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VERTICAL HYDROLOGIC EXCHANGE AND ECOLOGICAL STABILITY OF A DESERT STREAM ECOSYSTEM¹

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Abstract. The influence of hydrologic linkage between hyporheic and surface subsystems was investigated in sand-bottomed reaches of a desert stream. Direction of hydrologic exchange was measured as vertical hydraulic gradient (VHG) using mini-piezometers. Maps of VHG indicated upwelling (discharge from the interstitial regions into surface water) at the bases of riffles and heads of runs; downwelling (infiltration of surface water into the hyporheic zone) occurred at the bases of runs. Dissolved NO₃-N in surface water was higher over or immediately downstream from upwelling zones. Loss of continued supply from the hyporheic zone and intense assimilatory demand by surface autotrophs generated longitudinal declines in NO₃-N and lower nutrient concentrations in downwelling zones. Algal standing crop (as chlorophyll *a*) was significantly higher in upwelling zones than in areas without positive VHG. Postflood trajectories of chlorophyll *a* indicated that algae at upwelling zones recovered from disturbance significantly faster than those at downwelling zones. Recovery rate was related to supply of NO₃-N from enriched interstitial water in the hyporheic zone. Hydrologic linkage integrates surface and hyporheic subsystems and increases ecosystem stability by enhancing resilience of primary producers following flash flood disturbance.

Key words: *desert streams; disturbance; floods; hydrology; hyporheic zone; vertical hydraulic gradient.*

INTRODUCTION

Streams and rivers are open ecosystems that are heavily influenced by interaction with adjacent systems. Research has recognized the importance of material and energy exchange between streams and surrounding terrestrial environments (e.g., Fisher and Likens 1973, Vannote et al. 1980, Gregory et al. 1991), but the significance of groundwater–surface water interaction in streams is less well known. Following elegant pleas from Hynes (1975, 1983) and Danielopol (1980), stream ecologists have recently begun to include groundwater–stream water relationships in the study of lotic ecosystems.

It is well known that macroinvertebrates can penetrate the stream bottom and occupy interstitial spaces that are collectively known as the hyporheic zone (sensu Orghidan 1959). Hyporheic biota have been a long-standing focus of research, and their distribution, diversity, and abundance illustrate the size and complexity of hyporheic zones (Stanford and Gaufin 1974, Williams and Hynes 1974, Williams 1984, 1989, Penak and Ward 1986, Stanford and Ward 1988). Others studying biogeochemical processes have defined the hyporheic zone as the saturated sediments and interstitial spaces beneath streams that receive water from the surface (e.g., Triska et al. 1989a, b, Valett et al. 1990).

Water flowing on the surface of streams infiltrates interstitial spaces at discrete locations (downwelling zones) and hyporheic water enters the stream at upwelling zones (Vaux 1962, 1968, Grimm and Fisher 1984, White et al. 1987, Valett et al. 1990, White 1990, Stanley and Valett 1992). Nutrient transport from the hyporheic zone, where concentrations often are high (Dahm et al. 1987, Hendricks and White 1988, 1991, Carr 1989, Coleman and Dahm 1990, Duff and Triska 1990, Valett et al. 1990, Grimm et al. 1991, Stanley and Valett 1992), to nutrient-poor surface water may alleviate nutrient limitation in benthic subsystems. A few published reports begin to address the cumulative effect of exchange on surface conditions, however, results are equivocal. Hendricks and White (1991) hypothesized that phosphate-rich interstitial water failed to affect surface concentrations due to adsorption by hyporheic sediments. Triska et al. (1990) suggested that algal nutrient uptake precluded nitrate-nitrogen increases in surface water despite upwelling conditions following a rainstorm. Stewart (1988) hypothesized that increased benthic algal abundance reflected increased phosphate availability in flows emerging from anoxic interstitial regions. Upwelling water may support increased algal biomass and stimulate primary production, but a number of other processes occurring at the benthic–hyporheic interface may prevent such enrichment (see Gibert et al. 1990).

Sonoran Desert streams are frequently disturbed by flash floods that decimate biota (Fisher et al. 1982), alter channel morphology (Graf 1988, Grimm et al. 1991), and affect physical-chemical conditions in the

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hyporheic zone (Valett et al. 1990). Conversely, long periods of low precipitation generate spatial intermittency that causes significant mortality in the surface stream and alters conditions in the hyporheic zone (Stanley and Valett 1992). Disturbance and subsequent succession or recovery can be studied in the context of ecological stability (Holling 1973, Cairns et al. 1977, Connell and Slatyer 1977, Westman 1978, Van Vorris et al. 1980) and this approach has recently been applied to lotic ecosystems, including desert streams (Webster et al. 1983, Grimm and Fisher 1989, Peterson et al. 1990, Grimm et al. 1991). System stability is a synthesis of resistant (tendency to maintain character across a disturbance event) and resilient (capacity to quickly recover following disturbance) properties. Rates of primary production in Sycamore Creek, Arizona, can be exceptionally high (Busch and Fisher 1981) and rapid accumulation of algal biomass following removal by flash floods is a resilient feature of this desert stream ecosystem (Grimm and Fisher 1989).

Hyporheic water in streams of the Sonoran Desert is enriched in nitrate-nitrogen (Grimm and Fisher 1984, Valett et al. 1990, Boulton et al. 1992) compared with surface water where rates of primary production are limited by the availability of inorganic nitrogen (Grimm and Fisher 1986). Concentrations of total inorganic nitrogen (TIN) in hyporheic water were as much as 60 times greater than surface water concentrations in five Arizona streams (Boulton et al. 1992, Valett et al. 1992). In the surface water of Sycamore Creek, longitudinal declines and diel fluctuations of TIN have been attributed to the intense assimilatory demand of large standing crops of benthic algae (Grimm et al. 1981, Fisher et al. 1982, Grimm 1987, Valett 1993).

Given the potential for interaction between interstitial and surface water, we hypothesized that hydrologic linkage would promote ecosystem resilience through increased supply of the limiting nutrient. We predicted that benthic algal standing crops would be enhanced in upwelling zones, reflecting this nutrient subsidy from the hyporheic zone, and that the rate of algal recovery following disturbance would be greater in upwelling areas than in downwelling areas. These predictions were tested by direct measurement of algal standing crop and accrual rates during an 89-d post-flood recovery sequence. Samples were taken from sites where direction of vertical exchange and nutrient concentrations were measured once or concurrently monitored.

STUDY SITE

Sycamore Creek is 32 km northeast of Phoenix, Arizona, USA and flows ≈ 55 km from ephemeral headwaters to its confluence with the Verde River. Watershed area is 505 km² ranging from 2164 to 427 m elevation. Sonoran Desert streams exhibit distinct longitudinal changes in geomorphology along the drainage network (Wertz 1963, Graf 1988) that reflect the pri-

mary influence of floodwaters. Upstream phases are dominated by boulder-bedrock structure and reaches are usually dry due to small catchment area supplying run-off. Mid-elevation, transitional reaches are characterized by emergence and infiltration of surface flow caused by the proximity of less permeable substrata to overlying unconsolidated alluvium. Downstream phases include extensive alluvial deposits (up to 30 m deep in Sycamore Creek; Thomsen and Schumann 1968) that readily absorb all but the largest discharge events.

Three study sites were established at ≈ 650 m elevation in the transitional region. Study reaches included short segments (bases) of upstream riffles and the entire lengths of adjacent runs. Study sites I, II, and III were 165, 168, and 115 m long, respectively, and were separated by several pools and riffles. Field work was carried out in summer, fall, and early winter when modal flow in Sycamore Creek ranged from 0.01 to 0.04 m³/s. Flow was continuous but of variable discharge at sites I and III. Downstream portions of site II lacked surface water during part of the study period.

METHODS

Reach morphometry and hydrology

Measures of the direction and magnitude of the potential for advective exchange between hyporheic and surface water were obtained using mini-piezometers (Lee and Cherry 1978). Piezometers consisted of 9-mm (internal diameter) polyethylene tubes with lateral perforations protected by 300- μ m Nitex mesh near the tip of the tube. Piezometers were installed to depths of 20–30 cm beneath the stream bed surface and were immediately bailed to ensure unobstructed flow. Hydraulic heads (in centimetres) were determined in a manometer by measuring the heights of water columns drawn simultaneously from the inserted piezometer and overlying surface water. Details of mini-piezometer and manometer design and procedure are provided by Lee and Cherry (1978) and Winter et al. (1988). Vertical hydraulic gradient (VHG) was calculated as the difference in hydraulic head divided by depth of the piezometer (symbolized by dh/dl in Lee and Cherry 1978). Positive VHG indicates hyporheic discharge, or upwelling, where interstitial water enters the surface stream. Negative VHG values denote recharge, or downwelling, where stream water infiltrates the hyporheic zone, and sites where VHG = 0 were defined as stationary. Advective exchange was verified using subsurface injections of fluorescent dyes or by observing infiltration of dye introduced at the sediment surface.

Detailed information on reach morphometry and spatial patterns of hyporheic-surface exchange was obtained by mapping the stream and associated alluvial deposits and measuring VHG at points of intersection on a 1 \times 1 m grid established over 135 and 100 m at

sites I and II, respectively. Additional measures were occasionally taken at smaller intervals in areas of rapid change in hydraulic gradient. The hydrologic maps for sites I and II were established in September and June 1990, respectively, and were used to identify subreaches of sites I and II that differed in direction and intensity of hydrologic exchange.

Temporal variation in the magnitude of exchange was monitored at sites I and II in mini-piezometers permanently installed along longitudinal transects. Eight and 12 mini-piezometers at sites I and II, respectively, were monitored at 2-wk intervals with more intense sampling following floods from August 1990 to February 1991.

Stream water exchange and surface nutrient concentration

Surface water nutrients were analyzed in 125 mL samples taken from the well-mixed water column overlying upwelling, downwelling, and stationary regions in each study reach. Samples were analyzed for nitrate-nitrogen ($\text{NO}_3\text{-N}$) and soluble reactive phosphorus (SRP). Nitrate-nitrogen was determined by colorimetric analysis following reduction to nitrite in cadmium-copper columns (Wood et al. 1967). Molybdate-antimony analysis was used to measure SRP (Murphy and Riley 1962).

Single samples of surface water were collected along longitudinal transects at each site to assess continuous patterns in exchange and surface nutrient concentrations. Longitudinal patterns of VHGM ($n = 24$) and surface $\text{NO}_3\text{-N}$ ($n = 23$) were assessed at site I on 2 October 1990. Vertical hydraulic gradient was measured at 21 and 26 locations along sites II and III, respectively, on 14 June 1990. Concomitant, single samples of surface water were collected at equal intervals of $\approx 15\text{--}20$ m ($n = 8$ samples at each site). Nutrient concentrations in samples from locations with positive VHGM were averaged to generate mean values for $\text{NO}_3\text{-N}$ and SRP in upwelling zones at each site. Comparably, mean values for nutrients in downwelling zones were generated from surface samples collected in locations with negative VHGM. Because the magnitude of interstitial discharge was predicted to influence nutrient availability in surface water, Pearson product-moment correlations were used to relate water chemistry ($\text{NO}_3\text{-N}$ and SRP) to intensity of exchange (VHGM) in upwelling zones.

Hydrologic subreaches and periphyton standing crop

Subreaches of differing hyporheic-surface exchange were designated based on hydrologic maps of VHGM generated in an earlier portion of the study. Samples of benthic periphyton were collected according to random number tables and predetermined grids established within subreaches at each site. Three 24.63-cm² cores were collected from each subreach at site I in

December 1990. Six cores were collected within each subreach at site II in June of 1990. Both sites had experienced continuous surface flow and neither study site had been disturbed by flooding for over 80 d. Mini-piezometers were inserted to measure VHGM at algal sample locations. Benthic samples were analyzed for chlorophyll *a* (chl) and phaeophytin (phaeo) using methanol extraction (Tett et al. 1975). Percent chlorophyll was calculated from chlorophyll and phaeophytin measures $\{\%chl = [chl/(chl + phaeo)] \cdot 100\}$. Benthic organic matter (BOM) was estimated as ash-free dry mass (AFDM) after dried (60°C, 48 h) samples were ignited for 4 h at 500°C, rewetted, and redried. Percentage of BOM present as chl (chl/AFDM) was calculated from AFDM and chlorophyll values.

Comparisons of chl, phaeo, percent chl, AFDM, and chl/AFDM among subreaches were made using one-way ANOVAs. Separate ANOVAs were run for each site followed by Tukey's (HSD, $\alpha < .05$) test for multiple comparisons. Chlorophyll, phaeophytin, and AFDM concentrations were ln transformed before analysis. Percent chlorophyll and chl/AFDM values were arcsine transformed.

Data on VHGM at sampling locations and chlorophyll from sites I and II were combined and a correlation coefficient calculated to relate periphyton abundance to changes in hydraulic gradient. Periphyton abundance in sample locations with positive VHGM was compared to abundance in areas with negative VHGM by *t* test on ln-transformed chlorophyll.

Stream water exchange and periphyton recovery

Resilience of upwelling and downwelling subreaches was investigated by monitoring postflood recovery of periphyton and benthic organic matter. Following a flood of 2.45 m³/s on 15 September 1990 that reduced algal standing crop to <5% of late successional values (see Grimm and Fisher 1989), surface water samples and benthic algal cores were collected from the upwelling and downwelling subreaches at sites I and II. Upwelling and downwelling sample locations were separated by 80 and 50 m and intervening reach areas were 536 and 312 m² at sites I and II, respectively. Triplicate samples of benthic algae and surface water were collected from each zone at each site. Water samples were analyzed for $\text{NO}_3\text{-N}$ and SRP. Algal cores were analyzed for chl, phaeo, and AFDM. Samples were collected on days 4, 13, 34, 59, and 89 postflood during morning hours when study reaches were not shaded.

Effects of hydrology (upwelling, downwelling) and days postflood (DPF) were assessed using a repeated-measures ANOVA (GLM procedure, SAS 1985) on transformed data. Hydrology was treated as the independent variable and DPF was the repeated variable. Triplicate measures of chlorophyll and AFDM were combined and ANOVAs run on mean values ($n = 2$ for upwelling and downwelling zones on each date).

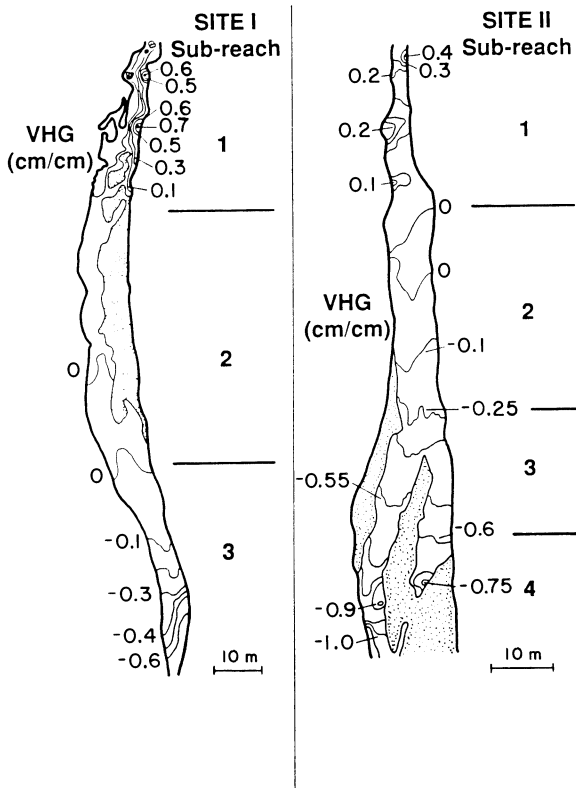


FIG. 1. Hydrologic map of sites I and II. Stippled areas are exposed alluvial deposits. Isoclines represent areas of equal vertical hydraulic gradient, VHG. Subreaches are identified to the right of each map.

Differences in chl and chl/AFDM between upwelling and downwelling zones were assessed for each of the five sample dates using Fisher's Least Significant Difference to compare the two factor levels. Recovery rates in upwelling and downwelling zones were analyzed by statistically comparing slopes of properly transformed chl, AFDM, and chl/AFDM vs. days post-flood. Slopes were considered to be significantly different following significant interaction between repeated and independent factors. Regression analysis was used to calculate accumulation rates (regression coefficients) for chl and AFDM in upwelling and downwelling zones for each site separately and for combined data. Correlation coefficients were calculated for differences in chlorophyll standing crop between upwelling and downwelling zones and concomitant differences in SRP and NO₃-N concentration.

RESULTS

Spatial variation in exchange

Piezometric surveys of runs at sites I and II illustrate the areal distribution of upwelling and downwelling regions (Fig. 1). Three subreaches were identified at site I: (1) upwelling, (2) stationary, and (3) downwelling. At site II four subreaches were identified: (1) up-

welling, (2) stationary-slight downwelling, (3) moderate downwelling, and (4) strong downwelling. Two major nodes of upwelling occurred in the first subreach at site I and strong positive VHG covered the upper 20 m of the run (Fig. 1). Maximum positive VHG was +0.7 and +0.6, and VHG decreased in a concentric manner to <+0.1 within 3-5 m lateral to areas of maximum upwelling. Moderate positive VHG (<+0.1) was measured for >30 m downstream. Vertical hydraulic gradient was zero throughout the stationary subreach. In the downwelling subreach, VHG decreased longitudinally from 0.0 to -0.6 over the lower 35 m of the study site.

The upstream subreach at site II also had two major nodes of upwelling (Fig. 1). Maximum VHG was less than at site I (+0.4 and +0.2), but strong upwelling (VHG > +0.1) persisted over 20 m of stream length. Moderate upwelling (VHG < +0.1) extended downstream an additional 15 m. Vertical hydraulic gradient in subreach 2 decreased from zero to <-0.1 over 30 m length. Vertical hydraulic gradient became increasingly negative in the remaining subreaches. Values decreased from -0.10 to -0.6 in subreach 3 and to as low as -1.1 in subreach 4 (Fig. 1).

Temporal variation in hyporheic-surface exchange

Temporal changes in the magnitude and direction of exchange between the hyporheic zone and the surface stream reflected effects of floods and the amount of time between floods. Four floods occurred during the study with the following magnitudes (*Q*) measured at site 2: three summer floods (*Q*_{max} = 50, 6.2, 2.4 m³/s) occurred between 15 August 1990 and 15 September 1990 and were followed by a 114-d interflood period. A single winter flood (*Q*_{max} = 4 m³/s) occurred on 6 January 1991.

Representative piezometers from each subreach illustrate temporal variation in VHG (Fig. 2). Vertical hydraulic gradient in upwelling subreaches generally increased following floods, but often did not achieve magnitudes greater than pre-flood values until 10-12 d after flooding (Fig. 2, Valett 1991). In general, however, changes in VHG magnitude over the entire monitoring period reflected decreasing magnitude of upwelling and increased downwelling. Compared to values obtained just after the final summer flood (15 September), VHG in the upwelling subreach decreased an average of 0.20 (58%) at site I and 0.12 (67%) at site II over a 76-d period (Valett 1991). Despite these decreases, VHG remained positive throughout the upwelling zones for the duration of the study (184 d) and for more than 12 wk postflood.

Changes in VHG in stationary subreaches were of smaller magnitude and effects of floods were less consistent. Early summer floods appeared to have little effect on hydraulic gradient. Changes in VHG during the long interflood period differed between sites (Fig.

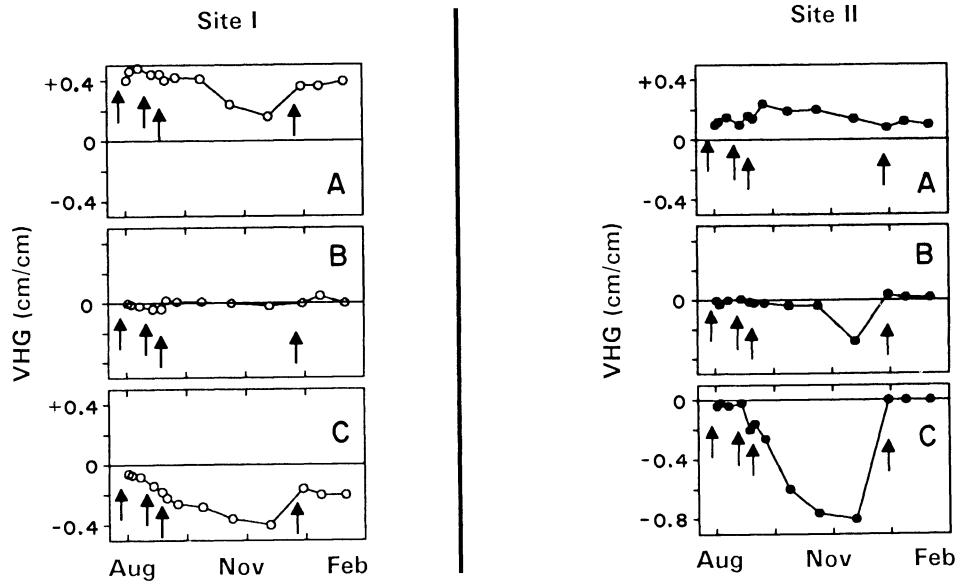


FIG. 2. Vertical hydraulic gradients at site I (○) and site II (●) from piezometers representative of: (A) upwelling subreach, (B) stationary subreach, and (C) downwelling subreach. Floods are indicated by black arrows.

2). Little change in stationary subreach VHG was observed at site I, whereas a strong decrease was measured at site II during late December (i.e., -0.28).

Summer floods had little effect on VHG in the downwelling zone at site I and produced only slight and transient increases in VHG at subreach 3 of site II. Temporal profiles of hydraulic gradient at both locations were dominated by a progressive increase in the magnitude of downwelling (Fig. 2). Vertical hydraulic gradient changed from -0.03 to -0.33 between 17 August and 14 December at site I. At site II, VHG magnitude increased 10-fold (-0.04 to -0.40) at subreach 3 and 20-fold (-0.04 to -0.80) at subreach 4 over the same time period.

Subreach 4 at site II rapidly lost surface flow during the study period. Downstream reaches of site II had been dry before the occurrence of summer floods. Flooding extended surface flow up to 50 m downstream, but water remained at the downstream areas for <11 d following the first summer flood and these areas were not rewetted until January.

The spatial extent of downwelling and upwelling zones was altered by floods. Following the winter flood in early January, downwelling intensity was greatly reduced at site I and some previously downwelling areas became stationary (i.e., $VHG = 0$) at site II. The same flood generated upwelling conditions in the stationary subreaches at both site I and site II (Fig. 2, Valett 1991).

Exchange effects on surface chemistry

Surface $\text{NO}_3\text{-N}$ concentrations in upwelling zones were 3.3, 3.1, and 2.0 times greater than in corresponding downwelling zones at sites 1, 2, and 3, respectively (Table 1). In contrast, SRP concentrations in upwelling zones were <1.5 times those in associated downwelling zones (Table 1). Across all sites and zones, $\text{NO}_3\text{-N}$ concentrations were more variable (mean $cv = 59\%$, Table 1) than SRP concentrations (mean $cv = 15\%$, Table 1). Within upwelling zones, SRP concentrations were not significantly related to the magnitude of upwelling ($n = 15$, $r = 0.51$, $P = .053$). Ambient $\text{NO}_3\text{-N}$, however, was significantly related to VHG ($n = 15$,

TABLE 1. Hydrologic and chemical characterization of upwelling and downwelling zones at three sites in Sycamore Creek, Arizona. Data for vertical hydrologic gradient (VHG), nitrate-nitrogen ($\text{NO}_3\text{-N}$), and soluble reactive phosphorus (SRP) are means ± 1 SE. Coefficient of variation (cv) is calculated as $cv = [sd/\text{mean}]100$.

Site	Zone	<i>n</i>	VHG (cm/cm)	$\text{NO}_3\text{-N}$ ($\mu\text{g/L}$)	cv (%)	SRP ($\mu\text{g/L}$)	cv (%)
I	upwelling	9	$+0.35 \pm 0.03$	86 ± 10	35	46 ± 1	6
	downwelling	10	-0.22 ± 0.05	26 ± 2	12	36 ± 2	17
II	upwelling	3	$+0.16 \pm 0.03$	19 ± 5	45	34 ± 2	10
	downwelling	4	-0.37 ± 0.12	6 ± 3	100	32 ± 2	12
III	upwelling	3	$+0.29 \pm 0.05$	49 ± 10	35	52 ± 4	13
	downwelling	4	-0.23 ± 0.07	24 ± 15	125	37 ± 6	32

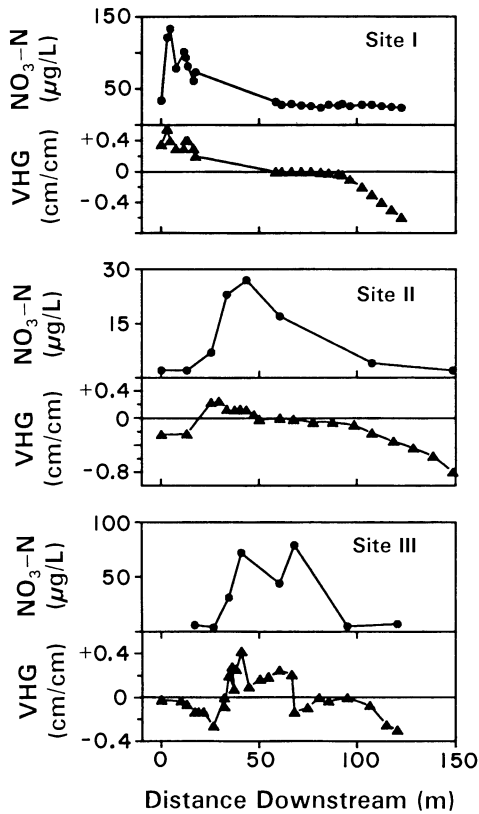


FIG. 3. Longitudinal profiles of NO₃-N concentration and vertical hydraulic gradient (VHG) at sites I-III. Data are single measures of NO₃-N (●) and VHG (▲).

$r = 0.74, P = .0014$) in upwelling zones. Over half the variation in NO₃-N observed across the three upwelling zones was explained by VHG magnitude.

Longitudinal patterns of VHG and water chemistry indicated that highest NO₃-N concentrations were found in upwelling zones or in surface water immediately downstream therefrom (Fig. 3). In addition, NO₃-N concentration decreased with increasing distance downstream from upwelling zones (Fig. 3).

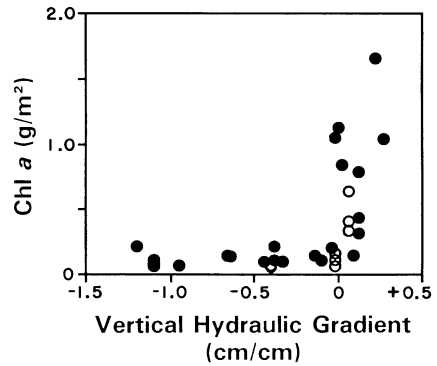


FIG. 4. Chlorophyll *a* vs. vertical hydraulic gradient for combined data from sites I (○) and II (●).

Exchange effects on benthic algal standing crops

Chlorophyll *a* standing crop decreased sequentially at site I from 459.7 mg/m² in the upwelling zone, to 140.2 mg/m² in subreach 2, to 66.9 mg/m² in the downwelling subreach (Table 2). All differences among subreaches were significant. Similarly, chlorophyll was significantly greater in the upwelling zone at site II than in either downwelling subreach (Table 2). Chlorophyll in the stationary subreach at site II was not significantly different from that in subreach 3, but was significantly greater than chlorophyll measured in subreach 4.

Phaeophytin in the upwelling zone at site I was significantly greater than in other subreaches (Table 2). Despite elevated phaeophytin, percent chlorophyll in the upwelling zone was significantly greater than in the downwelling zone (74.6 vs. 63.0%, Table 2). Phaeophytin in upwelling and stationary subreaches at site II was significantly greater than in subreach 4, but similar to subreach 3 (Table 2). Percent chlorophyll did not differ among subreaches at site II.

Ash-free dry mass at site I ranged from 105.4 to 147.3 g/m² (Table 2). No significant differences in AFDM existed among subreaches at site I, but chl/AFDM values were significantly greater in the up-

TABLE 2. Comparison of chlorophyll *a* (chl), phaeophytin (phaeo), percent chlorophyll (% chl, i.e., amount of total pigment, chl + phaeo, represented as chl), organic matter standing stock (AFDM: ash-free dry mass), and chlorophyll as percent AFDM (chl/AFDM) between subreaches at sites I and II. Chlorophyll, phaeophytin, and AFDM data were ln transformed and chl/AFDM and % chl values were arcsine-transformed before analysis. For each site, means within columns having the same superscript letter are not statistically different. Means ± 1 SE presented are calculated from nontransformed data.

Sub-reach	Chl (mg/m ²)	Phaeo (mg/m ²)	% chl	AFDM (g/m ²)	Chl/AFDM (%)
Site I					
1	459.7 ^a ± 92.0	154.7 ^a ± 26.5	74.6 ^a ± 0.7	147.3 ^a ± 19.2	0.322 ^a ± 0.066
2	140.2 ^b ± 15.1	67.6 ^b ± 16.1	68.0 ^{ab} ± 4.2	105.4 ^a ± 29.8	0.157 ^{ab} ± 0.051
3	66.9 ^c ± 4.5	39.6 ^b ± 4.4	63.0 ^b ± 1.1	135.8 ^a ± 41.2	0.069 ^b ± 0.032
Site II					
1	780.5 ^a ± 208.3	323.3 ^a ± 92.0	65.9 ^a ± 5.6	285.9 ^a ± 27.8	0.247 ^a ± 0.061
2	581.2 ^{ab} ± 178.7	253.3 ^a ± 68.7	63.4 ^a ± 5.7	418.7 ^a ± 73.0	0.131 ^{ab} ± 0.041
3	134.0 ^b ± 16.4	117.1 ^{ab} ± 12.6	53.2 ^a ± 1.3	289.3 ^a ± 48.9	0.049 ^b ± 0.005
4	97.4 ^c ± 22.7	81.1 ^b ± 12.1	52.9 ^a ± 2.0	247.9 ^a ± 47.6	0.047 ^b ± 0.016

TABLE 3. Results of repeated-measures ANOVA for the 89-d flood recovery period. The independent variable is hydrology (upwelling vs. downwelling) and the repeated variable is DPF (number of days postflood).

Dependent variable		Error mean square	Independent variables		
			Hydrology	DPF	Hydrology × DPF
			F statistic†		
Chlorophyll	between	0.092	79.12*
	within	0.146	...	38.05***	9.24**
AFDM	between	0.065	14.46
	within	0.032	...	15.05***	5.05*
Chl/AFDM	between	0.0019	56.00***
	within	0.0008	...	23.95***	11.87**

* $P < .05$; ** $P < .01$; *** $P < .001$.

† Degrees of freedom for all dependent variables are: (a) for between-subjects effects: hydrology, 1; and error, 2; and, (b) for within-subjects effects: DPF, 4; DPF × hydrology, 4; and error, 8.

welling zone than in the downwelling zone. Ash-free dry mass at site II did not differ significantly among subreaches. In contrast, chl/AFDM was significantly greater in the upwelling subreach than in either downwelling subreach.

At both sites, standing crop of chlorophyll was more variable (test for homogeneity of variances, $F_{10, 21} = 4.6$, $P < .005$) and significantly greater (703.4 vs. 156.3 mg/m^2 , $t = 6.98$, $P < .001$) in upwelling zones (VHG > 0) than in areas lacking positive VHG (Fig. 4). Correlation between VHG and chlorophyll was significant at site I ($n = 9$, $r = 0.80$, $P < .01$) and site II ($n = 24$, $r = 0.72$, $P < .01$) and when data from both sites were combined ($n = 33$, $r = 0.63$, $P < .01$).

Exchange effects on postflood recovery

Characteristic of postflood recovery in desert streams, chl and AFDM content of the benthic layer increased significantly with number of days postflood (repeated-measures ANOVA, test for the DPF effect, $P < .001$, Table 3). Chl/AFDM values also increased significantly during recovery ($P < .001$, Table 3).

Chlorophyll accumulated significantly faster in upwelling zones (repeated-measures ANOVA, test for factor interaction, $P < .001$, Table 3) than in downwelling zones (Fig. 5). Regression analysis indicated that number of days postflood explained 76 and 68% of the variance in chlorophyll *a* at upwelling and downwelling zones, respectively (Table 4). Slopes calculated from nontransformed data indicated that chlorophyll accumulation rate in upwelling zones was an order of magnitude greater than for downwelling zones (6.52 vs. 0.65 $\text{mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$; Table 4).

Rates of AFDM accumulation were also significantly greater in upwelling (repeated-measures ANOVA, test for factor interaction, $P < .01$, Table 3) than in downwelling zones (Fig. 5). When data from sites I and II were combined, AFDM accumulation rate in upwelling zones was 2.8 times that in downwelling zones, wherein slopes were not significantly different from zero (Table 4).

Significantly more chlorophyll was present in upwelling zones over the 89-d recovery sequence (test for independent factor effect, $P < .05$, Table 3). Amounts did not differ significantly until day 34 postflood (Fisher's LSD, $P < .05$) and significantly more chlorophyll was present in upwelling zones on all subsequent sampling dates. Due to high variability and small sample size ($n = 2$) AFDM concentrations did not differ significantly between upwelling and downwelling zones (Table 3). Significantly higher chl/AFDM occurred in upwelling zones (Table 3) during the recovery sequence for days 13, 34, 59, and 89 postflood (Fisher's LSD, $P < .05$).

Soluble reactive phosphorus concentration was initially elevated after flooding (Fig. 6), decreased over the following 30 d, then remained relatively unchanged at 30–35 $\mu\text{g}/\text{L}$. Direction of exchange did not have strong effects on SRP concentrations. Upwelling SRP averaged 100 and 96% of downwelling values over the

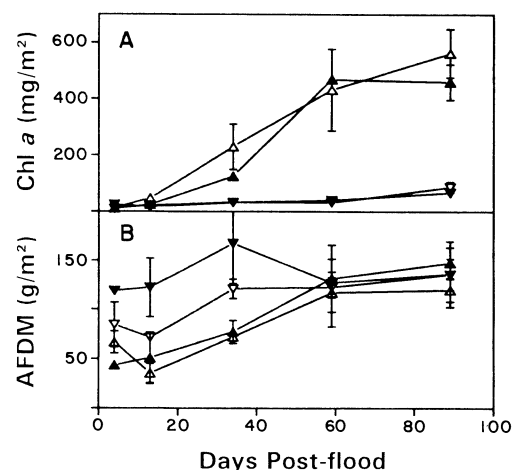


FIG. 5. Chlorophyll *a* (A) and ash-free dry mass (AFDM, B) vs. number of days postflood for samples taken from upwelling (triangles) and downwelling (inverted triangles) zones at site I (solid symbols) and site II (open symbols). Values are means ± 1 SE ($n = 3$).

TABLE 4. Regression coefficients (*b*: slope mean ± 1 SE), coefficient of determination (*r*²), and significance level (*P*) for regression analysis of chlorophyll *a* and ash-free dry mass on number of days postflood.

Source	<i>n</i>	Chlorophyll <i>a</i>			Ash-free dry mass		
		<i>b</i> (mg · m ⁻² · d ⁻¹)	<i>r</i> ²	<i>P</i>	<i>b</i> (mg · m ⁻² · d ⁻¹)	<i>r</i> ²	<i>P</i>
Site I							
Upwelling	15	6.20 ± 0.90	0.78	<.01	1.32 ± 0.27	0.46	<.01
Downwelling	15	0.53 ± 0.07	0.82	<.01	0.13 ± 0.40	0.01	>.05
Site II							
Upwelling	15	6.83 ± 1.09	0.75	<.01	0.91 ± 0.26	0.48	<.01
Downwelling	15	0.78 ± 0.16	0.66	<.01	0.70 ± 0.21	0.45	<.01
Combined							
Upwelling	30	6.52 ± 0.69	0.76	<.01	1.12 ± 0.19	0.55	<.01
Downwelling	30	0.65 ± 0.08	0.68	<.01	0.42 ± 0.24	0.09	>.05

course of recovery at sites I and II, respectively. Average difference between upstream and downstream SRP was 7.6 µg/L at site I and <1.0 µg/L at site II.

Surface water NO₃-N concentration differed between upwelling and downwelling zones at both sites and differences changed with time since disturbance (Fig. 6). Nitrate-nitrogen was more abundant in upwelling zones throughout the study period at site I (Fig. 6) and averaged 217% of downwelling concentrations. Difference in NO₃-N ranged from 17 to 47 µg/L over 80 m at site I and from 3 to 32 µg/L over 50 m at site II where upwelling concentrations averaged 1.25 times downwelling concentrations over the 89-d recovery.

Differences in chlorophyll amounts between upwelling and downwelling zones were significantly correlated with upstream-downstream differences in surface NO₃-N at both site I (*n* = 5, *r* = 0.81, *P* < .05) and site II (*n* = 5, *r* = 0.97, *P* < .01). Conversely,

differences in chlorophyll amounts were not correlated with differences in SRP concentrations at either site (*n* = 5, *P* > .05).

DISCUSSION

Spatial and temporal features of hyporheic-surface interaction

Patterns of hyporheic-surface exchange in Sycamore Creek are clearly related to differing vertical hydraulic gradient (Grimm et al. 1991, Stanley and Valett 1992, this study) such that upwelling and downwelling zones are spatially distinct areas characterized by a given direction of exchange between the hyporheic zone and surface water. No cases of local downwelling in upwelling zones, or isolated areas with positive VHG in downwelling subreaches, were encountered. While upwelling and downwelling zones appear to be spatially distinct at any one time, the direction and magnitude of exchange varies temporally. Floods occurring in late summer increased VHG in upwelling zones within 2 d, but magnitude decreased thereafter. Winter flooding decreased the intensity of downwelling following a long postflood period. In addition, run-off from storms can cause short-term changes in direction and magnitude of exchange. Lee and Hynes (1977) reported that an intense rainstorm momentarily reversed a +0.16 VHG and downwelling occurred for 10-30 min before upwelling was reestablished.

Flood-induced increases in VHG often occurred a number of days after the flood itself and this lag may reflect time required for floodwater entering the hyporheic zone somewhere upstream to reach the study site. Mulholland et al. (1990) reported considerable variation in subsurface flow following storm events in a forested watershed in karst terrain. Routes of flow differed among storms, depended on storm intensity and antecedent conditions, and hydrograph responses lagged 6-18 h behind storm initiation. Lags in VHG response in Sycamore Creek may result from complex routes of flow in the hyporheic zone. In addition, there may be specific reaches of the stream channel that act

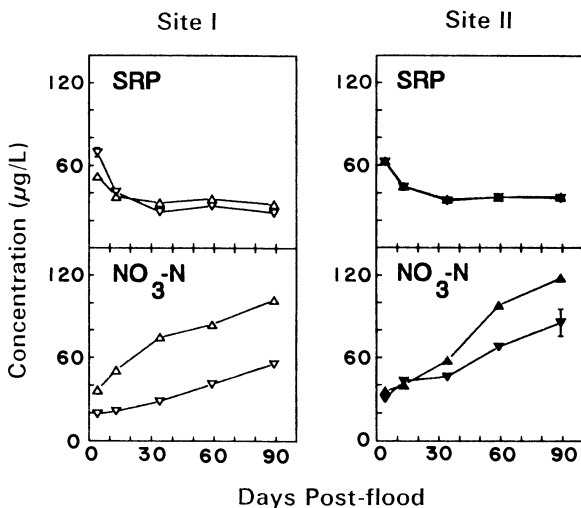


FIG. 6. Postflood nutrient profiles for soluble reactive phosphorus (SRP) and nitrate-nitrogen (NO₃-N) from upwelling (triangles) and downwelling (inverted triangles) zones at site I (open symbols) and site II (solid symbols). Values are means ± 1 SE (*n* = 3).

as entrances to the hyporheic zone and their location may depend on local geologic features such as bedrock profiles and channel storage capacity. This may explain why some floods affected VHG while others did not, since precipitation events in the Sonoran Desert are notoriously patchy and run-off may occupy different portions of the stream channel network.

Gibert et al. (1990) stressed that hydrologic features of ecotones, such as hyporheic zones, are variable and reflect changes in surface water levels and discharge. Our data support this assertion. Floods can extend the spatial extent of upwelling zones as they did at site II following the winter flood. On the other hand, long dry periods without floods cause decreases in upwelling and accentuate downwelling. Previously upwelling areas can become stationary, and then downwelling, as water is lost from the hyporheic zone to downstream areas (Stanley and Valett 1992).

Temporal variation in exchange should be assessed at differing scales. Diel patterns of VHG included changes of 0.05 in upwelling piezometers at Sycamore Creek (Valett 1993). Similarly, Lee and Hynes (1977) reported diel variation in exchange between groundwater and surface water in an Ontario stream. Seasonal changes in VHG include stream-wide decreases associated with drying (Stanley and Valett 1992, Fig. 2). Finally, effects of floods and the distribution of upwelling and downwelling zones will probably vary with long-term patterns of rainfall and run-off (*sensu* Molles and Dahm 1990, Grimm and Fisher 1992) reflecting the degree of saturation of channel alluvium.

Hydrologic exchange and nutrient supply

A large number of publications have illustrated the nutrient-rich nature of hyporheic water in Sycamore Creek (Grimm and Fisher 1984, Valett et al. 1990, 1992, Grimm et al. 1991, Boulton et al. 1992, Grimm 1992, Stanley and Valett 1992, Valett 1993). Concentration of surface $\text{NO}_3\text{-N}$ was strongly correlated with VHG magnitude in upwelling zones. These data indicate that inputs of nitrogen-rich hyporheic water increased $\text{NO}_3\text{-N}$ in the surface water of upwelling zones. Decreased concentration in downstream regions of groundwater recharge (downwelling zones) reflects $\text{NO}_3\text{-N}$ assimilation by high standing crops of benthic algae (Grimm et al. 1981, Fisher et al. 1982, Grimm and Fisher 1986) and lack of continued supply from the hyporheic zone. By contrast, SRP concentrations did not differ strongly between upwelling and downwelling zones and were not influenced by the magnitude of exchange occurring at upwelling zones. Concentrations of SRP are elevated in the hyporheic zone (Valett et al. 1990) and correlation between SRP and VHG in this study approached significance, but the low variability in SRP within and between zones of exchange suggests that SRP dynamics probably are controlled by physical-chemical processes, such as ad-

sorption. Biological processes in Sycamore Creek undoubtedly affect SRP concentrations, but spatial patterns are not striking because the nutrient is available in excess of required inorganic nitrogen (Grimm and Fisher 1986).

Increases in surface $\text{NO}_3\text{-N}$ occur in upwelling zones despite the intense assimilatory demand that must remove large amounts of inorganic nitrogen from upwelling water as it moves through the hyporheic-benthic interface. Others have not been able to show changes in surface water chemistry due to upwelling (Triska et al. 1990, Hendricks and White 1991). Cru ze des Ch telliens and Reygrobellet (1990), however, identified groundwater inputs to a reach of the Rh ne River as increased $\text{NO}_3\text{-N}$ in surface water. In Sycamore Creek, upwelling interstitial water supplies $\text{NO}_3\text{-N}$ in excess of assimilation by benthic algae. The ultimate source of this nitrate is incompletely known; however, it likely originates as nitrogen-rich floodwater stored in hyporheic sediments and/or from in situ nitrification in the hyporheic zone (Grimm et al. 1991).

Association between the degree of enrichment and upwelling potential as defined by VHG may be obscured by two important aspects of hydrologic flux: variation in hydrologic conductivity (K), and downstream transport of water and solutes from their site of emergence into surface water. The hydraulic gradient represents the energetic potential for hydrologic flux through the hyporheic-benthic interface, but rates of groundwater discharge (Q) are a product of K and VHG (Freeze and Cherry 1979). Measures of areal groundwater discharge were not taken during this study and successional development of the benthic layer may significantly alter exchange rates. Determining actual rates of exchange will require reliable measures of K and/or Q and will provide important information on nutrient fluxes between hyporheic and surface water.

Maximum surface $\text{NO}_3\text{-N}$ was observed at the bases of upwelling zones or in areas immediately downstream at two of the three study sites. This downstream displacement of response to upwelling has been documented in Sycamore Creek over a diel time frame as well (Valett 1993). It likely results from downstream transport of nitrogen-rich upwelling water and dilution by upstream water of lower $\text{NO}_3\text{-N}$ concentration.

While piezometric profiles were dominated by long-term decrease in VHG at all sites, concentration of $\text{NO}_3\text{-N}$ increased with time in both upwelling and downwelling zones. Surface $\text{NO}_3\text{-N}$ concentrations typically decrease rapidly during postflood recovery (Fisher et al. 1982, Grimm 1987). Patterns observed during our study reflected the influence of decreasing surface discharge and developing spatial intermittency (see Stanley and Valett 1992). Upstream surface inputs to both study reaches progressively decreased and were eventually lost due to drying. Loss of upstream input removed dilution by nitrogen-poor water from upstream areas. As a result of drying, the influence of the

hyporheic zone on surface processes increased over the recovery period.

Exchange, nutrient supply, and biotic responses

Upwelling zones supported higher standing crops of benthic algae, and differences in abundance were accentuated in the later stages of postflood recovery. In addition, algal physiological status appeared enhanced based on the higher percentage of chlorophyll in upwelling samples at one site. This result is consistent with the hypothesis that upwelling from the hyporheic zone supplies nitrogen-rich water that promotes algal growth and generates large standing crops of algae such as those observed in upwelling subreaches of this study.

Others have implicated linkage between nutrient-rich substrata or interstitial regions and elevated benthic algal standing crops in lakes (Jansson 1980, Keldermann et al. 1988, Hansson 1989), streams (Pringle and Bowers 1984, Dahm et al. 1987, Pringle 1987, 1990, Stewart 1988, Coleman and Dahm 1990), and marine systems (Capone and Bautista 1985, Höpner and Wonneberger 1985, McLachlan and Illenberger 1986, Sundback and Graneli 1988). Less common is the demonstration of advective exchange as the mechanism of supply (see, however, McLachlan and Illenberger 1986).

Many alternative hypotheses have been proposed to explain differences in algal abundance; of these factors, nutrient availability best explains the observed differences in algal standing crop between upwelling and downwelling zones in Sycamore Creek. Previous research on primary productivity of Sycamore Creek clearly demonstrated the importance of nitrogen limitation (Grimm and Fisher 1986, 1989, Grimm 1987). Other factors may also influence standing crop, but increased algal biomass in areas where hydrologic fluxes supply limiting nutrients emphasizes the importance of hyporheic-benthic linkages.

Stream ecosystems generally are stable by virtue of their capacity to recover quickly from disturbance (Webster et al. 1983, Grimm and Fisher 1989). Chlorophyll *a* accrual rates in upwelling zones were an order of magnitude greater than in downwelling zones. Westman (1978) stressed that the ecosystem parameter chosen for study will have great influence on the degree of stability or resilience observed. Chlorophyll *a* is an appropriate variable for this purpose because it is related to the potential for autochthonous primary production (McIntire 1973, Busch and Fisher 1981), a process of importance in ecosystem recovery (Cairns et al. 1977). As such, upwelling zones are more resilient than downwelling zones.

This research demonstrates that spatial variation in recovery within a season can be as great as temporal variation in resilience among seasons. Rates of chlorophyll accumulation in upwelling zones during the fall of 1990 were comparable to those for typical summer

recoveries based on 3-yr averages from Sycamore Creek (see Grimm and Fisher 1989). This form of spatial heterogeneity has strong implications for the dynamics of whole-system recovery. Upwelling subreaches may be viewed as a resource patch (sensu Pringle et al. 1988) with elevated rates of primary production. These patches may act as sources of algal colonists, or may attract consumers and affect the reestablishment of important trophic interactions.

Effects of positive VHG may extend beyond the supply of limiting nutrients to the surface stream and consequent stimulation of algal growth. Benthic organic matter accumulated at greater rates in upwelling zones, but initial concentrations were lower than, and final concentrations were similar to, those in downwelling zones. Low chlorophyll-to-AFDM ratios in benthic samples from downwelling zones suggest that organic matter at these sites was not closely associated with autochthonous production. Further, AFDM in downwelling zones did not change significantly over the course of the study, indicating that benthic organic matter in these regions was imported rather than produced in situ. The vast majority of this material was probably deposited immediately postflood. In downwelling zones, the negative hydraulic gradient will promote settling of fine particulate organic matter and sandy substrata of runs may act as a filter to retain it. Conversely, deposition may be reduced in upwelling zones. Besides affecting conditions for benthic recovery, accumulation of fine material in the pore spaces of downwelling zones may alter the degree and nature of exchange with the hyporheic zone (see Danielopol 1980).

CONCLUSIONS

Hyporheic and surface subsystems are integrated by complex hydrologic linkages that vary in space and time. Upwelling and downwelling zones represent windows of reciprocal influence through which interstitial and surface subsystems interact. The result is a thorough coupling of biogeochemical fluxes, linking hyporheic and benthic processes. The integrated hyporheic-surface system functions as a whole and its ability to respond to disturbance is greatly influenced by the nature of linkages between subsystems.

Specifically, hydrologic linkage supplies limiting nutrients from the nutrient-rich hyporheic zone to benthic regions. In this manner, hyporheic-surface interactions influence the distribution and abundance of primary producers and, by extension, rates of primary production. Further, upwelling zones may strongly influence species interactions and trophic structure. While these zones represent distinct, highly productive resource patches to which benthic consumers may be drawn, they may also be a source of algal drift and export.

In terms of understanding the mechanisms of stability that allow lotic ecosystems to regain their functional features following disturbance, interactions be-

tween the hyporheic zone and surface stream are of great importance. In this case, the open nature of streams promotes more rapid recovery following exogenous disturbance, i.e., resilience is the source of lotic ecosystem stability. As a medium of interaction between hyporheic and surface systems, hydrologic exchange can affect the physical (substrate composition, porosity), chemical (nutrient environment), and biological (population density and distribution) conditions under which recovery occurs.

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