Biodiversity and Conservation **14:** 1699–1718, 2005.
DOI 10.1007/s10531-004-0694-z

Primary producers in a Pampean stream: temporal variation and structuring role

ADONIS GIORGI[1,2,*], CLAUDIA FEIJOÓ[1] and GUILLERMO TELL[2,3,*]
*[1]Program de Investigación en Ecología Acuática, Departamento de Ciencias Básicas, Universidad Nacional de Luján, C.C. 221, 6700 Luján, Argentina; [2]CONICET; [3]Lab. Limnología, Facultad de Ciencias Exactas y Naturales (UBA), 1428 Buenos Aires, Argentina; *Author for correspondence (e-mails: adonis@coopenetlujan.com.ar; tell@bg.fcen.uba.ar; phone: +54-2323-423979; fax: +54-2323-425795*

Received 20 May 2003; accepted in revised form 9 February 2004

Key words: Current velocity, Herbivores, Macrophytes, Phytobenthos, Streams

Abstract. Low current velocities, high nutrient levels, the lack of riparian forest vegetation, and the development of dense and rich macrophyte communities characterize Pampean streams. The objective of this study was to describe the main physical, chemical, and biological characteristics of a headwater Pampean stream as well as to analyze the role of macrophytes and phytobenthos. The study was conducted in a stream considered to be not much disturbed by human activities. Samples of water and organisms (macrophytes, benthic algae and invertebrates) were taken monthly for 14 months in two sampling stations, in fast flow and slow flow sites. Macrophyte biomass and diversity increased in spring and summer, and they decreased in autumn, when the plant community was greatly affected by an important flood. Phytobenthos biomass was lower in late summer, possibly due to the establishment of a dense cover of the floating macrophyte *Lemna gibba* L. Density of amphipods and gastropods greatly increases in spring and summer, jointly with the macrophyte development. Analysis of correlation showed that current velocity is the most important factor influencing macrophyte biomass and phytobenthos structure, while depth, nutrients, and herbivores are linked factors. Pampean streams could be considered systems dynamically fragile, because habitat heterogeneity is generated by aquatic vegetation, a substratum that varies along time.

Introduction

In the last 20 years, the research on stream ecosystems has been greatly influenced by the theory of the River Continuum Concept (RCC) (Vannote et al. 1980), which have been developed mainly from studies conducted in forest streams in North America. This theory proposes that rivers show a longitudinal gradient, originated by changes in morphology and hydrology from headwaters to mouth. According to Vannote et al. (1980), headwater streams (orders 1–3):

'are strongly influenced by riparian forest vegetation which reduces autotrophic production by shading and contributes large amounts of allochthonous detritus'. In medium size streams (orders 4–6), 'the reduced importance of terrestrial organic input coincides with enhanced significance of autochthonous primary production and organic transport from upstream.'

Some authors have studied river systems that show different characteristics than those of temperate rivers; for example, subtropical rivers with warmer water temperatures, low gradient, and extensive floodplains (Meyer and Edwards 1990), or Mediterranean rivers that are more exposed to seasonal changes than temperate rivers (Guasch and Sabater 1994). Some types of rivers are primarily open in their upper reaches due to the lack of forest riparian vegetation, as prairie rivers (Wiley et al. 1990), streams in arid regions subjected to great floods (Fisher and Grimm 1988; Suárez and Vidal Abarca 2000), and lowland streams where macrophyte communities are well developed (Sand-Jensen et al. 1988; Young and Huryn 1996). Studies on non-temperate rivers have contributed to the redefinition of the RCC (Minshall et al. 1985); so, the description of streams of different environments could be useful to clarify the applicability of the RCC in a broader range of ecosystems.

Pampean streams have features that make them similar to the prairie streams described by Wiley et al. (1990), even though they have their own peculiarities. These streams are characterized by the lack of riparian forest vegetation, low current velocities, high nutrient levels occurring naturally in the water, the absence of dry periods or extreme temperatures, and the development of dense and rich macrophyte communities.

Even though these systems are different to many streams of the world, little information exists on the ecological characteristics of the Pampean streams (Claps 1991, 1996; Solari and Claps 1996; Feijoó et al. 1999). Particularly, Giorgi et al. (1998) pointed out the importance of the periphyton community in these systems. Moreover, the relative importance of other primary producers on the structure and function of stream communities was not investigated. The objective of this study was to describe the main physical, chemical, and biological characteristics of a headwater Pampean stream and to analyze the role of macrophytes and phytobenthos in this type of system. The study was conducted in Las Flores stream, which is considered to be not much disturbed by human activities (Feijoó et al. 1999).

Study area

Pampean streams run through the 'Pampa' – a vast grassy plain that covers central Argentina. The climate is temperate humid with mean annual precipitation between 600 and 1200 mm, and a mean annual temperature of 16 °C. Even though precipitation is distributed all along the year, maximum rainfall generally occurs in spring and autumn. Streams cross fertile soils formed by loess deposition during the Quaternary, characterized by large contents of clay in the B horizon and of organic matter in the upper layers, structural stability, and a high cation exchange capacity (Papadakis 1980). The natural vegetation in the region is grassland, with annual grasses being adapted to the occurrence of fires in summer and frosts in winter. Natural perennial plants are absent except for two species of trees (*Celtis tala* Gill. ex Planch and *Salix* *humboldtiana* Willd.) that develop isolated in areas with particular soil conditions. Small and occasional forested areas are comprised by introduced species.

Most Pampean streams usually originate in small depressions with emergent plants as *Juncus* or *Typha latifolia* L., which can also be found in their midcourses. These streams are fed by precipitation and groundwater, and they show slow water flow due to the gentle slope of the Pampean region. Streambeds are formed by hard and homogeneous substrata with fine sediments (primarily silt and clay), high content of calcium carbonate, and a total absence of stones or pebbles. Because of the lack of riparian forest vegetation, solar irradiation easily reaches the streambed allowing the development of dense plant communities. Vascular macrophytes establish themselves directly on the bottom, while algae grow over macrophytes (periphyton) or on the bottom (phytobenthos). Macrophyte architecture increases habitat heterogeneity and variation in the rather homogeneous substratum, and allows the development of a rich community of consumers that live associated to the plants.

Materials and methods

This study was carried out in Las Flores stream, which is considered to be representative of many Pampean streams. It is a second-order stream located in the Luján river basin (NE of Buenos Aires province).

Samples of water and organisms (macrophytes, benthic algae and invertebrates) were taken monthly for 14 months in two sampling stations (S1 and S2) located 2 km of each other (Figure 1). At each sampling station, separation between fast flow (FF) and slow flow (SF) sites was made. Slow flow sites were wide and deep areas (25–80 cm depth) with current velocities lower than 20 cm/sec, while fast flow sites were narrow and shallow areas (10–30 cm depth) with higher velocities (40–60 cm/sec).

Samples were collected from a metallic bridge with foldable sections to not disturb the bottom sediments and the macrophyte community. So, the conditions at the sample site underwent minimum modifications, which enabled monitoring to be carried out throughout the year.

Transparency, depth, current velocity, flow, water temperature, pH, and conductivity were recorded at each sampling site. Flow was estimated by the velocity-area method (Gordon et al. 1992). Concentrations of total dissolved solids (TDS), alkalinity, soluble reactive phosphorus (SRP), ammonia, nitrites, nitrates, dissolved oxygen, calcium, magnesium, silica, suspended particulate material (SPM), and particulate organic matter (POM) were determined according to APHA (1992) and Wetzel and Likens (1991). Loads of TDS, SPM and POM were also estimated considering the discharge in each sampling occasion.

Random samples of the macrophyte and phytobenthos communities were taken by triplicate at the different sites. The macrophyte community was

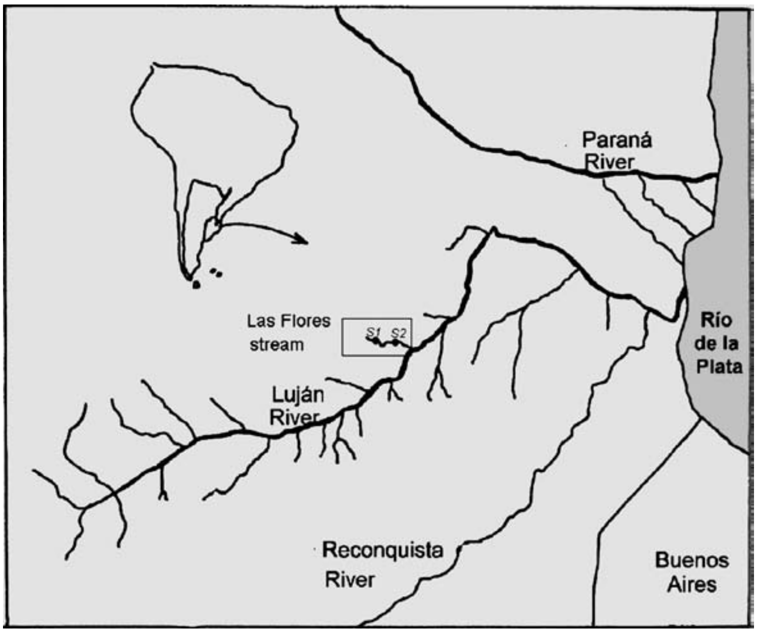

Figure 1. Map with the location of the Las Flores stream and the sampling sites.

sampled using a 25 × 25-cm quadrate, and the associated fauna was removed from the samples by sieves of different mesh sizes. Biomass of the different macrophyte species was determined drying the sample to 105 °C until constant weight (Wetzel and Likens 1991; APHA 1992), and these data were used to estimate richness, diversity and evenness of the plant community.

Phytobenthos samples were taken with a 4-cm diameter core and the samples were used to determine chlorophyll-*a* and phaeopigments, as well as for qualitative and quantitative analysis (Wetzel and Likens 1991). A Nikon Optiphot microscope with an underwater lens and phase contrast was used to identify algae. Algal density was subsequently calculated, together with species richness, evenness and diversity (Shannon index; Margalef 1983).

A multiple correlation analysis was carried out to assess the relations between different environmental variables and macrophytes, phytobenthos, and invertebrate fauna. Variables that did not conform to the assumption of normality were transformed to logarithms. The variable alkaline reserve could be not normalized; so, it was discarded from the statistical analyses.

Results

Las Flores stream can be characterized by having water with high conductivity and nutrient concentrations. However, most physical and chemical variables show a large range of variation due to the occurrence of a great flood in April 1993 and to seasonal changes in flow (Table 1).

Similar variations in flow, concentrations and loads of the transported material occurred at both sampling stations throughout the year, except for nitrite and ammonium concentrations that were higher at S2 ($p < 0.05$ and $p < 0.01$, respectively). Fast flow sites (S1FF and S2FF) differed significantly ($p < 0.01$) from slow flow sites in water velocity and depth.

After the flood, which was produced by an exceptional 240-mm rainfall within a single day, loads of the transported material increased significantly in both stations ($p < 0.01$) except for nitrogen load that showed no significant change (Table 2). This flood can be considered a catastrophic event as such a heavy rainfall occurs once in about every 75 years (Goldberg et al. 1995). The results shown in Table 2 for S1 correspond to the day after the flood, while for S2, data were taken 2 days after the flood because of the inaccessibility to this station after the event. Thus, these data are only indicative.

Table 1. General characteristics of physical and chemical variables measured at the sampling sites ($n = 336$).

Variables	Mean	Median	Minimum	Maximum
Water velocity (cm/s)	20.1	13.50	0.0	101.0
Dissolved oxygen (mg/l)	8.1	7.53	3.5	16.0
SRP (mgP-PO_4^-/l)	0.77	0.65	0.1	2.1
Nitrates (mg N-NO_3^-/l)	4.14	3.98	0.06	8.5
Ammonia (mg N-NH_4^+/l)	0.03	0.01	0.0	0.02
Silicate (mg Si-SiO_3^-/l)	0.64	0.65	0.12	2.58
pH	7.9	7.82	6.6	9
Calcium (mg/l)	23.4	22.8	11.20	40
Magnesium (mg/l)	18.9	18.5	4.86	34
Alkaline reserve (mg CO_3^-/l)	0.1	0.06	0.0	0.5
Alkalinity (mg CO_3^-/l)	0.5	0.42	0.18	1.0
Conductivity (μS/cm)	1067	1409	102	1458

Table 2. Mean values of flow and loads of particulate and dissolved substances in both sampling stations in Las Flores stream (samples taken during the flood of April 1993 are excluded and they are indicated separately).

			Flood	
	S1	S2	S1	S2
Flow (l/s)	40.64 (27.46)	79.60 (46.77)	491.89	240.15
TDS (mg/s)	0.69 (0.20)	0.70 (0.22)	0.42	0.20
SPM (mg/s)	637.3 (1022.0)	637.0 (570.7)	27378.0	6437.3
POM (mg/s)	63.67 (69)	97.98 (79.26)	1340.35	558.39
SRP (mg/s)	32.26 (25.71)	48.17 (35.68)	228.51	105.05
DIN (mg/s)	173.0 (154.7)	345.2 (342.3)	375.02	685.44

Values between brackets are standard deviations. DIN: Dissolved inorganic nitrogen ($NO_3 + NO_2 + NH_4$).

Submerged and floating macrophytes developed both in slow and fast flow sites and increased their biomasses in spring and summer. The April flood affected the macrophyte stands, especially in S2, where plant biomass was greatly reduced after the flood event. In S1, submerged macrophyte biomass was significantly higher in the slow flow site (S1SF) ($p < 0.01$). On the other hand, there were not significant differences between the macrophyte biomass of the other places although the macrophyte biomass showed more similar values in the fast flow zones than in the slow flow zones (Figure 2). Species richness increased in spring and summer, and it attained significantly higher values in S1SF than in S2SF while there were not significant differences between fast flow sites (Figure 3). Even though the same macrophyte species appeared at the different sites, the relative dominance of a given macrophyte species changed among sites producing a different community structure (Figure 2 and Table 3). At S1FF, the macrophytic stand was dominated by emergent plants, while submerged species like *Egeria densa* Planch. and *Ceratophyllum demersum* L. were dominant at the other sites. The floating macrophyte *Lemna gibba* L. appeared in the stream in summer, and rapidly developed high biomass, forming dense stands that completely covered the stream surface. This species decreased its biomass or disappeared from the sampling sites in autumn, with lower temperatures and/or higher water flow. In summer, the biomass of the submerged macrophyte vegetation in both stations seems to be affected by the presence of *L. gibba*, in spite of its low biomass in relation to submerged macrophytes. This influence is less important in S2 due to the late development of this species. The aquatic plant community was also affected by the flood of April, maintaining low biomass in autumn.

The phytobenthos community was dominated by diatoms, which were found in both types of environments (fast and slow flow sites), with similar composition but different relative abundance. *Gomphonema*, *Achnanthes*, *Cocconeis*, *Cymbella*, *Rhoicosphenia*, *Fragillaria*, *Navicula*, *Pinnularia*, and *Melosira* were the most common genera. Two green algae (*Cladophora* sp. and *Spirogyra* sp.) became extremely abundant in some periods of the year. *Cladophora glomerata* (L.) Kütz formed extensive mats in the fast flow sites from late winter to late summer (August–March). These mats were progressively colonized by epiphytic diatoms (*Gomphonema angustatum* (Kütz) Rabh., *Roicosphenia curvata* (Kütz) Grun, and *Synedra ulna* (Nitz.) Ehr. in spring (October–November) and by *Melosira varians* C.A. Ag. in summer (December–February). An explosive growth of *Spyrogira* sp. occurred in the slow flow sites between late winter and early spring (August–October). This green algae was only established in sites of fast flow during periods of very low flow.

Phytobenthos biomass estimated as mg chl-*a*/m^2 did not present significant differences among sampling stations or sites, showing lower values during late summer (February and March) (Figure 4). Phytobenthos species richness was generally higher in slow flow than in fast flow sites but these differences were not always statistically significant (Figure 5).

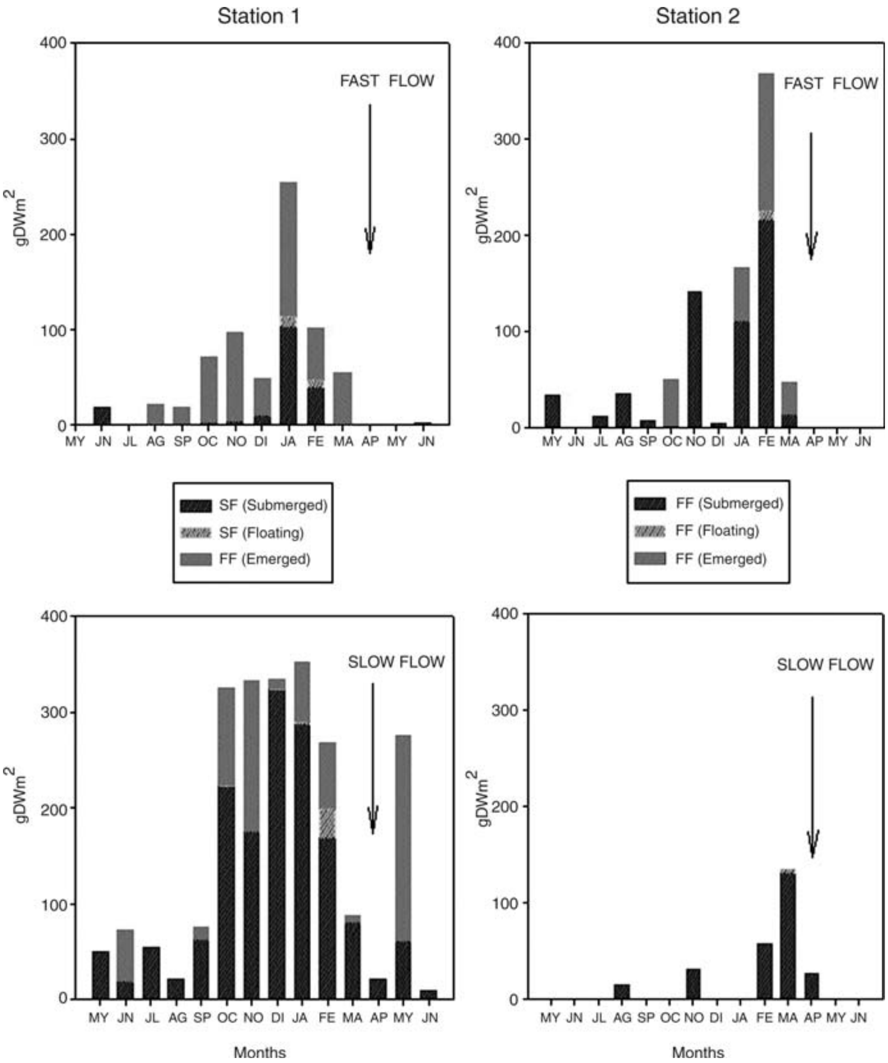

Figure 2. Macrophyte biomass (g DW/m^2) in both sampling stations at Las Flores stream. The arrow indicates the exceptional 240-mm rainfall.

Macrophytes provided refuge to both amphipods and gastropods, which stood out as the most important macroinvertebrates in terms of numbers and biomass, and acted as herbivorous on the phytobenthos, also as detritivorous. These invertebrates increased their numbers jointly with the macrophyte development in spring and summer, reaching densities of 30,000 individuals/m^2 (Figure 6). This is reflected by the positive correlation between submerged macrophyte biomass and the abundance of amphipods ($r = 0.72$; $p < 0.01$)

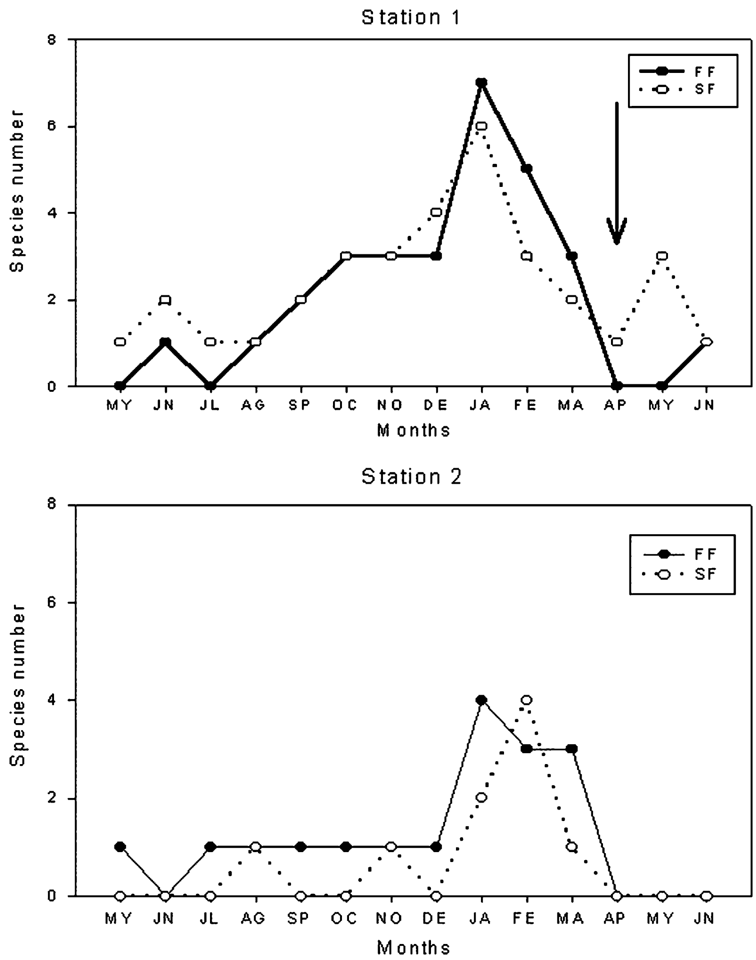

Figure 3. Macrophyte richness in both sampling stations at Las Flores stream. The arrow indicates the exceptional 240-mm rainfall.

and gastropods ($r = 0.62$; $p < 0.01$). Amphipods and gastropods numbers at S1F1 station with the higher biomass of submerged macrophytes, differed significantly from the other stations.

Multiple correlation analysis (Table 4) showed that current velocity had negative relationships with phytobenthos species richness, diversity and density, and positive relations with phytobenthos biomass and evenness. Current velocity was negatively associated to macrophyte biomass and macroinvertebrate abundance (amphipods: $r = -0.57$, $p < 0.01$; gastropods: $r = -0.43$, $p < 0.05$), and macrophyte richness had a positive correlation with water temperature and nutrient levels (SRP and silicates). The presence of herbivores associated with macrophytes seemed to favor the increase of phytobenthos

Table 3. Dominant and accompanying macrophyte species registered in the different sampling sites at Las Flores stream.

Site	Dominant species	Accompanying species
SIFF	*Ludwigia* sp. *Rorippa nasturtium-aquaticum* (L.) Hayek	*Hydrocotyle ranunculoides* L. *Egeria densa* Planch. *Ceratophyllum demersum* L. *Lemna gibba* L.
SIFF	*E. densa*	*Ludwigia* sp. *R. nasturtium-aquaticum* *L. gibba*
S2FF	*C. demersum*	*Ludwigia* sp. *R. nasturtium-aquaticum* *H. ranunculoides* *E. densa* *L. gibba*
S2SF	*E. densa*	*Ludwigia* sp. *R. nasturtium-aquaticum* *L. gibba*

diversity and density, while the abundance of the floating macrophyte *L. gibba* showed a negative relationship with phytobenthos biomass.

Discussion

Submerged macrophytes in Las Flores stream formed dense communities, and plant biomass estimated in this study reached higher values than those reported in other streams elsewhere. On the other hand, phytobenthos biomass was lower in relation to the values cited for other unforested streams (Table 5), possibly due to the competence for light and nutrients with macrophytes (Sand-Jensen et al. 1989b).

Physical and biological factors are undoubtedly associated in Las Flores stream because low water velocity, jointly with the lack of riparian forests and the occurrence of high nutrient levels in water, favor the establishment of dense stands of macrophytes in the stream. The complex architecture of submerged macrophytes like *E. densa* increases the heterogeneity of flow velocity, creating new microhabitats that can be occupied by invertebrate species (Champion and Tanner 2000). For example, it has been reported that invertebrates diversity increases within plant beds, where they can find food and refuge against predation (Suren 1991; Diehl and Kornijów 1998; Dodds and Biggs 2002).

Both macrophytes and sediments reduce the amount of light that reaches the streambed. Nevertheless, macrophytes are considered to be a more important light interference factor for phytobenthos (Giorgi and Malacalza 1994). Macrophytes are present in the stream for a long period of time, while turbidity only increases for periods up to 48 h following storms (Table 6). Moreover, the

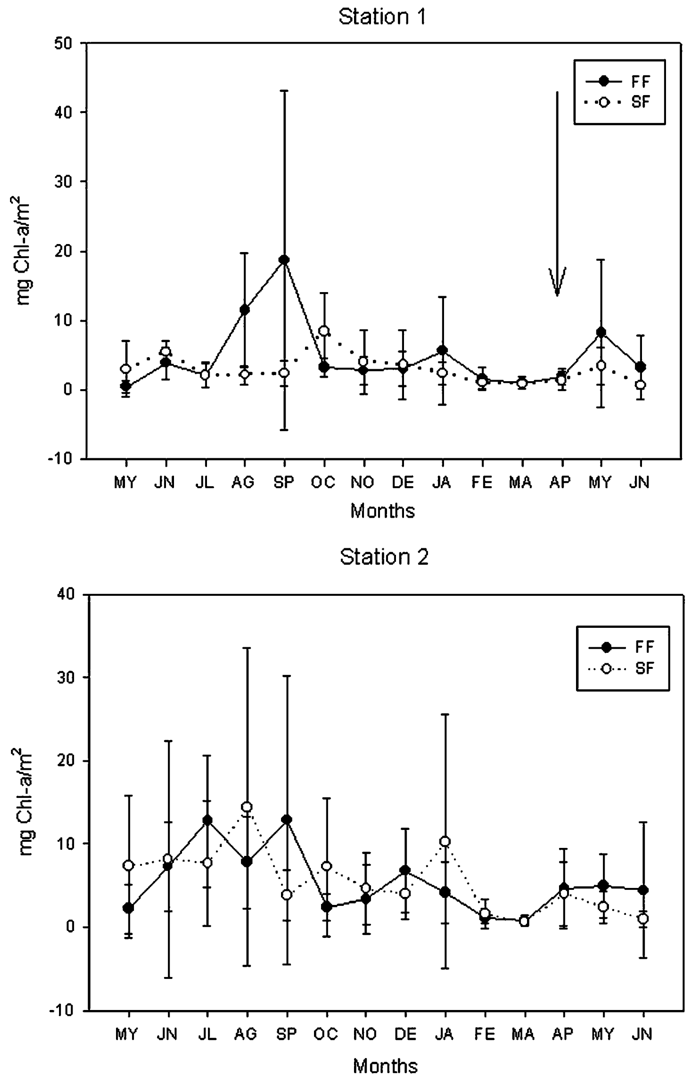

Figure 4. Phytobenthos biomass (mg chl-*a*/m^2) in both sampling stations in Las Flores stream. The arrow indicates the exceptional 240-mm rainfall.

influence of macrophytes is different according to their functional type. Floating plants reduce light penetration more than submerged plants, reaching reduction values of 99.9% in the case of an extensive covering of *L. gibba*. However, their effect is restricted to summer, while *E. densa* forms dense stands during spring and summer. Sand-Jensen et al. (1989b) observed a decrease in the abundance of the epiphytic cover associated with the reduced light availability produced by the increase of macrophyte biomass in summer. In Las

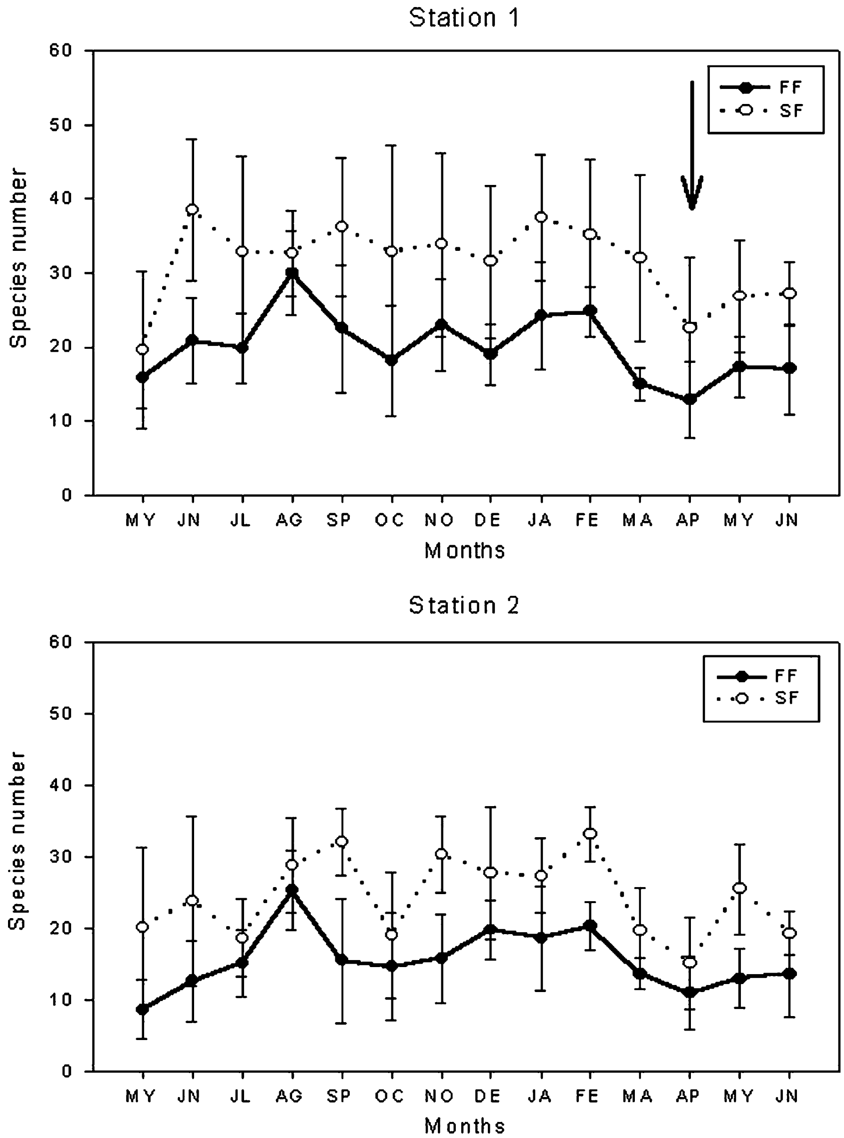

Figure 5. Phytobenthos species richness in both sampling stations in Las Flores stream. The arrow indicates the exceptional 240-mm rainfall.

Flores stream, floating macrophytes, as the observed negative relationship between the biomasses of *L. gibba* and phytobenthos shows, will have this effect. The reduction of underwater light levels can also produce changes in the physiognomy and taxonomic composition, modifying the algal community structure (Steinman and McIntire 1987). The presence of *L. gibba* seems to

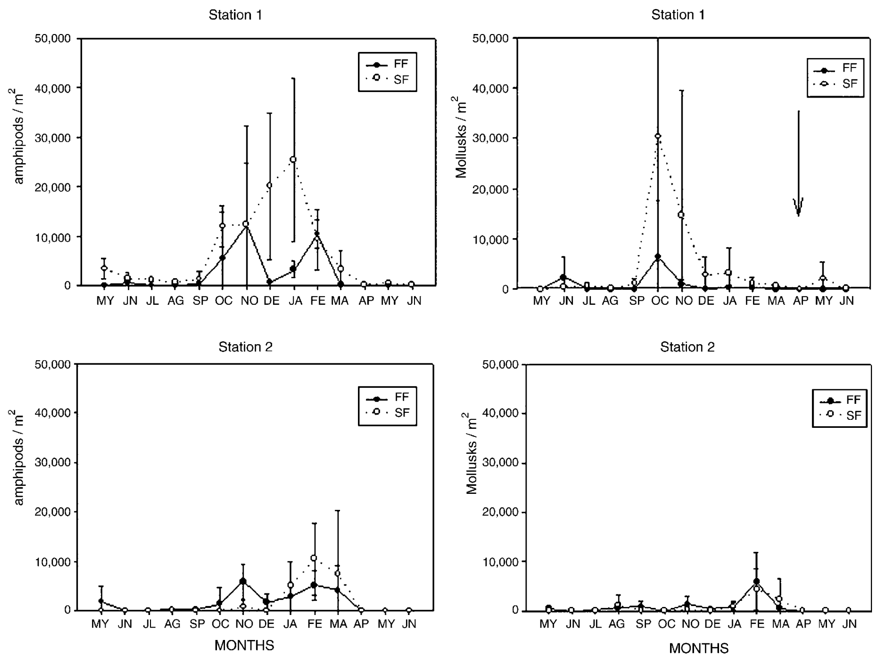

Figure 6. Abundance of amphipods and gastropods (individuals/m^2) in both sampling stations in Las Flores stream. The arrow indicates the exceptional 240-mm rainfall.

affect the development of the submerged macrophyte vegetation during summer as well. Indeed, the development of a dense cover of floating plants not only prevents the light penetration in the water but also affects the oxygen exchange between air and water, negatively affecting algal development as suggested by Bowker and Denny (1980).

In Las Flores stream, there is no marked seasonal response by the phytobenthos, because adequate growth conditions exist nearly all year long, and variations in algal biomass are mainly due to the effect of the above-mentioned factors. Diatoms dominated the phytobenthos community, even though at the end of winter and beginning of spring there were blooms of *C. glomerata* in the fast flow zones and of *Spyrogyra* sp. in the slow flow zones. Cushing et al. (1983) have shown that a community with a clear predominance of diatoms is indicative of intensive exploitation by grazing herbivores. In Las Flores stream, there are gastropods that could control species composition, but the scarcity of other algal groups could also be explained in terms of species competition for nutrients. Even though nutrient levels are high, ammonium concentration is low due to good oxygenation of stream water. According to Hillebrand (1983), the increase of ammonium concentrations produces blooms of *Cladophora* sp. and *Spyrogyra* sp. because they have a competitive advantage over other genera by the fast absorption of this ion (Dodds 1991) and their resistance to

Table 4. Significant Spearman coefficients of multiple correlation analysis among the environmental variables and macrophyte (Macro.) and phytobenthos (Phyto.) structural parameters.

	Phyto. richness	Phyto. diversity	Phyto. density	Phyto. eveness	Phyto. biomass	Macro. richness	Macro. diversity	Macro. eveness.	Macro. biomass
Current velocity	−0.50** (n = 94)	−0.29** (n = 94)	−0.49** (n = 94)	0.36** (n = 94)	0.28** (n = 94)				− 0,47* (n = 28)
Temperature	0.25** (n = 112)	0.26** (n = 112)				0.45** (n = 76)			
Depth			0.21* (n = 112)	−0.42** (n = 111)			−0.53** (n = 42)	− 0.43* (n = 28)	
Oxygen						− 0.27* (n = 76)	− 0.33* (n = 42)		
SRP	0.32** (n = 112)	0.32** (n = 112)	0.28** (n = 112)			0.49** (n = 76)			
Ammonia								0.51** (n = 27)	
Silicate	0.22* (n = 112)	0.32** (n = 112)	0.22* (n = 112)			0.43** (n = 76)		0.41* (n = 28)	
pH				− 0.24* (n = 112)					
Amphipods		0.33* (n = 39)							0.72** (n = 39)
Gastropods	0.34* (n = 37)	0.36* (n = 37)	0.32* (n = 37)						0.61** (n = 37)
Calcium		0.21* (n = 107)				0.30* (n = 73)			
Alkaline reserve					0.25* (n = 105)	− 0.28* (n = 74)			
Conductivity	0.22* (n = 112)	0.23* (n = 112)	0.26* (n = 112)						
SPM								− 0.41* (n = 28)	
L. gibba biomass					− 0.67* (n = 11)				

*: $p < 0.05$; **: $p < 0.01$

Table 5. Biomass of submerged macrophytes and phytobenthos in different streams of the world.

Stream	Phytobenthos (mg Chl- *a*/m^2)	Macrophyte biomass (g DW/m^2) and dominant species	Type of stream	Reference
River Sussá (Denmark)	40–80	100 *Potamogeton* sp.	Temperate/Cold Lowland	Prahl et al. 1991
Salmon River (USA)	1–144	–	Temperate/Cold Mountain Open forest	Cushing et al. 1983
Kakanui River (New Zealand)	10–18	–	Temperate Mountain Grassland	Biggs et al. 1998
La Solana stream (Spain)	42–78	–	Mediterranean Mountain Forested	Guasch et al. 1995
Bere stream (England)	50–271	*Rorippa* sp and *Ranunculus* sp. (5% of the streambed)	Temperate/Cold Lowland	Marker 1976
Riera Major (Spain)	16–77 (with forest) 16–834 (without forest)	–	Mediterranean Mountain	Sabater et al. 1998
Whakapiki stream (New Zealand)	–	36–324 *E. densa* and other species	Temperate Lowland Grassland	Champion and Tanner 2000
River Sussá	0–30	0–256 *Potamogeton pectinatus* and other species	Temperate/Cold Lowland	Sand-Jensen et al. 1989a
Badfish Creek (USA)	—	20–712 *Potamogeton* and other species.	Temperate Mountain	Madsen and Adams 1988
Las Flores stream (Argentina)	0–30	0–800 *E. densa*, *C. demersum* and other species.	Temperate Lowland Grassland	This study

Table 6. Percentage of the incidental light reaching different water depths with aquatic vegetation or sediments (from Giorgi 1998).

Water			Summer vegetation		
Depth	Before storm	After storm	*L. gibba*	*E. debsa*	*H. ranunculoides*
0	100	100	100	100	100
5			0.11		15
10	44	40	0.09	1	12
20	34	29	0.04	1	7
30	22	18	0.02	1	7
40	19	13	0.01	1	7

grazing (Dodds and Gudder 1992). Nevertheless, the abundance of these algae declines jointly with the reduction of ammonium concentration, as the biomass of floating and submerged macrophytes increases. Macrophytes may possibly be even more efficient in absorbing nutrients from the water than algae and both floating and submerged macrophytes would displace the Chlorophyceae by competition for both nutrients and light.

As Giorgi and Tiraboschi (1999) observed experimentally, amphipods and gastropods can have a very important effect on phytobenthos biomass in certain periods. However, this effect is not lineal: high herbivores densities decrease algal biomass whereas intermediate densities contribute to accelerate algal growth rate by the release of soluble nutrients to the water. A positive relationship was observed in this study between algal diversity and herbivores density, possibly because grazing produces an intermediate disturbance on the algal community (Connell and Slatyer 1977; Wetzel 1983; McCormick 1994).

Data on periphyton biomass is not presented here because it was previously studied by Giorgi et al. (1998). They reported that this community could reach high values of chlorophyll-*a* at the end of winter (36.31 mg/g DW of *E. densa)*. Macrophyte stands also support a dense community of invertebrates (Casset et al. 2001) that serves as a food source for other macroinvertebrates and fishes (mainly siluriforms, loricariforms and poeciliforms). The abundance of macrophytes favors the presence of large mollusks such as *Pomacea* sp. and *Anodontites* sp. and of small aquatic snakes. An abundant fauna of birds, especially herons of diverse species, and the indigenous rodent *Myocastor coypus* (coypu) complete the trophic web (Figure 7). It seems plausible that the primary production of the stream should be very high to support this large community diversity, in spite of the little dimensions of the lotic system.

Pampean streams and rivers, with their particular characteristics make a point of contrast to the RCC concept. For grassland prairie streams, Wiley et al. (1990) proposed an inversion of the longitudinal gradient predicted by Vannote et al. (1980). Consequently, they postulated the existence of autotrophic headwaters in these systems. While this is true for Las Flores stream, several differences arise between prairie and Pampean streams. First, high nutrient levels in Pampean streams are not associated with agricultural activities, but to the weathering of volcanic material transported from the Andes mountains and deposited in the plains during the Quaternary (Sala et al. 1983; Morrás 1993). Second, the macrophytic vegetation in Pampean streams is generally autochthonous unlike New Zealand lowland streams where *E. densa* is an invasive species (Champion and Tanner 2000). Third, streambeds are formed by fine sediments and lack boulders, cobbles or sands, making a difference with English chalk streams (Marker 1976) and Danish lowland streams (Sand-Jensen et al. 1988). Consequently, habitat heterogeneity in Pampean streams is not the result of different type and size of substrata but of submerged

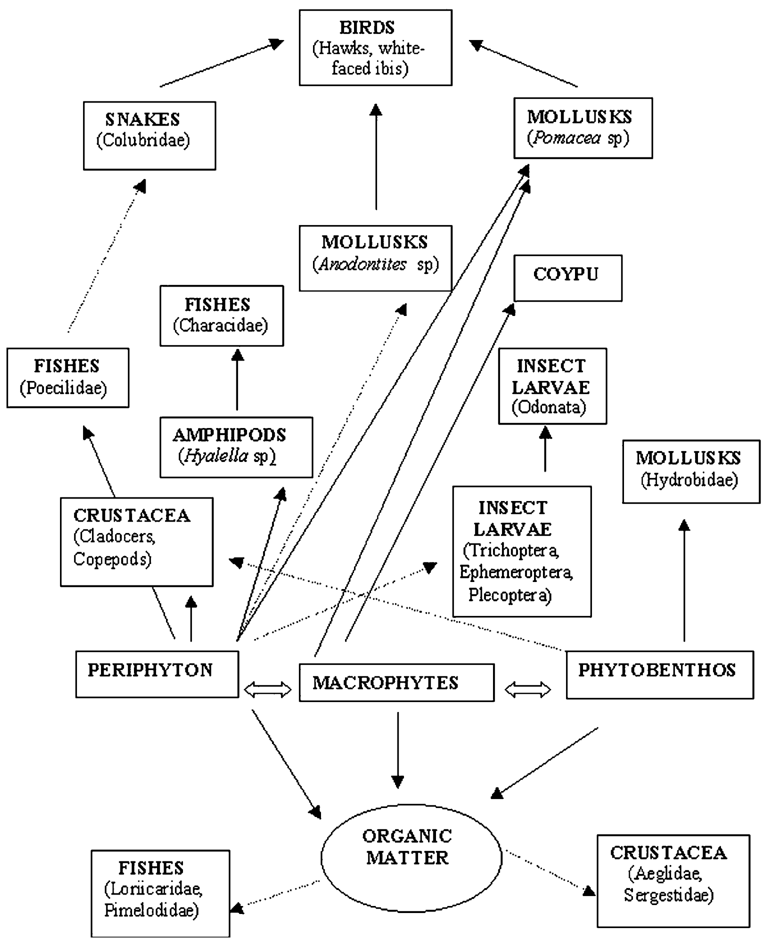

Figure 7. Hypothetical trophic web in Las Flores stream, based on our observations and on Gallardo (1977), Palermo (1984), Borgnia et al. (2000), and Casset et al. (2001). ┈┈▶: hypothetical relations; ──▶: reported relations; ⟺: relations of competence and mutualism.

vegetation, which plays and important structuring role in these systems. It is important to observe that all the streams with low slope, high nutrient levels and high irradiance show the 'structuring role' of macrophytes as it is described by Champion and Tanner (2000), which leads the macrophytes to regulate and modify the physicochemical and biological characteristics of the stream.

Westlake (1973) and Dawson (1988) considered that current velocity is the prime factor that regulates the growth and distribution of submerged macrophytes in streams and rivers. In this study, macrophyte biomass showed a negative relationship with velocity, a fact that was also observed by Gantes and Sánchez Caro (2001) in Pampean streams. Current velocity controls the establishment of macrophytes in the different microhabitats of the stream as well. Current velocity is also the most important factor influencing the phytobenthos community in this stream, while depth, nutrients, macrophytes and herbivores would be linked factors. Changes in current velocity have a more predictable pattern associated with seasonal water flow variation, and a stochastic component related to floods whose intensity vary in different years in relation to the quantity and frequency of precipitation.

Due to characteristics such as the gentle slope, the homogeneity of materials in streambeds, and the lack of strong restrictions to the growth of primary producers, it could be considered that Pampean streams have good conditions for the development of these communities. However, habitat heterogeneity is generated by the aquatic vegetation, a substratum that varies along time and could be easily removed by floods. Macrophytes, in turn, control the development of the other communities, creating a system where the components are linked by complex interactions. A system like this will be very vulnerable to the discharge of pollutants and to modifications in stream morphology and hydrology, as have occurred with the increase of non-controlled industries and urbanization in some Pampean streams.

Acknowledgements

The authors wish to acknowledge Ines O'Farrel and Carlos Coviella for the revision of the English text. Maria Adela Casco, Alfredo Salibián, and Joan Armengol for their comments and suggestions, and to Eric Pattee, Sergi Sabater and an anonymous reviewer for their useful critics of previous versions of the manuscript. This article was written during a stay of A.G. and C.F. in the Department d' Ecologia of the Universitat de Barcelona with the support of CONICET, AECI and the Universidad Nacional de Luján.

References

APHA (American Public Health Association) 1992. Standard Methods for the Examination of Water and Wastewater. APHA, Washington D.C.

Biggs B.J., Kilroy C. and Lowe R.L. 1998. Periphyton development in three valley segments of a New Zealand grassland river: test of a habitat matrix conceptual model within a catchment. Archiv für Hydrobiologie 143: 147–177.
Borgnia M., Galante M.L. and Cassini M.H. 2000. Diet of the coypu (nutria, *Myocastor coypus)* in agro-systems of Argentinean Pampas. Journal of Wildlife Management 64: 354–361.
Bowker D.W. and Denny P. 1980. The seasonal succession and distribution of epiphytic algae in the phyllosphere of *Lemna minor* L. Archiv für Hydrobiologie 90: 39–45.
Casset M.A., Momo F.R. and Giorgi A.D.N. 2001. Dinámica poblacional de dos especies de anfípodos y su relación con la vegetación acuática en un microambiente de la cuenca del río Luján (Argentina). Ecología Austral. 11: 79–85.
Champion P.D. and Tanner C.C. 2000. Seasonality of macrophytes and interaction with flow in a New Zealand lowland stream. Hydrobiologia 441: 1–12.
Claps M.C. 1991. Diatom communities on aquatic macrophytes of pampasic lotic environments (Argentina). Acta Hydrobiologica 33: 195–208.
Claps M.C. 1996. Structure and dynamics of epipelic algae from a plain river (Samborombon River, Buenos Aires, Argentina). Archiv für Hydrobiologie 137: 251–263.
Connell J.L. and Slatyer R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111: 1119–1144.
Cushing C.E., Cummins G.W., Minshall G.W. and Vannote R.L. 1983. Periphyton, chlorophyll-a, and diatoms of the Middle Fork of the Salmon River, Idaho. Holartic Ecology 6: 221–227.
Dawson F.H. 1988. Water flow and the vegetation of running waters. In: Symoens J.J. (ed.), Vegetation of Inland Waters. Kluwer Academic Publishers, Dordrecht, pp. 283–309.
Diehl S. and Kornijów R. 1998. Influence of submerged macrophytes on trophic interactions among fish and macroinvertebrates. In: Jeppesen E., Sondergaard M., Sondergaard M. and Christoffersen K. (eds), The structuring role of submerged macrophytes in lakes. Springer, New York, pp. 24–46.
Dodds W.K. 1991. Factors associated with the dominance of the filamentous green alga *Cladophora glomerata*. Water Research 25: 1325–1332.
Dodds W.K. and Biggs B.J.F. 2002. Water velocity attenuation by stream periphyton and macrophytes in relation to growth form and architecture. Journal of North American Benthological Society 21: 2–15.
Dodds W.K. and Gudder D.A. 1992. The ecology of *Cladophora*. J. Phycol. 28: 415–427.
Feijoó C., Giorgi A., García M.E. and Momo F. 1999. Temporal and spatial variability in streams of a pampean basin. Hydrobiologia 394: 41–52.
Fisher S.G. and Grimm N.B. 1988. Disturbance as a determinant of structure in a Sonoran Desert stream ecosystem. Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie 23: 1183–1189.
Gallardo J.M. 1977. Reptiles de los alrededores de Buenos Aires. Eudeba, Buenos Aires.
Gantes H.P. and Sánchez Caro A. 2001. Environmental heterogeneity and spatial distribution of macrophytes in plain streams. Aquatic Botany 70: 225–236.
Giorgi A. 1998. Factores reguladores del fitobentos en arroyos de llanura. Ph.D. thesis, Universidad Nacional de La Plata, La Plata, Argentina.
Giorgi A. and Malacalza L. 1994. Biomass variation of phytobenthos in a plain stream. Verh. Internat. Verein. Limnol. 25: 1883–1887.
Giorgi A., Feijoó C., Calviño P. and Dutweiller F. 1998. Annual variation of periphyton biomass in two plain streams with different macrophyte abundance. Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie 26: 1698–1701.
Giorgi A. and Tiraboschi B. 1999. Evaluación experimental del efecto de dos grupos de macroinvertebrados (anfípodos y gasterópodos) sobre algas epífitas. Ecología Austral 9: 35–44.
Goldberg S., Cirera I., Parella M., Benítez A., Bulos L. and Troncoso A. 1995. Caracterización climática y agroclimática de la Cuenca del Río Luján. Resúmenes de la Jornada sobre la Cuenca del Río Luján, Luján, Argentina, 29 November 1995. Programa de Ecología Acuática, Universidad Nacional de Luján, Argentina pp. 13–19.

Gordon N.D., Mc Mahon T.A. and Finlayson B.L. 1992. Stream Hydrology. J. Wiley & Sons, Toronto.
Guasch H. and Sabater S. 1994. Primary production on epilithic communities in undisturbed Mediterranean streams. Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie 25: 1761–1764.
Guasch H., Martí E. and Sabater S. 1995. Nutrient enrichment effects on biofilm metabolism in a Mediterranean stream. Freshwater Biology 33: 373–383.
Hillebrand H. 1983. Development and dynamics of floating clusters of filamentous algae. In: Wetzel R.G. (ed), Periphyton of freshwaters ecosystems, Dr. W. Junk Publishers, The Hague. pp. 31–39.
Madsen J.D. and Adams M.S. 1988. The seasonal biomass and productivity of the submerged macrophytes in a polluted Wisconsin stream. Freshwater Biology 20: 41–50.
Margalef R. 1983. Limnología. Omega, Barcelona.
Marker A.F.H. 1976. The benthic algae of some streams in southern England. Journal of Ecology 64: 343–358.
McCormick P.V. 1994. Evaluating the multiple mechanisms underlying herbivore-algal interactions in streams. Hydrobiologia 291: 47–59.
Meyer J.L. and Edwards R.T. 1990. Ecosystem metabolism and turnover of organic carbon along a blackwater river continuum. Ecology 71: 668–677.
Minshall G.W., Cummins K.W., Petersen R.C., Cushing C.E., Bruns D.A., Sedell J.R. and Vannote R.L. 1985. Developments in stream Ecosystem Theory. Canadian Journal of Fisheries and Aquatic Sciences 42: 1045–1054.
Morrás H. 1993. Fósforo total y materiales parentales de la región central de la República Argentina. Instituto de Suelos, INTA, Buenos Aires.
Palermo M.A. (ed.), 1984. Fauna Argentina. Centro Editor de América Latina, Buenos Aires.
Papadakis J. 1980. El suelo. Albatros, Buenos Aires.
Prahl C., Jeppesen E., Sand-Jensen K. and Moth-Iversen T. 1991. A continuous-flow system for measuring in vitro oxygen and nitrogen metabolism in separated stream communities. Freshwater Biology 26: 495–506.
Sabater S., Butturini A., Muñoz I., Romaní A., Wray J. and Sabater F. 1998. Effects of removal of riparian vegetation on algae and heterotrophs in a Mediterranean stream. Journal of Aquatic Ecosystems Stress Recovery 6: 129–140.
Sala J.M., González N. and Kruse E. 1983. Generalización hidrológica de la Provincia de Buenos Aires. Resúmenes Coloquio Internacional sobre Hidrología de Grandes Llanuras, Olavarría, Argentina, 11–20 April 1983. Comité Nacional para el Programa Hidrológico Internacional, Buenos Aires, Argentina. pp. 974–1009.
Sand-Jensen K., Moller J. and Olesen B.H. 1988. Biomass regulation of microbenthic algae in Danish lowland streams. Oikos 53: 332–340.
Sand-Jensen K., Borg D. and Jeppesen E. 1989a. Biomass and oxygen dynamics of the epiphytic community in a Danish lowland stream. Freshwater Biology 22: 431–443.
Sand-Jensen K., Moller J. and Hald Olesen B. 1989b. Biomass regulation of microbenthic algae in Danish lowland streams. Oikos 53: 332–340.
Solari L.C. and Claps M.C. 1996. Planktonic and benthic algae of a pampean river (Argentina): comparative analysis. Annals de Limnologie 32: 89–95.
Steinman A.D. and McIntire C.D. 1987. Effects of irradiance on the community structure and biomass of algal assemblages in laboratory streams. Can. J. Fish. Aquat. Sci. 44: 1640–1648.
Suárez L. and Vidal-Abarca R. 2000. Metabolism of a semi-arid stream of south east Spain. Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie 27: 756–761.
Suren A.M. 1991. Bryophytes as invertebrate habitat in two New Zealand alpine streams. Freshwater Biology 26: 399–418.
Vannote R.L., Minshall G.W., Cummings K.W., Sedell J.R. and Cushing C.E. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences: 37: 130–137.

Westlake D.F. 1973. Aquatic macrophytes in rivers. A review. Polskie Archiwum Hydrobiologii 20: 31–40.

Wetzel R.G. (ed.), 1983. Periphyton of freshwater ecosystems. Dr. W. Junk Publishers, The Hague.

Wetzel R.G. and Likens G.E. 1991. Limnological analyses. Springer-Verlag, New York.

Wiley M.J., Osborne L.L. and Larimore R.W. 1990. Longitudinal structure of an agricultural prairie system and its relationship to current stream ecosystem theory. Canadian Journal of Fisheries and Aquatic Sciences 47: 373–384.

Young R.G. and Huryn A. 1996. Interannual variation in discharge controls ecosystem metabolism along a grassland river continuum. Canadian Journal of Fisheries and Aquatic Sciences 53: 2199–2211.