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As productive and slow as a stream can be—the metabolism of a Pampean stream

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Abstract. Stream metabolism at both ecosystem and functional-compartment scales was measured in a low-order Pampean stream (La Choza) over a 3-wk period to characterize metabolic rates and discern the contribution of each functional compartment (submerged macrophytes, benthos, floating macroalgae, water column, and hyporheic zone) to ecosystem metabolism. La Choza stream is an autotrophic ecosystem during low flows and has gross primary production rates of up to 22 g O_2 $m^{-2}d^{-1}$, which are among the highest reported in the literature and set an upper bound on how productive streams can be in the absence of light and nutrient limitations. Floating macroalgae provided most of the primary production (30–90%), whereas the hyporheic zone provided most of the ecosystem respiration (40–80%). The differential effects of high flows on the different functional compartments depressed the production:respiration ratio, suggesting a strong relationship between flow and metabolism. Thus, low flows enhanced primary production and led to diel dissolved O_2 concentration oscillations between 0 and 25 g O_2/m^3. In contrast, high flow depressed primary production by an order of magnitude and increased ecosystem respiration. High production rates during the low-flow period and extreme physicochemical conditions (anoxia for 7–8 h on a daily basis) may be typical in this type of ecosystem during extended low-flow periods.

Key words: stream ecology, ecohydrology, ecosystem metabolism, Pampean streams, metabolism partitioning.

Measurements of ecosystem metabolism (gross primary production [GPP] and ecosystem respiration [ER]) provide information about energy and material fluxes through ecosystems (Odum 1956). In lotic ecosystems, metabolism is highly integrative and is sensitive to riparian cover (Bunn et al. 1999, Hill and Dimick 2002), nutrient status (Guasch et al. 1995, Mulholland et al. 2001, Mallin et al. 2004), organic pollution (Quinn and McFarlane 1989, Rutherford et al. 1991), siltation (Peterson 1996, Hill et al. 1998), metals (Hill et al. 1997, Niyogi et al. 2002), and changes in discharge (Young and Huryn 1997, Uehlinger and Naegeli 1998, Uehlinger 2000, Acuña et al. 2004). Differences in these factors explain variations in GPP and ER over time and space in river networks and among lotic ecosystems in different biomes (Webster et al. 2003).

Our knowledge of stream ecosystem metabolism is limited by 2 factors. Most research has been done in northern-hemisphere, forested streams and metabolism usually has been measured at either the ecosystem or the functional-compartment scales. Indeed, most studies on stream metabolism have been done in forested systems characterized by large inputs of terrestrial organic C and low light availability. The bias towards light- and nutrient-limited streams constrains our understanding of stream metabolism because there are few measurements of primary production under nonlimiting light and nutrient conditions. Streams in the Pampean biome

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might provide an upper bound on GPP because neither nutrients (mainly N and P) nor light are usually limiting in this biome (Feijoó et al. 1999, Mercado 2003, Giorgi et al. 2005).

Measurements at both the functional-compartment and the ecosystem scale have rarely been made at the same study site. Metabolism at the ecosystem level has been measured with the open-channel technique introduced by Odum (1956) and modified by others (Marzolf et al. 1994, Young and Huryn 1998, Reichert et al. 2009). Metabolism at the functional-compartment scale traditionally has been measured in chambers (McIntire et al. 1964). Most studies at this scale were focused on the benthic compartment (e.g., Bott et al. 1985), and few have quantified metabolism in the hyporheic compartment (Naegeli and Uehlinger 1997). The metabolism of the hyporheic compartment can be measured directly or estimated as the difference between ecosystem and benthic metabolism (Naegeli and Uehlinger 1997, Fellows et al. 2001).

The goal of our study was to characterize metabolic rates in a typical Pampean stream and to discern the contribution of each functional compartment (submerged macrophytes, benthos, floating macroalgae, water column, and hyporheic zone) to stream ecosystem metabolism. Initial expectations were that: 1) the high irradiance values in a Pampean stream might cause high GPP rates, and 2) most ER might occur in the surface compartment rather than in the hyporheic compartment because of the semi-impervious character of the stream beds in the Pampean region. We measured metabolic rates at the ecosystem and functional-compartment levels during 3 wk coinciding with the period of maximum light availability.

Methods

Site description

The Pampean biome (lat 30–39°S) occupies the eastern plains of Argentina, Uruguay, and the southern extreme of the state of Rio Grande do Sul in Brazil. The region is extremely flat with a warm-temperate climate, rainfall distributed throughout the year (range: 600–1200 mm), and mean annual temperatures between 13 and 17°C (Cabrera and Willink 1980). Under natural conditions, vegetation in the region is grassland, with annual grasses adapted to the occurrence of fires in summer and frost in winter. Most Pampean streams originate in small depressions with emergent plants, such as *Schoenoplectus californicus* or *Typha latifolia*, which also can be found in their midcourses. These streams cross plains with fertile soils formed after loess deposition during the Quaternary. Stream beds are characterized by fine sediments (primarily silt and clay) underlain by hard and homogeneous substrata with high $CaCO_3$ content. Stones and pebbles are absent (Giorgi et al. 2005).

We worked in a 100-m reach in La Choza stream that was representative of many Pampean streams (similar slope, composition, and extent of macrophytes) described in previous studies (Giorgi et al. 2005, Feijoó and Lombardo 2007). La Choza stream is a 2^{nd}-order stream draining a ~48-km^2 catchment within the Reconquista River basin of Buenos Aires, Argentina. It has a mean slope of 0.02%, no riparian tree vegetation, and flow ranging from 1 to 30 L/s. As is common in Pampean streams, La Choza stream has a trapezoidal cross-section. The flow regime of streams in this area can be classified as mesic groundwater sensu Poff and Ward (1989). Major land cover in the catchment upstream of the study reach consists of rangeland (75%), extensive cropland (22%), and residential development (3%).

Physicochemical characterization

We obtained a data series for photosynthetically active radiation (PAR) from a meteorological station 15 km from the study site (National University of Luján). We measured discharge at the beginning and end of the study reach and reach nominal travel time weekly during the study period. During each measurement, we released 10 L NaCl solution (2 kg NaCl; slug injection) 50 m upstream of the upstream reach edge to ensure complete mixing and recorded electrical conductivity in 1-min intervals at the upstream and downstream reach limits. Electrical conductivity was measured with YSI 600 OMS V2 multiparameter sondes (YSI Inc., Yellow Springs, Ohio), which were calibrated according to manufacturer specifications. We chose a mixing reach of 50 m on the basis of previous tracer experiments in which electrical conductivity was measured in cross-sections at increasing distances from the injection point until homogeneity in the cross-section was reached. The amount of discharged NaCl was sufficient to increase the background conductivity concentration by $\geq$200 μS/cm to ensure a robust signal-to-noise ratio in the measurements. We calculated discharge based on methods in Gordon et al. (2004). We calculated nominal travel time of water (τ) based on the time when the conductivity peak passed a station. We calculated mean flow velocity by dividing the length of the study reach by τ. We measured stream width (width of the wetted channel) every 10 m and calculated mean stream width between stations. We

calculated mean depth (z) as

$$z = \frac{Q}{vw} \quad [1]$$

where Q is discharge (m^3/s), v is mean flow velocity (m/s), and w is stream width (m).

We collected streamwater samples for nutrient analyses in prerinsed polyethylene bottles and filtered the samples within 2 h of collection through glass-fiber filters (pore size = 0.7 μm; Whatman GF/F filters, Maidstone, UK). We stored water samples at 4°C and transported them to the laboratory for analysis within 24 h. We measured soluble reactive P (PO_4^{3-}-P) with the ascorbic acid method (APHA 1998), NO_2^--N and NO_3^--N by reaction with sulfanilamide (with a previous Cd reduction in the case of NO_3^-) (APHA 1998), and NH_4^+-N with the phenol-hypochlorite method (Wetzel and Likens 1991). We analyzed all nutrients with a Hitachi U-2001 spectrophotometer (Hitachi Ltd, Tokyo, Japan).

Ecosystem metabolism

We measured ecosystem metabolism and metabolism of the existing functional compartments (submerged macrophytes, floating macroalgae, benthos, and water column) over a 3-wk period from 19 November to 6 December 2008, which is within the period of maximum light availability and temperature in the Pampean biome.

We installed 2 monitoring stations at the upstream and downstream edges of a 100-m homogeneous reach to estimate ecosystem metabolism with the open-channel 2-station technique (Odum 1956, Marzolf et al. 1994, Reichert et al. 2009). The length of the selected reach was within the range suggested by Reichert et al. (2009) for reliable estimates of ecosystem metabolism with the 2-station technique (0.4–3 × velocity × reaeration coefficient, 50–380 m in our case). At both stations, we recorded dissolved O_2, temperature, and conductivity at 10-min intervals with YSI 6150 optical dissolved O_2 probes connected to a YSI 600 OMS V2 multiparameter sonde. We deployed the probes in the thalweg of the stream, ~5 cm below the water surface during baseflow conditions, from 18 November to 6 December 2008. Before deployment, we calibrated the dissolved O_2 sensors according the manufacturer's manual. After field measurements, sonde-to-sonde variability was determined by immersing the 2 probes simultaneously in a thermoregulated and aerated water bath (± 0.1°C). We adjusted the temperature of the water bath successively to 20, 18, 16, 14, 12, 10, 8, and 6°C and recorded dissolved O_2 every 30 s for 8 h. We calculated saturation concentration of dissolved O_2 according to Bührer (1975) from recorded temperatures and barometric pressure from a nearby meteorological station at the same altitude above sea level (National University of Luján). We determined deviations from the calculated saturation concentration and used them to correct the field dissolved O_2 records. We estimated reaeration coefficients based on the decline of dissolved O_2 concentration after dusk (Hornberger and Kelly 1975). However, we used these reaeration coefficients only if the linear regression performed with the nighttime values had an $r^2 > 0.50$ (5 nighttime reaeration coefficient estimates were excluded from further analyses). Daily reaeration coefficients were the means of values from the nights before and after the day of interest.

We calculated net metabolism rate (NM, expressed as g O_2 m^{-2} min^{-1}) from the dissolved O_2 concentration, water temperature, atmospheric pressure, gas-exchange rate, and flow velocity using the open-channel 2-station technique originally developed by Odum (1956). Specifically, we calculated NM with the estimator for homogenous conditions (Reichert et al. 2009).

$$NM(t) = K\left(\left(C^{dn}\left(t + \frac{1}{K} - \tau\frac{\exp(-K\tau)}{1-\exp(-K\tau)}\right) - C^{up}\left(t + \frac{1}{K} - \tau\frac{\exp(-K\tau)}{1-\exp(-K\tau)} - \tau\right)\exp(-K\tau)\right) \div (1-\exp(-K\tau))\right) - C_{sat}(t)\Bigg) \quad [2]$$

where C^{dn} and C^{up} are the concentrations of dissolved O_2 at the upstream and downstream stations, respectively (g O_2/m^3), K is the reaeration coefficient (min^{-1}), t is time (min), and C_{sat} is the saturation concentration of dissolved O_2 according to Bührer (1975). We estimated NM with this equation and data from the deployed sensors. We based 3 daily metabolic parameters on NM: net ecosystem metabolism (NEM), ER, and GPP. We calculated NEM as the sum of NM over 24 h, ER as the sum of NM during the dark period and respiration rates during the light period (calculated as the linear interpolation between the NMs of sunrise and sunset of the nights before and after the day of interest), and GPP as the difference between NEM and ER.

Functional-compartments metabolism

We used the line–intercept method to map the distribution of substrata in the study reach along 51 equidistant transects spaced 2 m apart (Sokal and Rohlf 1995). Within each transect, we measured the %

stream bed covered by different primary producers (submerged macrophytes, floating macroalgae, benthos). We calculated the mean value of the coverage by each functional compartment across all transects for every sampling date.

We evaluated metabolism of the 4 functional compartments weekly during the study period (19 November, 25 November, 1 December). On each occasion, we ran 3 replicates (chambers) for each functional compartment (submerged macrophytes, floating macroalgae, benthos, water column) for a total of 12 chambers per occasion. We collected samples from random locations throughout the study reach on each sampling date. Samples for the benthic compartment were artificial substrata (trays measuring 130 cm^2 in planar area, 3 cm deep) with fine holes (~1 mm diameter) on all sides of the tray to allow water flow through the substrata. We immersed these trays at random locations in the study reach, filled them with streambed sediment, and allowed colonization for $\geq$60 d. We collected random samples of submerged macrophytes and floating macroalgae (surface area of each sample = 200 cm^2). We used the same chambers for measurements in the water-column compartment but filled them with only stream water.

We placed samples in clear acrylic rectangular chambers (600 cm^2 in planar area, 11 cm deep, volume = 6.6 L) that were operated simultaneously and submerged in the stream during incubations to minimize variability caused by differences in temperature and light conditions. We did not force recirculation inside the chambers because flow velocity in the stream was extremely low (~1 m min^{-1}) and the incubation times were not long enough to create conditions different from those in the stream channel. We measured community respiration (CR) in incubations lasting 2 h in darkness after covering the chambers with black sheets. We measured net community metabolism (NCM) in incubations lasting ~1 h to avoid supersaturated conditions inside the chambers. We did all incubations between 1030 and 1330 h to minimize water temperature differences between incubations for NCM and CR and among weeks. We used a handheld HQ40d O_2 meter (HACH Company, Loveland, Colorado) to measure dissolved O_2 and temperature at the beginning and end of the incubations.

Metabolic rates (CR and NCM) were calculated as

$$\text{CR or NCM} = \frac{\Delta O_2}{\Delta t}\frac{V}{S} \quad [3]$$

where rates are CR or NCM (g O_2 m^{-2} h^{-1}), ΔO_2 is the change in O_2 concentration between final and initial measurements (g O_2/m^3), Δt is the time interval between measurements (2 h for CR and 1 h for NCM) (h), V is the water volume in the chamber (m^3), and S is the surface of the stream bed (m^2). We minimized the distorting effect that metabolic rates occurring in the water column can have on measurements of the other functional compartments by subtracting water-column rates from the other 3 functional compartments (submerged macrophytes, floating macroalgae, and benthos). We transformed metabolic rates in the water column in units of g O_2 m^{-3} h^{-1} into surface units by multiplying them by water depth, measured as the vertical dimension of the metabolism chamber.

We estimated gross community production (GCP) from CR and NCM. We used mean community metabolic rates weighted by the relative spatial extent of each functional compartment to scale up metabolism data from the functional compartment to ecosystem levels.

$$\text{GPP} = \sum_{i=1}^{i=4} s_i \text{GCP}_i \quad [4]$$

$$\text{ER} = \sum_{i=1}^{i=4} s_i \text{CR}_i + \text{R}_{\text{hyporheic}} \quad [5]$$

where GCP_i and CR_i are metabolic rates of the substrate type i, s_i is the surface of the substrate type i in each m^2 of stream bed, and $R_{hyporheic}$ is respiration in the hyporheic zone (see below for details). The sum of individual areas was higher than the actual area of the stream because the area covered by floating macroalgae was counted twice (once for algae and once for benthos). We calculated variance for the product of the metabolic rate in the functional compartment (GCP_i, CR_i) and the spatial extent of each functional compartment assuming independent variables (Goodman 1960; see details above).

We compared GCP and GPP measurements from the incubation period between 1030 h and 1330 h (g O_2 m^{-2} h^{-1}) to discern if the measurements made at the functional-compartment and ecosystem scales matched, and then partitioned GPP and ER among functional compartments following the approach described by Naegeli and Uehlinger (1997). We assumed that the contribution of the hyporheic compartment to ER was the difference between ER and the sum of all the measured respiration values from the benthic compartment (Eqs 4, 5) (Naegeli and Uehlinger 1997, Fellows et al. 2001). The distinction between benthic and hyporheic compartments was set by the depth of the trays used to estimate NCP and CR of the benthic compartment (3 cm depth). The estimate of respiration in the hyporheic compartment

from the difference in the measurements at the ecosystem and benthic compartment levels had an intrinsic error term, which we estimated as the standard deviation of the estimates of the benthic compartment level, obtained from the $\sqrt{}$(sum of variances of each functional compartment), assuming that the estimates from each substrate were independent. After metabolism measurements, we dried the substrates used in the metabolism chambers at 105°C to a constant mass and combusted them at 450°C for ~4 h to estimate ash-free dry mass (AFDM).

We calculated the uncertainty associated with the estimates of GPP and ER from functional-compartment measures. Thus, we calculated variances from the products of the functional-compartment metabolic rates (GCP_i, CR_i) or AFDM and the spatial extent of each functional compartment (assuming independent variables) (Goodman 1960):

$$V(xy) = X^2V(y) + Y^2V(x) + V(x)V(y) \quad [6]$$

where x and y are independent variables, V is variance, and X and Y are the expected values of x and y (mean x and mean y).

To estimate the uncertainty of the calculations of GPP and ER from functional-compartment measures, we used the variances obtained from the field replicates (mainly metabolic rates) for x. However, we did not calculate the variance used for y (spatial extent of each functional compartment) directly from the 51 transects because that variance would express the spatial heterogeneity of the reach rather than the potential error of the method. Instead, we calculated the variance of y with the delete-d jackknife technique (Tukey 1958, Shao and Wu 1989). The basic idea behind the jackknife estimator lies in systematically recomputing the mean value of a set of measurements omitting one observation at a time from the sample set. An estimate for the variance of the mean value of measurements can be calculated from this new set of observations for the mean value of measurements. The delete-d jackknife technique leaves out d observations at a time instead of just 1 observation, where $d \approx \sqrt{n}$ (Shao and Wu 1989). Thus, the jackknife estimate of standard error was defined by:

$$se_{jack} = \sqrt{\frac{r}{\binom{n}{d}} \sum \left(\hat{y}_i - \hat{\bar{y}}\right)^2} \quad [7]$$

where $i = 1, 2, \ldots n$, are the jackknife samples, r is the ratio of n/d, $\hat{\bar{y}}$ is the overall mean, and $\hat{y}_i$ is the mean of the i^{th} jackknife sample (see details in Shao and Wu 1989).

Data analysis

We checked normality of all response variables (AFDM, ER, GPP, CR, and GCP) initially with the Shapiro–Wilkonson test, and transformed variables when necessary. Unless otherwise noted, all results are reported as mean ± standard deviation (SD). We used Pearson moment correlation analysis to identify the direction and strength of the relationships between variables and linear regression to estimate the reaeration coefficients (Hornberger and Kelly 1975). We used 2-way analysis of variance (ANOVA) to test for significant differences in AFDM and community metabolism (GCP and CR) rates among weeks and functional compartments. We used t-tests to compare ER and GPP before and after the high flow on 30 November. We considered all analyses significant at $p < 0.05$. We used R for all analyses (version 2.11; R Development Core Team, Vienna, Austria).

Results

Physicochemical characteristics

Stream width was relatively constant along the study reach (3.9 ± 1.69 m). Water depth also was relatively homogeneous along the reach (0.26 ± 0.18 m). Stream depth varied periodically on a daily basis during weeks 1 and 2, probably because of variation in evapotranspiration during the day. Both stream width and depth increased at the end of week 2 because of heavy rains. Water depth increased from 0.15 to 2.92 m (Fig. 1).

Estimates of Q did not differ between the upstream and downstream stations. Q was 19.9, 13.8, and 1300 L/s in weeks 1, 2, and 3, respectively (Table 1). Mean velocity ranged from 0.02 to 0.04 m/s during weeks 1 and 2, but rose to 0.96 m/s during week 3. The reaeration coefficient using the nighttime regression method ranged from 0.006 to 0.011 min^{-1} during weeks 1 and 2 and from 0.010 to 0.015 min^{-1} during week 3 (Table 1). Thus, the reaeration coefficient did not change to the same extent as water velocity during week 3.

Mean PAR integrated over the day was 44.9 E/m^2 ± 16.5 E/m^2 (Table 1). PAR instantaneous values ranged from 0 to 600 μE m^{-2} s^{-1} during weeks 1 and 2, and from 0 to 400 μE m^{-2} s^{-1} during week 3 as a result of increased cloudiness. Water temperature ranged from 15 and 32°C, with ~10°C of daily amplitude during weeks 1 and 2 and only 2.5°C during week 3. PO_4^{3-}-P ranged from 0.732 to 1.185 mg/L, with lower concentrations during week 1 and a maximum after the rain event during week 3. NH_4^+-N ranged from 0.070 to 0.301 mg/L, and NO_3^--N

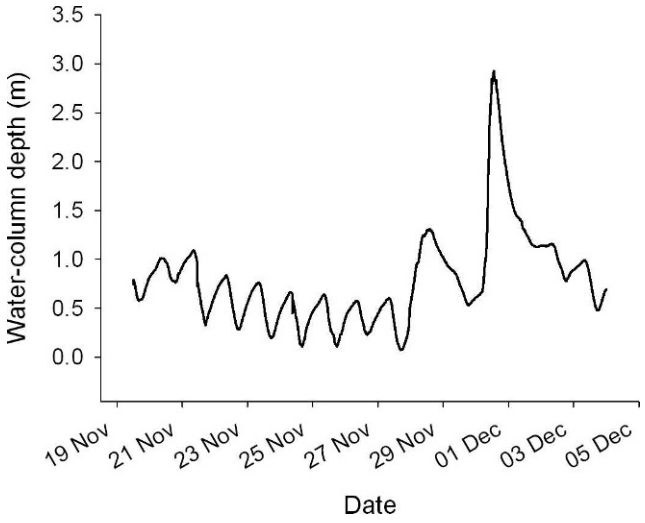

FIG. 1. Water-column depth in La Choza stream during the 2008 study period.

from 0.680 to 1.3 mg/L, both with the same pattern described for PO_4^{3-}-P (Table 1).

AFDM ranged from 210 to 360 g/m^2. AFDM differed significantly among functional compartments and weeks (Table 2). AFDM was higher in the benthic compartment than in the other compartments (Fig. 2A). AFDM in submerged macrophytes and floating algae decreased by 70 to 80% between weeks 2 and 3, whereas the opposite pattern was observed in the benthos (Fig. 2A). The increases between weeks 1 and 2 could have been related to high production rates. The decrease between weeks 2 and 3 probably was related to high flows at the end of week 2.

Metabolism of functional compartments

GCP ranged from 0.53 to 2.24 g O_2 m^{-2} h^{-1} and CR from 0.22 to 0.41 gO_2 m^{-2} h^{-1}. CR differed significantly among functional compartments (Table 2). Floating macroalgae and the benthic compartment had the highest rates (Fig. 2B). GCP differed significantly among weeks (Table 2). GCP was lowest during week 3. In contrast with the results for AFDM

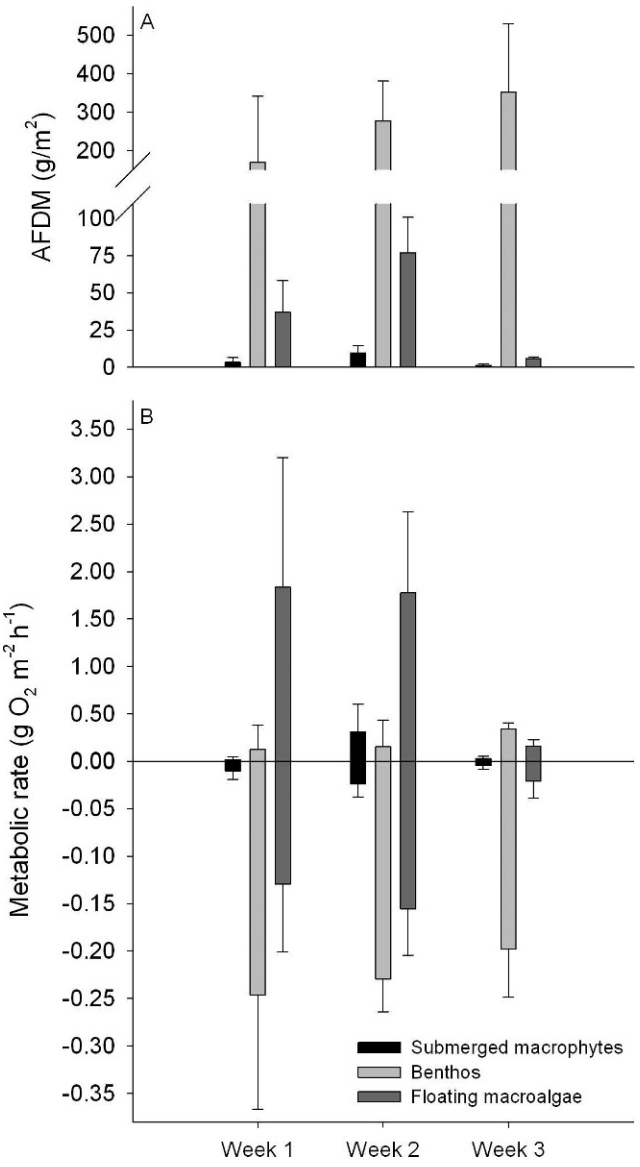

FIG. 2. Ash-free dry mass (AFDM) (A), and community gross primary production (GCP) and community respiration (CR) (B) measured as metabolic rate in various functional compartments in La Choza stream during the 3-wk study period. Note the difference in scale between GCP and CR.

TABLE 1. Values of physicochemical variables in La Choza stream. Discharge, PO_4^{3-}-P, and NH_4^+-N were measured once each week, whereas reaeration coefficients and daily photosynthetically active radiation (PAR) are presented as weekly means (±1 SD; n = 5–7).

Week	Discharge (L/s)	Reaeration coefficient (min^{-1})	Daily PAR (E/m^2)	PO_4^{3-}-P (mg/L)	NH_4^+-N (mg/L)
1	19.9	0.0089 ± 0.0022	53.70 ± 12.62	0.732	0.070
2	13.8	0.0108 ± 0.0016	48.48 ± 10.47	1.010	0.124
3	1300	0.0141 ± 0.0012	21.91 ± 6.98	1.185	0.301

TABLE 2. Results of the 2-way analysis of variance with week and functional compartment as independent factors and ash-free dry mass (AFDM), community respiration (CR), and community gross primary production (GCP) in various functional compartments as dependent variables.

	log(AFDM)			√(CR)			√(GCP)		
Source of variation	df	*F*	*p*	df	*F*	*p*	df	*F*	*p*
Week	2	18.87	<0.001	2	3.54	0.050	2	8.53	0.002
Functional compartment	2	157.49	<0.001	2	17.31	<0.001	2	65.72	<0.001
Interaction	4	7.88	<0.001	4	4.86	0.008	4	2.88	0.052

and CR, the effect of high flows on GCP was the same in all functional compartments and decreases occurred in all 3 compartments (Fig. 2B). GCP differed significantly among functional compartments (Table 2). GCP was higher for floating macroalgae than for the other compartments (Fig. 2B). CR did not differ significantly among weeks (Table 2). CR of submerged macrophytes and floating macroalgae decreased between weeks 2 and 3, whereas CR in the benthos remained similar between weeks 2 and 3 (Fig. 2B). Overall, temporal variation in GCP was 1 order of magnitude greater than temporal variation in CR (Fig. 2B).

Ecosystem metabolism

During the weeks 1 and 2, dissolved O_2 concentration showed a pronounced daily oscillation from 0 to ~25 g O_2/m^3 (Fig. 3A). After high flows, the daily variation in dissolved O_2 was greatly reduced, and dissolved O_2 oscillated from 2.5 to ~3.5 g O_2/m^3 (Fig. 3A). NM paralleled the daily oscillation of dissolved O_2. It ranged from −0.8 to 2.2 g O_2 m^{-2} h^{-1} during the first 2 wk and from −1.2 to −1.0 g O_2 m^{-2} h^{-1} during week 3 (Fig. 3B). Mean GPP was 16.34 g O_2 m^{-2} d^{-1}, and mean ER was 21.45 g O_2 m^{-2} d^{-1} (Table 3). The 3 daily metabolism variables showed considerable differences over time (Fig. 4), but these differences were more pronounced for GPP than for ER. During weeks 1 and 2, GPP was relatively stable (22.9 ± 2.2 g O_2 m^{-2} d^{-1}), whereas it decreased to 3–4 g O_2 m^{-2} d^{-1} during week 3. In contrast, ER rates were 17.0 ± 1.4 g O_2 m^{-2} d^{-1} during weeks 1 and 2 and increased with high flow. ER rates during week 3 were 30.2 ± 8.6 g O_2 m^{-2} d^{-1} (Fig. 4). The differences before and after the high-flow event on 30 November were significant, but the *t* statistics were higher for ER than for GPP (GPP: $t = 10.90$, $p < 0.001$; ER: $t = 13.03$, $p = 0.026$). Overall, the differential effect of high flows on GPP and ER led to a shift in the GPP:ER ratio (Fig. 4).

Partitioning of stream metabolism

GCP and GPP were correlated (Pearson moment correlation, $r^2 = 0.94$, $p < 0.001$; Fig. 5), and we were able to estimate the hyporheic contribution to ER. The major difference between GCP and GPP estimates occurred during week 1, when the SD was of the same

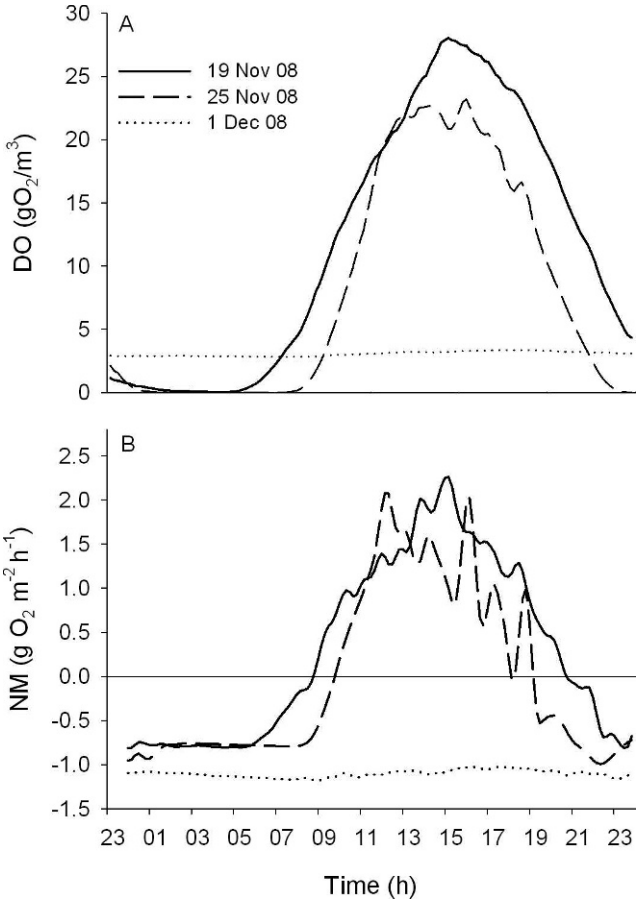

FIG. 3. Hourly dissolved O_2 (DO) concentration (g O_2/m^3) (A) and net metabolism rate (NM) (g O_2 m^{-2} min^{-1}) (B) in La Choza stream on 19 November, 25 November, and 1 December 2008.

TABLE 3. Mean (±1 SD) values of gross primary production (GPP), ecosystem respiration (ER), and GPP:ER ratios from low- to medium-sized streams reported in the literature.

Author	Method	Stream	GPP (g O_2 m^{-2} d^{-1})	ER (g O_2 m^{-2} d^{-1})	GPP:ER
This study	2-station	La Choza Stream	16.34 ± 10.07	21.45 ± 8.00	0.93
Acuña et al. 2007	1-station	Fuirosos Stream	0.48 ± 0.47	9.80 ± 11.88	0.05
Edwards and Owens 1962	1-station	Ivel River	9.6	8.5	1.13
Fellows et al. 2001	2-station	Rio Calaveras	0.5	0.19	2.63
Kaenel et al. 2000	1-station	Mühlibach	12.5 ± 4.5	8.9 ± 6.84	1.07
Marzolf et al. 1998	2-station	Walker Branch	1.4 ± 1.8	6.5 ± 1.9	0.21
Reichert et al. 2009	2-station	Luteren Stream	3.57 ± 1.61	10.68 ± 3.48	0.32
Uehlinger et al. 2002	1-station	Hassayampa River	0.3 ± 0.1	1.65 ± 0.13	0.17
Young and Huryn 1999	2-station	Three O'Clock	3.7 ± 0.9	2.7 ± 0.9	1.5
Wiley et al. 1990	1-station	Vermilion River	11.79 ± 9.94	16.07 ± 7.65	0.73

order of magnitude as the mean. However, during weeks 2 and 3, SD was lower than the mean, a result that supported the approach taken. Floating macroalgae made the largest contribution (~85%) to GPP during weeks 1 and 2, whereas the benthic compartment made the highest contribution (~60%) in week 3 (Table 4). The hyporheic compartment contributed ~57% of ER (Table 4). Among the surface compartments, the benthic compartment contributed the most (~15–35%) to ER. The effect of the high-flow event was reflected in the increase in the contribution of the hyporheic compartment from ~50 to ~80% (Table 4). The contribution of the water column was ~10% of the total ER and 30% of the total GPP.

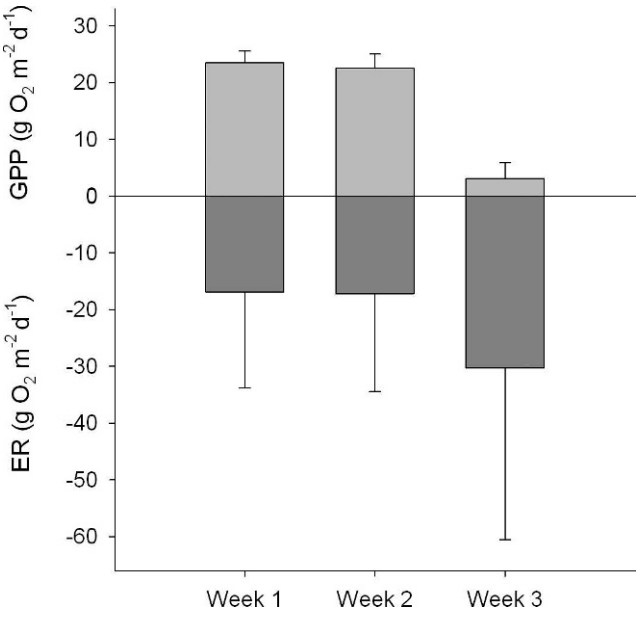

FIG. 4. Mean (±1 SD) gross primary production (GPP) and ecosystem respiration (ER) in La Choza stream during the 3-wk study period.

Discussion

Results obtained from La Choza stream indicate that this Pampean stream is among the most productive worldwide (at least at the time of year during which our study was conducted). GPP rates were as high as 22 g O_2 m^{-2} d^{-1}, a value that sets an upper bound on how productive streams can be with no irradiance or nutrient limitation (Table 3). Our study shows that further exploration of the key drivers of ecosystem metabolism and the interplay between these factors is warranted. Our results also highlighted the importance of flow to ecosystem metabolism. Very low flows enhanced GPP by

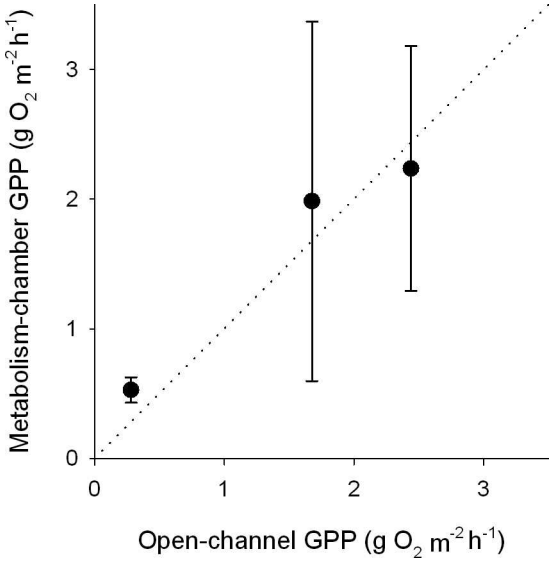

FIG. 5. Comparison of estimates of gross primary production (GPP) from the 2-station open-channel method and mean (±1 SD) estimates from the metabolism-chamber method (Goodman 1960) in La Choza stream during the 3-wk study period. The dotted line shows the expected 1:1 agreement between the methods.

TABLE 4. Estimated contribution of each functional compartment to ecosystem production and respiration. Values are expressed in percentages and reflect ecosystem rates. Uncertainty was based on the calculated variance of the product of the functional-compartment metabolic rates and the spatial extent of each functional compartment (Goodman 1960).

	Production			Respiration		
Functional compartment	Week 1	Week 2	Week 3	Week 1	Week 2	Week 3
Submerged macrophytes	1.07 ± 1.50	13.81 ± 13.16	5.15 ± 4.82	1.53 ± 1.30	2.91 ± 1.75	0.39 ± 0.36
Benthos	6.37 ± 12.81	6.82 ± 12.52	64.54 ± 12.03	36.65 ± 17.97	28.32 ± 4.29	17.75 ± 4.50
Floating macroalgae	92.54 ± 68.76	79.36 ± 38.13	30.29 ± 13.28	19.30 ± 10.62	19.20 ± 6.05	1.88 ± 1.58
Hyporheos	–	–	–	42.50 ± 20.92	49.54 ± 7.63	79.97 ± 4.79

submerged macrophytes and floating macroalgae, whereas high flows depressed GPP. However, high flows did not depress ER to the same extent as they enhanced GPP because a considerable portion of ER occurred in the hyporheic zone. Another remarkable aspect of the study system was the extreme diel fluctuation in O_2, which led to extended daily periods of anoxia and probably was a stressor for biota.

Functional partitioning of stream metabolism

We estimated stream community metabolism rates by incubating community samples from each functional compartment for 1 to 2 h and using these functional-compartment rates to estimate ecosystem-level rates. We followed a defined method during this process, but the specific characteristics of the method selected (e.g., substratum, incubation time, streambed mapping, and scaling approach) can strongly influence the estimates of metabolism. Therefore, a discussion is warranted of the specific advantages and limitations of the methods used to characterize metabolism and to quantify the uncertainty of the estimates.

Functional-compartment metabolism in streams usually is measured in chambers with internal circulation. However, extremely low water velocities (~0.016 m/s) in La Choza stream during weeks 1 and 2 of the study enabled us to mimic stream flow conditions in chambers with no water circulation. However, higher water velocities during week 3 were not properly reproduced inside the chambers and could have led to differences between metabolic rates in stream functional compartments and in our chambers. This potential source of error did not appear to influence our results because the differences between the scaled-up GCP and GPP values did not differ among weeks.

We weighted functional-compartment metabolic rates by the surface area occupied by the compartment in the stream to scale metabolic rates up to the ecosystem level. Errors introduced by the chambers and by our mapping methods were reflected in the slight mismatch between the scaled-up GCP estimates and the measured ecosystem-level GPP estimate and in the high SD in week 1 (Fig. 5). The magnitude of the difference between the 2 GPP estimates was small enough that we considered it feasible to determine hyporheic respiration as proposed by Naegeli and Uehlinger (1997).

Comparison of scaled-up GCP and GPP indicates that our methods led to reliable estimates of production at both functional-compartment and ecosystem scales. However, estimates of respiration might be less reliable than those of production because of the daily hours-long absence of dissolved O_2 in the ecosystem, which could have limited nighttime aerobic respiration. Thus, the reported ER rates might underestimate total respiration (aerobic + anaerobic). Overall, O_2 production rates can be used directly to quantify GPP, whereas O_2 consumption rates allow only an approximation of ER. Thus, our reported ER rates probably were underestimates, and the NEM was not as high in La Choza stream as reported here.

The metabolism of La Choza stream in a global perspective

To our knowledge, ours is the first study to estimate stream metabolism at both functional-compartment and ecosystem scales in a Pampean stream. Our goal was to characterize the metabolism of a typical Pampean stream in relation to the current knowledge of stream metabolism and to identify the contribution of each functional compartment (submerged macrophytes, water column, floating macroalgae, benthos and hyporheos) to ecosystem processes during the season of maximum light availability and highest temperature. The rates we obtained (NEM rates up to 9 g O_2 m^{-2} d^{-1}) identify this stream as among the most productive streams worldwide (Webster and Meyer 1997; Table 3). Similar NEM rates have been reported only in desert streams, which have no canopy cover and relatively high temperatures (Grimm and Fisher 1986). The complete absence of riparian tree vegetation in addition to low water

velocities, high water temperatures, and lack of nutrient limitation might explain the observed NEM rates in La Choza stream, which probably were limited by other factors, such as trace elements or cellular physiology. Riparian-zone vegetation has been identified by several authors as one of the most important explanatory variables for differences in GPP among biomes (Lamberti and Steinman 1997, Bunn and Davies 2000, Dodds 2007). Pampean streams have features such as low stream gradients, high nutrient concentrations and high light availability that make them similar to the prairie streams described by Wiley et al. (1990), but the GPP rates reported for prairie streams are considerably lower than those in La Choza stream (Wiley et al. 1990, Dodds et al. 2008). Gradient is another landscape attribute that influences primary production in lotic ecosystems (Lamberti and Steinman 1997). Indeed, low gradients typical of the Pampean region might favor biomass accumulation because they reduce stream power, i.e., streams with low gradients have reduced capacity to carry materials at a given flow compared to streams with higher gradients.

The role of hydrology and the hyporheic compartment in stream metabolism

Our results highlighted the role of flow in Pampean systems. Low flows facilitated biomass accumulation and enhanced primary production, whereas high flows removed biomass and reduced primary production. The effect of low flows in Pampean streams was first reported by Giorgi and Ferreira (2000), who studied accumulation rates of primary producers at different flow rates and concluded that community development and accumulation of new species were faster at low flows. High heterotrophic activity and low rates of gas exchange with the atmosphere during low flows caused daily anoxia (Fig. 5). Reaeration coefficients in La Choza stream were extremely low during low flows and remained lower than expected during high flows in week 3. The apparent decoupling between water velocity and reaeration rate probably was the result of the low turbulent flux under all observed flow conditions. This situation might be typical of most Pampean streams. Most have low streambed roughness (absence of stones) and homogeneous cross-sections that reduce turbulence. Extended droughts carry a high risk of anoxia and of failure to meet the standards set by Argentinean law (≥ 5 g O_2/m^3; DN 831/93 1993).

The daily periods of anoxia (0 g O_2/m^3 for 6–8 h) were lower than the tolerance limits of most invertebrates (0.9–2.1 g O_2/m^3; Surber and Bessey 1974). Furthermore, invertebrates experience other deleterious effects, such as disruption of feeding and reproductive behavior and invertebrate drift, at O_2 concentrations higher than lethal levels (1.8–2.5 g O_2/m^3 for 30 min; McCahon et al. 1991). No data on invertebrates or fish are available from La Choza stream, but massive fish mortalities observed in nearby aquatic environments during the study period highlight the toxic effect of anoxia on the aquatic biota.

Despite the periods of anoxia, NEM during low-flow conditions was positive and high because GPP rates were as high as 22 g O_2 m^{-2} d^{-1}. During low flow, benthic primary producers and floating macroalgae contributed 45% and 40% of total GPP, respectively. The low-flow period abruptly ended with 380 mm of rain in 11 h. This high-flow event considerably reduced submerged macrophytes and floating macroalgae and mobilized the streambed sediments locally and in sections upstream of the study reach. The various effects of high flow on different functional compartments were reflected in the measured metabolic rates. GCP decreased dramatically for submerged macrophytes and floating macroalgae but not for benthos. Resuspension of anaerobic sediments during high flow decreased water-column dissolved O_2 concentration for several days despite faster entrance of O_2 from the atmosphere because of higher gas-exchange rates. Reduction of primary producers and changes in water temperature, dissolved O_2, and nutrients reduced GPP but not ER, and the GPP:ER ratio shifted from 1.4 to 0.02 (Fig. 4). Uehlinger (2006) also found that high flows can decrease the GPP:ER ratio. However, changes in Uehlinger's study system were explained by a differential decrease in GPP and ER with flooding, whereas in La Choza stream, GPP decreased and ER increased. About 75% of the measured aerobic heterotrophic metabolism in La Choza stream occurred in the hyporheic compartment. The relatively high contribution of the hyporheic zone to ER may explain the different patterns of GPP and ER between our study and Uehlinger (2006). The role of the hyporheic zone, higher dissolved O_2 availability, and resuspension and consequent oxygenation of organic-matter-rich anaerobic sediments might explain the increase in ER with high flow. We were unable to determine whether the increase in ER with high flows was temporary because our study ended 1 wk after the rain event.

The magnitude of the contribution of the hyporheic zone to ER was contrary to our expectations, but similar rates have been reported elsewhere (Naegeli and Uehlinger 1997, Fellows et al. 2001). The hyporheic zone contributed 40 to 50% of total ER in Sycamore Creek, a desert stream (Grimm and Fisher 1984), and the estimated annual contribution of the

hyporheic zone was 70% in Buzzards Branch, a sand-bottom, black-water, coastal-plain stream (Fuss and Smock 1996). The contribution of the hyporheic zone was even greater (74–92% of ER) in the Necker, a 6th-order gravel-bed river (Naegeli and Uehlinger 1997). Fellows et al. (2001) found that the hyporheic zone contribution to whole stream ER ranged from 40 to 93%. Conceptual models presented by Findlay (1995) and Valett et al. (1996) propose that the contribution of the hyporheic zone to stream ecosystem functioning depends on the types and rates of metabolic processes occurring in the hyporheic zone, the proportion of stream discharge routed through the hyporheic zone, and its effect on hydrologic residence time. Hydrologic exchange between surface and hyporheic compartments in Pampean streams might be the limiting factor controlling the contribution of the hyporheic zone to the ecosystem metabolism. Previous work in Pampean streams indicated that the parent lithology of the stream bed (hard, homogeneous substrata with fine sediments [silt and clay] and high $CaCO_3$ content) does not allow large vertical hydrologic exchanges (Giorgi et al. 2005). Assuming limited vertical hydrologic exchange between functional compartments in La Choza stream, the active hyporheic zone probably was constrained to sediments deposited on the stream bed during low flows. The high contribution of this constrained layer (probably <40 cm deep) to whole-stream ER during the study period might be explained by high respiration rates resulting from the high organic content of this layer, which typically ranges from 3 to 8% by mass (AG, unpublished data).

In conclusion, ours is the first study to estimate stream metabolism in a Pampean stream, and one of a few studies to partition the contribution of different functional compartments to ecosystem metabolism. The high production rates and the extreme conditions experienced daily by the biota during low-flow conditions may be typical of this type of ecosystem. However, long-term records of stream metabolism and similar investigations in other Pampean streams are needed to reduce the limitations of a short and unreplicated study.

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