéristiques expliquent probablement la distribution relativement limitée des Characées dans les cours d'eau lotiques de l'état de São Paulo et la faible fréquence des observations dans la plupart des régions.

algues vertes d'eau douce / *Chara* / Characeae / microhabitat / *Nitella* / rapidité du courant / ruisseau / structure

INTRODUCTION

Occurrence of representatives of the green algal family Characeae has been sparsely documented as a component of the macroalgal communities in lotic ecosystems (Hendricks & White, 1988; Caffrey & King, 1989; Casanova, 1994; Bornette & Large, 1995; Bornette *et al.*, 1996; Hussain *et al.*, 1996). As a consequence, information on environmental factors affecting spatial and temporal distribution and plant structure of these algae is relatively scarce for such habitats. Responses of growth and reproduction to some variables, such as temperature, light, nutrients, depth and substratum, have been reported (Imahori, 1963; Imahori & Iwasa, 1965; Andrews *et al.*, 1984a, 1984b; Guerlesquin, 1990). Imahori & Iwasa (1965) described plastic responses in plant morphology to distinct treatments of light and nutrients. Light and temperature were reported as stimulating sexual reproduction and the induction of protandry in certain species (Guerlesquin, 1990). Influence of depth and particle size were evidenced by Andrews *et al.* (1984a, 1984b). However, there is no specific investigation on the influence of physical factors on small-scale spatial distribution and the morphology of these plants in lotic habitats.

The information is still scarcer for lotic ecosystems of tropical regions and is virtually restricted to areas in southeastern Brazil (Necchi & Pascoaloto, 1993; Necchi *et al.*, 1995a, 2000; Branco & Necchi, 1996, 1997, 1998b). These contributions refer to seasonal dynamics of macroalgal communities (including members of Characeae) or spatial distribution in distinct scales. A comprehensive approach has been initiated as to the microhabitat distribution of stream macroalgae in tropical regions of southeastern Brazil. Previous investigations have been published on populations of other well-represented algal groups: Rhodophyta – Batrachospermaceae, *Batrachospermum* (Necchi, 1997) and Compsopogonaceae, *Compsopogon* (Necchi *et al.*, 1999) and Chlorophyta – Chaetophoraceae, *Chaeto-*

phora and *Stigeoclonium* (Branco & Necchi, 1998a). This study is part of such approach and was carried out with the purpose to evaluate the influence of physical factors (current velocity, irradiance, depth and substratum type) on microhabitat distribution (on a scale of few centimeters) of some populations of *Chara* and *Nitella*, including distributional patterns and morphometric and reproductive adaptations to varying conditions and niche width.

MATERIALS AND METHODS

Field work was carried out from late winter (August) to early spring (October) in two years (1996 and 1997), the most favorable growth period for Characeae populations in the study region (Necchi & Pascoaloto, 1993; Branco & Necchi, 1997; Vieira & Necchi, unpublished), at three sites located in the northwest region of São Paulo State, southeastern Brazil (Tab. 1). Five populations (two of *Nitella subglomerata* and *Chara guairensis*, and one of *Nitella* sp.) were sampled once to avoid temporal influence. *Nitella* sp. is a probable new species to be published in a separate paper. Each sampling site consisted of stream segments ranging from 10 to 20 m in length, with abundant growth of *Chara* and *Nitella* populations. The Characean populations are typically annual in streams from this region (Vieira & Necchi, unpublished) and occur mostly in deposition zones (margins, pools or deeper and slower parts). All observations and collections were made on natural substrata (bedrock, gravel, sand-clay and others). Depths in the sampling sites are considerably variable seasonally and this pattern mostly determined by the precipitation regime with the highest and lowest values observed during the rainy and dry seasons, respectively (Necchi & Pascoaloto, 1993; Branco & Necchi, 1997; Vieira & Necchi, unpublished).

Sampling for microhabitat analyses was conducted by means of the quadrat technique (Necchi *et al.*, 1995b, 1999; Necchi, 1997; Branco & Necchi, 1998a). Details of sampling procedures are fully described in those publications, and here we will just refer to additional information or specifications to this particular study. Sampling units consisted of 20 cm circles (area = 314 cm^2) and 12 quadrats were sampled in each sampling site. In each sampling site, an equal number of quadrats without the alga (designated control) was randomly sampled to evaluate differences in microhabitat characteristics in comparison with those with the alga, according to the same criterion of 'presence' quadrats. This is essentially a within-site analysis and some between-site comparisons are purely descriptive and no conclusions are drawn from them.

Specimens collected within quadrats were measured in replicates of 15. This number was estimated on the basis of number of replicates *versus* variance curves. Five plants per quadrat were taken and three measurements or countings made from each plant. We included all morphometric characters considered to be important in previous studies (Imahori, 1963; Imahori & Iwasa, 1965; Wood & Imahori, 1964, 1965, Bicudo, 1974; Casanova, 1994) : plant, internode and whorl branchlet length, axis diameter, dactyl and sub-terminal ray length and number of whorl branchlets. The following reproductive characters were analyzed: head diameter, head peduncle length, number of nucules and globules per whorl and ratio of nucules per globules. Measurements were made with a micrometer eyepiece coupled to a Carl Zeiss Jena, Laboval 3 microscope and counts were made in three optical fields, each with a circular area measuring 12 mm^2.

Tab. 1. Location and characteristics of the sampling sites of Characeae populations. Abbreviations: BR = bedrock; GR = gravel; OT = others; SC = sand-clay.

	Characteristics								
Location, sampling date and species[a]	*Substratum* %*	*Temperature °C*	*Specific conductance $\mu S\ cm^{-1}$*	*Turbidity NTU*	*Current velocity* $cm\ s^{-1}$*	*pH*	*Dissolved Oxygen $mg\ l^{-1}$*	*Depth* cm*	*Irradiance* $\mu mol\ m^{-2}\ s^{-1}$*
Site 1									
São José do Rio Preto, Córrego da Lagoa, 20° 53’12” S, 49° 18’ 09” W, 3rd order, 26 August 1996 *Nitella subglomerata* *Chara guairensis*	SC 90 GR 5 OT 5	20.2	64	7	12.7	6.2	5.1 56 % saturated	10.4	1130
Site 2									
Ipiguá, Córrego do Barbosa, 20° 38’ 42” S, 49° 24’ 09” W 2nd order, 02 October 1997 *Nitella* sp. *Nitella subglomerata*	SC 75 BR 20 OT 5	24.6	61	6	10.8	7.2	5.5 65 % saturated	9.9	1670
Site 3									
São José do Rio Preto, Engo. Schmidt, Rio Preto, 20° 52’ 26” S, 49° 18’ 40” W, 3rd order, 07 October 1997 *Chara guairensis*	SC 100	24	84	15	11	6.7	3.2 38 % saturated	21.4	545

[a] Stream order according to Strahler (1957).

* Values represent means (N = 24), calculated from measurements taken within quadrats with Characeae plants and without them (controls).

For each population, niche width was calculated in order to evaluate the degree of microhabitat specialization, applying Levin's standardized index (Krebs, 1989): $B_A = (B - 1) / (n - 1)$, where $B = 1/\sum (p_{xi})^2$, p_{xi} = relative abundance (percent cover) of species x at sampling unit i (xi/X), $X = \sum xi$ and n = total sampling number. Values range along a scale of 0 to 1.

The following environmental variables were measured at the center of each sampling unit: current velocity, depth, underwater irradiance and substratum type. Temperature, turbidity, specific conductance, pH and dissolved oxygen were measured for the whole stream segment. Field procedures for measuring these parameters are the same described in details in previous microhabitat studies (Necchi *et al.*, 1999; Necchi, 1997; Branco & Necchi, 1998a).

Pairwise differences between 'presence' and 'control' quadrats within and among populations were determined by Student's *t* test and Analysis of Variance (ANOVA, one way), respectively, and associations among percent cover and morphometric data with stream variables were tested by Pearson's *r* product moment correlation coefficient (Sokal & Rohlf, 1981). Tests were performed with the Minitab statistical package (Ryan *et al.*, 1985).

RESULTS

Interspecific characteristics (populations of all species combined)

Characteristics of the sampling sites are summarized in Tab. 1. Variations in current velocity were relatively narrow (6.7-9.8 cm s^{-1}) with no significant difference among the populations of the three Characeae species, whereas depth varied significantly ($F = 7.8$, $p < 0.001$), with the lowest values in the population of *N. subglomerata* from site 1 (9 cm) and the highest in the population of *C. guairensis* of site 3 (18 cm, Fig. 1). Irradiances varied significantly among the populations ($F = 28.6$, $p < 0.001$), with the lowest value in the population of *C. guairensis* of site 3 (450 µmol m^{-2} s^{-1}) and the highest in the population of *Nitella* sp. in site 2 (1715 µmol m^{-2} s^{-1}, Fig. 1). Since irradiance is highly variable and dependent on water turbidity, itself dependent on precipitation, the differences in these values have not been accorded any significance. All populations occurred predominantly (68-97 %) in quadrats with substrata composed of small particle sizes (sand-clay) and only a small proportion (3-32 %) on other types of substrata (gravel or bedrock) (Tab. 1, Fig. 1). Sandy-clayish substrata are composed of 60-70 % sand and 30-40 % clay-silt.

ANOVA revealed a significant difference ($F = 23.3$, $p < 0.001$) for percent cover among the five populations of the three species. The lowest value was observed in the population of *Nitella subglomerata* from site 1 and the highest in the population of *C. guairensis* from site 3 (Tab. 2). Highly significant differences ($F = 5.0$-84.1, $p < 0.01$) were obtained for all morphometric and reproductive variables. The highest values for vegetative characters were observed in the population of *C. guairensis* from site 3, whereas the lowest for most characters in the population of *Nitella* sp. (Tab. 2). Total number of globules and nucules were highly positively correlated ($r = 0.91$-0.99, $p < 0.001$) with mature globules and nucules. Thus, data refer only to total numbers. The highest and lowest number of nucules were found in the population of *N. subglomerata* from site 1 and of *C. guairensis* from site 3, respectively, whereas the highest and lowest number of globules were encountered in the population of *Nitella* sp. and of *C. guairensis* from site 3.

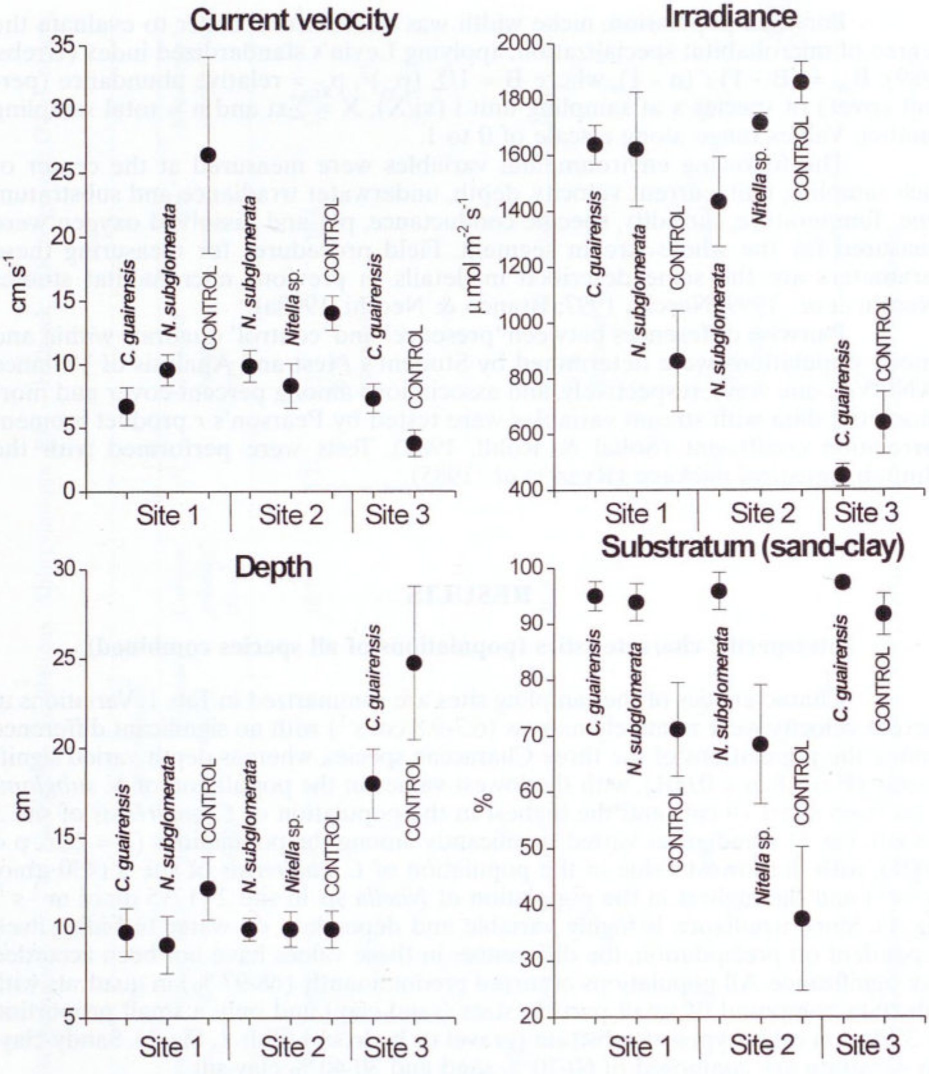

Fig. 1. Values of current velocity, depth, irradiance and dominant substratum values (mean ± 1 SD) for the Characeae populations within quadrats (presence and control) in the three sites studied. n = 12. Site numbers according to Tab. 1.

Some general trends in plant morphology and reproduction were observed (Tab. 5). Number of whorl branchlets was positively correlated with internode length in all populations, whereas this same variable was positively correlated with percent cover in three populations (*C. guairensis*, *N. subglomerata* and *Nitella* sp.). Plant length and axis diameter were positively correlated in three populations (*N. subglomerata* and *Nitella* sp.). Number of nucules were positively correlated with number of globules in all populations, whereas both were positively correlated with head diameter in all populations of *Nitella*, except for number of globules in one population of *N. subglomerata*. Plant length was significantly correlated with irradi-

Tab. 2. Characteristics (mean ± standard deviation) of Characeae populations. Site numbers according to Tab. 1.

	Chara guairensis		*Nitella subglomerata*		*Nitella sp.*
Variables	*Site 1*	*Site 3*	*Site 1*	*Site 2*	*Site 2*
Cover (%)[a]	32.5 ± 5.5	95.3 ± 2.2	28.9 ± 5.5	32.0 ± 5.8	53.0 ± 8.3
Plant length (cm)[b]	13.2 ± 5.3	41 ± 6.6	15.4 ± 4.9	12.5 ± 2.9	12.7 ± 3.4
Internode length (cm)[c]	2 ± 0.5	4.9 ± 0.5	2.9 ± 1	2.2 ± 0.6	1.9 ± 0.6
Branchlet length (cm)[c]	1.2 ± 0.3	3.6 ± 0.5	1.6 ± 0.4	1.9 ± 0.3	1.6 ± 0.3
Axis diameter (µm)[c]	692 ± 88	800 ± 38	568 ± 49	566 ± 71	406 ± 41
Nr whorl branchlets[c]	11.7 ± 0.6	14 ± 0.9	8.5 ± 0.7	8.6 ± 0.6	6.4 ± 0.3
Dactyl length (mm)[c]	–––	–––	2.5 ± 1.4	5.1 ± 1.4	2.0 ± 0.6
Subjacent branchlet length (mm)[c]	–––	–––	9.7 ± 3.9	10.1 ± 1.9	4.0 ± 0.8
Head diameter (mm)[c]	–––	–––	2.9 ± 0.4	3.5 ± 0.5	2.5 ± 0.4
Head peduncle length (mm)[c]	–––	–––	5.6 ± 2.7	8.6 ± 2.2	4.9 ± 1.7
Nr nucules[c]	3.2 ± 2.6	0.1 ± 0.1	15.3 ± 12	3.2 ± 4	8.7 ± 8.5
Nr globules[c]	2.2 ± 2.6	0.3 ± 0.3	6.4 ± 4.6	3.8 ± 3.8	13.4 ± 11
Ratio nucules/globules[c]	1.9 ± 1.7	0.4 ± 0.8	2.6 ± 1.6	0.6 ± 0.5	0.4 ± 0.3
Sampling units with sterile plants (%)[a]	25	30	8	10	23
Niche width (B_A)	0.60	0.99	0.89	0.74	0.76

[a] N = 12; [b] N = 60; [c] N = 180.

ance in three populations (Tab. 4): negatively in one population of *C. guairensis* and in *Nitella* sp. and positively in one population of *N. subglomerata*.

Niche width values (Tab. 2) were relatively high for the five populations of the three species, indicating a high degree of specialization to the microhabitat conditions prevailing in the stream segments sampled. Values also revealed considerable intraspecific variation between the two populations of *C. guairensis* and *N. subglomerata*. The proportion of sampling units with sterile plants (Tab. 2) was low in the populations of *N. subglomerata* but relatively high in those of *C. guairensis* and *Nitella* sp.

All populations occurred under microhabitat conditions of slow current velocities (Fig. 1). This was indicated by the significant differences of Student's *t* test (Tab. 3) found for current velocity in all populations between sampling units with presence of the alga and respective controls. Significant differences in *t* test were also observed for substrata composed of sand-clay in all populations, except for *C. guairensis* in site 3, where the predominant substrata in the controls was also of this same type.

Intra-specific characteristics (individual populations of each species)

In addition to the general trends commented above, a significant difference of Student's *t* test (Tab. 3) was found for irradiance in the population of *C. guairensis* from site 1 between sampling units with presence of the alga and controls. In this same site, the population occurred under similar conditions with the other species (*N. subglomerata*), since there were no significant differences among sampling units

Tab. 3. Significant values of Student's t test among environmental variables measured in sampling units with Characeae plants and respective controls. Site numbers according to Tab. 1. * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$ (N = 12). Abbreviations: BR = bedrock; SC = sand-clay. No significant value for depth.

	Chara guairensis		*N. subglomerata*		*Nitella sp.*
Variables	*Site 1*	*Site 3*	*Site 1*	*Site 2*	*Site 2*
Current velocity	6.50***	2.26*	5.13***	2.27*	2.62*
Dominant substratum	2.47*(SC)		2.05*(SC)	4.41***(SC) 2.50* (BR)	2.28*(SC)
Irradiance	3.65**			2.41*	

Tab. 4. Significant values of Pearson's r correlation coefficient among environmental variables and morphometric and reproductive characters for the Characeae populations. Site numbers according to Tab. 1. * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$ (N = 12). Abbreviation: SC = sand-clay.

		Chara guairensis		*N. subglomerata*		*Nitella sp.*
Variables	*Characters*	*Site 1*	*Site 3*	*Site 1*	*Site 2*	*Site 2*
Current velocity	nr nucules	0.60*				
	axis diameter			– 0.72*		
	internode length				0.60**	
	branchlet length				0.62**	
Depth	% cover	0.58*		– 0.94***		
	plant length	0.58*				
	nr nucules					– 0.53*
	nr globules					– 0.53*
Substratum (SC)	% cover		0.55*			
	axis diameter				– 0.76**	
	nr branchlets		0.69**			
Irradiance	plant length	– 0.73**			0.68**	– 0.53*
	internode length			– 0.83**		
	dactyl length			0.84**		

with these algae (Fig. 1). The population of *C. guairensis* from site 1 occurred under significantly higher irradiance ($t = 14.1$, $p < 0.001$) and lower depth ($t = 3.0$, $p < 0.01$) than the population from site 3 (Fig. 1). Among the vegetative characters, significantly higher values ($t = 3.8$-16.5 $p < 0.01$) were observed in the population from site 3 for plant, internode and branchlet length, axis diameter and number of whorl branchlets (Tab. 2). On the other hand, significantly higher values ($t = 3.3$-4.0 $p < 0.01$) were observed for reproductive characters in the population from site 1. Each population had a distinct pattern of association with the environmental variables and among the morphometric and reproductive characters (Tabs 4-5).

Tab. 5. Significant values of Pearson's *r* correlation coefficient among morphometric and reproductive characters and percent cover for the Characeae populations. Site numbers according to Tab. 1.* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$ (N = 12).

		Chara guairensis		*N. subglomerata*		*Nitella sp.*
Variables	*Characters*	*Site 1*	*Site 3*	*Site 1*	*Site 2*	*Site 2*
Plant length	% cover	0.82***				0.92***
	internode length	0.73*				0.73**
	nr branchlets	0.57*				
Axis diam.	internode length	0.80***			0.80**	
	branchlet length	0.92***				
	nr branchlets	0.75**				
	plant length			0.65*	0.69**	0.69**
Branchlet length	internode length	0.83***	0.69**	0.73*	0.80**	0.75**
	nr branchlets	0.74**	0.57*			
	% cover		0.59*	0.66*		0.57*
Nr globules	nr nucules	0.85***	0.53*	0.86**	0.90***	0.95***
	axis diameter			– 0.68*		
	head diameter				0.84***	0.73**
	plant length					0.57*
Nr nucules	plant length			– 0.71*		
	axis diameter			– 0.68*		
	head diameter			0.60*	0.72***	0.65*
	internode length		– 0.67**			

Significant differences of Student's *t* test (Tab. 3) were found for irradiance and substratum (bedrock) in the population of *N. subglomerata* from site 2 between sampling units with presence of the alga and controls. In this site, the population occurred under conditions similar with the other species (*Nitella* sp.) for all variables, except for significantly higher ($t = 2.5$, $p < 0.05$) occurrence on substratum composed of sand-clay in this species (Fig. 1). The populations of *N. subglomerata* occurred under similar conditions in both sites (Fig. 1), with no significant difference among them. Among the vegetative characters, both populations had similar values, except a significantly higher dactyl length ($t = 4.1$, $p < 0.001$) in the population from site 2 (Tab. 2). For reproductive characters, a significantly higher number of nucules ($t = 2.9$, $p < 0.05$) was observed in the population from site 1 and, as a consequence, the ratio of nucules/globules was also much higher in this population. Each population had a distinct pattern of association with the environmental variables and among the morphometric and reproductive characters (Tabs. 4-5). Higher production of gametangia was associated with shorter and thinner plants in population from site 1 and with larger heads in the other population (Tab. 5).

DISCUSSION

Variations in physical variables revealed some general trends of microhabitat distribution for the Characeae populations studied, with occurrence under the following conditions: 1) slow and narrow current velocities; 2) substrata predominantly composed of small particle size (sand-clay) ; 3) variable and generally low depths. French & Chambers (1996) reported the occurrence of *Chara* spp. under similar microhabitat conditions in segments of a large river: higher biomass (74-100 %) associated with lower current velocities (0-40 cm s^{-1}), shallower depths (0.1-1.5 m) and smaller sediment grain sizes (silt and sand). Caffrey & King (1989) reported three Characeae species to be tolerant to a wider range of flow conditions, from slow to moderate current velocities (12-53 cm s^{-1}). They argued that characean species are generally regarded as early colonizers, and it appears that they can colonize slow-flowing sites, which are later replaced by a phanerogam flora (with more robust and light-occluding, rooted plants) by competitive exclusion. Characean can secondarily affect their habitat characteristics (Caffrey & King, 1989; Hussain *et al.*, 1996), and not only being affected by them, such as an increase in sedimentation rates near or within the beds (especially in large ones), due to a decrease in current velocity and turbulence caused by their presence.

Substratum particle size can influence plant attachment by means of rhizoid development. Laboratory studies by Andrews *et al.* (1984a) showed that the extent of rhizoid development in *Chara hispida* was greatly dependent on grain size, with small particle sizes (sand) favoring plant growth. Irradiance can be the primary factor controlling lower depth limit of characean colonization in lakes (Andrews *et al.*, 1984a). They tend to occur under a considerably narrower range of depths in lotic habitats, ranging from few centimeters to a few meters (Caffrey & King, 1989; Casanova, 1994; French & Chambers, 1996; Hussain *et al.*, 1996), than in ponds and lakes, where they normally occur in depths up to 14-16 meters (Andrews *et al.*, 1984a). Hussain *et al.* (1996) described a luxuriant growth of *Chara zeylanica* in deeper waters (90-105 cm) and soft-sediment (sand) in an irrigation canal, whereas Caffrey & King (1989) found that the optimum depth for Characeae growth was 40 cm.

In terms of morphological adaptations, we found some general patterns (observed in at least three out of five populations): plants with longer whorl branchlets also had longer internodes in all populations studied, whereas longer plants had also thicker axis. The former were generally associated with higher biomass (percent cover). Few correlations of morphological characters were observed with environmental variables (e.g. plant length with irradiance: negative in two populations and positive in one population). The positive correlations of globules and nucules observed in all populations suggest synchrony in production and maturation of female and male gametangia, although this approach is exclusively spatial. In one population of *N. subglomerata* there was a negative correlation of gametangia number with plant length and axis diameter. This suggests resource allocation for reproduction in this species. Resource allocation was reported by Casanova (1994) in *N. sonderi* and was associated with water level variations. Wood & Imahori (1965) also reported that shallow-water forms tended to be heavily fertile.

Despite the general patterns of occurrence mentioned above, our results also indicated some intraspecific variations in microhabitat characteristics, i.e. each population differed in its responses to environmental variables and had particular morphological and reproductive adaptations. Casanova (1994) showed that characean species are not uniform in their adaptations to variations in environmental conditions, such as seasonal changes and water level fluctuations. In one population of *C. guairensis* higher biomass (in terms of percent cover) and longer plants were found under higher depths, corroborating the findings of Casanova (1994) that positive growth rates (including plant elongation) were recorded in response to depth increases. This is also expected according to Wood & Imahori (1965), who observed that deep-water forms tended to have elongate branchlets. On the other hand, this pattern was not observed in the other population of this same species. In addition, for one population of *N. subglomerata* an opposite trend was found, *i.e.* a negative correlation of percent cover with depth.

A comparison with other macroalgae from lotic habitats in similar studies (Necchi 1997; Branco & Necchi, 1998a; Necchi *et al.*, 1999) revealed that the Characean populations occurred under a narrower range of microhabitat conditions. Populations of Characeae occurred under lower current velocities ($\overline{x}$ = 6.7-9.8 for Characeae *vs* 12-132 cm s^{-1} for other macroalgae) and on distinct types of substrata, (small-sized particles, sand-clay or rocky substrata, bedrock or boulders) in comparison with those algae. In addition, populations of *Batrachospermum delicatulum* (Rhodophyta) tolerate wider variations in depth (5-23 cm) and higher irradiances (970-1820 mmol m^{-2} s^{-1}) (Necchi, 1997) than Characeae populations in this study (depth 9-18 cm and irradiance 450-1715 mmol m^{-2} s^{-1}). Populations of *Chaetophora elegans* and *Stigeoclonium helveticum* (Chlorophyta) were reported (Branco & Necchi, 1998a) under high irradiances (1100-1950 mmol m^{-2} s^{-1}) and variable depths (6-21 cm). *Compsopogon coeruleus* (Rhodophyta) was found under comparatively lower irradiances (400-900 mmol m^{-2} s^{-1}) and higher depths (20-25 cm) (Necchi *et al.*, 1999).

Niche width values of the Characeae populations studied indicate a high degree of habitat specialization, which corroborate the statement above. The values (0.60-0.99) are among the highest yet found in lotic macroalgae: *Batrachospermum macrosporum* (0.74), *B. delicatulum* (0.44-0.64) and '*Chantransia*' stage of *Batrachospermum* spp. (0.19-0.62) (calculated from data presented by Necchi, 1997); *C. elegans* (0.44-0.52) and *S. helveticum* (0.65-0.84) (Necchi & Branco, 1998a); *C. coeruleus* (0.70-0.83, Necchi *et al.*, 1999). French & Chambers (1996) reported that *Chara* spp. can have high niche overlaps (69-91 %) for variables such as current velocity, depth and sediment grain size with some macrophytes (e.g. *Callitriche hermaphroditica* and *Potamogeton gramineus*) but are differently distributed in relation to other species or some of these variables.

The relatively narrow variations in microhabitat conditions and high niche widths here reported for Characean populations, suggest high microhabitat specialization and, therefore, a lower tolerance to variations in current velocity, depth, irradiance and substratum type. These characteristics probably explain the relatively restricted distribution of Characeae species in streams of São Paulo State (Necchi *et al.*, 2000), with low frequency of records in all regions (0-9 %). The only exception was the northwest region, where conditions here reported as favorable to colonization by Characeae occurred more frequently: 32 % of sites with predominantly sandy-clayish substrata and 23 % with low to moderate current velocities (< 20 cm s^{-1}).

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