VERTICAL HYDROLOGIC EXCHANGE AND ECOSYSTEM METABOLISM IN A SONORAN DESERT STREAM[1]

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Abstract. Hyporheic metabolism in a Sonoran Desert stream was examined, focusing on the sources of detritus supporting hyporheic respiration. Two alternative hypotheses were specifically addressed: (1) organic matter derived from the surface stream supports hyporheic respiration, and (2) detritus buried during flash floods supports hyporheic respiration. As predicted for the surface-derived organic matter hypothesis, respiration was lowest immediately following flash floods and increased significantly with time after flood ($P < 0.001$). Hyporheic respiration ranged from 0.05 $mgO_2 \cdot L$ sediments$^{-1} \cdot h^{-1}$ immediately following a flash flood to as high as 4.41 $mgO_2 \cdot L$ sediments$^{-1} \cdot h^{-1}$ late in algal succession. Respiration was significantly correlated with surface algal biomass during two spring/summer successional sequences ($P < 0.05$; partial correlation coefficients 0.58 and 0.88). Respiration was also consistently higher in downwelling than upwelling zones with overall mean rates of 1.12 and 0.46 $mgO_2 \cdot L$ sediments$^{-1} \cdot h^{-1}$, respectively. Respiration exhibited a distinct diel pattern with highest rate coinciding with time of maximum photosynthesis and was also significantly correlated with dissolved organic carbon concentration ($P < 0.05$), further supporting the hypothesis of hyporheic dependence on algal production. Flash floods bury organic matter that is also respired in the hyporheic zone; however, based upon storage of organic carbon immediately following floods, an average of only 15% of the observed respiration could be supported. We conclude that hyporheic respiration in Sycamore Creek is tightly linked to surface production. It is spatially distributed in biotic "hot spots" where surface waters enter hyporheic sediments and is most likely supported by organic matter that is supplied as dissolved organic carbon, perhaps from algal production.

Key words: carbon dynamics; desert streams; disturbance; hydrology; hyporheic zone; Sonoran Desert; spatial heterogeneity; stream metabolism; vertical hydraulic gradients.

INTRODUCTION

Stream ecosystem respiration is spatially heterogeneous and depends on many factors including abundance and species composition of microorganisms (Characklis and Cooksey 1983, Rounick and Winterbourn 1983), organic matter quantity and quality (Kaplan and Bott 1985, Leff and McArthur 1990), inorganic nutrient availability, and availability of terminal electron acceptors (Dahm et al. 1991). Previous studies of stream respiration have focused on surface metabolism; however, sediments underlying the surface stream (the hyporheic zone) also are metabolically active (Grimm and Fisher 1984). The hyporheic zone is an important habitat for invertebrates (Bretschko and Leichtfried 1988, Stanford and Ward 1988, Strommer and Smock 1990), is a major site of detrital storage (Metzler and Smock 1990, Leichtfried 1991), and influences surface stream functioning through hydrologic exchange (Wallis et al. 1981, Munn and Meyer 1988, White 1990, Grimm et al. 1991, Valett et al. 1994). Organic matter within hyporheic sediments varies in abundance and

composition (Rutherford and Hynes 1987, Leichtfried 1991) which has important implications for respiration. Moreover, dissolved oxygen, the electron acceptor used in aerobic metabolism, also varies in space and time and can limit hyporheic metabolism (Dahm et al. 1991).

The surface stream and hyporheic zone are linked at areas of hydrologic upwelling (hyporheic to surface) and downwelling (surface to hyporheic) (Rutherford and Hynes 1987, White 1990, Valett et al. 1994). Previous research has demonstrated that the structure and functioning of the surface stream is influenced by hydrologic upwelling. Hyporheic waters are frequently enriched in nitrogen and phosphorus (Triska et al. 1989, Duff and Triska 1990, Valett et al. 1990, Grimm et al. 1991, Hendricks and White 1991), and may alleviate surface nutrient limitation at upwelling zones (Grimm et al. 1991, Valett et al. 1994). Valett et al. (1994) showed algal species composition was different and biomass higher in upwelling than in downwelling zones. Nutrient-poor water in downwelling zones limited algal production and favored cyanobacteria in comparison to chlorophytes.

The hyporheic zone is also reliant upon linkage with the surface stream and surrounding terrestrial environment. Grimm and Fisher (1984) reported respiration in the hyporheic zone of a Sonoran Desert stream nearly equal to that of the surface stream. This high respira-

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tory demand is ultimately dependent on the surface stream or surrounding terrestrial environment for organic matter as a substrate for respiration.

This research focused on two questions, (1) what is the source of organic matter supporting hyporheic respiration, and (2) by what mechanism does this material enter hyporheic sediments? Two alternative hypotheses were specifically addressed, (1) organic matter derived from the surface stream supports hyporheic respiration (surface stream-derived organic matter hypothesis), and (2) detritus buried during floods supports hyporheic respiration (flash flood-buried organic matter hypothesis). Desert streams have high algal production and biomass (Busch and Fisher 1981, Grimm 1987) that may be an important organic matter substrate for hyporheic respiration. If surface stream-derived organic matter supports hyporheic respiration then we predict (1) hyporheic respiration will increase with time after flood as algal biomass increases, and (2) hyporheic respiration will be highest in areas of downwelling where surface water containing labile organic carbon enters hyporheic sediments. Desert streams also are disturbed by flash floods that scour much of the substrate, remove algae, transport detritus into the stream from the watershed, and bury detritus in hyporheic sediments. If this detritus supports hyporheic respiration then we predict (1) hyporheic respiration will be greatest soon after flash floods when hyporheic particulate organic matter (POM) storage is highest and decrease as POM labile fractions are depleted by respiration, and (2) hyporheic respiration will be equal in upwelling and downwelling zones. These predictions were tested over 14 months that encompassed four floods and subsequent recovery sequences in downwelling and upwelling zones of three runs in Sycamore Creek, Arizona, USA.

STUDY SITE

Sycamore Creek is an intermittent Sonoran Desert stream located 32 km northeast of Phoenix, Arizona, USA. The stream drains a 505 km² mountainous watershed varying in elevation from 427 to 2164 m. The catchment is composed of igneous and metamorphic rocks with shallow overlying soils and unconsolidated sediments (Thomsen and Schumann 1968). Ponderosa pine and piñon–juniper woodlands predominate at higher elevations and Sonoran desert scrub at lower elevations. Precipitation is bimodal in winter and summer with annual means of 58.4 and 33.9 cm/yr at higher and lower elevations, respectively (Thomsen and Schumann 1968).

In mid-elevation runs (ranging in elevation from 600 to 760 m) of Sycamore Creek, where this study was performed, mean stream depth is 5 cm and average wetted channel width is 5–6 m. The wetted channel is bounded by an active channel of alluvium that is over 20 m wide (Fisher et al. 1982). Stream substrata consist primarily of sand and fine gravel with a mean depth to

bedrock of 62 cm (Valett et al. 1990). Riparian trees are restricted to high flow stream margin, consequently the stream receives full sunlight most of the day and has in-stream gross primary production as high as 12 $gO_2 \cdot m^{-2} \cdot d^{-1}$ and algal biomass (chl a) as great as 350 mg/m² (Grimm 1987).

Three study reaches were selected in sandy runs at ≈650 m elevation. Reaches I, II and III were 295, 115 and 104 m long, respectively, and were separated by pools and riffles.

METHODS

Spatial and temporal patterns of hyporheic respiration

Respiration rate was measured in one upwelling and one downwelling zone in each of three study reaches ($n = 3$ upwelling, $n = 3$ downwelling sites) approximately monthly from April 1992 through June 1993. Upwelling and downwelling zones were located at the tops and bottoms of each of the three study reaches based upon the work of Valett et al. (1994) in which this hydrologic pattern was originally reported for Sycamore Creek. Vertical hydraulic gradient (VHG) at the top and bottom of each run was confirmed during this study using mini-piezometers (Lee and Cherry 1978). Piezometers were 9-mm (internal diameter) polyethylene tubes with lateral perforations near the tip of the tube covered by 300 μm Nitex mesh. Piezometers ($n = 1$ measurement per site) were inserted to a depth of 25 cm below the stream bed and hydraulic head (cm) was measured using a manometer to determine difference in water column heights between water columns drawn simultaneously from the piezometer and surface stream. VHG was calculated as the hydraulic head divided by piezometer depth (cm/cm). Positive VHG indicates hyporheic waters upwelling into surface waters, whereas negative VHG indicates surface waters downwelling into hyporheic sediments. VHG was measured on all sampling dates except for three during spring 1993 when current velocity was too high for accurate measurement.

Subsurface respiration was measured as uptake of dissolved oxygen in chambers that contained hyporheic sediments and hyporheic water. Respiration chambers were constructed from clear plastic pipe (32 cm long, 4.4 cm inside diameter) that were sealed on both ends with rubber stoppers. Chambers were filled with hyporheic sediments that were collected from a depth of 2–17 cm below the sediment surface. Sediments to fill chambers were collected by scraping away benthic sediments and algae (top 2 cm of sediments) then inserting chambers to a depth of 17 cm and withdrawing the plastic pipe filled with 15 cm of sediments. Chambers were filled with water pumped from the hyporheic zone, gently inverted three times to allow any air trapped within sediments to escape, and sealed on the ends with rubber stoppers. Sealed chambers were then

buried in hyporheic sediments at a depth of 10 cm (to eliminate light) and incubated *in situ* for 3–4 h.

Three respiration chambers of replicated sediment samples were incubated from each upwelling and downwelling zone ($n = 18$ incubations per sampling date). Replicated incubations within a site were started immediately after filling chambers with sediments and water. Incubations at different sites were started ≈ 0.5 h apart (lag time between sites due to transit and set-up time) and alternated between downwelling and upwelling zones.

Water to fill respiration chambers was collected from the same piezometer used for VHG measurements. Water was drawn with a peristaltic pump and initially pumped into a 4-L polyethylene container, from which the three chambers and three dissolved oxygen bottles were filled for each sample site. Initial oxygen concentration in the three chambers for a given site was determined as the average of the three dissolved oxygen samples from that site. Samples for determination of final dissolved oxygen concentration in chambers were collected by inverting chambers three times (to mix water in chambers) and filling a dissolved oxygen bottle from a continuous column of water drawn from the core. The volume of sediments and water in a chamber were also determined and the sediments saved for later analysis of particulate organic carbon (POC). Three pre-acid washed polyethylene bottles were also filled from the 4-L polyethylene container for analysis of interstitial water chemistry ($n = 3$ samples from each upwelling and downwelling site, $n = 18$ subsurface samples total per sampling date). Triplicate samples of surface stream water were also collected ($n = 3$ samples per date).

Water chemistry samples were stored at 4°C, filtered upon return to the laboratory (Whatman GF/F glass fiber filters), and analyzed for dissolved organic carbon (DOC), total dissolved monosaccharides, ammonium nitrogen (NH_4-N), nitrate nitrogen (NO_3-N), total dissolved nitrogen (TDN), and soluble reactive phosphorus (SRP). Dissolved organic carbon was analyzed using persulfate oxidation on an Oceanography International Model 700 Total Carbon Analyzer (Menzel and Vaccaro 1964). Total dissolved monosaccharides were measured by MBTH (3-methyl-2-benzothiazolinone hydrazone hydrochloride) assay (Johnson and Sieburth 1977). Ammonium was measured with the phenolhypochlorite method (Solorzano 1969). Nitrate was analyzed colorimetrically following reduction to nitrite in cadmium-copper columns (Wood et al. 1967). Dissolved organic nitrogen (DON) was determined by difference between TDN and dissolved inorganic nitrogen (NH_4-N + NO_3-N); TDN was analyzed as nitrate following 4 h of ultraviolet oxidation (Manny et al. 1971). Molybdate-antimony analysis was used to measure SRP (Murphy and Riley 1962). Dissolved oxygen samples were analyzed by the Winkler method.

Sediment samples were stored on ice for transport to the laboratory after which samples were frozen until analyzed. POC was analyzed by sealing sediments (<1 mm size class separated by dry sieving) into glass ampules, digesting with persulfate oxidation, and measuring resulting CO_2 on a total organic carbon analyzer (Menzel and Vaccaro 1964).

Algal biomass was measured every 2 to 4 wk in study reach I by first mapping algal percentage cover by patch type and then randomly sampling all patches covering >10% area with a 25-cm^2 core to 2 cm depth ($n = 5$ cores per patch; Grimm 1987). Samples were stored on ice for transport to the laboratory then frozen until analyzed spectrophotometrically for chlorophyll *a* using a methanol extraction technique (Tett et al. 1975). Total chlorophyll *a* for the reach was calculated as the sum of patch specific chlorophyll *a* multiplied by the proportion of stream occupied by that patch. Thus, algal biomass values reported herein are for whole reaches.

Average respiration rate on annual and successional sequence bases was calculated as weighted means; respiration rate on each sampling date was weighted by the time interval between the previous and successive sampling dates. Effects of run location (run top vs. run bottom) and days postflood (DPF) on respiration, VHG, dissolved oxygen, DOC, monosaccharides and POC were assessed using a repeated measures ANOVA (SYSTAT: Wilkinson 1990). The correlations of algal biomass, dissolved oxygen, VHG, DOC, monosaccharides, POC, NH_4-N, NO_3-N, DON, SRP, atomic ratio of DOC:TDN (total dissolved nitrogen), and temperature with hyporheic respiration in upwelling and downwelling zones were analyzed by forward stepwise multiple linear regression ($\alpha = 0.05$-to-enter; Wilkinson 1990). Data were transformed prior to analysis, if necessary, to meet the assumptions of normality and equal variances.

Diel variation in hyporheic respiration

The surface stream-derived organic matter hypothesis was also examined by testing for a relationship between diel variation in algal production and hyporheic respiration. The relationship was examined by determining if hyporheic respiration rate varied over 24 h and if the character (e.g., amount of labile organic matter) of surface water changed on a diel basis. Hyporheic respiration rate was assessed on one sampling date late in time after a flood (181 days after flood; 8–9 July 1993), when algal biomass was high, in the downwelling zone of study reach I. Respiration rate was measured *in situ* using chambers previously described. Three chambers were filled with sediments (2–17 cm depth) and hyporheic water (drawn from 25 cm) every 4 h and incubated buried in stream sediments for 4 h. Thus, respiration rate was measured at 1000, 1400, 1800, 2200, 0200, and 0600 hours.

To differentiate between effects of diel temperature variation and changes in the character of stream water, sediments were also incubated in the laboratory using

surface water collected every 4 h during the diel sampling trip. In other words, temperature was constant and only temporal origin of water varied. Hyporheic sediments were randomly collected from the downwelling zone of reach I (collected from 2–17 cm depth) and transported to the laboratory at ambient temperature. Laboratory incubation chambers differed from field chambers in that they were plumbed to peristaltic pumps that recirculated water through the sediments (mean flow rate through sediments = 0.6 mm/s). Chambers (32 cm long, 4.4 cm inside diameter) were initially plumbed in-line to a reservoir to provide sufficient water volume for initial oxygen samples. Water circulated from the reservoir through chambers and then back to the reservoir for 1 h before incubation was initiated. Initial dissolved oxygen samples were collected by drawing water from the reservoir, through chambers and into dissolved oxygen bottles ($n = 3$). After initial oxygen samples were collected, the routing of flow through chambers and reservoir was changed so that water circulated from the top of a core through the pump and back to the bottom of the core. Sediments were incubated for 4 h ($n = 4$ chambers per point in time), and final dissolved oxygen samples were collected by drawing water from chambers into dissolved oxygen bottles ($n = 1$ per chamber). Effects of time of day on hyporheic respiration for both *in situ* and laboratory incubations were analyzed with repeated measures ANOVA on transformed data (Wilkinson 1990).

Hyporheic respiration vs. DOC and POC concentration

The surface stream-derived organic matter and flash flood-buried organic matter hypotheses were further examined by testing effects of surface DOC and hyporheic POC on hyporheic respiration using hyporheic sediments incubated in the laboratory. Concentration of DOC was manipulated by diluting stream water with distilled water producing four treatment levels (0, 33, 67, 100% stream water). Incubation chambers were those previously described for the diel laboratory experiment. Water samples for DOC analysis were collected from the outflow line from chambers (i.e., the return line to reservoir) and are an integration of treatment water and water stored in the sediments. Consequently, the distilled water treatment contained DOC from interstitial water.

The effects of POC were examined by amending sediments in respiration chambers with natural fine particulate organic matter (FPOM). FPOM was obtained from the hyporheic zone of study reach I by collecting sediments (using a trowel; sediments from 2–17 cm depth) and stream water into a bucket, swirling the container to separate dense inorganic particles from FPOM, and decanting supernatant (water and FPOM) through a sieve (0.053 mm mesh size). FPOM was transferred from the sieve into a polyethylene bottle

and stored at 4°C until incubations. Sediment cores were amended with FPOM creating four treatments (0, 45, 90, 180 g wet mass FPOM added per chamber). Following laboratory incubation, sediments from each chamber were analyzed for POC as previously described. POC in chambers ranged from 30 to 96 mgC/L sediment. Respiration vs. POC and DOC concentration was analyzed using simple linear regression (Wilkinson 1990).

RESULTS

During the study Sycamore Creek experienced four floods on 2 April 1992, 23 August 1992, 8 December 1992, and 8 January 1993 with peak discharges of 21.4, 113, 11.5, and 650 m³/s, respectively (discharge data from United States Geological Survey 1992, 1993). This range in flood magnitude encompassed discharges with return frequencies from 1 to 50 yr (flood frequency data for Sycamore Creek from Hedman and Osterkamp 1982).

Hydrologic exchange and hyporheic zone chemistry

The hydrologic pattern of upwelling zones at the tops of runs and downwelling zones at the bottoms of runs reported by Valett et al. (1994) was also observed in this study (Table 1). Vertical hydraulic gradient at the tops of the three runs ranged from 0 to 0.04 cm/cm (Fig. 1) and was significantly greater than at the bottoms of runs ($P < 0.05$; Table 2), where VHG ranged from 0 to -0.16 cm/cm. Hydraulic gradient also changed significantly with time after flood ($P < 0.05$; Table 2), becoming increasingly negative at the bottoms of the three study reaches.

Dissolved oxygen in the hyporheic zone of Sycamore Creek was highest in downwelling zones where aerated surface waters entered hyporheic sediments (Table 1). Dissolved oxygen concentration of surface and downwelling zone waters was similar averaging 7.70 and 7.62 mgO₂/L, respectively, but significantly greater than in upwelling zones where dissolved oxygen concentration averaged 3.89 mgO₂/L ($P < 0.001$; Table 2).

In contrast to the spatial variation observed in dissolved oxygen, organic carbon did not exhibit a consistent spatial pattern. All three measures of organic carbon (DOC, POC and total dissolved monosaccharides) were not significantly different among surface, downwelling, and upwelling waters ($P \geq 0.05$; Table 2).

During the spring/summer successional sequence of 1992 the temperature of Sycamore Creek increased from 18.5°C in April 1992 to 26°C in July 1992. Similarly, during the spring/summer successional sequence of 1993 temperature rose from 14°C in February 1993 to 25°C in June 1993. Over the autumn successional sequence, however, temperature declined from 24°C in August 1992 to 17°C in November 1992.

TABLE 1. Chemical and physical characteristics of surface stream, downwelling and upwelling waters, and hyporheic downwelling and upwelling sediments for study sites in Sycamore Creek, April 1992 through July 1993. Data are means $\pm$ SE ($n = 135$ for downwelling and upwelling zones, $n = 45$ for surface stream).

	Stream location					
	Surface		Downwelling zone		Upwelling zone	
	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
VHG (cm/cm)			−0.059*	0.008	0.013*	0.004
Dissolved oxygen (mg O_2/L)	7.70	0.13	7.62	0.33	3.89	0.38
DOC (mg C/L)	2.97	0.13	3.40	0.19	3.15	0.16
Monosaccharides (μg C/L)	324	32	248	61	276	69
POC (mg C/L sediment)			35.7	3.8	27.6	4.0
NH_4 (μg/L)	13	4	26	8	38	12
NO_3 (μg/L)	99	2	171	9	173	18
DON (μg/L)	117	13	127	10	122	14
SRP (μg/L)	47	2	57	4	73	10

* $n = 36$.

Spatial and temporal patterns of hyporheic respiration

Hyporheic respiration changed significantly over time ($P < 0.001$; Table 2, Fig. 2) with lowest rate immediately following floods and increasing thereafter. Respiration in upwelling and downwelling zones increased an average ninefold over the four successional sequences. Respiration was as low as 0.05 mgO_2·L sediments^{-1}·h^{-1} in upwelling zones in February 1993 and as high as 4.41 mgO_2·L sediments^{-1}·h^{-1} in downwelling zones in July 1992.

Hyporheic respiration exhibited a pattern similar to that of surface stream algal biomass (Fig. 2). Imme-
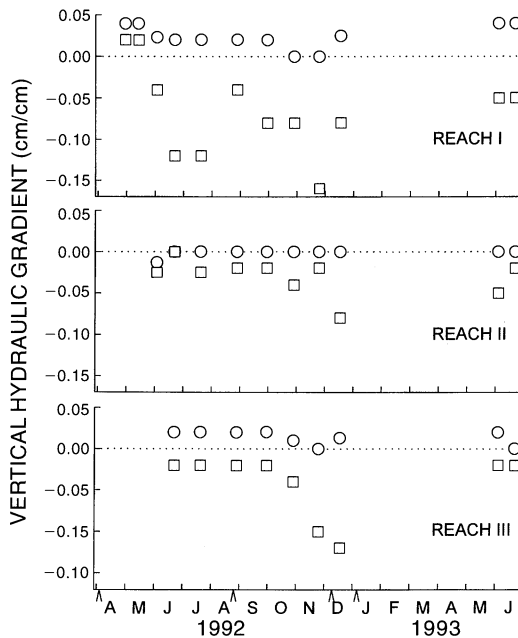

FIG. 1. Vertical hydraulic gradients (VHG) at the upstream (○) and downstream (□) ends of the three study reaches. Data are single measures of VHG. Arrow heads on abscissa denote timing of flash floods.

diately following the four floods algal biomass averaged only 10.7 mg/m² chl a. During the first and fourth successional sequences, which culminated in summer, algal biomass peaked at 201 and 333 mg/m² chl a by July 1992 and June 1993, respectively. Algal biomass over the second successional sequence (23 August–8 December 1992) rapidly reached 345 mg/m² chl a by late summer, but declined to 130 mg/m² chl a in late autumn as temperatures declined. Chlorophyll a during the third successional sequence in December 1992, which only lasted 30 d and was only sampled once, was 25.1 mg/m².

Respiration was higher in downwelling zones than in upwelling zones. In fact, respiration in downwelling zones was more than twice that of upwelling zones ($P < 0.01$; Table 2, Fig. 2), with weighted annual mean respiration of 1.12 and 0.46 mgO_2·L sediments^{-1}·h^{-1}, respectively. Over the four successional sequences, weighted mean respiration for downwelling and upwelling zones was, respectively, 1.99 and 0.77 mgO_2·L sediments^{-1}·h^{-1} from April 1992 through July 1992, 0.65 and 0.36 mgO_2·L sediments^{-1}·h^{-1} from August 1992 through November 1992, 0.99 and 0.51 mgO_2·L sediments^{-1}·h^{-1} from December 1992 through January 1993, and 0.75 and 0.33 mgO_2·L sediments^{-1}·h^{-1} from February 1993 through June 1993. The pattern of recovery after flood in downwelling and upwelling zones was similar in that there was no significant interaction between hydrology and time after the event ($P \geq 0.05$; Table 2, Fig. 2).

From 24 to 90% of the variation in hyporheic respiration was explained by a total of nine independent variables (Table 3). During the two spring/summer successional sequences respiration was associated with stream-surface algal biomass and within a spring/summer sequence the correlation between respiration and algal biomass was higher in downwelling than upwelling zones. Partial correlation coefficients between respiration and chlorophyll a in downwelling and upwelling zones were, respectively, 0.58 and 0.39 during

TABLE 2. Results of repeated measures ANOVA for the three postflood recovery periods. The independent variable is location (surface, bottom of run, top of run for dissolved oxygen, DOC and monosaccharides, and bottom of run and top of run for respiration, VHG, and POC), and the repeated variable is DPF (days postflood).

Dependent variable		Error mean square	F statistic		
			Location	DPF	Location × DPF
Respiration†	between	0.435	48.08**		
	within	0.397		12.68***	1.10^{NS}
VHG‡	between	0.005	13.48*		
	within	0.001		2.45*	1.54^{NS}
Dissolved oxygen§	between	0.079	90.0***		
	within	0.064		5.01***	3.28***
DOC§	between	0.079	5.37^{NS}		
	within	0.017		15.39***	1.56^{NS}
Monosaccharides§	between	0.004	0.18^{NS}		
	within	0.007		7.52***	2.18*
POC†	between	0.331	3.31^{NS}		
	within	0.071		25.18***	0.80^{NS}

^{NS} $P \geq 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

† Degrees of freedom are: (a) for between subject effects; location, 1; and error, 4; and (b) for within subject effects; DPF, 11; location × DPF, 11, and error, 44.

‡ Degrees of freedom are: (a) for between subject effects; location, 1; and error, 4; and (b) for within subject effects; DPF, 8; location × DPF, 8, and error, 32.

§ Degrees of freedom are: (a) for between subject effects; location, 2; and error, 4; and (b) for within subject effects; DPF, 11; location × DPF, 22, and error, 44.

the 1992 spring/summer sequence, and 0.88 and 0.77 during the 1993 spring/summer sequence. In contrast, during the autumn successional sequence, respiration and chlorophyll *a* were inversely related in downwelling zones (partial correlation coefficient = −0.55) and were not significantly related in upwelling zones ($P \geq$ 0.05). In upwelling zones, dissolved oxygen concentration was also consistently correlated with respiration (Table 3). Dissolved oxygen was never lower than 1.30 mgO$_2$/L and rarely lower than 2.00 mgO$_2$/L, hence probably not limiting to respiration. Dissolved oxygen declined with water residence time in sediments, however, and was likely a covariate with other factors such as amount of labile organic matter.

Diel patterns of hyporheic respiration

Hyporheic respiration exhibited a distinct diel pattern with highest rates coinciding with time of maximum photosynthesis (i.e., noon; Fig. 3). In situ respiration was significantly different over a day ($P <$ 0.01) with the daytime rate being more than three times the night time rate. The diel pattern of in situ respiration was similar to stream temperature which varied from a low of 23°C at 0130 and 0530 to a high of 29.5°C at 1330, thus suggesting temperature as a major influence. However, when measured in the laboratory with a constant temperature, respiration also exhibited significant changes with time ($P <$ 0.001; Fig. 3).

Patterns of POC storage

Storage of POC in hyporheic sediments varied significantly over time ($P <$ 0.001), but was similar in downwelling and upwelling zones ($P \geq$ 0.05; Table 2). Over the spring/summer 1992 and autumn 1992 suc-

cessional sequences, POC in hyporheic sediments was highest immediately following flash floods and decreased with time (Fig. 4). During the spring/summer 1992 sequence the decline of POC was especially great, decreasing 87% from an average of 155 to 20.4 mgC/L sediments. The floods in August and December 1992 scoured sediments and buried POC resulting in increased POC storage following disturbance. POC storage during the fourth successional sequence (spring/summer 1993) rose with time, in contrast to the other sequences; POC storage increased over sixfold from a low of 11.7 to 75.4 mgC/L sediments (Fig. 4). This final sequence was initiated by a 50-yr flood that scoured sediments to bedrock ($\approx$0.62 m) and continued with a sustained discharge of 11 m^3/s (baseflow discharge in Sycamore Creek is 0.53 m^3/s as reported by Thomsen and Schumann 1968) through March of the same year.

Hyporheic respiration vs. POC and DOC

The concentration of DOC from surface stream water and the amount of POC stored in hyporheic sediments both affected respiration. Respiration was positively correlated with POC and DOC ($P <$ 0.05; Fig. 5), supporting both hypotheses, and indicating that both forms of carbon are used in metabolism. There was, however, much unexplained variance (R^2 = 0.22 and 0.17 for POC and DOC, respectively) suggesting that other factors influence respiration in addition to organic matter quantity.

DISCUSSION

Hypotheses supported

The hypothesis that hyporheic respiration is dependent on organic matter derived from the surface stream

TABLE 3. Results of multiple regression analysis (partial correlations) of hyporheic respiration in downwelling and upwelling zones of runs for three successional sequences vs. twelve independent variables. Variables for which partial correlations are not listed were excluded from the model because of low F values.

| | Successional sequence* | | | | | |
| | I† | | II‡ | | IV§ | |
Independent variable	Down	Up	Down	Up	Down	Up
Chlorophyll	0.58	0.39	−0.55		0.88	0.77
Dissolved oxygen		0.19	0.28	0.60··	−0.65	0.29
VHG						
DOC	−0.53		0.60			
Monosaccharides						
POC			−0.32			
Ammonium	0.50					
Nitrate					−0.67	
DON				0.35	−0.25	
SRP					−0.57	
DOC:TDN‖						
Temperature				−0.21		
Multiple R^2	0.76	0.24	0.70	0.50	0.90	0.64
Sample size¶	29	30	36	36	45	45
F ratio	31.1	5.63	21.1	12.6	83.5	40.5
P value	<0.001	<0.01	<0.001	<0.001	<0.001	<0.001

* Successional sequence III (December 1992–January 1993) not included in analysis due to small sample size.
† April 1992–July 1992.
‡ August 1992–November 1992.
§ February 1993–July 1993.
‖ DOC:TDN = atomic ratio of dissolved organic C to total dissolved nitrogen (ammonium + nitrate + organic nitrogen).
¶ Sample size = total number of chambers incubated.

as a metabolic substrate was strongly supported by the results. As predicted for this hypothesis, hyporheic respiration is highest late in succession when algal biomass is greatest, and at downwelling zones where surface waters enter hyporheic sediments. Flash floods scour the substrate and reduce algal biomass. Over successional time algal biomass increases and thus the pool of surface organic matter also increases. This organic

matter-rich water enters hyporheic sediments at areas of downwelling, where a high subsurface metabolic rate is supported. As this water travels through sediments it is likely stripped of labile organic matter, thus reducing respiration in upwelling zones. Moreover, hyporheic respiration and photosynthesis exhibited similar diel patterns, further supporting the surface stream-derived organic matter hypothesis. We hypothesize that this variation is attributable to labile organic matter
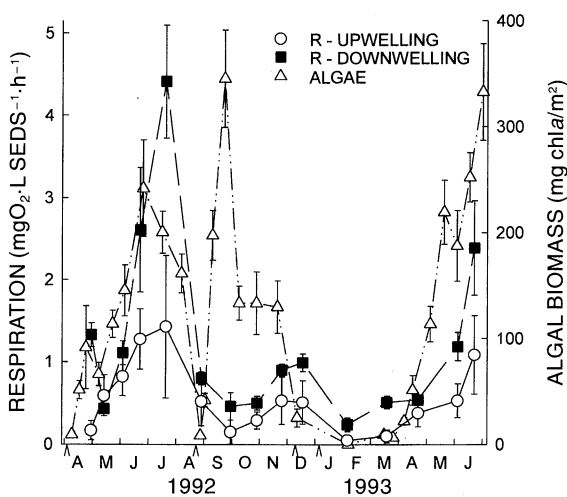

FIG. 2. Hyporheic respiration (R) in upwelling and downwelling zones, and algal biomass from April 1992 through June 1993. Respiration values are mean of three sites ± SE; algal biomass from areal abundance of algal patches in study reach I ± SE.
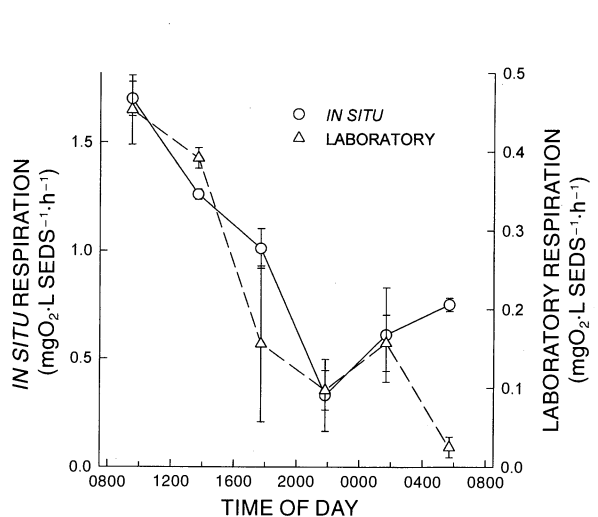

FIG. 3. Hyporheic respiration in a downwelling zone over a diel period as measured *in situ* and in the laboratory. Data are mean of incubation chambers ± SE ($n = 3$ for *in situ* and $n = 4$ for laboratory).
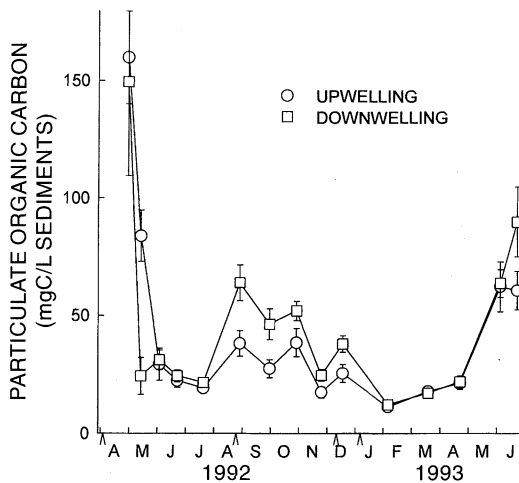
FIG. 4. Particulate organic carbon in hyporheic sediments of upwelling and downwelling zones from April 1992 through July 1993. Data are mean of three study sites ± SE ($n = 3$ upwelling and $n = 3$ downwelling zones).

produced during photosynthesis, and that respiration of hyporheic microorganisms responds to diel variation in that process.

The alternative hypothesis that hyporheic respiration is supported by organic matter buried during floods was supported by the data but to a lesser degree. POM was buried by flash floods during the first two successional sequences. POM decreased with time, presumably via decomposition and downstream transport through sediments. However, the amount of respiration that could be supported by POM buried during floods is small. Based upon the amount of hyporheic POC on the first sampling date following a flood, and assuming all POC is respired, an average of only 15% (range 3 to 28% for individual successional sequences) of the observed respiration could be supported. Moreover, the difference in respiration rate between downwelling and upwelling zones, and the increase of respiration with time after flood did not support predictions based on the flood hypothesis. Therefore, while floods bury organic matter that supports hyporheic respiration, it is more likely that most organic matter (>85%) is supplied from algal production in the surface stream.

Sources of surface-derived organic matter

Extracellular release of DOM during algal photosynthesis is an important source of DOC in both lotic and lentic ecosystems (e.g., Manny and Wetzel 1973, Cole 1982). Baines and Pace (1991), in a review of literature values of extracellular release of photosynthate, reported phytoplankton losses averaging 13% of total fixation. Kaplan and Bott (1982, 1989) reported diel patterns of DOC concentration in a piedmont stream in Pennsylvania with an afternoon maximum as much as 40% higher than the daily minimum, resulting

from photosynthetic fixation and subsequent extracellular release of carbon. DOC release for two species averaged 78 μgC·mg chl a^{-1}·h^{-1} and was as high as 132 μgC·mg chl a^{-1}·h^{-1} (Kaplan and Bott 1982). Assuming the same rate of DOC production by algae in Sycamore Creek, photosynthesis could contribute an average 8.8 mgC·m^{-2}·h^{-1} (annual mean algal biomass = 113 mg/m^2 chl a; Fig. 2) and as much as 46 mgC·m^{-2}·h^{-1} (study maximum algal biomass = 345 mg/m^2 chl a; Fig. 2). These production rates translate into an average contribution to the DOC pool of 0.2 mgC·L^{-1}·h^{-1} and potentially 0.9 mgC·L^{-1}·h^{-1} (assuming a stream depth of 5 cm). Moreover, DOC production by algae could support upwards of 25% of an average hyporheic respiration rate of 185 mgC·m^{-2}·h^{-1} (assuming a respiratory quotient of 1 and sediment depth of 0.62 m; Valett et al. 1990).

Organic matter produced by algae is labile and readily used by bacteria. Cole et al. (1982) described a tight linkage between phytoplankton photosynthesis and planktonic microbial production, in which photosynthetic production of DOC supported about a third of total microbial production. In lentic systems, planktonic bacteria and algae have close spatial association that results in algal exudates being rapidly metabolized near the site of release (Cole 1982).

Kaplan and Bott (1982) observed a longitudinal time lag for maximum DOC concentration in a stream in-
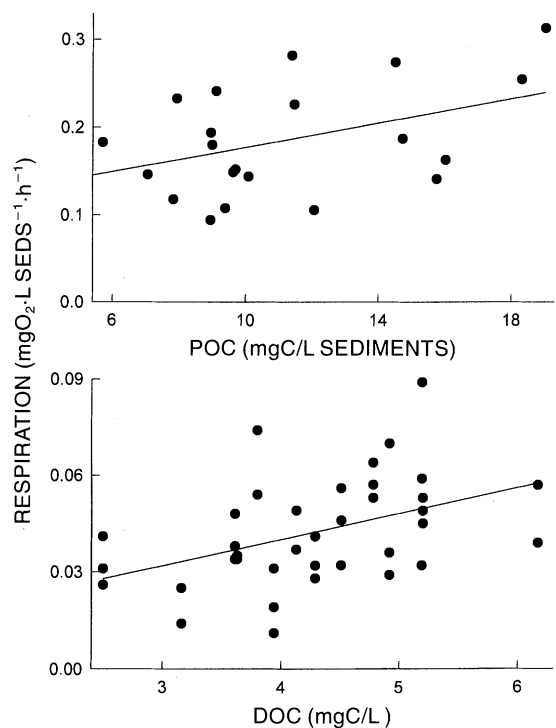

FIG. 5. Hyporheic respiration vs. particulate organic carbon content of hyporheic sediments and dissolved organic carbon concentration of hyporheic interstitial water.

dicating that not all was used at the point of production, but at least a portion was transported downstream. Furthermore, as the daily pulse of DOC was transported, microorganisms responded with increased metabolism. Benthic bacterial activity increased 1.4 to 3.0 times from morning to afternoon (Kaplan and Bott 1989). In Sycamore Creek, one estimate of the labile fraction of the DOC pool (dissolved monosaccharides) was not significantly greater in the surface stream than in the hyporheic zone (Tables 1 and 2) suggesting that the pool rapidly turns over. Bacteria in the surface stream and hyporheic zone may respire labile DOC as rapidly as it is produced, thus maintaining the concentration of monosaccharides at a low level.

In addition to extracellular release of photosynthetic DOM, algae also lose biomass through sloughing and senescence (Stockner 1968, Naiman 1976, Cole et al. 1984). In Sycamore Creek, POM transport is typically greater during the day than night (Grimm 1987) due to POM generation from flotation of highly productive algal mats and diurnal feeding by fishes (Fisher et al. 1981). Moreover, FPOM can be transported through porous sediments of Sycamore Creek (Boulton et al. 1991); thus algal production of POM can also enter the hyporheic zone by vertical hydrologic exchange.

Surface-stream–hyporheic linkage

To drive the linkage between the surface and hyporheic zone there must be sufficient hydrologic exchange; in Sycamore Creek the potential for exchange is high (Valett et al. 1994). Flow through sediments is the product of hydraulic conductivity and hydraulic gradient (Lee and Cherry 1978). Sycamore Creek's sediments are coarse, resulting in high hydraulic conductivity (Shepherd 1989) of ≈1 cm/s (*unpublished data*). Flux into hyporheic sediments is therefore potentially as high as 0.2 cm/s based upon VHG data from this study and may be as high as 0.8 cm/s in areas of intense downwelling (Valett et al. 1994).

Once DOM and POM enters hyporheic sediments much of it is immobilized by metabolically active microorganisms in sediments. Fiebig and Lock (1991) perfused groundwater through sediment cores resulting in a 10 to 26% immobilization of DOC. Vervier and Naiman (1992) and Findlay et al. (1993) both reported DOC concentration to decrease 50% along subsurface flowpaths in gravel bars in a sixth order river in Washington and a fourth order stream in New York, respectively. Moreover, Findlay et al. (1993) found bacterial abundance and production to decrease as DOC declined, presumably due to degradation of labile DOC, and speculated that the surface stream was the source of organic matter supporting sediment respiration. Vervier et al. (1993), working in the Garonne River in France did not, however, find a consistent decrease in DOC along a gravel bar flowpath; they suggested DOC patterns along flowpaths were controlled by not only input and downstream sequestering of DOC, but also

by microhabitat variation in POM and microbial activity within sediments.

Numerous authors have reported groundwater to be high in DOC (Wallis et al. 1981, Rutherford and Hynes 1987, McDowell and Likens 1988) and have hypothesized groundwater to be a source of organic matter for surface streams (Hynes 1975, Ford and Naiman 1989, Fiebig et al. 1990). In Sycamore Creek, most of the water in the hyporheic zone, at least at the depth addressed in this study (15 cm), originated from the surface and not from groundwater inputs. Hyporheic dissolved oxygen was high, especially in downwelling zones, and similar to the surface suggesting that hyporheic waters originated from the surface (Hill 1990, Hendricks and White 1991). Using differences in dissolved oxygen between the surface and hyporheic zone, and hyporheic respiration rate, we estimate that hyporheic residence time in Sycamore Creek is just 0.1 and 2.5 h in downwelling and upwelling zones, respectively.

Spatial heterogeneity and stream functioning

Spatial heterogeneity has been examined extensively by terrestrial ecologists and recognized as an important determinant of ecosystem functioning (e.g., Pickett and White 1985, Wiens et al. 1985, Forman and Godron 1986, Urban et al. 1987, Turner 1989). Ecosystems are composed of a mosaic of patches that differ in species composition (Watt 1947, Whittaker 1975, Sousa 1984) and material and energy distributions (Bormann and Likens 1979, Vitousek 1985, Schlesinger et al. 1990). Patches are linked to other patches through material, energy, and organism exchanges, and may act as sources or sinks for abiotic and biotic elements (Wiens et al. 1985, Pulliam 1988, Grimm 1994). Ecosystem structure at the next higher scale is describable by this mosaic of patch types, and functioning is a product of linkages between these patches.

Stream ecologists have historically viewed streams as a continuum of spatial variation and processes (Vannote et al. 1980). Streams, however, are composed of different patches linked via a strong hydrologic transport vector that results in potentially high interactions between patches (Naiman et al. 1988, Pringle et al. 1988). The functioning of surface and hyporheic subsystems are clearly interdependent. The two subsystems are linked through hydrologic exchange that is a transport vector for materials and nutrients. Valett et al. (1994) demonstrated a connection from the hyporheic zone to surface in which subsurface nutrient rich waters up-well into the surface stream and alleviate local nutrient limitation. Conversely, the surface represents a source of labile organic matter to fuel hyporheic respiration. Materials from algal production are transported to the hyporheic zone via regions of hydrologic downwelling and produce biotic "hot spots", where surface waters enter hyporheic sediments. Thus,

the hyporheic zone is a source of nutrients to the surface stream where primary production is stimulated, which in turn provides a labile organic carbon source for hyporheic respiration. Future concepts of stream ecosystem functioning must incorporate interactions between the surface and hyporheic zone. Stream ecosystems can only fully be understood by expanding definitions of ecosystem boundaries to include all component subsystems and the interactions between these patches.

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