Hydrologic exchange and N uptake by riparian vegetation in an arid-land stream

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Abstract. Riparian zones can strongly influence the exchange of nutrients between streams and their watersheds. Most riparian studies have been done in mesic watersheds, which differ significantly from arid-land watersheds hydrologically. The goals of our work were to determine the strength and direction of hydrologic linkages between stream and riparian zone, and to estimate the extent of uptake of streamwater N by riparian trees in Sycamore Creek, a Sonoran Desert stream. Br⁻ and ¹⁵NH₄⁺ were added simultaneously to the surface stream to trace water and N from stream to riparian zone. Br⁻ concentrations in riparian wells installed downstream of the release point increased during the addition, demonstrating a strong hydrologic linkage from stream to riparian zone. Percentage stream water in wells increased in a downstream direction, suggesting little or no input of water laterally from uplands or vertically from deep groundwater. Leaf and wood samples collected from willow trees downstream of the addition point became significantly labeled with ¹⁵N during the addition, indicating uptake of streamwater N. Other tree species did not become labeled, most likely because they were located farther from the stream channel than the willows. Results from our study provide evidence of strong hydrologic linkage between stream and riparian zone and suggest that N demand by riparian vegetation is a potentially significant sink for streamwater N.

Key words: riparian, nitrogen retention, hydrologic exchange, nitrogen uptake, tracer tests.

Riparian zones influence the exchange of materials between streams and their watersheds because of their unique position in the landscape. The strength of that influence depends on the hydrogeologic setting in which riparian– stream interactions take place (Hill 1996, 2000, Cirmo and McDonnell 1997, Lowrance et al. 1997, Hill et al. 1998). Much of the work reviewed in these papers was done in mesic watersheds, where rainwater generally infiltrates upland soils and flows horizontally through riparian soils before entering the stream. Riparian zones in these watersheds often act as efficient nutrient filters, particularly of N, as water flows

¹ Present address: Department of Integrative Biology, University of California, Berkeley, California 94720-3140 USA. E-mail: jschade@berkeley.edu through riparian soils (Lowrance et al. 1984, Peterjohn and Correll 1984, Groffman et al. 1992, Pinay et al. 1993, Lowrance 1998, Sabater et al. 2003). In many agricultural watersheds, riparian buffer strips have significantly reduced N loads in runoff water from fertilized agricultural fields, thereby maintaining streamwater quality (Lowrance 1998).

In our study, retention is defined as the difference between input and output of N in water moving through riparian soils. Therefore, retention includes dissimilatory mechanisms of N removal, such as denitrification. N retention is particularly effective when riparian soils are underlain by geologic features that force groundwater to move laterally through organic-matterrich soils in the rooting zone of vegetation, and it is less effective when water mainly flows deeper in mineral soils below the rooting zone (Groffman et al. 1992, Hill 1996, 2000, Cirmo and McDonnell 1997, Lowrance et al. 1997). Furthermore, retention often occurs rapidly in a

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narrow zone adjacent to upland–riparian or riparian–stream boundaries as water carries electron acceptors (i.e., NO_3^- and O_2) from the oxidizing environment of upland soils or the surface stream into the reducing environment of organic-matter-rich riparian soils (McClain et al. 1994, Hedin et al. 1998, Hill et al. 1998).

The mechanisms responsible for retention of N from groundwater in the rooting zone remain unclear; in particular, the influence of vegetation is poorly understood (Hill 1996). Most work to date has focused on 2 main mechanisms: 1) plant uptake with subsequent incorporation of N into biomass, and 2) denitrification. The ultimate fate of N depends strongly on the relative importance of these mechanisms. N in plant biomass eventually is recycled back to the pool of available N in the ecosystem, whereas denitrification removes N permanently by returning it to the atmosphere as N_2 , which is unavailable to most organisms. The relative importance of each of these mechanisms in any given riparian ecosystem has been difficult to establish with much confidence because both mechanisms act simultaneously, and riparian ecosystems are not easily manipulated experimentally (Nelson et al. 1995, Hill 1996, Jacinthe et al. 1998; but see Verchot et al. 1997, Schade et al. 2001).

In arid-land watersheds, soils are relatively impermeable and, as a result, runoff flows overland into small rills and ephemeral channels before emptying into large, perennial stream channels (Fetter 1994). Once in these perennial stream channels, water infiltrates the subsurface through coarse channel sediments, and then moves laterally out into the riparian zone (Martí et al. 2000). Therefore, the dominant direction of groundwater movement is from stream to riparian zone, under both baseflow (Fetter 1994) and flood (Martí et al. 2000) conditions. The distribution, extent, and species composition of riparian vegetation in arid lands is dependent on the maintenance of minimum stream flows and shallow groundwater tables (Stromberg and Patten 1991, Stromberg et al. 1996), and this relationship suggests a hydrologic connection between stream and riparian zone in arid-land streams. The stream could be a source of nutrients for riparian vegetation in desert watersheds because stream water carries solutes with it as it moves into the riparian zone. Furthermore, the riparian zone may influence water quality by retaining nutrients from stream water as it moves into and out of the riparian zone during downstream transport. This hydrologic interaction could have important implications for primary production by riparian vegetation and for N dynamics in both the stream and riparian zone. At this point, however, little is known about the influence of riparian zones on streamwater chemistry in arid lands.

Hydrologic differences between mesic and arid-land watersheds generate contrasting linkage characteristics between upland, riparian zone, and stream. Preliminary observations of flowpath direction in Sycamore Creek, a Sonoran Desert stream, suggest that flowpaths from stream to riparian zone dominate at this site, at least during floods (Martí et al. 2000). The objective of our study was to address 2 questions: 1) How strong, and in what direction, is the hydrologic linkage between stream and riparian zone in Sycamore Creek? 2) Does N in stream water enter the riparian zone, and is it used by riparian vegetation? Our working hypothesis was that water generally moves from the stream to the riparian zone and carries with it N, which is then available for use by vegetation. Our approach was to add a conservative tracer (Br⁻) and ¹⁵NH₄⁺ to Sycamore Creek surface water (see Mulholland et al. 2000). We expected to find elevated Br- in water from riparian wells and ¹⁵N enrichment in riparian vegetation if our hypothesis was correct.

Site Description

The study site was a 400-m run in the middle reaches (~700 m elevation) of Sycamore Creek, a stream northwest of Phoenix, Arizona. Sediments in the channel of the main study reach consist primarily of sand and fine gravel, and the depth of alluvial sediments averages ~ 1.5 m (Holmes et al. 1994). Surface flow occurs during most of the year; however, at base flow, the surface stream typically occupies <25% of the active channel, with the remainder of the channel consisting of extensive gravel bars. The riparian zone consists of a strip of vegetation dominated by large trees such as Gooding's willow (Salix goodingii), ash (Fraxinus pennsylvanica velutina), sycamore (*Platanus wrightii*), mesquite (*Prosopis* sp.), and woody shrubs such as seepwillow (Baccharis salicifolia) and burro bush (Hymenoclea monogyra). These plants are distributed in a narrow strip bounded on one side by upland Sonoran Desert scrub and restricted on the other side to high-flow stream margins by severe flash floods that prevent the establishment of large trees in the active channel.

Methods

Tracer addition

In summer 1997, Br^- and ${}^{15}NH_4^+$ were added simultaneously to the surface stream at the top of the study reach. Prior to the addition, one longitudinal transect of 20 piezometers was installed on each bank of the riparian zone in the reach. Piezometers were spaced 20 m apart on the transects, which were 3 to 4 m from the stream channel. Piezometers were constructed of polyvinyl chloride (PVC) tubing that was 16 mm in diameter and 2 m in length, and piezometers were slotted over the bottom 5 to 10 cm. The piezometers reached a depth ~1.5 m below the soil surface (initially 50–100 cm below the water table). Tubes were cut 10 to 15 cm above the soil surface after installation.

Tracer additions began on 1 May 1997. Target concentrations were 2 mg/L for Br⁻ and 500% for ¹⁵NH₄⁺, and were achieved by adding the solutes to the stream at a constant rate with 2 solar-powered metering pumps. Br⁻ was added for 15 d, whereas ¹⁵NH₄⁺ was added for 42 d. The stream remained at base flow throughout the addition, i.e., no flash floods occurred during this time, although discharge did decline over the 42 d from 70 L/s to 42 L/s by day 15 and to 15 L/s by day 42.

Initial Br⁻ samples were collected from each piezometer 24 h after the addition began, with continued sampling at 24 to 72 h intervals throughout the 15-d Br⁻ addition and for several weeks after the end of the Br⁻ addition. Br⁻ concentrations were measured with an Orion Br⁻ specific electrode. The % of stream water in each piezometer was calculated by comparing the background-corrected, peak Br⁻ concentration in the piezometer to the background-corrected, plateau, or steady state Br⁻ concentration in the surface stream. Sampling for Br⁻ concentration in the surface stream followed procedures outlined in Triska et al. (1989).

Water samples for analysis of NO₃⁻ and NH₄⁺ concentrations were collected from the riparian zone and the surface stream several times during the injection. Samples from the surface

stream were collected every 20 to 40 m downstream of the addition point on days 0, 20, and 40 of the addition. Subsets of riparian wells were sampled using a peristaltic pump on days 20 (16 wells) and 40 (10 wells). All samples were collected in 60-mL, acid-washed, polyethylene sample bottles. Samples were placed on ice and returned to the laboratory, where they were filtered and analyzed for NO₃⁻ and NH₄⁺ concentrations. All analyses were completed within 24 h of collection. NO₃⁻ concentration was analyzed on a Braun and Leubbe TRAACS 800 autoanalyser using Cd reduction, and NH₄⁺ concentration was measured using the phenol-hypochlorite method (Solorzano 1969).

Plant tissue ¹⁵N

Leaves and wood were sampled to determine if N in stream water entering the riparian zone was retained via uptake by riparian vegetation. Leaves were collected from all individuals of the dominant tree species in the riparian zone of the study reach (willow, ash, sycamore, and mesquite) just prior to and at the end of the addition (April and June 1997, respectively). Leaves were sampled from willow trees only (n = 40) in April, May, and June 1998. Leaves from all species were sampled in September 1998 and April 1999. Leaves from willow trees upstream of the addition point were sampled in June 1997, September 1998, and April 1999. Wood cores were collected from 40 willow trees, 20 upstream and 20 downstream of the addition point, in the summer of 1999. Cores were returned to the laboratory, and wood from individual tree rings corresponding to 1995 (pre-addition year), 1997 (addition year), and 1998 (post-addition year) was collected and analyzed separately by year. All leaf and wood samples were dried, milled, and analyzed for N isotopic composition on a Europa Scientific 20/20 stable isotope analyzer (analytical precision for plant tissues ~0.08/ mil). N isotopic composition was reported in terms of $\delta^{15}N$ values, a measure of the ^{15}N content of a sample relative to the atmospheric N standard. An increase in 15N signifies an increase in ¹⁵N content.

Data analysis

All statistical analyses were performed using Systat for Windows (version 10, Systat, Point



FIG. 1. Temporal pattern of change in groundwater Br⁻ concentration following start of continuous Br⁻ addition to Sycamore Creek, Arizona, in the 4 riparian piezometers furthest from the addition point. Streamwater plateau averaged ~1.8 mg/L. Each type of symbol represents a different piezometer. Arrow indicates termination of the Br⁻ addition.

Richmond, California). NO_3^- and NH_4^+ concentrations were compared between surface water and riparian groundwater with *t*-tests. Leaf $\delta^{15}N$ was compared among sampling dates with separate analyses of variance (ANOVA) for each species. Leaf $\delta^{15}N$ was compared among species with separate ANOVAs for each sampling time. Tukey's tests were used to detect differences among means when ANOVAs were significant.



FIG. 2. Longitudinal changes in % stream water in riparian piezometers, calculated from peak Br⁻ concentration (measured on day 15 of the addition) in piezometers and at plateau in stream water. Distances are measured from the addition point.

Wood $\delta^{15}N$ was compared between years using 2 repeated-measures ANOVAs, one for upstream and one for downstream sites. Paired *t*-tests were used to compare $\delta^{15}N$ values between years when ANOVAs were significant. Enrichment of ¹⁵N in wood samples was calculated by subtracting 1995 $\delta^{15}N$ values from 1997 $\delta^{15}N$ values for upstream and downstream sites, and enrichment values were compared using *t*-tests. A *p*-value <0.05 was considered significant for all statistical tests.

Results

Tracer addition and water chemistry

Br- concentration in the surface stream reached a plateau at 1.8 mg/L within several hours of the beginning of the addition (not shown), whereas Br⁻ concentration in riparian groundwater began to increase within 24 to 72 h of the beginning of the addition (Fig. 1). All piezometers were labeled, to some extent, with Br- at the end of the addition but, in many piezometers, Br⁻ concentrations never reached a plateau. However, peak Br- concentrations generally were close to the streamwater plateau concentration in most piezometers (including the 4 farthest downstream; Fig. 1) that did not reach a plateau. This result suggested that piezometers were close to plateau conditions all along the reach. Percent stream water ranged from $\sim 20\%$ at the upstream end, near the addition point, to $\sim 80\%$ at the downstream end of the reach and generally increased with distance downstream (Fig. 2). Streamwater ¹⁵NH₄⁺ was between 300‰ and 700‰ 10 m below the addition site, declined to values as low as 12‰ at the downstream end of the reach, and averaged 101‰ over the 42-d addition. Streamwater $\delta^{15}NO_3^{-}$ was not enriched early in the addition, but by day 42, streamwater $\delta^{15}NO_3^{-}$ showed enrichment ranging from $\sim 8\%$ to nearly 40%along the reach (EM, unpublished data).

Concentrations of NO_3^- and NH_4^+ in the surface stream showed no consistent longitudinal pattern on any dates, so data were pooled, and a single mean was calculated for the injection period. NO_3^- concentrations were slightly higher than NH_4^+ concentrations, but mean concentrations were similar (Table 1). On 20 May 1997 (day 20), NH_4^+ concentrations were significantly higher in riparian wells than in surface water.

TABLE 1. Mean (SE) concentrations of NO₃⁻-N and NH₄⁺-N in surface water and riparian wells. Mean surface-water concentrations are averages across all locations and times. BDL = below detection limits, with detection limit for the TRAACS 800 ~1 μ g/L.

	Surface water				Riparian wells	
	$\begin{array}{l} \text{Day 0}\\ (n=7) \end{array}$	Day 20 $(n = 7)$	Day 40 $(n = 7)$	Mean $(n = 21)$	Day 20 $(n = 16)$	Day 40 $(n = 10)$
NO ₃ ⁻ (μg/L) NH ₄ ⁺ (μg/L)	6.4 (0.9) 7.6 (0.3)	8.5 (0.5) 8.6 (0.2)	14.2 (2.9) 6.6 (0.6)	9.7 (2.3) 7.6 (0.6)	14 (1) 32 (7)	BDL 19 (6)

 NO_3^- concentrations were similar in riparian wells and surface water. By the end of the injection (9 June 1997, day 40), NO_3^- concentrations in riparian wells were below detection limits (BDL), and NH_4^+ concentrations in riparian wells had declined, although they were still significantly higher than NH_4^+ concentrations in surface water (Table 1). On both dates, NH_4^+ was the dominant form of inorganic N in riparian wells.

Plant tissue ¹⁵N

Willow leaves accumulated ¹⁵N label during the addition and had significantly higher $\delta^{15}N$ values on the last day of the addition (June 1997) than prior to addition (April 1997) (Fig. 3A). Sycamore, ash, and mesquite leaves showed no significant change in $\delta^{15}N$ during the addition (Fig. 3A). By April 1998, willow leaves showed further accumulation of ¹⁵N and had significantly higher $\delta^{15}N$ values than leaves collected in April and June 1997. Between April and September 1998, willow-leaf $\delta^{15}N$ values declined linearly ($r^2 = 0.984$, p = 0.008) to pre-addition values (Fig. 3A). By September 1998, 1.5 y after the addition, δ^{15} N values were similar in willow, sycamore, and mesquite leaves, but $\delta^{15}N$ was higher in willow than in ash leaves.

At the end of the addition (June 1997), $\delta^{15}N$ values were significantly higher in leaves collected from willows downstream of the addition point than in leaves collected from willows upstream of the addition point (Fig. 3B). However, $\delta^{15}N$ values in willow leaves did not differ between upstream and downstream sites in September 1998 or April 1999. Leaf $\delta^{15}N$ values for all species, including upstream willows, increased between September 1998 and April 1999 (Fig. 3A, B).

Wood $\delta^{15}N$ values were significantly lower in 1995 than in 1997 (addition year) and 1998 for

willow trees downstream of the addition point (Fig. 4A). Wood δ^{15} N values did not differ between 1997 and 1998 for trees downstream of the addition point. Wood δ^{15} N values did not differ among years for willow trees upstream of the addition point (Fig. 4A). Enrichment was significantly higher in wood from trees downstream of the addition point than in wood from trees upstream of the addition point (Fig. 4B).

Discussion

Surface water-groundwater linkages

Our results clearly show a strong hydrologic linkage between stream and riparian zone. The appearance of Br- in riparian piezometers showed that stream water was moving into the riparian zone. This result was consistent with previously reported results from the same reach under flood conditions (Martí et al. 2000). The downstream increase in % stream water in the riparian zone differed from the results of other studies, typically done in mesic streams, in which % stream water decreased with distance from the addition point (e.g., Triska et al. 1993). These studies generally were done in gaining reaches in which the decrease in % stream water was a consequence of dilution by unlabeled water moving laterally from the uplands or up from deep groundwater sources (Triska et al. 1993, Hedin et al. 1998). Our results suggest that the only major source of unlabeled water to our study site was from bypass flow upstream of the addition point, with the volume of labeled stream water entering the riparian zone increasing downstream. Our observations indicated little dilution from groundwater sources moving laterally from uplands, or up from deep groundwater sources, a result characteristic of losing reaches. Stream water was clearly the pri-



FIG. 3. Changes in $\delta^{15}N$ of riparian tree leaves in Sycamore Creek following ${}^{15}NH_4^+$ addition. Sampling period includes 6-wk ${}^{15}NH_4^+$ addition to surface water (April–June 1997) and 2 y post-addition. A.—All riparian tree species. B.—Willow trees upstream and downstream of the addition point. Horizontal lines represent $\delta^{15}N = 0$. Error bars are ± 1 SE.

mary source of water to the subsurface during baseflow conditions.

Accumulation of 15N

Accumulation of ¹⁵N in willow leaves and wood clearly showed that N in stream water was taken up by willow trees. Lack of enrichment of other tree species suggested that these species did not have access to streamwater N as a resource, perhaps because of their spatial arrangement in the riparian zone. With a few exceptions, sycamore and ash trees grew significantly farther from the stream channel than willows (Fig. 5). We hypothesize that either these species were using a different source of water than willow trees, or N in stream water was removed before water penetrated far enough into the riparian zone to reach more distal trees. We believe an alternative water source for more distal trees is unlikely because the results of the Br⁻ addition showed that stream water provided most water to the subsurface. The proximity of the willow trees to the stream channel may have given them greater access to streamwater N, partly because willow roots grew into the stream channel. Thus, willows may have been able to withdraw N directly from surface or subsurface water in the channel. In turn, this direct access may have depleted streamwater N



FIG. 4. Changes in δ^{15} N of riparian willow-tree wood in Sycamore Creek following 15 NH₄⁺ addition. A.— δ^{15} N in willow trees upstream and downstream of the addition point in a pre-addition year (1995), the addition year (1997), and a post-addition year (1998). Stars indicate significant differences (p < 0.05) between pre- and post-addition years. B.—Enrichment of 15 N in willows upstream and downstream of the addition point, calculated as δ^{15} N in 1997 minus δ^{15} N in 1995. Star indicates significant difference (p < 0.05) between upstream and downstream wood samples. Error bars are ± 1 SE. Up = upstream, Down = downstream.

at the stream–riparian edge, thereby reducing the availability of streamwater N to species that grew further inland.

 δ^{15} N in willow leaves collected in April 1998 was higher than δ^{15} N in leaves collected in June 1997 at the end of the addition (Fig. 3A). Furthermore, leaf δ^{15} N was high in spring 1999 for all species downstream of the addition point and for willows upstream of the addition point. The elevated δ^{15} N in leaves in April 1998 could be explained by storage of streamwater N in the riparian zone, possibly in roots or soil organic



FIG. 5. Mean distance of willow, ash, and sycamore trees from the stream channel in the addition reach. Bars with different letters are significantly different (p < 0.05). Error bars are +1 SE.

matter or through sorption to soil particles. This stored N could have been released to the available pool or translocated from roots to leaves during spring leafout. The surface stream was not labeled during this period, so the additional accumulation of 15N suggests that uptake of N from stream water may be less important than recycling of N in soils and roots for initial allocation to leaves in the spring. This explanation is consistent with previous work showing the importance of soil-N recycling as a source of nutrients for willow trees in Sycamore Creek (Schade et al. 2002). An alternative explanation is that the increases in both spring 1998 and 1999 may have reflected a shift in nutrient-processing rates in riparian soils. Winter precipitation in both 1998 and 1999 was higher than winter precipitation in 1997. Higher precipitation is likely to have increased soil moisture and, possibly, mineralization rates, in 1998 and 1999. N mineralization favors 14N, leading to enrichment of the remaining soil-N pool. Therefore, high N mineralization rates in riparian soils may lead ultimately to isotopic enrichment of soil-N pools, even in the absence of added ¹⁵N. Given the importance of N recycling to riparian trees in Sycamore Creek, this enrichment would be reflected in higher $\delta^{15}N$ in tissues of plants using soil-N pools than in plants not using those pools.

N mass-balance calculations

The mechanism by which N is removed from groundwater flowing through riparian soils remains unclear and has been difficult to establish unequivocally in any particular ecosystem. The importance of uptake often has been inferred using mass-balance methods, which compare calculations of N retention in incremental biomass of riparian vegetation to measures of total mass of N lost from groundwater (Lowrance et al. 1984, Hill 1996). However, N in plant biomass can come from a variety of sources, including groundwater, surface water, or N recycled from soil organic matter (Schade et al. 2002). The shortcoming of this mass-balance method is its inability to determine from which source plant N is derived, and this inability may lead to overestimates of the use of groundwater N by plants. In our experiment, streamwater N was labeled with ¹⁵N without significantly increasing inorganic N concentrations. With a few assumptions, this label can be used to estimate uptake of streamwater N by riparian trees. A modified mass-balance approach was used to estimate N uptake by willow trees in the riparian zone and the proportion of streamwater N input this uptake represented.

The Br- addition showed that all of the piezometers received water from the stream and, in fact, the stream appeared to be the only source of water to the riparian zone. Assuming that all piezometers were directly connected to the stream by similar flowpaths, the flux of NO_{3}^{-} and NH_{4}^{+} from stream to riparian zone can be calculated using streamwater inorganic-N concentrations, cross-sectional area of the stream-riparian edge (saturated zone, corrected for porosity of riparian soils = 0.3; Jones et al. 1995), and velocity of water moving across this edge. Velocity was estimated by dividing the average nominal travel time by the average distance of piezometers from the stream. Crosssectional area was estimated by multiplying the total length of the reach (800 m, using both banks), by the depth of the riparian zone, assumed to be 1.5 m (based on measurements of the depth of alluvial sediments; Holmes et al. 1994). Flux of inorganic N (NO₃⁻ and NH₄⁺) was calculated to be 0.6 kg during the 6-wk addition, or 5 kg ha⁻¹ y⁻¹. This input is comparable to atmospheric deposition to the desert (3 kg ha⁻¹ y⁻¹; Peterjohn and Schlesinger 1990), but small when compared to groundwater NO_3^- inputs to the riparian zone in 2 agricultural watersheds, estimated to be 50 (Peterjohn and Correll 1984) and 29 kg ha⁻¹ y⁻¹ (Lowrance et al. 1984).

Estimates of uptake use ¹⁵N labeling of stream water and the increase in $\delta^{15}N$ in willow leaves and wood. It was assumed that 15N in leaves and wood increased solely because of uptake of labeled streamwater N, and that uptake did not cause any fractionation of N isotopes, i.e., did not favor ¹⁴N, causing changes in isotopic signature. Both assumptions were reasonable because of the magnitude of the increase in $\delta^{15}N$ in stream water, which was likely to have swamped other potential sources of N or the effects of fractionation. Moles of 15N taken up by willow trees during the injection were calculated using the increase in δ^{15} N in leaves and wood and the estimates of total N in leaf and wood tissue in the reach. Total mass of N in leaves and wood was estimated as 24 and 4 kg, respectively, based on estimates of production multiplied by % N of leaves and wood (JRW, unpublished data). On average, leaf $\delta^{15}N$ values were enriched by 2.18‰, whereas wood was enriched by 8.7‰. These enrichment levels were the equivalent of 0.05 and 0.04 kg of streamwater N in leaves and wood, respectively, or a total of 0.09 kg N removed from stream water by plant uptake. Based on this calculation, uptake was responsible for retention of 15% of the total N inputs from the stream to the riparian zone, and streamwater N represented a very small proportion of the total N demand by willow trees (0.3%). This level is likely to be an underestimate, however, because the injection began after leaves were fully expanded. A major source of error in this calculation is the omission of N uptake and storage in belowground biomass.

Our first assumption in calculating uptake was that all piezometers were hydrologically connected to the stream along similar flowpaths. If this were the case, then variation in nominal travel time simply would have reflected variation in the velocity of water caused by variation in some factor, such as hydraulic conductivity of the soil. If, however, variation in nominal travel time reflected differences in the flowpaths, or the tightness of the connection between the stream and the piezometers, then stream water may have been entering the riparian zone only at specific locations. Assuming that water entered the riparian zone only at the piezometers with the shortest nominal travel time (4 d), then the total length of the zone of exchange would have been $\sim 10\%$ of the total length of the reach, or ${\sim}80$ m. Estimates of velocity would increase to 0.3 m/h. Substituting these values into our calculation, total input of N to the riparian zone would become 0.15 kg. Because our uptake calculation is unaffected by changes in our assumptions about connections, 60% of these inputs would have been stored in plant biomass. Thus, the riparian zone may have been an effective filter of N from stream water in Sycamore Creek. Furthermore, the lack of enrichment of the tree species growing further from the stream suggests that retention occurred rapidly at the interface between stream and riparian zone, a conclusion consistent with results from several other studies (Peterjohn and Correll 1984, McClain et al. 1994, Hedin et al. 1998, Hill et al. 1998, Schade et al. 2001, 2002).

A more detailed understanding of hydrologic exchange between stream and riparian zone is clearly necessary for a deep understanding of spatial and temporal variation in N retention. Combining ¹⁵N labeling of sources with detailed hydrologic studies is a potentially powerful approach to improving our understanding of mechanisms of N retention by riparian zones and our understanding of sources of nutrients for the production of riparian vegetation.

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