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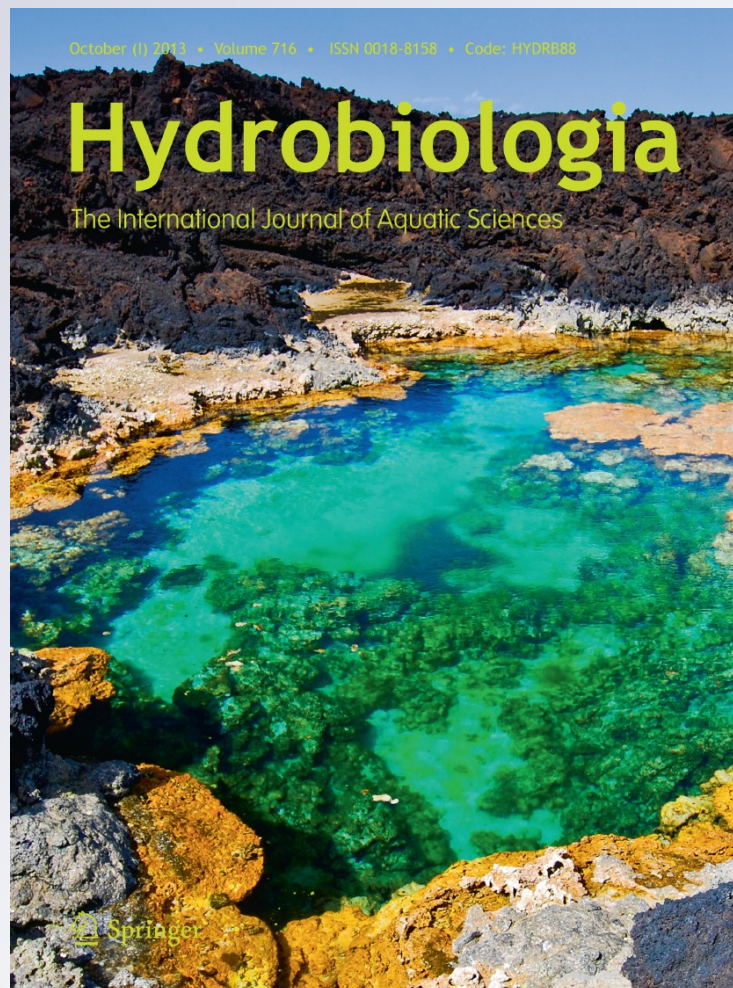
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# Seasonal weather effects on hydrology drive the metabolism of non-forest lowland streams

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**Abstract** Weather variations change stream hydrological conditions, affecting the stream function. A seasonal study in three well-conserved first-order Pampean streams was carried out to test the hypothesis that rainfalls are the main drivers of whole-stream metabolism, through their effects on hydrology. We estimated the stream metabolism and metabolic contribution of six relevant communities (angiosperms, macroalgae, seston, epiphyton, epipelon,

and hyporheos) during late spring, summer, and winter and examined the relation between gross primary production (GPP) and photosynthetic active radiation (PAR). Our results showed that the decrease in available streambed light due to the dissolved organic carbon after rainfalls was the main factor related to the decrease in the ecosystem and community metabolisms. For instance, GPP oscillated from  $\sim 10 \text{ gO}_2 \text{ m}^{-2} \text{ d}^{-1}$  in early spring (low flows) to  $\sim 3 \text{ gO}_2 \text{ m}^{-2} \text{ d}^{-1}$  in summer (high flows). Ecosystem respiration (ER) was less sensitive than GPP to rainfalls due to the increase of hyporheic respiration. Rainfalls also caused a significant loss of downstream macroalgal biomass. At a day scale, the high PAR of late spring and summer saturated GPP during the afternoon, and the low temperature of winter mornings constrained GPP. Hence, the knowledge of weather changes is key to understanding the main hydrological drivers of stream function.

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**Keywords** Whole-stream metabolism · Weather conditions · Community metabolism · Streambed light · Dissolved organic carbon

## Introduction

The magnitude and frequency of low and high flows regulate the structure and diversity of aquatic ecosystems, thus modifying the energy flow, nutrient cycling,

and population dynamics (Poff et al., 1997; Galat et al., 1998; De Loe, 2008). Low flows lead to ecosystem stability, allowing the development of the biota, whereas high flows lead to ecosystem instability, shear forces, and abrasion by transported bed sediments that severely damage or eliminate organisms of the stream, rejuvenating the biological community and allowing many species with fast life cycles and good colonizing ability to reestablish (Fisher, 1983; Uehlinger & Naegeli, 1998). Hence, the knowledge of meteorological variations and flow dynamics is key to understanding the stream functioning. In this context, ecosystem metabolism is a suitable variable to evaluate the effects of hydrological variation on streams, given its integrative nature (e.g., Fisher et al., 1982; Uehlinger & Naegeli, 1998; Acuña et al., 2011).

Pampean streams run over the flat topography of the Wet Pampa sedimentary plains in Argentina and are usually disturbed by annual rainfall cycles. In late summer, precipitations and flooding events are the most frequent and the most intense of the year, whereas in winter and early spring, rainfalls are scarce and streams show high hydrological stability (Scian et al., 2006). This is, the flow instability and sunlight incidence relatively coincided at a seasonal scale. Based on previous evidence in the region (Vilches & Giorgi, 2010; Acuña et al., 2011), we hypothesized that rainfalls are the main driver of whole-stream metabolism through their effects on hydrology. Our prediction is that the hydrological conditions after rainfalls, such as the available light to autotrophs, will decrease the primary production and respiration rates of Pampean streams and their communities. In addition, since we did not know how rainfalls stress the stream biota, we considered as many physical, chemical, hydrological, and biological factors as possible. The goal of our study was to characterize the whole-stream metabolism and to discern the contribution of six communities (angiosperm macrophytes, macroalgae, seston, epiphyton, epipelon, and hyporheos), under the different meteorological and limnological conditions of each season, as an attempt to know the main drivers of stream function. Finally, to detect light and temperature effects on stream metabolism at a day scale, we examined the relation between daily gross primary production and photosynthetic active radiation.

## Methods

### Study area

The Wet Pampa region is located in the central-east region of Argentina and presents a mean annual temperature of 17°C and rainfall of 1000 mm (Soriano et al., 1992). The region is a fertile sedimentary plain covered by grasslands. Lowland Pampean streams drain these soils, being usually eutrophic (SAGPyA & CFA, 1995; Feijoó & Lombardo, 2007). These streams are highly productive and support a high biodiversity (Giorgi et al., 2005; Acuña et al., 2011). Their streambeds are characterized by fine sediments (primarily silt and clay), without stones or pebbles (Feijoó & Lombardo, 2007). The study was conducted in 350-m-long reaches of the three first-order streams: La Choza (34°08'10''S–60°03'50''W), De La Cruz (34°24'20''S–59°15'35''W), and El Contador (34°42'10''S–59°04'40''W). The three streams are tributaries of the Paraná-La Plata river system and originate in small depressions (~15 km upstream of the reaches). Their floodplains are relatively wide (50–100 m). The stream reaches and the upstream riparian vegetation are well conserved in at least the first 30 m of the water edge, with dominance of grass and the absence of trees.

### Meteorological factors

Fieldwork was carried out in September and December 2009 and in February, May, and July 2010 (which correspond to early spring, late spring, summer, autumn, and winter of the Southern hemisphere, respectively). Data of daily rainfalls and daily evaporation rates of the water surface were obtained from the meteorological station of the National University of Luján, located between 20 and 120 km from the study sites. The water that rained during the 20 days ( $R_{20}$ ) prior to the sampling dates was estimated as the mean daily mm rained during this period. The water balances ( $\Delta W$ ) were calculated from the data of the previous 20 days as precipitation (mm) minus evaporation (mm). Photosynthetically active radiation (PAR) was continuously recorded every 10 min using a PAR sensor (PAR-Lite, Kipp & Zonen, Delft, the Netherlands) and a datalogger (CR1000, Campbell Scientific Inc., Utah, USA). Adding all the PARs measured during the sampling dates, we obtained a



daily PAR value (dPAR). PAR attenuation coefficients ( $k$ ) were calculated according to Gordon et al. (2004) using a quantum sensor to measure PAR at different depths at midday.

#### Hydrological and physicochemical factors

The physical structure of the channel was determined according to Elosegui & Diez (2009) at regular intervals of 35 m. The hydraulic ratio ( $m$ ) was calculated by dividing the mean cross-sectional area ( $m^2$ ) by the length of the wetted perimeter ( $m$ ). Discharge was calculated using the slug-injection method (Gordon et al., 2004). Water samples for nutrient analyses were collected in triplicate in polyethylene bottles and then stored at 4°C, transported to the laboratory, and analyzed within 4 h. The samples were filtered (glass fiber filters: pore size = 0.7  $\mu\text{m}$ ; Whatman GF/F, Maidstone, UK) and analyzed for soluble reactive P (SRP) with the ascorbic acid method, for nitrates and nitrites through a reaction with sulfanilamide, and for ammonia with the phenolhypochlorite method (Wetzel & Likens, 1991; APHA, 1998). Total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP) were determined using the methods described in the previous sentence with previous oxidation with peroxydisulfate (APHA, 1998). The dissolved organic fractions (DON and DOP) were calculated by the difference between total nutrients and dissolved inorganic nutrients. The trophic state was established based on total dissolved nutrient criteria (Dodds et al., 1998). Dissolved organic carbon (DOC) was estimated with the methodology proposed by Zhang et al. (2005).

#### Biomass

The line–intercept method was used to map the distribution of five autotrophic communities (angiosperm macrophytes, macroalgal macrophytes, epiphyton, epipelton, and seston) in 70 equidistant transects spaced 5 m apart (Feijoó & Menéndez, 2009). Three samples of each were collected. The biomass of the dominant species of angiosperms (*Ludwigia* sp. in La Choza stream and *Stuckenia* sp. in De la Cruz and El Contador streams) and filamentous macroalgae (*Spirogyra* sp. or *Cladophora* sp.) was estimated according to Feijoó & Menéndez (2009). Epiphyton biomass was estimated according to Vilches & Giorgi (2010).

Epipelton and seston were sampled according to Gómez et al. (2009). The epipelton samples were dried at 60°C to constant dry weight (DW) and ashed at 500°C for 2 h. Epipelton biomass was estimated as the difference between the DW and the ash-free DW. Filters with seston, obtained from the filtered stream water, were also dried at 60°C to DW. Combining the data of community DW with the data of map plotting, we calculated the mean biomass of every community per surface of stream ( $\text{g DW m}^{-2}$ ; used to scale up the community metabolism to ecosystem levels; see “Community Metabolism” section).

#### Community metabolism

The metabolism of the five communities in late spring, summer, and winter was calculated by the incubation chamber method (Bott et al., 1978). Samples of each community were randomly collected and placed in clear acrylic rectangular chambers (volume  $\sim 6$  l) that were simultaneously submerged in the stream during incubations to minimize temperature and light variability. We did not force circulating pumps inside the chambers because flow velocities in the streams were low (Velasco et al., 2003). The five treatments were (a) seston (stream water); (b) epipelton + seston (three 4-cm-diameter corer samples of epipelton per chamber plus stream water); (c) macroalgae + seston; (d) angiosperm macrophytes + seston (plants without epiphyton); and (e) angiosperm macrophytes + epiphyton + seston (macrophyte fragments). Three replicates for each treatment were run. For the (d) chambers, angiosperm macrophyte samples were previously separated and carefully shaken and washed to remove the epiphytic algae growing on them (Vilches & Giorgi, 2010).

Community respiration (CR) was estimated by covering the chambers with black sheets for 2 h. Then, the same chambers were used to estimate net community metabolism (NCM) during 1-h incubations to avoid oversaturation conditions inside the chambers. All the incubations were performed between 10 h 30 min and 13 h 30 min to minimize water temperature differences between incubations for CR and NCM and among sampling dates. Dissolved oxygen concentration and temperature were measured with an oxygen meter HQ30D (HACH Company, Colorado, USA) at the beginning and at the end of the incubations. The temperature in the chambers never

exceeded stream temperature by more than 2°C. The community biomass from the chambers was estimated in the same way as indicated above (see “Biomass” section). The metabolic rates (CR, NCM) of seston were subtracted from the metabolic rates of the other communities, and the metabolic rates of angiosperm were subtracted from the metabolic rates of epiphyton-angiosperm. The metabolic rates (CR, NCM) of communities were expressed as (mgO<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>). Gross community productions (GCP) were assumed as the sum of CR and NCM, also expressed as (mgO<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>). Then, we scaled up these CR and NCM data to ecosystem levels by multiplying the biomass of each community (g DW m<sup>-2</sup>) and thus obtained the CR and NCM per stream reach surface (mgO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup>; Naegeli & Uehlinger, 1997; Fellows et al., 2001).

### Ecosystem metabolism

The ecosystem metabolism was measured with the open-channel 1-station technique on each sampling date (Odum, 1956; Uehlinger & Naegeli, 1998). We selected one homogeneous segment in each stream and determined the length of each studied reach within segments as ( $\Delta x \sim 3v/k$ ), where  $v$  is the average flow velocity and  $k$  is the reaeration coefficient (Chapra & Di Toro, 1991). Based on preliminary measures of  $\Delta x$  length, we found a mean  $\Delta x$  of 354 m ( $\pm 126$  m). So, we standardized the reach lengths at 350 m. All fieldwork was carried out in these stream reaches. Metabolism was measured at least 5 days after the last rainfalls, reducing the interference of rain in the stream metabolism. The oxygen meter was placed at the downstream edge of a 350-m reach. The probe was deployed in the thalweg of the stream, about 5 cm below the water surface. The oxygen meter recorded DO, DO saturation percentage, temperature, and pressure in 10-min intervals for 24 h. The net metabolism of the ecosystem (NM, expressed as gO<sub>2</sub> m<sup>-2</sup> · min<sup>-1</sup>) was calculated with the following equation:

$$NM = \left[ k(DO(t) - DO_s(t)) + \frac{dDO(t)}{dt} \right] z$$

where  $k$  is the reaeration coefficient (min<sup>-1</sup>) corrected by temperature ( $k = k_{20^\circ C} \times 1.024^{(T-20^\circ C)}$ ; Elmore & West, 1961; Bott, 2006); DO is the dissolved oxygen concentration (g m<sup>-3</sup>); DO<sub>s</sub> is the saturated

concentration of DO under the given temperature and atmospheric pressure (g m<sup>-3</sup>) condition; and  $z$  is the mean stream depth (m). We estimated  $k$  based on the decrease in DO during the night (PAR < 1 - μEm<sup>-2</sup> s<sup>-1</sup>; Marzolf et al., 1994). Given that only ten of the 15 linear regressions to obtain  $k$  showed  $r^2 \geq 0.60$ , we also estimated the  $k$  based on a hydrological characteristic:

$$k_H = 8784v^{0.734}z^{-0.420}S^{0.930}$$

where  $S$  is the slope in m m<sup>-1</sup> (Thyssen et al., 1987). Since the regression to compare both estimators was significant ( $k = 0.962 k_H + 0.094$ ,  $r^2 = 0.66$ ), we calculated the  $k$  of the five cases that had  $r^2 < 0.60$  as a function of  $k_H$ . The DO and the temperature series were smoothed: each time  $t_i$  (min) was fitted with a normal distribution centered at  $t_i$  and with a standard deviation of 0.05 days (Uehlinger et al., 2000). The calculation of the derivative with the polynomial fitting technique strongly reduces the possibility of errors in DO and temperature measurements, which is greatly amplified by the differentiation process (Shoup, 1983). Daily NM was calculated as the sum of NM over 24 h, daily ecosystem respiration (ER) as the sum of NM during the night and respiration rates during the day (calculated as the linear interpolation between the NMs of sunrise and sunset of the nights before and after the day, respectively), and daily gross primary production (GPP) as the sum of daily NM and daily ER (Odum, 1956).

The uncertainties ( $u$ ) of daily metabolism descriptors were calculated according to Demars et al. (2011). The relative uncertainties of net metabolism ( $u_{(NM)}/NM$ ) were calculated and propagated for each time step (10-min interval) based on one standard deviation ( $\pm 1\sigma$ ), using the square root of the  $\Sigma(\sigma)^2$  for sums and the square root of the  $\Sigma(\sigma/x)^2$  for multiplications. The  $u_{(GPP)}$  were based on every 10-min time step  $i$  (1, ...,  $n$ ) of the NM and ER minus 1 standard deviation ( $-1\sigma$ ):

$$u_{(GPP)} = \left( GPP - \sum_{i=1}^n \left( \frac{NM_{-1\sigma} - ER_{-1\sigma}}{n} \right) \right)$$

The  $u_{(ER)}$  were calculated as the average of all the relative uncertainties calculated for each time step during the night. The  $u_{(GPP/ER)}$  were calculated according to the error propagation (Bevington & Robinson, 2002)

$$u_{(GPP/ER)} = GPP \sqrt{\left(\frac{u_{GPP}}{GPP}\right)^2 + \left(\frac{u_{ER}}{ER}\right)^2}$$

The metabolism measurements made at community scales (scaled  $\Sigma GCP$  and  $\Sigma CR$ ) and ecosystem scales (GPP and ER, respectively) were compared to discern if the methodologies were comparable using a correlation analysis (Naegeli & Uehlinger, 1997). The comparison was made with the chamber incubation data and with the open-channel data from the period between 10:30 h and 13:30 h. The sum of CR ( $\Sigma CR$ ) was subtracted to the ER to estimate the hyporheic contribution to the ER (Naegeli & Uehlinger, 1997; Fellows et al., 2001). Then, GPP and ER were partitioned among five communities and hyporheos to estimate the relative contribution of each community as a percentage (Naegeli & Uehlinger, 1997). Finally, the photosynthesis–irradiance relation was tested using a nonlinear regression analysis according to the hyperbolic tangent function (Jassby & Platt, 1976)

$$GPP = GPP_{\max} \tanh\left(\frac{\gamma PAR}{GPP_{\max}}\right)$$

where  $GPP_{\max}$  is light-saturated photosynthesis and  $\gamma$  is the initial slope of the GPP-PAR curve.

#### Data analysis

The normality of all the response variables was checked with the Shapiro–Wilkinson test, and response variables were transformed when necessary. Unless stated otherwise, the results of stream variables are the means of three replicates. Variance of each community metabolism at the ecosystem scale ( $\text{mgO}_2 \text{ m}^{-2} \text{ h}^{-1}$ ) was calculated from the variances of biomass ( $\text{g m}^{-2}$ ) and community metabolism ( $\text{mgO}_2 \text{ g}^{-1} \text{ h}^{-1}$ ) according to Goodman (1960). To examine which variables contributed to variation among seasons, we conducted a principal component analyses (PCA) with the group of meteorological and limnological variables (SPSS 11.5 Inc., Chicago, Illinois, USA). The weight of a variable on a PCA component was considered relevant when its loading was  $>0.6$ . The relation of metabolism descriptors (GPP, ER, GPP/ER, and the relative contributions of GCP and CR to stream metabolism) and community biomass with the meteorological–limnological variables was examined using multiple linear regression (MLR),

with the scores of the components of the PCA as independent variables and the metabolism parameters (GPP, ER, and GPP/ER) as dependent variables (SPSS 11.5). MLR were performed for each possible model, and the model with the highest  $r^2$ -value was chosen. The importance of the selected component in each of the MLR models was assessed on the basis of their final significance level in the complete model (Borcard et al., 1992). We only showed the best models.

## Results

### Meteorological, hydrological, and physicochemical factors

Temperature, sunlight, and evaporation rates were maximum in summer and minimum in winter. The frequency and quantity of rainfalls prior to the sampling dates were higher in spring and summer than in autumn and winter, determining a seasonal difference of accumulated rainfalls. Consistent with the flat topography of the Wet Pampa, the three Pampean streams presented high conductivity ( $>900 \mu\text{S cm}^{-1}$ ) and pH ( $>7.5$ ), and low slopes ( $<0.15\%$ ), velocities ( $<0.3 \text{ ms}^{-1}$ ), and oxygen reaeration rates ( $<15 \text{ day}^{-1}$ ). The inorganic nutrient concentrations were higher than the nutrient limitation for primary producer growth (Table 1). The stream water was classified as eutrophic (P-TDP =  $0.31 \pm 0.20$  ppm, N-TDN =  $5.93 \pm 4.30$  ppm,  $n = 15$  of all data) because the total dissolved nutrients were always higher than the meso-eutrophic boundary (P-TDP  $> 0.075$  ppm; N-TDN  $> 1.50$  ppm).

The first component of the PCA (PC1) explained 34.83% of the variance, with a positive loading of DOC (0.85), rainfalls  $R_{20}$  (0.81), water balance  $\Delta W_{20}$  (0.67), width  $w$  (0.71), and hydraulic ratio  $h$  (0.63), and a negative loading of streambed light ( $-0.67$ ; Fig. 1A). The second component of the PCA (PC2) accounted for 27.55% of the variance, with a positive loading of discharge  $Q$  (0.86), depth  $z$  (0.81), reaeration  $k$  (0.80), velocity  $v$  (0.74), and DIN (0.65; Fig. 1A). Finally, the third component (PC3) accounted for 13.56% of the variance, with a positive loading of mean daily temperature (0.85) and water surface dPAR (0.74), and a negative loading of water balance  $\Delta W_{20}$  ( $-0.71$ ). The seasonality of the meteorological and hydrological conditions could be

**Table 1** Meteorological, hydrological, and physicochemical characteristics and community biomass during the sampling dates

		Early spring	Late spring	Summer	Autumn	Winter
Climatic factors	d PAR (mE m <sup>-2</sup> day <sup>-1</sup> )	728 (70)	817 (246)	876 (58)	429 (69)	370 (12)
	Daytime (h)	12.4 (0.4)	14.4 (0.0)	13.2 (0.4)	10.4 (0.4)	10.1 (0.1)
	Water temp. (°C)	17.1 (4.7)	23.8 (6.4)	25.9 (3.7)	14.6 (3.8)	9.4 (3.3)
	R <sub>20</sub> (mm day <sup>-1</sup> )	2.4 (0.6)	4.7 (1.0)	7.9 (1.1)	1.8 (0.8)	1.6 (0.4)
	ΔW <sub>20</sub> (mm day <sup>-1</sup> )	– (1.0)	– (2.7)	1.3 (1.3)	0.0 (1.2)	1.0 (0.8)
		1.4	2.3			
Hydrological factors	z (m)	0.28 (0.05)	0.43 (0.20)	0.48 (0.19)	0.40 (0.06)	0.40 (0.04)
	w (m)	3.88 (0.73)	4.25 (0.49)	4.28 (0.91)	4.22 (0.43)	4.27 (0.38)
	h (m)	0.22 (0.01)	0.30 (0.08)	0.36 (0.08)	0.30 (0.03)	0.30 (0.02)
	v (m s <sup>-1</sup> )	0.09 (0.03)	0.19 (0.08)	0.27 (0.06)	0.24 (0.05)	0.26 (0.10)
	Q (L s <sup>-1</sup> )	134 (89)	361 (298)	461 (131)	87 (33)	222 (92)
	k (day <sup>-1</sup> )	4.6 (3.1)	7.2 (3.8)	12.6 (3.5)	9.6 (0.1)	8.6 (2.3)
Physical & chemical factors	K <sub>light</sub> (m <sup>-1</sup> )	1.87 (0.53)	1.42 (0.21)	1.48 (0.34)	1.64 (0.73)	0.94 (0.08)
	Streambed dPAR (mE m <sup>-2</sup> day <sup>-1</sup> )	252 (129)	255 (192)	212 (165)	119 (64)	159 (12)
	P-SRP (ppm)	0.09 (0.04)	0.18 (0.06)	0.39 (0.15)	0.18 (0.09)	0.27 (0.17)
	P-DOP (ppm)	0.04 (0.02)	0.13 (0.04)	0.10 (0.03)	0.13 (0.01)	0.04 (0.02)
	N-DIN (ppm)	1.80 (1.12)	2.42 (0.63)	2.78 (0.53)	2.60 (0.50)	2.03 (0.77)
	N-DON (ppm)	0.18 (0.17)	4.10 (2.64)	4.15 (2.17)	3.17 (2.78)	6.85 (4.27)
	DOC (ppm)	1.78 (0.06)	1.77 (0.06)	1.79 (0.09)	1.78 (0.08)	1.71 (0.01)
Community biomass (gDW m <sup>-2</sup> )	Angiosperms	11.6 (8.9)	23.8 (12.9)	19.4 (10.3)	14.9 (9.6)	16.2 (12.3)
	Macroalgae	9.1 (7.9)	1.1 (1.9)	–	5.3 (4.6)	25.0 (11.9)
	Seston	6.4 (5.3)	12.1 (8.6)	12.0 (6.6)	4.1 (2.8)	7.5 (2.1)
	Epiphyton	7.0 (5.3)	6.7 (5.1)	7.9 (5.5)	0.9 (0.4)	4.2 (3.6)
	Epipelon	3.9 (0.5)	2.8 (0.5)	2.8 (1.1)	2.2 (0.4)	1.9 (0.7)

Values are mean of data from the three studied streams (La Choza, de la Cruz, and El Contador) and standard deviation is between parentheses

dPAR daily photosynthetic active radiation, R<sub>20</sub> accumulated rainfalls in the previous 20 days, ΔW<sub>20</sub> water balance in the previous 20 days, z depth, w width, h hydraulic ratio, v velocity, Q discharge, k reaeration coefficient, K<sub>light</sub> light attenuation coefficient, SRP soluble reactive phosphorus, DOP dissolved organic phosphorus, DIN dissolved inorganic nitrogen, DON dissolved organic nitrogen, DOC dissolved organic carbon

differentiated with the first two principal components (Fig. 1B).

**Biomass**

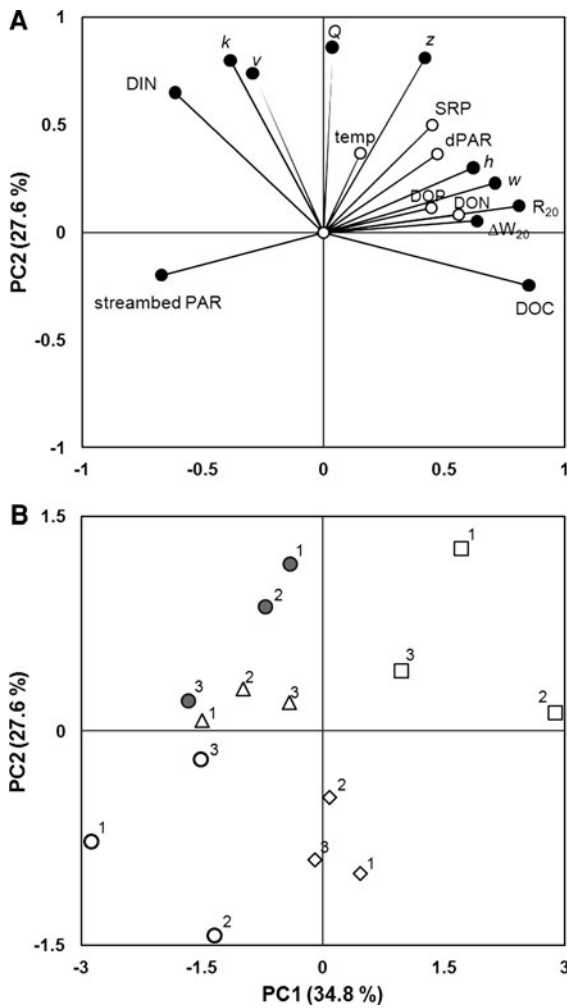
In general, the epipelon had the lowest biomass of the ecosystem (~2 to 4 g DW m<sup>-2</sup>), while macrophytes had the highest biomass (~10 to 20 g DW m<sup>-2</sup>). The seasonal variation of macroalgal biomass was the highest one, being the most important community biomass in winter and being almost nil during the summer (Table 1). The biomass (B) of macroalgae was negatively related to PC1 and PC3 (log<sub>10</sub>B = 0.49 – 0.27PC1 – 0.26PC3, r<sup>2</sup> = 0.41, P < 0.05), whereas that of angiosperms was

positively related to PC2 (log<sub>10</sub>B = 1.06 + 0.28PC2, r<sup>2</sup> = 0.34, P < 0.05).

**Metabolism of communities**

The epipelon showed the highest primary productivity and respiration. Only the macrophytes and the epiphyton showed a clearly autotrophic metabolism (GCP/CR > 1). Neither the GCP nor the CR of angiosperms varied among seasons. The GCP of seston, epiphyton, and epipelon and the CR of seston and epiphyton were lower in summer than in late spring and winter (Table S1). At the ecosystem level, the epipelon was the main contributor to ER and GPP. The second main contributors





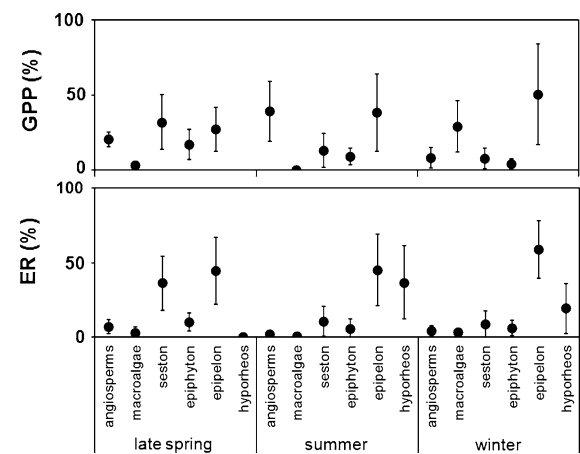
**Fig. 1** Principal component analysis of the selected variables, where closed circles denote relevant variables (loading >0.6; see Table 1 for variable definitions) (A); and multivariate space with the distribution of the 15 sampling units (3 streams × 5 dates) (B). Streams are shown as La Choza (1), de la Cruz (2), and El Contador (3). Seasons are shown as early spring (white circles), late spring (gray circles), summer (squares), autumn (diamonds), and winter (triangles). The percent values on each axis represent the amount of variance explained by each component

to GPP were seston in late spring, angiosperms in summer, and macroalgae in winter. The second main contributors to ER were seston in late spring and hyporheos in summer and winter (Fig. 2). The contribution of epipelton to ER was negatively related to PC1 ( $r^2 = 0.38$   $P < 0.05$ ). The contribution of macroalgae to GPP and ER was negatively related to PC1 ( $r^2 = 0.54$  and  $r^2 = 0.48$ ,  $P < 0.05$ , respectively). The contribution of the hyporheic zone to ER was positively related to PC1

( $r^2 = 0.56$ ,  $P < 0.01$ ). Finally, the contribution of epiphyton and angiosperms to GPP was positively related to PC3 ( $r^2 = 0.39$  and  $r^2 = 0.76$ ,  $P < 0.05$ , respectively).

### Ecosystem metabolism

The ecosystem GPP was associated with the total biomass of the producers ( $r = 0.93$ ,  $P < 10^{-5}$ ). Respiration increased from early spring to winter, leading to a decrease in NM. GPP and ER were also positively correlated ( $r = 0.59$ ,  $P < 0.05$ ). Both GPP and ER were reduced in summer, but GPP increased in early spring and ER increased in winter (Fig. 3). The mean relative (min–max) uncertainties in GPP, ER, and GPP/ER were 37% (20–58%), 33% (18–46%), and 46% (25–65%), respectively. The primary production obtained with the chamber method ( $\Sigma$ GCP) and the open-channel method (GPP) was highly correlated ( $r = 0.87$ ,  $P < 0.005$ ). The respiration obtained by the chamber method ( $\Sigma$ CR) and the open-channel method (ER) was marginally related ( $r = 0.54$ ,  $P = 0.09$ ). This non-relationship was an expected result given that the  $\Sigma$ CR does not consider hyporheic respiration. Therefore, we assumed that both the primary production and the respiration obtained by the chamber method are comparable to those obtained by the open-channel method. The contribution of the hyporheic zone (ER minus  $\Sigma$ CR) to ER varied with seasons,



**Fig. 2** Relative contribution (%) of each autotrophic community and hyporheic zone to the gross primary production (GPP) and the ecosystem respiration (ER). Values in percentages are means ( $\pm$ SD,  $n = 3$ )

being close to zero in late spring, highest in summer, and with intermediate values in winter (Fig. 2).

The ecosystem metabolism descriptors and PC1 were negatively related:  $\log_{10}GPP = 0.65 - 0.20PC1$ ,  $r^2 = 0.69$ ,  $P < 0.001$ ;  $ER = 7.84 - 3.24PC1$ ,  $r^2 = 0.71$ ,  $P < 0.001$ ; and  $GPP/ER = 0.77 - 0.32PC1$ ,  $r^2 = 0.59$ ,  $P < 0.005$  (Fig. 4). Hence, ecosystem metabolism increased with streambed light and decreased with accumulated rainfalls in the previous days, affecting more GPP than ER.

The relation between the GPP rate and PAR varied with the seasons (Fig. 5), showing three different patterns: (a) In early spring, the relations were almost linear; (b) in late spring, summer, and autumn, the relations showed a light saturation of GPP and a clockwise hysteresis (GPP was lower than expected during the afternoon); and (c) in winter, the relation showed a counterclockwise hysteresis (GPP was lower than expected during the morning). The degree of light saturation of GPP was estimated from the  $GPP_{max}$  and  $\gamma$  parameters, being maximal in early spring and winter (Table 2).

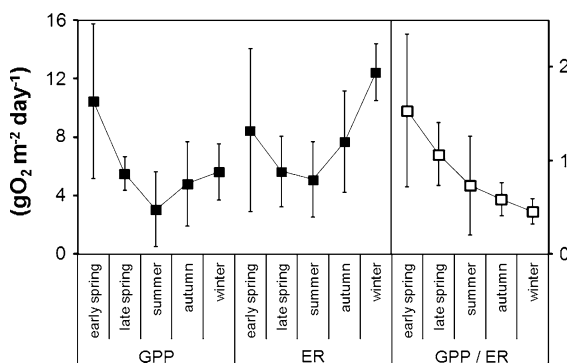
## Discussion

The hypothesis that the hydrological conditions after rainfalls negatively affected stream metabolism is fully supported by our results. The rainfalls in the previous days caused hydrological instability, principally affecting the water color (DOC) and thus the light availability to the autotrophic activities of the

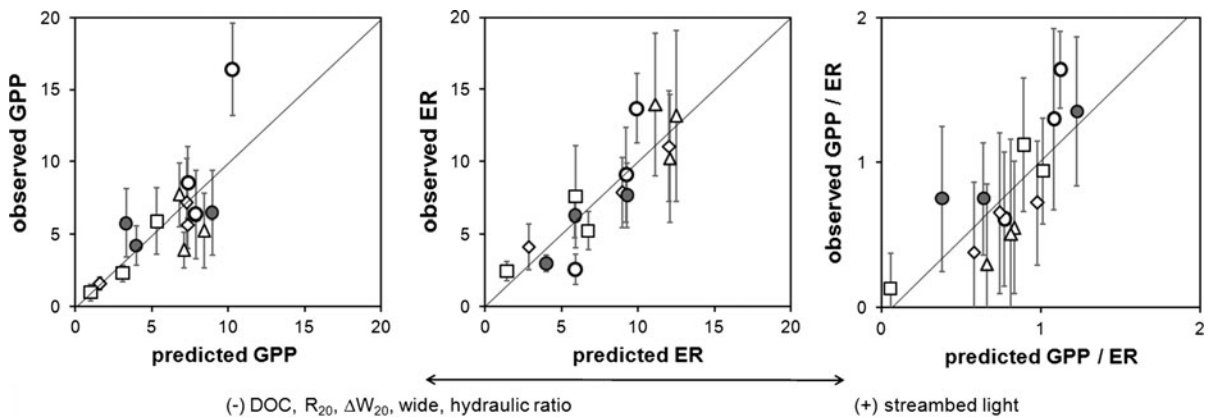
stream biota. Flow events not only reduced both GPP and ER but also reduced GPP/ER. ER was less sensitive than GPP to rainfall periods because the respiration of hyporheos was increased by the increase in the size of the hyporheic zone and groundwater levels (Uehlinger & Naegeli, 1998; Aragón et al., 2011). Hence, ER is probably less affected by high flows than the channel surface to which GPP is restricted. The decrease in biomass and community metabolism after a flood event in Pampean streams has been previously reported (Vilches & Giorgi, 2010; Acuña et al., 2011). Additionally, several studies have shown that floods drive key ecological processes, such as energy flow, nutrient cycling, and population dynamics, as well as photosynthesis and respiration of stream communities (Uehlinger & Naegeli, 1998; Johnson et al., 2005; De Loe, 2008).

Flood events could affect the availability of factors relevant for autotrophs, such as nutrients and light. Phosphorus and nitrogen concentrations in the water were not scarce for the primary producer activity in any season (the trophic state was always eutrophic). In contrast, the seasonal pattern of streambed light (5 days after the last rainfalls) showed a decrease from early spring to summer, being negatively related to the rainfalls, principally due to the increase in DOC from runoff inputs. DOC affects primary production through physical and chemical processes, decreasing the underwater light climate to autotrophs (colored water) and scavenging nutrients and micronutrients from the water (Jackson & Hecky, 1980). So, primary production was restricted by the light availability, even during periods of the greatest radiation such as summer.

It is interesting that the discharge was not associated with stream metabolism. Probably, the kinetic hydrological factors (discharge, velocity; PC2) also depend on seasonal differences of groundwater inputs (Aragón et al., 2011). For instance, the mean discharges of winter were higher than expected based on the scarce previous rainfalls, due to the low evaporation and the groundwater inputs. We found an increase in DOC with rainfalls (PC1) but not with discharge (PC2). The runoff water often contains higher concentrations of humic compounds than groundwater. Hence, the light attenuation in the increased flow due to groundwater inputs, such as that observed during winter, could be lower than in the increased flow from runoff inputs, such as that observed during summer.



**Fig. 3** Temporal variation of gross primary production (GPP), ecosystem respiration (ER), and GPP/ER. Means ( $\pm$ SD) were estimated with the data registered at three streams (La Choza, de la Cruz, and El Contador)



**Fig. 4** Observed vs predicted gross primary production (GPP,  $\text{gO}_2 \text{ m}^{-2} \text{ day}^{-1}$ ), ecosystem respiration (ER,  $\text{gO}_2 \text{ m}^{-2} \text{ day}^{-1}$ ), and GPP/ER of the three streams. Seasons are shown as early

spring (white circles), late spring (gray circles), summer (squares), autumn (diamonds), and winter (triangles). Error bars indicate the uncertainty of measurements

### Role of communities in stream metabolism

Flood events could affect the ecosystem metabolism by shifting the community metabolisms. We found that the lowest ecosystem primary production and respiration during summer—a period of high rainfalls—was due to the diminished primary production of the epipelton, epiphyton, and seston and the diminished respiration of epiphyton and seston. In contrast, hyporheic respiration depends on the size of the hyporheic zone and, consequently, on the water volume of the channel (i.e., width, hydraulic ratio). We found an increase in hyporheic respiration with rainfalls, determining a lower decrease in ER with rainfalls with respect to GPP. Rainfalls increased the water volume of the channel and the connectivity between ground and surface water, allowing an increase in the size of the hyporheic zone (Aragón et al., 2011). During late spring, the net loss of surface water to the atmosphere caused the reduction of channel water levels, determining nearly null hyporheic respiration. During summer, heavy rainfalls caused a positive balance for water, determining an increase in the size of the hyporheic zone by high levels of ground, subsurface, and surface water and determining the highest hyporheic respirations (~37%). Similar results were found in a previous study on the metabolism of a Pampean stream, where almost half of the ecosystem respiration was provided by hyporheos (Acuña et al., 2011). Finally, during winter, the water balance was positive again for land

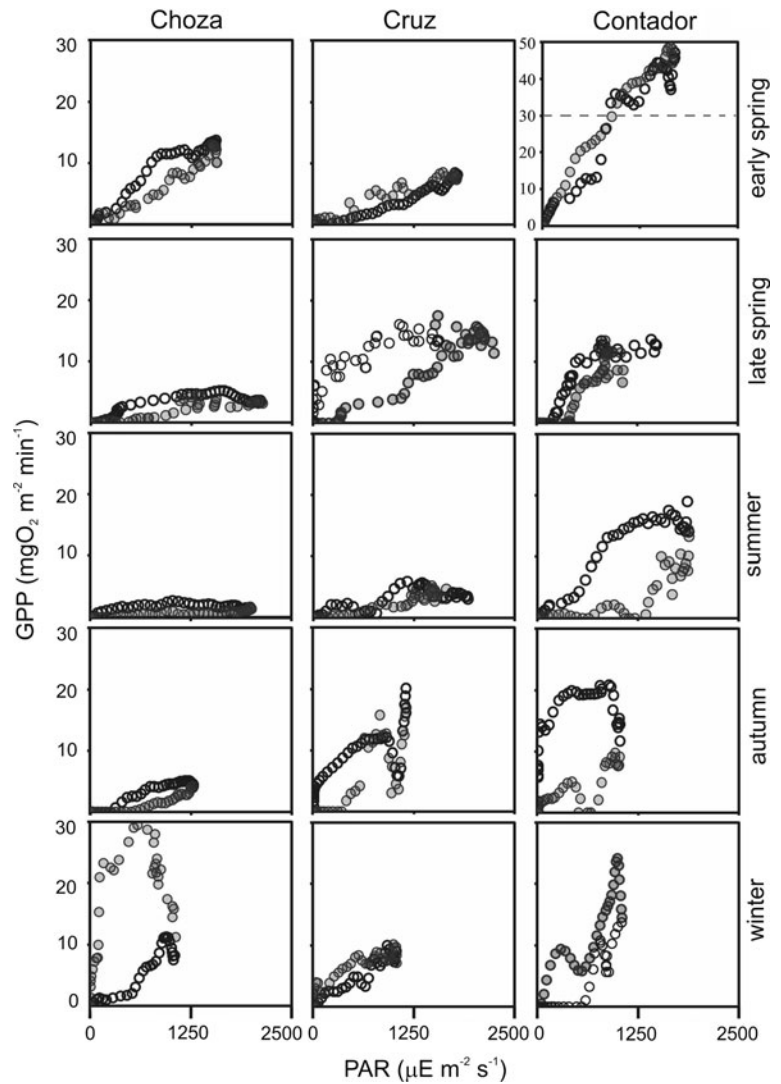
water (Table 1), allowing an increase in the size of the hyporheic zone and an increase in hyporheic respiration (20%; Fig. 2).

Flood events also affect the ecosystem metabolism by dragging the community biomass downstream. Macroalgae showed the lowest resistance to flow events because of their morphological characteristics such as low or absent root development and high buoyancy. The high macroalgal growth rates explain their ability to recover quickly after flooding disturbances in winter (Wetzel, 2001; Acuña et al., 2011).

### Effects of light and temperature on stream metabolism at day scale

Daily GPP was not directly related to light or temperature (PC3). Nevertheless, the nonlinear GPP-PAR curves in the course of the day could be the consequence of light and temperature effects. During early spring, ecosystem autotrophs presented highly efficient GPP all day long (Mann & Wetzel, 1999). Instead, during late spring and summer, the GPP of ecosystem autotrophs was saturated at noon and decreased more than expected in the afternoon, possibly due to the higher sensitivity of ER to temperature than GPP and the increase in photorespiration and photoinhibition of autotrophs during the day (Hough, 1974; Parkhill & Gulliver, 1998; Wetzel, 2001). During autumn, low flows could have constrained GPP due to the low oxygen diffusion from the water to the cells (Wetzel, 2001), and during winter,

**Fig. 5** Gross primary production (GPP) versus PAR measured every 10 min in the three streams during the five sampling dates (the GPP of Contador stream during early spring is shown at a different scale). Measurements in the morning are indicated as white open circles and measurements in the afternoon as gray circles



**Table 2** Light-saturated photosynthesis  $GPP_{max}$  ( $gO_2 m^{-2} day^{-1}$ ) and the initial slope ( $\gamma$ ) of the GPP-PAR relation estimated in the La Choza, de la Cruz, and El Contador streams

	Early spring	Late spring	Summer	Autumn	Winter
$GPP_{max}$	40.8 (32.1)	17.7 (9.4)	12.7 (15.4)	23.9 (13.7)	40.3 (25.5)
$\gamma$	0.017 (0.017)	0.011 (0.007)	0.005 (0.002)	0.020 (0.019)	0.046 (0.054)

Values are means ( $\pm$ SD)

the low temperature at sunrise ( $\sim 7^\circ C$ ) could have constrained GPP in the mornings (Acuña et al., 2004). Hence, the high light intensities affected GPP and water temperature variations affected both GPP and ER at the day scale, but their effects were not detectable at the season scale.

Conclusions about seasonality of the metabolism of Pampean streams

In early spring, moderate radiation and negative water balance led to high hydrological stability and high light available for the growth of the primary producers,



explaining the highest net and gross production. In contrast, the intense rainfalls of late spring and summer decreased the flow stability and the light availability, and caused the washout of macroalgae. In addition, the high light intensity saturated GPP during the afternoon. These conditions caused the lowest metabolism of communities living in the channel and the highest hyporheic respiration, determining a higher decrease in GPP than in ER. In autumn and winter, the few flood events and the positive water balance caused, in turn, a mean discharge and a high hydrological stability, allowing the expansion of filamentous macroalgae and a mean hyporheic respiration. At the day scale, the lowest temperatures constrained GPP during the morning. Hence, the hydrological stability favored GPP and ER, but the low temperature and low sunlight promoted heterotrophic processes over autotrophic ones.

Our results support the hypotheses that whole-stream metabolism is mainly driven by rainfalls through its effects on the available light to primary producer metabolisms, the hyporheic respiration, and the community biomass. Furthermore, on a daily timescale, stream metabolism was also modulated by light and temperature. These insights into the ecology of non-forest lowland streams must be, however, treated with caution because of the low number of replications. Hence, more empirical and theoretical studies need to be performed for the complete understanding of how weather conditions affect the metabolisms of non-forest lowland streams.

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