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Nitrogen budget of a subarctic stream altered by beaver (*Castor canadensis*)*

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Abstract. Beaver (*Castor canadensis*) influence stream ecosystems through their wood cutting and dam building activities. To quantify this influence we have used measured rates of nitrogen dynamics to construct a nitrogen budget for a section of a second order stream in eastern Québec and a beaver dam in that stream. The budget demonstrates the importance of sediment accumulations and an expanded wetted area to the annual nitrogen economy and to pathways of nitrogen cycling. Major changes after impoundment (per unit area) include a reduction in allochthonous nitrogen and an increase in nitrogen fixation by sediment microbes. Overall, the beaver-modified section accumulated $\sim 10^3$ times more nitrogen than before alteration. The ecosystem implications of beaver activity suggest that current concepts of patterns and processes in running waters require modification.

Introduction

Beaver (*Castor canadensis*) affect the structure and dynamics of stream ecosystems by transferring organic matter from the terrestrial to the aquatic system and by building dams. The more noticeable effects are the retention of sediment, organic matter and water by the dam, an increase in wetted surface area, modification of nutrient cycling and decomposition dynamics, and alterations to the riparian zone (Naiman et al. 1984; Francis et al. 1984). These changes have a long-lasting influence on the nature of stream ecosystems, on wetlands, and on the surrounding forest. Nevertheless, there are few instances where changes in any ecosystem component by beaver have been quantified (see literature reviews by Yeager and Hay 1955; Jenkins and Busher 1979; Hodgdon and Larson 1980).

Historically, beaver were extraordinarily abundant and widely dispersed in North America. Prior to the arrival of Europeans the population was estimated to be about 60 million individuals ranging over 15.5 million km^2 (Seton 1929; Jenkins and Busher 1979). The density was about 4 beaver/km^2, which is in accord with densities in remote regions today (Naiman, unpublished data). Since near extinction around 1900 A.D., the beaver population has increased substantially throughout its former range. Beaver are again becoming a significant component of aquatic ecosystems.

In Québec, beaver influence a substantial percentage of the total stream length within catchment basins; in some cases as much as 30–50% of the total length of second to fourth order streams is affected. This alteration has important implications for sediment movement, biogeochemical processes, and aquatic communities. Compared to a typical riffle, beaver activities produce an alteration to nutrient cycling and decomposition dynamics through entrainment of sediment and organic matter, there is an alteration to the light regime through the opening of the forest canopy, and there are alterations to precipitation, throughfall, and the character of allochtonous inputs (Fig. 1). Concomitant with these changes, the extent of wetted surface area increases, influencing the nature and intensity of interactions between the stream channel, biological components of the ecosystem, and the surrounding forest. The objectives of this paper are to quantify the influence of beaver activities on the nitrogen dynamics of a small, nutrient poor, subarctic stream and to examine this influence in reference to current perspectives in running water ecology.

Study site

We studied nitrogen dynamics in both a beaver pond and a riffle in Beaver Creek, a second order stream located $\sim$25 km east of Sept-Iles, Québec, Canada. This region is Precambrian Shield with waters characterized by low nutrient concentrations ($<$0.3 mg N/L as nitrate and $<$0.003 mg P/L as orthophosphate), 5–15 mg C/L of dissolved organic carbon, about 2100 degree days annually (°C/yr), and generally acidic brown waters (pH: 4.8–7.2).

The Beaver Creek drainage is a pristine watershed with no evidence of human disturbance. The forest is predominantly black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*), with paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), speckled alder (*Alnus rugosa*), and willow (*Salix* sp.) composing the riparian community. The catchment drains 1.8 km^2, has a large beaver pond in its headwaters, and over its 1.4 km length there are 12 abandoned or recolonized dams separated by riffles. Mean annual discharge is $\sim$0.113 m^3/s. Several geomorphological, hydrological, and biological components of this stream have been described by Naiman (1982, 1983a, b, c), Melillo

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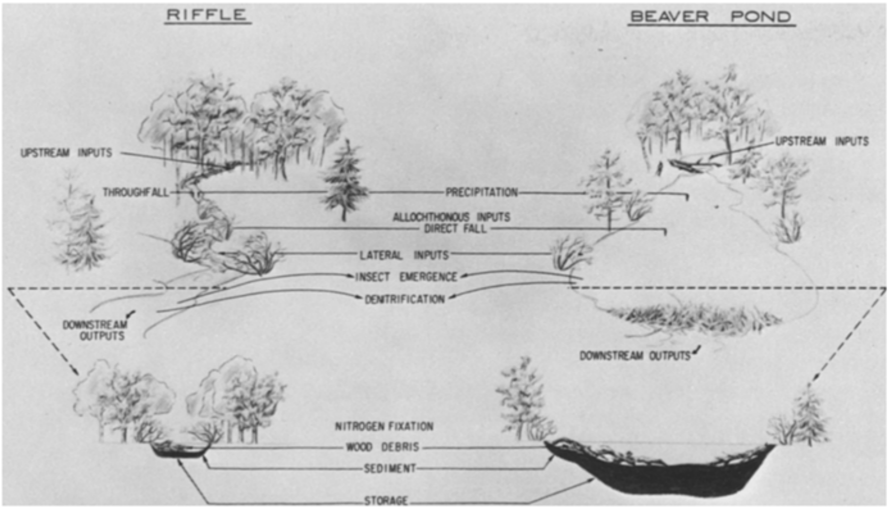

Fig. 1. The activities of beaver influence stream ecosystem components primarily by opening of the forest canopy, by increasing the water surface area, and by increasing the amount of sediment and organic matter in the channel. The schematic drawing depicts ecosystem components addressed by this study

et al. (1983, 1984), Conners and Naiman (1984), Francis et al. (1984), and Naiman et al. (1984).

Methods

The entire stream was mapped using standard survey techniques. Sediment accumulations behind each dam were estimated by using trigonometric interpolations of valley contour and measuring channel slope, pond width, pond length, dam height, and the bulk density and percentage organic matter of sediment cores taken from ponds. Accumulation of woody debris >10 cm diameter was measured, by species, over a 1383 m transect. Woody debris between 1–10 cm diameter was measured, also by species, in 1 m wide transects every 10 m for 300 m (Naiman et al. 1982). The erosion rate of particulate organic carbon (POC: >0.5 μm) suspended in the water column was reported by Naiman (1982). The amount of nitrogen associated with this carbon was estimated from C:N ratios given by Naiman (1983c) for Beaver Creek seston. Water samples for total dissolved nitrogen, and nitrogen in precipitation and throughfall under riparian zone species, were collected regularly between 1979–1983 and analyzed for total nitrogen by the method of D'Elia et al. (1977). Nitrate, nitrite, and ammonia in stream water were determined by the methods of Solorzono (1969) and Wood et al. (1967). The sum of nitrate, nitrite, and ammonia (dissolved inorganic nitrogen; DIN) was substracted from total nitrogen to estimate dissolved organic nitrogen (DON). Allochthonous inputs were collected from riffles and dam sites, sorted into component types, and the percentage nitrogen determined by the Kjeldahl technique or taken from the literature (Conners and Naiman 1984; Melillo et al. 1983). Nitrogen fixation associated with wood species and sediments was measured using the acetylene reduction technique (Hardy et al. 1973; Francis et al. 1984). Insect emergence was estimated using surface traps and literature data on percentage nitrogen associated with major insect groups (Naiman et al. 1984; Allen et al. 1974).

Results and discussion

From measurements of nitrogen dynamics at a number of dam and riffle sites along Beaver Creek and similar streams, we have constructed composite nitrogen budgets for a

Table 1. Details of nitrogen budgets calculated for a riffle and a beaver pond in Beaver Creek, Québec

Nitrogen Source	Riffle[a] ($g N/m^2/yr^1$)	Beaver pond[b]	
		($g N/m^2/yr^1$)	($g N/m^1/yr^1$)
Throughflow			
Dissolved inorganic	712	102	712
Dissolved organic	3,265	467	3,265
Particulate	861	123	861
Standing Stock ($g N/m^2$ or $g N/m$)			
Water column	0.1	0.5	3.7
Woody debris	17.8	> 14.5	>101.2
Sediment	4.3	542.5	3,797.5
Precipitation	0.4	0.7	4.9
Throughfall	0.5	0	0
Allochthonous inputs			
Direct fall	4.1	1.7	11.4
Aspen	(0.4)	(0.1)	(0.5)
Birch	(0.8)	(0.4)	(2.7)
Alder	(2.6)	(1.1)	(7.6)
Conifer needles	(<0.1)	(<0.1)	(0.1)
Seeds and flowers	(0.2)	(<0.1)	(0.1)
Fine wood	(<0.1)	(0.1)	(0.4)
Lateral movement	1.9	0.1	1.0
Leaves	(1.9)	(0.1)	(1.0)
Fine wood	(<0.1)	(<0.1)	(<0.1)
Nitrogen fixation			
Woody debris	0.2	<0.1	0.1
Aspen	(<0.1)	(<0.1)	(<0.1)
Birch	(0.2)	(<0.1)	(<0.1)
Alder	(<0.1)	(<0.1)	(<0.1)
Balsam fir	(<0.1)	(<0.1)	(<0.1)
Spruce	(<0.1)	(<0.1)	(<0.1)
Sediment	<0.1	5.1	35.7
Denitrification	?	?	?
Insect emergence	0.1	0.1	0.4

[a] Surface area 100 m^2; 1 kg/m^2 sediment, and 15.9 kg/m^2 woody debris
[b] Surface area 700 m^2; 125 kg/m^2 sediment, and 12.9 kg/m^2 woody debris

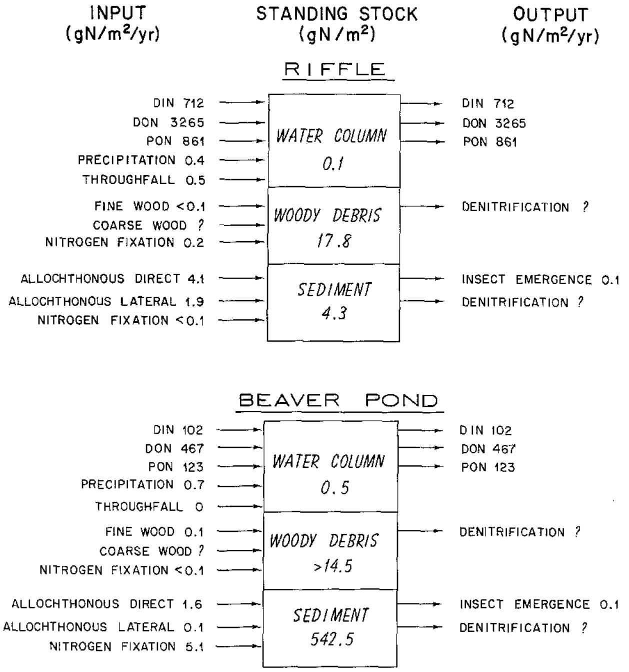

Fig. 2. The nitrogen budget of a riffle is compared to that of a beaver pond, per unit of area. See Table 1 for specific details of the budget

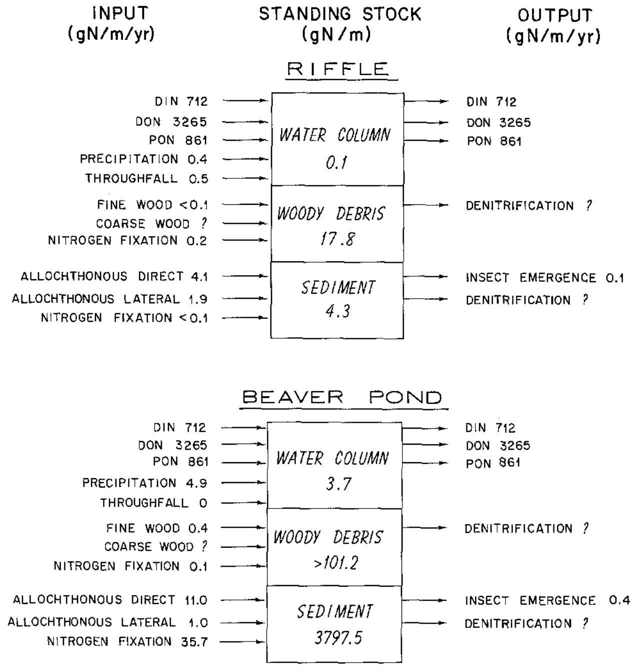

Fig. 3. The nitrogen budget of a riffle is compared to that of a beaver pond, per unit of channel length. See Table 1 for specific details of the budget

beaver pond and a stream riffle. For this exercise we assumed a situation where beaver have taken a 100 m reach of Beaver Creek, which has an average width of 1 m and a mean water depth of 15 cm, and transformed it into a pond with an average width of 7 m and a mean water depth of 150 cm. Further, the riffle has 1 kg/m^2 of sediment and 15.9 kg/m^2 of wood; the beaver pond has 125 kg/m^2 of sediment and 12.9 kg/m^2 of wood. These dimensions, amounts of material, and general assumptions are in agreement with actual field data from 2nd and 3rd order streams of this region (Naiman et al. 1982). In that study we made detailed surveys of five streams covering ~4.3 km and 42 beaver dams. The details of the nitrogen budget are given in Table 1.

Budget calculations

Standing Stock. Per unit area, the standing stock of nitrogen in the water column and associated with woody debris is similar in the riffle and beaver pond (Fig. 2). The water column contains 0.1–0.5 g N/m^2 and woody debris accounts for >14.5–17.8 g N/m^2. The amount of wood-associated nitrogen in the beaver pond is a minimal estimate since wood buried in sediments was not measured. However, per linear meter of channel, there are substantial differences between the two habitat types. The water column in the beaver pond contains 37 times more nitrogen than the riffle and the wood sequesters at least six times more nitrogen (Fig. 3).

The standing stock of nitrogen in sediments differs greatly between the riffle and pond (Figs. 2, 3). This is solely a function of the amount of accumulated sediment since cores taken from both sites had an average nitrogen content of 0.43% as dry weight. The beaver pond stores approximately 1000 times more nitrogen in sediments, per linear meter of stream channel, than does the riffle (Fig. 3).

Throughflow. The average annual discharge since 1979 in Beaver Creek is 1.04×10^6 m^3/yr (Naiman 1982 and unpublished data). Since 1979 we have monitored dissolved nitrogen (DIN and DON) concentrations in a riffle; in 1981 water leaving a beaver pond was added to the biweekly sampling program. We found the average concentrations to be statistically identical (riffle DIN = 0.066 mg N/L, DON = 0.304 mg N/L; pool DIN = 0.071 mg N/L, DON = 0.323 mg N/L). Most of the dissolved nitrogen is organic (riffle = 82.1%, pond = 81.5%). Using average concentrations, the throughflow of DIN available to the 100 m^2 of riffle is 712 g N/m^2/yr versus 102 g N/m^2/yr for the 700 m^2 beaver pond (Fig. 2); the corresponding values for DON are 3265 g N/m^2/yr and 467 g N/m^2/yr. The difference between the riffle and pond in available nitrogen is due to the larger surface area of the pond.

Every 2nd or 3rd order stream in this region has significant beaver activity. Therefore, we have no control by which to judge how upstream activity has influenced nitrogen concentrations entering the study reach. We do have data on a small 1st order stream (First Choice Creek) with no history of beaver activity (Naiman 1982, 1983a, c). Between 1979 and 1983 the average concentration of DIN in that stream was 0.050 mg N/L, 72% of the level measured in the beaver influenced watershed; DON was 0.134 mg N/L, only 43% of that measured in Beaver Creek. Since we were unable to detect a significance difference in total dissolved nitrogen between water entering and leaving a beaver pond, we can only speculate that perhaps a series of ponds is required to raise the nitrogen concentration and, once a stabilized level is reached, no further increases can be detected. Water exiting the Beaver Creek watershed has essentially the same DIN and DON concentrations as water in large rivers downstream (Naiman 1982, 1983a). For the present budget we are assuming net changes in DIN or DON cannot be detected as water passes through a single beaver pond.

The situation for particulate organic nitrogen (PON) is similar. From 1980 to 1982 we monitored PON suspended in water entering and leaving a beaver pond and could not detect any net change. Using the average concentration (0.083 mg N/L), the total amount of particulate nitrogen in stream water available annually to the riffle is 861 g N/m^2, compared to 123 g N/m^2 to the beaver pond (Fig. 2). Again, we are not certain how upstream activity has influenced suspended particulate nitrogen concentrations since we could not locate a similar stream lacking beaver activity. Indications are, however, that beaver activity may significantly increase the export of particulate nitrogen since First Choice Creek has an export rate of only 0.54 g C/m^2/yr compared to 3.37 g C/m^2/yr for Beaver Creek (Naiman 1982). We suspect that the higher export rate may result from the increased organic matter loading cause by beaver feeding activities and that the water must pass through a series of ponds in order to raise the concentration.

The throughflow of dissolved and particulate nitrogen is large compared to that in storage or received via other pathways (see below). This represents a fundamental problem in budget calculations (Meyer and Tate 1983; Cummins et al. 1983). Since we cannot calculate error estimates for the throughflow components, we cannot be certain if there was a significant difference between the input and export of nitrogen. We conclude, as did Cummins et al. (1983), that a budget approach towards comparing two stream ecosystems may be inappropriate if one is trying to assess differences in biological processes. An input-output budget for nitrogen obscures important in-stream processes such as organic nitrogen formation and utilization.

Meterologic inputs. The beaver pond receives only direct precipitation since the forest canopy has been completely opened by flooding and cutting. Between 1979 and 1982 the 109 cm/yr of rainwater and snow averaged 0.625 mg N/L. This is an annual input of 0.7 g N/m^2 or 4.9 g N/m of stream channel (Figs. 2, 3). For the riffle segment, precipitation during the leaf-off period (approximately 1 October – 15 May) averages 65.5 cm. This amounts to an annual nitrogen input of 0.4 g N/m^2.

The riffle section of Beaver Creek is heavily shaded by speckled alder from about 15 May to 1 October. During this period an average of 43.5 cm of rain falls. Water dripping from alder leaves between 1980–1983 averaged 1.031 mg N/L, nearly 65% greater than unaltered precipitation, resulting in an estimated input of 0.5 g N/m^2/yr (Fig. 2). Annually, the pond receives 0.7 g N/m^2 from precipitation while the riffle receives 0.9 g N/m^2 from precipitation and throughfall.

Allochthonous inputs are an important source of nitrogen for small streams (Conners and Naiman 1984). Most direct inputs of nitrogen to the riffle is in the form of alder, birch, and aspen leaves; together they account for 3.9 g N/m^2/yr (Table 1, Fig. 2). Since there is no canopy over the beaver pond, direct inputs of allochtonous material are less (1.6 g N/m^2/yr), but the collecting width of the channel is 7 times that of the riffle, with the amount collected per linear meter of channel being large (11.4 g N/m/yr; Fig. 3).

Beaver, by opening the canopy and expanding the width of the stream channel, effectively increase the stream order from 2 to 3 in terms of annual direct inputs of allochthonous organic matter. Second order streams with a closed canopy receive ~260 g AFDM/m^2/yr of litter whereas, in the ponded reach, the annual input averages ~110 g AFDM/m^2, a level predicted for 3rd order streams in this region (Conners and Naiman 1984). Nevertheless, alder, birch, and aspen leaves remain the dominant litter types.

Lateral inputs of organic matter from the forest floor are less than direct allochthonous inputs (Conners and Naiman 1984). For the riffle, nearly 81% of the annual 119 g AFDM/m was leaves or tree products (e.g., seeds and catkins) and 19% was fine wood. This amounts to an input of 1.9 g N/m^2/yr (Table 1; Fig. 2). For the beaver pond, 76% of the annual 63 g AFDM/m was leaves or tree products, and 24% was fine wood, accounting for an annual input of only 0.1 g N/m^2. The annual input per unit of stream channel was 1.0 g N/m (Fig. 3).

One form of allochthonous input not directly measured in this study was the annual contribution of nitrogen in coarse wood. This is a difficult component to accurately measure in streams. Nevertheless, an estimate can be made for the beaver pond. An individual beaver requires about a metric ton of wood for growth and maintenance annually (Howard 1982), and a pond of this size would contain one lodge with a minimum of six beaver (Jenkins and Busher 1979). Feeding activities by these beaver could contribute as much as 10.3 g N/m^2/yr if their diet consists entirely of paper birch and trembling aspen and if all of that wood is transferred to the pond. This gives a minimum turnover time of 1.4 yr for the standing stock of wood in the pond, which is in agreement with estimates of wood decay rates made in Beaver Creek by Melillo et al. (1983), especially when the inherent uncertainties in our assumptions are considered. This estimated input rate for coarse wood mediated by beaver is more than twice that estimated for other forms of allochthonous inputs and for nitrogen fixation (see below).

In-stream processes. Francis et al. (1984) examined nitrogen fixation associated with wood and sediment in riffles and ponds on Beaver Creek. Wood, in general, had low and patchy fixation rates, accounting annually for 0.2 g N/m^2 in the riffle and <0.1 g N/m^2 in the pond (Fig. 2). This despite the fact that both sites had substantial standing stocks of woody debris (e.g., 12.9 to 15.9 kg/m^2).

For sediment, mass specific nitrogen fixation rates did not differ significantly ($P>0.10$) between aerobic and anaerobic sediment or between riffles and ponds. Fixation rates remained at approximately 3.3×10^{-3} μmoles C_2H_4 g $AFDM^{-1}hr^{-1}$ during the ice-free season. The difference between riffles and ponds in the absolute amount of nitrogen fixed results from the substantial amount of sediment accumulated behind the beaver dam. In riffles, with only about 1 kg/m^2 of sediment, the annual nitrogen fixation is <0.1 g N/m^2 (Fig. 2); ponds average about 125 kg/m^2 of sediment with organisms fixing 5.1 g N/m^2 annually or 35.7 g N/m of channel length (Figs. 2, 3).

Other than erosion (see above) there appears to be only two major pathways for loss of nitrogen from streams: denitrification and insect emergence. Denitrification was not measured in this study. However, in other studies it has ranged between 0.2–14.0 g N/m^2/yr (Sain et al. 1977; Chatarpaul et al. 1980; Smith and DeLaune 1983; P.A. Steudler, unpublished data).

The exit of insects from the water column represent a small annual loss of nitrogen during the ice-free season (Table 1; Naiman et al. 1984). In both the riffle and the

Table 2. Percentage composition of major nitrogen sources when the throughflow of nitrogen suspended in the water is excluded

Nitrogen Source	Riffle (%)	Beaver Pond (%)
Precipitation	5.6	9.1
Throughfall	6.9	0.0
Allochtonous inputs		
Direct	56.9	22.1
Lateral	26.4	1.3
Nitrogen fixation		
Wood	2.8	1.3
Sediment	1.4	66.2
Total standing stock (g N/m^2)	22.2	557.5
Annual input (g N/m^2)	7.2	7.7
Turnover time (yr)	3.1	72.4

beaver pond, annual insect emergence accounts for 0.1 g N/m^2, and only 0.4 g N/m of stream length from the pond. These are minimal rates since insect emergence from stream margins has not been measured.

Budget analysis. If the large annual throughflow of nitrogen suspended in stream water is excluded and only in-stream processes examined, it is clear that fundamental pathways of nitrogen cycling have been altered by beaver (Table 2). In riffles, 83.3% of the annual nitrogen inputs (7.2 g N/m^2) are accounted for by direct allochthonous inputs (56.9%) or as lateral inputs from the forest floor (26.4%). Nearly all this nitrogen enters the stream in the form of leaves, most of which is speckled alder. Precipitation, throughfall, and nitrogen fixation are not especially important to the riffle's nitrogen budget. Together they account for only 16.7% of the annual nitrogen inputs (Table 2). Cycling of nitrogen is rapid in the riffle, with a turnover time of 3.1 yr; sediment nitrogen turns over faster (0.6 yr) than that of wood (~90 yr).

In the beaver pond, most of the annual input (7.7 g N/m^2) is accounted for by nitrogen fixation associated with accumulated sediment (66.2%); direct allochthonous inputs have been reduced to 22.1% and lateral inputs to 1.3% of the budget. Precipitation contributes 9.1% but throughfall and nitrogen fixation associated with wood are negligible (<1.3%). The turnover time for nitrogen is a slow 72.4 yrs. It appears that much of the nitrogen is sequestered in sediments until the site is abandoned, the dam decays and the pond dries. Only when the pond dries does it appear that the nitrogen is released to higher trophic levels (Naiman et al. 1984). This scenario is similar when considered per unit length of channel.

In one other nitrogen budget study DON was also the major form of throughflow (Watershed 10, Oregon; Triska et al. 1984). In that study the dissolved nitrogen fraction consisted of 95% DON and 5% DIN, which contrasts sharply with Meyer et al. (1981) who found that only 13% of the dissolved nitrogen in Bear Brook, New Hampshire, was DON. Watershed 10 had annual allochthonous input rates (3.1 gN/m^2) slightly less, and nitrogen fixation rates on a variety of organic materials (0.8 gN/m^2), that were slightly higher than those measured in our study. Overall, the nitrogen budget reported by Triska et al. (1984) is similar to that reported here for the riffle.

Ecosystem implications

Historically, small streams throughout North America had different features than they do today (Morgan 1868; Sedell and Froggett 1984). Beaver undoubtly exerted a much stronger and wider influence on ecosystem structure and dynamics by ponding headwater streams and by intensifying interactions between the terrestrial and aquatic environments. The fact that large amounts of sediment and nitrogen were sequestered high up in the watershed, rather than being eroded downstream, suggests that watercourses throughout North America were significantly altered by the removal of beaver long before extensive research began. In fact, the influence of beaver activity can still be seen today in the terrestrial vegetation of meadowlands centuries after extirpation (Ives 1942, Neff 1957).

Beaver mediated alterations to streams have far reaching implications when viewed in an ecosystem perspective. In pristine and semi-pristine regions of Oregon and Québec, nearly 1500 km of stream have been surveyed recently with the conclusion that today beaver may directly influence ~30% of that length (J.R. Sedell and R.J. Naiman, unpublished data). In Wyoming, Smith (personal communication) recently surveyed 1,840 km of stream and found that beaver dams averaged 0.8/km. In these studies only dams of significant size and water ponding were counted. If this was a general situation throughout the historical range of beaver, as we suspect, then nitrogen fixation by sediment organisms, long-term cycles of nitrogen storage and release, and elevated nitrogen concentrations in waters flowing downstream would have been dominant features of running waters. These features would have had strong effects on community composition and productivity, especially in regions where nitrogen is a limiting nutrient.

Finally, the storage of sediment and nitrogen by beaver dams has strong implications for the river continuum concept (Vannote et al. 1980), the nutrient spiraling concept (Elwood et al. 1983) and the intermediate-disturbance hypothesis (Connell 1978; Ward and Stanford 1983). Specifically, the continuum concept must be modified to include numerous zones of beaver altered reaches in small order streams, and concomitant changes in community processes and composition. Nutrient retention is increased within streams altered by beaver as nitrogen is sequestered for longer time periods, thus decreasing spiraling length and increasing ecosystem retention and processing efficiency. Beaver ponds also increase the diversity of habitat available for aquatic organisms. As ponds pass through their ontogeny from formation to erosion, they act to enhance the biotic diversity of headwater streams by creating small "disturbance" zones analogous to those in marine intertidal areas. Overall, these features suggest that beaver, through their feeding and dam building activities, act as a keystone species (sensu Paine 1966) to affect ecosystem structure and dynamics far beyond their immediate requirements for food and space. This being the case, the role of beaver in influencing interactions between terrestrial and aquatic ecosystems, and in the structuring of those ecosystems, deserves serious consideration.

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