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PERSPECTIVES

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Is in-stream N_2 fixation an important N source for benthic communities and stream ecosystems?

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Abstract. We evaluate the current state of knowledge concerning the ecosystem- and community-level importance of N_2 fixation in streams. We reviewed the literature reporting N_2-fixation contributions to stream N budgets and compared in-stream N_2-fixation rates to denitrification and dissolved inorganic N (DIN)-uptake rates. In-stream N_2 fixation rarely contributed >5% of the annual N input in N budgets that explicitly measured N_2 fixation, but could contribute higher proportions when considered over daily or seasonal time scales. N_2-fixation rates were statistically indistinguishable from denitrification and DIN-uptake rates from the same stream reach. However, published N_2-fixation rates compiled from a wide variety of streams were significantly lower than denitrification or DIN-uptake rates, which were indistinguishable from one another. The data set we compiled might be biased because the number of published N_2-fixation measurements is small (9 studies reporting rates in 22 streams), the range of stream conditions (NO_3^--N concentration, discharge, season) under which N_2-fixation and other N-processing rates have been measured is limited, and all of the rate estimates have associated methodological artifacts. To broaden our understanding of how N_2 fixation contributes to stream ecosystems, studies must measure all rates concurrently across a broad range of stream conditions. In addition, focusing on how N_2 fixation supports food webs and contributes to benthic community dynamics will help us understand the full ecological ramifications of N_2 fixation in streams, regardless of the magnitude of the N flux into streams from N_2 fixation.

Key words: nitrogen fixation, DIN uptake, denitrification, nitrogen cycle, ammonium, nitrate, stream.

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Thousands of types of bacteria fix N_2 (gas) in many different aquatic and terrestrial microhabitats. In aquatic systems, N_2 fixation is carried out mainly by cyanobacteria, which are specialized autotrophic prokaryotes (Whitton and Potts 2000), although heterotrophic bacteria similar to those found in terrestrial environments also might be important stream N_2 fixers (Buckley and Triska 1978). Nitrogenase is the enzyme responsible for N_2 fixation, and because O_2 strongly inhibits nitrogenase activity, researchers initially thought that heterocysts, specialized thick-walled cells, were necessary for cyanobacteria to carry out the 2 seemingly incompatible processes of photosynthesis and N_2 fixation (Walsby 1985). However, in oceans, N_2 fixation also can be carried out by nonheterocystous cyanobacteria (Bergman et al. 1997) that use mechanisms such as within-cell or temporal separation to allow co-occurence of photosynthesis and N_2 fixation (Giani and Krumbein 1986, Reddy et al. 1993). In streams, the dominant autotrophic N_2 fixers are heterocystous cyanobacteria, such as *Nostoc*, *Anabaena*, *Calothrix*, and *Phoridium*, and unicellular cyanobacterial endosymbionts of diatoms of the order Rhopalodiales, including *Epithemia* and *Rhopalodia* (Wehr and Sheath 2003). No researchers have confirmed the existence of free-living, N_2-fixing unicellular cyanobacteria in streams, but endosymbionts within *Rhopalodia gibba* are closely related to 2 strains of the unicellular N_2-fixing cyanobacterium *Cyanothece* sp. (Prechtl et al. 2004), which is commonly found in ocean environments (Reddy et al. 1993).

N_2 fixation represents a source of N at both the organism and ecosystem levels. In lakes, N_2 fixation by heterocystous cyanobacteria influences competitive interactions (Sterner 1989) and can make up as much as 82% of annual N budgets (Howarth et al. 1988). In the oceans, N_2 fixation is proportionally less important than in lakes, but recent work has shown that marine nonheterocystous cyanobacteria are significant contributors to the global N cycle (Zehr et al. 2001, Montoya et al. 2004). Despite intensive study of N_2 fixation in the open ocean, estuaries, and lakes (Howarth et al. 1988), and the common presence of N_2 fixers in stream benthic communities, N_2-fixation rates in streams have seldom been measured. A few notable exceptions have shown that N_2-fixation rates in streams can be quite high where periphyton communities are dominated by cyanobacteria (Horne and Carmiggelt 1975, Grimm and Petrone 1997) or when ambient NO_3^- levels are low (Grimm 1994).

N cycling is currently a broad focus of ecosystem ecology because human activities have approximately doubled the amount of N cycling globally (Vitousek et al. 1997). Increased N loads to coastal ecosystems and subsequent eutrophication and hypoxia in areas such as the Gulf of Mexico (Rabalais et al. 2002) have led stream ecologists to study how N is transported from terrestrial areas to rivers and estuaries further downstream. Stoddard (1994) proposed that increased N loading to terrestrial systems would result in predictable alterations in the amount and timing of N transport and export from watersheds. Headwater streams are thought to be important sinks of N in the landscape (Alexander et al. 2000), and the application of nutrient spiraling theory (Newbold et al. 1981, Stream Solute Workshop 1990) has led to the discovery that small headwater streams have high rates of uptake of inorganic N (Peterson et al. 2001). Intersite research programs have produced large data sets of N-uptake parameters for streams in a variety of ecosystems (e.g., Webster et al. 2003). Recently, researchers have focused on quantifying denitrification, which represents a permanent loss of N from stream ecosystems (Seitzinger 1988, Royer et al. 2004, Mulholland et al. 2004b). These new, readily available data provide an opportunity to examine the importance of N_2 fixation in streams relative to other N-processing rates.

We evaluate the current state of knowledge concerning the importance of N_2 fixation in streams. We use several criteria to evaluate the potential importance of N_2 fixation because few authors report N_2-fixation rates in these ecosystems. First, we summarize studies where N_2-fixation contributions to stream N budgets have been considered. We then compare N_2-fixation rates to denitrification and uptake rates of dissolved inorganic N (DIN; NH_4^+-N and NO_3^--N) from the published literature. Comparing N_2 fixation to denitrification provides insight into gaseous inputs and outputs from the stream N pool, whereas comparing N_2 fixation to DIN-uptake rates provides insight into sources of N for autotrophic and heterotrophic production. We restrict our comparison to rates measured in the channel itself rather than including rates measured in riparian areas and terrestrial uplands because we know the least about N_2-fixation contributions to surface water and benthic processes. This comparison identifies a major gap in the stream ecology literature. We conclude with a discussion of the potential limitations of N budgets and our rate comparison, and the importance of N_2 fixation and cyanobacteria to stream communities and ecosystems.

Contribution of N_2 Fixation to Stream N Budgets

At the ecosystem level, the importance of in-stream N_2 fixation has been considered in several N-budget studies where N_2 fixation was included as an N source.

For the purposes of this comparison, we selected only N budget studies in which N_2 fixation was measured directly (typically with the acetylene reduction assay) rather than studies in which it was estimated as a remainder of the N budget. Studies in which the contributions of N_2 fixation to stream N budgets are measured directly are rare, and such data are available for only a few streams.

N budget studies suggest that N_2 fixation might not be a large source of N to stream ecosystems and rarely contributes >5% of the N input on an annual basis. N_2 fixation contributed only 0.01% of the annual N input in Bear Brook, a small headwater forested stream (Meyer et al. 1981). Bear Brook is heavily shaded, and when that N budget was constructed, periphyton were essentially absent from the stream biota (Fisher and Likens 1973). N_2 fixation contributed 4.2% of the N annually to a riffle in a 2nd-order Quebec stream, but when a similar reach was dammed by beaver, N_2 fixation by sediment microbes contributed 68% of the annual N budget (Naiman and Melillo 1984). This increase did not occur because of a difference in N_2-fixation activity between the 2 habitat types, but rather because of the greater sediment area available for microbial colonization in the beaver pond compared with in the riffle reaches (Francis et al. 1985). N_2 fixation supplied 5% of the annual N input, compared with 73% from upstream (hydrological inputs as NO_3^--N and dissolved organic N [DON]) and 22% from terrestrial organic matter, in another small forested stream (Triska et al. 1984). N_2 fixation contributed 4%, an amount similar to the input from atmospheric deposition to the pond surface, of the annual N budget in an oligotrophic, streamlike pond with significant water flow and abundant *Nostoc pruniforme* (Dodds and Castenholz 1988). Overall, these contributions are generally greater than or within the range of contributions of N_2 fixation observed in mesotrophic lakes (0.1–0.3% of annual budget), but less than in the budgets of eutrophic lakes (5–82%) (Howarth et al. 1988).

These annual budgets suggest that, overall, N_2 fixation contributes less N to stream reaches than do hydrologic or litter inputs, but they do not take into account seasonal or successional variations in N flux and N_2 fixation. For example, N_2 fixation in a 3rd-order montane stream reach was far less than the annual hydrologic input of total N or NO_3^--N; however, N_2 fixation was greater than the NO_3^--N flux during late summer, when discharge and NO_3^--N concentration were low and biological activity was high (Marcarelli 2006). Annual rates of N_2 fixation were very high (8.0–12.5 g/m^2) in Sycamore Creek, a desert stream, and were comparable with rates measured in eutrophic lakes and rice fields (Grimm and Petrone 1997). However, daily contributions of N_2 fixation to the total N input to stream benthos ranged from 0 to 85% depending on the season and abundance of cyanobacteria (Grimm and Petrone 1997). In Sycamore Creek, contributions from N_2 fixation to the N budget were controlled directly by DIN availability, which was controlled by algal community composition and biomass, which were, in turn, controlled by floods that scoured the periphyton community (Fisher et al. 1982, Grimm 1987).

When considering the contribution of N_2 fixation to annual N budgets, N_2 fixation is often compared with hydrologic and litter N inputs without considering how N inputs are assimilated by stream biota. In marine systems, ⅔ of the N obtained by cyanobacteria via N_2 fixation is assimilated directly into cellular material (Mulholland et al. 2004a), and the remaining ⅓ is released from the cell as DON, which can be used by the surrounding algal and bacterial community (Brookshire et al. 2005). Therefore, it is likely that most N introduced into a stream via N_2 fixation is stored at least temporarily in benthic biomass either by direct incorporation or by DON assimilation. In contrast, the fate of hydrologic N cannot be quantified once it enters a stream reach; it might pass through the stream reach unaltered, be retained temporarily through cycling by the biota, be transformed and exported as dissolved or particulate organic N, or be lost permanently through denitrification.

Last, nutrient budgets are susceptible to problems related to stream size. Nutrient inputs, such as N_2 fixation, that are measured per unit stream area are dependent on the overall area of the stream bottom and are not directly comparable with hydrologic or linear inputs, such as NO_3^--N transported from upstream or laterally from the riparian zone, which are independent of stream size (Cummins et al. 1983). Some studies have avoided this problem by estimating nutrient budgets for the entire watershed (e.g., Triska et al. 1984). However, this approach is not feasible for large watersheds or studies with a more limited research scope. Comparison of N_2 fixation to N-transformation rates, such as denitrification and DIN uptake, that also are measured on an areal basis might provide more insight than comparisons with hydrologic or linear input processes when trying to evaluate the importance of N_2 fixation in stream ecosystems.

Comparing N_2-fixation, DIN-uptake, and Denitrification Rates in Streams

We compared whole-stream biological DIN-uptake rates with in-stream rates of N_2 fixation and denitrification. These comparisons are appropriate because DIN uptake, N_2 fixation, and denitrification are all measured on an areal basis and are independent of system size. From an ecosystem perspective, N_2 fixation and denitrification are an important source and sink, respectively, for N, whereas NH_4^+-N and NO_3^--N uptake are transformations of N into organic form where N will be stored temporarily within a stream. Comparing N_2 fixation and denitrification in streams is logical because these inverse processes convert N_2 gas to inorganic form and inorganic N to N_2 gas, respectively, and thus, indicate true input to and output from the available N pool. N_2 fixation also can be compared appropriately to DIN uptake in streams because the N obtained via N_2 fixation is incorporated into autotrophic or heterotrophic biomass, temporarily stored, and then released into the water column through mineralization in a manner similar to DIN spiraling. Therefore, comparing DIN-uptake rates to N_2 fixation allows assessment of the relative contributions of N obtained from uptake of inorganic material from the water column and N obtained from fixation for biological production. In addition, a rich literature provides comparisons with N_2-fixation rates because most stream N-cycling literature in the recent past has focused on measuring DIN-uptake rates and denitrification.

Multirate streams

We surveyed the literature to find all possible reports of N_2-fixation, denitrification, and DIN-uptake rates measured in the same stream. We located references with Web of Science (Thomson Scientific, Philadelphia, Pennsylvania), Water Resources Abstracts (ProQuest-CSA, Bethesda, Maryland), reference sections of other studies, and personal communication with researchers. This search identified 9 studies in which N_2-fixation rates were reported for 22 stream reaches (Appendix). We then searched for NO_3^--N-uptake, NH_4^+-N-uptake, and denitrification rates measured in the same stream reaches for which N_2-fixation rates had been reported. We called these systems *multirate streams*. We compared N_2-fixation, denitrification, NH_4^+-N-uptake, and NO_3^--N-uptake rates with Kruskal–Wallis tests with $\alpha = 0.05$ (SAS, version 9; SAS Institute, Cary, North Carolina; Zar 1999). When this test was significant, we assessed post hoc differences with pairwise comparisons on the basis of Mann–Whitney U tests. We corrected p values from the post hoc tests for multiple tests using the Dunn–Sidak method (Gotelli and Ellison 2004). The data sets we have compiled here cannot be considered a random analysis of all streams, and therefore, the conclusions we reach should be treated with caution.

Our literature review revealed that N_2 fixation, denitrification, and DIN uptake are very rarely measured in the same stream system. We identified only 1 study that measured N_2-fixation and DIN-uptake rates as part of a comprehensive study (Howard-Williams et al. 1989), and this study excluded denitrification. We identified 17 study reaches in which N_2 fixation and ≥ 1 of the other rates had been measured (Table 1). These rates typically were measured in the same month or season, although for at least a few reaches, the rate estimates were made years or decades apart (e.g., Watershed 2, Oregon, and Watershed 6, New Hampshire; Appendix). All measurements were made between March and November. Rates were measured only during summer in most (15 of 17) studies and during spring, summer, and autumn in 2 studies. Study reaches in multirate streams were 1st to 4th order with discharge (Q) from 0.001 to 13.7 m^3/s.

Comparisons in multirate streams indicated that N_2-fixation rates are frequently similar to other N-processing rates. However, the relative importance of N_2 fixation is extremely variable when considered on a stream-by-stream basis (Table 1). N_2-fixation, denitrification, and DIN-uptake rates did not differ from each other in the multirate streams (Kruskal–Wallis, $\chi^2_{3\,df} = 6.03$, $p = 0.11$). N_2-fixation rates were higher than denitrification rates in 5 of the 9 streams in which both were measured and lower in 4. N_2 fixation ranged from 1250× lower than denitrification in Watershed 6, New Hampshire, to 117× greater than denitrification in Sycamore Creek, Arizona (Table 1). N_2-fixation rates were greater than NO_3^--N uptake rates in 5 of 17 streams in which both were measured, lower in 10, and approximately equal in 2 (Sycamore Creek and Toxaway–lake outlet, Idaho). N_2 fixation ranged from 8650× lower than NO_3^--N uptake in Warm Spring Creek–lake inlet, Idaho, to 13.1× greater than NO_3^--N uptake in Watershed 2 (Table 1). N_2-fixation rates were greater than NH_4^+-N uptake in 2 of 6 streams where both were measured and lower in 4. N_2 fixation ranged from 1100× lower than NH_4^+-N uptake in Warm Spring Creek–lake inlet to 4.8× greater than NH_4^+-N uptake in Sycamore Creek (Table 1).

Literature-review streams

We also did a wider literature search to compile N_2-fixation, DIN-uptake, and denitrification rates from a wide variety of stream studies. We used N_2-fixation rates from all 22 stream reaches identified in the 1st

Table 1. Mean N_2-fixation, denitrification, NO_3^--N-uptake, and NH_4^+-N-uptake rates (range). All rates were converted to μg N m^{-2} h^{-1}. See Appendix for citations for rate studies and specific measurement methods. Cr. = Creek, Br. = Brook, — = data not available.

Stream	N_2 fixation	Denitrification	NO_3^--N uptake	NH_4^+-N uptake
Adams Stream, Antarctica	460 (0.6–1360)	1470[a] (630–2300)	8100 (4800–14,500)	18,800 (9400–37,000)
Farley–lake inlet, Idaho	5	—	14,700	—
Farley–lake outlet, Idaho	9	—	0	—
Fryxell Stream, Antarctica	410 (2.7–820)	1470[a] (630–2300)	4160 (1670–6700)	240 (95–380)
Stanley Lake Cr.–reference, Idaho	27	—	440	—
Stanley Lake Cr.–lake inlet, Idaho	5.7	0	540 (300–1170)	—
Stanley Lake Cr.–lake outlet, Idaho	620	0	0 (0–0)	—
Sycamore Cr., Arizona	8400 (0–51,000)	72 (1–180)	9130	1750
Toxaway–lake inlet, Idaho	10	—	970	—
Toxaway–lake outlet, Idaho	4	—	0	—
Warm Spring Cr.–reference, Idaho	6	—	1700	—
Warm Spring Cr.–lake inlet, Idaho	0.1	0	865	110 (37–193)
Warm Spring Cr.–lake outlet, Idaho	8.7	26	0 (0–418)	825 (267–1804)
Watershed 2, Oregon	1920	—	146 (70–290)	—
Watershed 6, New Hampshire	2[b]	2500 (2000–3000)	810 (690–930)	350 (290–470)
Yellow Belly Cr.–lake inlet, Idaho	8.7	—	4270	—
Yellow Belly Cr.–lake outlet, Idaho	410	0	0 (0–0)	—

[a] Rates from a nearby Antarctic stream with a similar biological community
[b] Rough estimate on the basis of annual budget data for Bear Br.

literature survey. We identified studies of whole-stream DIN-uptake rates from the review by Ensign and Doyle (2006). This data set was supplemented with rates from the multirate streams (if not included) and from several recently published studies (Appendix). We found denitrification rates by searching the Web of Science. We compiled rates from these references, references cited therein, and from the multirate stream studies (Table 1). We included rates only if they were measured directly in enclosures or at the reach scale; we excluded rates if they were estimated using reach-scale total N or NO_3^--N mass-balance methods. However, we did include rates from denitrification studies that measured whole-reach N_2:Ar balance using membrane-inlet mass spectrometry (e.g., Laursen and Seitzinger 2002). For comparison, we converted all rates to units of micrograms of N per square meter per hour. We excluded studies where rates could not be converted to similar units (e.g., rates given per unit biomass with no report of biomass per unit area) from the data set. For each study, we noted the method used to measure the rate, the month and year of measurement, study location, Q, stream order, and nutrient concentration when available (Appendix). We call these systems *literature-review streams*. We compared rates as described above in *Multirate streams*.

We found fewer estimates of N_2 fixation ($n = 22$) than of any other rates (denitrification: $n = 62$, NH_4^+-N uptake: $n = 67$, NO_3^--N uptake: $n = 87$). NH_4^+-N uptake varied across 4, N_2 fixation varied across 5, denitrification varied across 6, and NO_3^--N uptake varied across 7 orders of magnitude (Fig. 1). The median N_2-fixation rate (10 μg N m^{-2} h^{-1}) was 1 to 2 orders of magnitude lower than the median of the other 3 rates (denitrification median = 1605 μg N m^{-2} h^{-1}, NH_4^+-N uptake median = 1300 μg N m^{-2} h^{-1}, NO_3^--N uptake median = 870 μg N m^{-2} h^{-1}; Fig. 1). N_2-fixation, denitrification, and DIN-uptake rates differed in the literature-review streams (Kruskal–Wallis, $\chi^2_{3\,df} = 25.7$, $p < 0.001$; Fig. 1). N_2-fixation rates were significantly lower than the other 3 N-processing rates, which did not differ from each other (Fig. 1).

The literature-review streams were much more

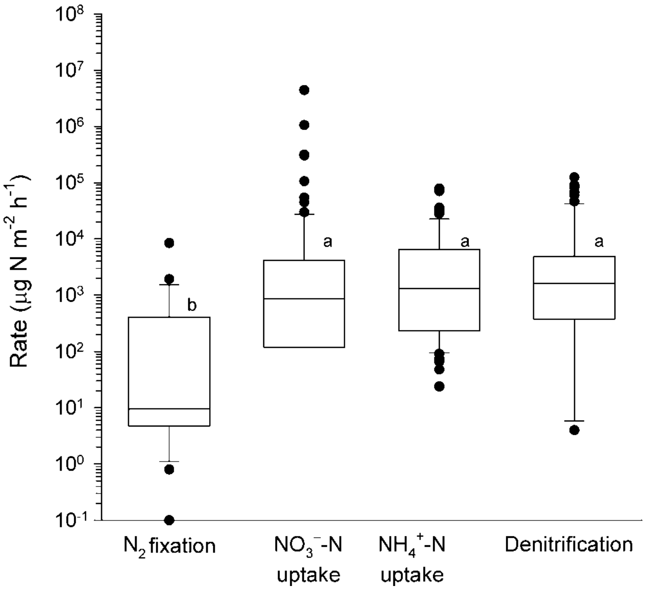

FIG. 1. Box-and-whisker plots of N_2-fixation (n = 22), NO_3^--N-uptake (n = 87), NH_4^+-N-uptake (n = 67), and denitrification (n = 62) rates from the literature-review streams. The box plot shows the median (middle line), 1st and 3rd quartiles (top and bottom of box), 95% confidence intervals (whiskers), and outlier values (dots). Rates were converted to hourly rates to facilitate comparison. Plots with the same letters are not significantly different (post hoc Mann–Whitney U tests with a Dunn–Sidak-corrected α value).

variable than the multirate streams in terms of timing of studies and stream characteristics, such as Q and NO_3^--N concentration. Fifty-four percent of N_2-fixation, 49% of NH_4^+-N-uptake, and 60% of NO_3^--N-uptake rate measurements were made during summer (Fig. 2A, D). In contrast, denitrification rates were measured throughout the year (Fig. 2A). Q ranged from 0.001 to 13.7 m^3/s in studies of N_2-fixation, from 0.0001 to 2.4 m^3/s in studies of NH_4^+-N and NO_3^--N uptake, and from 0.0004 to 13,100 m^3/s in studies of denitrification rates (Appendix). Frequency analysis indicated that denitrification, N_2 fixation, and NO_3^--N uptake were most often measured in streams where Q was 0.1 to 1 m^3/s, whereas NH_4^+-N uptake tended to be measured in streams where Q ranged from 0.01 to 0.1 m^3/s (Fig. 2B, E). Therefore, we also analyzed rates in streams grouped by Q in the same order of magnitude (e.g., rates in streams where Q = 0.01–0.1 m^3/s; Fig. 2B, E). The 4 N-processing rates were statistically indistinguishable in every group except Q = 0.1 to 1 m^3/s ($\chi^2_{3\,df} = 10.7$, $p = 0.01$). For this group, which also had the largest number of rate estimates (total $n = 72$), NO_3^--N- and NH_4^+-N-uptake rates were significantly different from N_2-fixation rates, and denitrification rates were not distinguishable from the other rates. This result indicates that our literature-review analysis of the relative importance of N-processing rates probably was affected by the fact that the frequency of measurement of each N-processing rate differed with Q (Fig. 2B, E). NO_3^--N concentrations in the study streams varied from 1 to 16,520 μg/L, and the distribution of studies across this range also varied among the 4 N-processing rates (Fig. 2C, F). N_2 fixation, NO_3^--N uptake, and NH_4^+-N uptake were most often measured in streams where NO_3^--N concentrations averaged 10 to 100 μg/L, whereas denitrification was most frequently measured in streams with NO_3^--N concentrations of 1000 to 10,000 μg/L (Fig. 2C, F).

Implications and Potential Data Biases

Several biases are inherent in the N-cycling literature and should be recognized when N-processing rates and N budget summaries are compared across studies. First, studies are not randomly distributed across stream types; many were done in preselected habitats where rates were expected to be high. For example, 12 of 17 N_2-fixation rate estimates from multirate streams were from our work on central Idaho streams, where we expected N_2 fixation to be an important contributor to the N budget because of low ambient DIN concentrations. We would expect N_2 fixation to be high in streams where communities are strongly limited by DIN availability and low in streams with high DIN availability because of the high energetic cost of N_2 fixation compared with the costs of NH_4^+-N or NO_3^--N uptake (Howarth et al. 1988). Nevertheless, rates of N_2 fixation in the central Idaho streams were low compared with other rates reported in the literature (Marcarelli 2006).

Second, the denitrification rates found in our review might be skewed toward streams where denitrification was a large contributor to the N cycle because they were measured most frequently in streams with high NO_3^--N concentrations (Fig. 2C). Denitrification rates can increase with increasing availability of NO_3^- as an oxidization substrate (Bernot and Dodds 2005). Therefore, streams with high rates of denitrification might not support high rates of N_2 fixation and vice versa. In the literature-review streams, denitrification rate increased significantly with NO_3^--N concentration ($\log_{10}[y + 1] = 0.64 + 0.86 \log_{10}[x + 1]$, $F_{1,48} = 47.4$, $p < 0.0001$, $r^2 = 0.50$; Fig. 3A). In contrast, N_2-fixation rate was not related to NO_3^--N concentration (Fig. 3B), probably because of the limited number of rates reported in the literature and the small range of

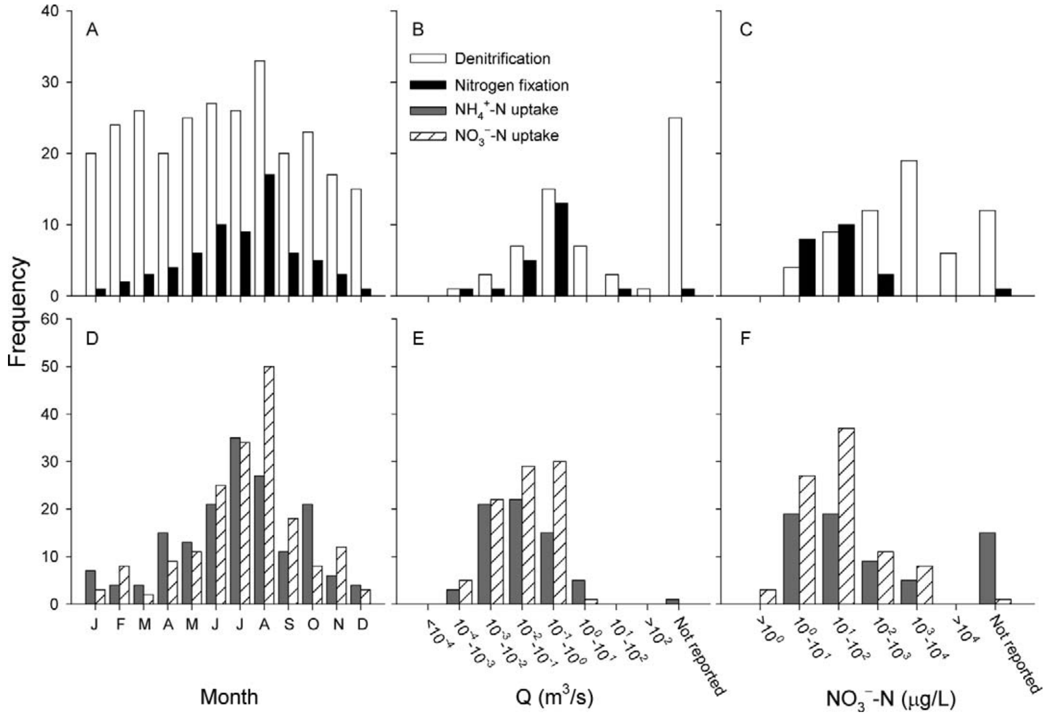

Fig. 2. Frequency plots of N_2-fixation and denitrification rates by month of study (A), stream discharge (Q) (B), and NO_3^--N concentration (conc) (C), and of NO_3^--N- and NH_4^+-N-uptake rates by month of study (D), stream discharge (E), and NO_3^--N concentration (F). All data are from the literature-review streams (Appendix). For studies done in the Southern Hemisphere, months were coded as the equivalent Northern-Hemisphere month (e.g., January was coded as July).

NO_3^--N concentrations across which N_2-fixation rates were measured.

The narrow and low range of N concentrations across which N_2-fixation rates have been examined in streams is in stark contrast to the range in lakes, where N_2 fixation is associated (counterintuitively) with high N concentrations and eutrophic conditions. A review of N budget studies in lakes showed that N_2 fixation contributes 6 to 82% of the annual N budget in eutrophic lakes (Howarth et al. 1988). The lakes with the highest N_2-fixation contributions are nutrient-rich systems that support cyanobacterial blooms. However, it is unclear whether cyanobacterial dominance in these nutrient-rich lakes is the result of the ability of cyanobacteria to fix additional N to support growth and outcompete other taxa, or of competition for some other resource, such as light (e.g., Ferber et al. 2004). To our knowledge, no estimates of benthic N_2-fixation rates have been made in nutrient-rich 1st- to 5th-order streams, probably because the periphyton communities in these streams are sometimes nutrient saturated (Bernot and Dodds 2005, Earl et al. 2006). The high N contribution from N_2 fixation in eutrophic lakes suggests that N_2 fixation in eutrophic streams should be examined more closely.

The lowest rates of denitrification in our data set were from central Idaho streams (MAB and L. Jeffs, Utah State University, unpublished data). It is possible that 0 or low rates of denitrification have been measured in other streams with low NO_3^--N concentrations but not published. A low publication rate for negative results is a common problem in biological research (Csada et al. 1996), and could lead to overestimation of the importance of denitrification in streams.

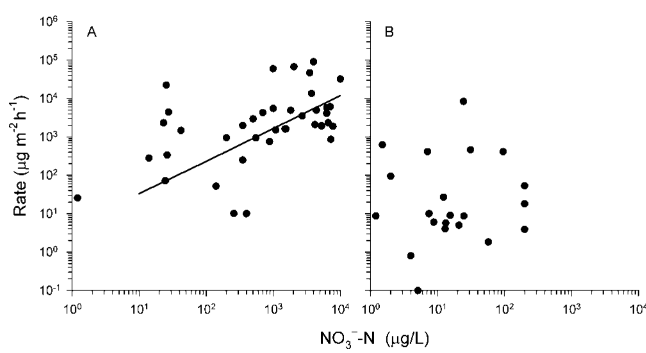

Fig. 3. Denitrification (A) and N_2-fixation (B) rates vs NO_3^--N concentration for studies where NO_3^--N concentrations were available (denitrification $n = 50$, N_2 fixation $n = 20$). Note similarity of both rates at low NO_3^- concentrations.

Seasonal variation in denitrification is well represented in the literature, but seasonal variations in DIN uptake and N_2 fixation are not; most studies have been done during summer. This focus on summer undoubtedly has biased our understanding of the relative importance of N-processing rates. For example, in subalpine streams, small increases in water temperature (3–5°C) stimulate N_2 fixation (Marcarelli and Wurtsbaugh 2006). The small number of N-processing studies during seasons when Q is high, such as spring snowmelt in the western montane US, is especially troubling because most nutrients move during high-flow periods (e.g., Wurtsbaugh et al. 2005). A full understanding of N-cycling rates in streams will require more effort across the entire year and at a variety of Q values.

In every study we reviewed, N_2-fixation rates were measured per unit area of substrate in enclosed containers (most frequently using the acetylene-reduction assay; Stewart et al. 1967), and then scaled to stream area. In contrast, denitrification and nutrient-uptake rates sometimes were measured with whole-stream techniques that account for spatial heterogeneity. Whole-stream techniques for measuring denitrification and nutrient uptake include both surface and hyporheic-zone processes (Findlay 1995), whereas enclosure techniques typically focus on surface processes. Development of a whole-stream N_2-fixation technique would permit more direct comparisons of N_2-fixation rates with whole-stream uptake and denitrification rates, could be applied to a larger range of stream and river sizes, and would eliminate some of the uncertainty concerning the effects of methods on the rates compared in our study.

Whole-stream nutrient-uptake techniques are most commonly applied in small streams (Ensign and Doyle 2006). In contrast, whole-stream denitrification techniques, particularly those based on changes in N_2 gas concentrations, can be applied in small streams and large rivers (Laursen and Seitzinger 2002). Thus, denitrification has been measured in systems that are much larger than the systems used for studies of N_2 fixation or whole-stream nutrient uptake. However, denitrification metrics on the basis of changes in N_2 gas concentrations actually represent a balance between N_2 loss via N_2 fixation and N_2 gain via denitrification. An assumption of the method is that N_2-fixation rates will be negligible when NO_3^--N concentrations are high; thus, this technique has been applied most often in N-rich large rivers. In contrast, whole-stream denitrification methods that use ^{15}N tracers (e.g., Mulholland et al. 2004b) measure only denitrification.

Although some denitrification rates reported in our review were made with whole-stream techniques (e.g., Laursen and Seitzinger 2002, Mulholland et al. 2004b), others were made in enclosed containers with the acetylene-block technique. The acetylene-block technique can underestimate denitrification rates by 50% compared to ^{15}N-tracer methods (Seitzinger et al. 1993) because it inhibits coupled nitrification–denitrification and can incompletely inhibit N_2O production, although many studies used a modified acetylene-block technique that accounted for this inhibition (Bernot et al. 2003). We took care to exclude potential denitrification rates (e.g., rates measured with additions of NO_3^--N or DON) when extracting data from denitrification studies for the literature-review data set.

NO_3^--N- and NH_4^+-N-uptake rates reviewed in our study were made in streams that spanned a large geographic area, included a large number of estimates (compared with the number of N_2-fixation estimates), and probably represented the potential range of DIN-uptake rates in small streams ($<5^{th}$ order). Some of the NO_3^--N- and NH_4^+-N-uptake rates were measured with traditional enrichment injections, whereas others were measured with ^{15}N tracers (Ensign and Doyle 2006). Enrichment experiments overestimate the nutrient uptake length (S_w) 2 to 3$\times$ compared with tracer experiments (Mulholland et al. 2002, Payn et al. 2005), and therefore, underestimate the mass-transfer coefficient (uptake velocity; mm/h). However, because they elevate nutrient concentrations, enrichment experiments also overestimate uptake rates (Dodds et al. 2002). Therefore, many of the DIN-uptake rates in our review are probably overestimates, and N_2 fixation might be even more important than our analysis suggests. Future work should focus on comparing N_2-fixation rates to DIN-uptake rates measured with ^{15}N-tracer additions or the promising multilevel release technique of Payn et al. (2005).

Ecological Importance of N_2 Fixation for Stream Communities

Our review examined N_2 fixation relative to N budgets and N-processing rates from an ecosystem perspective, but N_2 fixation by particular taxa could have important consequences at the level of stream community dynamics. Cyanobacteria probably have a competitive advantage over other periphyton taxa in N-limited streams because of their ability to fix atmospheric N_2, as has been observed in lakes (e.g., Sterner 1989). This advantage can have important implications for the patch dynamics of algal community structure. For example, cyanobacterial abundance in Sycamore Creek is controlled spatially by hyporheic exchange patterns. Cyanobacteria are abundant at

N-poor downwelling edges of sandbars, and taxa that do not fix N_2 are abundant at N-rich upwelling edges of sandbars (Henry and Fisher 2003). In other stream studies, P enrichment increased the abundance of N_2-fixing taxa (e.g., Elwood et al. 1981) and, in turn, increased N_2-fixation rates (Marcarelli and Wurtsbaugh 2006, 2007). These results suggest that cyanobacteria do not become dominant only when N concentrations are low, but rather are controlled by a combination of chemical factors that includes P availability (e.g., Marcarelli and Wurtsbaugh 2007). Nutrient concentrations can vary spatially even within a nutrient-limited stream reach (Dent and Grimm 1999), and this spatial variability might affect patch-level community composition and, in turn, contributions of N_2 fixation to whole-stream N budgets.

The ability of cyanobacteria to fix N_2, and therefore to gain a competitive advantage in streams, also might be constrained by physical factors. For example, temperature is an important factor controlling the spatial distribution of N_2-fixation rates in central Idaho streams because warm temperatures favor N_2-fixing taxa in the periphyton assemblage (Marcarelli and Wurtsbaugh 2006). N_2 fixation is an energetically expensive reaction, and many N_2 fixers in streams are autotrophs that obtain the energy required to fix N_2 through photosynthesis. Therefore, N_2 fixation might be less important in shaded streams than in streams where light, and therefore autotrophic activity, is high. N_2 fixation appears to be particularly important in streams in deserts, where in-stream primary production might be the predominant energy source (e.g., Minshall 1978). The importance of light for N_2 fixation also is suggested by diel studies in streams, in which N_2-fixation rates are greater during the day than at night (Horne 1975, Livingstone et al. 1984, Grimm and Petrone 1997).

Some stream and lake foodweb studies have questioned whether cyanobacteria are a high-quality food source for higher trophic levels because they are N rich or whether they are a poor-quality food source because they are defended against grazers. In general, experimental manipulations indicate that grazers in streams avoid feeding on cyanobacteria, and grazer avoidance can increase the relative abundance of cyanobacteria by removing competing algal taxa (Power et al. 1988, Dudley and D'Antonio 1991, Abe et al. 2006). Cyanobacteria have a variety of grazing defense mechanisms, such as mucilage that makes them difficult to ingest (Power et al. 1988, Dudley and D'Antonio 1991), toxins that deter macroinvertebrate feeding (Aboal et al. 2002), and basal trichomes that allow rapid regeneration of filaments (Power et al. 1988). Diatoms with cyanobacterial endosymbionts might be more palatable than cyanobacteria for stream grazers. Some work suggests that *Epithemia* can become dominant under grazed conditions because of its adnate growth form (Hill and Knight 1987), but in other systems, this genus does not appear to be particularly resistant to grazing (Peterson and Grimm 1992). In some grazing studies, cyanobacteria were not the preferred food source, but some grazers still ingested cyanobacteria (Power et al. 1988, Abe et al. 2006). If cyanobacteria are abundant they might provide a significant amount of food to higher trophic levels regardless of food preference, provided they are not toxic to grazers. Stable-isotope studies in streams where N_2 fixation occurs might provide insight into this question.

Data Gaps and Research Needs

Our review of N processing in streams highlighted gaps in the N-cycling literature that could influence our understanding of these processes. First, measurements of denitrification, DIN uptake, and N_2 fixation are not distributed in similar ways across streams with differing NO_3^--N concentrations or Q. Measurements of rates tend to be biased toward streams with either high or low DIN concentration, depending on which state should favor the given rate; e.g., N_2 fixation is more often measured in streams with low DIN concentrations, whereas denitrification is more often measured in streams with high DIN concentrations. This bias certainly hampers our ability to compare the importance of these rates across streams with varying N loads. In addition, all rates were measured more frequently in streams where $Q < 1$ m^3/s, although denitrification also has been measured in larger rivers. This bias could cause severe limitations in our understanding of N cycling because ecosystem processes change with river size (Vannote et al. 1980). Last, studies of DIN uptake and N_2 fixation are heavily biased toward summer months (June–August). In some systems this focus might be appropriate because snow cover or stream freezing might essentially stop some biotic processes during the winter. However, in other systems this bias could alter our ability to evaluate the relative importance of different N-processing rates on annual timescales.

The general importance of N_2 fixation in streams is difficult to assess given our current state of knowledge. N_2-fixation rates clearly are high in some streams, particularly ones with low DIN concentrations, but too little evidence is available for us to conclude why N_2 fixation appears to be important in some streams and not in others. Further examination of how physical and biological characteristics such as temperature, light, nutrient concentrations, and grazing control N_2 fixation might help us understand patterns of N_2 fixation within and among streams.

Our analysis suggests that assessing the importance of N_2 fixation as part of an annual N budget might underestimate its importance, perhaps because of scaling issues or seasonal changes in the importance of different N sources. To broaden our knowledge of how N_2 fixation contributes to stream ecosystems, N_2 fixation must be measured in concert with other N processes, including denitrification, hydrologic N import and export, and DIN-uptake rates across a broad range of stream conditions. Future work should compare N_2-fixation rates to other inputs and losses of N that are not commonly considered in stream N budgets, such as N_2 fixation by riparian organisms (Compton et al. 2002), groundwater N contributions (Wondzell and Swanson 1996), and losses of N via biogeochemical pathways other than denitrification (Burgin and Hamilton 2007). In addition, focusing on how N_2 fixation supports food webs will help us understand how N_2 fixation contributes to benthic community dynamics, regardless of the overall contributions of N_2 fixation to stream N budgets.

Streams throughout much of the industrialized world are polluted with DIN, either directly through point- or nonpoint-source pollution or indirectly through N deposition (Vitousek et al. 1997). Our finding that N_2 fixation is negatively related and denitrification is positively related to DIN concentration implies that N pollution should promote denitrification and favor a less important role for N_2 fixation in streams. If true, N pollution might inherently change the N cycle in stream ecosystems by changing the balance between N_2 fixation and denitrification. Without understanding how environmental conditions control N_2-fixation rates in streams, we will be unable to understand how increasing N loads have altered, and will alter, the N cycle and the community and populations dynamics of stream organisms.

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APPENDIX. Studies used in the literature review. Superscripts indicate the measurement method used in each study. See individual references for details. Q = discharge, R. = river, Cr. = creek, Br. = brook, Dr. = drain, DOC = dissolved organic C, nr = not recorded, — = not measured in the study stream.

Stream name	Location	Stream order	Q (m^3/s)	Sampling date
Adams	Miers Valley, Antarctica	nr	0.15	December–January 1984–1986
Agricultural	Kalamazoo R. watershed, Michigan	1	0.001–0.063	January 2002–January 2003
Agua Fria	110 km N of Phoenix, Arizona	nr	0.010	April–November 2003
Bailey Cr.	Grand Teton, Wyoming	2	0.12	July–August 1999–2000
Barbours	Otago province, New Zealand	3–4	0.046	March and August 2001
BDO	Upper Sangamon R. watershed, Illinois	2	0.41	April–January 2002
BDT	Upper Sangamon R. watershed, Illinois	1	0.052	April–January 2002
Bear Br.	Hubbard Brook Experimental Forest, New Hampshire	2	0.004	June 1997
Beaver Cr.	Sawtooth Mountain stream–lake district, Idaho	3	0.33	August 2004
Beaver Cr.	Matamek R. watershed, Quebec, Canada	2	0.033	May–October 1982
Big Cr. (headwater)	Southern Illinois	1	nr	March 2000–April 2001
Big Cr. (channelized)	Southern Illinois	3	nr	March 2000–April 2001
Big Ditch	Sangamon R. watershed, Illinois	3	0.42	May–November 2002
BLS	Upper Embarras R. watershed, Illinois	1	0.17	April–January 2002
Blueberry Cr.	Kuparuk R. watershed, Alaska	2	0.40	July 1994
Bremer	Bremer subcatchment, Queensland, Australia	1–4	nr	August and September 2000
Broad	Otago province, New Zealand	3–4	0.16	March and August 2001
Buskirk Dr.	Kalamazoo R. watershed, Michigan	1	0.002	Baseflow 2002
Canal	Southwest Cr., coastal North Carolina	2–3	0.014	August 2003–January 2004
Canal Two	Yaqui Valley, Mexico	nr	0.48	July 2001
Carnagigue	Grand R. watershed, Ontario, Canada	nr	nr	nr
Cascade Br.	Hubbard Brook Experimental Forest, New Hampshire	1	0.002	June 1999
Chatterick Bridge	Swale–Ouse R. system, UK	nr	5.76	August 1995–December 1996
Charente R.	France	nr	nr	May 1991–April 1992
Chiangjiang R.	China	nr	39,100	August and October 2003
Cliff Cr.	Frank Church Wilderness of No Return, Idaho	2	0.088	August 1994
Cobb Ditch	Iroquios–Kankakee watershed, Indiana	3	0.58	Baseflow 2002
Cone Pond Outlet	White Mountains, New Hampshire	nr	0.002	July 1998
Convict Cr.	Sierra Nevada, California	nr	0.6–2.1	August 1979–October 1980

APPENDIX. Extended.

N_2 fixation	Denitrification	NO_3^--N uptake	NH_4^+-N uptake	Notes
Howard-Williams et al. 1989[a]	—	Howard-Williams et al. 1989[b]	Howard-Williams et al. 1989[b]	Mean of 3 mat types on 1 date
—	Inwood et al. 2005[c]	—	—	Annual mean of 3 streams: Buskirk Cr., Little Rabbit R., Red Run R.
—	—	Grimm et al. 2005[d]	—	1 measurement made sometime during study period
—	—	Hall and Tank 2003[e]	Hall and Tank 2003[e]	1 measurement
—	—	Niyogi et al. 2004[e]	—	Mean of summer and winter measurements
—	Royer et al. 2004[c]	—	—	Mean of 6 dates
—	Royer et al. 2004[c]	—	—	Mean of 5 dates
—	—	Webster et al. 2003[d]	Webster et al. 2003[d]	1 measurement
—	—	Arp and Baker 2007[e]	—	1 measurement
Francis et al. 1985[a]	—	—	—	Mean of biweekly measurements for the entire study period
—	O'Brien and Williard 2006[f]	—	—	Mean of biweekly measurements for the entire study period
—	O'Brien and Williard 2006[f]	—	—	Mean of biweekly measurements for entire study period
—	Schaller et al. 2004[c]	—	—	Mean of 12 dates, weighted for relative cover of plant and sediment substrates
—	Royer et al. 2004[c]	—	—	Mean of 6 dates
—	—	—	Wollheim et al. 2001[g]	
—	Bartkow and Udy 2004[f]	—	—	Median of 3 sites
—	—	Niyogi et al. 2004[e]	—	Mean of summer and winter measurements
—	—	Bernot et al. 2006[d]	Bernot et al. 2006[e]	1 measurement for each rate
—	—	—	Ensign et al. 2006[e]	Mean of 6 dates
—	Harrison et al. 2005[h]	—	—	One 24-h study period
—	Chatarpaul et al. 1980[i]	—	—	
—	—	Bernhardt et al. 2002[e]	Hall et al. 2002[e]	1 measurement for each rate
—	Pattinson et al. 1998[f]	—	—	Mean of 17 sample dates
—	Torre et al. 1992[f]	—	—	In French
—	Yan et al. 2004[h]	—	—	Mean of 2 dates
—	—	Davis and Minshall 1999[e]	—	Mean of 2 reaches on 1 study date
—	—	Bernot et al. 2006[d]	Bernot et al. 2006[e]	1 measurement for each rate
—	—	Bernhardt et al. 2002[e]	Hall et al. 2002[e]	1 measurement for each rate
Leland and Carter 1985[a]	—	—	—	Mean of 13 dates

Appendix. Continued.

Stream name	Location	Stream order	Q (m^3/s)	Sampling date
Cunningham Cr.	Coweeta Hydrologic Laboratory, North Carolina	2	0.004–0.29	June 1988, July–August 1987
Dempsters	Otago province, New Zealand	3–4	0.015	March 2001
Ditch	Southwest Cr., coastal North Carolina	2–3	0.003	August–October 2003
Ditch Cr.	Grand Teton, Wyoming	2	0.23	July–August 1999–2000
Dode A	Denmark	nr	nr	nr
Duffin Cr.	Toronto, Ontario, Canada	nr	2.5	May–October 1973–1975, 1978
E1 Outlet	Kuparuk R. Watershed, Alaska	2	0.017	July 1997
Eagle Cr.	Kalamazoo R. watershed, Michigan	2	0.20	June–July 1998
East Fork Walker Branch	Oak Ridge National Research Park, Tennessee	1	0.0004	October 2002
East Tributary	Kye Burn, South Island, New Zealand	nr	0.015	October 2000–September 2001
Elk Cr.	Sawtooth Mountain stream–lake district, Idaho	3	0.30	August 2004
EMC	Upper Embarras R. watershed, Illinois	4	0.90	April–January 2002
Farley–lake inlet	Sawtooth Mountain stream–lake district, Idaho	3	0.41	August 2002, 2003
Farley–lake outlet	Sawtooth Mountain stream–lake district, Idaho	3	0.62	August 2002, 2003
Fir Cr.	Sawtooth Mountain stream–lake district, Idaho	3	0.22	August 2004
First Choice Cr.	Quebec, Canada	1	0.013	May–October 1982
Flat Shoals	Chattahoochee R. watershed, Georgia	3	0.61	September 1996–June 1998
Forested	Kalamazoo R. Watershed, Michigan	1	0.006–0.009	January 2002–January 2003 (annual mean)
Fryxell Stream	Taylor Valley, Antarctica	nr	0.06	December–January 1984–1986
Gallina Cr.	Carson National Forest, New Mexico	2	0.006	August 1997
Gelbaek and Rabis Baek	Jutland, Denmark	nr	0.02–0.4	March–December 1985
Gila Dr.	Phoenix, Arizona	nr	0.11	April–November 2003
Glade Cr.	Grand Teton, Wyoming	1	0.15	July–August 1999–2000
Gold Coast	Gold Coast subcatchment, Queensland, Australia	1–4	nr	August and September 2000
Green Cr.	Taylor Valley, Antarctica	nr	0.003–0.028	Austral summer, 1998–1999
Hammonton Cr.	Pinelands Region, New Jersey	nr	nr	nr
Hell Roaring Cr.	Sawtooth Mountain stream–lake district, Idaho	3	0.610	August 2004
Hiline Canal	Phoenix, Arizona	nr	0.50	April–November 2003
Hubbard Br.	Hubbard Brook Experimental Forest, New Hampshire	4	0.089	July 1998–June 1999
Hugh White Cr.	Coweeta Hydrologic Laboratory, North Carolina	2	0.003–0.005	June–July 1995, August 1999
Imnavit Cr.	Kuparuk R. watershed, Alaska	2	0.06	July 1995

APPENDIX. Extended. Continued.

N_2 fixation	Denitrification	NO_3^--N uptake	NH_4^+-N uptake	Notes
—	—	Wallace et al. 1995[e]	Wallace et al. 1995[e]	1 measurement made before experimental manipulation sometime during the study period
—	—	Niyogi et al. 2004[e]	—	1 summer measurement
—	—	—	Ensign et al. 2006[e]	Mean of 3 dates
—	—	Hall and Tank 2003[e]	Hall and Tank 2003[e]	1 measurement
—	Nielsen et al. 1990[f]	—	—	Methods; little environmental data reported
—	Hill 1979[i]	—	—	
—	—	Webster et al. 2003[d]	Webster et al. 2003[d]	1 measurement
—	—	Hamilton et al. 2001[g]	Hamilton et al. 2001[g]	6-wk experiment, mean of days 0, 20, 41
—	Mulholland et al. 2004b[d]	Mulholland et al. 2004b[d]	—	1 measurement
—	—	Simon et al. 2005[e]	Simon et al. 2005[e]	Mean of 12 dates
—	—	Arp and Baker 2007[e]	—	1 measurement
—	Royer et al. 2004[c]	—	—	Mean of 5 dates
Marcarelli and Wurtsbaugh 2007[j]	—	Arp and Baker 2007[e]	—	N_2 fixation measured in 2002, uptake in 2003
Marcarelli and Wurtsbaugh 2007[j]	—	Arp and Baker 2007[e]	—	N_2 fixation measured in 2002, uptake in 2003
—	—	Arp and Baker 2007[e]	—	1 measurement
Francis et al. 1985[a]	—	—	—	Mean of biweekly measurements for the entire study period
—	—	—	Meyer et al. 2005[e]	Mean of 4 dates
—	Inwood et al. 2005[c]	—	—	Means of 3 streams: Bear Cr., Sand Cr., Swan Cr.
Howard-Williams et al. 1989[a]	—	Howard-Williams et al. 1989[b]	Howard-Williams et al. 1989[b]	Mean of 3 mat types on 1 date
—	—	Webster et al. 2003[d]	Webster et al. 2003[d]	1 measurement
—	Christensen and Sorensen 1988[f]	—	—	Mean of 12 dates
—	—	Grimm et al. 2005[e]	—	1 measurement made sometime during study period
—	—	Hall and Tank 2003[e]	Hall and Tank 2003[e]	1 measurement
—	Bartkow and Udy 2004[f]	—	—	Median of 7 sites
—	Gooseff et al. 2004[f]	—	—	Mean of 15 incubations
—	Seitzinger 1994[k]	—	—	Mean of 2 core measurements
—	—	Arp and Baker 2007[e]	—	1 measurement
—	—	Grimm et al. 2005[d]	—	1 measurement made sometime during study period
—	—	Bernhardt et al. 2002[e]	Hall et al. 2002[e]	Mean of 3 dates
—	—	Fellows et al. 2006[e]	Hall et al. 1998[g]	NH_4^+-N uptake measured in 1995 (23-d release), NO_3^--N uptake measured in 1999 (mean of day/night uptake rates)
—	—	—	Wollheim et al. 2001[g]	

Appendix. Continued.

Stream name	Location	Stream order	Q (m^3/s)	Sampling date
Indian Bend Wash	Scottsdale, Arizona	nr	0.069	April–November 2003
Iroquois R.	Illinois R. drainage, Indiana	nr	13.1	June 1999, May 2000
Ivel and Gade R.	USA (location not reported)	nr	nr	January–May 1963
Ivelet Bridge	Swale–Ouse R. system, UK	nr	nr	August 1995–December 1996
Juday Cr.	South Bend, Indiana	nr	nr	nr
Kings Cr.	Konza Prairie Biological Station, Kansas	3	0.016–0.059	April–May 1998 (uptake), February 1999–November 2000 (denitrification)
Kuparuk R.	Kuparuk R. watershed, Alaska	4	2.4	Summer 1983–1986
Kyeburn	Otago province, New Zealand	3–4	0.024	March and August 2001
La Solana	90 km N of Barcelona, Spain	2	0.021	Summer 1990–spring 1992
Lee	Otago province, New Zealand	3–4	0.071	March 2001
LFK	Lake Fork Kaskaskia watershed, Illinois	3	1.13	April–January 2002
Little Demp	Otago province, New Zealand	3–4	0.044	August 2001
Little Lost Man Cr.	Humboldt County, California	3	0.007	August 1981
Little Miami R.	Southeastern Ohio	5	0.85	Aug 1998
Little Rabbit R.	Kalamazoo R. watershed, Michigan	1	0.063	Baseflow 2002
Lizard Cr.	Grand Teton, Wyoming	2	0.025	July–August 1999–2000
Lockyear	Lockyear subcatchment, Queensland, Australia	1–4	nr	August and September 2000
Logan Albert	Logan Albert subcatchment, Queensland, Australia	1–4	nr	August and September 2000
Lower Brisbane	Lower Brisbane subcatchment, Queensland, Australia	1–4	nr	August and September 2000
Mack Cr.	H. J. Andrews Experimental Forest, Oregon	3	0.060	July–September 1998
Maroochy–Mooloolah	Maroochy–Mooloolah subcatchment, Queensland, Australia	1–4	nr	August and September 2000
Matamek R.	Matamek R. watershed, Quebec, Canada	6	13.7	May–October 1982
Meandering	Rio Cipo watershed, southeast Brazil	1	0.002	April 2003
Millstone R.	Central New Jersey	nr	6.8	October 1999, March 2000
Montesina Stream	Cordoba province, Spain	nr	0.004	November 1991
Moose–Wilson Road Cr.	Grand Teton, Wyoming	1	0.035	July–August 1999–2000
Naburn Weir	Swale–Ouse R. system, UK	nr	24.0	August 1995–December 1996
Nickajack	Chattahoochee R. watershed, Georgia	3	0.60	April–September 1997
Noosa	Noosa subcatchment, Queensland, Australia	1–4	nr	August and September 2000
North Moran Bay Cr.	Grand Teton, Wyoming	2	0.009	July–August 1999–2000
North Tributary	Kye Burn, South Island, New Zealand	nr	0.023	October 2000–September 2001
Ovens R.	Southeastern Australia	4	nr	August–September (year not reported)

APPENDIX. Extended. Continued.

N_2 fixation	Denitrification	NO_3^--N uptake	NH_4^+-N uptake	Notes
—	—	Grimm et al. 2005[d]	—	1 measurement made sometime during study period
—	Laursen and Seitzinger 2002[h]	—	—	Mean of 2 dates
—	Edwards and Rolley 1965[i]	—	—	
—	Pattinson et al. 1998[f]	—	—	Mean of 17 dates
—	Laursen and Carlton 1999[i]	—	—	
—	Kemp and Dodds 2002[f]	Dodds et al. 2000[g]	Dodds et al. 2000[g]	6-wk experiment used to calculate uptake rates, mean August denitrification rate, scaled for cover of benthic stream substrates
—	—	Peterson et al. 1993[g]	Peterson et al. 1993[g]	Means from 6-wk addition period
—	—	Niyogi et al. 2004[e]	—	Mean of summer and winter measurements
—	—	—	Martí and Sabater 1996[e]	Mean of 13 dates
—	—	Niyogi et al. 2004[e]	—	1 summer measurement
—	Royer et al. 2004[c]	—	—	Mean of 5 dates
—	—	Niyogi et al. 2004[e]	—	1 winter measurement
—	Duff et al. 1984[f]	—	—	1 measurement
—	—	Webster et al. 2003[d]	Webster et al. 2003[d]	1 measurement
—	—	Bernot et al. 2006[d]	Bernot et al. 2006[e]	1 measurement for each rate
—	—	Hall and Tank 2003[e]	Hall and Tank 2003[e]	1 measurement
—	Bartkow and Udy 2004[f]	—	—	Median of 9 sites
—	Bartkow and Udy 2004[f]	—	—	Median of 7 sites
—	Bartkow and Udy 2004[f]	—	—	Median of 4 sites
—	—	Ashkenas et al. 2004[g]	Ashkenas et al. 2004[g]	6-wk experiment, mean of days 0, 20, 41
—	Bartkow and Udy 2004[f]	—	—	Median of 10 sites
Francis et al. 1985[a]	—	—	—	Mean of biweekly measurements for the entire study period
—	—	—	Gücker and Boëchat 2004[e]	Mean of 3 reaches
—	Laursen and Seitzinger 2002[h]	—	—	Mean of 2 dates
—	—	Maltchik et al. 1994[e]	—	1 measurement
—	—	Hall and Tank 2003[e]	Hall and Tank 2003[e]	1 measurement
—	Pattinson et al. 1998[f]	—	—	Mean of 17 dates
—	—	—	Meyer et al. 2005[e]	Mean of 2 dates
—	Bartkow and Udy 2004[f]	—	—	1 measurement
—	—	Hall and Tank 2003[e]	Hall and Tank 2003[e]	1 measurement
—	—	Simon et al. 2005[e]	Simon et al. 2005[e]	Mean of 12 dates
—	Baldwin et al. 2006[f]	—	—	Mean of 6 sites

APPENDIX. Continued.

Stream name	Location	Stream order	Q (m^3/s)	Sampling date
Paintbrush Canyon Cr.	Grand Teton, Wyoming	1	0.004	July–August 1999–2000
Paradise Br.	Hubbard Brook Experimental Forest, New Hampshire	4	0.005	July 1998–June 1999
Pasture	Central Volcanic Plateau, North Island, New Zealand	1	0.003	August 1982–June 1983
Peachtree	Chattahoochee R. watershed, Georgia	4	1.3	April 1997–May 1998
Petit–north lake inlet	Sawtooth Mountain stream–lake district, Idaho	4	0.069	August 2004
Petit–south lake inlet	Sawtooth Mountain stream–lake district, Idaho	4	0.18	August 2004
Petit–lake outlet	Sawtooth Mountain stream–lake district, Idaho	4	0.41	August 2004
Pilgrim Cr.	Grand Teton, Wyoming	3	0.029	July–August 1999–2000
Pine	Central Volcanic Plateau, North Island, New Zealand	1	0.002	August 1982–June 1983
Pine R.	Pine Ridge subcatchment, Queensland, Australia	1–4	nr	August and September 2000
Pioneer Cr.	Frank Church Wilderness of No Return, Idaho	2	0.083	August 1994
Polecat Cr.	Grand Teton, Wyoming	nr	1.5	July 2000–August 2001
Price Road Dr.	Eastern Phoenix, Arizona	nr	0.19	April–November 2003
Quebrada Bisley	Luquillo Experimental Forest, Puerto Rico	2	0.020	January–February 1998
Ravenseat	Swale–Ouse R. system, UK	nr	nr	August 1995–December 1996
Red Run Dr.	Kalamazoo R. watershed, Michigan	1	0.017	Baseflow 2002
Riera Major	90 km north of Barcelona, Spain	2	0.058	Summer 1990–spring 1992
Rio Callaveras	New Mexico	1	0.001	July 1999
Rio Ranch Dr.	Albuquerque, New Mexico	nr	0.014	April–November 2003
R. Dorn	Northwest of Oxford, UK	nr	nr	nr
R. Raan	Southern Sweden	nr	1.8	December 1987–March 1989
R. Wiske	Swale–Ouse R. system, UK	nr	0.56	August 1995–December 1996
Rivers	Toronto, southern Ontario, Canada	2–6	nr	May–June, year nr
Rocky Cr.	Eel R. watershed, California	nr	nr	February–June 1971
Rottenwood	Chattahoochee R. watershed, Georgia	3	0.44	September 1996–October 1997
Run	Rio Cipo watershed, southeast Brazil	1	0.002	April 2003
Salto R.	La Selva Biological Reserve, Puerto Rico	3	0.43	February 1989
San Francisquito Cr.	North of San Francisco, California	nr	nr	August–September 1982
Sand Cr.	Kalamazoo R. watershed, Michigan	1	0.007	Baseflow 2002
Shane Cr.	Konza Prairie Biological Station, Kansas	3	0.073	February 1999–November 2000
Shingobee R.	North-central Minnesota	2	0.23	September 1998
Skit Br.	Pinelands region, New Jersey	nr	nr	nr
Slocum Cr.	North Carolina coastal plain	1	0.065	October 2003, January 2004
Snake	Chattahoochee R. watershed, Georgia	3	1.3	September 1996–June 1998

APPENDIX. Extended. Continued.

N_2 fixation	Denitrification	NO_3^--N uptake	NH_4^+-N uptake	Notes
—	—	Hall and Tank 2003[e]	Hall and Tank 2003[e]	1 measurement
—	—	Bernhardt et al. 2002[e]	Hall et al. 2002[e]	Mean of 2 dates for each rate
—	—	Cooper and Cooke 1984[e]	—	Mean of 3 streams
—	—	—	Meyer et al. 2005[e]	Mean of 4 dates
—	—	Arp and Baker 2007[e]	—	1 measurement
—	—	Arp and Baker 2007[e]	—	1 measurement
—	—	Arp and Baker 2007[e]	—	1 measurement
—	—	Hall and Tank 2003[e]	Hall and Tank 2003[e]	1 measurement
—	Cooper and Cooke 1984[f]	Cooper and Cooke 1984[e]	—	Mean of 3 streams
—	Bartkow and Udy 2004[f]	—	—	Median of 2 sites
—	—	Davis and Minshall 1999[e]	—	Mean of 2 reaches on 1 date
—	—	—	Hall et al. 2003[e]	Mean of 4 dates
—	—	Grimm et al. 2005[e]	—	1 measurement made sometime during study period
—	—	Merriam et al. 2002[g]	Merriam et al. 2002[g]	6-wk experiment, mean of days 0, 20, 41
—	Pattinson et al. 1998[f]	—	—	Mean of 17 dates
—	—	Bernot et al. 2006[d]	Bernot et al. 2006[e]	1 measurement for each rate
—	—	—	Martí and Sabater 1996[e]	Mean of 13 dates
—	—	Fellows et al. 2006[e]	—	Mean of day/night uptake rate
—	—	Grimm et al. 2005[d]	—	1 measurement made sometime during study period
—	Cooke and White 1987[f]	—	—	
—	Jansson et al. 1994[f]	—	—	Mean of 4 dates
—	Pattinson et al. 1998[f]	—	—	Mean of 17 dates
—	—	Hill and Sanmugadas 1985[i]	—	Mean of 3 rivers: Nottawasaga, West Humber, Duffin Cr.
Horne and Carmiggelt 1975[a]	—	—	—	Mean of 10 dates
—	—	—	Meyer et al. 2005[e]	Mean of 3 dates
—	—	—	Gücker and Boëchat 2004[e]	Mean of 3 reaches
—	Duff et al. 1996[f]	—	—	
—	Duff et al. 1984[f]	—	—	
—	—	Bernot et al. 2006[d]	Bernot et al. 2006[e]	1 measurement for each rate
—	Kemp and Dodds 2002[f]	—	—	Mean August rate, scaled for cover of benthic stream substrates
—	Sheibley et al. 2003[f]	—	—	
—	Seitzinger 1994[i]	—	—	Mean of 2 core measurements
—	—	—	Ensign and Doyle 2005[e]	
—	—	—	Meyer et al. 2005[e]	Mean of 5 dates

APPENDIX. Continued.

Stream name	Location	Stream order	Q (m^3/s)	Sampling date
Snake Den Branch	Coweeta Hydrologic Laboratory, North Carolina	2	0.004	September 1999, May 2000
Sope	Chattahoochee R. watershed, Georgia	4	1.2	May 1998
South Platte R.	Colorado	nr	12	May 2000–August 2001
Spread Cr.	Grand Teton, Wyoming	3	0.087	July–August 1999–2000
Stanley	Stanley subcatchment, Queensland, Australia	1–4	nr	August and September 2000
Stanley Lake Cr.–reference site	Sawtooth Mountain stream–lake district, Idaho	3	0.45	August 2002, 2004
Stanley Lake Cr.–lake inlet	Sawtooth Mountain stream–lake district, Idaho	3	0.67	August 2000, 2003, 2004
Stanley Lake Cr.–lake outlet	Sawtooth Mountain stream–lake district, Idaho	3	0.83	August 2000, 2003, 2004
Step-pool	Rio Cipo watershed, southeast Brazil	1	0.001	April 2003
Stony	Otago province, New Zealand	3–4	0.070	March 2001
Sugar Cr.	Illinois R. drainage, Indiana	nr	1.62	May 2000
Sutton	Otago province, New Zealand	3–4	0.053	March and August 2001
Swamp	Rio Cipo watershed, southeast Brazil	1	0.002	April 2003
Sycamore Cr.	Sonoran Desert, central Arizona	4	0.03–0.08	July 1992–October 1993, May 1997
Thornton Manor	Swale–Ouse R. system, UK	nr	9.5	August 1995–December 1996
Toxaway–lake inlet	Sawtooth Mountain stream–lake district, Idaho	1	0.078	August 2002, 2003
Toxaway–lake outlet	Sawtooth Mountain stream–lake district, Idaho	2	0.25	August 2002, 2003
Two Ocean Lake Cr.	Grand Teton, Wyoming	2	0.14	July–August 1999–2000
Unnamed stream A	High Tatra Mountains, eastern Europe	nr	0.002	July 1991
Unnamed stream B	Bio-Environmental Engineering Research Center, Nova Scotia Agricultural College, Nova Scotia, Canada	1	nr	May–September 2000
Upper Ball Cr.	Coweeta Hydrologic Laboratory, North Carolina	2	0.062	November–December 1996
Urban	Kalamazoo R. watershed, Michigan	1	0.022–0.071	January 2002–January 2003
Urban drain	Dorr, Michigan	2	nr	Baseflow 2002
Warm Spring Cr.–reference site	Sawtooth Mountain stream–lake district, Idaho	2	0.16	August 2002–2003
Warm Spring Cr.–lake inlet	Sawtooth Mountain stream–lake district, Idaho	2	0.23	July–August 2002–2004

APPENDIX. Extended. Continued.

N_2 fixation	Denitrification	NO_3^--N uptake	NH_4^+-N uptake	Notes
—	—	Thomas et al. 2003[d]	—	Mean of 2 dates
—	—	—	Meyer et al. 2005[e]	1 measurement
—	Pribyl et al. 2005[h]	—	—	Mean of 13-mo study period
—	—	Hall and Tank 2003[e]	Hall and Tank 2003[e]	1 measurement
—	Bartkow and Udy 2004[f]	—	—	Median of 12 sites
Marcarelli and Wurtsbaugh 2007[j]	—	Arp and Baker 2007[e]	—	N_2 fixation measured in 2002, uptake in 2004
Marcarelli 2006[a]	MAB, unpublished data[c]	Arp and Baker 2007[e]	—	Denitrification measured in 2000, N_2 fixation in 2003, uptake in 2004
Marcarelli 2006[a]	MAB, unpublished data[c]	Arp and Baker 2007[e]	—	Denitrification measured in 2000, N_2 fixation in 2003, uptake in 2004
—	—	—	Gücker and Boëchat 2004[e]	Mean of 3 reaches
—	—	Niyogi et al. 2004[e]	—	1 summer measurement
—	Laursen and Seitzinger 2002[h]	—	—	1 measurement
—	—	Niyogi et al. 2004[e]	—	Mean of summer and winter measurements
—	—	—	Gücker and Boëchat 2004[e]	Mean of 3 reaches
Grimm and Petrone 1997[a]	Holmes et al. 1996[f]	Webster et al. 2003[d]	Webster et al. 2003[d]	N_2 fixation measured July 1992–August 1993 (12 dates), denitrification in August and October 1993, N uptake in May 1997
—	Pattinson et al. 1998[f]	—	—	Mean of 17 dates
Marcarelli and Wurtsbaugh 2007[j]	—	Arp and Baker 2007[e]	—	N_2 fixation measured in 2002, uptake in 2003
Marcarelli and Wurtsbaugh 2007[j]	—	Arp and Baker 2007[e]	—	N_2 fixation measured in 2002, uptake in 2003
—	—	Hall and Tank 2003[e]	Hall and Tank 2003[e]	1 measurement
—	—	—	Kopáček and Blažka 1994[e]	Mean of 2 dates
—	Kellman 2004[i]	—	—	
—	—	Tank et al. 2000[g]	Tank et al. 2000[g]	6-wk experiment, mean of days 0, 20, 41
—	Inwood et al. 2005[c]	—	—	Annual mean of 3 streams: Leila Arboretum, Brickyard, Portage
—	—	—	Bernot et al. 2006[e]	1 measurement
Marcarelli and Wurtsbaugh 2007[j]	—	Arp and Baker 2007[e]	—	N_2 fixation measured in 2002, uptake in 2003
Marcarelli 2006[a]	MAB and L. Jeffs, unpublished data[c]	Arp and Baker 2007[e]	Koch 2005[e]	Denitrification measured 2002, N_2 fixation and NO_3^--N uptake in 2003, NH_4^+-N uptake in 2003–2004 (mean of 6 measurements)

Appendix. Continued.

Stream name	Location	Stream order	Q (m^3/s)	Sampling date
Warm Spring Cr.–lake outlet	Sawtooth Mountain stream–lake district, Idaho	2	0.17	July–August 2002–2004
Watershed 1	Hubbard Brook Experimental Forest, New Hampshire	1	0.002	June 1999
Watershed 2	Hubbard Brook Experimental Forest, New Hampshire	1	0.001	July 1998–April 1999
Watershed 2	H. J. Andrews Experimental Forest, Oregon	2	0.001	April 1975–May 1976, summer 1987
Watershed 3	Hubbard Brook Experimental Forest, New Hampshire	2	0.006	July 1998–June 1999
Watershed 4	Hubbard Brook Experimental Forest, New Hampshire	2	0.004	July 1998–April 1999
Watershed 5	Hubbard Brook Experimental Forest, New Hampshire	2	0.002	July 1998–April 1999
Watershed 6	Hubbard Brook Experimental Forest, New Hampshire	1	0.002	July 1998–August 1999
West Branch Whiteface R.	Bowl Research Natural Area, North Sandwich, New Hampshire	nr	0.078	October 1998
West Fork Walker Branch	Oak Ridge National Research Park, Tennessee	1	0.009	April–May 1997
West Inlet Mirror Lake	Hubbard Brook Experimental Forest, New Hampshire	1	0.001	October–June 1999
Yellow Belly Cr.–lake inlet	Sawtooth Mountain stream–lake district, Idaho	3	0.70	August 2003
Yellow Belly Cr.–lake outlet	Sawtooth Mountain stream–lake district, Idaho	3	0.76	August 2000, 2003

[a] Acetylene reduction assays in enclosures or bottles
[b] ^{15}N uptake in enclosures or bottles
[c] Chloramphenicol-amended acetylene block assays in enclosures or bottles
[d] Short-term ($\leq$24 h) whole-stream ^{15}N-injection experiments
[e] Whole-stream enrichment experiments (Stream Solute Workshop 1990)
[f] Acetylene block assays in enclosures or bottles (no chloramphenicol amendments)
[g] Long-term whole-stream ^{15}N-injection experiments
[h] Whole-reach changes in N_2 concentration (Laursen and Seitzinger 2002)
[i] NO_3^- flux in cores
[j] Acetylene reduction assays on artificial substrates
[k] N_2 flux in cores

APPENDIX. Extended. Continued.

N_2 fixation	Denitrification	NO_3^--N uptake	NH_4^+-N uptake	Notes
Marcarelli 2006[a]	MAB and L. Jeffs, unpublished data[c]	Arp and Baker 2007[e]	Koch 2005[e]	Denitrification measured 2002, N_2 fixation and NO_3^--N uptake in 2003, NH_4^+-N uptake in 2003–2004, mean of 6 measurements
—	—	Bernhardt et al. 2002[e]	Hall et al. 2002[e]	1 measurement for each rate
—	—	Bernhardt et al. 2002[e]	Hall et al. 2002[e]	1 measurement for NO_3^--N uptake, NH_4^+-N uptake is mean of 3 dates
Buckley and Triska 1978[a]	—	Munn and Meyer 1990[e]	—	N_2 fixation measured on wood substrates in 1975–1976, scaled to whole-stream area; NO_3^--N uptake measured in 1987, mean of 3 reaches
—	—	Bernhardt et al. 2002[e]	Hall et al. 2002[e]	NO_3^--N uptake is mean of 2 dates, NH_4^+-N uptake is mean of 6 dates
—	—	Bernhardt et al. 2002[e]	Hall et al. 2002[e]	1 measurement for NO_3^--N uptake, NH_4^+-N uptake is mean of 3 dates
—	—	Bernhardt et al. 2002[e]	Hall et al. 2002[e]	1 measurement for NO_3^--N uptake, NH_4^+-N uptake is mean of 3 dates
Meyer et al. 1981[a]	Bernhardt and Likens 2002[f]	Bernhardt et al. 2002[e]	Hall et al. 2002[e]	N_2-fixation rates estimated from unpublished measurements by J. Roskoski (see Meyer et al. 1981 for discussion); denitrification rates are mean of before and reference treatments of a dissolved organic carbon (DOC) addition experiment (July–August 1999); NO_3^--N uptake is mean of 3 dates; NH_4^+-N uptake is mean of 5 dates
—	—	—	Hall et al. 2002[e]	1 measurement
—	—	Mulholland et al. 2000[g]	Mulholland et al. 2000[g]	6-wk experiment, mean of days 0, 20, 41
—	—	Bernhardt et al. 2002[e]	Hall et al. 2002[e]	1 measurement for NO_3^--N uptake, NH_4^+-N uptake is mean of 3 dates
Marcarelli 2006[a]	—	Arp and Baker 2007[e]	—	N_2 fixation and uptake measured within 24 h in 2003
Marcarelli 2006[a]	MAB, unpublished data[c]	Arp and Baker 2007[e]	—	Denitrification measured in 2000, N_2 fixation and uptake measured within 24 h in 2003