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Metabolism in a macrophyte-rich stream exposed to flooding

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Abstract The aim of this study was to investigate the effect of floods on the metabolic autotrophic rates of a Pampean stream. We hypothesized that there would be high productivity because of the macrophyte-rich community and the high nutrient levels but that this productivity would be reduced by flooding. Net community production (NCP) and community respiration (CR) were measured using clear and opaque acrylic chambers in the same reach of the stream. Community metabolism was analyzed in relation to biomass and the colonized streambed surface. Prior to the flood, epiphyton was the most productive compartment of the stream, whereas after the flood, the bottom algae compartment was the most productive one. Therefore, the relative contribution of each compartment to the entire ecosystem was influenced by the varying flow conditions. The primary gross production values of the Las Flores stream communities before the flood were higher than most of those reported in other streams worldwide and sustain the complex trophic web associated to the stream. Consequently, production decrease due to the lower relative contribution of macrophytes and epiphyton would lead to a more simplified trophic network.

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Introduction

Extreme flows and droughts are natural disturbances that cause important changes in the properties of many streams (Fisher et al., 1982; Resh et al., 1988; Boulton & Lake, 1990). The changes produced by floods may modify community production and respiration and the relative contribution of communities to ecosystem metabolism (Vis et al., 2007).

Stream metabolism depends on the hydrology and riparian forest inputs that affect both primary producers and organic matter accumulation and respiration. Flooding reduces production and increases ecosystem respiration (Acuña et al., 2004). In large rivers, it has been reported that spates reduce primary

production by 49% and ecosystem respiration by 19% (Uehlinger, 2006). Disturbance caused by frequent bed-moving floods may also lead to major stochastic variation in production and respiration.

The contribution of each specific autotrophic community to primary production varies in different environments. Low order streams have lower production than higher order ones and the epilithic community is more important in small streams (Vannote et al., 1980). For instance, it has been estimated that in a headwater stream in an arid area, epipelic algae assemblage contributes to 84% of gross primary production and to 86% of CR (Velasco et al., 2003), whereas in a marked widening of the St. Lawrence River (Canada), the estimated annual primary production is roughly equally divided among phytoplankton (34%), submerged macrophytes (27%), emergent macrophytes (23%) and epiphyton (16%) (Vis et al., 2007).

In spite of the differences between ecosystems, no clear effect of floods on community metabolism at headwater streams has been established because the studies so far have been generally carried out in base flow conditions. Increases in water flow caused by storms may produce drastic declines in periphytic biomass and, hence, a reduction in the primary production and respiration rates, shifting the system from autotrophy to heterotrophy due to the disproportional reduction in gross primary production (Roberts et al., 2007).

It has been hypothesized that, in macrophyte-rich streams, floods frequently wash away the macrophytes, thus reducing the ecosystem biomass and changing stream metabolism. The results of a previous study, however, did not support this hypothesis given that no changes were found in ecosystem production and respiration (Kaenel et al., 2000). Floods change the biomass and metabolism of some autotrophic communities, although these changes either may or may not affect stream metabolism, depending on the degree of disturbance and the resilience of the dominant communities (Roberts et al., 2007). Floods are probably the main drivers of Pampean stream functioning in Argentina because they lead to the loss of macrophytes. High macrophyte and epiphyton biomasses are common in Pampean streams and promote the development of large number of grazers related to macrophytes and epiphyton (Casset et al., 2001; Giorgi et al., 2005).

The aim of this study was to investigate the effect of a large flood on the autotrophic productivity contribution to stream metabolism in a Pampean stream. We hypothesized that the high productivity of macrophytes, maintained by high nutrient concentrations, would be markedly reduced during periods of high floods.

Materials and methods

Study area

The 'Pampa' is a vast grassland system covering central Argentina (500,000 km^2). The climate is mild and humid with mean annual precipitations between 600 and 1200 mm, and a mean annual temperature of 16°C. Rainfall is distributed throughout the year, with maximum levels in spring and fall. Soil water deficits over the last 80 years have been recorded during the summer season, particularly in December and January (Gantes, 2000).

Pampean streams begin at small depressions with emergent plants, such as *Schoenoplectus californicus* (C. A. Mey) Sojak or *Typha latifolia* L. Streambeds have a hard, homogeneous substratum, with fine sediments (primarily silt and clay), high calcium carbonate content, and a total absence of stones or pebbles. These streams are fed by rains and groundwater infiltration. These particular streams crisscross fertile soils with high organic matter and nutrient contents, formed by loess deposition during the Quaternary period (Papadakis, 1980; Sala et al., 1983). There is little drainage not only because of the gentle slopes (0.02% or less) but also due to the silt content (Fidalgo, 1983). Water flow is usually low, but is prone to increase drastically due to flooding. Because of the absence of riparian forest vegetation in unmodified areas, solar radiation easily reaches the streambed, allowing the development of dense plant communities. Macrophytes play a key role in open streams (without riparian forest) by increasing physical heterogeneity, trapping fine sediments, and providing a habitat for epiphyton, invertebrates, and fish. The general pattern over the year shows a reduction in the amount of macrophytes during the fall-winter season and an increase in submerged plants towards spring, which reaches its peak in summer (Feijoó et al., 1996; Giorgi et al., 1998,

Fig. 1 Map showing the location of the Las Flores stream
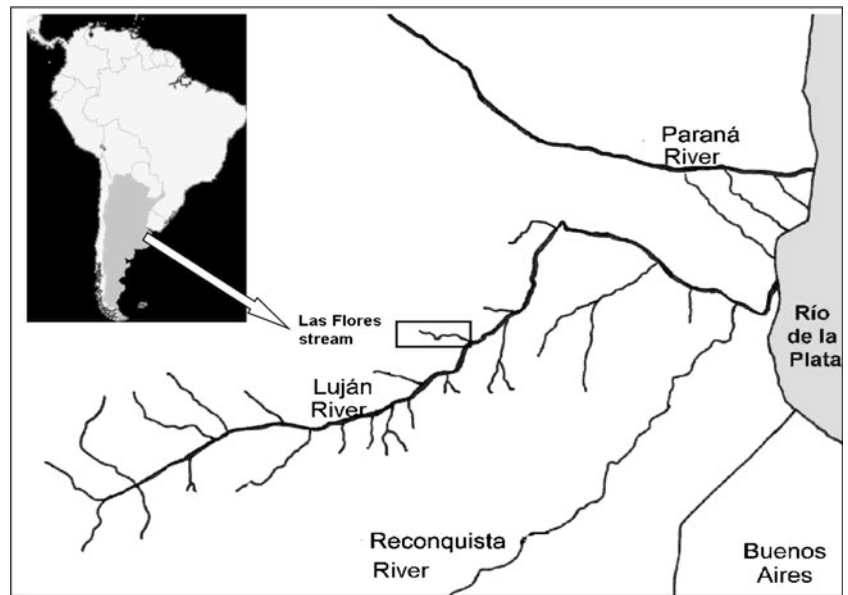
Feijoó et al., 1999). In Pampean streams, the high submerged vegetation biomass (up to 500 g DW m^{-2}) suggests that macrophytes and epiphytic algae contribute a substantial part of overall stream productivity. However, flooding events could bring about significant changes in the way the stream works (Giorgi et al., 2005).

This study was carried out in the Las Flores stream, a second-order reach located in the Luján River basin in the northeast of the province of Buenos Aires, Argentina (Fig. 1). This stream is considered representative of most Pampean streams. It has been affected by human activities only to a small extent because in this region only horse breeding and a few other farming and rural activities take place (Feijoó et al., 1999, Giorgi et al., 2005). The stream is inhabited by a variety of primary producer communities (i.e., submerged vascular plants, epiphytic and bottom algae). Dominant submerged macrophytes are *Egeria densa* Planch and *Ceratophyllum demersum* L.

Study design

One experiment was carried out during the summer of 2005 and another in the winter of that same year. These experiments were repeated during the summer and winter of 2006. At the beginning of 2006 (January), heavy rainfalls led to a severe week-long flood that increased the stream flow to 50 times its normal flow. Throughout the text, the experiments

carried out the year before the flood are called summer before the flood (SBF) and winter before the flood (WBF), whereas the experiments carried out during 2006 are called summer after the flood (SAF) and winter after the flood (WAF). The latter were carried out after the flooding took place, but once the baseflow hydrological conditions had been recovered.

Stream compartment characterization

Distribution of substrata within the study reach was mapped plotting all the type of substrate present in 20 areas made up of equidistant transects (with a distance of 5 m between them). Within each area, the percentage of streambed covered by the different primary producers (macrophytes, macrophytes and epiphyton, bottom algae) was determined. Also, the biomass in the different substrates was estimated by harvesting the different communities at sampling areas of 0.0625 m^2. Submerged macrophyte samples were dried at 60°C to constant dry weight (DW) and then combusted at 480°C for 4 h to estimate the ash-free dry weight (AFDW) content. Epiphyton biomass was estimated by removing the epiphyton algae and carefully shaking, rinsing and cleaning the submerged macrophytes with filtered stream water. The 500 ml suspension obtained was filtered using a Sartorius funnel and a vacuum pump through Whatman GF/F filters. Bottom algae were obtained from artificial substrata submerged for more than 60 days

(colonized bricks). The bottom algae biomass was estimated by scraping and cleaning the surfaces of the colonized bricks to remove all attached organisms and this suspension was also filtered through Whatman GF/F filters. DW and AFDW were determined in the same way as that described above.

All producers biomass were first estimated per unit surface. Then, considering the percentage of stream bed covered by each community, biomass were expressed as DW of reach for each substrate and sampling date.

Experiment organization

Vegetation samples were randomly collected from the study reach, and placed in rectangular acrylic glass chambers (400 cm^2, 11 cm deep, 5 l volume) before the beginning of the experiment. A total of twelve chambers were used for each experiment. Three were used as control chambers to evaluate metabolism in free water because all the other chambers with different substrates were filled with stream water. Three chambers were prepared with colonized submerged macrophytes. Another three were prepared with cleaned submerged macrophyte samples. For this, macrophyte samples were previously separated and carefully shaken and washed to remove the epiphytic algae growing on them. The efficiency of epiphyton removal was analyzed by microscopic inspection of the macrophyte leaves. When checking for damage to macrophyte leaves, we found that only a few organisms, such as the diatom *Cocconeis placentula,* remained attached after cleaning. A 90% reduction in the incidence of this diatom on macrophyte leaves was achieved using this procedure. All the submerged macrophytes were collected from the same reach and similar biomass was distributed in each chamber. Submerged macrophytes were *E. densa* and *C. demersum* and showed no roots. Finally, the other three chambers were prepared with substrates colonized with bottom algae. This substrate was made up of regular pieces of brick that were previously submerged for more than 60 days in the stream. Previous studies at the same location revealed a high degree of similarity in benthic algae composition between this substrate and natural ones (tuff layer) (Giorgi & Ferreyra, 2000).

Community metabolism

Community respiration (CR) and net community production (NCP) of the three types of primary producers were measured with incubations in metabolic chambers. All chambers were prepared according to the methods described above. The temperature in the chambers never exceeded stream temperature by more than 2°C. The chambers did not require circulating pumps because of the low current velocity of this system (Velasco et al., 2003).

Dissolved oxygen and temperature were measured at the beginning and end of the incubations using a handheld HI9142 oxygen meter (0.1 mg O_2 l^{-1} precision Hanna instruments, Woonsocket, Rhode Island, USA). CR was estimated during 2-h incubations in darkness after covering the metabolic chambers with black sheets, and then extrapolated to a 24-h period. Then, the same chambers were used to evaluate NCP during 1-h incubations to avoid over-saturation conditions inside the chambers, and then extrapolated to daylight hours (Velasco et al., 2003). The same communities were used for CR and NCP estimation to avoid the variation produced by the change of substrates. Gross community production (GCP) was calculated by adding NCP and CR. The water column rates were subtracted from the other three compartments (macrophytes, epiphyton and bottom algae). In the chambers with epiphyton, macrophyte-related oxygen variation was also discounted using oxygen variation values per gram of macrophytes obtained in the chamber with cleaned macrophytes. Dissolved oxygen results were converted to carbon units by applying a 1.2 coefficient to GCP and a 0.85 coefficient to CR, and multiplying by 0.375 that is the relation between the atomic weight of carbon and oxygen in photosynthetic equation (Bott et al., 1978; Margalef, 1983; Bott et al., 1997). The biomass for each community was estimated in the same way as that described above (see "Stream compartment characterization" section).

CR, NCP, and GCP were calculated in units of oxygen production or consumption per unit of AFDW and time for each chamber and transformed to mg C m^{-2} day^{-1} in relation to the proportion of streambed covered by the different primary producers.

Physico-chemical characterization

Photosynthetically active radiation (PAR) reaching the streambed was measured using an underwater spherical quantum sensor (LI-193 sensor fitted to LI-250 Quantum Meter, both LICOR Inc., Lincoln, NA, USA). Measurements were carried out during the experiments.

Stream water for nutrient analyses was filtered in situ through glass fiber filters (Whatman GF/F filters) and stored at 4°C until analyzed. Soluble reactive phosphorus (SRP) was analyzed using the ascorbic molibdate method (APHA 1995), and N-NH4 was analyzed with the indophenol blue method following APHA (1995). Water temperature, pH (portable pH meter Hanna HI9023 Hanna instruments, Woonsocket, Rhode Island, USA), and conductivity (portable conductimeter Hanna HI9033) values in each chamber were also recorded on each sampling occasion. These measurements were also carried out at the beginning and end of each experiment to study any possible changes in the water characteristics during the incubations as nutrient depletion that should affect production or respiration rates.

Results

Phosphorus and ammonia were not exhausted in the chambers during the experiment due to the high initial concentration. The short incubation times caused only a 5% reduction in SRP concentration and a 3% increase in ammonia concentration during the experiments. Highest temperatures and PAR were recorded at SAF. These conditions positively contribute to increasing GCP. pH and conductivity did not present significant changes on each sampling date. Flow velocity was lower than 10 cm s^{-1} each time measurements were taken (Table 1).

Epiphyton was the most productive community in the stream; the highest NCP was recorded in SAF, with values different from those obtained in WBF. Macrophyte NCP and bottom algae were also higher in SAF than those performed on the remaining sampling dates. Only bottom algae showed differences in respiration between SAF and WAF. The highest values of GCP expressed as mg C g C^{-1} day^{-1} were recorded during SAF (Table 2).

The flooding in 2006 took place in January and was associated with the higher rainfall during this period (Fig. 2). This rainfall level increased the basal flow more than 100 times, and most of the macrophytes were washed away. As a result, macrophyte coverage in SAF and WAF fell from ca. 50% to less than 1% of the surface area of the reach. In addition, during WAF, macrophytes and epiphyton biomasses were lower than 4 g DW m^{-2} and 2, respectively (Fig. 3).

Figure 4 shows values of production by unit of reach surface considering the relative contribution of each community at each sampling date (expressed as mg C m^{-2} day^{-1}). Epiphyton was the community with the highest variability in the estimates. On the other hand, bottom algae NCP mean values were higher in SAF than in SBF. This relative variation was also evident when comparing the results of NCP for both winters (Fig. 4).

The contribution of macrophytes to the total stream production was over 59% in both summers, 44% in WBF, and only 16% in WAF. The highest contribution of epiphyton was noted in WBF and the lowest in SAF (54% and 16, respectively), and the contribution of bottom algae was higher after the flood than before it (22–65 and 1.9–1.1%, respectively) (Fig. 4).

Table 1 Principal characteristics of the Las Flores stream on each sampling date

|	Temperature (°C)	Conductivity (µS cm^{-1})	pH	Radiation (W/m^2)	NH$_4^+$ (mg l^{-1})	SRP (mg l^{-1})	Water flow (cm s^{-1})
SBF	20	961.4	7.7	302.24	0.018	0.21	8
WBF	17.5	983.33	8.1	378.02	0.061	0.18	4.3
SAF	24.5	834.5	7.7	742.75	0.044	0.24	9.1
WAF	9	913.17	8.1	555.8	0.05	0.67	3.7

SBF summer before flood, *WBF* winter before flood, *SAF* summer after flood, *WAF* winter after flood, *SRP* soluble reactive phosphorus

Table 2 Metabolism measures (mean ± SD) for macrophytes, epiphyton and bottom algae on different sampling dates

	NCP	CR	GCP
Macrophytes			
SBF	152.86 ± 27.49	41.86 ± 7.54	194.73 ± 34.21
WBF	147.03 ± 50.68	24.76 ± 7.39	171.79 ± 58.01
SAF	334.37 ± 44.39	13.27 ± 18.35	347.64 ± 31.63
WAF	153.89 ± 29.42	27.86 ± 21.25	181.75 ± 46.28
Epiphyton			
SBF	1253.53 ± 559.73	205.83 ± 180.68	1441.1 ± 757.91
WBF	752.97 ± 391.25	275.16 ± 108.79	1028.13 ± 335.02
SAF	3324.07 ± 1323.56	1004.87 ± 1141.53	4132.4 ± 1132.96
WAF	1515.13 ± 520.41	215.24 ± 225.27	1730.37 ± 747.49
Bottom algae			
SBF	373.5 ± 60.63	125.91 ± 16.22	499.42 ± 75.67
WBF	526.57 ± 2082.73	242.85 ± 107.87	769.42 ± 277.76
SAF	1099.1 ± 202.87	315.55 ± 132.56	1414.66 ± 293.42
WAF	219.08 ± 23.85	70.17 ± 23.42	289.26 ± 35.63

SBF summer before flood, *WBF* winter before flood, *SAF* summer after flood, *WAF* winter after flood, *NCP* net community production, *CR* community respiration, *GCP* gross community production. All the values are in mg C g C^{-1} day^{-1}

Fig. 2 Mean monthly air temperature (°C; line and diamonds) and precipitation (mm; bars) recorded in the months surveyed. *White arrows* indicate the sampling date. *Dark arrow* indicates the flooding
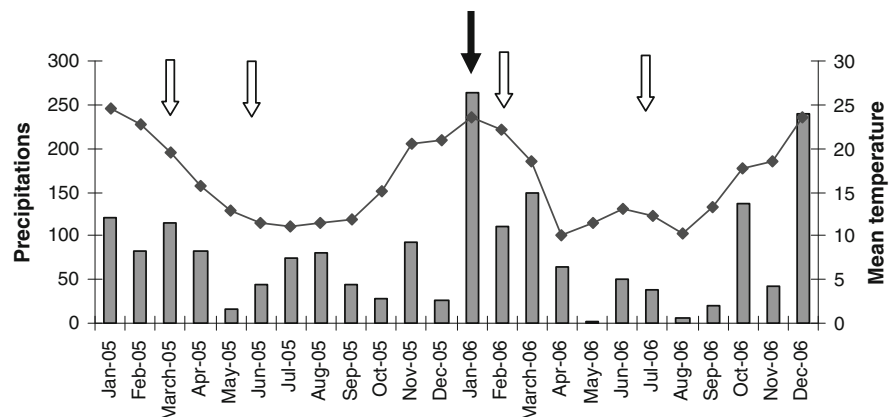
Discussion

In our study in Las Flores stream with a macrophyte-rich community, changes in the relative contribution of macrophytes and the associated epiphyton after the flood were conspicuous. When the flood occurred, both macrophytes and epiphyton reduced their biomasses. The decrease in macrophyte and epiphyton biomass contributed to the development of bottom algae and to an increase in their biomass. It can therefore be concluded that the flood modified the relative importance of macrophytes and epiphyton, and thus noticeably affected the ecosystem metabolism.

An event of this magnitude is not particularly frequent and usually takes place in cycles of 4 or more years. Other studies in the same reach of the stream have shown that the base flow hydrological conditions are swiftly recovered, but that biological recolonization is much slower (Feijoó et al., 1996).

The presence and development of macrophytes in lotic systems is primarily controlled by the frequency of high velocity floods; therefore, the main mechanism causing the decrease in macrophyte abundance was probably the uprooting associated with stream-bed sediment erosion (Riis & Biggs, 2003). The removal of aquatic vegetation changes the relative contribution to the overall ecosystem production (Vis et al., 2007); however, Kaenel et al. (2000) found little effect on the entire stream metabolism where macrophytes were cut off.
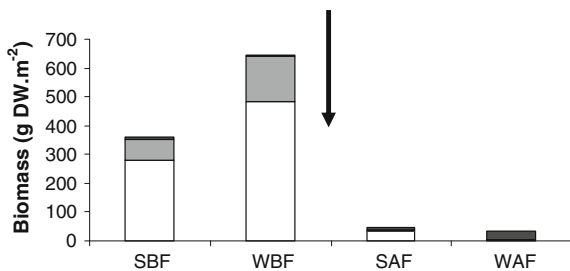
Fig. 3 Macrophyte (*white*), epiphyton (*gray*), and bottom algae (*black*) biomass recorded on each sampling occasion. The *arrow* indicates the flooding
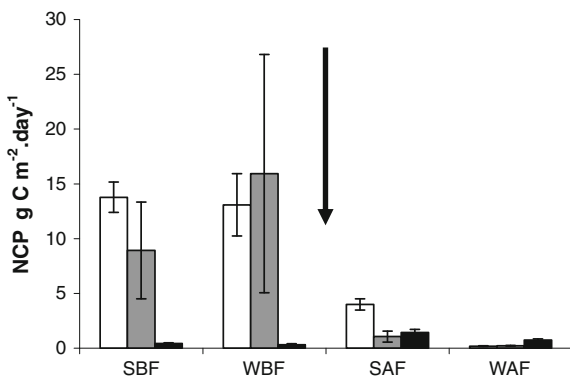

Fig. 4 Net community production (NCP) g C m^{-2} day^{-1} for each community. The *arrow* indicates the flooding. Macrophyte (*white*), epiphyton (*gray*), and bottom algae (*black*) biomass recorded on each sampling occasion

In the SAF, autotrophic communities showed the highest production values in the chambers. This is probably accounted for by the high irradiation and temperature values which reduce competition for light and nutrients after the flood; although in WAF the low temperature would reduce the rate of development of macrophytes. Epiphyte productivity was at all times higher than that of the other two communities. However, epiphyton representation and the relative contribution of this community to ecosystem productivity decreased after the flooding because the macrophytes and epiphytes wash away.

Young et al. (2008) warned of associated errors when small-scale measurements of different stream components are related to an entire stream reach. In spite of this, the important differences recorded between the conditions before and after the flooding provide a basis for the comparison. Likewise, the chamber methods made it possible to make the comparison between communities and to compare the same community on

different occasions. There is no doubt that further studies will be necessary to evaluate the respiration of the entire stream and consider all the consumers involved (Fellows et al., 2001; Acuña et al., 2004).

After the flood, the Las Flores stream took a long time to recover its initial biomass and production values, which suggests its low resilience level. In other streams, although the disturbance decreased gross production, the epiphyton recovered within a shorter span of time (Uehlinger & Naegeli, 1998; Uehlinger et al., 2003; Acuña et al., 2007). The high resilience level of these streams is related to the generational time of producers. In Pampean stream, the main substrates for epiphyton are macrophytes that are also affected by floods. Macrophyte colonization and development are slow compared to those of algae. Start macrophyte regrowth time are between 1 and 6 months according flood level (Maltchik & Pedro, 2001). In addition, epiphyton developing in areas of slow flow is more susceptible to dislodgement during flooding than communities from fast flow regions (Steinman & McIntire, 1990). Other authors have reported that after a flood epiphyton was more productive because of the greater availability of light and nutrients (Hoagland et al., 1982; Steinman & McIntire, 1987; Stevenson et al., 1996). The Las Flores stream has adequate conditions for algae recovery, but macrophytes have slow development. These characteristics lead us to believe that the Las Flores stream sustains a highly fragile ecosystem because both macrophytes and epiphyton, the two communities that contribute to the establishment of invertebrates, can be washed away by floods and thus the macroinvertebrate-rich community loses shelter and food (Giorgi & Tiraboschi, 1999; Giorgi et al., 2005).

When comparing our results in baseflow conditions and those reported by other authors using chamber methods, the highest GCP was recorded among communities studied during summer in the Chicamo stream, which is located in an arid environment (chaparral), followed by communities in the Las Flores stream (Velasco et al., 2003). In both the areas, macrophytes are more productive in summer and epiphyton in winter. The production of bottom algae is lower than the other communities. Autotrophic production of the Las Flores stream during the summer and WBF is higher than in various other streams belonging to other climatic regions (Sand-Jensen et al., 1989; Fellows et al., 2001; Hill et al.,

2001). Many of these streams have other dominant substrates as rocks, sand or sediments.

The high gross production values found in the Las Flores stream in baseflow conditions led to an excess of production that was available for aquatic organisms and other fauna associated with this stream, such as birds (heron, white-faced ibis), mammals (coypu), amphibians (frogs), reptiles (snakes) and insects. Under these conditions, it is reasonable to hypothesize that, after the flooding, the stream production would sustain a less complex trophic network because macrophytes and epiphyton reduce their production and would therefore develop a lower biomass of herbivorous and carnivorous. Flooding also increases the homogeneity of available habitats due to the reduction in macrophyte representation and an increased connection among different habitats (Gantes & Sánchez Caro, 2001; Thomaz et al., 2007).

The results of this study confirmed the initial hypothesis that stream productivity is high both in summer and winter because of the macrophyte abundance but lower after the flooding because this community is dragged away. The flooding increased the metabolic rate of autotrophic communities—principally epiphyton—but reduced the entire stream production due to the decrease in biomass. It also changed the relative contribution of the various primary producers to the stream ecosystem. In the two summer experiments, before and after the flood, macrophytes were shown to be the principal support for stream production whereas in the winter experiments, the relative contribution of epiphyton was more important before the flooding, while after it bottom algae became more important.

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