A HETEROTROPHIC DESERT STREAM?
THE ROLE OF SEDIMENT STABILITY

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ABSTRACT.—In autumn 1998 stream metabolism was measured in the Hassayampa River, Arizona, a Sonoran Desert stream, using single-station diel oxygen curves and an oxygen mass balance model. Oxygen consumption rates of parafluvial and channel sediments were determined with respiration chambers. Bedload of channel sediments (sand) prevented significant primary production by benthic autotrophs, despite favorable nutrient, light, and temperature conditions. Ecosystem respiration was relatively low (1.50 g O_2 $m^{-2}d^{-1}$) and presumably fueled by production in the riparian zone and riverine marshes. Respiration rates in the parafluvial zone and in channel sediments ranged from 0.6 to 1.4 g O_2 m^{-3} sediment h^{-1}. Sediment organic matter (ash-free dry mass) was 4.0 ± 1.8 kg m^{-3} sediment and did not significantly differ between the channel and the parafluvial zone. Results indicate that heterotrophic processes may dominate the metabolism of desert stream segments over extended periods of time if unstable sandy bed sediments prevail.

Key words: *desert stream, stream metabolism, diel oxygen curve, sediment respiration, disturbance, sediment stability.*

Environmental conditions in streams of warm arid or semiarid climates favor high primary production rates that may exceed ecosystem respiration (Minshall 1978, Cushing and Wolf 1984, Grimm 1987, Lamberti and Steinman 1997, Sinsabaugh 1997). Respiration in streams mainly occurs in hyporheic and parafluvial sediments (Grimm and Fisher 1984, Mulholland et al. 1997, Naegeli and Uehlinger 1997). Jones et al. (1995) found that in Sycamore Creek, a warm desert stream, benthic production fueled more than 80% of the hyporheic respiration through leaching dissolved material. Input of allochthonous organic matter is of minor importance if a riparian zone is narrow and upland vegetation is sparse as in arid environments (Cushing 1997, Schade and Fisher 1997). However, river corridors may include floodplain marshes, shrubs, and trees (e.g., Prach et al. 1996, Stromberg et al. 1997) that provide organic matter through aerial deposition of plant litter, fine root production or release of organic matter by roots, or processing of particulate organic matter buried during floods (Robertson et al. 1999).

The stability of bed sediments is an important determinant of the biologically mediated energy flow through lotic ecosystems. Bed-moving spates damage benthic primary producers but have only a minor influence on the heterotrophic community of the hyporheic zone (Grimm and Fisher 1984, Naegeli and Uehlinger 1997). These disturbances shift stream metabolism toward heterotrophy (Fisher et al. 1982, Uehlinger and Naegeli 1998, Uehlinger 2000). Flash floods in desert streams decimate primary producers, but recovery can be rapid due to favorable light and temperature conditions and stable substrata after flood recession (Fisher et al. 1982, Grimm and Fisher 1989).

This study focuses on the metabolism of a warm desert stream, where light availability, temperature, and nutrient concentrations are ample to support high primary production rates. However, bed sediments consisted of sand, the superficial layer of which was in continuous motion even at low flow. We hypothesized that the metabolism of this desert stream would be dominated by respiration because of this persistent bedload. Further, we expected that metabolism rates in the wetted channel would be smaller than in the parafluvial zone because low in-stream primary production was thought to result in low organic matter supply compared to inputs from the riparian vegetation and riverine marshes to the parafluvial zone.

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METHODS

Study Reach

The Hassayampa River drains a catchment of about 2000 km^2 into the Gila River (central Arizona). Perennial, intermittent, and ephemeral reaches characterize the river. The study was conducted downstream of Wickenburg (Maricopa County, AZ, USA), where a shallow bedrock layer causes perennial surface flow for about 8 km. Sand dominates channel sediments in the bedrock-confined reach (Stromberg et al. 1993), which is an upwelling zone of alluvial- and basin-filled groundwater (Jenkins 1989). The study reach is 1 km downstream of The Nature Conservancy's Hassayampa River Preserve, close to the end of the perennial river section. Elevation is about 610 masl, and channel slope averages 0.006 (m/m). The reach is relatively homogenous with respect to channel structure (pool-riffle-run frequency), depth, slope, and riparian vegetation. At the Hassayampa River Preserve, mean annual discharge averages 0.1 m^{3}s^{-1} (Jenkins 1989). Effluent from a municipal wastewater treatment plant upstream of the study area makes up 0.01 to 0.02 m^{3}s^{-1} of the flow. Large floods (Q$_{max}$ > 500 m^{3}s^{-1}), which change channel area and in-stream riparian habitat structure, occur predominantly in winter (Stromberg et al. 1997). Emergent macrophytes, such as *Typha domingensis* Pers., is occasionally dominant within the river channel and abundant in adjacent marshlands (Wolden et al. 1994). *Baccharis salicifolia* [Ruíz et Pavón] Pers. occurs along stream margins; more distal riparian vegetation is dominated by cottonwood (*Populus fremonti* Wats.) and willow (*Salix goodnigii* Ball). Floodplain width ranges from 100 to 200 m. Adjacent uplands consist of Sonoran Desert scrub vegetation (Stromberg et al. 1993). The study reach is unreplicated; therefore, only tentative conclusions about ecosystem metabolism and sediment respiration of desert streams may be drawn.

Physics and Chemistry

Channel width and depth were measured along a 260-m reach. In the wetted channel and the parafluvial zone of a 75-m sub-reach, we installed 15 permanent piezometers with sampling depths of 10 cm (6), 30 cm (6), and 80 cm (3) for sampling interstitial water. A small side channel longitudinally divided the parafluvial zone.

Interstitial water temperatures were measured using 2 temperature loggers (StowAway, Onset Corporation, North Falmouth, MA, USA) that were installed 20 cm below the sediment-water interface in the wetted channel and 20 cm below the water table in the parafluvial zone. Surface water temperatures were continuously recorded with a combination temperature-oxygen probe (see below). We measured discharge with the slug injection method (Gordon et al. 1992), using NaCl as tracer and a conductivity meter (WTW LF 340, Wissenschaftlich-Technische Werkstätten GmbH, Weilheim, Germany) as detector. Discharge records of the Hassayampa River at the Morristown gage (about 6 km downstream of the study site) were recorded by the USGS (http://waterdata. usgs.gov/nwis-w/AZ/).

Surface and interstitial water samples for chemical analyses were collected in triplicate on 28 October and 1 November 1998 (surface water was also sampled on 27 October 1998). Samples were stored on ice, filtered in the laboratory (Whatman GF/F glass fiber filters), and analyzed for nitrate (NO$_3$) and ammonium (NH$_4$) nitrogen, soluble reactive phosphorus (SRP), and dissolved organic carbon (DOC). Analyses were performed as described by Holmes et al. (1998). Dissolved oxygen (O$_2$) and temperature of subsurface water were measured in the field with an oxygen meter (ATI Orion model 830).

Metabolism

We measured sediment respiration as changes in O$_2$ concentration over time in sealed Plexiglas cores (4.5-cm diameter, 32 cm long), filled with sediments from 10 or 30 cm depth and water from the respective depths, and sealed with rubber stoppers (after Jones et al. 1995). Cores were incubated in situ for 2 to 3 hours. Oxygen concentrations and temperatures were measured with an oxygen meter (ATI Orion model 830). After incubation, sediments were analyzed for particulate organic matter as ash-free dry mass (loss on ignition) and grain-size distribution. Sampling sites were located in the main channel and in the parafluvial zone.

To assess gross primary production and ecosystem respiration in the channel, oxygen concentrations and temperatures were continuously measured at the end of the study reach

from 27 October to 1 November 1998 with Orbisphere equipment (probe 2115 with O_2-meter 2607 of Orbisphere, Geneva, Switzerland). Temperature and O_2 signals were averaged for 5 minutes and stored (datalogger LI-1000, LI-COR Inc., Lincoln, NE, USA). We used an oxygen mass-balance model to calculate gross primary production *GPP* (g $O_2m^{-2}d^{-1}$) and ecosystem respiration *ER* (g $O_2m^{-2}d^{-1}$). A detailed description of the model is given by Uehlinger et al. (2000). Model simulations and parameter estimations were performed with the computer program AQUASIM (version 2.0; Reichert, 1994, 1995). Respiration per volume *r* (g $O_2m^{-3}d^{-1}$) was parameterized as:

$$r = -\frac{ER}{z} \qquad (1)$$

where *ER* is the respiration rate per area (g $O_2m^{-2}d^{-1}$) and *z* the mean water depth (m). Gross primary production was described as a linear function of incident light (*I*):

$$GPP = pIz \qquad (2)$$

where *p* is the slope of the linear *P–I* curve (g $O_2m^{-1}d^{-1}W^{-1}$) and *I* is incident light intensity (Wm^{-2}). Linear or almost linear relationships between ecosystem primary production and light intensitiy are usually obtained with open system methods (e.g., Duffer and Dorris 1966, Hornberger et al. 1976, Uehlinger 1993, Uehlinger et al. 2000). We described temperature dependence of *ER* and *GPP* with the following Arrhenius equation:

$$X(T) = X(20^{o}C)\beta_x^{(T-20)} \qquad (3)$$

where the subscript *X* is *p* or *r* and β_X is a constant ($\beta_X > 1$; Bowie et al. 1985). Saturation concentrations of O_2 at the study site were calculated using water temperature and the barometric pressure recorded at Wickenburg Airport (about 6 km from the study site). We determined the reaeration coefficient K_s with propane as tracer gas (Genereux and Hemond 1992). Temperature dependence of K_s was described according to Elmore and West (1961). Estimates of the parameters *r, p,* and β_X were based on the minimization of the sum of squares (*SS*):

$$SS = \sum_{i=1}^{n}(O_2(t_i)-O_{2meas,i})^2 \qquad (4)$$

where $O_{2meas,i}$ is the O_2 concentration measured at the end of the reach at the time t_i, $O_2(t_i)$ is the O_2 concentration at the end of the reach at the time t_i is calculated with the model, and *n* is the number of observations. To judge the identifiability for model parameters, we calculated the collinearity index (γ), which is a measure for the degree of approximate linear dependence of sensibility functions (Brun et al. 2001). Critical values of γ are in the range of 5 to 20. To evaluate the relative importance of *ER, GPP,* and the influence of temperature on both processes, we performed model runs by activating and deactivating primary production, respiration, and temperature dependence of both processes (i.e., by setting $\beta = 1$ or *p* or *r* = 0).

To assess differences in sediment respiration rates and sediment organic matter, we used 2-way ANOVA. Prior to the analysis, respiration data were transformed (log(x + 1)). Temperature dependence of sediment respiration was evaluated using linear regression analysis. Differences or regressions were considered significant when *P* < 0.05.

RESULTS

Discharge measured on 3 occasions averaged 0.094 ± 0.007 m^3s^{-1}. At this flow rate, width and depth of the wetted channel averaged 6.6 m and 0.034 m, respectively, and mean current velocity was 0.41 ms^{-1}. Between 0900 and 1200 hours, the main channel stage decreased by about 1 cm (presumably due to diel transpiration cycles of the riparian vegetation). As a consequence, the upper part of the small side channel fell dry each day during the investigation. A transient flow increase due to a rainstorm during the night of 31 October/1 November 1998 (flood marks indicated a stage increase by 3–5 cm) scoured some of the algal patches located along the margins of the wetted channel.

Main channel surface water temperature varied between 12.4°C and 26.7°C (Table 1, Fig. 1). The high diel temperature variation of the interstitial water in the sediments of the wetted channel ($\Delta T = 9.5°C$) indicated a substantial water exchange between sediment and surface water. Temperature in the parafluvial

TABLE 1. Temperature of surface water and interstitial water (°C) in the Hassayamapa River. Temperatures were recorded in 10-minute intervals.

	Surface water	Sediment below the main channel[a]	Saturated sediments of the parafluvial zone[b]
Period	27–31 Oct	27–30 Oct	30 Oct–2 Nov
Minimum	12.4	14.1	13.0
Maximum	26.7	23.6	15.3
Average	17.4	17.6	14.3

[a]25 cm below the sediment water interface
[b]25 cm below the water table

zone averaged only 14.3°C, and diel variations were small (ΔT = 2.3°C). This pattern suggests minor water exchange between surface water and parafluvial sediments.

Relatively high concentrations of nitrate and SRP characterize the surface and interstitial water of the main channel (Table 2). Vertical concentration gradients of the interstitial water were small or absent, and even at 80 cm depth O_2 was surprisingly high. In the parafluvial zone, O_2 and nitrate concentrations were lower than in the channel sediments, and SRP increased with depth. We found higher DOC concentrations in parafluvial sediments than in channel sediments. Ammonium concentrations were relatively high and uniform at all sites.

Differences in grain-size distribution between the channel and the parafluvial zone were small (Fig. 2). Apart from a narrow zone along the channel margins, surface bed sediments (D_{90} about 2 mm) were in continuous motion (based on average channel characteristics such as width, depth, slope, and D_{90}, the discharge threshold for initiation of sediment transport, was estimated to be 0.078 m^3s^{-1}; Günther 1971). Sediment movement occurred between the beginning of October 1998 (1st visit to the site) and the end of the study in mid-November 1998, and also when we returned to the reach in February 1999. This bedload restricted habitats suitable for algae to small patches along the channel margins; we observed that more than 95% of the wetted channel area was free of algal patches visible by eye. Site (main channel, parafluvial zone) and depth had no significant effect on sediment organic matter, which averaged 4.0 ± 1.8 kg m^{-3} sediment (Table 3).

Site and depth significantly influenced sediment respiration. Average respiration rates decreased by about 40% from the parafluvial zone to the main channel and by 30% from 10
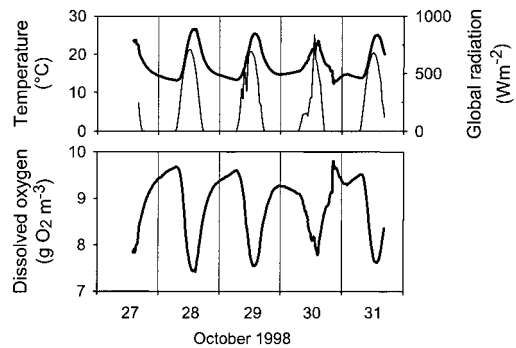

Fig. 1. Top: Surface water temperature (bold line) in the main channel of the Hassayampa River and global radiation (fine line) at Wickenburg airport. Bottom: Dissolved oxygen concentration in the surface water of the main channel.

to 30 cm depths (Table 3). During incubation, average temperatures in the sediment tubes ranged from 15.8°C to 24.5°C in the channel and from 12.5°C to 22.7°C in the parafluvial zone. However, the regression between the respiration rates and temperature was significant only for parafluvial sediments (R^2 = 0.198).

Oxygen concentrations in the surface water were always below saturation concentration and showed distinct diel variation (ΔO_2 = 2.3 ± 3 mg O_2 L^{-1}) with daily minimum in the early afternoon (between 1300 and 1500 hours; Fig. 1). The small spate of 30 October resulted in a distinct but transient increase in O_2. The re-aeration coefficient K_s (20°C) for O_2 determined with the gas tracer method was 89 ± 18 d^{-1}. Table 4 summarizes the results of a series of calculations with models of different complexity (number of active processes). The value of the collinearity index (γ < 5) points out that the 4

TABLE 2. Concentrations of oxygen, major nutrients, and DOC on 28 October and 1 November 1998 between 1100 and 1400 hours (channel surface water was also sampled on 27 October 1998).

	O_2 (mg L^{-1})	NH_4-N (μg L^{-1})	NO_3-N (μg L^{-1})	SRP (μg L^{-1})	DOC (mg L^{-1})
Main channel					
Surface water	7.7 ± 0.4	28 ± 15	230 ± 15	53 ± 1	1.67 ± 0.12
Sediments (depth 10 cm[a])	6.8 ± 1.1	20 ± 11	278 ± 32	48 ± 7	1.61 ± 0.12
Sediments (depth 30 cm[a])	7.1 ± 0.7	26 ± 23	296 ± 20	42 ± 14	1.53 ± 0.07
Sediments (depth 80 cm[a])	7.3 ± 0.4	26 ± 19	302 ± 9	51 ± <1	1.52 ± 0.05
Parafluvial zone					
Sediments (depth 10 cm[b])	3.3 ± 3.6	23 ± 9	165 ± 139	58 ± 20	2.71 ± 1.58
Sediments (depth 30 cm[b])	2.8 ± 2.1	31 ± 14	288 ± 343	63 ± 15	2.30 ± 0.88
Sediments (depth 80 cm[b])	1.0 ± 0.3	30 ± 16	171 ± 164	73 ± 16	1.83 ± 0.39

[a]Below the sediment-water interface
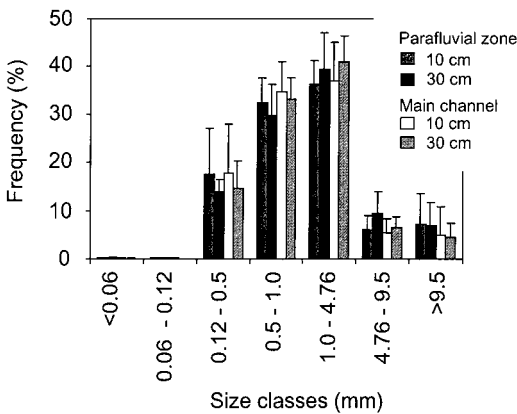[b]Below the water table

Fig. 2. Grain-size distribution of main channel sediments (10 and 30 cm below the bed surface) and parafluvial sediments (10 and 30 cm below the water table) in the Hassayampa River.

model parameters (ER, p, β_r, β_p) can be identified. The sum of squares (SS) of the basic model, which considered only gas exchange, was 145.9. Respiration had the largest influence on SS through all levels of model complexity and indicates the importance of this process for oxygen balance. In contrast, primary production had no (fits 1, 3, 4) or only a small effect (fits 6, 7). Temperature dependence of gross primary production and ecosystem respiration reduced SS to 17.0. However, we did not consider this model in the estimation of metabolism rates because β_p became unrealistically high (a value $\beta_p = 1.2311$ means an 8-fold increase in gross primary production if temperature rises from 10°C to 20°C). Fit 5

was the most parsimonious fit and led to good agreement between calculated and measured oxygen data. Estimates of daily gross primary production and ecosystem respiration based on fits 5, 6, and 7 are given in Table 5. We assume that the values provided by fits 5 and 6 most probably delimited the range of gross primary production and ecosystem respiration during the investigation.

DISCUSSION

As expected, heterotrophic processes dominated the metabolism of this desert stream. The permanent motion of the uppermost bed sediments in most parts of the wetted channel prevented substantial periphyton accrual and thus any substantial primary production. Apart from sediment stability, environmental conditions were favorable for the growth of benthic algae; the river was open canopied, the water was clear, and concentrations of major nutrient were high. Algal patches were restricted to areas with stable substrata such as channel margins, backwater areas, and parafluvial sediments inundated for only a few hours a day. However, the contribution of these stable areas to the wetted channel area was small (< 5%).

The metabolism of the Hassayampa River was heterotrophic during this study; estimates of P/R ranged from 0 to 0.10 depending on the model applied (fits 5 and 6) to calculate metabolism rates. Ecosystem respiration rates were relatively small (1.33–1.50 g O_2 $m^{-2}d^{-1}$) compared to rates reported from other desert streams (3.6–6.5 O_2 $m^{-2}d^{-1}$; Grimm 1987, Cushing and Wolf 1984). Algae can provide significant quantities of dissolved and particulate

TABLE 3. Sediment respiration rates and sediment organic matter (mean and standard deviation) in the Hassayampa River measured on 29 and 31 October, and 10 November 1998. N = number of samples.

Location	Depth (cm)	Respiration rate (g O_2 m^{-3} sediment h^{-1})	Organic matter (kg m^{-3} sediment)	N
Main channel	10[a]	0.96 ± 0.11	3.8 ± 1.8	22
	30[a]	0.55 ± 0.31	4.4 ± 1.9	9
Parafluvial zone	10[b]	1.39 ± 0.82	4.2 ± 1.9	21
	30[b]	0.78 ± 0.31	4.4 ± 1.2	6

[a]Below the sediment-water interface
[b]Below the water table

TABLE 4. Evaluation of the processes influencing the oxygen balance in the Hassayampa River. Reaeration, $K_s(20\,°C)$, was measured (see text). The other parameters were fitted to the models defined by equations 1, 2, and 3. Standard error estimates are in parentheses; empty cells mark the parameters not included in a fit.

Fit no.	Number of parameters fitted	$K_s(20\,°C)$ (d^{-1})	ER (g O_2 m^{-2}d^{-1})	P (g O_2 W^{-1}d^{-1})	β_r	β_p	SS	γ
—	0	89					145.9	—
1	1	89		2.90 10^{-7} [a]			145.9	1.00
2	1	89	1.290 (0.021)				25.8	1.00
3	2	89		2.77.10^{-7} [a]		1.00001[a]	145.9	4.04
4	2	89	1.295[a]	0.00[a]			25.8	1.82
5	2	89	1.476 (0.022)		1.0502 (0.0034)		20.3	1.53
6	3	89	1.707 (0.038)	9.04 10^{-4} (1.27 10^{-4})	1.0698 (0.0046)		19.0	3.19
7	4	89	1.958 (0.049)	9.72 10^{-4} (1.30 10^{-4})	1.1087 (0.0060)	1.2311 (0.0216)	17.0	4.47

[a]Standard error could not be estimated.

organic matter supporting respiration in the hyporheic zone (Jones et al. 1995). We suggest that the lack of a substantial algal community may account for the low ecosystem respiration rates, and we hypothesize that organic matter released by macrophytes of the riverine marshes and the riparian vegetation, in addition to organic matter buried during floods, may have fueled sediment respiration. Organic matter from riverine marshlands and the riparian vegetation bordering the investigated parafluvial zone may have accounted for the differences in respiration rates between parafluvial and channel sediments; the differences in DOC concentrations between the parafluvial zone and channel sediments may reflect different organic matter sources. Sediment organic matter in the Hassayampa River averaged 4.0 kg m^{-3} sediment in the uppermost 30 cm, which is in the range of values reported from Sycamore Creek (2.8–5.7 kg m^{-3} sediment in the top 15 cm; Valett et al. 1990). This material is presumably of suboptimal quality, but it is an

energy reservoir that may increase the resistance of stream metabolism to short-term environmental fluctuations. Sediment organic matter was homogeneously distributed in the uppermost 30 cm of the sediments (channel and saturated parafluvial zone), but respiration rates significantly decreased from 10 to 30 cm depth. This may reflect the increasing refractory nature of the sediment organic matter with depth.

One prediction of the river continuum concept is that changes in the relative importance of primary production and respiration for energy flow through lotic ecosystems can be attributed to changes in stream size and riparian vegetation (Vannote et al. 1980); for example, environmental settings in arid or semiarid regions were found to favor high rates of primary production exceeding ecosystem respiration (Minshall 1978, Lamberti and Steinman 1997, Sinsabaugh 1997). However, this study and recent investigations indicate that the stability of bed sediments has to be considered in

TABLE 5. Gross primary production, ecosystem respiration, and P/R (average and standard deviation) in the Hassayampa River, 28–31 October 1998. Daily rates (g O_2 $m^{-2}d^{-1}$) were calculated with 3 models of different complexity (fits 5, 6, and 7; Table 4).

Model (fit)	Gross primary production	Ecosystem respiration	P/R
5	0.00	1.33 ± 0.05	0.00
6	0.15 ± 0.03	1.50 ± 0.07	0.10 ± 0.01
7	0.29 ± 0.10	1.65 ± 0.13	0.17 ± 0.05

predictions on the relative importance of stream metabolism (Uehlinger and Naegeli 1998, Uehlinger 2000). During high flow, bed sediments may become unstable, which mainly affects benthic algae and primary production (Fisher et al. 1982, Uehlinger and Naegeli 1998). But the effects of such events are usually transient because spates are limited in time and primary production recovers more or less rapidly depending on environmental conditions (Fisher et al. 1982, Uehlinger and Naegeli 1998, Uehlinger 2000). At the Morristown gage (about 6 km downstream of our study site), spates were recorded on 29 March 1998 ($Q_{max} = 21$ m^3s^{-1}) and on 12 August 1998 ($Q_{max} \approx 2$ m^3s^{-1}). During the spate-free period between August 1998 and the beginning of our measurements, permanently moving bed sediments apparently prevented periphyton accrual in most parts of the channel; i.e., sediment instability seems to account for a persistent dominance of heterotrophic processes in the metabolism of this warm desert stream. Streams with sandy, unstable sediments can be found throughout the semiarid Southwest of North America, though we do not know the extent to which they comprise a significant proportion of southwestern river habitat. Conditions of high bedload may be restricted to certain segments or transient (e.g., during the wet season). In the Hassayampa River, for example, the study reach represented a particular successional stage of a desert river corridor. Large floods dramatically change prevailing substrata and the spatial extent of the wetted channel, parafluvial zones, riverine marshes, floodplain forests, and shrublands within the river corridor (Stromberg et al. 1997). Such flood-induced alterations in the configuration of the river corridor may affect stream metabolism.

Studies of stream metabolism in the arid West of North America indicate that desert streams are autotrophic ecosystems (Minshall 1978, Cushing and Wolf 1984, Grimm 1987). The results of this investigation suggest that heterotrophic processes may dominate the metabolism of desert stream segments over extended periods of time if unstable sandy bed sediments prevail. However, a test of this hypothesis needs reliable estimates of annual metabolism rates. Such estimates require measurements at least during one annual cycle and with a temporal resolution that accounts for the hydrological disturbance regime of these systems.

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