Exchange between interstitial and surface water: Implications for stream metabolism and nutrient cycling

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Abstract

Metabolism of a Sonoran Desert stream was investigated by both enclosure and whole system oxygen techniques. We used recirculating chambers to estimate surface sediment metabolism and measured deep sediment respiration in isolated sediment cores. Metabolism of the stream ecosystem was determined for a 30-m reach as dark and light oxygen change with and without black plastic sheeting that darkened the stream and prevented diffusion. Average ecosystem respiration for two dates in August (440 mg O_2 m^{-2} h^{-1}) exceeded respiration of either the surface sediment community (155 mg O_2 m^{-2} h^{-1}) or the hyporheic community (170 mg O_2 m^{-2} h^{-1}) alone. Deep sediments show substantial oxygen and nitrate uptake when isolated. In the stream, this low nitrate interstitial water is exchanged with surface water. Metabolism of the isolated surface community suggests a highly productive and autotrophic system, yet gross production is balanced or exceeded by community respiration when ecosystem boundaries include the hyporheic zone. Thus, despite high rates of gross primary production (600–1200 mg O_2 m^{-2} h^{-1}), desert streams may be heterotrophic ($P_G < R$) during summer.

Introduction

Recent studies of stream ecosystem metabolism have stimulated interest in the prevalence of naturally autotrophic streams (Minshall 1978). The widely held view that streams are dependent on organic matter imported from the watershed to support ecosystem respiration (R) in excess of *in situ* gross primary production (P_G), and are thus heterotrophic systems, has been challenged by data from streams in regions of high insolation, high temperature, and infrequent disturbance (Busch & Fisher 1981, Fisher *et al* 1982, Minshall 1978). In truly autotrophic systems organic material must be either exported or stored (Busch & Fisher 1981). Since increases in storage may not continue indefinitely, organic material accrued during periods of autotrophy must be consumed on site during periods of heterotrophy or exported to downstream, heterotrophic systems during floods.

Stream metabolism includes processes of synthesis and decomposition of organic material. Whole system methods (e.g. diel oxygen curves; Odum 1956) and light-dark enclosure (chamber) measurements of oxygen change (e.g. Hansmann *et al* 1971, Marker 1976, Pfeiffer & McDiffett 1975, Sumner & Fisher 1979) have been used to determine rates of net primary production and ecosystem respiration. An assumption of enclosure methods is that chambers contain realistic subsamples of organisms (algae, microorganisms, and invertebrates) responsible for both metabolic processes. Such an assumption is warranted if streams are considered as two-layered systems (sediments and water) in which organisms associated with surface sediments affect chemistry of water flowing over them. The assumption is invalid, however, when processing by deep sediment communities contrib-

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utes to whole system metabolism. Such activity will not be measured by surface enclosures if active hyporheic sediments are excluded or if influx of interstitial water to the surface water column is precluded by chamber design.

Limnologists and marine ecologists have long been aware of the influence of sediment metabolism on overlying water. In lakes, salt marshes, and coastal systems biological activity in sediments is significant, but rates of exchange of interstitial with surface water are largely controlled by hydrodynamic factors (Keeney 1973). Salt marsh interstitial water has a long residence time (Teal & Kanwisher 1961) and exchange may occur solely because of animal activity (Everest & Davis 1979). Exchange between pore water and surface water is common in salt marsh embayments, estuaries, and coastal systems (Hale 1975, Nixon *et al* 1975) and must be included in nutrient budgets (Rowe *et al* 1975).

A few stream studies implicate deep sediments in nitrogen dynamics (Chatarpaul & Robinson 1979, Hill 1981). Most work on stream metabolism, however, has emphasized surface sediment processes, yet data have existed for quite some time that imply biological activity beneath the sediment surface (Coleman & Hynes 1970, McNeil 1962), as well as interchange between surface and interstitial water (Vaux 1962, 1968). In salmon spawning gravels, for example, embryo success is correlated with interstitial dissolved oxygen which in turn is related to velocity of intragravel flow and hence residence time of intragravel water (Coble 1961, McNeil 1962). Exchange between interstitial water and surface water may be expected in any stream where variations in streambed concavity, sediment permeability, or sediment cross sectional area exist (Vaux 1962).

This paper reports an investigation of summertime stream metabolism in a 30-m reach of Sycamore Creek, Arizona. We present simultaneous measurements of metabolism for the whole system and for enclosures of both surface sediments (chambers) and deep sediments (cores). Our results are from two dates in August, 1982, when water temperatures and solar radiation were both high, thus both primary production and respiration should be near maximum hourly rates for this system. Data are used to compare a two-layer (surface sediment + water column) to a three-layer (deep sediment + surface sediment + water column) model of the desert stream ecosystem. We will test the null hypothesis that deep sediments have no effect on stream metabolism. We then explore implications of our results for metabolism and nutrient cycling of desert streams in particular and streams in general.

Study site

Sycamore Creek (33° 45′ N, 111° 30′ W), 32 km northeast of Phoenix, Arizona, USA, is a tributary of the Verde River. The stream drains a 505 km^2 catchment which ranges in elevation from 427 to 2 164 m. Like many mid-sized streams of the Sonoran Desert, Sycamore Creek is spatially and temporally intermittent and is fed primarily by high elevation precipitation (Thomsen & Schumann 1968). Annual precipitation is from 39 cm a^{-1} at 510 m to 51 cm a^{-1} at 1 040 m, and peaks bimodally in winter and summer. Localized summer thunderstorms may cause flash flooding during which discharge rises abruptly and falls to preflood levels within 1–2 days (Fisher & Minckley 1978). A more complete description of the stream is in Fisher *et al* (1982).

Work reported here was done on 6 and 17 August 1982, 14 and 25 days after a resetting flash flood of 2 $m^3 \cdot s^{-1}$ occurred at the study site. The study reach is at 640 m elevation, approximately 1 km downstream from a source of surface flow. Riparian vegetation consists of seepwillow (*Baccharis salicifolia*) and willow (*Salix goodingii*), but the stream is unshaded for most of the day. During the study period, the algal community was dominated by diatoms. The blue green alga *Anabaena* was also present. *Cladophora glomerata,* which is common in Sycamore Creek, was absent at the time of the study as were aquatic macrophytes. Discharge was 0.01 $m^3 \cdot s^{-1}$ during the study period. Sediments are coarse sand of 0.42 m average depth (limits 0.2–1.0 m), mean stream width is 1.4 m, and average water depth is 3.6 cm in the study reach.

Methods

Surface and Deep Sediment Metabolism

Metabolism of the surface sediment community was measured using open-bottom, circular plexi-

glas chambers enclosing 90.8 cm^2 of sediment buried to 15 cm depth. Floating plexiglas lids with submersible motors attached to stirring paddles enclosed and gently stirred the water column. Respiration (R) was measured as oxygen consumed in 30 min in chambers darkened by aluminum foil. Immediately thereafter, foil was removed and net production (P_N) measured as oxygen generated during 20–30 min. Water samples taken with 10 ml syringes through sample ports in chamber lids were analyzed for dissolved oxygen using a micro-Winkler technique (Busch & Fisher 1981). Gross production (P_G) was calculated as the sum of R and P_N. Surface and interstitial waters do not mix in chambers. Fluorescein dye added to either interstitial or surface water of chambers remains stationary during the time required for measurements, probably because convectional exchange is stopped. Chamber R and P_N therefore reflect metabolism of only the surface sediment community.

Deep sediment respiration was determined in 10–30 cm sediment cores (15.5 cm^2) taken after diatom-covered sediments (to about 2 cm) were removed. Cores were sealed at each end with rubber stoppers. Initial oxygen samples were taken from the bottom of the core with a 10 ml syringe inserted through the rubber stopper. Cores were incubated in the dark for 1–2 h, then sampled again for dissolved oxygen. The final sample was of 25–50% of total interstitial volume. Rate of change of interstitial oxygen was then used to calculate metabolism (respiration) of the deep sediments. Columns were drained after measurements to calculate interstitial volume and percent interstitial space.

Chlorophyll *a* was determined on half of the chamber surface sediments (to 2 cm depth) by a methanol extraction technique (Tett *et al* 1977). The other subsample was dried at 95 °C and combusted at 550 °C to determine ash-free dry mass (hereafter referred to as biomass). Ash-free dry mass (including microbial biomass and detritus) was determined for entire columns of deep sediments (2 cm < depth < 15 cm).

Whole System Metabolism

Metabolism of the study reach was determined from dissolved oxygen change (ΔO_2) between up and downstream termini of the study reach in light and dark (flow time = 2 min). Net ecosystem production was measured as light ΔO_2 minus diffusion. To measure ecosystem respiration, the 30-m reach was covered with black plastic sheeting which floated on the water surface, darkening the stream and preventing diffusion in or out. To measure diffusion alone, the leading edge of the plastic sheet was pushed into the sandy substrate which allowed the entire stream to flow over the plastic. Morphometry of the channel was unchanged by this manipulation. ΔO_2 with the plastic so placed is attributable to diffusion alone, as the benthic community is isolated from the flowing water. The diffusion constant (f, m h^{-1}) was calculated by dividing the diffusion rate (g m^{-2} h^{-1}) by mean saturation deficit (g m^{-3}) of the 0 and 30 m stations.

Oxygen was measured on 6 August with a YSI model 5 400 electrode, and on 17 August by the Winkler method (azide modification). Residence time was determined both as system volume/discharge, and as time required for fluorescein dye to travel 30 m. Morphometry was determined by measuring width and depth on transects at 5 m intervals. All oxygen changes in mg l^{-1} were converted to mg O_2 m^{-2} h^{-1} by multiplying by system volume and dividing by system area × flow time.

Sediments and interstitial water

To investigate interstitial-surface water exchange, we injected 30–50 ml fluorescein dye 10 cm into sediments at 0, 5, 8, 10, 12, 15, 18, 20, 26, and 30 m. Times of appearance of dye at the surface, peak flow, cessation of dye flow, and distance of travel beneath the surface were recorded.

Interstitial water was sampled from plastic pipes perforated at the end and driven into the sediments to depths of 15, 20, and 30 cm above the study reach and at 4 and 17 m. Water was pumped from these pipes into a 60 ml glass bottle held in a sealed vessel. Oxygen in these samples was determined with the Winkler method. Interstitial water volume was determined from sediment volume and percent interstitial space.

Nitrogen (N) utilization by deep sediments was investigated in the laboratory. Nitrogen uptake by sediments was determined for samples collected in late July from a site 50 m above the study reach. Sediments (200 g fresh weight) were placed in nine 250 ml erlenmeyer flasks. Sediments were first rinsed three times with the appropriate solution,

then three flasks received 20 ml 5 mg nitrate-N l^{-1}, three received 20 ml 5 mg nitrate-N l^{-1} in 2% formalin solution, and three were first autoclaved, and then received 20 ml sterilized 5 mg nitrate-N l^{-1}. These treatments were intended to separate physicochemical and biological effects. Flasks were sealed with parafilm and stored in the dark at 25 °C for one and four days. Nitrate-N remaining after incubation was determined by cadmium-copper reduction to nitrite (Wood *et al* 1967).

Results

Between 6 and 17 August, surface chlorophyll *a* remained steady at 44.58 (SE = 1.18; n = 3) and 41.24 (SE = 3.12; n = 3) mg m^{-2} and biomass increased from 80.8 (SE = 5.9; n = 3) to 101.4 (SE = 7.0; n = 3) g m^{-2}. Sediment organic matter content as ash-free dry mass remained constant, averaging 0.31% of sediment dry mass.

Oxygen concentration increased at the upstream station during the measurement period on both dates and exceeded saturation at upstream and downstream stations during most of that time (Fig. 1). Water temperature increased gradually from 23.9 to 28.2 °C on 6 August, and from 25.6 to 30.9 °C on 17 August.

Net production and respiration of the surface sediment community, measured in chambers, averaged 479 and 128 mg O_2 m^{-2} h^{-1} on 6 August and 489 and 180 mg O_2 m^{-2} h^{-1} on 17 August (Table 1). Mean deep sediment R (cores) was 53.5 mg m^{-2} h^{-1} on 6 August and 44.4 mg m^{-2} h^{-1} on 17 August. These

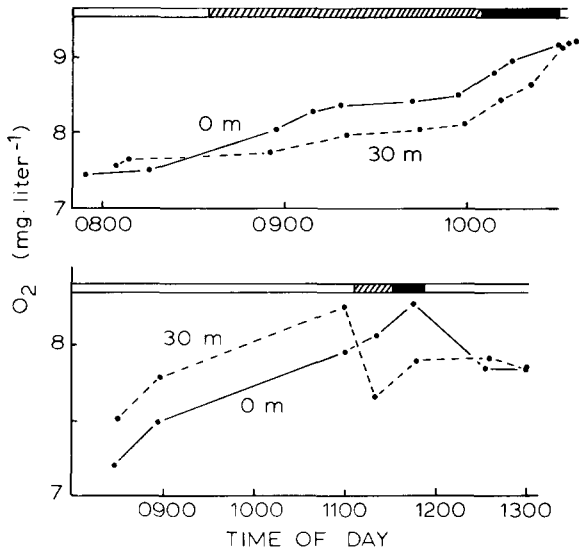

Fig. 1. Oxygen concentration of surface water at upstream (0 m) and downstream (30 m) termini of the study reach in Sycamore Creek, Arizona, during experiments on 6 August (upper) and 17 August (lower), 1982. Horizontal bars refer to manipulations of the black plastic sheet: open bar – plastic removed; hatched bar – plastic floating on the water surface; shaded bar – stream flowing over plastic.

values were applied to the 42 cm mean sediment depth of the reach to estimate total deep sediment respiration: 195 and 147 mg m^{-2} h^{-1} on 6 and 17 August, respectively (Table 1). These two values are not significantly different ($T = 1.44$; $p > 0.05$; $df = 8$).

Over half the nitrate-N added to two samples of fresh sediment was lost from the water column (Table 2). When sediment microorganisms were

Table 1. Metabolism of the surface sediment (chambers, A) and deep sediment (cores, B) communities in Sycamore Creek, Arizona, measured in enclosures. Values given are means of replicate enclosures. Parenthetical values are standard errors.

A.	Date	Time	n*	P_N	R	P_G
				(mg O_2 m^{-2} h^{-1})		
	8- 6-82	0915	3	479 (9.69)	128 (5.54)	607
	8-17-82	1250	3	489 (25.3)	180 (20.4)	669
B.				R	R core^{-1}	R 42 cm^{-1}**
				(mg O_2 l^{-1} h^{-1})	(mg O_2 m^{-2} h^{-1})	
	8- 6-82	1100	6	2.41 (0.132)	53.5 (5.07)	195 (16.3)
	8-17-82	1300	4	1.64 (0.230)	44.4 (11.4)	147 (32.9)

* n = number of replicate enclosures.

** Areal respiration extrapolated to the mean sediment depth (42 cm) in the reach.

Table 2. Uptake of nitrogen from interstitial water by deep sediment columns enriched with nitrate-N. (A) Sediment 1, (B) Sediment 2. Values are means for triplicate cores; parenthetical values are standard errors.

Treatment	Incubation time (h)	NO_3-N added (μg)	NO_3-N remaining (μg)	% NO_3-N lost
A				
Fresh	91	100	29.3 (1.76)	71
Formalin-killed	89	100	91.3 (1.37)	9
Autoclaved	91	100	89.5 (1.80)	10
B				
Fresh	24	89	42 (5.0)	53
Formalin-killed	24	85	87 (8.0)	0
Autoclaved	24	90	101 (11.6)	0

Table 3. Metabolism of a 30 m reach of Sycamore Creek, Arizona, measured as whole-system oxygen change in light and dark. Values expressed in mg O_2 m^{-2} h^{-1}.

Date	Time*	P_N	R	P_g
8- 6-'82	0800	107	421	528
	0815	161	421	582
	1030	546	421	967
	1035	624	421	1 045
8-17-'82	0830	356	455	811
	0900	616	455	1 071
	1100	763	455	1 218
	1230	506	455	961
	1300	403	455	858

* Time given is for measurement of P_N. Respiration was determined on 8-6-82 at 0910, 0919, 0943, and 0958 (standard error = 0, n = 4) and on 8-17-82 at 1120 (n = 1).

killed by sterilization or formaldehyde, losses of nitrate-N were minor (Table 2). Although these results must be interpreted cautiously (concentrations of 5 mg nitrate-N l^{-1} are rare in Sycamore Creek), they suggest that sediment microbial metabolism rather than physicochemical reactions is primarily responsible for nitrate uptake and release in sediments.

Diffusion for the 30 m study reach was -458 mg O_2 m^{-2} h^{-1} on both 6 and 17 August at 1015 and 1145, respectively. The diffusion constant (f) for 6 August was 0.31 m h^{-1}, and this was used for calculation of net production on that date. On 17 August, f was 0.41 m h^{-1}, a value we consider more reliable for Sycamore Creek since it is derived from Winkler determinations, not electrode readings. The electrode was prone to drift, even between frequent calibrations and thus absolute oxygen values (which are critical to diffusion estimates) are less reliable. Respiration was 421 mg O_2 m^{-2} h^{-1} on 6 August and 455 mg O_2 m^{-2} h^{-1} on 17 August, nearly 3 times chamber respiration on both dates (Table 3). Gross production was higher on 17 August (811 mg O_2 m^{-2} h^{-1} at 0830) than on 6 August (582 mg O_2 m^{-2} h^{-1} at 0815), increased continuously

Table 4. Morphometric characteristics of deep sediments and seepage velocities for six sections of the study reach. Parenthetical values are standard errors and number of determinations.

Section	Mean sediment depth (m)	Sediment volume (m^3)	Seepage velocity (cm s^{-1})
0-5 m	0.38	2.85	0.136 (0.022; 9)
5-10 m	0.33	2.07	0.136 (0.032; 7)
10-15 m	0.49	2.94	0.0827 (0.0349; 4)
15-20 m	0.51	3.83	N.A.*,** (n = 7)
20-25 m	0.41	3.08	0.0589 (n = 1)
25-30 m	0.38	3.07	0.0473 (0.0041; 4); N.A.* (n = 4)

* N.A. = dye injected into sediments did not appear at the sediment surface.

** Dye was not found at depth of injection after 60 min.

Table 5. Interstitial oxygen concentrations at 3 transects in Sycamore Creek.

Transect	Surface O_2 (mg l^{-1})	Depth of sample (cm)	Interstitial O_2 (mg l^{-1})		
			W Bank	Middle	E Bank
10 m > study reach	7.96	15	7.34	7.97	6.88
4 m	7.91	15	6.33	7.79	7.50
17 m	7.75	15	7.03	7.54	
		30	5.32	6.78	
17 m - on bank		20			7.28
		52			3.85

on 6 August but declined slightly after noon on 17 August (Table 3).

Seepage of interstitial water into the stream occurred through most of the reach. Dye injected 5–30 cm into sediments usually appeared at the sediment surface downstream of the injection point within 1–80 min as a discrete dye trail which flowed for 9–30 min. Seepage velocity (distance of travel divided by time until first appearance at surface) was highest for the upper 10–15 m of the reach (Table 4). Seven injections at 15, 17, and 18 m never surfaced. One h after injection we were unable to locate the dye bolus by digging into the sediments. At these sites, water apparently moves from the stream into the sediments. Higher seepage velocities are associated with small cross sections or low volumes of sediments. The section of greatest sediment volume had no upward seepage whatsoever (Table 4). Variations in hydrologic and presumably morphometric characteristics at any given transect contribute to high variances in estimates of seepage velocity.

Oxygen in interstitial water was generally slightly lower than in surface water but no anoxic water was found (Table 5). Like interstitial flow, oxygen concentration varies widely at each transect. Deep interstitial water is lower in oxygen than shallow interstitial water, but even at 0.5 m depth outside the wetted stream perimeter, oxygen is present at 3.85 mg l^{-1} (Table 5).

Discussion

Metabolic rates of the surface sediment community suggest a highly productive and potentially autotrophic system. Rates of surface sediment P_N and R agree well with those reported by Busch and Fisher (1981) for Sycamore Creek in summer. Hourly primary production is higher and hourly respiration somewhat lower in Sycamore Creek than in small to midsized streams elsewhere (Hornick *et al* 1981, Marker 1976, Sumner & Fisher 1979). Metabolism of deep sediments is approximately equal to surface respiration on an areal basis. We are aware of no other studies of deep sediment respiration in streams. Mulholland (1981) reported respiration by swamp sediment cores of up to 194 mg O_2 m^{-2} h^{-1}; however, these data are not strictly comparable to ours since they exclude sediments deeper than 10 cm and reflect only oxygen changes in water overlying the sediment. Sediment core oxygen consumption ranges from 6.5–34 mg O_2 m^{-2} h^{-1} in lakes and from 0.3–15 mg O_2 m^{-2} h^{-1} in coastal ecosystems (calculated from annual rates given in Hargrave 1973).

A few recent studies have documented nitrate demand of stream sediments. Sain *et al* (1977) demonstrated removal of 90% of nitrate-N from a 10 mg l^{-1} solution overlying columns of stream sediment. Chatarpaul & Robinson (1979) used ^{15}N incubations of sediments to show loss of N to denitrification by stream sediment microorganisms. Finally, Hill (1981) reported a loss of 50% of nitrate input in an Ontario stream by sediment bacterial denitrification. Our data suggest that desert stream sediments may be similarly active in nitrate removal, although we are unable to attribute this to denitrification and doubt its occurence in these well oxygenated, low organic matter waters.

Sediment oxygen consumption averaged 2.41 and 1.64 mg O_2 l^{-1} h^{-1} on 6 and 17 August, respectively. At this rate of O_2 decline, interstitial oxygen at 8 mg l^{-1} would be depleted in 3–4 h. Influx of surface water into sediments is therefore likely; interstitial oxygen was 6–7 mg l^{-1} at most sampling sites (Table 5). Given these interstitial oxygen con-

centrations we estimated residence time of the water using oxygen consumption rates in cores. Residence times are <1 h and as low as 4 minutes for interstitial water at 15 cm depth. These data, coupled with seepage velocity data, indicate significant flux of water both into and out of deep sediments. Indeed in any stream, oxygenated interstitial water is evidence for significant surface-interstitial exchange.

Respiration rates for the whole ecosystem measured as oxygen change under the plastic sheet are near the highest chamber R values reported by Busch & Fisher (1981) for Sycamore Creek algal mats of 427 g m^{-2} biomass. However, biomass of the surface community in this study was only about 100 g m^{-2}, thus these high rates must include metabolism of deep sediments. If deep sediment core R is added to surface chamber R, their sum approaches our whole system measurements (Table 6). Sources of error may include underestimation of total sediment depth and undetermined variation in organic matter content of deep sediments, for example pockets or lenses of buried organics. Despite the discrepancy between the summed component estimate and measured whole system respiration, either value gives a respiration rate for the stream that exceeds any previously determined estimates for Sycamore Creek.

Diffusion of oxygen from the stream to the atmosphere occurred at all times during the sampling periods. The diffusion constant for Sycamore Creek (0.41 m h^{-1}) is about half that predicted from nomograms derived from studies of large rivers (Churchill *et al* 1962, Hart 1967); however, these nomograms are inappropriate for small, slow-moving, shallow streams.

Whole system P_N was lower than chamber P_N, but a summed component estimate of P_N (chamber P_N + core P_N) shows somewhat closer agreement with whole system rates (Table 6). Gross production is oxygen production by the photosynthetic organisms associated with the stream sediment surface only, thus P_G estimates by whole system and chamber methods should agree. Our whole system estimates were higher than chamber estimates (Table 6). Sampling error in placement of chambers may have resulted in underestimation of gross production by the chamber method. Our purpose, however, is not to compare the two methods but to show that chamber measurements, and hence a

Table 6. Comparison of whole system to component (chambers and cores) metabolism in Sycamore Creek, Arizona during August, 1982. (A) hourly rates in mg O_2 m^{-2}. (B) estimated daily rates (g O_2 m^{-2}) assuming P_g and P_N are constant over 12 h and R is constant over 24 h.

Parameter	Date	Time*	Surface	Surface + sediment**	Whole system
A					
P_G	8-6	0915	607	607	785
	8-17	1250	669	669	858
R	8-6	–	128	323	421
	8-17	–	180	327	455
P_N	8-6	0915	479	284	364
	8-17	1250	489	342	403
P_G/R	8-6		4.7	1.9	1.9
	8-17		3.7	2.0	1.9
B					
$P_G \times 12$	8-6	0915	7.3	7.3	9.4
	8-17	1250	8.0	8.0	10.3
$R \times 24$	8-6	–	3.1	7.8	10.1
	8-17	–	4.3	7.8	10.9
$P_N \times 24$	8-6	0915	4.2	-0.5	-0.7
	8-17	1250	3.7	0.2	-0.6
P_G/R	8-6	–	2.4	0.94	0.93
	8-17	–	1.9	1.0	0.94

* Time given is for measurement of chamber P_N and R. Whole system values corresponding to the time of chamber measurements on 8-6-'82 were calculated from a regression on the raw data.

** Surface + sediment is summed chamber and core metabolism: $R = R_{sed} + R_{surf}$, $P_G = P_{Gsurf}$, $P_N = P_{Gsurf} - R_{surf+sed}$.

view of streams as two-layered systems, may result in substantial underestimation of ecosystem respiration.

Although our data are hourly rates, we have calculated daily P/R (gross primary production/ecosystem respiration) for this stream based on 12 h of gross production and 24 h of ecosystem respiration (Table 6). P_G is probably overestimated since early morning and late afternoon rates would be lower than those measured here. Even with this overestimate, the system was slightly heterotrophic both days (P/R = 0.93 and 0.94 on 6 and 17 August, respectively). Chamber measurements however, yielded P/R = 2.4 on 6 August and P/R = 1.9 on 17 August. Thus exclusion of deep sediment R gives an erroneous picture of desert stream metabolism.

Implications for stream metabolism and nutrient cycling

Given the high rates of whole system respiration revealed by the use of black plastic, and supported by high rates of deep sediment metabolism, we propose that even this highly productive, algal-based desert stream may be heterotrophic. Minshall (1978) rightly points out that many more streams may be dependent on autochthonous organic matter as a food base than previously believed. The question of system autotrophy, however, revolves around the balance of gross primary production and ecosystem respiration. Despite high rates of P_G, streams remain heterotrophic by definition, if R exceeds P_G. As Fisher (1977) points out, system autotrophy must at some time or place be balanced by heterotrophic consumption of excess organic matter, or autotrophic streams would inexorably fill with organic matter. Consumption of net biomass increment may of course take place outside the system, if organic matter is exported to downstream ecosystems – lakes, large rivers, or the ocean. To say that a stream is heterotrophic says nothing about its relative dependence upon allochthonous or autochthonous organic matter, but simply that ecosystem utilization of organic matter exceeds supply by photosynthesis. In productive Sycamore Creek, daily $P/R < 1$ occurs even at a time of year when P_G is highest, because of high respiration of the hyporheic community.

Significant biological activity within deep sediments is probably not unique to desert streams. Such activity is possible wherever organic matter substrates supporting respiratory activity of microorganisms are present within deep sediments. Translation of chemical effects to surface waters requires interstitial-surface water exchange. Literature from salmon spawning riffles suggests depletion of oxygen in intragravel water (McNeil 1962, Woods 1980). Problems of deoxygenation of intragravel water may be exacerbated by intrusion of fine particles into gravels (Moring 1982), perhaps because surface-interstitial exchange is slowed (Beschta & Jackson 1979) or because of addition of organic matter to intragravel spaces. Burial of coarse particulate material during floods in many rocky streams provides a deep sediment organic substrate (Herbst 1980). In Sycamore Creek, flash floods transport nearly 50 g dry mass l^{-1} suspended solids of which 10–30% may be organic fine particulates. Most of this is allochthonous material exported from terrestrial watersheds by sheetflow (Fisher & Minckley 1978, McGee 1897), which is deposited as an admixture of organic and inorganic particles, producing a sediment layer of a meter depth or more. In the present study, organic matter was approximately 0.3% of dry sediment weight; for the study reach this represents a total of 23.5 kg organic material m^{-3} interstitial water. At an average consumption rate of 4.2 g organic matter m^{-3} h^{-1} (assuming oxygen consumption is 50% of organic matter utilization), this amount of organic material would last 233 days. Since average flood return frequency is less than this, there is continual supply of organic material for deep sediment respiration, in addition to that supplied by photosynthesis.

If deep sediments are important in whole system metabolism, they undoubtedly also play a role in nutrient dynamics. Measureable nitrate uptake occurs in desert stream reaches below high-nitrate springs. This has been attributed to algal uptake (Grimm *et al* 1981); deep sediment microbial communities may play a role as well. Our demonstration of sediment nitrate demand is preliminary, but we propose that allochthonous fine organic substrates of deep sediments are low in nitrogen relative to carbon, and therefore may be a sink for nitrate as are leaves in temperate streams (Howarth & Fisher 1976, Kaushik & Hynes 1968, Triska *et al* 1975). Alternatively, nitrate loss may be attributable to denitrification. Rates of denitrification are

low when oxygen is present (Van Kessel 1977), thus we feel that few sites are likely to exist in Sycamore Creek where conditions are conductive to rapid denitrification. However, in streams where interstitial water movement is slow or organic matter high, denitrification is a potentially important pathway of N loss (Chatarpaul & Robinson 1979, Hill 1981, Kaushik & Robinson 1976). Other biological reactions unique to anaerobic environments, such as detrital electron flux (Rich 1979, Rich & Devol 1978), may occur in streams, obscuring metabolic pathways that do not involve oxygen when oxygen methods are used to measure respiration.

We are only able to speculate on the extent of hyporheic metabolic activity and its surface chemical manifestations among streams worldwide. We feel that the data presented here dictate a modification of the two-layer model of stream ecosystems, at least for desert and other streams with permeable substrates. Certainly the stream ecosystem extends to some degree below the surface of sediments in all but streams on bedrock. Investigations of the physical process of interstitial-surface water exchange and of biological processing within sediments are needed if the extent of this phenomenon is to be known. Until such time, it is incumbent upon individual investigators to make a rational case for exclusion of deep sediments from models of stream metabolism.

Summary

The subtantial contribution of the hyporheic community to whole ecosystem metabolism argues strongly for inclusion of deep sediments in conceptualizations of stream ecosystems. While whole system and chamber estimates of gross primary production agree reasonably, open system respiration exceeds respiration estimated with enclosure methods by almost three fold (440 vs 155 mg O_2 m^{-2} h^{-1} respectively). This is because chambers neither enclose deep sediments nor permit vertical exchange between surface and interstitial water. This exchange is common in streams with porous substrates such as Sycamore Creek. In such situations, use of chambers to estimate ecosystem metabolism will grossly overestimate ecosystem autotrophy (P/R) by underestimating sediment respiration.

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