

Sources of Nitrogen to the Riparian Zone of a Desert Stream: Implications for Riparian Vegetation and Nitrogen Retention

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ABSTRACT

Riparian zones effectively remove nitrogen (N) from water flowing through riparian soils, particularly in agricultural watersheds. The mechanism of N removal is still unclear, especially the role of vegetation. Uptake and denitrification are the two most commonly studied mechanisms. Retention of groundwater N by plant uptake is often inferred from measurements of N in net incremental biomass. However, this assumes other sources of N are not contributing to the N demand of plants. The purpose of this work was to investigate the relative importance of three sources of available N to riparian trees in a desert stream—input in stream water during floods, input during baseflow, and mineralization of N from soil organic matter. Two approaches were used; a mass balance approach in which the mass of available N from each source was

estimated, and a correlational approach in which indexes of each source were compared to leaf N for individual willow trees. Total N from all sources was $396 \text{ kg ha}^{-1} \text{ y}^{-1}$, with $172 \text{ kg ha}^{-1} \text{ y}^{-1}$ from mineralization, $214 \text{ kg ha}^{-1} \text{ y}^{-1}$ from the stream during baseflow, and $9.6 \text{ kg ha}^{-1} \text{ y}^{-1}$ from floods. Leaf N was significantly related to N mineralization rates and flood inputs; it was not related to baseflow inputs. We conclude that mineralization is a major source of available N for willow trees, subsidized by input of N from floods. Baseflow inputs are most likely removed by rapid denitrification at the stream–riparian edge, while higher rates of flood supply exceed the capacity of this “filter.”

Key words: riparian zone; nitrogen retention; denitrification; plant uptake; N mineralization; desert stream.

INTRODUCTION

Riparian zones often are effective nutrient sinks, rapidly removing nutrients, particularly nitrogen (N), from groundwater flowing through riparian soils (Peterjohn and Correll 1984; Lowrance and others 1984; Groffman and others 1992; Hill and others 1998; Hill 2000). In agricultural watersheds, riparian buffer strips have been particularly effective

at removing N in runoff from fertilized fields and thereby aiding in the maintenance of stream water quality (Lowrance 1998). Furthermore, N removal often occurs rapidly, with most removal taking place within a narrow strip of the upland–riparian or riparian–stream boundary (Peterjohn and Correll 1984; Jacobs and Gilliam 1985; Haycock and Burt 1993; McClain and others 1994; Hedin and others 1998; Hill and others 1998). The mechanism by which N is removed from groundwater remains unclear, particularly the role of riparian vegetation (Jacinthe and others 1998; Hill 1996;

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Nelson and others 1995); however, denitrification or plant uptake and storage in biomass are the most likely mechanisms (Hill 1996). The ultimate fate of N input to riparian zones is strongly determined by the relative importance of these mechanisms. Plant uptake only temporarily retains N, which returns to the available pool when the plant, or part of the plant, dies and is mineralized. Denitrification is a permanent loss of N to the atmosphere as N₂, which is unavailable for use by most organisms.

Several indirect lines of evidence give support to both possible N removal mechanisms, and both are likely to have some influence, depending on the biological and hydrogeological characteristics of the watershed (Hill 1996, 2000; Lowrance and others 1997; Cirimo and McDonnell 1997). Experimental manipulations distinguishing these mechanisms are difficult and have rarely been performed. Two recent studies have used experimental approaches that suggest that denitrification is more important than uptake in retaining N, at least during certain times of the year (Verchot and others 1997; Schade and others 2001). Furthermore, high potential and in situ denitrification rates have been measured in riparian soils at several sites. Denitrification is difficult to measure and varies spatially, making it difficult to accurately scale up to the whole riparian zone for the purposes of constructing a mass balance (Parkin 1987; Murray and others 1995). Nevertheless, N losses due to denitrification are potentially high, leading to the possibility that denitrification removes nitrate at interfaces between the riparian zone and upland or stream before riparian plants gain access to it. As Hill (1996) puts it, "many riparian areas have significant unused potential for nitrate depletion" because most nitrate is lost in a narrow perimeter near the upland-riparian boundary (see also Hedin and others 1998; Hill and others 1998).

The main line of evidence for the importance of plant uptake comes from measurements of N stored in plants when net biomass increment is positive compared to estimates of total loss of N entering the riparian zone from groundwater flow. In some cases, uptake of N can exceed N input in groundwater (Lowrance and others 1984). A major assumption of this method is that other unmeasured sources of N are not contributing significantly to plant production. For example, mineralization of N from soil organic matter is known to be an important source of available N in upland forests (Pastor and others 1984) and may provide a large amount of available N in riparian forests as well. If so, N supplied through mineralization may meet a large proportion of the plants' N requirement; yet N min-

eralization rates in riparian soils are rarely measured. If N mineralization does provide a substantial mass of available N for plants, then the importance of uptake in N retention from groundwater is overestimated by this method. A thorough accounting of all sources of N and their relative importance under various conditions for riparian vegetation would be a large step forward in our understanding of the importance of plant uptake in the removal of N from groundwater by riparian forests. One goal of this research is to determine the importance of several possible sources of N for riparian vegetation.

Most of what we know about ecosystem processes in riparian zones is derived from studies of the mesic watersheds of North America. In arid land streams, riparian zones have received attention mainly because they are important habitat for many animal species and are rapidly disappearing due to human activities (Stromberg 1993). Unfortunately, we know little about N cycling in desert riparian zones, or the influence of riparian zones on other subsystems. The linkages among upland, riparian zone, and stream in arid land watersheds are quite different from those for mesic watersheds. In mesic watersheds, rainfall infiltrates upland soils and moves laterally as groundwater from uplands, through riparian soils, to the stream. In arid land watersheds, rainwater typically does not infiltrate less permeable desert soils, but flows overland into small rills, eventually infiltrating coarse sediments in larger stream channels. In these arid watersheds, water moves from stream to riparian zone under baseflow and flood conditions (Marti and others 2000; Fetter 1994) and may be an important source of nutrients for riparian vegetation. To understand the consequences of this difference in hydrology for ecosystem processes in riparian zone or stream, more information is needed on N cycling in desert riparian zones. A second goal of this work is to increase our understanding of N cycling in riparian zones in southwestern deserts.

Our specific objectives were (a) to describe spatial and temporal patterns in N concentrations in surface water and groundwater and N mineralization rates in riparian soils, and (b) to determine the sources of N for riparian trees. For objective (a), a portion of the data reported here is also reported in Marti and others (2000). Those analyses are included here for completeness and are indicated accordingly. For objective (b), we hypothesized three potentially important N sources for riparian trees, including the pulse input of N due to the movement of flood water and its solute load into the riparian zone, chronic input of N from the movement of water and nitrogen from stream to riparian zone

during baseflow, and the conversion of organic N in riparian soils to available N—that is, mineralization. If these hypothetical mechanisms are providing N for riparian trees, we predicted (a) that input of N from each source will be a significant proportion of N demand by trees and (b) that variation in input from these sources will be associated with variations in the characteristics of trees. These mechanisms are not mutually exclusive, and tests were designed to estimate the relative importance of each. To test prediction (a), we used a mass balance approach in which total mass of available N provided to the riparian zone from each source was estimated and then compared to an estimate of total N demand by riparian trees. Prediction (b) was tested using a correlational approach in which variation in the leaf N content of willow trees was compared to variation in the input of each potential source. Many tree species are known to respond to variation in N availability with a change in foliar N concentrations (Vitousek and others 1995); therefore, foliar N of willow trees should correlate with sources of N that contribute significantly to willow production. We focused on willow trees because they are the most abundant tree species in the study reach.

SITE DESCRIPTION

The study site is a 400-m run in the middle reaches of Sycamore Creek, located at an elevation of approximately 700 m. The riparian zone is dominated by large deciduous trees such as Gooding's willow (*Salix goodingii*), ash (*Fraxinus pennsylvanica velutina*), sycamore (*Platanus wrightii*), mesquite (*Prosopis glandulosa*), and woody shrubs such as seepwillow (*Baccharis salicifolia*) and burro bush (*Hymenoclea monogyra*). Riparian vegetation is contained in a narrow strip, on average 13 m wide, 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. The total area of the riparian zone along both banks of this reach is approximately 1 ha (800 m length \times 13 m width). Sediments in the stream channel consist primarily of sand and fine gravel, at an average depth of approximately 1.5 m (Holmes and others 1994). Surface flow occurs during most of the year; however, at baseflow the surface stream typically occupies only a fraction of the active channel, with the remainder dominated by extensive gravel bars (the parafluvial zone).

The distribution of riparian vegetation is determined by the hydrologic regime, which is characterized by severe flash floods in which discharge

may increase several orders of magnitude in the span of a few minutes. These floods scour vegetation from the active channel, leaving large gravel bars behind as the water recedes. Discharge declines to baseflow levels within a few hours to a few days of peak flood flows. Previous work on Sycamore Creek has shown that water and nutrients are transported into the riparian zone both during floods (Marti and others 2000) and baseflow (C. L. Dent personal communication; J. D. Schade unpublished). Flood water has a high concentration of N, and the steepness of the hydraulic gradient between the stream and the riparian zone during floods leads to large hydrologic input to the riparian zone; however, the duration of flood input is short (on the order of hours) and depends on hydrologic conditions, particularly the hydraulic gradient, in the reach at the time of the event (Marti and others 2000). At baseflow, stream water is low in N relative to flood water; however input typically occurs over the course of several weeks.

METHODS

Water Chemistry

Wells were installed in the riparian zone of the study reach every 20 m downstream along both left and right banks. Each well was located 3–4 m from the riparian–stream edge and was installed to a maximum depth, initially 50–100 cm below the water table. An additional set of six wells was installed at the riparian–stream edge, one well on each side of the channel at 90, 150, and 270 m, with each edge well adjacent to a riparian well. Three transects of five wells each were installed in the parafluvial zone, stretching from bank to bank perpendicular to the stream at 30, 90, and 150 m along the same reach.

Riparian wells and surface water were sampled monthly from March to May 1996 and from August 1996 to July 1997. Wells were dry in June and July 1996 and could not be sampled. Parafluvial and edge wells were sampled at the same time as riparian wells, except for March and April 1996, which was prior to the installation of these wells. Four floods occurred during the study period—on 22 August 1996, 5 September 1996, 14 January 1997, and 28 February 1997. Surface water samples from each event were collected within 1 day of the flood peak. On each sampling date, duplicate samples were collected from each well and triplicate samples were taken from the surface stream in acid-washed polyethylene bottles. Well samples were collected using a peristaltic pump.

All samples were stored on ice for return to the laboratory, where they were analyzed for NO_3 , NH_4 , and dissolved organic nitrogen (DON) concentration within 24 hs. NO_3 analyses were performed on a Braun and Leubbe TRAACS 800 autoanalyzer. NH_4 was analyzed using the phenolhypochlorite method (Solorzano 1969). DON was measured by UV oxidation, followed by NO_3 analysis.

Nitrogen Mineralization

Mineralization of N in riparian soils was measured during the leaf-out period of the growing season monthly between 8 March and 15 June 1998. Thirteen willow trees were selected; for each of these trees, the mineralization rates were measured at three locations at a 1-m radial distance from the trunk of the tree, for a total of 39 locations. Mineralization rates were measured using the buried-bag method (Hart and Firestone 1989). Soil samples were collected from the bottom of pits dug at each spot to a depth of 50 cm. This depth was chosen following preliminary observations of a small number of deeper (more than 2 m) soil pits that showed that willow roots are rarely found shallower than about 30 cm and that surface soils are densely populated by the roots of Bermuda grass (*Cynodon dactylon*). We also observed in these pits a layer of soil roughly 1 m thick extending from around 30 cm down to 1–1.5-m depths that was densely rooted by riparian trees, including willow. We chose 50 cm because our observations suggest that this depth is in that layer of soil and fairly representative of the rooting zone of willow trees.

Soil samples collected from these 50-cm-deep pits were divided in half. One half was returned to the laboratory on ice for analysis of initial available N concentrations; the other half was sealed in a polyethylene bag, placed back into the pit, and buried. After an incubation period of roughly 1 month, the bags were dug up and returned to the laboratory on ice for analysis of available N. Three consecutive month-long incubations were conducted at each location. All soil samples (a total of 230 for all three mineralization experiments) were analyzed for NO_3 and NH_4 concentration by KCl extraction. Samples were homogenized and 20-g subsamples were collected and shaken for 30 min in 2 N KCl. Extractant was filtered and analyzed for NO_3 and NH_4 concentrations using the analytical methods described for water chemistry samples.

Mass Balance Calculations

For the following calculations, we used a riparian zone of 1 ha in area (see site description) and 1 m

depth (based on preliminary observations described above), for a total volume of riparian soil of 10,000 m^3 . Total flood N input for the study period was estimated by summing the calculated inputs for each individual flood occurring between August 1996 and July 1997. For each flood, the volume of water added to the riparian zone during the event was multiplied by the concentration of NO_3 , NH_4 , and DON in flood water, giving an estimate of the mass of N entering the riparian zone during each flood. The total volume of water entering the riparian zone was calculated by measuring the average increase in water table height in riparian wells during the flood, multiplying that number by the area of the riparian zone, and adjusting for porosity of riparian soil (estimated to be 0.3) (Jones and others 1995). The height of the water table in each well was measured at least biweekly; frequency of measurement was increased in response to floods. Change in water table height was calculated by subtracting the water table height in wells at the last sampling date before the flood from the water table height measured the day after the flood. Concentrations of NO_3 , NH_4 , and DON in each flood were estimated using surface water samples collected within 1 day of the flood peak.

The input of N from the movement of water from stream to riparian zone during baseflow was estimated by calculating the flux of NO_3 , NH_4 , and DON across the stream-riparian edge. Previous work using a conservative tracer suggests that water moves from stream to riparian zone all along this reach (C. L. Dent personal communication; J. D. Schade unpublished). Because, along most of the reach, water flows through the parafluvial zone on its way to the riparian zone, this flux was calculated by multiplying the average concentration of NO_3 , NH_4 , and DON (g/m^3) in parafluvial wells times the area across which the water was moving (length of stream-riparian edge [800 m]) times the depth of the riparian zone [1.5 m] times the velocity of movement (0.2 m/h). This value was also adjusted for the porosity of riparian soil, as in the flood input calculation. Velocity was estimated to be 0.2 m/h, based on the results of the Br^- tracer experiment (C. L. Dent personal communication). The total input was calculated for the whole year and for the growing season (March–October) using average NO_3 and NH_4 concentration in the parafluvial zone—both that is, the annual average and the average for the growing season alone.

Production of available N from mineralization was calculated from measurements of mineralization rates made from March to June of 1998, as described above. No measurements were made dur-

ing fall or winter. Extrapolating these rates beyond the period of study is problematic because the rates are likely to be different during other seasons. Because the temperature is lower during late fall and winter (November–March), we are probably overestimating annual production of available N via mineralization. If we confine ourselves to the growing season, this source of error is reduced. The period from mid-May through the beginning of the monsoonal rains in July is the driest and warmest period. Our last incubation (May–mid-June) is representative of this period. Soils were already dry at the beginning of this incubation, and temperatures were high. Because mineralization rates during the May incubation ($0.06 \text{ mg kg}^{-1} \text{ d}^{-1}$) were the highest measured in this study, it seems reasonable to apply our mean mineralization rate ($0.03 \text{ mg kg}^{-1} \text{ d}^{-1}$) to the entire dry period (June–July). During the monsoon season (August–September), high temperatures combined with higher moisture conditions should lead to comparable to higher mineralization rates during this period. Again, it seems reasonable to apply our mean rate to these months. For these reasons, we feel confident that applying our mean rate to the entire growing season is a reasonable, although admittedly rough, approximation. Total mass of available N produced was calculated by multiplying the average mineralization rate ($0.03 \text{ mg kg}^{-1} \text{ of soil}^{-1} \text{ d}^{-1}$) by an estimate of the total mass of soil in the riparian zone and time (3, 8, or 12 months). Total mass of soil was calculated by multiplying the volume of the riparian zone by bulk density of riparian soils; the latter was measured by weighing a known volume of soil from samples used for initial values in mineralization experiments ($n = 38$).

Relative Importance of Potential Sources

For this approach, we selected 13 willow trees in the spring of 1998. At each tree during the growing season, we measured leaf %N, N mineralization rate, an index of baseflow input, and an index of flood input. All measurements were carried out each month for three consecutive months between 8 March and 15 June 1998. The approach was to use all of these variables in a multiple regression analysis to determine the proportion of variance between trees in leaf %N explained by each independent variable. Because plants are known to respond to variation in N availability with variation in tissue N (Vitousek and others 1995; Hobbie 1992; Chapin and others 1982), we can infer that the source that explains the most variation in leaf N is likely to be the most important. Furthermore, because foliar N integrates the effects of all processes

influencing N availability over the period of growth, only June leaf %N values were used in the statistical analysis and were compared to mean values for N mineralization rate and the index of baseflow input, and to total flood inputs for the 3-month period.

Mineralization rate was measured at three replicate locations at each tree and averaged to produce a mean rate for each tree during each month. Mineralization incubations defined the three month-long periods. On the last day of each mineralization experiment, three replicate samples of full sunlight leaves were collected from each tree. Leaf samples were returned to the laboratory, dried for at least 48 h, and milled in a Wiley mill. Percent N in each sample was measured on a Europa Scientific 20/20 stable isotope analyzer. As an index of flood input, we used the change in water table height in wells adjacent to each of the 13 willow trees during two floods that occurred in March during the study period. Changes due to individual floods were summed to produce one value for the flood index. In the regression analysis, total flood input for the entire 3-month period was used as an independent variable.

As an index of input from stream to riparian zone during baseflow, we used the difference in water table height between the stream channel and the riparian zone, or the hydraulic gradient. If the water table is higher in the channel than the riparian zone, then water will move from stream channel out into the riparian zone, and vice versa, with the strength of that movement proportional to the difference in water table height. To determine the hydraulic gradient, wells were installed in the parafluvial zone adjacent to riparian wells at each tree ($n = 13$). Water table height was measured in the parafluvial wells at the same time as riparian wells. The height of the top of the wells relative to each other was determined using surveying equipment for each riparian–parafluvial pair, and the distance between the two wells was measured. The difference in height of water table between the wells was divided by the distance between the wells to determine the hydraulic gradient (cm/m). The water table was measured several times during each incubation period, and the mean hydraulic gradient for the 3-month period was used in the statistical analysis.

All statistical analyses were performed on Systat version 5.02 (SPSS Inc., Chicago, IL, USA). Mean water chemistry from all wells and surface stream was compared using analysis of variance (ANOVA), followed by Tukey's multiple comparison. Monthly mean mineralization rates were also compared using ANOVA. Simple linear regression was used to estimate the relative importance of sources by re-

Table 1. Mean concentrations of NO₃ and NH₄ in Surface Water and Wells Installed in Gravel Bars at the Stream–Riparian Edge and 3–4 m into the Riparian Zone

Form of N (µg/L)	Riparian	Edge	Gravel Bar	Surface Stream
NO ₃	8 ^a (2)	7 ^a (2)	156 ^b (12)	28 ^c (6)
NH ₄	33 ^a (5)	28 ^a (6)	17 ^{a,b} (3)	6 ^b (2)
DON	185 ^a (5)	180 ^a (8)	166 ^b (5)	207 ^a (21)

Modified from Marti and others 2000.

^a, ^b, and ^c denote significant differences ($P < 0.05$).

Values in parentheses are standard errors of the mean (SEM).

gressing each independent variable (flood input, hydraulic gradient, and N mineralization rate) individually against leaf %N in June. Multiple regression was also used to determine the importance of each independent variable by estimating the proportion of variance in leaf %N in June explained by each independent variable when all variables were included in the regression model. Results from all analyses were considered significant if P was greater than 0.05.

RESULTS

Water Chemistry

The mean concentrations of both NO₃ and NH₄ in riparian wells were not significantly different from edge wells (Table 1). Stream water was significantly higher in NO₃ and lower in NH₄ than both edge and riparian wells; it was also significantly lower in NO₃ than parafluvial wells (Table 1). Parafluvial wells were significantly higher in NO₃ than all other subsystems, but they were not significantly different in NH₄ from either surface water or riparian or edge wells. No differences in DON concentrations were found among riparian, edge, and surface stream, but they were significantly lower in parafluvial wells than all other subsystems. Furthermore, although DON was the dominant form of N in all subsystems, NH₄ was the dominant form of inorganic N in riparian and edge wells, whereas NO₃ dominated in surface stream and parafluvial wells (Table 1). Temporal variation in both NO₃ and NH₄ concentrations in all subsystems was associated with floods, with no apparent seasonal variation (Figure 1). Floods caused large, rapid increases in NO₃ in all subsystems and smaller increases in NH₄ in riparian and edge wells only. The similarity in temporal variation between riparian and edge wells is clear (Figure 1).

Nitrogen Mineralization

Mineralization rates varied severalfold both temporally (-0.01 – 0.03 mg kg⁻¹ d⁻¹), (Figure 2A) and

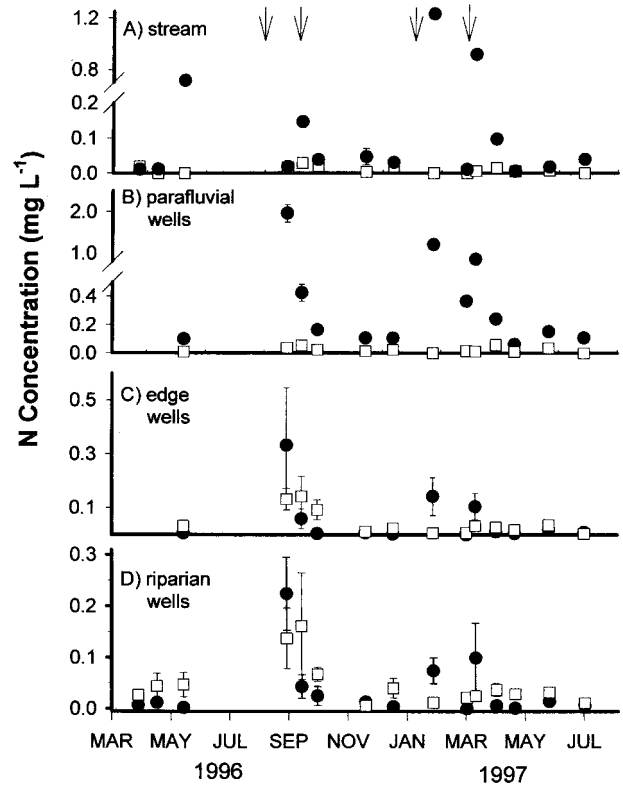


Figure 1. NH₄ (□) and NO₃ (●) concentrations in water collected monthly from A surface stream, B parafluvial wells, C edge wells, and D riparian wells. Note the difference in the scale of the y-axis between edge–riparian wells and parafluvial wells and stream. Graph of riparian wells reprinted from Marti and others (2000, with permission from Academic Press). Arrows indicate floods.

spatially (-0.025 – 0.06 mg kg⁻¹ d⁻¹), (Figure 2B). The mean rate for the riparian zone was higher in March and May than April. In April, the mean rates were negative; thus, net immobilization was occurring during this incubation period (Figure 2A). Spatial variation occurred at a relatively small scale, with rates at locations in close proximity varying up to two orders of magnitude. No significant longitudinal pattern in mineralization rate was found (Figure 2B).

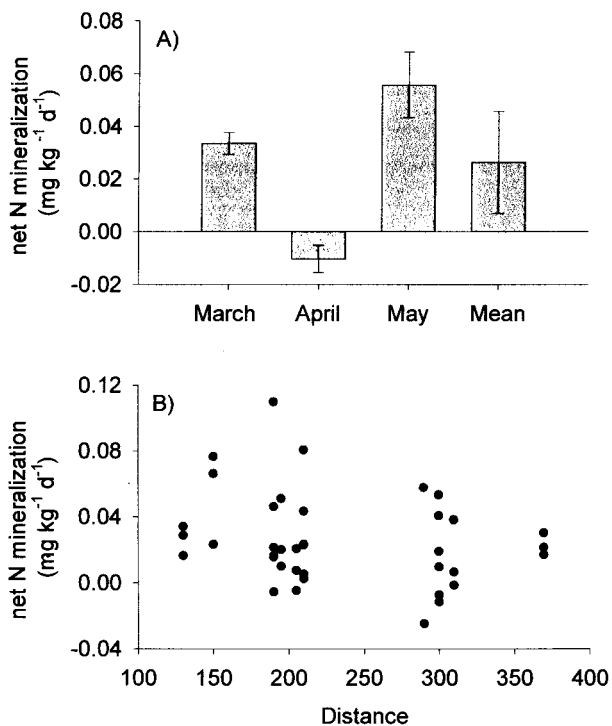


Figure 2. N mineralization rates averaged across A all locations each month for temporal variation ($n = 39$ for each bar) and B all times at each location for longitudinal variation. Each dot represents the mean of three experiments.

Mass Balance Calculations

All of the following calculations apply to a riparian zone 400-m long and 13 m wide on both sides, or roughly 1 ha in area. Four floods occurred between August 1996 and July 1997. Input of N from these floods ranged from 1.9 to 2.9 kg and averaged 2.4 kg. Total annual flood input was 9.6 kg, of which 6.7 kg entered as NO_3 , 1 kg as NH_4 , and 1.9 kg as DON. Three of these floods occurred during the growing season, providing an estimated total N input of 6.5 kg (4.6 kg NO_3 , 0.6 kg NH_4 , 1.3 kg DON) (Table 2).

Annual baseflow input of NH_4 , NO_3 , and DON was calculated for the study period using the following equations:

$$\begin{aligned} \text{Total annual } \text{NH}_4 \text{ input} &= 0.017 \text{ g/m}^3 \\ &\times 1200 \text{ m}^2 \times 0.2 \text{ m/h} \times 0.3 = 11 \text{ kg/y} \quad (1) \end{aligned}$$

$$\begin{aligned} \text{Total annual } \text{NO}_3 \text{ input} &= 0.156 \text{ g/m}^3 \\ &\times 1200 \text{ m}^2 \times 0.2 \text{ m/h} \times 0.3 = 98 \text{ kg/y} \quad (2) \end{aligned}$$

$$\begin{aligned} \text{Total annual DON input} &= 0.166 \text{ g/m}^3 \\ &\times 1200 \text{ m}^2 \times 0.2 \text{ m/h} \times 0.3 = 104 \text{ kg/y} \quad (3) \end{aligned}$$

The first term is the average concentration of each form of N in parafluvial wells; the second is the area of the zone of exchange between stream and riparian zone; the third is the velocity of movement of water between the two; and the last is an estimate of the porosity of riparian soils. Inputs for just the growing season were calculated using concentrations in parafluvial wells of 0.014 g m^{-3} for NH_4 , 0.123 g m^{-3} for NO_3 , and 0.134 for DON. Total input for the growing season was 6, 51, and 55 kg, respectively (Table 2). Average N mineralization rate for the study period was $0.03 \text{ mg kg}^{-1} \text{ d}^{-1}$, and total mass of soil in the riparian zone was estimated at $1.1 \times 10^7 \text{ kg}$. Total annual input of N from mineralization was calculated to be 117 kg for the year and 77 kg for the growing season (Table 2).

Relative Importance of Potential Sources

Leaf %N in willow trees declined steadily from April to June (Figure 3). Declines were significant both between April and May and between May and June. Simple linear regression of leaf %N in June against mean N mineralization rate and total flood input showed a significant positive relationship to both (Figure 4A and B). In contrast, leaf %N was not significantly related to mean hydraulic gradient (Figure 4C). A multiple regression analysis using all three potential sources as independent variables was significant ($r^2 = 0.624$, $P = 0.026$) and consistent with simple linear regressions. Mineralization rate was the most significant variable, explaining 34% of the variation in leaf N; flood input was also significant, explaining 20%. Hydraulic gradient explained less than 2% of the variance in leaf N, despite being a larger total source of N than flood input (Table 2), and its inclusion in the regression model did not improve model fit significantly.

DISCUSSION

The similarity in water chemistry between riparian and edge wells and the large decrease in NO_3 between parafluvial and edge wells during baseflow (Table 1 and Figure 1) strongly suggest a rapid removal of NO_3 from water moving from stream to riparian zone at the stream-riparian edge. This indicates that stream water nitrate may not be available to much of the vegetation, particularly trees growing farther from the stream in the riparian zone. This is consistent with the results of a previous experiment in which $^{15} \text{NH}_4$ was added to surface water in the same reach of Sycamore Creek. Only willow trees, which grow significantly closer to the stream channel than other species, received a

Table 2. Summary of N Inputs to the Riparian Zone from Floods, Movement of Water during Baseflow, and N Mineralization (N. Min.) both Annually and during the Growing Season

Source	Annual (kg ha ⁻¹)				Growing Season (kg ha ⁻¹)					
	NH ₄	NO ₃	DON	Total Avail.	Total	NH ₄	NO ₃	DON	Total Avail.	Total
Flood	1	6.7	1.9	7.7	9.6	0.6	4.6	1.3	5.2	6.5
Baseflow	11	98	105	109	214	6	51	55	57	112
N. Min.				117	117				77	77
Total	12	104.7	106.9	234	341	6.6	55.6	56.3	139	196

Growing season typically runs from March to October.
 Total available N = (NH₄ + NO₃ + N. Min.)

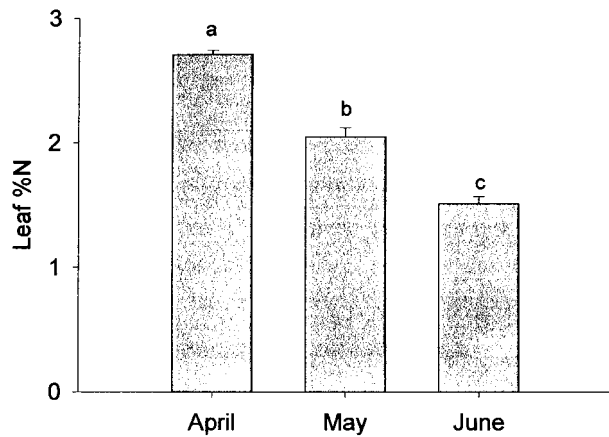


Figure 3. Mean monthly values for leaf %N from willow trees ($n = 13$). Letters indicate significant differences (ANOVA followed by Tukey's test; $P < 0.05$).

detectable amount of stream water N (J. D. Schade unpublished). This is also consistent with work in mesic riparian zones showing that most N input from groundwater from uplands was removed just a few meters from the upland–riparian boundary (Hill 1996). In this case, however, due to hydrologic differences in arid land streams, N in water moving in from the stream, rather than from the uplands, is being removed at the stream–riparian edge.

These patterns suggest that stream water may be a substantial source of N for riparian vegetation, at least for willow trees growing near the stream–riparian edge. Mass balance calculations reinforce this idea, by showing that 63% of total estimated N input and 47% of inorganic N input (NO₃ + NH₄), enter in stream water during baseflow and that another 3% of total N and 3% of inorganic N enters from the stream during floods (Table 2). The demand of N by all riparian trees in this 400-m reach has been estimated to be 103 kg annually (J. R. Welter unpublished). This figure is based on esti-

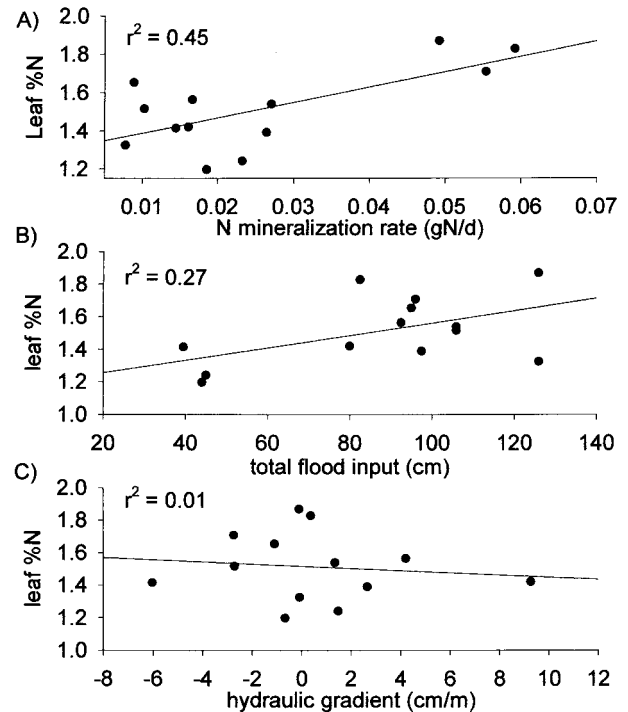


Figure 4. Relationship between leaf %N and A average nitrogen mineralization, B total flood input, and C average hydraulic gradient. Reported r^2 values are from simple linear regression of leaf %N against each independent variable.

mates of tree production calculated from regression relationships correlating tree height and diameter at breast height (DBH) to the production of leaves, wood, and roots. Total N demand was calculated by multiplying estimates of leaf, wood, and root production by %N in tissues. No herbaceous production is included in this estimate.

Furthermore, because a proportion of this demand may be met by the retranslocation of N from leaf tissue to wood or roots, we are likely overesti-

mating the total uptake of N by trees. Stream water input of inorganic N during baseflow alone could account for 109 kg, or all of this demand. Flood inputs alone could account for only 8%; at the average input per flood calculated here, it would take more than 50 floods to provide all of the inorganic N required by vegetation. Together, inorganic N input to the riparian zone in stream water during floods and baseflow was estimated to be 117 kg for the year—more than enough to satisfy the demands of riparian vegetation.

If these were the only sources of N for vegetation, then uptake by vegetation would explain a large proportion of the decline in NO_3 concentration between the stream and the riparian zone. However, mineralization was also found to provide 117 kg of available N annually. Combined with estimates of input from the other two sources, 341 kg of total N is provided through recycling (that is, mineralization) and new input, with 34% of the total and 50% of available N (mineralized + inorganic N) due to recycling of N from soil organic matter. Mineralization of N by itself exceeds estimated N demand by vegetation. Total annual available N from these three sources is more than double the estimated demand by vegetation. It seems likely that mineralized N would provide a significant proportion of N for plant production, reducing both the importance of stream water N as a source for riparian vegetation and the influence of plant uptake on N concentrations in water moving into the riparian zone from the stream.

Consistent with the mass balance analysis, N mineralization explained the most variation in leaf %N. However, the cause-and-effect relationship between these two variables is difficult to interpret because high leaf %N may also cause high mineralization. We believe that N mineralization is causing variation in leaf%N within the limits of our study because the leaves are responding to current growth conditions. Current mineralization rates are certainly influenced by the leaf%N of previous years, but our focus is on the relative importance of N sources within a growing season. In contrast to the results of the mass balance analysis and the stable isotope study, the index of stream water input—the hydraulic gradient—was not found to be significantly related to leaf%N (Figure 4C) in either the simple linear regression or the multiple regression analysis. Furthermore, although it provided the lowest mass of N (Table 2), total flood input was significantly related to leaf%N (Figure 4B), suggesting that floods were an important source of available N for the growth of plants, whereas baseflow inputs were not. This conclusion should be viewed

with caution, however, because the hydraulic gradient is only one of several variables that influence the input of water and N from stream to riparian zone. Variation in the hydraulic conductivity of soils, or of N concentrations in the parafluvial zone from site to site, could be obscuring the relationship between leaf%N and baseflow inputs.

Our two approaches, then, lead to opposite conclusions about the importance of baseflow and flood inputs. How can we reconcile these contradictory conclusions? The mass balance approach assumes that all of the input from each source is available to vegetation. To reconcile the two approaches, we need to determine the fate of N from each source. Several observations from this and previous work on Sycamore Creek provide some clues.

First, the stable isotope tracer experiment referred to earlier showed that only willow trees, which grow closest to the stream channel, were using detectable amounts of stream water N during baseflow, even though a conservative tracer (Br^-) showed that stream water was penetrating deeper into the riparian zone (J. D. Schade unpublished). Second, Holmes and others (1996) showed that the potential denitrification rate was high in sediments at the stream–riparian edge. Third, NO_3 concentrations declined sharply between parafluvial and edge wells, while NH_4 concentrations did not significantly change and DON increased only slightly (Table 1). All of these observations indicate that NO_3 may be removed from stream water by denitrification before it penetrates into the riparian zone. As a result, most trees do not have access to it as a resource.

Flood input was equivalent to 8% of the N required by vegetation. If we assume that all of the baseflow input of NO_3 was denitrified, but all of the NH_4 was available to vegetation, then we can account for another 11% of N demand by plants. We assume here that DON inputs from baseflow and flood are of a refractory nature and are not available to vegetation. Much of the other 81%, or 83 kg, of required N presumably came from the mineralization of N from soil organic matter. This assertion is supported by both approaches. Mineralization provided 40% of the remaining N demand (33 kg) in just the 3-month study period and the largest mass of available N when extrapolated to the growing season (77 kg, or 93% of the remaining N demand) and the entire year (117 kg, or more than 100%) (Table 2). Finally, mineralization explained the most variation in leaf%N in both simple linear and multiple regression analyses. Our calculations also suggest that there is excess available N beyond tree

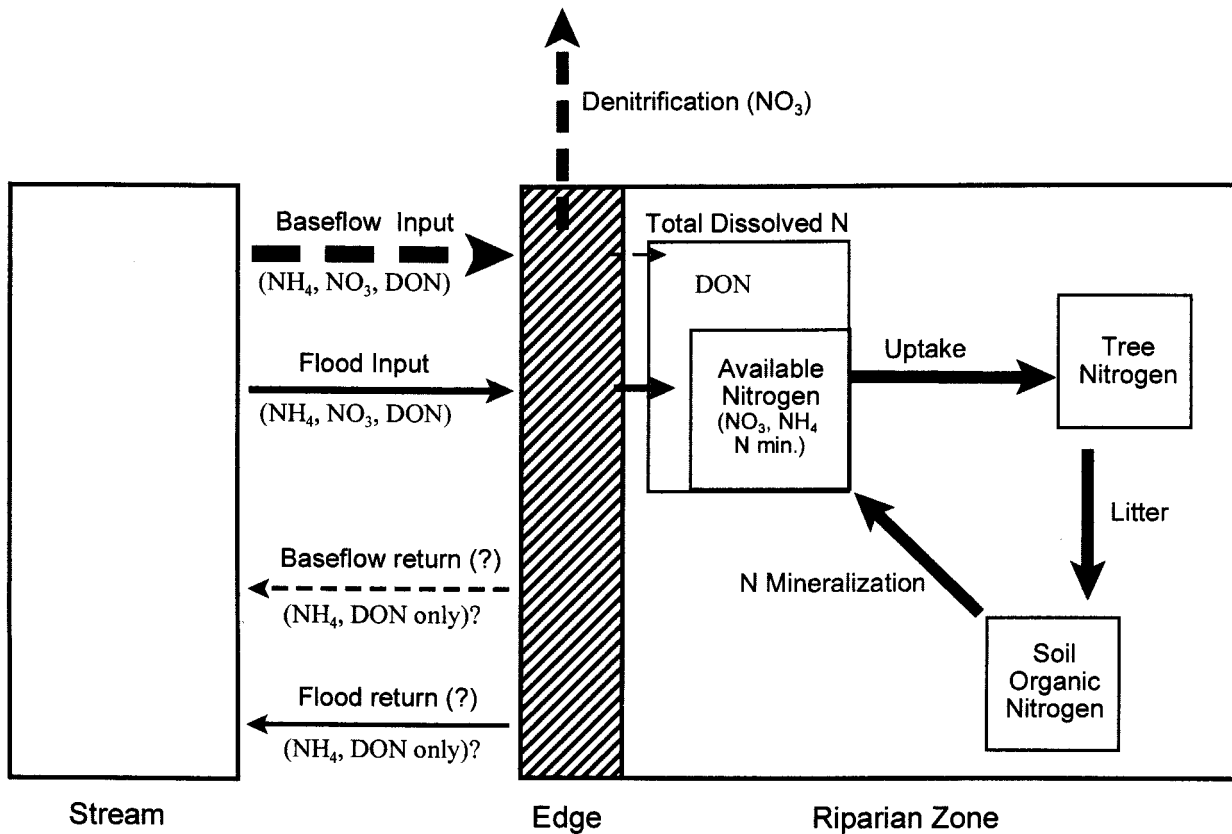


Figure 5. Conceptual model of N dynamics in the riparian zone and exchange of N with the surface stream. Much of baseflow NO₃ input is denitrified and lost from the riparian–stream ecosystem. The largest sources of available N come from recycling within riparian soils, with a smaller input during floods.

demand; however, this conclusion should be regarded with caution due to imprecisions in both our estimates of N demand and our calculations of N inputs.

These results have several important consequences for N cycling in riparian soils and N retention. First, mineralization provides a significant proportion of N for willow trees in Sycamore Creek and likely for species growing farther from the stream channel. Mineralization by itself, however, is simply recycling N from organic matter provided by the plants and cannot sustain net ecosystem production in the riparian zone. An outside source of N is required as a supplement. In this case, the source appears to be flood inputs of N and inputs of NH₄ from baseflow (Figure 5).

Other potential outside sources not considered here are atmospheric deposition and N fixation. Atmospheric deposition has been estimated at 3 kg ha⁻¹ y⁻¹ in the desert (Peterjohn and Schlesinger 1991). At this rate, atmospheric deposition would contribute a very small mass of N to the riparian zone relative to the sources discussed here. Mes-

quite trees (*Prosopis glandulosa*) are abundant and are known to fix N through associations with *Rhizobium* in their roots. This may provide N, either in available forms directly or through the production of organic matter that eventually enters the soil organic matter pool. In the latter case, this source would be reflected in measurements of N mineralization and may explain why N mineralization rates are higher than estimated N demand by trees. Both atmospheric deposition and N fixation may take on a greater significance in forests lacking the fluvial input of N in floods and baseflow. In upland forests, which are relatively disconnected from hydrologic interaction with streams, aboveground net primary production (ANPP) has been shown to be related to N recycling rate (Pastor and others 1984), and the N mineralization rate is a major indicator of N availability (Binkley and Hart 1989). These systems rely on atmospheric deposition and N fixation as subsidies to maintain positive net ecosystem production.

Several indirect lines of evidence from this study and other work suggest that most of the NO₃ entering the riparian zone in stream water at baseflow

is not used by trees but is lost to denitrification. Furthermore, both DON and NH_4 were slightly higher in riparian and edge wells than parafluvial wells. This finding raises the possibility that these N forms are produced in riparian soils, presumably through microbial processes associated with the decomposition and ammonification of soil organic matter. At the very least, there is little net retention of them by the riparian zone. These patterns strongly suggest that uptake by trees is not retaining significant amounts of N from stream water. The production of vegetation in the riparian zone is relatively disconnected from processes occurring in the stream, except during floods. Interestingly, the N in flood water comes primarily from runoff from the upland desert, which moves into small rills and eventually into large channels where it infiltrates, carrying solutes with it, and moves out into the riparian zone. Floods provide a spatial link between N cycling in the upland and the riparian zone; the upland may, in fact, be the ultimate source of N in flood water. If this is the case, then the production of riparian vegetation in both arid and mesic watersheds is tightly connected to processes that occur in the upland, such as atmospheric deposition and N-fixation, although the routing of water is quite different.

According to our results, the retention of N from stream water entering the riparian zone is most likely accomplished by soil microbes, and N is permanently lost to the atmosphere as N_2 by denitrification. Not surprisingly, soil microbes play a dominant role in N cycling in riparian zones in Sycamore Creek through a number of processes, including mineralization, denitrification, and probably N fixation. All of these processes are dependent on the production of organic matter by the plants; however, denitrification is the only one that leads to the loss of available N from the ecosystem. Of particular importance for N retention is the observation that high denitrification rates are associated with the presence of plants and especially with the production of belowground biomass (Schade and others 2001; Bakken 1988; Smith and Tiedje 1979; Bailey 1976; Woldendorp 1962). This association provides a link between plants and microbes that can lead to high rates of NO_3 removal.

As a result of this work, we have developed a conceptual model of N cycling in arid-land riparian zones and the linkage between the riparian zone and the stream, in terms of nutrient exchange (Figure 5). In this conceptual model, a large mass of N enters the riparian zone from the stream during baseflow. Much of this N input is removed from the water by denitrification in organic matter-rich soils

located at the interface between the stream and the riparian zone. This loss happens very quickly and prevents plants from using stream water N to support growth. This contention is supported by previous research in a number of systems that has shown the rapid removal of NO_3 from water moving into riparian soils from upland soils (Hedin and others 1998; Peterjohn and Correll 1984) or from the stream (Hill and others 1998); these NO_3 losses have been attributed to high rates of denitrification. The retention of N occurs mainly through the removal of NO_3 ; other forms of N pass through the stream-riparian interface relatively unaffected. In fact, DON concentrations were significantly higher in the riparian zone than in gravel bars (Table 1), suggesting that the riparian zone may be a source of organic N to the stream at locations of groundwater movement from riparian zone to stream (Figure 5).

The bulk of N for riparian production in our model, as in more traditional upland forest studies, comes from the mineralization of N from soil organic matter, with a supplement of available N through the movement of water from stream to riparian zone, particularly during floods (Figure 5). Unfortunately, the importance of floods as a source of N is difficult to determine, because we do not know the fate of flood water N and because flood inputs vary tremendously from flood to flood and from year to year, depending on their frequency and magnitude. In general, though, the structure and function of riparian zones is intimately tied to floods for several reasons. First, large-magnitude floods remove tree biomass (Stromberg 1993), maintaining the forest in an early successional stage and creating the potential for positive net ecosystem production. Second, floods are required for the dispersal and germination of the seeds of some riparian tree species (Stromberg 1993). We can now add a third—the input of available N and presumably other nutrients required for the growth of trees.

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