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Nutrient Dynamics and Retention in Land/Water Ecotones of Lowland, Temperate Lakes and Rivers.

The role of water exchange between a stream channel and its hyporheic zone in nitrogen cycling at the terrestrial–aquatic interface

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Abstract

The subsurface riparian zone was examined as an ecotone with two interfaces. Inland is a terrestrial boundary, where transport of water and dissolved solutes is toward the channel and controlled by watershed hydrology. Streamside is an aquatic boundary, where exchange of surface water and dissolved solutes is bi-directional and flux is strongly influenced by channel hydraulics. Streamside, bi-directional exchange of water was qualitatively defined using biologically conservative tracers in a third order stream. In several experiments, penetration of surface water extended 18 m inland. Travel time of water from the channel to bankside sediments was highly variable. Subsurface chemical gradients were indirectly related to the travel time. Sites with long travel times tended to be low in nitrate and DO (dissolved oxygen) but high in ammonium and DOC (dissolved organic carbon). Sites with short travel times tended to be high in nitrate and DO but low in ammonium and DOC. Ammonium concentration of interstitial water also was influenced by sorption-desorption processes that involved clay minerals in hyporheic sediments. Denitrification potential in subsurface sediments increased with distance from the channel, and was limited by nitrate at inland sites and by DO in the channel sediments. Conversely, nitrification potential decreased with distance from the channel, and was limited by DO at inland sites and by ammonium at channel locations. Advection of water and dissolved oxygen away from the channel resulted in an oxidized subsurface habitat equivalent to that previously defined as the hyporheic zone. The hyporheic zone is viewed as stream habitat because of its high proportion of surface water and the occurrence of channel organisms. Beyond the channel's hydrologic exchange zone, interstitial water is often chemically reduced. Interstitial water that has not previously entered the channel, groundwater, is viewed as a terrestrial component of the riparian ecotone. Thus, surface water habitats may extend under riparian vegetation, and terrestrial groundwater habitats may be found beneath the stream channel.

Introduction

Holland (1988) defined an ecotone as a zone of transition between adjacent ecological systems having a set of characteristics uniquely defined by space and time scales and by the strength of the interaction between adjacent ecological systems. A riparian corridor separating agricultural land from the riverine ecosystem is an ideal example. Waterfowl can use the corridor longitudinally for migration while they and other bird species simultaneously exploit the agricultural field, riparian zone and lotic system for food, cover and nesting habitat (Décamps *et al.*, 1987). Similar longitudinal and lateral exploitation can be employed by large terrestrial mammals such as deer. Riparian mammals, such as beaver, also exploit both terrestrial and aquatic resources. Beaver activity has direct riparian feedback through the selective harvesting of bankside species for food, and dam building, which raises the water table creating specific habitat patches of variable permanence (Johnston & Naiman, 1987). In addition, litter input from beaver activity loads the aquatic ecosystem with reduced carbon for microbial metabolism and consumption by shredder invertebrates. Finally, many aquatic invertebrates alternately use the aquatic habitat for development of juvenile instars while adults exploit the riparian corridor as paths of dispersion, cover, swarming and reproduction. All of these are strong between-system linkages as described by Holland (1988).

Biotic linkage is strong between the riparian ecotone and the riverine ecosystem because the primary direction of material flux is toward the channel (Fig. 1A). For example, channel fauna, such as fish, benefit from bankside inputs of wood, which provide cover and protection (Triska & Cromack, 1980). Litter inputs also provide an energy and nutrient source for invertebrates and fish. The loss of this source can significantly reduce their production (Karr & Schlosser, 1978). The canopy also can indirectly regulate nutrient uptake by shading, which controls periphyton primary production (Gregory, 1980). By contrast, instream production of algae, fish and invertebrates typically constitutes a far weaker linkage to terrestrial flora and fauna.

The riparian ecotone also links terrestrial to riverine ecosystems below ground. Like above-ground materials, below-ground transport is toward the channel. Pinay & Décamps (1988) described the fate of dissolved allochthonous nitrogen moving through the riparian ecotone perpendicular to the Louge River. The overall direction of transport was toward the channel, during which time complete removal of nitrate over a 30-meter flow path was attributed to denitrification and assimilation. Lowrance *et al.* (1984) reported 75% retention (input minus stream export) of nitrate transported across the riparian ecotone of a coastal plain watershed in Georgia, USA. Schnabel (1986) reported up to 50% decreases in nitrate concentration within 16 m of an upland-wetland ecotone. Similar observations of riparian ecotones that serve as nutrient filters have been reported by Peterjohn & Correll (1984), Jacobs & Gilliam (1985) and Chauvet & Décamps (1989).

Below ground, linkage between the stream channel and riparian ecotone is dependent upon complex hydrologic exchange which is only poorly understood. This linkage involves the continuous bi-directional exchange of water, nutrients and fauna. This zone of bi-directional exchange is a hydrologic manifestation of what lotic ecologists identify as the hyporheic zone (Fig. 1C).

Early hyporheic studies reported aquatic invertebrates deep beneath the channel surface and emphasized the importance of this habitat as a refuge during storms (Coleman & Hynes, 1970; Hynes, 1974; Williams & Hynes, 1974; Hynes *et al.*, 1976). Bretschko (1981) reported invertebrate fauna to depths of 80–100 cm and up to 10 m from the channel in an Austrian stream. Stanford & Gaufin (1974) and Stanford & Ward (1988) found riverine invertebrates up to 2 km inland 10 m beneath the Flathead River, Montana. Observations of complex lotic communities adjacent to and below the surface channel imply effective, subsurface exchange of food resources and nutrients.

Production of invertebrate fauna in the sub-stream requires an oxidized environment to sustain aerobic metabolism and a source of particulate or dissolved carbon and nutrients (Fig. 1C). When reducing conditions occur in groundwater (Dahm *et al.*, 1987; Johnston & Naiman, 1987), exchange of aerated surface water between the channel and hyporheic zone is required to maintain aerobic metabolism. Triska *et al.* (1989b) attributed primary oxygen transport to advective exchange, defined as the mean transport of surface water which results from localized pressure variations in the channel that force water into the

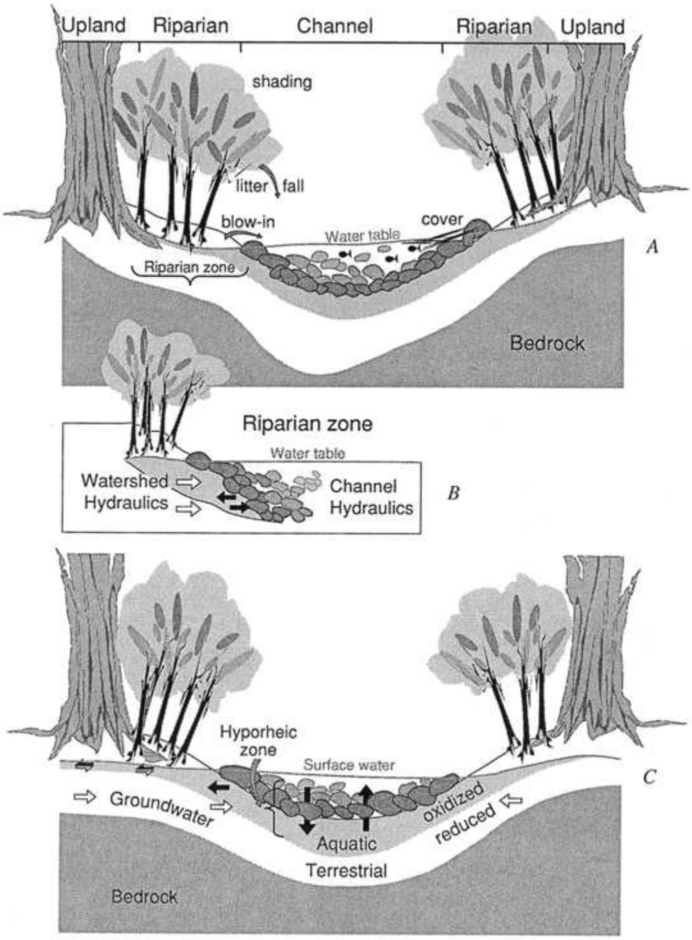

Fig. 1. Schematic diagram of the stream-riparian ecotone in cross section indicating: (A) above-ground aquatic-terrestrial linkages, (B) subsurface hydrodynamic linkages dominated by watershed hydraulics inland (clear arrows) and channel hydraulics streamside (shaded arrows), and (C) subsurface groundwater-surface water exchange, resulting in an oxidized hyporheic zone. Oxidized interstitial waters are viewed as aquatic (surface water) habitat. Reduced interstitial waters are viewed as terrestrial (groundwater) habitat.

subsurface (Vaux, 1962; Savant *et al.*, 1987; Thibodeaux and Boyle, 1987). Surface water (Fig. 1) consists of water currently or previously transported along the exposed surface channel, whereas groundwater has not been exposed to the surface channel. Thus, below ground, the riparian corridor effectively contains two distinct interfaces: (1) an upland-riparian interface where transport is dominated by upland hydrodynamics and movement of water and dissolved solutes is toward the channel, and (2) a streamside interface where movement of water and solutes is bidirectional and strongly influenced by channel hydrodynamics (Fig. 1B).

From a watershed perspective, the hyporheic zone is the edge of the channel or floodplain. As a result, the lateral-vertical dimensions and interstitial volume of the hyporheic zone are a dynamic product of the landscape's physical properties that include the watershed area, the groundwater contributing area, the hillslope and channel gradient, and annual precipitation. From a channel perspective, the depth and lateral extent of advective exchange (i.e. hyporheic zone) within localized reaches are determined by geomorphologic features of the surface channel such as roughness, permeability and pool-riffle sequence. Nutrient cycling studies at fine scales (e.g. reach) are advantageous because they afford an opportunity to examine biological processes within a qualitatively-defined hydrologic setting.

This report is a compilation of experiments done over several years in a third-order stream at summer base flows. These experiments were designed to examine the exchange of flow between the channel and lateral hyporheic zone and the role of water exchange in nitrogen cycling at the groundwater-surface water interface. This report is divided into four sections that examine: (1) the hydrologic exchange of water between the riparian ecotone and the riverine ecosystem that defines the hyporheic zone, (2) the chemical gradients of dissolved gases, organic nutrients and inorganic nutrients that result from hydrologic exchange, (3) the biotic processes, especially those related to nitrogen cycling, that occur along physical-chemical gradients, and (4) the lithologic properties that control the flux of dissolved inorganic nitrogen to the channel. We close with a conceptual model describing the interaction of flows, nutrients, biological processes and lithology on nutrient flux across the hyporheic zone.

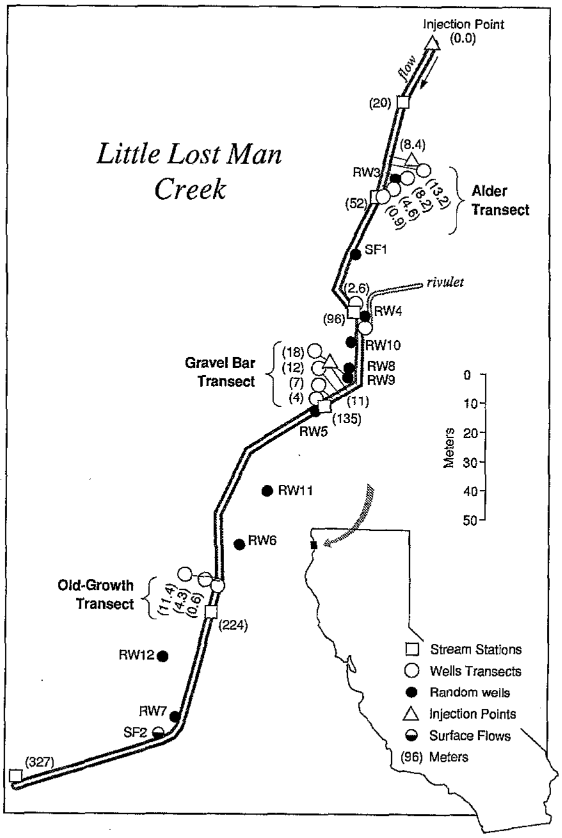

Fig. 2. Map of the experimental reach at Little Lost Man Creek, California, USA. Stream and bankside stations are coded as indicated.

Methods

Site description and techniques

Linkages between the riparian ecotone and the stream channel were studied at Little Lost Man Creek, a small, gravel-cobble stream in northwestern California, USA (Fig. 2). Precipitation in the watershed is highly seasonal, with wet winters and dry summers. As a result, base flow steadily declines May–October. The streambed is highly permeable and overland flows are minimal compared with seepage through the porous soils. The stream is oligotrophic, with very low background concentrations of biologically-influenced nutrients ($NO_3 + NO_2$, 25–40 μg N l^{-1}; NH_4, 6 μg N l^{-1}; PO_4, 9–13 μg P l^{-1}). Biotic production is nitrogen limited relative to atomic N:P ratio (Redfield *et al.* 1963).

Water chemistry was studied along a 327 m reach of channel and at the top of the water table in the riparian zone. Sampling protocol and techniques are presented in detail in Duff & Triska (1990). Lateral transport of stream water was estimated using water table wells installed in the riparian zone, at distances of 1–20 m from the wetted channel. Wells were of two types: (1) temporary sites that consisted of randomly-placed pits dug to the water table (random wells), and (2) permanent transects of cased wells installed at four bankside habitats. Cased wells were located along: (1) the base of a hillslope dominated by an old-growth stand of redwood *Sequoia sempervirens* Endl. (old-growth transect), (2) the base of a hillslope clearcut in 1965 co-dominated by nitrogen fixing *Alnus rubra* Bong. (alder transect), (3) the junction of the channel and a small tributary seepage that increased discharge < 1% (rivulet), and (4) a bankside gravel deposit (gravel-bar transect). Well construction and installation are described elsewhere (Triska *et al.*, 1989a, 1989b; Duff & Triska, 1990; Triska *et al.* 1990).

The role of hydrologic exchange on nutrient cycling was studied using solute injection experiments both in the stream channel and lateral subsurface flows (Fig. 2). The experiments occurred over several summers and involved the same general protocol. The stream injections included an upstream injection point in the channel surface, a turbulent mixing reach, and paired stations either upstream-downstream or a downstream station-riparian well combination. Injections in the lateral hyporheic zone included a subsurface injection well and one downstream sampling well. Tributary inputs were an insignificant component of discharge, and discharge was nearly constant during the experiments. The injectate solutions typically consisted of both a conservative tracer (nonreactive biologically and lithologically) and a biotically reactive (uptake) or sediment reactive (sorption) solute. Preferred conservative tracers included chloride and bromide, although sulfate was used with some experiments (Triska *et al.*, 1990).

Injection experiments

When an injection begins, the hydrologic tracer is rapidly transported through the mixing reach and the concentration raised to a maximum plateau at the upstream station (Fig. 3A, Head). At the downstream station (Base), the time interval for

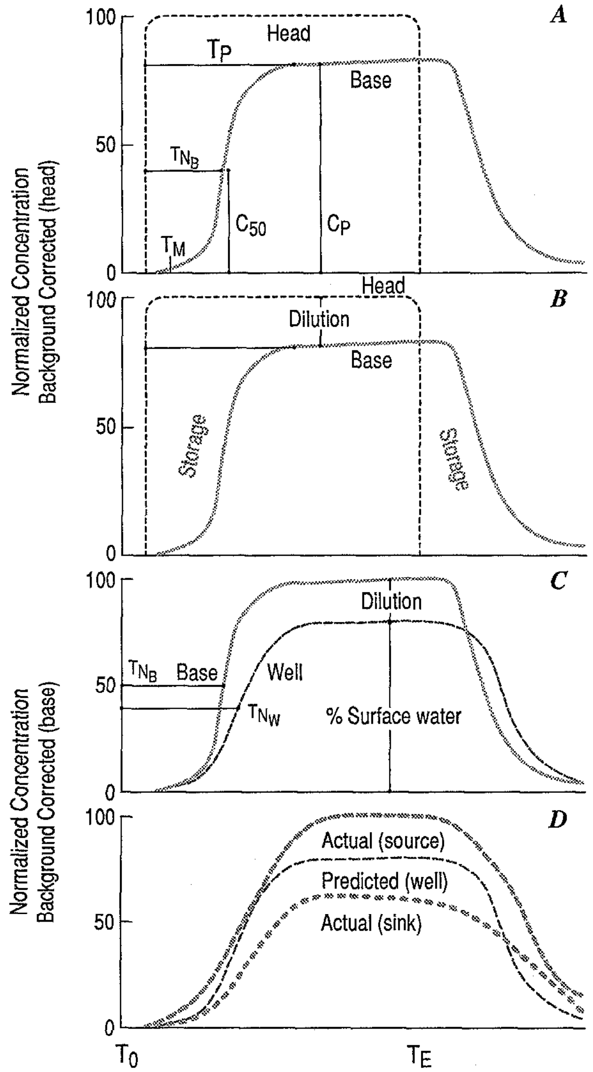

Fig. 3. Idealized time-concentration plots of injected conservative (A–C) and reactive (D) solutes that determine hydrologic and biologic properties of a stream reach. T_o = time a solute injection begins. T_E = time a solute injection ends. Background-corrected normalized concentrations are based on the plateau concentration at the top of the reach (Head) as 100% (A–B) or at the terminus of the reach (Base) as 100% (C–D). (A) T_M = minimum travel time for a solute to be transported from Head to Base, T_P = time required to reach plateau concentration (Head = T_{Ph}, Base = T_{Pb}). T_{Nb} = Nominal travel time between Head and Base (interval for concentration to reach 50% of C_{Pb}). (B) Dilution = proportional reduction of normalized concentration at Base due to groundwater input. Storage = cumulative proportion of injectate transiently retained between Head and Base. (C) Comparison of concentration time plots between a channel station and an adjacent inland well. T_{N_W} = nominal travel time to the well. Normalized plateau concentration in the well is equal to the contribution of surface water. The difference between C_{Pb} and C_{Pw} is the groundwater contribution. (D) Comparison of normalized concentration of an injected reactive solute to the conservative tracer (predicted). Concentrations in excess of predicted indicate sources of reactive solute; concentrations lower than predicted indicate sinks for the reactive solute.

tracer concentration to first rise above background is the minimum travel time (T_M). The concentration of tracer at Base eventually reaches a plateau (C_P) at time (T_P). The time to attain 50% of the background-corrected plateau concentration on the rise, or to decrease to 50% from the background-corrected plateau concentration on the fall, is the nominal travel time (T_{Nb}). T_P is longer than T_M due to longitudinal dispersion and storage in the hyporheic zone (Bencala, 1984; Jackman *et al.*, 1984). With sufficient samples, C_P is reached asymptotically and can be estimated. C_P is lower at Base than at Head due to groundwater input (dilution). Once C_P is reached, discharge (Q_h) can be estimated at Head then at Base (Q_b) using their respective C_P values (Table 1). The difference between (Q_h) and (Q_b) is groundwater input.

Corrected for groundwater dilution, total storage of conservative solute in the channel and hyporheic zone can be estimated by integrating the area labeled 'storage' (Fig. 3B). Disappearance of tracer into storage after T_o should be equivalent to solute elution from storage after T_E. If significant tracer enters the hyporheic zone and travel paths are complex, tracer concentrations may require a considerable period of time to return to background, resulting in a concentration 'tail'. Storage at plateau concentration consists of solutes stored in channel features that range from rapid flow down the thalweg to dead zones in nearly stagnant waters of the hyporheic zone. To obtain estimates of actual interstitial storage, the amount of tracer injected during one nominal travel time can be subtracted from total storage.

The depth, lateral extent and timing of hydrologic exchange to various hyporheic locations is determined by comparing the nominal travel time of the conservative solute between a hyporheic well (T_{Nw}) and the channel location (Base) (T_{Nb}) (Fig. 3C). The nominal travel time to the hyporheic location provides a qualitative index of the permeability of channel sediments. Flow through the lateral wells comes from two sources: (1) surface water from the channel, and (2) groundwater from upland terrestrial environments. As a result, the plateau concentration of the well is less than that of the nearby channel, and the proportion of surface water in the well (percentage surface water) can be calculated (Table 1). When both a reactive solute and tracer are injected into the channel, the transport response

Table 1. Equations used to calculate the parameters from injection studies at Little Lost Man Creek.

Discharge:

$$Q_o = \frac{C_i - C_b}{C_p - C_b} \times Q_I \qquad (1)$$

C_i = Concentration of tracer in injectate
C_b = Background concentration of tracer at site
C_P = Plateau concentration at site
Q_I = Flow rate of injectate

Normalized concentration:

$$C_n = \frac{C_t - C_b}{C_p - C_b} \times 100 \qquad (2)$$

C_t = Concentration at time t
C_b = Background concentration
C_P = Plateau concentration at Head

Percentage surface water:

$$\%\,\text{Surfacewater} = \frac{C_w - C_g}{C_s - C_g} \times 100 \qquad (3)$$

C_w = Tracer concentration in the well
C_g = Tracer concentration in groundwater
C_s = Tracer concentration in the stream

Predicted reactive solute concentratrion at a hyporheic well:

$$R_{wt} = R_{wb} + (C_{wt} - C_{wb}) \times \frac{(R_{st'} - R_{wb})}{(C_{st'} - C_{wb})} \qquad (4)$$

w = well
s = stream
t = time t
t′ = time t − nominal travel time
b = background concentrations
R = reactive solute
C = conservative solute

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of the tracer serves as a basis to determine the fate of the reactive solute (Fig. 3D). Three fates are possible: (1) If the normalized concentration of the reactive solute is identical to the conservative tracer, then either no reaction occurred or uptake plus sorption equaled regeneration. (2) If the reactive solute has a higher normalized concentration than that predicted from the tracer, then that site in the hyporheic zone is a source for the reactive solute. (3) If the reactive solute has a lower concentration than that predicted from the tracer, then that hyporheic location is a sink for the reactive solute. By sink we imply a net loss of the reactive solute from solution either through biotic transformation or sorption to sediments. Nitrate undergoes insignificant exchange with most sediments; therefore, gain or loss of nitrate is due to biotic processes. Both biotic transformations and sediment sorption can be significant for cations such as ammonium.

Results and discussion

Hydrologic exchange

At the stream edge of the riparian ecotone, transport of water is the dominant observable property of a channel. Despite dominance by transport, the retentive properties of a channel enable the stream to function as biological habitat. Retention is controlled both by physical and biotic mechanisms. Biotic mechanisms include uptake of dissolved constituents and consumption of particulate organic matter by riverine flora and fauna. Physical retention is controlled by the surficial geomorphology of the channel that includes deep pools, debris dams and bed roughness. Physical retention ranges from the long-term, as in burial of particulates for periods of years (Cummins *et al.*, 1983), to the short-term, as in transient storage of solutes in zones of slow-moving water. Even transient storage for periods of hours is biologically-important because such scales are consistent with biotic transformation of solutes in transport. The sequential uptake and remineralization of nutrients results in alternating transport and retention phases, which have been called spiralling (Newbold *et al.*, 1983; Elwood *et al.*, 1983; Newbold, 1987).

Most of the water and dissolved nutrients transported through a reach reflect upstream input. However, there also is an incremental addition of groundwater within a reach. During transport through the reach, groundwater and stream water exchange vertically in the subchannel and laterally at sites far under the riparian zone. Where subchannel exchange occurs, dissolved solutes in groundwater become available to hyporheic biota and subsequently to the surface water community. Dissolved solutes and particulates in surface water also have an opportunity to be either transported to hyporheic uptake sites or transiently stored by physical mechanisms in the subsurface.

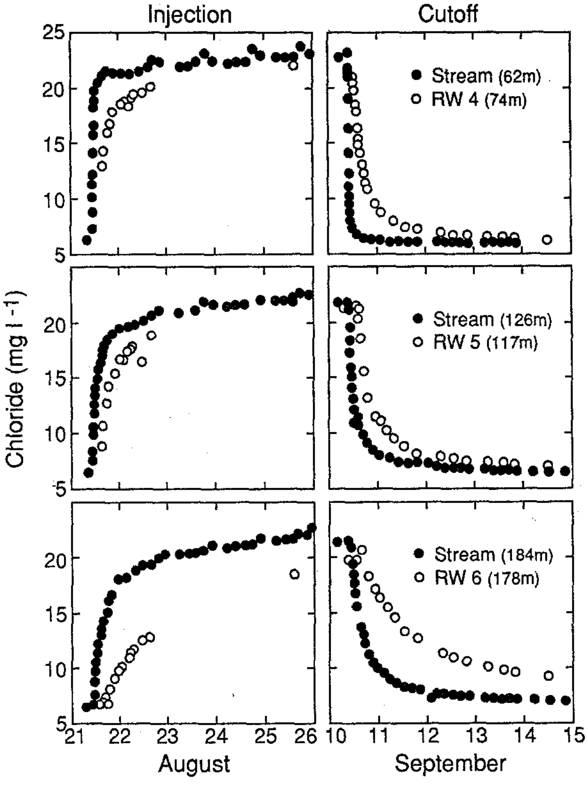

Fig. 4. Left: (○) rise in tracer concentration in random wells RW4, RW5 and RW6 compared with those at the nearest channel location (●) after the start of solute injection (To = 1000 August 21). Right: decline in tracer concentration in the same wells after cut-off (T_E = 1000 September 10) (Triska *et al.*, 1989b).

The magnitude of hydrologic exchange between the channel and the hyporheic zone was estimated at Little Lost Man Creek by using conservative tracers (Fig. 3A, Table 1). Injection studies indicated that exchange of surface and hyporheic waters was not directly related to distance from the channel. Lateral transport was usually rapid to zones within 5 m of the wetted channel, and bankside water-table wells commonly attained concentrations equivalent to that of channel water (Fig. 4). For example, in RW4 and RW5 (3.5 and 1.0 m, respectively, from the channel), tracer response was observed within 8 hours, indicating rapid mixing of channel water with hyporheic water. A similar response was observed after solute injection was cut-off. Within three days, added chloride was nearly cleared by exchange with channel water. However, at RW6, three meters inland, chloride took longer both to arrive and clear (Fig. 4). After 5 days of continuous injection, chloride in well water was not equivalent to that of channel water. Even after 21 days of continuous injection, well water was only about 90% of channel water concentration, indicating steady input of groundwater from the riparian ecotone. After cutoff, chloride decreased slowly in the well compared to the channel. Chloride concentration at RW6 remained significantly higher than background for 12 days following cut-off.

Transport time relative to the distance of inland transport was estimated from the nominal travel time calculated after cutoff (Table 2). Random wells closest to the stream generally had the shortest travel times, although there were some exceptions. For example, RW3, which was 4.3 meters from the wetted channel, had the shortest nominal travel time (3.3 h), whereas RW5, 1.0 m from the wetted channel, had a travel time more than twice as long. With one exception (RW10), all wells > 5.0 m from the channel had nominal travel times > 45 h. Ten meters from the channel, nominal travel time ranged from 121–450 h. Nonetheless, effective exchange occurred at these locations, as indicated by the high percentage of surface water. High variation in nominal travel time presumably indicates that permeability of the sediments was highly heterogeneous throughout the hyporheic zone.

Although hydrologic properties of individual wells vary, storage can be estimated as a unit-property of the reach (Fig. 3B). After the first 10 days of a 21-day chloride injection in a 327 m reach of Little Lost Man Creek, Triska *et al.* (1989b) reported that total chloride (tracer) input

Table 2. Physical parameters of random well sites (RW) and subsurface flows (SF) during a 21 day injection in Little Lost Man Creek.

Well #	Longitudinal distance (m)	Bank[1] side	Lateral distance	Nominal travel time (h)	Percentage surface water[2]	
					Day 10	Day 21
SF1	80	L	0	6.1	93	
SF2	277	R	0	24.9	93	
RW3	37	R	4.3	3.3	97	93
RW4	74	L	3.5	5.6	96	96
RW5	117	R	1.0	8.7	102	96
RW6	178	L	3.0	22.6	93	87
RW7	265	R	1.8	33.6	88	79
RW8	126	R	5.0	45.8	–	92
RW9	129	R	5.0	134.0	–	60
RW10	108	R	5.0	9.2	–	93
RW11	169	L	10.0	450.0	–	47
RW12	247	R	10.0	121.0	–	76

[1] Right bank (old growth forest) left bank (clearcut 1965).

[2] Continuous injection of chloride for the period indicated. A storm occurred on Day 14.

exceeded output by 11.1 kg. Instantaneous storage of this dissolved load consisted of many interacting components that included solute dissolved in the fastest flows, solute delayed in midchannel pools or along stream margins, and solute stored in the hyporheic zone. The mass of tracer transported in one nominal travel time (4.7 kg) was subtracted to correct for the maximum solute load in transport. By mass balance, 6.4 kg of chloride was attributed to storage. Even if well water was entirely surface water, transient storage volume in the hyporheic zone was nearly 60% of the instantaneous water volume for the reach (channel plus hyporheic zone). Thus, the hyporheic volume exceeded the channel volume. This conclusion was supported by Bencala (1984), who used simulation modeling with the same data set to estimate solute transport processes at Little Lost Man Creek. He found that simulations lacking subchannel storage inadequately represented solute transport. Estimates of storage-area cross-sections equivalent to 30%–250% of stream-area cross-sections were required to effectively simulate tracer transport through four successive subreaches of the channel.

Chemical gradients

Solute concentration gradients that include DO, nitrate, ammonium, and DOC are formed across the riparian ecotone when chemically reduced groundwater and oxidized surface water mix in the hyporheic zone.

Table 3. Distance (D), nominal travel time (NTT), surface water composition (SW), and background concentration of biologically-influenced solutes in the stream and hyporheic habitats of Little Lost Man Creek, August, 1984. NA = not applicable, NS = not sampled.

Station	D	NTT	SW	O_2	NO_3	NH_4	DON	DOC
	m	h	%	mg l^{-1}	μg N l^{-1}			mg l^{-1}
(A) Gravel bar								
Stream	0	1	100	9.5	19	4	47	2.0
Well 1	4.0	7	96	8.5	52	3	47	1.3
Well 2	7.0	8	94	7.6	45	2	40	1.4
Well 3	12.0	50	78	5.2	55	1	31	1.2
Well 4	18.0	140	25	2.5	7	240	NS	5.3
(B) Alder riparian								
Stream	0	0.3	100	9.5	17	4	48	1.7
Well 1	0.9	1	97	8.9	20	3	38	2.0
Well 2	4.6	44	34	3.3	93	3	34	1.7
Well 3	8.2	124	8	3.0	135	122	34	2.7
Well 4	13.2	NA	0	1.5	86	21	58	4.3
(C) Old-growth riparian								
Stream	0	2	100	9.5	20	5	37	1.5
Well 1	0.6	3	100	8.0	26	4	45	2.0
Well 2	4.3	7.5	100	7.2	42	1	38	1.9
Well 3	11.4	NA	0	1.0	6	14	83	4.4
(D) Tributary-stream junction								
Rivulet	NA	NA	0	9.0	38	6	117	1.7
Sub-surface	1.0	89	14	1.8	10	95	77	10.6

At Little Lost Man Creek, DO concentration was inversely related to nominal travel time and distance from the wetted channel. DO typically was saturated in channel water, and nearly anoxic at sites isolated from exchange with surface water (Table 3). The gravel bar sediments were the most permeable of the three bankside transects. Surface water was effectively transported up to 18 m from the wetted channel and DO ranged between 2.5 and 9.5 mg l^{-1}. At both the alder and old-growth riparian transects, lateral penetration of surface water was less than 10 m and, correspondingly, DO concentrations were lower. Linkage between channel water advection and DO concentration in hyporheic waters was established by comparing percentage surface water with DO concentration between the gravel bar transect and the alder riparian transect (Fig. 5). High permeability of the gravel bar resulted in a subsurface habitat composed of $>75\%$ stream water and DO concentrations >5.0 mg l^{-1} up to 12 m inland. At the alder riparian transect, subsurface waters 5.0 m from the wetted channel were less than 35% surface water and DO was <3.0 mg l^{-1}.

Nitrate was typically higher in aerobic interstitial waters than in either the channel or groundwater (Table 3). This was the case along all three transects. Nitrate was approximately 20 μg N l^{-1} in channel water, and 2.0–2.5 times higher in the hyporheic zone of the old-growth and gravel bar sites. Nitrate was more than 6 times higher than channel concentration in the hyporheic zone of the alder riparian transect.

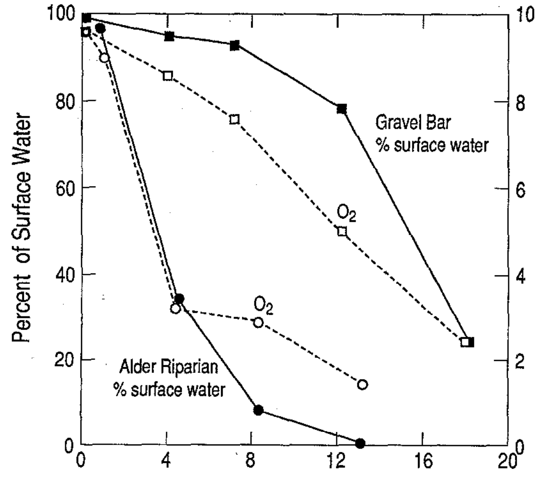

Fig. 5. Comparison of dissolved oxygen concentration and percentage surface water ln the hyporheic zone in relation to distance from the wetted channel.

Coinjection of chloride and nitrate demonstrated effective inland transport of nitrate. Both solutes were injected into the stream at the head of a 327 m reach and sampled at 12 sites; ten random wells and two subchannel flows that emerged as springs adjacent to the wetted channel but within the incised channel (Fig. 2). The high concentration of chloride indicated that these flows consisted of surface water; however, the length and location of their respective flow paths are unknown. The fate of nitrate at the random well locations was determined by comparing observed nitrate concentration with that predicted from chloride assuming absence of either uptake or regeneration (Table 1). Of eight wells with sufficient data for statistical analysis, four had mean observed nitrate concentrations significantly higher than mean predicted concentrations (Table 4), two had mean observed nitrate concentrations significantly lower than mean predicted and two had mean nitrate concentrations not significantly different from predicted. Statistical significance (95% confidence level) was determined with a t-test on the signed ranks (Wilcoxon signed ranks test of Iman & Conover, 1983). The fate of injected nitrate at a specific hyporheic location was related to its distance from the wetted channel (Fig. 6). In the box plot, apparent regeneration or loss is the difference between predicted and observed nitrate concentrations (either above or below zero on the y axis). Wells 2.0–4.2 m from the wetted channel had significantly higher median nitrate concentrations than predicted. The exception, RW5, only 1.0 m from the bank, was significantly lower than predicted. Wells >4.3 meters from the channel were typically sinks for injected nitrate. These wells also had the lowest proportion of surface water.

Ammonium concentration typically increased with distance from the wetted channel as dis-

Table 4. Difference between mean measured nitrate and mean calculated nitrate in random wells (RW) and subsurface flows (SF) along the experimental reach of Little Lost Man creek. The significance of the difference, either positive, $H_0(2)$, or negative, $H_0(3)$, was determined at locations where the null hypothesis, $H_0(1)$, was rejected.

Sta	*n*	Mean[1] diff; (μg N l^{-1})	t-Test on signed ranks					
			$H_0(1)$: $\mu_{meas} = \mu_{calc}$		$H_0(2)$: $\mu_{meas} > \mu_{calc}$		$H_0(3)$: $\mu_{meas} < \mu_{calc}$	
			Result	p-value	Result	p-value	Result	p-value
SF1	75	− 4	Diff.	0.000			Loss	0.000
SF2	52	+ 12	Diff.	0.000	Gain	0.000		
RW3	21	− 27	Diff.	0.000			Loss	0.000
RW4	36	+ 6	Diff.	0.000	Gain	0.000		
RW5	29	− 35	Diff.	0.000			Loss	0.000
RW6	22	+ 6	Same	0.088				
RW7	17	+ 10	Diff.	0.022	Gain	0.011		
RW8	19	− 19	Diff.	0.011			Loss	0.006
RW9	15	− 117	Diff.	0.000			Loss	0.000
RW10	11	+ 3	Same	0.680				

[1] A negative number represents apparent loss of nitrate from the water.

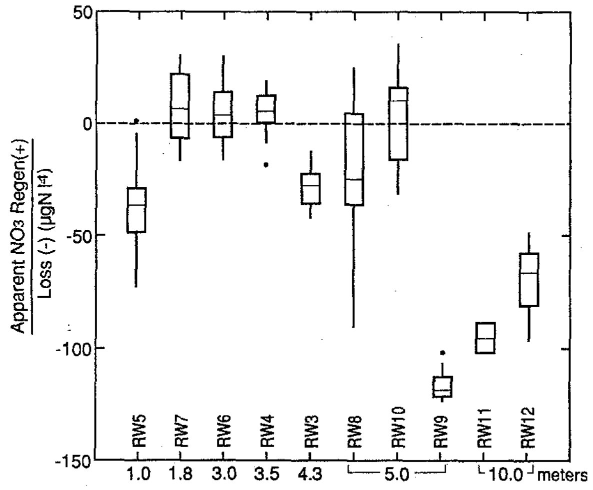

Fig. 6. Apparent loss (−) or regeneration (+) during transport of nitrate-nitrogen at Little Lost Man Creek. Wells are graphed in order of increasing distance (in meters) from the wetted channel. Regeneration or loss is the difference between calculated and measured nitrate concentration (zero on the y-axis). The box is drawn from the 25th percentile to the 75th percentile of differences actually observed. The horizontal line is the median difference between predicted and observed nitrate concentrations. The total height of the box from the 25th to 75th percentile is the interquartile range (IQR). Lines extending either above or below the box show the largest absolute differences between calculated and measured concentration ≤ the upper (above) or lower quartile (below) plus 1.5 times the IQR. Differences lying outside this range are recorded as points (Triska *et al.*, 1989b).

solved oxygen decreased (Table 3). Ammonium concentration was highest at the most inland gravel bar well (240 μg N l^{-1}) and beneath the small tributary (95 μg N l^{-1}). In the alder and old-growth transects, we observed three- to eight-fold differences in ammonium concentration between bankside and inland wells. These results are consistent with previous results from the same site (Triska *et al.*, 1989b, 1990). Dahm *et al.* (1987) similarly reported a steep concentration gradient for ammonium among surface water (0.023 mg l^{-1}), aerobic interstitial water (0.334 mg l^{-1}) and anaerobic interstitial water (1.887 mg l^{-1}) at Sulfur Creek, Oregon, USA.

Dissolved organic nitrogen (DON) lacked the steep concentration gradient of nitrate or ammonium. DON concentrations ranged between 30 and 50 μg N l^{-1} at most locations. The highest DON concentrations were found in wells dominated by groundwater. Steeper concentrations might have been observed if any of our wells had been far enough inland to yield samples that consisted of anaerobic groundwater. Dahm *et al.* (1987) report DON concentrations of 23 μg l^{-1} in stream water, 300–400 μg N l^{-1} in aerobic interstitial water and 460–4100 μg l^{-1} in anaerobic interstitial waters.

DOC in stream water and all hyporheic areas dominated by stream water ranged between 1. 2 and 2.0 mg l^{-1}. DOC at sites dominated by groundwater (>75%) ranged between 2.7 and 5.3 mg l^{-1}. The highest DOC concentrations were in surface and interstitial waters of the tributary rivulet. Our findings are within the general range of DOC concentrations reported by Dahm *et al.* (1987), although in anaerobic waters beneath a debris dam pond, they report DOC as high as 82.6 mg l^{-1}. Crocker & Meyer (1987) also found interstitial DOC concentration consistently higher than channel DOC in a two year study of a North Carolina, USA, stream. Wallis *et al.* (1981) found that saturated-zone DOC, in the vicinity of two springs, was 5.9 mg l^{-1}, twice as high as that of adjacent surface water. Mickelburg (1984), however, concluded that subsurface gravels can be a major site of DOC disappearance. Finally, Rutherford & Hynes (1987) concluded that subsurface water neither consistently diluted nor enhanced stream water concentrations of DOC. At some locations, DOC concentration was random with depth, whereas at other locations, DOC was consistently higher at the deepest and shallowest locations. The variation in findings by these authors may be a function of the proportion of groundwater to surface water in subsurface locations. Unfortunately, these proportions were not estimated in any of the above studies.

Biological processes

In the preceding discussion we related chemical gradients to hydrologic exchange. In reality, the observed chemical gradients are an interactive result of the hydrologic properties of the hillslope and channel, and the biologic processes that transform solutes during transport (Fig. 7).

In hyporheic sediments, microbial processes and rates are controlled by the availability of DO, DOC, DIC (dissolved inorganic carbon) and DIN (dissolved inorganic nitrogen). Aerobic metabolism, the basis of virtually all stream studies,

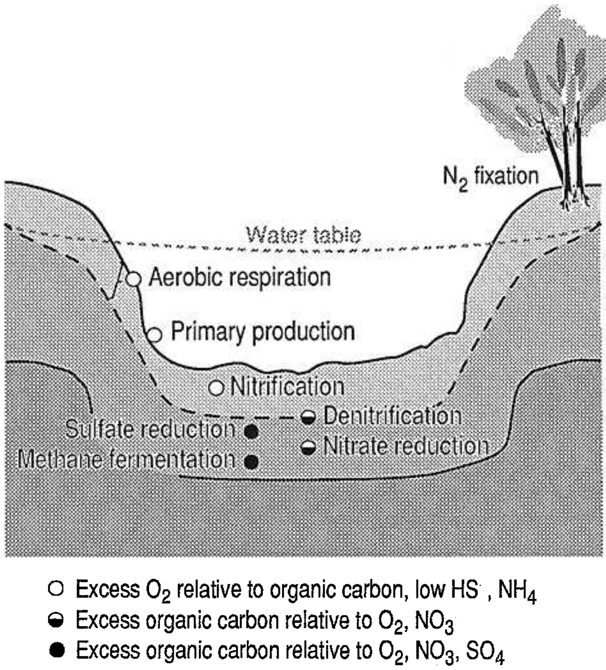

Fig. 7. Major biological processes in reduced groundwater in the riparian ecotone (dark grey), oxidized waters of the hyporheic zone (medium grey), and surface water (unshaded).

characteristically dominates microbial activity in low-ammonium environments with excess DO relative to organic carbon. One form of aerobic metabolism that is often overlooked is nitrification. Nitrification may be either chemolithotrophic or heterotrophic, although in nature the former process dominates ammonium oxidation (Keeney, 1973). The conversion of ammonium to nitrate provides an easily transported source of nitrogen to stream biota. It also is a sink for oxygen, contributing to low-oxygen hyporheic waters. As DO is depleted, facultative anaerobes switch from oxygen to nitrate for the terminal electron acceptor in the oxidation of organic carbon. Nitrate can be reduced completely to dinitrogen or, under some conditions, to ammonium. The former process, denitrification, is an important sink for nitrate because it results in total removal of nitrogen from the system. Strictly anaerobic processes, such as sulfate reduction or methane fermentation, occur under more extreme reducing conditions. These processes dominate metabolism beyond the effective zone of surface water exchange and, therefore, would be considered terrestrial functions of the riparian ecotone.

Near the aerobic-anaerobic interface, hydrologic advection of surface water is inadequate to replenish DO. In this region of the hyporheic zone, the interactions of hydrologic, physical and biotic processes establish an effective hyporheic boundary, the terrestrial-aquatic interface. This boundary is dynamic, readily shifting temporally in response to either hydrologic or metabolic changes, and spatially due to variations in bankside permeability. The aerobic-anaerobic interface is characterized by an excess of organic carbon relative to either DO or nitrate. The flexibility of facultative anaerobes to use both DO and nitrate as terminal electron acceptors makes them dominant here. Heterogeneity in DO concentration also can be caused by microbial metabolism in pockets of organic matter stored in the hyporheic zone, forming patches of oxygen-depleted habitat in an otherwise oxidizing environment (Cummins *et al.*, 1983).

As an interface between oxygen-saturated channel water and oxygen-depleted groundwater, the hyporheic zone is a region of intense nitrogen cycling, especially between denitrification and nitrification. Denitrification is controlled by the oxygen, carbon and nitrogen concentrations, which have distinct gradients in the hyporheic zone of Little Lost Man Creek. To assay for denitrification, subsurface sediments were harvested from wells in the old-growth and alder transects (Fig. 8). Sediments were slurried with well water and incubated under anaerobic conditions without added nutrients, with nitrate alone and with nitrate plus glucose. Denitrification potential (measured by the acetylene block technique) increased with distance from the channel. In slurries without added nutrients, the denitrification potential was higher along the alder transect than along the old-growth transect, presumably due to higher background nitrate (Table 3). Addition of nitrate enhanced the denitrification potential at all locations. The low response in the channel sediments was probably due to the absence of con-

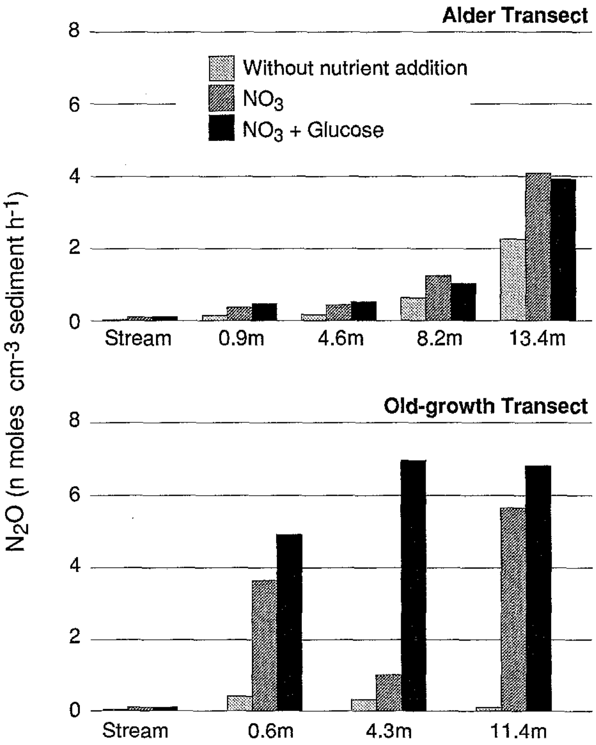

Fig. 8. Spatial gradients of nitrous oxide formation rates in sediment slurries incubated under various nutrient treatments from two bankside habitats (Duff & Triska, 1990).

stitutive denitrifying enzymes. Nitrate amendment enhanced nitrous oxide formation to a greater extent in slurries from the old-growth transect than from the alder transect. Adding glucose in addition to nitrate had little effect over nitrate alone with one exception, the 4.3 m well at the old-growth transect. DOC addition alone typically failed to promote the process (Duff & Triska, 1990). Although background DOC was low at most locations, it tended to be significantly higher at nearly anoxic sites, where denitrification potential was the highest. As a result, DOC rarely limits denitrification at Little Lost Man Creek. Rather, denitrifying activity is limited primarily by nitrate at locations where DO is consistently low, and by DO at locations where nitrate concentration is consistently high. These findings are similar to those of Pinay and Decamps (1988) across the riparian zone of the River Louge.

In situ denitrifying activity was demonstrated under field conditions. An injectate solution that consisted of stream water amended with nitrate and acetylene was injected directly into a subsurface flow path at the alder transect, 8.4 m inland from the stream channel (Fig. 2). Nitrous oxide concentration was monitored in a well 13 m downflow of the injection well. The leading edge of the injected nitrate traveled through the subsurface riparian zone in less than 5.5 h. Nitrous oxide accumulated in the presence of acetylene at an increasing rate as nitrate concentration increased from 10 to 40 μmoles l^{-1} over 24 hours (Fig. 9). Nitrous oxide continued to increase but at a slower rate over the next 24 hours before cutoff. The experiment indicated that the indigenous bacterial population was capable of transforming nitrate to nitrous oxide at anaerobic microsites under oxic background and natural hydrodynamic conditions in the hyporheic zone.

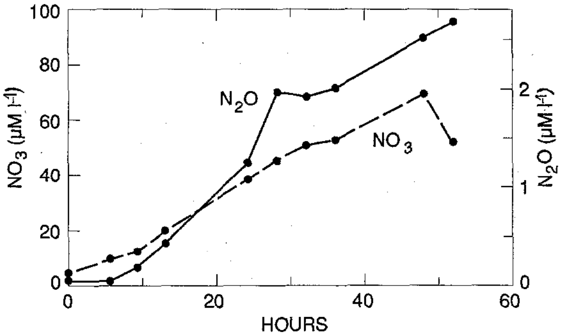

Fig. 9. Nitrate and nitrous oxide concentration 13 meters downgradient during a 48-hour nitrate + acetylene co-injection in a hyporheic flow 8.4 m inland from the wetted channel (Duff & Triska, 1990).

Nitrification, the oxidation of ammonium to nitrate, is promoted by conditions that are not conducive for denitrification: (1) oxygen, (2) dissolved inorganic carbon (DIC), and (3) ammonium (energy source). DIC is rarely limiting in the hyporheic zone at Little Lost Man Creek because of continuous aerobic respiration and atmospheric exchange with channel water. Like denitrification, nitrification rates in the field are regulated by a balance of opposites: the DO gradient, which decreases with distance from the channel, and the ammonium gradient, which decreases with distance toward the channel. Nitrification assays were conducted at summer base flows using sediment slurries that consisted of 20 cm^3 of sediment and 100 ml of stream water amended with DIC. Selected flasks were incubated with and without ammonium plus phosphate (Fig. 10). Nitrate production in slurries from wells closest to the channel ($<$4.6 m) was an order of magnitude higher at the alder transect than at the old-growth transect. Nitrification potential decreased with distance from the stream channel at the alder transect. Ammonium amendment enhanced nitrate production in slurries from all locations. When nitrapyrin, an inhibitor of ammonium oxidation, was added to slurries nitrate production was not observed (data not shown). During August, when water from the most inland wells is nearly anoxic, nitrate production was not observed in slurries even though they were incubated aerobically with ammonium. Thus, under summer base-flow conditions, nitrate observed in channel water is most likely produced by nitrification as ammonium-rich groundwater is transported through hyporheic sediments adjacent to the channel.

Nitrification potential of the hyporheic zone was demonstrated in a coinjection study. Ammonium $[(NH_4)_2\ SO_4]$ and sulfate $[MgSO_4]$ were

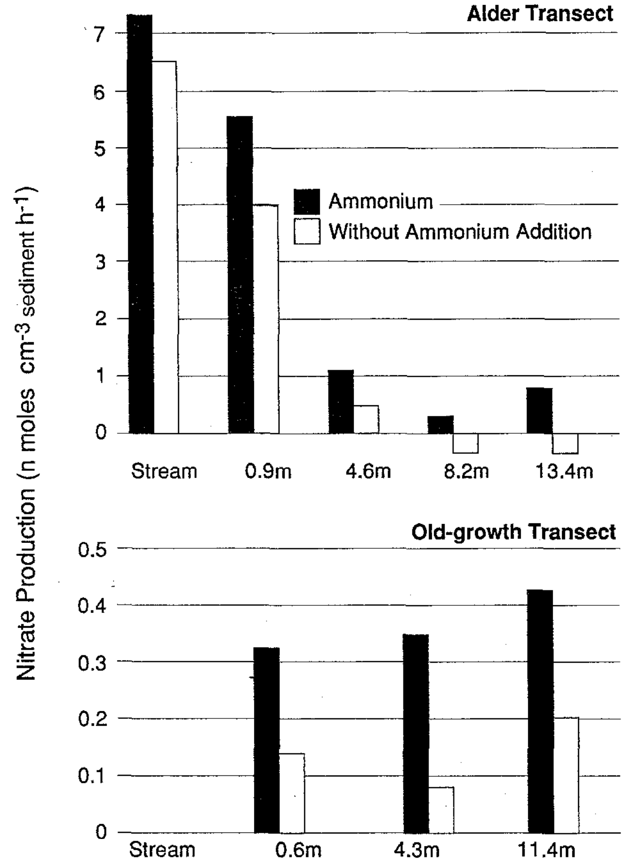

Fig. 10. Spatial gradient of nitrate production rate in sediment slurries incubated with and without ammonium, from two bankside habitats.

co-injected into a pit approximately three meters upflow of a gravel bar well and 12 m inland from the channel (Fig. 2). Nitrate concentration was assayed during ammonium transport under natural hydrologic conditions (Triska *et al.*, 1990). Sulfate concentration rose within three hours (Fig. 11A). Co-injected ammonium was not detected in early samples, and within the first two days most ammonium was removed from the subsurface flow. Nitrate concentration increased about 12% within hours of the ammonium amendment (Fig. 11B), from approximately 75 μg N l^{-1} to a maximum of 130 μg N l^{-1} during the eight-day injection. Lack of a nitrate increase in an adjacent control well confirmed a nitrification response to ammonium amendment. The amount of ammonium converted to nitrate was only a small proportion of total retention. Thus, other retention processes, such as sorption to sediment, were factors in ammonium transport.

Lithologic factors

Ammonium is readily sorbed and exchanged on clay minerals and clay-humic complexes (Boatman & Murray, 1982). The degree of ammonium

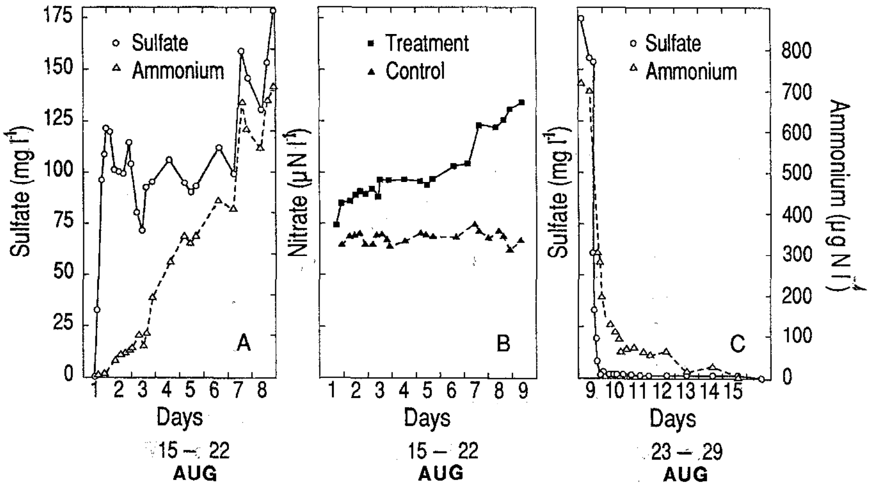

Fig. 11. Concentration of sulfate and ammonium during rise (A) and fall (C) of a 9-day co-injection in a hyporheic flow path. The injection site was 3 m upflow from the sampling well, and 12 m inland from the wetted channel at the gravel-bar transect. (B)-rise in nitrate concentration in response to the ammonium injection compared with an adjacent unamended flow path.

sorption to sediment is dependent on mineralogic properties of the sediments, particularly the cation exchange capacity. The surface of clay minerals are the predominant sites of cation exchange, and all clay minerals have some exchange capacity although it is highly variable depending on the clay's chemical structure and other factors such as pH, the sorbing ion and the amount of organic coating on the sediment (Drever, 1982). X-ray diffraction studies of sediment from Little Lost Man Creek indicated a predominance of largely non-sorptive minerals, particularly quartz and plagioclase. However, approximately 30% of grains smaller than 1 mm were clay minerals that are sorptive for ammonium ions, including illite-mica and chlorite-smectite (Table 5).

Ammonium injected into the subsurface gravel bar was rapidly sorbed to sediments in the initial stage of the injection, and was readily desorbed after cutoff (Fig. 11C). The sulfate tracer declined to background concentration rapidly after cutoff, whereas ammonium had a two-phase desorption that lasted for several days. Initial rapid desorption of ammonium supported nitrate production at pre cut-off rates for eight hours. Desorption then continued at slower rates allowing nitrate concentration to remain elevated for six days after cutoff. This amount of retention is remarkable considering the high hydrologic conductivity of hyporheic sediments at the site. Closer to the groundwater-surface water interface, where ammonium transport is controlled by upslope hydrodynamics, and grain size is smaller, the retardation factor could be higher.

Table 5. X-Ray diffraction analyses of sediments from the channel of Little Lost Man Creek (Jackman & Ng, 1986).

Size class (mm)	Mineral content of sediments (%)			
	Quartz	Plagioclase	Chlorite/ Smectite	Illite/ Mica
0.25–0.5	52	21	7	20
0.5–0.83	48	23	9	20
0.83–1.0	49	21	8	22
1.0–2.0	49	27	8	16
2.0–6.3	62	25	6	7
6.3–9.5	60	23	7	10

Conceptual model

Examination of the hyporheic zone suggests that the aquatic-terrestrial interface is a complex environment where nitrogen cycling is regulated by interactive hydrologic, chemical, biologic and geologic factors. At the upland edge of the riparian ecotone, hillslope hydrodynamics control the transport rate of groundwater towards the hyporheic zone, whereas at the streamside edge, channel hydrodynamics control bi-directional exchange of water between the stream channel and riparian ecotone. The permeability of bankside sediments also regulates the proportion of stream water and groundwater in the hyporheic zone. Gradients of essential biological elements are formed in the hyporheic zone that include DO, DOC, DON, nitrate, and ammonium. These concentration gradients reflect linkage between the biotic metabolism and hydrodynamics in the hyporheic zone. Lithologic factors, including the sorptive properties of sediments, also regulate availability of DIN (dissolved inorganic nitrogen) to biota.

Our observations of transport, chemistry and biologic processes have resulted in a conceptual model for nitrogen cycling in the hyporheic zone of Little Lost Man Creek (Fig. 12). In anaerobic groundwater, decomposition processes result in high ammonium concentrations compared with

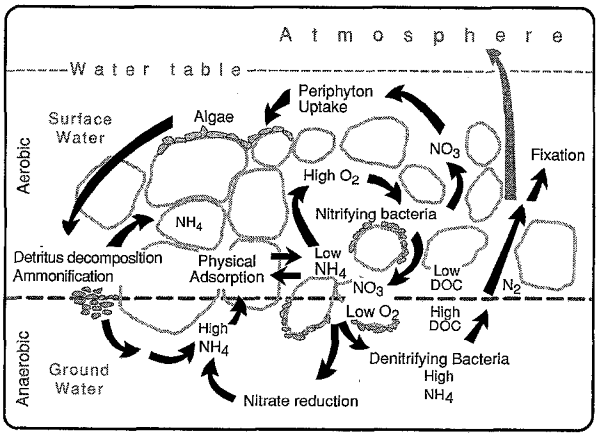

Fig. 12. Conceptual model of nitrogen cycling in the hyporheic zone as groundwater crosses the terrestrial–aquatic interface.

nitrate. Ammonium that enters the hyporheic zone is sorbed to clay sediments where a large reservoir is formed that is in equilibrium with interstitial water. Under aerobic conditions, nitrifying bacteria that occupy the sediment surface oxidize ammonium to nitrate. If nitrate is transported to the stream channel, it can be taken up by periphyton in conjunction with primary production. If nitrate is transported to low-DO regions of the hyporheic zone, it can either be denitrified or reduced to ammonium in the presence of DOC. Reduction to dinitrogen results in permanent loss from the system unless it is fixed by riparian species such as alder. Nitrate that is reduced to ammonium can re-enter the biological cycle. For streams like Little Lost Man Creek, the magnitude of nitrogen flux through the hyporheic zone depends on the background concentrations, the permeability of the bed (which determines the depth and lateral extension of habitat for various nitrogen transformations) and the lithology of the sediments (which partially regulates nutrient availability to biological pathways).

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