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Ecology, Vol. 67, No. 5. (Oct., 1986), pp. 1254-1269.

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ECOSYSTEM ALTERATION OF BOREAL FOREST STREAMS BY BEAVER (*CASTOR CANADENSIS*)¹

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Abstract. Beaver (*Castor canadensis*) alter the structure and dynamics of aquatic ecosystems with a minimum of direct energy or nutrient transfer. Through dam building and feeding activities, beaver act as a keystone species to alter hydrology, channel geomorphology, biogeochemical pathways, and community productivity. Here we consider the effects of beaver activity on several major ecosystem components and processes in boreal forest drainage networks in Quebec, Canada. The density of dams on the small streams (≤ 4 th order) we studied averages 10.6 dams/km; the streams retain up to 6500 m³ of sediment per dam, and the wetted surface area of the channel is increased up to several hundred-fold. Beaver are also active in larger order streams (≥ 5 th order), but their effects are most noticeable along riverbanks and in floodplains.

Comparative carbon budgets per unit area for a riffle on 2nd order Beaver Creek and a beaver pond downstream show the pond receives only 42% of the carbon acquired by the riffle annually. However, because the pond has a surface area seven times greater than the riffle, it receives nearly twice as much carbon as the riffle per unit of channel length. Carbon in the pond has an estimated turnover time of ≈ 161 yr compared to ≈ 24 yr for the riffle. Beaver ponds are important sites for organic matter processing; the stream metabolism index (SMI), a measure of ecosystem efficiency for the utilization or storage of organic inputs, is 1.63 for the pond compared to 0.30 for the riffle; the turnover length (S) for particulate carbon is 1.2 km for the pond compared to 8.0 km for the riffle. Beaver-induced alterations to the structure and function of streams suggest removal of beaver prior to 1900 AD had substantial effects on the dynamics of lotic ecosystems. Our results suggest that current concepts of the organization and diversity of unaltered stream ecosystems in North America should recognize the keystone role of beaver, as drainage networks with beaver are substantially different in their biogeochemical economies than those without beaver.

Key words: beaver; biogeochemistry; carbon budget; *Castor canadensis*; ecosystem; keystone species; landscape; Quebec; watershed.

INTRODUCTION

The activities of beaver (*Castor canadensis*) in streams provide an outstanding example of a natural alteration to ecosystem structure and dynamics. Beaver activity results in alterations that: (1) modify channel geomorphology and hydrology, (2) increase retention of sediment and organic matter, (3) create and maintain wetlands, (4) modify nutrient cycling and decomposition dynamics by wetting soils, by altering the hydrologic regime, and by creating anaerobic zones in soils and sediments, (5) modify the riparian zone, including the species composition and growth form of plants, their chemistry (lignin, nitrogen, and defensive compounds), and the quantity of allochthonous inputs, (6) influence the character of water and materials transported downstream, and (7) modify habitat, which ultimately influences community composition and diversity. These alterations are not localized or unusual.

Where beaver remain largely unexploited, their activities may influence 20–40% of the total length of 2nd to 5th order streams (Naiman and Melillo 1984; J. R. Sedell and R. J. Naiman, *personal observations*), with the alterations remaining as part of the landscape for centuries (Rudemann and Schoonmaker 1938, Ives 1942, Neff 1957). Surprisingly, few studies have addressed the effects of beaver on the structure and dynamics of aquatic or terrestrial ecosystems (reviewed by Yeager and Hay 1955, Jenkins and Busher 1979, Hodgdon and Larson 1980).

Prior to the arrival of Europeans in North America, the beaver population was estimated to be between 60×10^6 and 400×10^6 individuals (Seton 1929) with a geographical range of $\approx 15.5 \times 10^6$ km² extending from the arctic tundra to the deserts of northern Mexico (Jenkins and Busher 1979). In the early 17th century extensive removal of beaver began; between 1620 and 1630 over 10 000 were trapped annually from Connecticut and Massachusetts (Moloney 1967). From 1630 to 1640, ≈ 80 000 were taken annually from the Hudson River and western New York (Hays 1871). Historically, nearly every lake, pond, river, and brook in

¹ Manuscript received 10 December 1984; revised 3 February 1986; accepted 6 February 1986.

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New York, and probably most of New England, was occupied by beaver (Rudemann and Schoonmaker 1938). As the eastern beaver population declined, exploring expeditions to the West (1800–1850) were often made solely for the purpose of discovering new trapping areas (Cline 1974). Eventually there was an overharvest (Dugmore 1914, Johnson and Chance 1974) and beaver became almost extinct in North America by 1900 (Jenkins and Busher 1979). In addition, since 1834, about 195 000–260 000 km² of beaver habitat in primitive marshes, swamps, and seasonally flooded bottomlands of the United States were converted to dry land (Shaw and Fredine 1971). Today the population is thought to number between 6×10^6 and 12×10^6 . For most of North America the present beaver population represents only a small fraction of earlier numbers; this suggests that basic features of stream ecosystems were substantially changed long before extensive research began.

The objectives of this article are: (1) to examine the ecological role of beaver as natural agents of alteration, in light of current concepts addressing the ecosystem organization and dynamics of running waters; and (2) to present a conceptual model of a pristine stream–river continuum.

STUDY AREA

The study sites are located ≈ 25 – 50 km east of Sept-Iles, Quebec, largely within the Matamek (673 km²) and Moisie River (19 871 km²) watersheds (Fig. 1). This subarctic region on the Precambrian Shield is vegetated by black and white spruce (*Picea mariana* and *P. glauca*; 47% of the area) and balsam fir (*Abies balsamea*; 44%). Paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), speckled alder (*Alnus rugosa*), and willow (*Salix* spp.) are the dominant streamside vegetation. The area receives ≈ 1.12 m of precipitation annually, mostly as snow from October to April. The mean annual air temperature is 1°C. Most streams are relatively low gradient ($< 1.5\%$ slope) with high concentrations of dissolved organic carbon (10–15 mg/L), ≈ 2100 annual degree days ($^{\circ}\text{C}$ above 0°), and an aquatic growing season of ≈ 105 d. The area and some biogeochemical components of the streams were described further by Naiman (1982, 1983a, b, c), Melillo et al. (1983, 1984), and Naiman and Melillo (1984).

The Matamek River watershed is a nearly pristine basin reserved for scientific research. There are no roads or timber harvesting. The lower one-third of the watershed historically received only light and controlled beaver trapping, and there has been no trapping since 1979. The Moisie River watershed is similarly unique. Less than 1% of the area has been disturbed and the lower 170 km of the river is controlled by a private fishing club. The lower part of the watershed is subject to controlled trapping but, due to its remote location

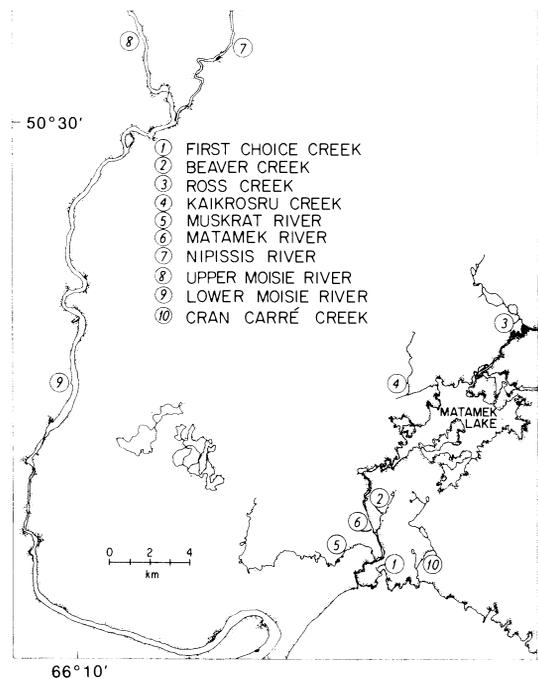


FIG. 1. Locations of principal study sites in the subarctic region east of Sept-Iles, Quebec, Canada.

and vast area, the beaver population is only slightly affected.

METHODS

General approach

We designed this study to evaluate how beaver might alter ecosystem structure and function. Important geomorphological and biological parameters such as distribution of beaver dams, sediment accumulation, woody debris standing stocks, and insect emergence were examined in streams of several different orders. We also measured processes such as allochthonous inputs, decomposition dynamics, seston export, and benthic metabolism, comparing beaver-modified reaches with unmodified reaches immediately upstream. This approach allowed us to study the influence of beaver in a landscape perspective as well as within a single small stream. The synthesis presented in this paper is based upon both previously published and unpublished results. Data are reported for the first time on geomorphology, sediment and organic matter accumulations, wood debris, carbon export, and benthic metabolism. These data are combined with additional data on carbon export (Naiman 1982), allochthonous inputs (Connors and Naiman 1984), primary production and respiration (Naiman 1983a, b), insect emergence (Naiman et al. 1984), and methane flux (T. E. Ford and R. J. Naiman, *personal observation*) to develop the carbon budgets.

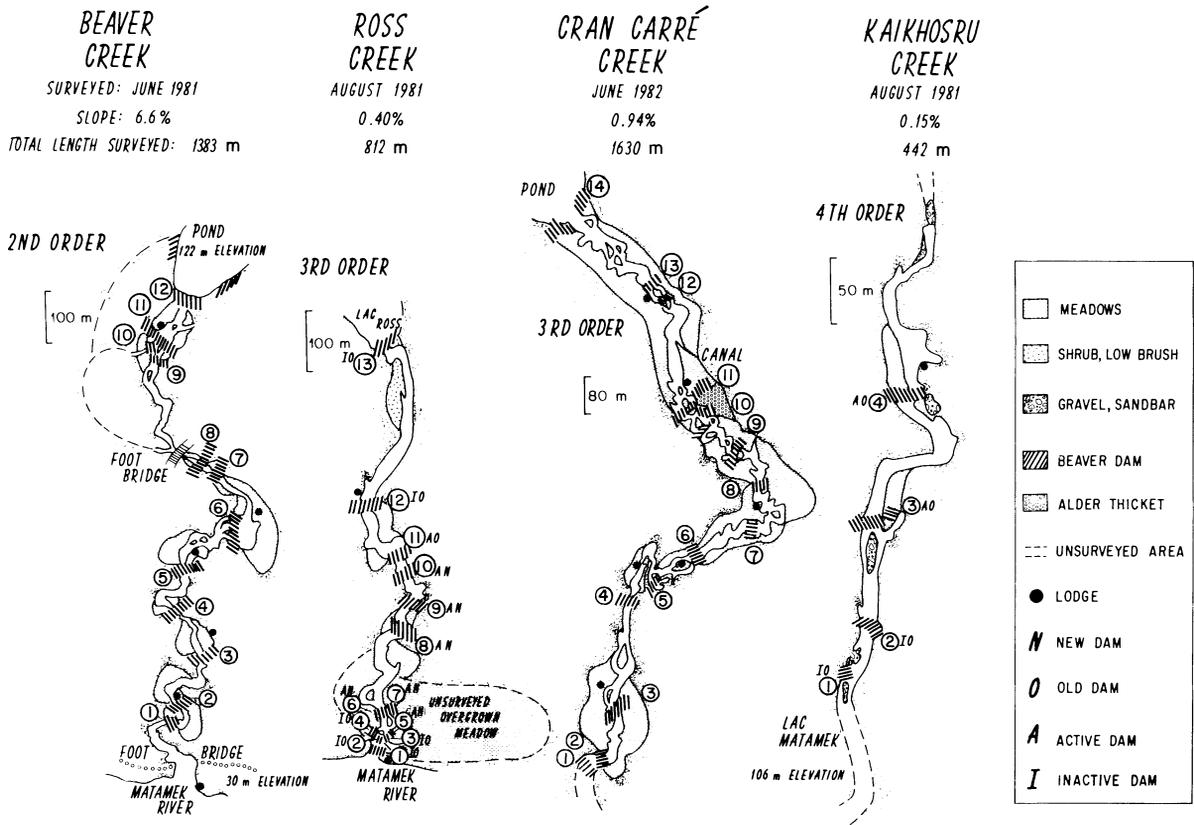


FIG. 2. Partial results of the survey of beaver dams (circled numbers) and ponds on 2nd–4th order streams in the study area (mapped in Fig. 1). The horizontal dimension in the illustrations (i.e., width) has been increased 2–4 \times relative to the vertical dimension to show meadows and sediment accumulations better.

Standing stock

Benthic organic carbon.—Sections of 10 streams ranging in size from 1st to 9th order (Fig. 1) were mapped using standard surveying techniques. Woody debris, extent of sediment accumulation, channel geometry, gradient, and position and condition of dams and lodges were noted. Coarse particulate organic matter (CPOM: > 1 mm diameter), fine particulate organic matter (FPOM: 0.5 μ m to 1 mm), and inorganic sediment accumulated behind each dam were estimated by measuring channel slope, valley contours, pond width and length, dam height, and the bulk density and percentage of CPOM and FPOM in sediment cores. Bulk density was measured by drying (60°C) a known volume of sediment taken from various depths. The percentage of organic matter was determined by sieving and then ashing samples at 525° for 2–4 h. For these and other components, organic matter was assumed to be 47% carbon. Autotrophic standing stock was estimated by extraction of chlorophyll *a* in 90% acetone, then using the phaeophytin correction and the equation of Lorenzen (1967). Chlorophyll content was converted to carbon content by assuming a ratio of 120:1 (Naiman and Sedell 1979a).

Wood debris.—Wood debris in 9 of the 10 streams

was surveyed for biomass and identified to species, and the probable input agent (e.g., wind, erosion, beaver, other) was determined by visual inspection. Biomass of coarse wood (≥ 10 cm diameter) was estimated from measurements of length, diameter, and bulk density. For whole trees, the diameter at breast height (dbh) and species-specific equations developed for northern trees (Young et al. 1980; H. E. Young, *personal communication*) were used to estimate total mass from dbh. Transects for coarse wood either encompassed the entire stream or covered a minimum of 367 m. The mass of fine wood (1–10 cm diameter) was determined by measuring all pieces in 1 m wide transects across the channel every 10–50 m and species-specific bulk densities. Depending upon the stream, the total number of transects for which all fine wood was measured ranged from 10 to 180 ($\bar{X} = 50$). In riffles, wood biomass was measured to bedrock or a depth of ≈ 8 cm, whichever was less; in beaver ponds only wood in the upper 5–8 cm of sediment was measured. Wood buried in the accumulated sediment could not be measured accurately.

Water column.—One-litre water samples were taken at least weekly during the ice-free season for 2 yr at a well-mixed riffle and at a pond outlet on Beaver Creek

(Naiman 1982). Particulate organic matter (POM: $\geq 0.5 \mu\text{m}$) was concentrated onto a pre-ashed and preweighed Gelman AE glass fiber filter. The filter with the sample was dried at 80° , weighed, ashed at 525° for 2–4 h, and weighed again on a Cahn 25 electrobalance. The POM was assumed to be 47% carbon. Dissolved organic carbon (DOC: $< 0.5 \mu\text{m}$) was measured by collecting 50 mL of water passing through the pre-ashed Gelman filter, preserving it with 2% phosphoric acid (by volume), and measuring the carbon concentration with a Dohrman Model 54 analyzer.

Throughflow

Discharge.—Average annual discharge at Beaver Creek was measured from 1979 to 1983 (Naiman 1982, Naiman and Melillo 1984). Daily discharge was estimated by injecting fluorescent dye into a narrow section of the creek previously charted for depth, width, and volume at various water stages, and determining the discharge from the time it took the dye to traverse the area. Daily discharge was converted to annual discharge by summation.

Carbon throughflow.—Samples used to estimate the standing stock of DOC and POC (carbon content of POM) in the water column were also used to estimate throughflow.

Meteorologic inputs

Precipitation.—Rain and snowfall were measured daily between 1979 and 1983. Collectors for determination of carbon in precipitation were set in an open area adjacent to the Matamek River. Samples were collected after each rainstorm during the snow-free season, and DOC was measured with the Dohrman analyzer. Carbon in snowfall was measured by cores taken in March and extrapolated to total snowfall for the year.

Throughfall.—Trees in the Matamek River watershed have leaves from approximately 15 May to 1 October. Throughfall collectors ($n = 8$) were set beneath pure stands of red alder, paper birch, trembling aspen, and willow. The water was collected after each storm, and carbon measured with the Dohrman analyzer. Stemflow was not measured.

Allochthonous inputs

Allochthonous inputs were measured by Connors and Naiman (1984). Direct litterfall was measured with 10 0.089-m² traps at each of five sites. Lateral inputs were measured with 0.4 m wide traps, using 6–10 traps at each site. Samples from both types of traps were collected weekly or biweekly, May through November, and again in the spring. Samples were dried (80°), weighed, and corrected for ash content.

Metabolism

Primary production.—Annual gross production and respiration by periphyton in a riffle were estimated by

TABLE 1. Standing stocks of fine (1–10 cm diameter) and coarse (> 10 cm diameter) wood debris, by stream order.

	Stream order	Fine wood (g/m ²)*	Coarse wood (kg/m ²)†
First Choice Creek	1	548.2	12.2
Beaver Creek	2	1797.2	39.7
Ross Creek	3	506.5	3.4
Kaikrosru Creek	4	555.8	10.1
Muskrat River	5	405.3	2.1
Matamek River	6	595.9	1.0
Nipissis River	8	36.4	0.1
Upper Moisie River	8	70.3	0.3
Lower Moisie River	9	46.0	0.1
\bar{X}		506.8	7.8
SD		537.5	12.8

* Ash-free dry mass per unit surface area. The relationship between standing stock of fine wood and stream order is significant ($r^2 = 0.75$; $P < .01$) and is described by the equation: fine wood mass = $2244.4e^{-0.41x}$, where x is order.

† Ash-free dry mass per unit surface area. The relationship between standing stock of coarse wood debris and stream order is significant ($r^2 = 0.87$; $P < .01$) and is described by the equation: coarse wood mass = $64.8e^{-0.70x}$, where x is order.

Naiman (1983a). Metabolism was measured by the diel oxygen technique using recirculating Plexiglas chambers (Bott et al. 1978) during the ice-free season.

Primary production in a beaver pond was measured in a similar manner. Shallow (5 cm) plastic trays were filled with either FPOM or fine wood and incubated in the stream at the site of collection for 3–4 wk before metabolic measurements were made. Samples were placed in separate recirculating 17-L Plexiglas chambers, oxygen changes were monitored with YSI Model 54 meters connected to a strip chart recorder, and metabolic parameters were measured by the oxygen method. Each month, from June to September 1981, five chambers were operated simultaneously for 24-h periods over three consecutive days.

Surface respiration.—Daily surface respiration (i.e., top 5 cm of sediment) was also measured by the diel oxygen method, with the same samples used for gross production. Respiration rates were assumed to remain constant over the 24-h period (Bott et al. 1978).

Methane flux.—Bubbles of gas from sediments were collected in bell jars at the water surface and analyzed for methane by flame ionization using a gas chromatograph (Carle) with a Poropak Q column at 75° (T. E. Ford and R. J. Naiman, *personal observation*). Sampling was done weekly during the 1984 ice-free season (May–October). Measures of methane production represent minimums due to bacterial oxidation of methane at the aerobic-anaerobic sediment boundary.

Decomposition.—Mass loss and nitrogen dynamics of speckled alder, paper birch, black spruce, balsam fir, and trembling aspen wood chips were studied by Melillo et al. (1983) using a mesh bag technique (mesh size = 2 mm). Materials were analyzed for loss of mass, lignin concentration, ash content, and total Kjeldahl nitrogen concentration over the 16-mo study. Decomposition

TABLE 2. Distribution of fine wood (1–10 cm diameter) and coarse wood (>10 cm diameter) inputs, classified by most probable input agent. Data are averages across all stream orders.

Species	Fine wood				Coarse wood
	Beaver	Wind	Erosion	Other	Beaver
	Percentage of total mass of the species ($\bar{X} \pm 1$ SD)				
Deciduous					
Speckled alder	13.4 ± 23.8	32.8 ± 22.0	52.6 ± 31.6	1.2 ± 2.2	0.0
Paper birch	16.5 ± 22.6	69.9 ± 26.3	13.5 ± 26.1	0.0 ± 0.1	8.1 ± 14.8
Trembling aspen	53.1 ± 40.6	39.7 ± 4.4	4.4 ± 6.8	2.6 ± 5.7	36.7 ± 29.8
Willow	56.2 ± 39.9	20.9 ± 22.7	17.4 ± 37.3	5.4 ± 14.4	0.0
Conifers					
Balsam fir	0.5 ± 1.5	52.3 ± 29.5	46.4 ± 29.0	0.7 ± 1.5	1.0 ± 2.6
White and black spruce	0.0	79.0 ± 32.5	19.9 ± 32.6	0.1 ± 0.3	0.2 ± 0.7
Unidentified	4.4 ± 5.3	70.2 ± 28.7	14.3 ± 15.1	0.0	2.4 ± 4.7

rate (k) was calculated using the exponential decay model of Olson (1963).

Insect emergence

Insects were collected weekly, from May to mid-October 1982, using 2–4 floating emergence traps (Naiman et al. 1984) on each stream. Traps were constructed with a wooden frame on styrofoam floats, Nitex netting (200 μ m), and a glass jar at the apex to concentrate insects; each trap samples 0.25 m² (Mundie 1971). Insects were preserved in the field with 70% ethanol. In the laboratory they were sorted and identified to genus. Biomass of individual genera in each collection was estimated by drying representative samples at 60° for 24 h, weighing the specimens on a Cahn 25 electrobalance, and then multiplying the unit dry mass by the number of individuals in that collection. Annual emergence was calculated by summing the biomass for each weekly collection over the ice-free season.

RESULTS AND DISCUSSION

Geomorphology

Beaver noticeably alter the main channels of 2nd–4th order streams (Fig. 2). Rarely do beaver build dams in 1st order streams and, in streams \geq 5th order, dams in the main channel are often destroyed by the spring flood. The density of intact dams in the 2nd–4th order streams examined ranged from 8.6 dams/km in Cran Carré (3rd order) to 16.0 dams/km in Ross Creek (3rd order); the mean was 10.6 dams/km. Old abandoned dams and small dams made of stone and mud were not included. This density of dams is not unexpected when one considers that the number of colonies may reach 3 colonies/km² (Voigt et al. 1976), with typical values in favorable habitat ranging between 0.4 and 0.8 colonies/km² (Aleksiuk 1968, Voigt et al. 1976, Bergerud and Miller 1977). Areas in the Matamek and Moisie River watersheds unsuitable for beaver, because of stream gradient or inadequate food supply, account for only \approx 30% of the total length of 2nd–4th

order streams. In streams \geq 5th order, beaver alterations to channel geomorphology are largely seen along river banks and in backwater wetlands and floodplains.

Beaver dams significantly alter the nature of streams by impounding water and sediment. We could not accurately measure the amount of water impounded, especially in saturated soils some distance from the original stream channel; however, we did measure the amount of sediment retained by dams. There was no relationship between the size of the dam and the amount of sediment retained ($r^2 = 0.03$, $n = 18$, $P > .05$). There was, however, a significant relationship between the surface area of the meadow or pond and the amount of sediment (sediment volume = $47.3 + 0.39 \cdot [\text{surface area}]$; $r^2 = 0.85$, $P < .01$; where sediment volume is in cubic metres and surface area is in square metres). Surface area of the ponds varied from ≈ 100 to $\approx 14\,650$ m², and sediment volumes varied from ≈ 35 to 6500 m³. In several instances a small dam (4–18 m³) of wood, properly positioned, could retain 2000–6500 m³ of sediment.

The sediment accumulation can be important when viewed in a landscape perspective. In the Matamek River watershed, 21% of the 1532 km of streams are 2nd–4th order (Naiman 1983a, c). If we estimate that these streams contain 10 dams/km and each dam retains 1000 m³ of sediment, then beaver may be directly responsible for the retention of 3.2×10^6 m³ of sediment in small-order streams. If the sediment were evenly distributed throughout all streams in the watershed (stream surface area = 7.7×10^6 m²), the stream bottom would be covered with an additional 42 cm of sediment.

Biological processes

Wood debris.—There were significant relationships between the mass of fine wood (≤ 10 cm diameter) and of coarse wood (> 10 cm diameter), and stream order (Table 1). Most fine wood was speckled alder, balsam fir, and spruce, with these species accounting for 18.2–25.3% of the biomass. Coarse wood estimates include

TABLE 2. Continued.

Coarse wood		
Wind	Erosion	Other
Percentage of total mass of the species ($\bar{X} \pm 1$ SD)		
47.9 \pm 50.1	52.3 \pm 50.1	0.0
47.3 \pm 31.5	41.0 \pm 24.6	3.5 \pm 7.7
27.3 \pm 21.3	35.9 \pm 29.0	0.0 \pm 0.0
53.6	46.4	0.0
49.8 \pm 26.1	44.9 \pm 25.1	4.2 \pm 7.7
63.8 \pm 27.9	34.9 \pm 28.0	1.0 \pm 1.5
73.2 \pm 20.5	23.9 \pm 18.1	1.3 \pm 2.0

all the wood in the stream channel, whether above the channel or actually submerged in the water. Paper birch, balsam fir, and spruce were the major portion of this coarse wood biomass (21.2–38.4%). Nevertheless, there were few statistically reliable trends relating stream order to mass of a particular wood species. For particular species, coefficients of variation among stream orders were generally large (44–308%); the only exceptions were for coarse spruce ($r^2 = 0.87$) and coarse birch ($r^2 = 0.74$).

Beaver eat the leaves, twigs, and bark of most species of woody plants growing near water, as well as many herbaceous plants, especially aquatic macrophytes. However, beaver are usually selective. Jenkins (1975) found that 16 of 17 tree genera in central Massachusetts were cut over a 2-yr period, but 6 genera accounted for >90% of all trees cut. We attempted to quantify the importance of beaver as an agent transferring wood to streams in comparison to other possible agents (i.e., wind and erosion). Beaver cut 53.1% of the fine wood mass of trembling aspen, 56.2% of the willow, 13.4% of the alder, 16.5% of the paper birch, and <1% of the conifers (Table 2). Wind was important for all species, with erosion important only for speckled alder and balsam fir, two species growing on the riverbank. For coarse wood, beaver were an important input agent only for trembling aspen (36.7%), with wind and erosion being about equal for the remaining species (Table 2).

Data in Tables 1 and 2 may, however, underestimate the role of beaver in several respects. First, no significant difference was found in the mass of wood cut by beaver when stream orders were compared. It appears that beaver may be equally active in small streams and larger rivers. Second, beaver have an important role, especially in 2nd–4th order streams, as an indirect input agent. The trees surrounding the original stream channel are killed where beaver build dams and raise the water table; eventually the trees fall into the pond (Lawrence 1954). In these streams, we estimated that as much as 50–60% of the wood input categorized by us as wind-induced resulted from conditions changed

by beaver. Third, the relative standing stocks of wood species do not imply relative input rates. We have already shown that species with a low lignin : nitrogen ratio and preferred by beaver (e.g., alder, birch, aspen, willow) decompose relatively rapidly ($< \approx 20$ yr), while wood with a high lignin : nitrogen ratio decomposes slowly (≈ 50 –200 yr; Melillo et al. 1983, 1984). Finally, in beaver ponds a large proportion of the wood is buried in sediment; therefore, data in Tables 1 and 2 underestimate total amounts and the percentages contributed directly and indirectly by beaver to the ponds. Nevertheless, the amount and quality of this organic material has some important implications for decomposition dynamics and nutrient chemistry in streams.

Decomposition dynamics.—Melillo et al. (1983, 1984) concluded that the initial quality of organic material strongly determines its decay rate and its tendency to sequester nutrients. Quality is measured as the initial percentage of nitrogen and lignin of the material, or the lignin : nitrogen ratio. In our experiments a high-quality wood (speckled alder; lignin : nitrogen ratio = 42) and a low-quality wood (black spruce; lignin : nitrogen ratio = 647) were placed in a riffle and a pond on Beaver Creek. As would be predicted from the initial wood quality, alder chips in the riffle decayed faster ($k = -0.64$ yr $^{-1}$) than spruce chips ($k = -0.18$ yr $^{-1}$). However, alder incubated aerobically on pond surface sediments decayed substantially more slowly than in the riffle ($k = -0.12$ yr $^{-1}$), and spruce wood in the pond decayed more slowly than spruce wood in the riffle ($k = -0.07$ yr $^{-1}$). By changing stream channels into ponds, beaver substantially decrease the rate of organic matter decay, possibly by a reduction in the nutrient supply rate caused by a slower water velocity. We believe this reduction in nutrient supply rate to be important, since nutrient immobilization dynamics during decay did not differ in the pond vs. the riffle (Fig. 3). For both alder and spruce the patterns of nutrient immobilization in the two sites did not fundamentally differ (Fig. 3: data points for pond and riffle were collinear), but the rate and which the material moved through the decay-nutrient immobilization process was significantly slower in the pond (Fig. 3: values of k).

Carbon and sediment export.—No significant difference ($P > .05$) in suspended DOC, POM, or sediment concentrations entering and leaving a pond on Beaver Creek was observed during the 2-yr study. This may be because the pond was mature (i.e., it no longer appeared to be rapidly accumulating material), and because this section of Beaver Creek had 10 additional ponds upstream. However, when annual suspended export from the Beaver Creek watershed is compared to other watersheds, substantial differences in export rates are evident (Table 3). In addition, virtually every 2nd or 3rd order stream in this region has significant beaver activity. Therefore, we have no control stream by which to judge how upstream activity has influenced carbon

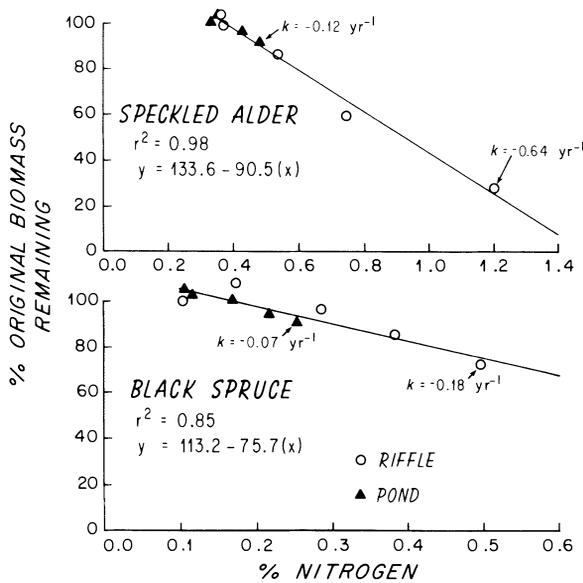


FIG. 3. Mass loss and nitrogen dynamics of speckled alder (high-quality) and black spruce (low-quality) wood chips placed in a riffle and in a beaver pond in Beaver Creek, Quebec, Canada. Data represent a time series, over 16 mo; each data point represents 5 samples. For each wood species, the decomposition was faster (decomposition rate k more negative) in the riffle.

concentrations entering the study reach. We do, however, have data on a small 1st order stream (First Choice Creek) with no history of beaver activity (Table 3 and Naiman 1982). Between 1979 and 1981 the average loss rate of DOC in that watershed was $2.5 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, only 5.2% of the level measured in the beaver-influenced watershed; the POC loss rate was $0.5 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, only 16.0% of that measured in Beaver Creek. Since we were unable to detect a significant difference in either DOC or POC between water entering and leaving a beaver pond, we can only speculate that a series of ponds is required to raise carbon concentrations and, once a certain concentration is reached, further increases are difficult to detect. Water leaving the Beaver Creek watershed has higher DOC and POC concentrations and the stream has higher export rates than large rivers downstream (Naiman 1982), suggesting that exported carbon is stored or oxidized in

middle order streams. We suspect the higher export rate in Beaver Creek may result from the increased organic matter loading caused by beaver activities.

This situation is somewhat paradoxical, for, as we suggest later (Ecosystem Efficiency), beaver increase ecosystem processing efficiency for organic matter, yet erosional yields of organic matter are greater in beaver-modified watersheds. The apparent conflict may be reconciled if one considers that the wetted area of the stream channel and the mass of organic matter in contact with the water are substantially increased by beaver activity. Although the absolute mass of organic material moved downstream increases, the amount of material exported relative to that in contact with the water may eventually prove to be less.

FPOM and wood debris metabolism.—Mass-specific metabolism of FPOM (milligrams of O_2 consumed per gram ash-free dry mass per day) was significantly altered by beaver activity in two ways. First, opening the canopy resulted in more primary production; net community production, net daily metabolism, and the $P:R$ ratio (ratio of gross primary production to community respiration) were significantly greater in the pond ($P = .01-.03$), while respiration in the upper 5 cm of sediment was significantly less ($P = .02$). There was no difference in gross production ($P = .60$). Second, when mass-specific rates are applied to the standing stock of surface FPOM in the riffle and pond, the difference between the two sites in total metabolism (measured as carbon consumed) becomes obvious. In the riffle, FPOM respired $\approx 5.8 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, while primary production was negligible (Naiman 1983a). In contrast, FPOM in the pond respired an estimated $55.5 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ while periphyton associated with surface sediments produced carbon at the rate of $1.7 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ and respired $1.6 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$.

The mass-specific metabolism of fine wood debris was not significantly different between riffle and pond. The difference in areal respiration by fine wood debris (riffle: $11.3 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$; pond: $41.2 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) was due to the larger standing stock of wood in the pond. Metabolism by coarse wood debris was not measured. Until it is demonstrated otherwise, we assume that metabolism by organisms associated with coarse wood debris is not significant when compared to organisms associated with materials with larger surface-to-vol-

TABLE 3. Annual yield of sediment and organic carbon per unit area for the five study watersheds in 1980.

Stream	Watershed area (km ²)	Sediment yield (g·m ⁻² ·yr ⁻¹)	POM yield* (g·m ⁻² ·yr ⁻¹)	DOC yield (g·m ⁻² ·yr ⁻¹)	Total carbon† yield (g·m ⁻² ·yr ⁻¹)
First Choice Creek	0.25	2.21	1.08	2.53	3.07
Beaver Creek	1.83	7.62	6.73	48.38	51.75
Muskrat River	207	3.32	1.92	12.44	13.40
Matamek River	673	1.50	1.33	9.78	10.45
Moisie River	19 871	5.99	0.95	4.26	4.74

* Particulate organic matter ($\geq 0.5 \mu\text{m}$); yield is ash-free dry mass.

† Calculated by assuming POM to be 47% carbon (Naiman 1982).

ume ratios (Naiman 1983a), even though in Georgia, wood has been shown to be an important site for invertebrate production (Wallace and Benke 1984).

Carbon budgets

From the previous measurements of carbon dynamics at a number of pond and riffle sites along Beaver Creek and similar streams nearby, we constructed partial carbon budgets for a "typical" beaver pond and stream riffle. Due to the wide variety of pond ages and sizes encountered, we assumed a situation where beaver had taken a 100-m reach of stream, with a mean 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/m² of sediment (including FPOM) and 3.9 kg/m² of coarse wood (measured as carbon) submerged in the water; the beaver pond has 125 kg/m² of sediment and 3.1 kg/m² of wood (measured as carbon) actually in the water. These dimensions, amount of material, and general assumptions agree with the field data from local 2nd and 3rd order streams where we made detailed surveys of five streams covering 4.3 km and 42 beaver dams (Naiman et al. 1982, Naiman and Melillo 1984). Two partial budgets were developed: one per unit area, to emphasize concentration effects (Fig. 4), and one per unit length of channel, to emphasize absolute effects (Fig. 5).

Standing stock.—The pond contains substantially more carbon per unit area than the riffle, except for coarse wood and periphyton (Fig. 4). As a result of the damming of the stream, the standing stock of FPOM is increased 110-fold and the fine wood debris is increased to four times the previous value. Both DOC and POC in the water column are minor components of both budgets, but in the pond there is ≈ 10 times as much carbon in the water column than in the riffle. The major difference between the two sites is in the accumulated benthic organic carbon behind the dam; cores taken from riffles and ponds both contained 6.25% organic carbon as dry mass.

There are substantial differences between the riffle and the pond in the budgets computed per linear metre of channel (Fig. 5). Every carbon standing stock component in the pond is substantially larger than in the riffle. The magnitude of these comparisons ranges from 1.4:1 for periphyton to 347:1 for benthic FPOM plus CPOM.

Throughflow.—The average annual discharge between 1979 and 1983 in Beaver Creek was 1.04×10^6 m³/yr (Naiman and Melillo 1984). Since the average concentrations of suspended DOC and POC in water from a riffle and water leaving a beaver pond were not statistically different, we used export rate equations reported by Naiman (1982) to estimate the throughflow of carbon annually available to the biotic communities. The amount of DOC available to the 100 m² of riffle

was 8.9×10^5 g·m⁻²·yr⁻¹ vs. 1.3×10^5 g·m⁻²·yr⁻¹ for the 700-m² pond (Fig. 4). The corresponding values for POC were 5.8×10^4 g·m⁻²·yr⁻¹ and 8.3×10^3 g·m⁻²·yr⁻¹; the difference was due only to the larger surface area of the pond. We assumed no net change in DOC or POC concentrations as water passes through a single beaver pond for the present budget.

Meteorologic inputs.—The beaver pond receives mostly direct precipitation, since the forest canopy cover became only 10% due to flooding and cutting. Between 1979 and 1983 the 112 cm/yr of rainwater and snow provided an average carbon input of 4.86 mg/L (R. J. Naiman, *personal observation*). This is an annual input of 5.5 g/m² or 38.5 g/m of stream channel (Figs. 4 and 5). For the riffle, precipitation during the leaf-off period (≈ 1 October to 15 May) averaged 65.5 cm, an annual carbon input of 3.4 g/m².

The riffle section of Beaver Creek is heavily shaded by speckled alder during the growing season, when an average of 43.5 cm of rain falls. The carbon content of water dripping from alder leaves between 1980 and 1983 averaged 11.85 mg/L (R. J. Naiman, *personal observation*), 244% greater than unaltered precipitation, resulting in an estimated input of 13.5 g·m⁻²·yr⁻¹ (Fig. 4). Only $\approx 10\%$ of the pond is covered by riparian vegetation, resulting in a throughfall of 1.4 g·m⁻²·yr⁻¹. Annually, the pond receives 16.9 g/m² via meteorologic pathways.

Allochthonous inputs.—Allochthonous inputs are an important source of carbon for these small streams (Connors and Naiman 1984). Most direct inputs (92%) of carbon to the riffle are in the form of alder, birch, and aspen leaves; together they account for 112.8 g·m⁻²·yr⁻¹ (Fig. 4). Since there is little canopy over the beaver pond, direct inputs of allochthonous leaf material are less (48.8 g·m⁻²·yr⁻¹), but the amount collected per linear metre of channel (341.9 g·m⁻¹·yr⁻¹; Fig. 5) is about three times that of the riffle, due to the wider collecting surface.

Lateral inputs of organic matter from the forest floor are less than direct allochthonous inputs (Connors and Naiman 1984). For the riffle, nearly 81% of the annual 55.8 g/m is leaves or seeds and catkins, an input of 45.2 g·m⁻²·yr⁻¹ exclusive of fine wood (Fig. 4). For the beaver pond, 76% of the annual 29.7 g/m consists of leaves or tree products, accounting for an annual input of only 3.2 g/m². The annual input of leaves per linear metre of pond is 22.4 g/m (Fig. 5).

Fine wood, falling directly from the forest canopy or moving downhill on the forest floor, also constitutes a significant input. For the riffle, 8% of the direct allochthonous carbon and 19% of the lateral allochthonous carbon is fine wood (20.9 g·m⁻²·yr⁻¹). For the pond, 9% of the direct allochthonous carbon and 24% of the lateral allochthonous carbon is fine wood, contributing 4.8 g·m⁻²·yr⁻¹ or 33.6 g·m⁻¹·yr⁻¹ (Figs. 4 and 5).

Primary production.—The standing stock (0.5 g/m²)

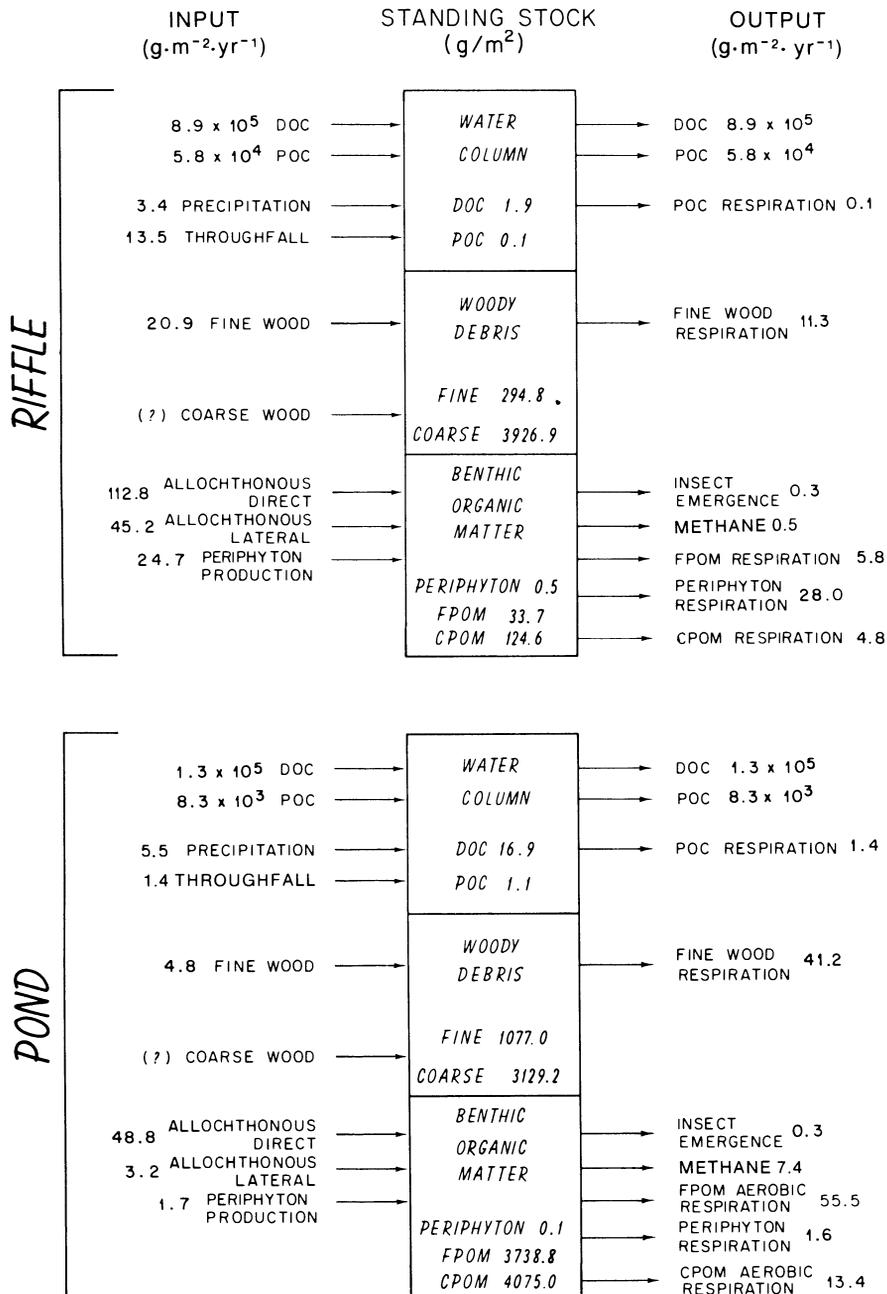


FIG. 4. Comparison of carbon budgets, per unit area, for a riffle and for a pond on Beaver Creek, Quebec, Canada. The budget is calculated for a 100-m reach of stream.

of periphyton in the riffle, although low when compared to periphyton from streams in other biomes and even to larger streams in this watershed, has an annual gross production of $24.7 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (Fig. 4 and Naiman 1983a). Diatoms and algae associated with FPOM on the benthic surface also fix carbon photosynthetically. In the riffle, where the forest canopy filters out 89% of the available light, the contribution is miniscule. However, in the pond, where light availability is less restricted, a small standing stock of photosynthetic

organisms ($0.1 \text{ g}/\text{m}^2$) has a gross production of $1.7 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (Fig. 4) or, in terms of stream channel, $11.9 \text{ g}\cdot\text{m}^{-1}\cdot\text{yr}^{-1}$ (Fig. 5). Primary production by diatoms and algae on wood debris in the pond was so low that it could not be accurately measured by our techniques.

Respiration.—In the riffle, most respiration is accomplished by periphyton ($28.0 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), followed by fine wood ($11.3 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), benthic FPOM ($5.8 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), benthic CPOM ($4.8 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), and POC suspended in the water column ($0.1 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$). In

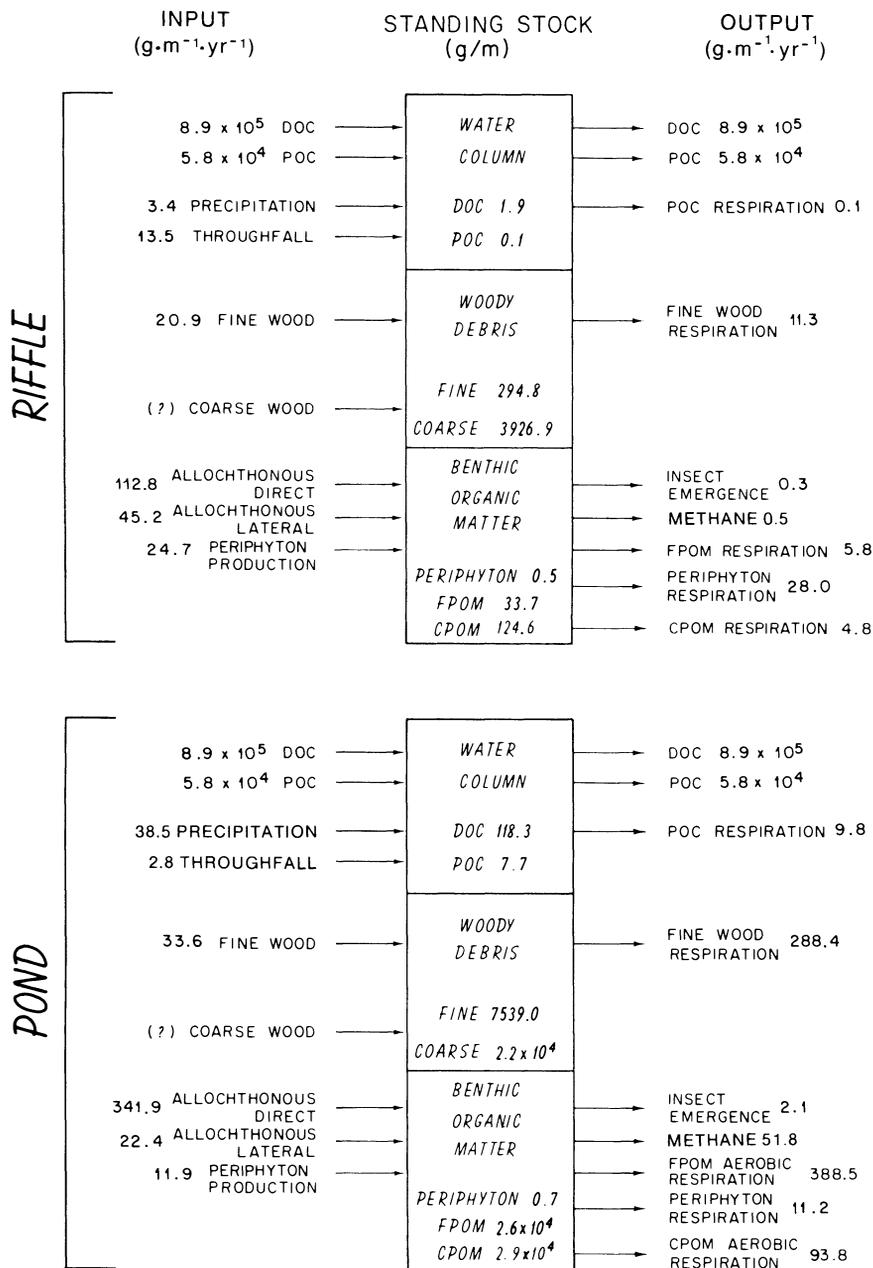


FIG. 5. Comparison of carbon budgets, per unit length of channel, for a riffle and for a pond on Beaver Creek, Quebec, Canada. As in Fig. 4, the budget is calculated for a 100-m reach of stream.

the pond the situation is quite different as a result of the larger standing stocks of benthic FPOM, CPOM, and fine wood, the lower standing stock of periphyton, and the fact that FPOM in the pond has a significantly lower mass-specific respiration rate. Pond respiration in the upper 5 cm of sediment is dominated by FPOM ($55.5 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$), followed by fine wood debris ($41.2 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$), CPOM ($13.4 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$), periphyton ($1.6 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$), and POC suspended in the water column ($1.4 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$). Overall, areal aerobic respiration in the pond is 2.3 times that in the riffle, while the total

standing stock of carbon is 2.8 times that in the riffle. Total aerobic pond respiration, per linear metre of channel, is 15.8 times that in the riffle.

Beaver activities result in extensive accumulations of anaerobic organic matter suitable for methane-producing organisms. Methane evasion was 15 times as great in the beaver pond than at the riffle site (T. E. Ford and R. J. Naiman, *personal observation*). At the riffle site methane escaping the water surface accounted for only $0.5 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, while in the pond, methane accounted for $7.4 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, or $\approx 6\%$ of the total

TABLE 4. Relative composition of carbon budget: inputs, outputs, and standing stocks, each evaluated per unit area.

Component	% of carbon budget*		Riffle : pond ratio
	Riffle	Pond	
Inputs			
Precipitation	1.9	7.3	0.26
Throughfall	8.4	1.3	6.46
Allochthonous inputs			
Direct	60.3	75.0	0.80
Lateral	15.6	5.6	2.79
Primary production	10.3	2.4	4.29
Outputs			
Respiration	91.7	92.9	0.99
Methanogenesis	0.9	6.0	0.15
Standing stocks			
Wood debris	96.3	34.9	2.76
Benthic organic matter	3.6	65.0	0.06
	Mass/length or area		
Areal annual input (g/m ²)	179.5	74.9	2.40
Channel annual input (g/m)	179.5	524.3	0.34
Areal standing stock (g/m ²)	4383.0	12 038.0	0.36
Channel standing stock (g/m)	4383.0	84 266.0	0.05
Areal annual output (g/m ²)	54.7	121.8	0.45
Channel annual output (g/m)	54.7	852.6	0.06
	Time (yr)		
Turnover time (yr)	24.4	160.7	0.15

* Neither inputs nor outputs total 100% because minor components have been excluded.

carbon output from the system. These are minimal estimates, since we did not directly measure the rate of methanogenesis in the anaerobic sediments. In another study, 18 g·m⁻²·yr⁻¹ were produced as methane from the sediments of an artificially eutrophic shield lake in Canada (Rudd and Hamilton 1978).

Insect emergence.—The exit of insects from the water column represents a small annual loss of carbon during the ice-free season (Naiman et al. 1984). In the riffle, annual carbon loss from insect emergence is 0.3 g/m²; for the pond it is 0.3 g/m², or 2.1 g/m of stream length. These are minimal rates since insect emergence from stream margins has not been measured.

In-stream comparisons

Beaver activity not only alters the total amount of available carbon, it also alters the relative proportion contributed by each input-output category (Table 4). Major differences between the riffle and the pond, per unit area, include a decrease in the pond in the relative importance of lateral inputs and primary production. Also, although the pond receives only 42% of the total carbon received by the riffle, annual carbon inputs per unit length of channel for the pond are three times those of the riffle (Table 4). Outputs of carbon from

the pond, primarily by respiration and methanogenesis, are more than twice those from the riffle on an areal basis, and nearly 16 times those from the riffle per unit length of channel. The projected carbon turnover time is longer (≈ 161 yr) in the pond than in the riffle (≈ 24 yr), largely due to the mass of benthic organic carbon in the pond.

Comparisons with other studies

Measurements for the Beaver Creek riffle components, in most cases, fell within the range of values measured at two comparable streams in northern latitudes (Table 5). Excluding coarse wood debris, the general range was 68–710 g/m² for FPOM plus the CPOM standing stock (Naiman and Sedell 1979b, Iversen et al. 1982, Minshall et al. 1983); Beaver Creek riffle contained 453 g/m². Most studies ignore coarse wood debris, but in Oregon, where the forest attains a mature age of ≈ 450 yr, Naiman and Sedell (1979b) reported 6698–11 163 g/m² in 1st and 2nd order coniferous forest streams. In Beaver Creek, where the mature forest has an age of 60–90 yr, the riffle had 3927 g/m².

Carbon in precipitation and throughfall is a small but measurable component of most budgets. Fisher and Likens (1973) examined throughfall only during the leaf-on period at Bear Brook, New Hampshire, and found that it contributed 3.3 g·m⁻²·yr⁻¹, or 9.5% of their budget. Triska et al. (1982) measured rates of 25.2–35.0 g·m⁻²·yr⁻¹ in Oregon, where total precipitation ranges from 160 to 300 cm/yr and the forest canopy has a high degree of interception and leaching; these rates were 7–8% of their budget. The Beaver Creek riffle received 16.9 g·m⁻²·yr⁻¹ in precipitation and throughfall, 7.6% of the annual budget (Tables 4 and 5).

Other northern forested, 2nd order streams receive 128–309 g·m⁻²·yr⁻¹ as allochthonous carbon inputs (Triska et al. 1982, Connors and Naiman 1984); Beaver Creek riffle receives 168 g·m⁻²·yr⁻¹. Except for Watershed 10, Oregon, where the stream is deeply incised into the mountain slope (Triska et al. 1982), most of the allochthonous inputs occur in autumn as direct litterfall; lateral inputs are usually only 14–34% of the total (Fisher and Likens 1973, Connors and Naiman 1984); for Beaver Creek riffle lateral inputs are 33% of the total.

Bott et al. (1985), in a study of periphyton of several streams from northern regions, found the following ranges of values: 0.1–7.2 g/m² for standing stock, ≈ 0.0 –0.5 g·m⁻²·d⁻¹ for gross production, and 0.1–0.7 g·m⁻²·d⁻¹ for respiration. Comparable values for Beaver Creek were 0.5 g/m², 0.1–0.5 g·m⁻²·d⁻¹, and 0.1–0.6 g·m⁻²·d⁻¹, respectively.

Triska et al. (1984) reported that insect emergence accounted for only 0.2% of the nitrogen budget of an Oregon stream. Meyer et al. (1981) estimated this component accounted for only 0.1% of the carbon losses

TABLE 5. Comparison of mean annual standing stocks and annual fluxes of carbon (g/m^2) for Watershed 10, Oregon (Triska et al. 1982, 1984), Bear Brook, New Hampshire (Fisher and Likens 1973, Meyer et al. 1981), and a riffle and pond in Beaver Creek, Quebec.

Component	Watershed 10*	Bear Brook	Beaver Creek	
			Riffle	Pond
Input				
Fluvial transport	83.0	321.0	9.4×10^5	1.3×10^5
Precipitation/throughfall	30.1	3.3	16.9	6.9
Direct allochthonous	101.7	248.3	123.1	52.6
Lateral allochthonous	163.8	41.7	55.8	4.3
Periphyton production	14.5	1.0	24.7	1.7
Total input, excluding fluvial transport	310.1	294.3	220.5	65.1
Standing stock				
Water column	<0.1	<0.1	2.0	18.0
Coarse woody debris†	5342.1	218.0	3926.9‡	3129.2‡
CPOM§	896.1	235.0	419.4	5152.0
FPOM	196.7	20.0	33.7	3738.8
Primary producers	19.0	1.3	0.5	0.1
Invertebrates	0.5	0.7	—¶	—
Total standing stock	6456.2	475.1	4382.5	12 038.1
Outputs				
Fluvial transport	211.4	385.0	9.4×10^5	1.3×10^5
Detritus respiration	113.4	202.6	22.0	111.5
Primary producer respiration	9.4	—	28.0	1.6
Insect emergence	1.2	2.1	0.3	0.4
Methanogenesis	—	—	0.5	7.4
Total outputs, excluding fluvial transport	124.3	204.7	50.8	120.9

* Average of water years 1973 and 1974 (from Triska et al. 1982).

† Coarse woody debris ≥ 10 cm diameter.

‡ Naiman and Melillo (1984) reported a standing stock (dry mass basis) of $15.9 \text{ kg}/\text{m}^2$ for the riffle and $12.9 \text{ kg}/\text{m}^2$ for the pond; these values were incorrect. The correct values, expressed as grams of carbon per square metre, are reported here.

§ Coarse particulate organic matter 1 mm to 10 cm diameter; includes fine wood (1–10 cm diameter) for Beaver Creek.

|| Fine particulate organic matter $0.5 \mu\text{m}$ to 1 mm diameter.

¶ — = no data.

from Bear Brook; in our study, insect emergence also accounted for only 0.1% of the measured carbon losses from the riffle.

The only comparable data from a beaver pond are those given by Hodkinson (1975). His Alberta pond was a highly accretive heterotrophic system where significantly less organic carbon was exported than could be accounted for in the total measured inputs. This beaver pond system differs from the one described here in that it was spring-fed and did not have such a large volume of water passing through each year. Furthermore, the $141 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ of direct litterfall carbon inputs was over three times the amount measured in our study, lateral inputs ($45 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) were over 10 times as great, and primary production ($495 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) was several orders of magnitude greater. We suspect the high primary production rate measured by Hodkinson may be an artifact of his method of using static cylinders left in the sediments for 24 h. Respiration in the Alberta pond was much greater than respiration reported in this study (607 vs. $121 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, respectively), since we measured respiration only in the upper few centimetres of sediment. No information is given on the relative or total standing stocks of periphyton or detritus in Hodkinson's study. He did measure an annual carbon accrual of $1268 \text{ g}/\text{m}^2$ to the

benthos and a $P:R$ ratio of 0.8; we could not measure any net accrual to the benthos, but the mean $P:R$ ratio was also 0.8.

Ecosystem efficiency

Fisher (1977) developed the stream metabolism index (SMI), defined as:

$$\text{SMI} = (R + \Delta Z)/(P + L + T + M + G) - Q_f/M,$$

where, R = ecosystem respiration; Z = organic matter storage; P = gross primary production; L = litter input; T = organic matter input via tributaries; M = organic matter input at mainstem upstream site; G = groundwater input; and Q_f = discharge at the mainstem input site. Cummins et al. (1983) noted many limitations of this index. In general, however, it is useful as a gross comparative measure of ecosystem efficiency for the utilization or storage of organic inputs, while avoiding the problem of comparing reaches of different length.

We calculated SMI's for the riffle and pond on Beaver Creek and compared them to SMI's calculated from carbon budgets for Watershed 10, Oregon (Triska et al. 1982, 1984), and Bear Brook, New Hampshire (Fisher and Likens 1973, Meyer et al. 1981). For free-flowing stream sections the SMI's are 0.30 (Beaver Creek), 0.46 to 0.84 (Watershed 10), and 1.00 (Bear

Brook). The SMI's < 1.00 indicate that if these streams are in a steady state they should be exporting "excess" organic matter. These values contrast sharply with an SMI of 1.63 for the beaver pond. This calculated value suggests the pond is accruing and/or processing organic inputs, and less material is being transported downstream than is being received. This contradicts our previous statement that there was no net change in throughflow. The discrepancy is probably due to our inability to calculate precise error estimates for downstream throughflow (Meyer and Tate 1983).

Another measure of ecosystem efficiency is the carbon turnover length (S), defined as the average or expected downstream distance traveled by a carbon atom during its residence in the stream in a fixed or reduced form (Newbold et al. 1982). It can be calculated as the ratio of the downstream transport flux of carbon (per unit width of stream) to the respiratory utilization of carbon (per unit area of stream bottom). The carbon turnover length is a measure of the rate at which the ecosystem utilizes carbon relative to the rate at which it is transported downstream. If S is short, organic carbon inputs are respired near the location of entry or fixation. If it is long, organic carbon is "lost" from the local stream reach, to be oxidized or deposited somewhere downstream. Newbold et al. (1982) speculated that headwater sections of drainage networks are the most efficient for the retention and oxidation of carbon, and that, as a rule, S should increase with increasing distance from the headwaters. Minshall et al. (1983) examined this hypothesis for stream-river continua in four biomes and found it to be generally true, with S ranging from 0.9 to 246 km.

We calculated S for the POC fraction, assuming all respiration is associated with particulate carbon. For Beaver Creek riffle, $S = 8.0$ km; for the pond, $S = 1.2$ km. The beaver pond substantially shortens S , making this stream section more efficient than a nearby headwater stream (First Choice Creek) where $S = 15.4$ km, and than downstream reaches where S ranges from 35.9 to 435.8 km (R. J. Naiman, *personal observation*). In total, these indices clearly suggest that beaver ponds can be viewed as sites where substantial organic matter storage and processing occurs within a physically diverse stream channel.

ORGANIZATIONAL PATTERNS IN RUNNING WATERS

The preceding discussion of ecosystem efficiency, beaver-induced alterations of stream dynamics, and biogeochemical pathways becomes especially significant when viewed in an historical perspective. Unfortunately, few unaltered watersheds remain in North America, and most of these are small. Historically, streams throughout North America had different features than they do today (Morgan 1868, Sedell and Froggett 1984). Most large rivers had extensive floodplains and backwater areas, many woody snags, and often clear water with light reaching the bottom (Bar-

tram 1791, Bates 1863, Bakeless 1961, Triska 1984). That large amounts of carbon and nutrients were sequestered high up in the watershed, rather than being transported downstream, suggests that watercourses throughout North America were significantly altered by the removal of beaver. The fact that the effects of beaver activity can still be seen today in the terrestrial vegetation of meadowlands centuries after their extirpation (Rudemann and Schoonmaker 1938, Ives 1942, Neff 1957) is testimony to the beaver's influence on landscape ecology.

There are many contrasts between a stream-river continuum where beaver are present and a continuum where beaver are absent. The beaver-influenced system has the following notable features: (1) In low order streams (e.g., approximate orders 1-4) there are numerous zones of open canopy, large accumulations of detritus and nutrients, an expanded wetted area, and substantial shifts to anaerobic biogeochemical cycles. (2) In middle-order streams (e.g., orders 5-8), beaver-cut wood from upstream and the immediate riparian zone augment local allochthonous inputs. Debris accumulations set up conditions for massive storage of sediment and detritus in the mainstream channel, often forming small islands. (3) In large rivers (e.g., orders ≥ 9) beaver utilize floodplains and backwaters, where they construct dams, lodges, and canals and cut large amounts of wood. The net effects are to increase the diversity of wetland habitat; by creating canals, beaver help keep wetlands open for species utilizing these areas for feeding, reproduction, and shelter. Wood debris accumulations in the main channel, cut directly by beaver or entering the channel via bank erosion, create conditions for sediment storage and for the formation of braided channels and islands.

The physical and biological consequences of a dam on a small stream are not always clear. Effects vary with biome, stream morphology, discharge, dam age, and other physical factors. Studies of large impoundments with surface water release (Ridley and Steel 1975, Baxter 1977, Ward 1982) similar to that of a beaver dam, have shown that turbidity decreases downstream, nutrients are stored in accumulated sediments, plankton productivity is enhanced in the impoundment, variability in the discharge regime is often damped, the temperature range is increased, and dissolved oxygen in outflowing waters is increased. These effects, even though some may be relatively small, can have substantial downstream impacts.

Beaver also have an effect on the relative stability of stream ecosystems (the theory is described by Webster et al. 1983). Current ecosystem theory predicts that streams have low resistance to state perturbations relative to forest, lakes, and oceans (Reichle et al. 1975, Webster et al. 1975, O'Neill et al. 1979). That is, streams are most easily displaced from a reference state but have a high resiliency, returning rapidly to the reference point soon after the disturbance. A factor contributing to the predicted low resistance is the absence of large

stable pools of biomass and nutrients with slow turnover rates to buffer the system from perturbations. Our data suggest that beaver ponds function as large-mass, slow-turnover components in stream ecosystems, and that streams with beaver ponds probably have a high resistance to perturbation. Beaver also return streams to the reference point soon after displacement as they rebuild dams and water and sediment are accumulated. This view is partially supported by the theoretical analyses of O'Neill et al. (1979), who found that stream systems with a high degree of spatial heterogeneity were more resistant to perturbation.

Moreover, beaver activity and the resultant ecosystem level effects have important implications for the river continuum concept. Vannote et al. (1980) viewed river systems as longitudinally interconnected channels where physical variables present a continuous gradient of physical conditions from the headwaters to the mouth. One cannot question the influence and usefulness of this concept as a general framework within which to organize and examine data on stream ecosystems. However, the concept does not fully address natural interruptions (e.g., ponds and lakes) to this continuum. Small streams (approximate orders 1–3), in particular, are envisioned as narrow and heavily shaded channels, receiving a large proportion of their energy inputs from the surrounding forest and having large standing stocks of coarse detritus. We suggest that where beaver are present the implied characterization of small streams needs to be redefined to include numerous zones of open canopy, large accumulations of fine detritus, increased wetland area, increased biogeochemical interactions with riparian plants and soils, reduced inputs of allochthonous inputs per unit area, and concomitant adjustments in the functional attributes of the invertebrate community. In fact, before the widespread removal of beaver, we believe conditions described here were characteristic of many low order streams.

We conclude that beaver have a substantial influence on the stability, retention capacity, and processing efficiency of drainage networks in North America. Treating beaver as significant and essential components of the landscape should be required of most management programs. Overall, our field observations and data show that beaver, through their feeding and dam-building activities, act as a keystone species (*sensu* Paine 1966, 1969, 1974) to affect ecosystem structure and dynamics far beyond their immediate requirements for food and space. As such, within their natural range beaver should be integrated into resource management plans as well as considered in the development of stream ecosystem theory.

ACKNOWLEDGMENTS

We thank M. M. Francis, B. S. Farr, D. M. McDowell, G. Lebel, K. N. Eshleman, A. Kane, and A. Turner for assistance in the field and laboratory; J. R. Sedell, and C. Dahm for discussions of landscape and biogeochemical aspects; and

J. B. Wallace, P. J. Mulholland, R. Morin, C. E. Cushing, J. R. Webster, and J. D. Newbold, and two anonymous referees for critically reviewing the manuscript. The research was supported by the National Science Foundation (DEB 81-05677), the Matamek Research Program of the Woods Hole Oceanographic Institution, and the Ecosystem Center of the Marine Biological Laboratory. This is contribution Number 5827 of the Woods Hole Oceanographic Institution and Number 99 of the Institution's Matamek Research Station.

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