Parafluvial nitrogen dynamics in a desert stream ecosystem

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Abstract. We investigated nitrogen dynamics over a 15-mo period in the parafluvial zone (the part of the active channel without surface water) of Sycamore Creek, Arizona, a nitrogen-limited Sonoran Desert stream. The parafluvial zone and surface stream are linked hydrologically; thus, nitrogen dynamics in the parafluvial zone potentially influence whole-system functioning. We identified discrete parafluvial flowpaths by following the movement of fluorescent dye through gravel bars over time, sampled subsurface water along these flowpaths, and collected parafluvial sediments for measurement of nitrification rate. Water samples were analyzed for nitrate-N, ammonium-N, dissolved oxygen, temperature, and conductivity. Nitrate-N concentration increased along parafluvial flowpaths, with the largest increases occurring in summer. Although ammonium-N concentration was low and did not vary with season or location on flowpath, dissolved oxygen declined as water moved through parafluvial gravel bars. Net nitrification rate was highest in the summer and at the heads of flowpaths where surface water entered the parafluvial zone, suggesting that nitrification may be dependent upon ammonium, dissolved organic nitrogen, or particulate organic nitrogen imported from the surface stream. Overall, the parafluvial zone of Sycamore Creek was a source of nitrate to the nitrogen-limited surface stream, and may play an important role in the productivity of the stream ecosystem.

Key words: Nutrient dynamics, desert streams, nitrate, nitrification, parafluvial zone, hyporheic zone.

Nutrient dynamics in stream ecosystems are a function of processes occurring in the surface stream as well as interactions between surface waters and subsurface regions (Fisher and Likens 1973, Likens and Bormann 1974, Hynes 1975, Peterjohn and Correll 1984). In nutrient-limited streams, these interactions are of particular importance if subsurface zones are sources or sinks of the limiting nutrient. For example, nitrogen-fixing cyanobacteria are a source of fixed nitrogen (Howarth et al. 1988, Paerl 1990), whereas denitrification in riparian sediments is a nitrogen sink (Peterjohn and Correll 1984, Lowrance et al. 19865, Cooper 1990, Duff and Triska 1990, Pinay et al. 1993). Because ecosystem properties such as primary productivity or nutrient transport and retention are products of the interactions of ecosystem components, it is useful to investigate functioning of individual system components to better understand the entire system.

Desert stream ecosystems are composed of four interacting subsystems: the surface stream, and hyporheic, parafluvial, and riparian zones (Fig. 1). Most research in desert streams and in stream ecology generally has focused on the surface stream. For example, we know that nitrogen availability limits primary productivity in surface waters of Sycamore Creek, Arizona (Grimm and Fisher 1986a), and that nitrogen is potentially limiting in many streams of the southwestern United States (Grimm and Fisher 1986b).

There is, however, a growing awareness of the importance of subsurface waters to stream structure and functioning (Hynes 1983, Ward 1989, Triska et al. 1989). Surface–hyporheic interactions have been investigated in several streams (e.g., Grimm and Fisher 1984, Triska et al. 1989, Hendricks and White 1991, Valett et al. 1994). In Sycamore Creek, the hyporheic zone is a source of nitrate to surface waters (Valett et al. 1990, Valett et al. 1994). This input alleviates nitrogen limitation at sites of hyporheic upwelling, and consequently algal productivity in Sycamore Creek is higher in upwelling than in downwelling zones (Valett et al. 1994). Algal recovery following disturbance is also accelerated in upwelling zones; thus, surface–hyporheic exchange increases ecosystem stability through enhanced resilience (Valett et al. 1994).

Less is known about processes in interstitial waters of the parafluvial zone, the region of the active channel without surface water. The parafluvial zone of Little Lost Man Creek, California, is a source of nitrate to the surface stream (Triska et al. 1989, Triska et al. 1990), whereas in the Garonne River, France, it is a nitrate sink (Pinay et al. 1994). In desert streams such as
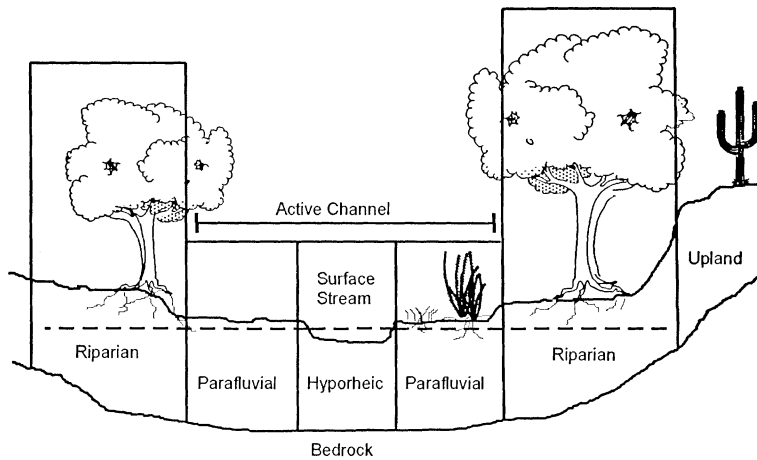
FIG. 1. Diagrammatic representation of surface stream, hyporheic, parafluvial, and riparian components of a desert stream ecosystem. The dashed line represents the water table, which may slope toward or away from the surface stream.

Sycamore Creek, the parafluvial zone is extensive and hydraulic conductivity is high, resulting in high potential for surface–subsurface exchange. The effect of this exchange depends in part upon the kinds and rates of parafluvial processes and their consequences for chemical change in interstitial water. Whether the parafluvial zone acts as a nitrogen source or sink to Sycamore Creek is the focus of this investigation.

The objectives of this study are 1) to determine hydrologic flowpaths within the parafluvial zone and demonstrate hydrologic linkage between parafluvial gravel bars and surface waters, 2) to investigate nitrogen dynamics along parafluvial flowpaths and determine whether the parafluvial zone is a source or sink of inorganic nitrogen to the surface stream, and 3) to evaluate the importance of parafluvial nitrogen dynamics to whole-system functioning.

Study Site

Sycamore Creek is about 35 km northeast of Phoenix, Arizona. Elevations reach 2164 m at the headwaters and drop to 427 m at its confluence with the Verde River. Catchment area is 505 km² and stream length is about 65 km. The geomorphology of Sycamore Creek is characteristic of Sonoran Desert streams and can be broadly divided into three sections (Wertz 1963). The channel in the upper section of the watershed is composed of boulders and exposed bed-rock. Mid-reaches are characterized by coarse sand and gravel sediments averaging 80 cm deep. The surface stream in this region typically occupies only part of the active channel, creating extensive gravel bars that form the parafluvial zone. The downstream section of the stream channel has deep alluvial sediments that rarely support surface flow.

The study site is a 300-m reach in the middle section of Sycamore Creek. Elevation is ~650 m and alluvial sediments in the reach average >1.5 m deep. The active channel is ~25-m wide, with the water table generally being within 25 cm of the surface of parafluvial gravel bars (Fig. 1). Channel slope is 0.006 and typical baseflow discharge is ~0.05 m³/s (range 0 to >400 m³/ s). Vegetation of parafluvial gravel bars has been sparse since 1991 when several large floods scoured the bars clear. However, at times the parafluvial zone is densely covered by seep-willow (*Baccharis salicifolia*) and/or Bermuda grass (*Cynodon dactylon*), as well as seedlings of common riparian species such as cottonwood (*Populus freemontii*), sycamore (*Platanus wrightii*), and mesquite (*Prosopis glandulosa*).

Methods

Parafluvial hydrology and linkage with the surface stream

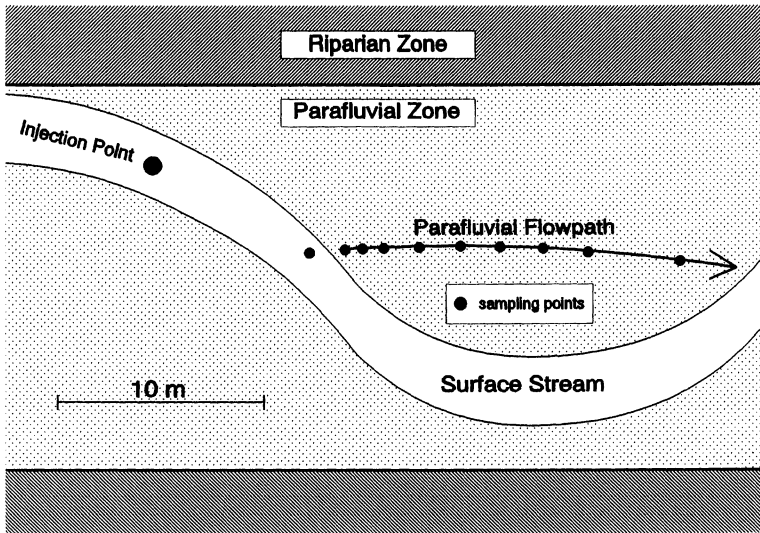The areal extent of the parafluvial zone was determined by measuring the percent of the

FIG. 2. Areal view of solute injection site. Solutes were injected into the surface stream and sampled in parafluvial wells (sampling points are indicated by solid circles).

active channel occupied by parafluvial gravel bars. Measurements were made using a series of 11 transects at 20-m intervals along the study reach, or estimates were made from photographs of the study site. These estimates were made 33 times during the study.

We sampled a total of 28 parafluvial flowpaths on 13 days from October 1992 to January 1994. Subsurface flow direction and rate in parafluvial gravel bars was determined by injecting fluorescent dye at the upstream margins of gravel bars and at several points within the bars and tracing its progress through the bar over time. We injected dye by adding it to shallow pits, and followed its movement by digging a series of trenches perpendicular to the predicted flowpath roughly 1 h after injection. Injection time, distance from injection point to the farthest trench where dye was seen, and time when dye was located were recorded to determine flow rate. Discrete flowpaths of at least 10 m in length were identified.

Hydrologic exchange from the surface stream to the parafluvial zone was investigated by injecting a conservative tracer (chloride as NaCl) into the surface channel and sampling parafluvial wells downstream from the injection point. Chloride injections were performed in July 1993, and parafluvial wells up to 14 m from the surface stream were sampled. Parafluvial to surface

exchange was examined by searching for parafluvially injected dye in the surface stream.

Physico-chemical characteristics along parafluvial flowpaths

Physico-chemical characteristics of interstitial water along parafluvial flowpaths were determined by sampling with mini-piezometers (Lee and Cherry 1978) inserted to a depth of 25 cm below the water table. Piezometers, with tips covered by Nitex® mesh to minimize clogging, were inserted along discrete flowpaths at 0.1, 1.0, 2.0, 5.0, and 10.0 m (and occasionally up to 30.0 m) from the upstream parafluvial-stream interface. Samples were collected using a battery-powered peristaltic pump fitted with an in-line filter. At each sampling point we first measured dissolved oxygen (Leeds & Northrup Instruments D.O. probe), temperature, and conductivity, and then collected triplicate water samples in acid-washed 60-mL polyethylene bottles for nitrate analysis. Separate triplicate 25-mL water samples were collected and fixed in the field with phenol reagent before spectrophotometric ammonium analysis (Shimadzu UV160U) by the phenolhypochlorite method (Solorzano 1969). Before November 1993, samples were field-filtered through 0.8-μm cellulose-acetate filters (Geofilter®, 142 mm diame-

ter), thereafter with Whatman® GFF filters (nominal pore size = 0.7 μm). Comparison of the two filtration methods showed their equivalence for nitrate and ammonium analyses. Nitrate samples were analyzed on a Bran and Luebbe TRAACS 800® autoanalyzer using a modified version of Technicon Industrial Method No. 818-87T.

Net nitrification

Net nitrification rate was determined using sediments from 15 parafluvial flowpaths. Sediments were taken from 5 to 15 cm below the water table, at 0.1 m and 5.0 m from the stream-parafluvial interface. We also collected sediments at 1.0 m, 2.0 m, and 10.0 m (in addition to 0.1 m and 5.0 m) from the stream-parafluvial interface along eight flowpaths during summer 1993. Net nitrification rate was measured by placing approximately 160 g (wet weight) sediments in 250-mL Erlenmeyer flasks, and incubating with 100 mL distilled water for 15–22 hours in the dark at 25°C. Sediments from each sampling point were run in triplicate. After the incubation period, a 5-mL water sample was collected from each flask and analyzed for nitrate-N. Net nitrification rate was expressed per unit dry sediment mass. Initial nitrate-N samples were not taken. We later determined that ~10% of the nitrate-N increase is due to leaching when distilled water is first added to sediments. Net nitrification rates for sediments collected at 0.1 m and 5.0 m were log-transformed to correct for non-normality and analyzed using two-factor analysis of variance, with season and location on flowpath as factors. Net nitrification along the eight intensively-sampled flowpaths was analyzed using one-way ANOVA. Season was not a factor in this analysis because all samples were collected in summer. All statistical analyses were done with the SYSTAT (1992) software package.

Co-injection of ammonium and chloride

We co-injected the conservative tracer chloride (as NaCl) and ammonium (as NH_4Cl) to the surface stream to demonstrate surface-parafluvial hydrologic linkage and to investigate potential ammonium limitation of nitrification. Our objective was to determine whether nitrate production in parafluvial sediments was limited
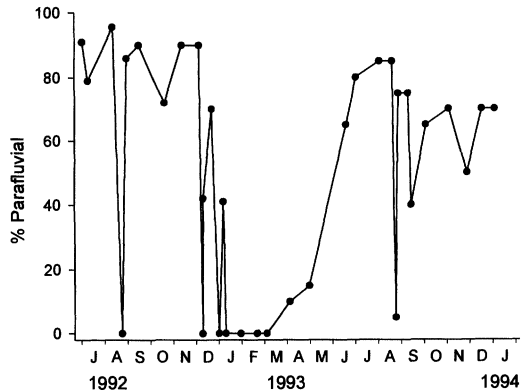

FIG. 3. Percent of the active channel composing the parafluvial zone. During spates when the entire active channel is underwater, the parafluvial zones does not exist. Conversely, when surface flow ceases completely, as it sometimes does, the parafluvial zone occupies 100% of the active channel.

by ammonium availability. On 19 July 1993, we sampled subsurface water at nine points along a parafluvial flowpath, as well as surface water adjacent to the head of the parafluvial flowpath (Fig. 2). All samples were analyzed for nitrate-N, ammonium-N, dissolved oxygen, temperature, and conductivity by previously described methods. Chloride was analyzed on a Bran and Luebbe TRAACS 800® using Technicon Industrial Method #783-86T.

Solute injection into the surface channel began at 9:30 am on 20 July 1993 and continued for 20 h. Surface water and parafluvial wells were sampled 1, 2, 4, 24, 48, and 72 h after the initiation of the injection. If nitrification was limited by ammonium availability, we expected to find increased nitrate-N concentrations in the parafluvial zone after initiation of the injection due to increased rates of nitrification. Conversely, lack of change in nitrate-N concentration would indicate that nitrification was independent of the rate of ammonium supply.

Results

Parafluvial hydrology and linkage with the surface stream

The parafluvial zone occupied from 0 to 95% of the active channel of the 300-m study reach over the period of the study (Fig. 3). Parafluvial coverage was generally greatest in summer, al-

TABLE 1.   Variation of chemical and physical characteristics with distance along parafluvial flowpaths. Data are presented as means (± 1 SE) over all sites and seasons ($n = 26$).

Distance along flowpath	NO_3-N (μg/L)	NH_4-N (μg/L)	D.O. (mg/L)	Temperature (°C)	Conductivity (μS/cm)
Surface stream	45 ± 9	2 ± 1	8.8 ± 0.3	21.5 ± 1.3	467 ± 10
0.1 m	51 ± 8	1 ± 1	8.7 ± 0.3	21.5 ± 1.4	469 ± 10
1.0 m	59 ± 9	3 ± 3	8.6 ± 0.3	20.8 ± 1.3	468 ± 10
2.0 m	67 ± 11	1 ± 0	8.5 ± 0.4	19.6 ± 1.2	470 ± 10
5.0 m	78 ± 12	5 ± 4	7.9 ± 0.4	18.9 ± 1.1	473 ± 11
10.0 m	98 ± 12	2 ± 1	7.2 ± 0.4	20.5 ± 1.3	476 ± 10

though the parafluvial zone often composed much of the active channel in winter as well. An unusually large flood (>400 m³/s) beginning 8 January 1993 inundated the active channel for almost 3 months, and thus eliminated the parafluvial zone for that period (Fig. 3).

During the solute injection experiment, surface-injected chloride appeared in all parafluvial wells, verifying surface–parafluvial linkage. Likewise, parafluvially injected dye was often found in the surface stream, confirming parafluvial–surface linkage. Surface water typically entered gravel bars at meanders and re-entered the surface stream farther downstream. Parafluvial water velocity averaged 1.96 m/h and ranged from 0.5 to 5.0 m/h, although velocities at different locations along a flowpath on a given day were similar. No seasonal trends were apparent in flowpath velocity, although flow direction fluctuated as stream water level changed relative to the parafluvial water table. Visual inspection of dye plumes downstream of injection points suggested lateral dispersion of water flowing through gravel bars was minimal as dye plumes remained constricted even 5–10 m from the injection point.

Physico-chemical characteristics along parafluvial flowpaths

Physico-chemical parameters along parafluvial flowpaths are summarized in Table 1. Nitrate-N concentration increased as water flowed through parafluvial gravel bars (repeated measures ANOVA, test for repeated-factor, $p < 0.001$, Table 2). The mean nitrate-N increase along 10-m parafluvial flowpaths was >50 μg/L and the maximum exceeded 200 μg/L. There was a significant seasonal effect on parafluvial nitrate-N concentration (test for independent factor effect, $p < 0.05$, Table 2), with the greatest concentration increase in summer (Fig. 4A, B). Overall, 25 of the 26 flowpaths sampled exhibited higher nitrate-N concentration at 10 m than in surface-stream water. One winter-sampled flowpath showed a small nitrate-N decline (2 μg/L). In contrast to nitrate, ammonium concentrations were generally low, often below limits of detection (<5 μg/L, Table 1), and did not vary as a function of distance along flowpath or season (Table 2).

Dissolved oxygen declined as water flowed through the parafluvial zone ($p < 0.001$, Table

TABLE 2.   Results of repeated measures ANOVA for chemical variables along parafluvial flowpaths. The independent variable is season and the repeated variable is distance along flowpath.

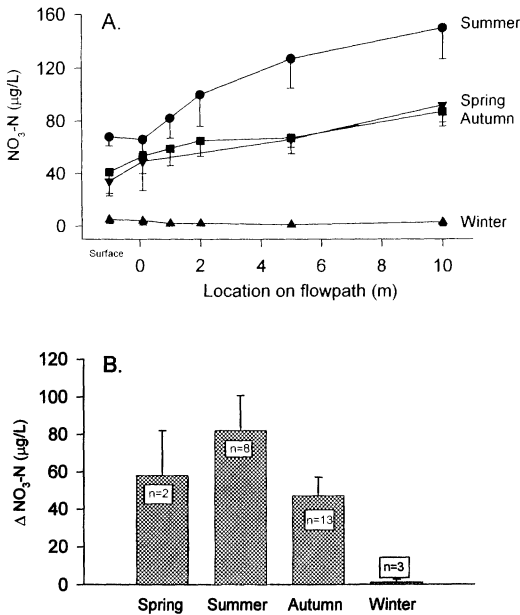| Dependent variable	Mean squared error		F statistic		
			Season	Distance	Season × distance
Nitrate	between	0.011	3.930*	—	—
	within	0.000	—	13.446***	3.352***
Ammonium	between	0.000	3.229	—	—
	within	0.000	—	0.821	0.698
Dissolved Oxygen	between	9.365	10.192***	—	—
	within	0.252	—	17.576***	3.941***

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

FIG. 4. A. Nitrate-N concentration along parafluvial flowpaths as a function of season. Each data point represents the mean (−1 SE) concentration of several flowpaths (see Fig. 4B for number of flowpaths sampled). B. Change in nitrate-N concentration between the surface stream and the 10.0-m sampling point along parafluvial flowpaths. Numbers of flowpaths sampled in each season are indicated. Error bars represent +1 SE.

2, Fig. 5A) and also varied as a function of season (repeated measures ANOVA, test for independent factor, $p < 0.001$, Table 2). The greatest decline occurred during summer, followed by spring, autumn, and winter (Fig. 5B). For flowpaths that were sampled over distances >10 m, the greatest dissolved oxygen declines were generally within the first 5–10 m of the flowpaths (Fig. 6). Conductivity and temperature did not vary significantly along flowpaths (Table 1, $p > 0.05$ in both cases).

Net nitrification

Net nitrification rate varied seasonally ($p < 0.001$), with summer rates being significantly higher than autumn or winter (Fig. 7). Mean summer net nitrification was much higher in sediments from the 0.1-m sampling point than from 5.0 m, but not in autumn and winter (Fig. 7). Thus, location was not a significant factor in explaining net nitrification in this analysis

overall ($p > 0.05$). Location was significant, however, for the eight flowpaths that were intensively investigated in the summer of 1993 ($p < 0.05$). Tukey multiple comparison analysis showed sediments from 0.1 m exhibited higher net nitrification rates than sediments collected 5.0 m into the parafluvial flowpaths ($p < 0.05$, Fig. 8), which is consistent with the summer nitrification rates shown in Figure 7.

Ammonium and chloride co-injection

All parafluvial wells exhibited elevated solute concentrations in response to the surface stream injection. Pre-injection nitrate-N and ammonium-N in the surface stream were 36 $\mu g/L$ and below detection level (<5 $\mu g/L$), respectively. During the injection, surface-water nitrate-N near the head of the parafluvial flowpath ranged from 49 $\mu g/L$ to 82 $\mu g/L$, while ammonium-N reached 1554 $\mu g/L$. Surface-in-
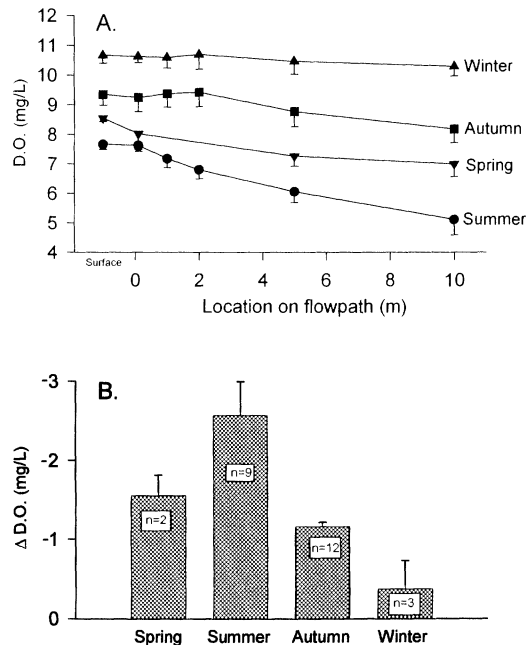

FIG. 5. A. Dissolved oxygen concentrations along parafluvial flowpaths as a function of season. Each data point represents the mean (−1 SE) concentration of several flowpaths (see Fig. 5B for number of flowpaths sampled). B. Change in dissolved oxygen concentration between the surface stream and the 10.0-m sampling point along parafluvial flowpaths. Numbers of flowpaths sampled in each season are indicated. Error bars represent +1 SE.
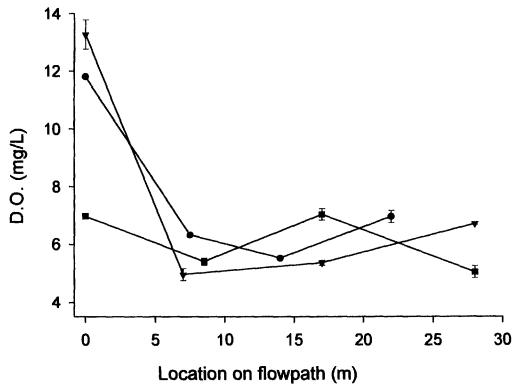
FIG. 6. Oxygen concentration along three parafluvial flowpaths that were sampled over distances greater than 10 m. Each line represents a distinct flowpath. Note the rapid initial dissolved oxygen decline followed by a levelling-off. Error bars represent ± 1 SE, $n = 3$.

jected solutes arrived rapidly in parafluvial wells, with chloride appearing first, followed by increases in nitrate-N and ammonium-N. For example, at the sampling well 4 m along the flowpath, pre-injection nitrate-N was 67 μg/L and the highest recorded concentration (585 μg/L) was 24 h after the injection began (Fig. 9). Highest recorded ammonium concentration was also at 24 h (352 μg/L).

Discussion

Parafluvial hydrology and linkage with the surface stream

Hydrologic linkage is the primary interaction between parafluvial and surface-water environments. Aerial linkage may be important when parafluvial vegetation is dense and leaf litterfall is heavy; however, the absence of vegetation on parafluvial gravel bars made this vector insignificant.

Frequent hydrologic exchange between surface and subsurface environments increases the probability that subsurface processes will influence surface-stream functioning. Parafluvial to surface-stream linkage was demonstrated when parafluvially injected dye was detected in the surface stream. Surface to parafluvial exchange was suggested when dye injected at the stream–parafluvial interface was transported into parafluvial gravel bars. This linkage was verified by the tracer experiment when surface-injected

ammonium and chloride appeared in parafluvial wells (Fig. 9).

Although lateral exchange between the parafluvial zone and riparian and upland ecosystems cannot be ruled out, we found no evidence for this linkage. We never observed parafluvially injected dye enter the riparian zone, nor did dye injected into riparian bank sediments move into the parafluvial zone. Sediments at the riparian–parafluvial interface are fine-grained and rich in organic matter, and may restrict the exchange of water between these zones.

Deep groundwater inputs were not investigated. However, indirect evidence suggests that deep groundwater inputs are not important in Sycamore Creek. For example, hyporheic and parafluvial concentrations of dissolved organic carbon are similar to surface-stream values (J. Jones, Arizona State University, personal communication), in contrast to systems with significant groundwater inputs (Ford and Naiman 1989, Fiebig and Lock 1991). In addition, conductivity and temperature did not vary significantly along flowpaths (Table 1, $p > 0.05$), which further suggests that a distinct groundwater source was not entering the stream ecosystem. Thus, it appears that most of the water in the
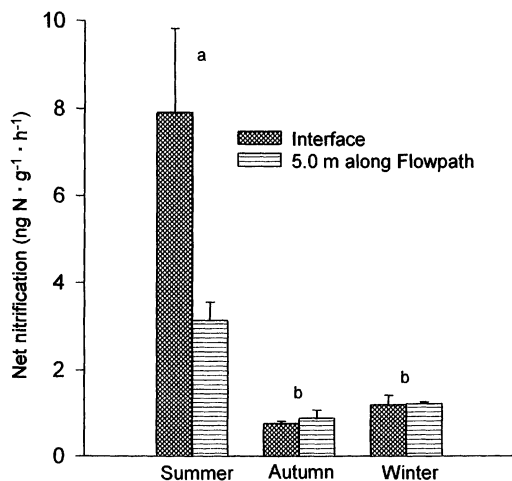

FIG. 7. Net nitrification rate (per unit sediment dry mass) in parafluvial sediments at the stream–parafluvial interface and at 5.0 m along parafluvial flowpaths. Error bars represent +1 SE. Statistically significant differences among seasons (Tukey's multiple comparison, $p < 0.05$) are denoted by different lower case letters.
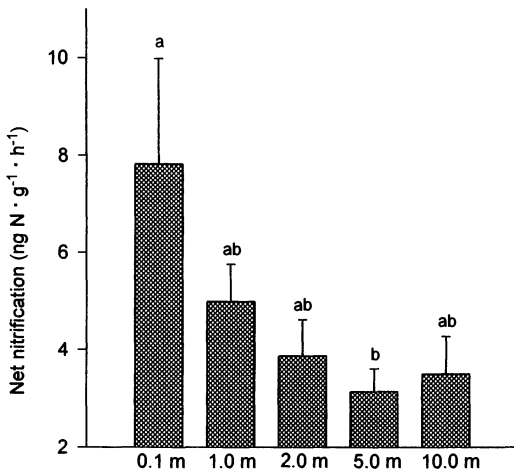
FIG. 8. Net nitrification rate (per unit sediment dry mass) for eight intensively sampled flowpaths. All of these flowpaths were sampled in the summer of 1993. Error bars represent +1 SE. Statistically significant differences (Tukey's multiple comparison, $p < 0.05$) are denoted by different lower case letters.

hyporheic zone (mean = 2.2 m/h; Valett et al. 1990). These rates are greater than typical groundwater velocities and probably are at the upper extreme for interstitial water velocity in stream sediments. The high parafluvial water velocity found in Sycamore Creek may influence nutrient dynamics. That is, rapid interstitial velocity decreases hydrologic residence time, and therefore may influence the relative contribution of aerobic and anaerobic processes, as shorter residence times should minimize dissolved oxygen declines.

Parafluvial flowpath length varied from less than 1 m to greater than 100 m. For logistical reasons, we sampled only flowpaths at least 10 m long and then generally restricted sampling to the first 10 m. This approach facilitates comparison between dates and locations, but it fails to describe the full range of variability present in the system. For example, the net effect of many small bars is probably different from the effect of a few large bars. At times the parafluvial zone occupies 95% or more of the active channel, whereas at other times the parafluvial zone is absent (Fig. 3). Moreover, the distribution of flowpath lengths is not constant but varies in response to flooding and drying as the configuration of the active channel changes, further influencing stream–parafluvial interactions.

parafluvial zone had been within the active channel for an extended period, as opposed to recently entering the active channel from the riparian, upland, or groundwater systems.

Parafluvial water velocities in Sycamore Creek (mean = 1.96 m/h) were similar to those in the
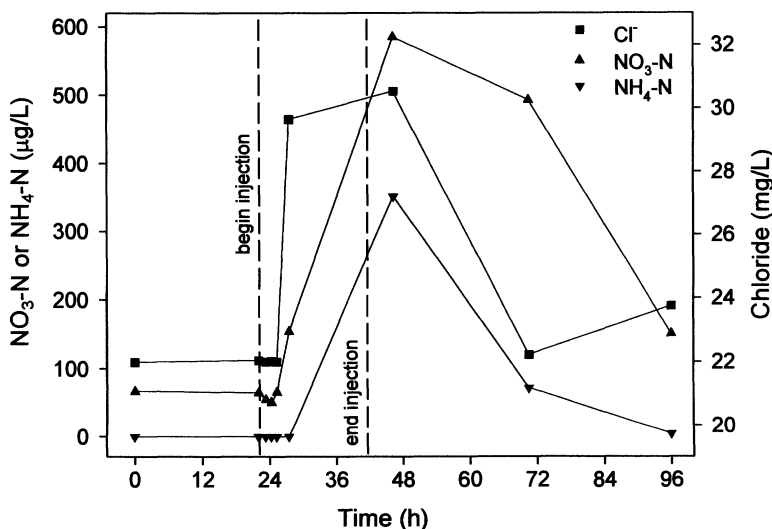

FIG. 9. Ammonium-N, nitrate-N, and chloride concentrations in parafluvial well 4 m from stream–parafluvial interface. Similar patterns were found at the other sampling locations.

Physico-chemical characteristics along
parafluvial flowpaths

Dissolved oxygen concentration influences
nitrogen dynamics, as some transformations are
obligately aerobic whereas others are anaerobic.
In Sycamore Creek, dissolved oxygen declined
along parafluvial flowpaths, with the extent of
the decline being seasonally variable (Fig. 5,
Table 2). Lowest initial dissolved oxygen con-
centration, as well as the greatest decline along
parafluvial flowpaths, occurred during summer.
However, over the course of this study, dis-
solved oxygen seldom dropped below 5 mg/L.
At these levels, aerobic processes (e.g., nitrifi-
cation) would predominate over anaerobic pro-
cesses (e.g., denitrification), except at active an-
oxic microsites.

For flowpaths that were sampled over dis-
tances greater than 10 m, dissolved oxygen gen-
erally decreased most rapidly within the first
6–8 m of the flowpaths (Fig. 6). Similarly, dis-
solved oxygen decline along 10-m flowpaths
sampled in summer was greatest in the first few
metres of the flowpaths (Fig. 5A). These obser-
vations are consistent with the hypothesis that
subsurface respiration is dependent upon sur-
face inputs of dissolved or particulate organic
matter. Jones (Arizona State University, per-
sonal communication) found higher hyporheic
respiration in downwelling zones (where sur-
face water entered the hyporheic zone) than in
upwelling zones (where hyporheic water en-
tered the surface stream). He suggested that the
higher respiration in downwelling zones is re-
lated to the import of labile, surface-derived
organic matter. A similar dependence on stream-
parafluvial linkage to support parafluvial res-
piration may be inferred from our oxygen data.

Although ammonium in surface and paraflu-
vial waters of Sycamore Creek was always low
(Table 1), and did not vary as a function of
season or location along flowpath (Table 2), am-
monium production through mineralization
may be high, with rapid nitrification, adsorp-
tion, or uptake accounting for the low ambient
concentration. At a minimum, ammonium-N
supply must equal nitrate-N production, assum-
ing that the entire nitrate increase is from ni-
trification.

In summer, algal productivity is generally
highest and nitrogen is typically limiting in
Sycamore Creek (Grimm and Fisher 1986a).

Similarly, nitrate-N increases along parafluvial
flowpaths were greatest in summer (Fig. 4A, B).
Thus, nitrate production in the parafluvial zone
is greatest at the time when it is most needed
by surface autotrophs, increasing the likelihood
that parafluvial processes influence primary
productivity in the surface stream.

Net nitrification

Elevated nitrate concentration in hyporheic
waters of Sycamore Creek may be due to storage
of nitrate-rich floodwaters or in-situ nitrifica-
tion (Grimm et al. 1991); substantial nitrification
potential in hyporheic sediments supports the
nitrification hypothesis. High discharge spates
have 6.1 times higher nitrate-N concentration
than baseflow (Grimm and Fisher 1986b), so
spates also may recharge the hyporheic zone
with nitrate. As pointed out by Grimm et al.
(1991), these sources are not mutually exclusive.
For example, organic matter could be imported
into the stream ecosystem during floods and
later mineralized and nitrified within intersti-
tial sediments. However, storage of nitrate-rich
floodwater alone would not explain the ob-
served nitrate increases along parafluvial flow-
paths. That is, if floodwater storage were re-
sponsible for elevated subsurface nitrate-N, we
would expect nitrate-N in the hyporheic and
parafluvial zones to be high and spatially con-
stant immediately following a spate, and then
to gradually decrease following flushing with
lower nitrate-N surface water.

Results of the present study support the hy-
pothesis that nitrification within parafluvial
sediments in Sycamore Creek is responsible for
elevated nitrate-N concentration in this zone.
The period of highest net nitrification rate
(summer) corresponded with the time of great-
est nitrate increase along parafluvial flowpaths
(Fig. 4). Although higher summer temperature
might increase rates of microbially mediated
reactions including nitrification (Focht and
Verstraete 1977), temperature alone cannot ex-
plain the observed seasonal differences in net
nitrification rate because all lab nitrification
analyses were done at the same temperature.
Therefore, nitrifier populations were either
larger or more active in summer than in other
seasons.

In summer, the highest net nitrification rates
occurred at the stream–parafluvial interface,

suggesting that nitrification in subsurface sediments is closely linked to surface-derived sources (ammonium, dissolved organic nitrogen [DON], or particulate organic nitrogen [PON]). Ammonium injection into surface water demonstrated that nitrate production (nitrification) was limited by ammonium supply (Fig. 9). Because surface water ammonium concentration is low (Table 1), it appears that surface-derived DON or PON mineralized in parafluvial sediments provides the ammonium substrate for nitrification. Algal production and standing crops are normally highest in the summer (Grimm and Fisher 1986a). Thus, algal-derived DOM or POM are potential sources of organic matter for fueling parafluvial metabolism. This creates the potential for a positive feedback loop (or spiral; sensu Newbold et al. 1981) between surface primary production, which is nitrogen-limited, and nitrification along parafluvial and hyporheic flowpaths. That is, algal leachates may fuel nitrification in subsurface sediments, leading to elevated nitrate-N in subsurface waters, which later re-enters the surface stream and stimulates primary production.

Ecosystem implications

Previous research has shown the importance of surface–hyporheic hydrologic exchange to the structure and functioning of stream ecosystems (Grimm and Fisher 1984, Valett et al. 1994). Our study demonstrates the significance of the parafluvial zone as an additional source of nitrate to a nitrogen-limited stream ecosystem. Casual observation suggested that algal biomass was higher in areas where parafluvial water entered the surface stream, as in upwelling zones where nitrate-rich hyporheic water enters the surface (Valett et al. 1994). As with hyporheic-surface exchange, parafluvial nitrate inputs might be expected to contribute to ecosystem resilience following disturbance (sensu Webster et al. 1983).

The relative importance of hyporheic and parafluvial subsystems to whole-stream ecosystem functioning depends upon channel configuration, rates of supply and distribution of sand and gravel substrates, hydraulic conductivity of bed materials, and channel geomorphology which generates the hydraulic heads that determine the direction and velocity of flowpaths.

In wide, sandy streams of the desert Southwest, these attributes tend to accentuate the significance of hyporheic and parafluvial subsystems. Similar studies in streams in redwood forests of California (Triska et al. 1989, Triska et al. 1993), the Oak Ridges moraine of southern Ontario (Hill 1990), New Mexico highlands (C. Dahm, University of New Mexico, personal communication), and southwest France (Pinay et al. 1994) suggest that these processes are widespread. A comprehensive understanding of stream ecology will increasingly require a broadened view of what constitutes the stream ecosystem.

Acknowledgements

Literature Cited

COOPER, B. A. 1990. Nitrate depletion in the riparian zone and stream channel of a small headwater catchment. Hydrobiologia 202:13–26.

DUFF, J. H., AND F. J. TRISKA. 1990. Denitrification in sediments from the hyporheic zone adjacent to a small forested stream. Canadian Journal of Fisheries and Aquatic Sciences 47:1140–1147.

FIEBIG, D. M., AND M. A. LOCK. 1991. Immobilization of dissolved organic matter from groundwater discharging through the stream bed. Freshwater Biology 26:45–55.

FISHER, S. G., AND G. E. LIKENS. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem analysis. Ecological Monographs 43:421–439.

FOCHT, D. D., AND W. VERSTRAETE. 1977. Biochemical ecology of nitrification and denitrification. Advances in Microbial Ecology 1:135–214.

FORD, T. E., AND R. J. NAIMAN. 1989. Groundwater-surface water relationships in boreal forest watersheds: dissolved organic carbon and inorganic nutrient dynamics. Canadian Journal of Fisheries and Aquatic Sciences 46:41–49.

GRIMM, N. B., AND S. G. FISHER. 1984. Exchange be-

tween surface and interstitial water: implications for stream metabolism and nutrient cycling. Hydrobiologia 111:219–228.

GRIMM, N. B., AND S. G. FISHER. 1986a. Nitrogen limitation in a Sonoran Desert stream. Journal of the North American Benthological Society 5:2–15.

GRIMM, N. B., AND S. G. FISHER. 1986b. Nitrogen limitation potential of Arizona streams and rivers. Journal of the Arizona-Nevada Academy of Science 21:31–43.

GRIMM, N. B., H. M. VALETT, E. H. STANLEY, AND S. G. FISHER. 1991. Contribution of the hyporheic zone to stability of an arid-land stream. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 24:1595–1599.

HENDRICKS, S. P., AND D. S. WHITE. 1991. Physicochemical patterns within a hyporheic zone of a northern Michigan river, with comments on surface water patterns. Canadian Journal of Fisheries and Aquatic Sciences 48:1645–1654.

HILL, A. R. 1990. Ground water flow paths in relation to nitrogen chemistry in the near-stream zone. Hydrobiologia 206:39–52.

HOWARTH, R. W., R. MARINO, J. LANE, AND J. COLE. 1988. Nitrogen fixation in freshwater, estuarine, and marine ecosystems. I. Rates and importance. Limnology and Oceanography 33:688–701.

HYNES, H. B. N. 1975. The stream and its valley. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 19:1–15.

HYNES, H. B. N. 1983. Groundwater and stream ecology. Hydrobiologia 100:93–99.

LEE, D. R., AND J. A. CHERRY. 1978. A field exercise on groundwater flow using seepage meters and mini-piezometers. Journal of Geological Education 27:6–10.

LIKENS, G. E., AND F. H. BORMANN. 1974. Linkages between terrestrial and aquatic ecosystems. BioScience 24:447–456.

LOWRANCE, R. R., R A. LEONARD, AND L. E. ASMUSSEN. 1985. Nutrient budgets for agricultural watersheds in the southeastern coastal plain. Ecology 66:287–296.

NEWBOLD, J. D., J. W. ELWOOD, R. V. O'NEILL, AND W. VAN WINKLE. 1981. Measuring nutrient spiralling in streams. Canadian Journal of Fisheries and Aquatic Sciences 38:860–863.

PAERL, H. W. 1990. Physiological ecology and regulation of N_2 fixation in natural waters. Advances in Microbial Ecology 11:305–344.

PETERJOHN, W. T., AND D. L. CORRELL. 1984. Nutrient dynamics in an agricultural watershed: obser-

vations on the role of a riparian forest. Ecology 65:1466–1475.

PINAY, G., N. E. HAYCOCK, C. RUFFINONI, AND R. M. HOLMES. 1994. The role of denitrification in nitrogen retention in river corridors. Pages 107–116 in W. J. Mitsch (editor). Global wetlands: Old World and New. Elsevier, Amsterdam.

PINAY, G., L. ROQUES, AND A. FABRE. 1993. Spatial and temporal patterns of denitrification in a riparian forest. Journal of Applied Ecology 30:581–591.

SOLORZANO, L. 1969. Determination of ammonia in natural waters by the phenolhypochlorite method. Limnology and Oceanography 14:799–801.

SYSTAT, INC. 1992. SYSTAT for windows: statistics. Version 5 Edition. Evanston, Illinois.

TRISKA, F. J., J. H. DUFF, AND R. J. AVANZINO. 1993. Patterns of hydrological exchange and nutrient transformation in the hyporheic zone of a gravel-bottom stream: examining terrestrial-aquatic linkages. Freshwater Biology 29:259–274.

TRISKA, F. J., J. H. DUFF, AND R. J. AVANZINO. 1990. Influence of exchange flow between the channel and hyporheic zone on nitrate production in a small mountain stream. Canadian Journal of Fisheries and Aquatic Sciences 47:2099–2111.

TRISKA, F. J., V. C. KENNEDY, R. J. AVANZINO, G. W. ZELLWEGER, AND K. E. BENCALA. 1989. Retention and transport of nutrients in a third-order stream in northwestern California: hyporheic processes. Ecology 70:1893–1905.

VALETT, H. M., S. G. FISHER, N. B. GRIMM, AND P. CAMILL. 1994. Vertical hydrologic exchange and ecological stability of a desert stream. Ecology 75:548–560.

VALETT, H. M., S. G. FISHER, AND E. H. STANLEY. 1990. Physical and chemical characteristics of the hyporheic zone of a Sonoran Desert stream. Journal of the North American Benthological Society 9:201–215.

WARD, J. V. 1989. The four-dimensional nature of lotic ecosystems. Journal of the North American Benthological Society 8:2–8.

WEBSTER, J. R., M. E. GURTZ, J. J. HAINS, J. L. MEYER, W. T. SWANK, J. B. WAIDE, AND J. B. WALLACE. 1983. Stability of stream ecosystems. Pages 355–395 in J. R. Barnes and G. W. Minshall (editors). Stream ecology. Plenum Press, New York.

WERTZ, J. B. 1963. Mechanisms of erosion and deposition along channelways. Journal of the Arizona Academy of Science 2:146–163.

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