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BEAVER INFLUENCES ON THE LONG-TERM BIOGEOCHEMICAL CHARACTERISTICS OF BOREAL FOREST DRAINAGE NETWORKS[1]

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Abstract. Beaver (*Castor canadensis*) affect biogeochemical cycles and the accumulation and distribution of chemical elements over time and space by altering the hydrologic regime. Aerial photograph analyses of beaver activities on the 298-km^2 Kabetogama Peninsula, Minnesota, were coupled with site-specific studies of soil and pore water concentrations of nutrients (nitrogen, phosphorus) and other ions (potassium, calcium, magnesium, iron, sulfate, chloride), nitrogen cycling processes (nitrogen fixation and denitrification), and biophysical environmental variables (vegetation, temperature, organic matter, soil structure, pH, and oxidation–reduction potential). Our analyses demonstrate that beaver influence the distribution, standing stocks, and availability of chemical elements by hydrologically induced alteration of biogeochemical pathways and by shifting element storage from forest vegetation to sediments and soils.

Over the 63 yr of aerial photo records (1927–1988), beaver converted 13% of the peninsula to meadows and ponds. Elemental concentrations in soils (in micrograms per cubic centimetre) and in pore water (in milligrams per litre) revealed complex patterns within and among the principal hydrologic zones (e.g., forest, moist meadow, wet meadow, pond, stream). Principal components analysis (PCA) suggested that anaerobic conditions caused by saturation of soil by water was the fundamental control over subsequent alterations of biogeochemical pathways. Although few clear statistical trends were detected for mass- or volume-specific elemental concentrations among habitats, organic horizon (O and A) depths were greatest in the wet meadows and ponds (>15 cm), causing the standing stocks of chemical elements to be greatest there. We argue that the net effect of beaver activities has been to translocate chemical elements from the originally inundated upland forest vegetation to downstream communities and to pond sediments. As the upland vegetation dies and decays after dam construction, only a portion of the chemical elements are exported downstream (except for calcium and magnesium) or returned to the atmosphere (C and N only). Consequently, the organic horizons of pond sediments accumulate substantial standing stocks of chemical elements that are available for vegetative growth when dams fail, the ponds drain, and meadows are formed. Since 1927 beaver activities have augmented the standing stock of chemical elements in the organic horizons by 20–295%, depending on the element. These influences are spatially extensive and long lasting, affecting fundamental environmental characteristics of boreal forest drainage networks for decades to centuries.

Key words: aerial photography; beaver; biogeochemical cycles; boreal forest; Castor canadensis; *landscape ecology; Minnesota; nutrients; stream.*

INTRODUCTION

The vast populations of mammals and birds that once inhabited the grasslands, forests, and waterways of North America had substantial long-term influences on the structure and dynamics of ecological systems by foraging and by physically altering habitat (Naiman 1988, Pastor and Naiman 1992). Beaver (*Castor canadensis*) provide an excellent example of how long-term ecosystem and landscape-level changes are induced by herbivory, physical habitat alteration, and population dynamics (Naiman and Melillo 1984, Naiman et al. 1986, 1988, Remillard et al. 1987, Johnston and Naiman 1990*a, b, c*). Beaver modify drainage network morphology and hydrology by cutting wood and building dams. These activities retain sediment and organic matter in the channel, create and maintain physically diverse wetlands, modify biogeochemical cycles, alter the structure and dynamics of the riparian vegetation, influence the character of water and ma-

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TABLE 1. Vegetative and physical characteristics of the hydrologic categories of study sites. Annual mean ± 1 SE is given, where appropriate. ND = not determined.

Parameter	Hydrologic zone Forest	 Moist meadow	 Wet meadow	 Beaver pond
Dominant species	*Populus tremuloides, Betula papyrifera, Picea glauca, Abies balsamea*	*Calamagrostis canadensis*	*Scirpus cyperinus, Calamagrostis canadensis, Carex lacustris*	*Calamagrostis canadensis, Carex pseudocyperus, Sparganium*
Total live biomass (g/m^2, as dry mass)	12 330 ± 1363	340 ± 32.1	362 ± 52.0	348 ± 64.5
Litter dry biomass (g/m^2)	ND	253 ± 45.5	143 ± 30.0	214 ± 117.2
Number of species	ND	19	28	17
Dominant soil	Typic Eutroboralf	Typic Ochraqualf	Typic Argiaquoll	Typic Haploquept
Soil bulk density (g/cm^3)	0.53 ± 0.11	0.39 ± 0.06	0.32 ± 0.04	0.47 ± 0.05
Soil organic matter (% soil dry mass)	39 ± 2	35 ± 2	38 ± 2	26 ± 1
Soil carbon* (g/m^2)	4247 ± 429	9619 ± 658	5285 ± 405	5920 ± 809
Depth of water table (cm)	<−70	−2 ± 3.7	5 ± 2.2	>10
Water-logging conditions	Not flooded	Temporarily flooded	Seasonally flooded	Permanently flooded
Annual Celsius degree-days†	2084 ± 21	2078 ± 18	2760 ± 19	2784 ± 21
Redox potential (Eh, mV)	536 ± 15	338 ± 22	−18 ± 25	−64 ± 45
Soil/sediment pH	5.06 ± 0.26	5.13 ± 0.15	5.78 ± 0.07	6.06 ± 0.06

* From Naiman et al. 1991.

† SE calculated from the array of sampling probes.

terials transported downstream, and broadly influence biotic composition and diversity. The net result is a mosaic of temporally and spatially variable biophysical patches with strong long-term influences on landscape-level features.

Alterations to the hydrologic regime are especially important in influencing system-level characteristics and processes. Hydrologic changes modify the sediment water content, which in turn governs aerobic–anaerobic status, biogeochemical cycles, and metabolic activity. The hydrologic regime is of primary importance to microbial processes such as nitrogen mineralization, organic carbon decomposition, phosphorus availability, and ionic reactions that determine water quality and biogeochemical reactions (Johnston 1991, Pinay and Naiman 1991, and references therein). Physiological responses to the hydrologic regime also alter vegetative composition, causing mortality in some species while promoting production in others. Hydrologically induced changes result in productive beaver-created meadows and wetlands with long-term consequences for vegetative succession in the boreal forest (Naiman et al. 1986, 1988, Pinay and Naiman 1991). In addition, the hydrologic alterations may remain as functional features of the landscape for centuries (Rudemann and Schoonmaker 1938, Ives 1942, Johnston and Naiman 1987).

Our previous research has examined the effects of beaver on stream community characteristics (McDowell and Naiman 1986, Naiman et al. 1986, 1988), specific biogeochemical cycles (Ford and Naiman 1988, Naiman et al. 1991, Pinay and Naiman 1991), and landscape features (Johnston and Naiman 1987, 1990*a*, *b*, *c*). Here, we report on changes in biogeochemistry of the organic horizons (O and A) as ponds are created, used, and abandoned, while comparing the resultant soil properties with the adjacent upland forests. We examine oxidation–reduction potential (redox), temperature, percentage organic matter, ion and nutrient concentrations and standing stocks, and vegetation characteristics associated with altered hydrologic regimes. We show that changes in soil biogeochemical properties in abandoned beaver meadows persist far longer than active occupation by beaver and that beaver may cause substantial reallocation of standing stocks, chemical forms, and flux rates for nutrients and ions. Through these collective processes beaver initiate a long-term legacy that significantly influences boreal forest drainage networks.

STUDY AREA

The 298-km^2 Kabetogama Peninsula of Voyageurs National Park, Minnesota, USA (48°34′ N, 93°23′ W) has been subjected to a dramatic reinvasion of beaver

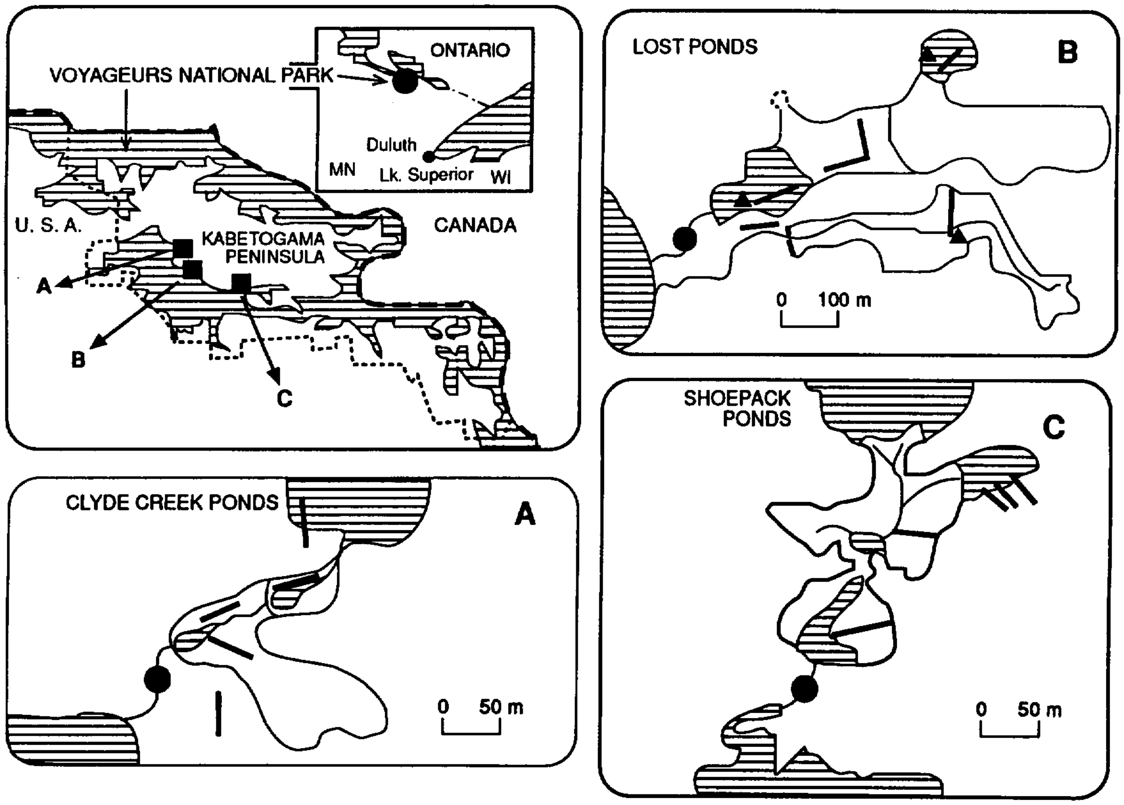

FIG. 1. Location of study sites (■) and major sampling transects (——), Kabetogama Peninsula, Voyageurs National Park, Minnesota. Location of stream sampling sites (●) and hydrologic recorders (▲); (A) Clyde Creek Ponds, (B) Lost Ponds, (C) Shoepack Ponds; ▤ represents surface water in ponds and lakes.

since ≈1925. Fire and logging in the early part of this century created abundant food reserves in trembling aspen (*Populus tremuloides*) and willow (*Salix* spp.). This, combined with a reduction in predatory wolf (*Canis lupus*), allowed the beaver population to expand rapidly. In 1927 there were only 64 beaver ponds, whereas by 1988 there were 835 ponds. Beaver impoundment density increased from 0.2/km^2 in 1927 to 3.0/km^2 in 1988 as the total area of beaver-created habitat expanded from 200 ha (< 1% of peninsula study area) to 2661 ha (13% of peninsula study area) over the 63-yr period (Johnston and Naiman 1990*a*, *c*). Additionally, ≈12–15% of the uplands were altered by beaver foraging during the same period (Naiman et al. 1988). The impounded area constitutes a mosaic of beaver dams representing a large array of vegetative and hydrologic environments ranging from newly created ponds to abandoned meadows (Table 1).

The Kabetogama Peninsula lies in the Northern Lakes and Forests ecoregion (Omernik 1986). Trembling aspen, paper birch (*Betula papyrifera*), white spruce (*Picea glauca*), and balsam fir (*Abies balsamea*) are the primary tree species. The area is well known for its cold climate, caused by the arrival of continental polar air throughout most of the year. Mean annual temperature is 1.4°C. The average first and last occurrences of freezing temperatures are 15 September and 26 May, respectively. In winter, frost penetrates to depths up to 150 cm, varying with soil moisture and snow depth (NOAA 1986).

Three drainage systems were chosen (Shoepack, Lost Ponds, Clyde Creek), each of which contain three beaver-influenced sites and a stream site (Fig. 1). We chose these particular drainage systems because they were accessible and representative of beaver-created environments on the peninsula and to avoid pseudoreplication by sampling in only one drainage. Wet meadow and moist meadow sites were distinguished prior to sampling by the presence or absence of surface water in late spring: water was below the soil surface at moist meadow sites and at or above the surface at wet meadow sites.

The streams for all three systems were small (second to third order), heavily shaded, and on bedrock, had little summer discharge, and were located below the pond–meadow complexes. Unimpounded streams were exceedingly rare on the peninsula due to the extent of beaver activity, necessitating the selection of stream sites below pond–meadow complexes. The effects of upstream beaver activities on these sites remain unknown, although the sites chosen appear to be typical boreal forest streams (Naiman et al. 1987).

METHODS AND MATERIALS

Sampling strategies

The primary growing season in northern Minnesota is ≈100 d, compressing the vegetative seasons into a few short months. In 1986 samples were collected in May (spring), June (late spring/early summer), July (summer), August (late summer), and October (autumn). In 1987 samples were collected in April (winter), May, June, July, September (autumn), and October. Ice conditions on access lakes between mid-April and mid-May in both years prevented sampling during the spring thaw period. A total of 113 sampling points were established as 15 transects within four hydrological zones; 94 sampling points were monitored seasonally.

Site characterization

Oxidation–reduction potential and temperature.—Soil oxidation–reduction potential (redox; Eh) and temperature were measured at the time of soil or pore water collection using a millivolt meter, a calomel reference electrode, and platinum-tipped redox probes (Delaune et al. 1980). In May 1986 and 1987 three probes were placed 10 cm deep in the soil at each site and left in situ throughout the ice-free season to minimize soil disturbance. Redox measurements from the replicate probes were averaged and the means compensated for soil temperature, soil pH, and individual variations among the electrodes (Bohn 1968). After the field season, all probes were checked in the laboratory for conformity to theoretical values.

Hydrologic regime.—Leupold-Stevens strip chart recorders (Model 71-A) were used to continuously monitor water levels at the ponds and meadows, and stream discharge in the Lost Ponds system during the ice-free (May–October) seasons of 1986 and 1987 (Fig. 1B). Perforated standing pipes ($N = 94$) were implanted at all meadow and upland sites in the Lost Ponds, Clyde Creek, and Shoepack systems to give a relative depth to water table at the time of sampling.

Soil morphology.—Sixteen pits were dug and described in the forest and meadows, and a "Dutch" hand auger was used to examine impounded soils. Soils were described and classified using standard field techniques (Soil Survey Staff 1975, Cornell University Department of Agronomy 1985) subject to laboratory verification. Detailed soil maps were prepared based on the results of the field studies, supplemented by information from topographic maps and aerial photographs. In order to determine the influence of beaver impoundments on soil morphology, specific profiles were described for: (1) a beaver-impounded moist meadow, (2) an adjacent unimpounded forest soil, and (3) an isolated wet depression (i.e., a wetland without a surface water inlet or outlet) that was never impounded.

Vegetation.—Vegetative composition and aboveground standing stock were determined for pond and meadow sites by clipping 10 randomly selected 0.25-m^2 plots per zone in late August 1986, during the period of maximum annual biomass. Species taxonomy follows Gleason and Cronquist (1963). Species were separated, dried to a constant mass at 60°C, and weighed. Litter biomass on the soil surface was obtained from the same plots.

Aboveground biomass for the forest was determined by measuring the diameter of all trees ≥5 cm dbh (taken 1.4 m above ground surface) within 33 50-m^2 circular plots adjacent to but beyond the browse zone of the beaver ponds, and converting to biomass using regression equations developed by Freedman (1983). The biomass of shrubs and herbs was negligible in comparison to tree biomass and was not measured.

Chemical studies

Sampling design.—Analyses of environmental conditions were based on sediment and pore water samples taken at points along transects. The transects follow natural hydrologic gradients that reflect changes in the aerobic–anaerobic status of sediment (Fig. 1). Pore water was considered to be in a quasi-dynamic or near equilibrium with the solid and gas phases of the sediment (Ponnamperuma 1972). A pressure-vacuum pore water lysimeter was installed at each sampling point at 25 cm below the soil surface (average depth of root penetration) at 94 sites. Water from "stream" locations was collected as pore water from the sediments in order to facilitate comparisons with the other habitats.

Analytical analyses.—The lysimeters were evacuated (20 kPa) 2 d before sampling and then flushed with nitrogen gas to avoid microbial oxidation of reduced forms of nitrogen, iron, and other water constituents. Pore water samples were immediately passed through 0.45-μm mesh filters (Schleicher and Schuell ME 25, Keene, New Hampshire), stored at 4°C, and analyzed with a Lachat Quick Chem autoanalyser (Lachat Instruments, Milwaukee, Wisconsin) within 2 d for total nitrogen (Indophenol blue method after reduction of all nitrogen forms to ammonium on a block digester), nitrite (modified Griess–Ilosvay method), nitrate (modified Griess–Ilosvay methods after copperized cadmium reduction), ammonium (Indophenol blue method), total phosphorus (orthophosphate method after reduction on a block digester), and orthophosphate (automatic ascorbic acid method). Dissolved potassium, calcium, magnesium, and iron were analyzed with an atomic absorption spectrophotometer (Varian Spectran 30) and sulfate and chloride with a Dionex ion chromatograph (Model 2000/SP).

Although the sites contained several soil horizons important in biogeochemical cycling, we restricted sampling to the surface organic horizons (O and A) above clay and sand deposits because of the complexities introduced by the deeper soil patterns (C. A. Johnston et al., *unpublished manuscript*). Soils were collected with a hand-held 5-cm diameter corer from all sites within 1–2 d of pore water collection from the lysimeters. Samples were collected to 15 cm depth or the thickness of the organic horizon, whichever was less. Soil subsamples were oven-dried for 24 h at 105°C in order to determine the fresh : dry mass ratio and percent moisture by mass, which allows calculation of soil nutrient and ion contents. Percentage organic matter was determined by loss on ignition at 525°C for 24 h. Samples were stored at 4°C for 1–2 d before chemical analysis. Nitrate-N and ammonium-N were extracted with 2 mol/L KCl and analyzed in the same manner as the pore water samples. Total nitrogen was analyzed using the Kjeldahl method (Bremner 1965). Total phosphorus was determined using molybdenum blue, and ascorbic acid as a reducing agent, after treatment of the samples according to Saunders and Williams (1955) followed by neutralization. Inorganic sulfate was determined by the method of Tabatabai (1982) after extraction with 0.1 mol/L lithium chloride (LiCl). Total iron was determined by decomposition of soil samples with hydrofluoric acid (HF) in the presence of perchloric acid ($HClO_4$) and measurement on the atomic absorption spectrometer (Olson and Roscoe-Ellis 1982). Exchangeable potassium, calcium, and magnesium were extracted with 1mol/L ammonium acetate (NH_4OAc) and then analyzed with the atomic absorption spectrophotometer (Kundsen et al. 1982, Lanyon and Heald 1982). In this article we refer to K, Ca, Fe, Mg, $S0_4$, and C1 as "ions" and N and P as "nutrients."

Additional soil samples were collected for nitrogen fixation and denitrification measurements from the surface organic horizons (6–15 cm depth, depending on the site). We used a closed chamber incubation technique for nitrogen fixation (acetylene reduction, Bergersen 1980) at ambient soil temperatures. Denitrification was assayed by a static core acetylene inhibition technique (Yoshinari and Knowles 1976). Intact cores were capped with rubber serum stoppers and then amended with acetone-free acetylene to bring core atmosphere concentrations to 10 Pa (10% volume/volume) acetylene and 90 Pa air. Headspace samples were removed from all cores and stored in evacuated collection tubes. Samples were analyzed with a gas chromatograph (GC Hewlett Packard 5890 A) equipped with electron capture detector (ECD 63 Ni) and Porapak Q columns.

Statistical treatment.—Data were grouped by location and by hydrologic zone (e.g., stream, pond, wet meadow, moist meadow, and forest). Two-way ANOVA revealed no significant interaction between location and hydrologic zone, thus allowing analysis to proceed with a one-way ANOVA with hydrologic zone as the key variable. Where data did not conform to ANOVA assumptions, the nonparametric Kruskal-Wallis test was used. The Tukey procedure was used to identify which means differed significantly. In addition, soil and pore water data were analyzed separately by principal components analysis (PCA) based on the linear correlation matrix of all variables to examine factors responsible for observed patterns. All statistical analyses were performed with the PC SAS statistical package (SAS 1988).

RESULTS

Hydrologic regime

Water levels.—Total annual precipitation in 1986 and 1987 was only 73 and 79%, respectively, of the long-term (1940–1987) average of 63 cm/yr. A shortfall in average precipitation occurred in 10 of 12 mo for each year. Droughts of this magnitude would be expected to occur every 16.3 yr for 1986 and every 7.0 yr for 1987.

The effect of the drought on water levels in the meadows and ponds was substantial. In the Lost Ponds drainage, the water level in the gauged beaver pond declined by nearly 50 cm in 1986 during the ice-free season; in 1987 the water level increased by nearly 40 cm immediately after the spring thaw and remained relatively stable over the summer (Fig. 2). In the gauged wet meadow the water level declined ≈10–15 cm below the soil surface for nearly 100 d in the summer of 1986. In 1987 the water level declined ≈10 cm below the soil surface for only ≈25 d in spring, remaining above the soil surface for the reminder of the summer and autumn (Fig. 2). In the gauged moist meadow the water level was normally 15–40 cm below the soil surface for nearly all of 1986 but was 10–15 cm below the soil surface for nearly all of 1987.

The effects of the drought were also reflected in the standpipes established at soil sampling stations. At the wet meadow sites the water was above or within 8 cm of the soil surface for both years (Fig. 3). For the moist meadow sites the water level regimes differed between years. In 1986 when the sites were established the water levels remained 25–40 cm below the surface; in 1987 they remained 5–12 cm below the surface until autumn when the water level rose to 15–20 cm above the surface after a series of storms and remained at that level for 6 wk. At the forest sites the water level was >70 cm below the surface in both years.

Discharge.—Stream discharge from all watersheds was low for both years except for brief periods following heavy rains. In the Lost Ponds system major discharge periods in 1987 were of short duration (normally <3 d). However, during these periods, discharge would increase by an order of magnitude from <0.02 m^3/s to >0.2 m^3/s (Fig. 2). The pattern in 1986 was similar but because of a calibration error the data could not be converted to exact discharge rates and are not shown for comparison.

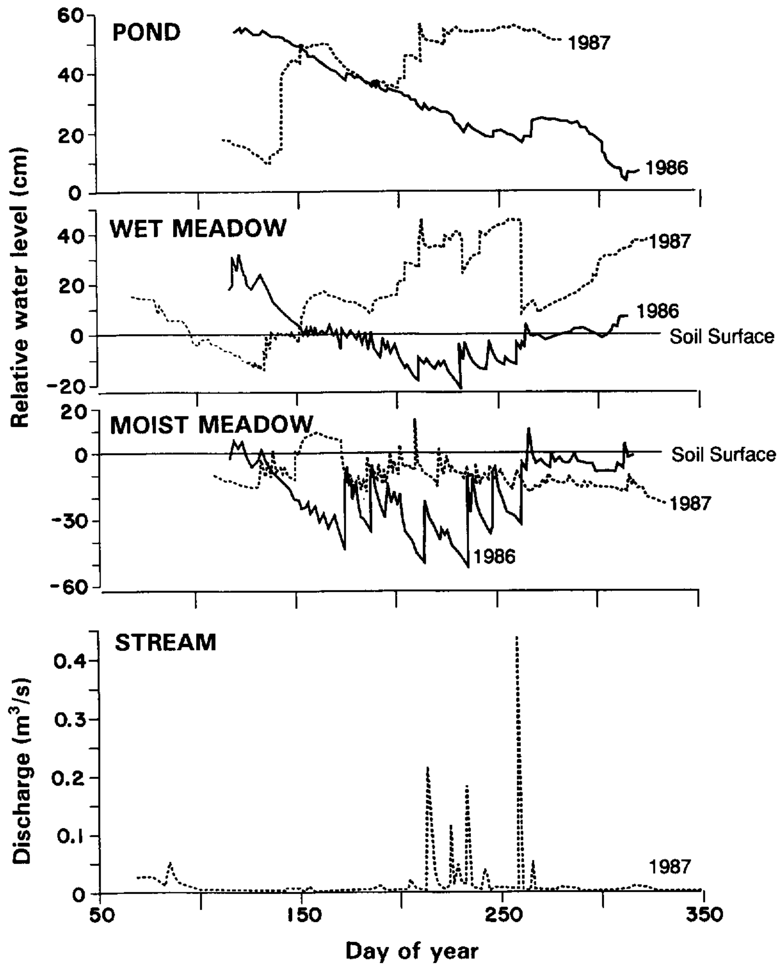

FIG. 2. Water table fluctuations in the gauged beaver pond, wet meadow, and moist meadow in the Lost Ponds drainage basin for the ice-free season of 1986 and 1987, and stream discharge for 1987.

Vegetation

Species diversity and biomass.—The number of plant species was greatest in the wet meadows (n = 28), followed by the moist meadows (19), and the beaver ponds (17) (Table 1). In the shallow (<20 cm depth) areas of beaver ponds five species (*Calamagrostis canadensis, Carex pseudo-cyperus, Sparganium chlorocarpum, Sagittaria latifolia,* and *Scirpus cyperinus*) made up 74% of the 348 g/m² of dry biomass. *Nuphar* was locally

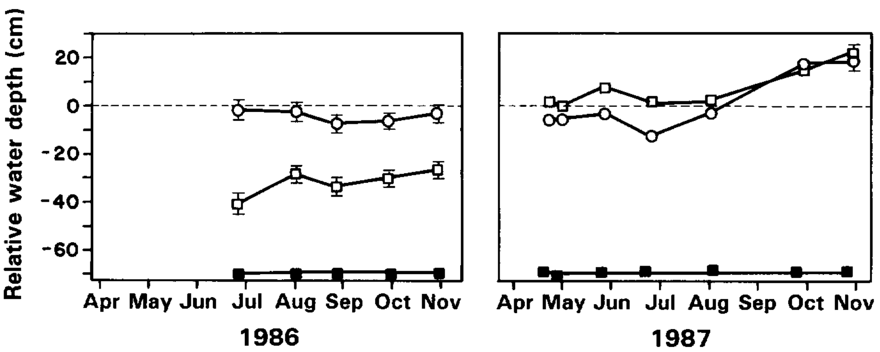

FIG. 3. Relative water depths in stand pipes ($\bar{X}$ ± SE) at the soil sampling stations in the forest (■), moist meadow (□), wet meadow (○), for 1986 and 1987.

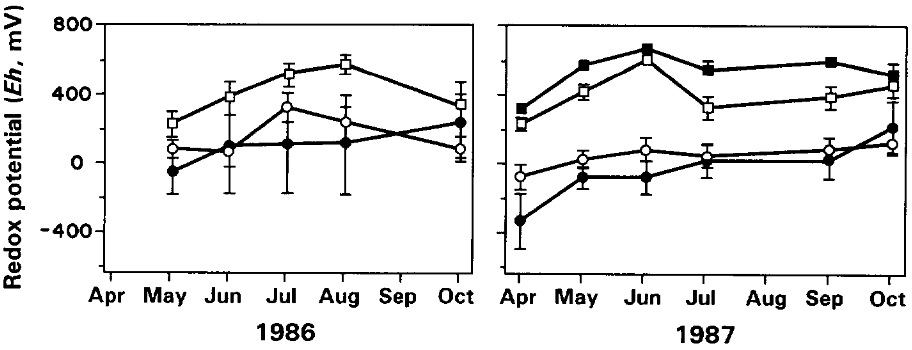

FIG. 4. Monthly redox potentials ($\bar{X}$ ± SE) during 1986 and 1987 for the four hydrologic zones: forest (■), moist meadow (□), wet meadow (○), beaver pond (●).

abundant in submerged areas but was not measured. The dry mass of dead litter >1 mm diameter on the surface sediments was 214 g/m^2 (Table 1).

In wet meadows the dominant five species were *Scirpus cyperinus, Calamagrostis canadensis, Carex lacustris, Glyceria canadensis,* and *G. grandis.* Together their dry biomass accounted for 67% of the 362 g/m^2. Dry mass of litter on the soil surface was 143 g/m^2.

In the moist meadows *Calamagrostis canadensis* dominated (72%) the live biomass; as dry mass this totaled 340 g/m^2. Fourteen of the 19 recorded species accounted for <1% of the total mass. The annual dieback of the aboveground *Calamagrostis* stems produced a thick thatch with a dry mass of 253 g/m^2 (Table 1).

In the riparian forest the dominant tree was *Populus tremuloides* (60% of total biomass), followed by *Betula papyrifera* (24%), *Picea glauca* (7%), and *Abies balsamea* (6%). Six other tree species comprised only 3% of total biomass. Aboveground dry biomass in the forest was more than an order of magnitude greater (12 330 g/m^2 vs. 340–362 g/m^2) than that in the ponds and meadows (Table 1).

Soil profiles

The soil survey revealed that the organic horizons differed substantially between the hydrologic zones (C. A. Johnston et al., *unpublished manuscript*). The mean thickness of the organic horizon was 7 ± 1.7 cm in the forest (mean ± 1 SD), 13 ± 9.6 cm in the moist meadows, and consistently >15 cm in the wet meadows and beaver ponds.

The three specific soil profiles described were in the Alfisol order, with surface litter layers (Oe) 6–9 cm thick, dense E horizons overlying textural B horizons indicative of clay eluviation/illuviation, and clay subsoils derived from glaciolacustrine deposits (Table 2). The beaver-impounded and wet depression soils both

TABLE 2. Morphological characteristics of soil profiles in an abandoned beaver meadow, an unimpounded forest, and an unimpounded wetland. Nomenclature follows U.S. Department of Agriculture Soil Survey Manual (USDA 1962). Horizon depths measured relative to the mineral soil surface. NA = not applicable, ND = not determined.

Horizon	Depth (cm)	Matrix color (Munsell)	Mottle color (Munsell)	Texture	Sand (%)	Silt (%)	Clay (%)	Bulk density (g/cm^3)
		Moist meadow soil in abandoned beaver pond (Typic Ochraqualf)						
Oe	6–0	10 YR 3/2	none	hemic	NA	NA	NA	0.26
E	0–12	5 Y 5/1	10 YR 4/6	silt loam	23	54	23	1.75
Btg	12–32	5 Y 5/2	10 YR 4/6	clay	12	8	80	1.23
Bg	32–44	5 GY 5/1	10 YR 5/6	clay	12	24	64	1.27
Ckg	44+	5 GY 5/1	5 G 5/1	clay	ND	ND	ND	ND
		Forest soil, never impounded (Typic Eutroboralf)						
Oe	6–0	10 YR 2/1	none	hemic	NA	NA	NA	0.17
E	0–13	10 YR 6/2	none	sandy loam	56	36	8	1.64
Bt1	13–30	10 YR 4/3	none	silt clay loam	10	50	40	1.49
Bt2	30–63	10 YR 5/3	10 YR 5/6	silt loam	4	76	20	1.43
Ck	63+	2.5 Y 5/2	10 YR 5/6	clay	6	22	72	1.30
		Wet depression, never impounded (Typic Ochraqualf)						
Oe	9–0	10 YR 3/2	none	hemic	NA	NA	NA	0.25
A	0–10	10 YR 2/1	none	silt loam	ND	ND	ND	0.75
E	10–27	2.5 Y 5/2	7.5 YR 5/6	silt loam	20	60	20	1.54
Btg1	27–40	5 Y 5/2	7.5 YR 5/6	clay	12	12	76	1.13
Btg2	40–53	5 Y 5/2	5 G 4/1	clay	12	8	80	1.44
Cg	53+	5 Y 5/3	5 G 4/1	clay	20	16	64	1.48

TABLE 3. Specific concentrations ($\bar{X}$ ± SE) of nutrients and ions associated with soils during 1986–1987 for the five hydrologic zones. Values connected by a line in the Tukey comparison are not significantly different ($P > .05$).

Parameter	Hydrologic zone		
	Forest (A)	Moist meadow (B)	Wet meadow (C)
Sample size (*n*)	9–42	50–124	72–157
Total nitrogen (μg/cm³)*	278.83 ± 35.98	290.98 ± 24.58	218.63 ± 22.36
Nitrate-N (μg/cm³)*	0.13 ± 0.02	0.66 ± 0.15	0.39 ± 0.10
Ammonium-N (μg/cm³)*	8.98 ± 1.31	11.00 ± 1.50	9.32 ± 0.81
Total phosphorus (μg/cm³)*	34.65 ± 5.10	26.36 ± 2.87	24.26 ± 2.72
Potassium (μg/cm³)*	153.15 ± 18.68	116.22 ± 18.38	54.72 ± 8.64
Calcium (μg/cm³)*	921.72 ± 206.67	988.60 ± 105.46	785.92 ± 89.68
Magnesium (μg/cm³)*	161.38 ± 38.09	211.07 ± 23.79	166.46 ± 20.58
Iron (μg/cm³)*	5.34 ± 1.97	2.54 ± 0.30	2.75 ± 0.65
Sulfate (μg/cm³)*	15.92 ± 7.75	17.66 ± 1.93	13.55 ± 1.75

* Volume of either soil or sediment, depending upon hydrologic zone.
† SE not available.

had the same taxonomic classification (Typic Ochraqualf), gleyed matrix colors in the B and C horizons (indicative of iron reduction under anaerobic conditions), and rust-colored mottles within 10 cm of the soil surface. The primary difference between the wet soils was that the beaver-impounded profile lacked an A horizon (i.e., a horizon in which the organic carbon was incorporated into the mineral soil surface), whereas the wet depression did not (Table 2). The unimpounded forest soil lacked gleyed colors and had mottles much deeper in the profile (30⁺ cm), indicative of its deeper water table.

Temperature and oxidation–reduction potential

Soil and sediment temperatures were ≤0°C from November to April, rising to ≈7–11°C in May. In the wet meadows and beaver ponds, temperatures rose steadily until June, remaining at a relatively constant 13–22°C until October when they rapidly declined with the onset of winter. Cumulative soil and sediment temperatures (expressed as annual degree-days) in the wet meadows and beaver ponds were 33% greater than in the forest or the moist meadow zones ($P < .01$). Annual degree-days in the beaver ponds and wet meadows could not be distinguished from each other, nor could degree-days in the forest and moist meadows (Table 1).

Soil oxidation–reduction (redox) potential was significantly higher (mean = 536 mV; $P < .01$) at the forest sites than in the other habitats. The redox potential decreased as waterlogging conditions increased, resulting in an average redox potential of −64 mV in the pond sediments (Fig. 4, Table 1). Seasonal and spatial coefficients of variation for individual hydrologic zones were 1–5% of the mean.

Soil ion and nutrient dynamics

Ion concentrations.—Cation and anion concentrations associated with the soils showed the same range of concentrations and seasonal patterns in both years.

TABLE 4. Pearson correlation (*r*) analysis of soil ion and nutrient concentrations for all sites in 1986 and 1987 combined. Sample size = 61–748; * $P < .05$; ND = not determined.

	% Organic	Bulk density	Soil pH	Eh	Total N	NO_3-N
Bulk density	−0.459*					
Soil pH	−0.066	−0.035				
Eh	0.043	0.075	−0.256*			
Total N	−0.208*	0.428*	−0.156	0.141		
NO_3	0.075	0.027	−0.071	0.075	0.050	
NH_4	−0.075	0.301*	0.131	−0.190*	0.237*	−0.021
Total P	−0.003	0.607*	−0.179	0.120	0.804*	0.013
Fe	−0.027	0.142*	ND	−0.204*	0.177*	0.077
K	0.018	0.329*	ND	0.059	0.265*	0.150*
Ca	0.075	0.431*	ND	−0.176*	0.547*	0.117*
Mg	0.054	0.396*	ND	−0.134*	0.506*	0.102
SO_4	0.017	0.218*	ND	0.152	0.203	0.252*
Nitrogen Fixation	0.007	−0.011	−0.149	−0.054	0.004	−0.010
Denitrification	−0.082	−0.066	0.245	−0.139*	0.003	0.011

TABLE 3. Continued.

Hydrologic zone		Tukey comparison
Beaver pond (D)	Stream (E)†	
53–122	0–3	
252.99 ± 42.32	···	$\overline{\text{BAD}}\text{C}$
0.09 ± 0.02	···	$\overline{\text{BC}}\kern-0.75em\overline{\phantom{\text{C}}\text{AD}}$
31.67 ± 6.25	···	$\text{D}\overline{\text{BCA}}$
27.15 ± 3.80	···	$\overline{\text{ADBC}}$
89.79 ± 14.47	41.90	$\overline{\text{ABDCE}}$
1380.85 ± 294.92	570.80	$\overline{\text{DBACE}}$
289.10 ± 53.71	82.76	$\overline{\text{DBCAE}}$
9.13 ± 2.70	3.04	$\overline{\text{DAECB}}$
14.96 ± 2.49	23.39	$\overline{\text{EBADE}}$

Although, in general, concentrations were slightly higher during the wetter 1987 season. In most cases, coefficients of variation were less than ≈25% of the mean (Table 3). The only exceptions were iron (37%) and sulfate (49%) from the forest, and iron (30%) from beaver ponds.

There were no statistically significant differences in ion concentrations between the five hydrologic zones (Table 3). Pearson correlation coefficients showed significant relationships between ion concentrations and sediment bulk density but explained <19% of the variation in concentrations (Table 4). Relationships between ion concentrations and percentage organic matter or sediment pH were not significant. Ion concentrations showed only three weak but significant relationships with oxidation–reduction potential. Predictably, in 23 of 30 possible cases there were weak ($r^2 < 0.25$) but significant relationships between the individual ion concentrations or between the individual ions and specific nutrient concentrations.

Statistically significant differences in ion stocks between the hydrologic zones only appear when specific concentrations are adjusted for the depth of the organic horizon (to a maximum depth of 15 cm) and converted to mass per unit land area (Table 5). Average organic horizon depths were ≥15 cm in ponds and wet meadows, 13 cm in moist meadows, and 7 cm in the forest. Streams were excluded from this analysis because of a small sample size. There was statistical overlap between zones but in four of five cases the standing stocks were largest in the beaver ponds and were significantly different from the forest, with meadows being intermediate.

Nutrient concentrations.—Soil nutrient concentrations were highly variable within and between years, with no discernible seasonal pattern. Pearson correlation analyses showed relatively weak relations (r^2 = 0.09–0.37) between total nitrogen, ammonium, total phosphorus, and the bulk density of soil and sediment (Table 4). Other relationships with physical variables were either nonsignificant or extremely weak. Predictably, there was a strong correlation between total nitrogen and total phosphorus (r^2 = 0.64). There were no significant relationships with either nitrogen fixation or denitrification rates.

Discernible patterns again emerged between hydrologic zones only when volumetric nutrient concentrations (in micrograms per cubic centimetre) were converted to standing stock (in kilograms per hectare) in the upper 15 cm of the organic horizons (Table 5). For total nitrogen, ammonium, and total phosphorus the standing stocks were significantly higher in the beaver ponds than in the forest. The wet and moist meadows were intermediate, overlapping with other zones. Nitrate standing stock was highest in the aerobic moist meadow and statistically significantly different from the other hydrologic zones.

Nitrogen cycling.—Nitrogen fixation was statistically similar at all sites, acetylene fixation ranging from 1.5 to 2.9 mol·m^{-2}·h^{-1} (Table 6). However, within a hydrologic zone and between seasons there was consid-

TABLE 4. Continued.

NH_4-N	Total P	Fe	K	Ca	Mg	SO_4	Nitrogen fixation
0.348*							
0.166*	0.197*						
0.385*	0.323*	0.199*					
0.551*	0.524*	0.252*	0.462*				
0.568*	0.476*	0.309*	0.468*	0.940*			
0.002	0.149	0.268*	0.193*	0.092	0.076		
0.001	−0.015	−0.077	−0.013	−0.061	−0.022	ND	
−0.012	−0.009	−0.137	0.031	−0.194	0.182	ND	−0.023

TABLE 5. Standing stocks in the organic horizons, to a maximum of 15 cm depth ($\bar{X}$ ± SE), of nutrients and ions associated with soils during 1986–1987 for four of the five hydrologic zones. Values connected by a line in the Tukey comparison are not significantly different ($P > .05$).

	Hydrologic zone				
Parameter	Forest (A)	Moist meadow (B)	Wet meadow (C)	Beaver pond (D)	Tukey comparison
Sample size (n)	9–42	50–124	72-157	53-122	
Total Nitrogen (kg/ha)	195.2 ± 25.2	378.3 ± 31.9	327.9 ± 33.5	379.5 ± 63.5	DBCA
Nitrate-N (kg/ha)	0.1 ± 0.0	0.9 ± 0.1	0.6 ± 0.2	0.1 ± 0.0	B$\overline{\mathrm{CDA}}$
Ammonium-N (kg/ha)	6.3 ± 0.9	14.3 ± 2.0	14.0 ± 1.2	47.5 ± 9.4	D$\overline{\mathrm{BCA}}$
Total phosphorus (kg/ha)	24.3 ± 3.6	34.2 ± 3.8	36.4 ± 4.1	40.7 ± 5.7	DCBA
Potassium (kg/ha)	107.2 ± 13.1	151.1 ± 23.8	82.1 ± 13.0	134.7 ± 21.7	$\overline{\mathrm{DBAC}}$
Calcium (kg/ha)	645.2 ± 144.7	1285.1 ± 137.1	1178.9 ± 134.5	2071.3 ± 442.3	DBCA
Magnesium (kg/ha)	112.9 ± 26.7	274.4 ± 30.9	247.7 ± 30.9	433.6 ± 80.6	DBCA
Iron (kg/ha)	3.7 ± 1.4	3.3 ± 0.4	4.3 ± 1.0	13.7 ± 4.1	D$\overline{\mathrm{CAB}}$
Sulfate (kg/ha)	11.2 ± 5.5	23.0 ± 2.5	20.3 ± 2.6	22.4 ± 3.7	BDCA

erable variation in rates, with coefficients of variation ranging from 27 to 48%.

Denitrification rates were statistically similar in the moist meadows, wet meadows, and beaver ponds (N_2O production 0.30–0.39 × 10^{-5} mol·m^{-2}·h^{-1}) and nearly double that measured in the forest (N_2O production 0.14 × 10^{-5} mol·m^{-2}·h^{-1}; $P < .01$; Table 6). The highest rates for the meadows and pond were in the warm July–August period, whereas rates in the forest were low and relatively constant across all seasons.

Principal components analysis.—A principal components analysis (PCA) was performed on soil data for 1987 to search for factors responsible for the observed results. Soil data for 1986 were not included because of problems with completeness of the data matrix. The first three factors of the PCA explained 74% of the variance among the original variables with, respectively, 32% for PC_1, 25% for PC_2, and 18% for PC_3.

Principal component 1 (PC_1) was mainly correlated with total nitrogen ($r = 0.93$) and total phosphorus ($r = 0.86$). Wet meadow soils presented the largest variations in total nitrogen and total phosphorus contents during the ice-free period (Fig. 5A). However, PC_1 was not especially useful in distinguishing between hydrologic zones.

Principal component 2 (PC_2) was positively correlated with soil moisture ($r = 0.92$) and soil organic matter ($r = 0.80$). Wet meadows, moist meadows, and forest soils had large variations in their moisture and organic matter content during the ice-free period, while pond sediments were stable (Fig. 5B). This large variation, however, minimized the usefulness of PC_2 in distinguishing between hydrologic zones.

Principal component 3 (PC_3) was positively correlated with soil ammonium content ($r = 0.62$) and negatively with soil oxidation–reduction potential ($r = -0.76$). This axis (PC_3) was related to the aerobic–anaerobic status of the soil since low Eh values and, to a lesser extent, high ammonium contents reveal anaerobic conditions. The four hydrologic zones were well separated along this third axis (Fig. 5A, B), with pond sediments on the most anaerobic side and forest soils on the most aerobic one.

Pore water ion and nutrient dynamics

Ion concentrations.—Cation and anion concentrations below the average depth of the rooting zone, as expected, showed little annual or seasonal variation. The only exceptions were iron, magnesium, and potassium from the stream and meadows during an unusually dry period in August 1986. Coefficients of variation remained between 6 and 22% of the annual mean.

TABLE 6. Annual nitrogen fixation and denitrification rates ($\bar{X}$ ± SE) associated with surface soils (0–15 cm) from four habitats for 1987. Underlined values are not significantly different ($P > .05$; Tukey comparison).

	Hydrologic zone			
Process	Forest	Moist meadow	Wet meadow	Beaver pond
Annual sample size (n)	75–95	82–105	105–135	78–105
Nitrogen fixation (measured as acetylene fixation, mol·m^{-2}·h^{-1})	$\underline{2.9 \pm 0.9}$	$\underline{2.9 \pm 1.4}$	$\underline{2.3 \pm 0.6}$	$\underline{1.5 \pm 0.4}$
Denitrification (N_2O production) (10^{-5} mol·m^{-2}·h^{-1})	0.14 ± 0.02	$\underline{0.33 \pm 0.06}$	$\underline{0.39 \pm 0.05}$	$\underline{0.30 \pm 0.04}$

There were significant differences in pore water ion concentrations between hydrologic zones but the differences were not consistent (Table 7). For example, calcium and magnesium were similar ($P > .05$) for the forest, moist meadows, and streams but significantly different ($P < .05$) from the wet meadows and beaver ponds. The results were similarly complicated for potassium, sulfate, iron, and chloride where concentrations do not sort by the degree of water saturation. Pearson correlation analyses of ion concentration data revealed a large number of significant but weak relationships among ions and with physical features of the soil (Table 8). In most cases <25% of the variation in concentrations can be explained by the percentage of organic matter, soil bulk density, pH, or oxidation–reduction potential.

Nutrient concentrations.—Nitrogen and phosphorus concentrations had greater year-to-year and seasonal variations than most ions below the average depth of the rooting zone. This was reflected in coefficients of variation, which ranged from 0 to 67% of the annual mean (Table 7). Pearson correlation analyses again showed a number of significant but weak ($r^2 < 0.15$) relationships among nutrient species and with physical features of the soil (Table 8). Relations are stronger among nutrient species but only ≈30% of the variation was explained in the best cases.

There were significant differences in pore water nutrient concentrations between hydrologic zones. However, the differences are only consistent for the ponds where total nitrogen, total phosphate, ammonium, and orthophosphate concentrations were greater than in the other habitats (Table 7). There were no consistent trends across the hydrologic gradient for nitrate, ammonium, total phosphorus, and orthophosphate concentrations. Often concentrations of these nutrients in the meadows were more similar to the forests than to the beaver ponds or streams.

Principal components analysis.—Principal components analysis (PCA) of pore water chemistry for the 2 yr of observation were grouped by month and hydrologic regime (i.e., pond, wet meadow, moist meadow, and forest). The first three factors of PCA explained 65% of the variance among the original variables with, respectively, 40% for PC_1, 14% for PC_2, and 11% for PC_3. Only PC_1 and PC_3 were considered further since PC_2 did not give any information that could be interpreted ecologically.

Principal component 1 (PC_1) was positively correlated with pore water ammonium ($r = 0.80$), total ni-

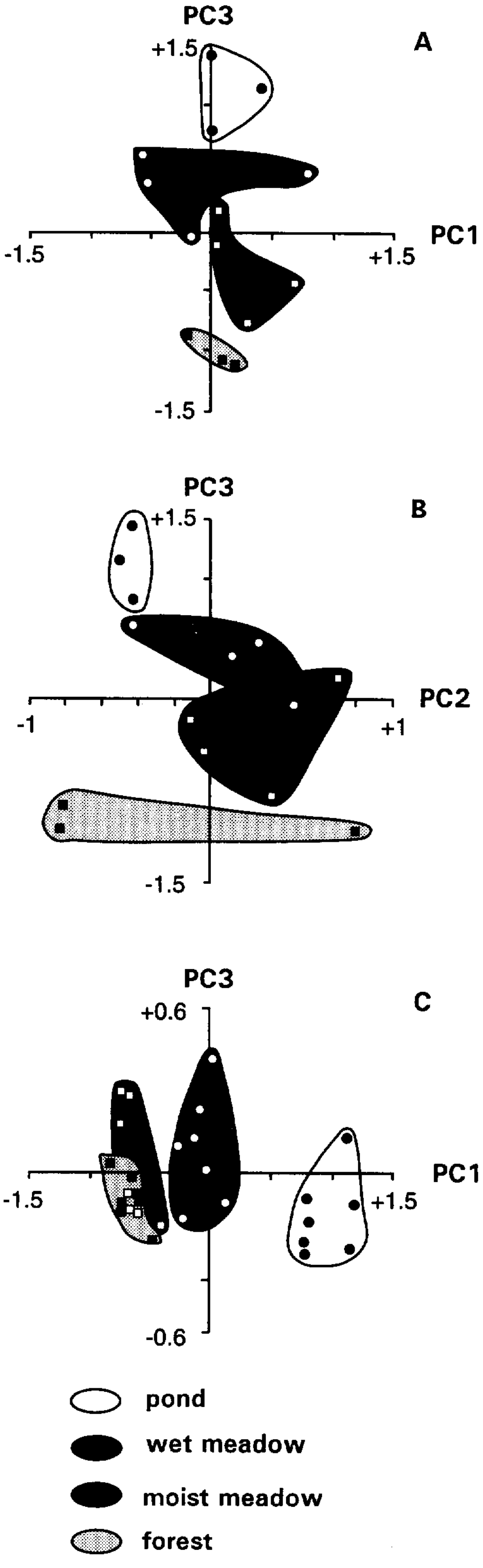

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FIG. 5. (A) Projection of the mean factorial coordinate for a given month and hydrologic regime for PCA factors 1 and 3 for 1987 soil analyses. (B) Projection of the mean factorial coordinate for a given month and hydrologic regime for PCA factors 2 and 3 for 1987 soil analyses. (C) Projection of the mean factorial coordinate for a given month and hydrologic regime for PCA factors 1 and 3 for pore water.

TABLE 7. Concentrations ($\bar{X}$ ± SE) of nutrients and ions associated with pore water during 1986–1987 for the five hydrologic zones. Values connected by a line in the Tukey comparison are not significantly different ($P > .05$).

Parameter	Forest (A)	Moist meadow (B)	Wet meadow (C)	Beaver pond (D)	Stream (E)	Tukey comparison
	Hydrologic zone					
Sample size (*n*)	108–127	140–215	178–306	135–232	35–59	
Total nitrogen (mg/L)	0.92 ± 0.07	1.23 ± 0.17	1.88 ± 0.15	4.35 ± 0.52	1.99 ± 0.41	DECBA
Nitrate-N (mg/L)	0.03 ± 0.02	0.08 ± 0.07	0.06 ± 0.04	0.00 ± 0.00	0.01 ± 0.00	BCAED
Ammonium-N (mg/L)	0.09 ± 0.02	0.05 ± 0.01	0.38 ± 0.08	2.94 ± 0.51	1.01 ± 0.41	DECAB
Total phosphorus (mg/L)	0.04 ± 0.01	0.02 ± 0.00	0.03 ± 0.00	0.11 ± 0.02	0.10 ± 0.03	DEACB
Orthophosphate-P (mg/L)	0.03 ± 0.01	0.02 ± 0.01	0.03 ± 0.01	0.14 ± 0.03	0.11 ± 0.07	DECAB
Potassium (mg/L)	1.19 ± 0.18	0.71 ± 0.09	1.24 ± 0.20	2.31 ± 0.33	1.56 ± 0.19	DECAB
Calcium (mg/L)	4.46 ± 0.49	6.76 ± 0.94	17.44 ± 2.02	23.86 ± 3.01	8.54 ± 2.40	DECBA
Magnesium (mg/L)	1.52 ± 0.23	2.79 ± 0.44	7.94 ± 1.12	11.15 ± 1.50	3.68 ± 1.01	DECBA
Iron (mg/L)	0.41 ± 0.10	2.03 ± 0.44	10.80 ± 1.68	12.61 ± 2.85	7.37 ± 2.88	DCEBA
Sulfate (mg/L)	5.97 ± 0.38	6.72 ± 0.57	2.45 ± 0.76	0.72 ± 0.18	0.58 ± 0.12	BACDE
Chloride (mg/L)	3.87 ± 0.61	3.09 ± 0.25	3.35 ± 0.23	4.53 ± 0.36	2.19 ± 0.21	DACBE

trogen ($r = 0.86$), total phosphorus ($r = 0.65$), orthophosphate ($r = 0.68$), calcium ($r = 0.72$), magnesium ($r = 0.70$) and iron ($r = 0.48$). Together with the negative correlation of PC_1 with sulfate content ($r = -0.44$), the pattern suggests that the components of PC_1 were strongly related to anaerobiosis. PC_3 was mainly correlated with nitrate ($r = 0.86$) and thus expressed nitrate availability in pore water. The four hydrologic zones sorted along the PC_1 axis representing the anaerobic status of the soils (Fig. 5C). Overall, in all seasons, ponds were more anaerobic than wet meadows, which were more anaerobic than moist meadow and forest sites, and this was represented in the pore water and soil chemistry for each hydrologic zone. Moreover, the wide range of variation of wet and moist meadow measurements through time along the PC_3 axis indicated large variations in pore water nitrate availability compared to forests and ponds.

DISCUSSION

A landscape perspective

The total area impounded by beaver increased dramatically between 1927 and 1988 (Table 9), a period of beaver population expansion (Broschart et al. 1989). Despite occasional abandonment and drainage, none of the impoundments established during the 63-yr period had reverted to forest (Naiman et al. 1988, Johnston and Naiman 1990*a*, *c*). Therefore, all areas impounded during the 63 yr were still distinct biophysical patches, and the total area affected by impoundment was cumulative over time (Table 9). The fastest rate of new impoundment occurred between 1940 and 1961, when the proportion of the landscape impounded increased by an order of magnitude (Table 9). The rate of new impoundment formation was much less after 1961.

TABLE 8. Pearson correlation (*r*) analysis of pore-water ion and nutrient concentrations for all sites in 1986 and 1987 combined. Sample size = 765; * $P < .05$.

	% Organic	Bulk density	Soil pH	Eh	Total N	NO_3-N
Bulk density	−0.459*					
Soil pH	−0.066	−0.035				
E	0.043	0.075	−0.256*			
Total N	−0.181*	0.062	0.411	−0.332*		
NO_3-N	0.020	0.024	0.040	0.073	0.043	
NH_4-N	−0.184*	0.100*	0.299*	−0.336*	0.904*	−0.008
Total P	−0.138*	0.153*	0.354*	−0.176*	0.567*	−0.032
PO_4-P	−0.145*	0.107*	0.281*	−0.251*	0.464*	−0.032
Fe	−0.194*	−0.009	0.260*	−0.410*	0.319*	−0.038
K	−0.140*	0.072*	0.259*	−0.044	0.331*	0.003
Ca	−0.109*	−0.024	0.528*	−0.483*	0.497*	−0.045
Mg	−0.121*	−0.009	0.494*	−0.457*	0.451*	−0.034
SO_4	0.003	0.181*	−0.401*	0.349*	−0.295*	0.187*
Cl	−0.105*	0.004	0.195	−0.041	0.159*	0.020

Table 9. Area associated with forest, moist meadow, wet meadow, and beaver ponds on a 214-km² portion of the Kabetogama Peninsula, 1927–1988. The 214-km² region represents 72% of the Kabetogama Peninsula, and is the area for which there was aerial photo coverage on all nine dates.

Generalized habitat type	Area (ha)								
	1927	1940	1948	1961	1972	1981	1986	1987	1988
Land not impounded	21 180	21 119	20 569	19 611	19 368	19 168	18 887	18 871	18 719
Impoundable forest	2563	2502	1952	994	751	551	270	254	102
Moist meadow	134	216	269	694	866	727	768	850	880
Wet meadow	19	27	148	312	422	514	457	425	457
Beaver pond	47	18	394	763	723	971	1268	1234	1323
Total impounded	200	261	811	1769	2012	2212	2493	2509	2661

Concomitant with the creation and abandonment of impoundments is a dramatic alteration of the dominant hydrologic zones. Moist meadows, those with saturated soils or a seasonally high water table, dominate from 1940 to 1972 (Table 9); wet meadows, wetlands with shallow standing water and emergent vegetation, are intermediate in areal extent. Beaver ponds, with water too deep to support emergent vegetation, dominate by 1981. The sharp increase in beaver ponds between 1981 and 1988 is not related to precipitation nor beaver population trends (Johnston and Naiman 1990*a*). It is believed that a slightly declining population was creating more impoundments in search of new food supplies. This is supported by the fact that new ponds established prior to 1961 were significantly larger ($\bar{X} = 3.6$ ha) than new ponds established after 1972 ($\bar{X} = 1.2$ ha; Johnston and Naiman 1990*a*) as beaver began to colonize less desirable habitat.

Standing stocks of ions and nutrients in the organic horizons of soils and sediments increased as a result of beaver-induced habitat alterations throughout the peninsula (Table 10). The extrapolations to the landscape scale that follow are conservative estimates since many beaver-influenced sites have organic horizons >15 cm in depth as well as deeper soil horizons that may represent historical beaver activities. Deeper soil horizons are complex in beaver-influenced areas and could not be fully characterized as part of this study. Nevertheless, with the exception of potassium (20%), the increases in the upper 15 cm of the organic horizon are substantial. For example, calcium, magnesium, iron, and sulfate increased by 82–169%, total phosphorus by 43%, and total nitrogen, nitrate, and ammonium by 72–295%. The nitrogen increases are particularly noteworthy because even though total nitrogen increased by only 72%, the plant-available forms of nitrogen (NO_3, NH_4) increased by 208 and 295%, respectively. These results are despite the fact that measured rates of nitrogen fixation are less than or equal to that found in the forest (not statistically significant) and denitrification rates are significantly higher in the beaver-altered habitats (Table 6). (Data reported here for total nitrogen accumulations are an order of magnitude lower than that reported by Naiman et al. [1988]. The correct values are reported here, and the conclusions remain the same.) Overall, beaver have created meadow and pond patches with high standing stocks of ions and nutrients in surface organic profiles and, for nitrogen, in plant-available forms. The high standing stocks and availability are important in a boreal forest environment where ions and nutrients are generally scarce.

Table 8. Continued.

NH_4-N	Total P	PO_4-P	Fe	K	Ca	Mg	SO_4
0.553*							
0.452*	0.597*						
0.218*	0.095*	0.254*					
0.297*	0.269*	0.298*	−0.023				
0.441*	0.251*	0.367*	0.488*				
0.398*	0.176*	0.303*	0.386*	0.357*	0.845*		
−0.241*	−0.156*	−0.171*	−0.280*	−0.083*	−0.336*	−0.280*	
0.163*	0.061	0.052	0.111*	0.162*	0.235*	0.195*	−0.053

TABLE 10. Absolute amounts of ions and nutrients in 1927 and 1988 associated with habitat potentially influenced by beaver activities*. Habitat data are from Table 9 and ion and nutrient data are from Table 5.

Parameter	Absolute amounts (kg) 1927	Absolute amounts (kg) 1988	Percentage change (%)
Total nitrogen	5.8×10^5	1.0×10^6	72
Nitrate-N	3.9×10^2	1.2×10^3	208
Ammonium-N	2.1×10^4	8.3×10^4	295
Total phosphorus	7.0×10^4	1.0×10^5	43
Potassium	3.0×10^5	3.6×10^5	20
Calcium	1.9×10^6	4.5×10^6	137
Magnesium	3.5×10^5	9.4×10^5	169
Iron	1.1×10^4	2.4×10^4	118
Sulfate	3.3×10^4	6.0×10^4	82

* For 1927 we included the total forest area (2563 ha) that could be potentially impounded by beaver.

Ion and nutrient sources

There are several possible reasons why the beaver-created patches had standing stocks of ions and nutrients greater than that of the original forest soil: (1) the beaver ponds and meadows may have acted as efficient sinks for material eroding from the landscape, (2) the rising water from dam construction may have captured sufficient nutrients and ions contained in the preexisting forest vegetation, and (3) biogeochemical processes may have transformed elements in the habitats themselves.

It is already established that beaver ponds retain large amounts of material that would normally be transported downstream by streamflow (Naiman et al. 1986). This is demonstrated by the accumulation of materials behind dams to depths that may exceed 1 m. Yet, it has also been established that export rates of dissolved ions, nutrients, and fine particulate organic matter are greater in beaver-influenced streams than in similar-sized streams without beaver (Naiman 1982). This presumably results from the increase in contact area with soils caused by the ponding of water. Export rates (mass per unit land area) of dissolved organic carbon and fine particulate organic carbon may be several times higher in streams with beaver ponds than in similar-sized streams without beaver ponds. The balance between a pond acting as a net sink or source of elements to downstream communities appears to be equivocal, depending on pond age, ecological maturity, channel morphology, and other factors related to the maintenance of system properties. However, beaver-impounded soils on the Kabetogama Peninsula generally lack the morphological characteristics that would indicate substantial postglacial sediment deposition. Beaver-impounded soils were morphologically similar to soils in an unimpounded wetland depression, and different from upland forest soils only in color, implying that the primary influence of beaver impoundment at this location is on in situ biogeochemistry rather than waterborne particulates from the uplands.

Evidence supporting the contention that, by building dams, beaver initially capture virtually all the elements eventually found in the pond sediments is strong. Of the ions and nutrients measured, there is seldom a significant difference in mass per unit volume (in micrograms per cubic centimetre) concentrations between the pond, meadow, and forest soils, there are no clear trends in gradients between the forest and the ponds (Table 3), and pore water concentrations (Table 7) below the rooting zone suggest little leakage to deeper aquifers. When unit volume concentrations are converted to standing stock (in kilograms per hectare) in the upper 15 cm of the organic horizon, a number of significant differences appear between the beaver-created habitat and the forest soils (Table 5). The general trend is for the highest standing stocks to be associated with pond sediments and the least with forest soils. This is because pond and wet meadow organic matter accumulations are, on average, deeper (≥15 cm) than in moist meadows (13 cm) or the forest (7 cm). In some cases this could result from the ponds and meadows acting as depositional zones for organic matter transported to the site or generated in situ by herbaceous vegetation. However, it may also result from the forest vegetation captured by the initial inundation of the forest by beaver (Johnston and Naiman 1990*b*).

We do not have measurements of how much vegetative material was captured by the initial water inundation at dam construction or how much was actively transported from uplands by beaver over the life of ponds used in this study. However, estimates from studies of forest biomass composition (Johnston and Naiman 1990*b*) and from ion and nutrient data measured for an aspen–mixed hardwood–Spodosol ecosystem in northern Wisconsin (Pastor and Bockheim 1984) suggest that the standing stock of ions and nutrients in the upland vegetation prior to pond creation were as follows: total nitrogen (222 kg/ha), total phosphorus (38 kg/ha), potassium (300 kg/ha), calcium (680 kg/ha), magnesium (58 kg/ha), and sulfate (22 kg/ha). When added to the standing stocks measured for the forest soils, the total amounts exceed, in most cases, the standing stocks in the organic horizon of the meadows and ponds. For example, estimated total nitrogen standing stocks for the forest vegetation and soils are 2–48% larger than that measured for the existing meadows and ponds, for total phosphorus the standing stocks are 44–146% larger, for potassium 190–378%, for calcium 5–39% (meadows only), and for sulfate 41–99%. These estimates do not include vegetation cut by beaver and transported to the pond from the uplands. The only exceptions are for calcium in the beaver pond where the standing stock in the organic horizon is 68% larger than in the original forest and for magnesium where the standing stocks at all sites are 23–180% larger than the original forest. We suspect that the excess calcium and magnesium may be solubilized from carbonate sources deeper in the soil profile than the depth used to make the standing stock calculations (Table 2; Ck and Ckg horizons). There was effervescence when hydrochloric acid was applied to deeper soils, an indication of free carbonates.

Collectively, these results suggest that beaver activities may be depleting ion and nutrient stocks in the original forest system (Mg, and possibly Ca, being exceptions), altering the distribution of ions and nutrients (soils vs. vegetation) at the ecosystem scale, and increasing the depth of the organic horizon. Ions and nutrients are moved from the vegetation component to the soil component in the first decade following dam construction, a portion is eroded from the landscape by water movement, and the remainder is stored in anaerobic pond sediments until the site is abandoned and meadows are formed. With the return of aerobic conditions ions and nutrients become readily available to vegetation, resulting in productive communities during succession.

In addition, biogeochemical transformation of ions and nutrients in response to altered hydrologic and redox regimes is an important part of this process (Keeney 1973, Ponnamperuma 1972). Beaver ponds have concentric patches of redox conditions within soils and sediments. These redox conditions occur throughout the year (Fig. 4) and are at different depths in each hydrologic zone, ponds being the most reduced sites. Due to their intermediate position, wet and moist meadows present large variation in redox conditions through time, especially with annual variation in precipitation, which enhance nitrogen bioavailability (Patrick and Tusneem 1972). The formation of anaerobic zones with low redox potentials and altered hydrogen ion concentrations has strong effects on ionic affinities and microbial processes. Nitrogen fixation rates are reduced, denitrification rates increase (especially if the water table fluctuates; Reddy and Patrick 1975), ratios between elements are severely altered as a result of linked biogeochemical cycling, and shifts occur in the form of the element (Johnston 1991, Pinay and Naiman 1991). This latter point is especially true for nitrogen where total nitrogen and ammonium accumulate under anaerobic conditions. However, organic nitrogen mineralization and vegetative uptake proceeds rapidly once aerobic conditions return, and may explain why beaver ponds are initially so productive once they drain.

Animal–system interactions

Our results support the general concept that beaver, although less widespread and ecologically influential than in the past, continue to have significant ecological roles that go far beyond their immediate requirements for food and habitat. Due to their size, longevity, and food and habitat requirements, beaver have substantial impacts on drainage networks throughout many areas of the United States and Canada. Beaver feeding strategies and physical alteration of the stream environment affect the hydrologic regime as well as community composition (McDowell and Naiman 1986, Naiman et al. 1988, Johnston and Naiman 1990*a, b*). These changes, in turn, alter biogeochemical cycling and accumulation of nutrients and ions in soils, sediments, and water. Specific alterations influence maintenance of the habitat, the forage base, and the beaver population itself. Some changes may benefit the habitat or the forage base, resulting in increased production and greater beaver population density (e.g., plant available nitrogen), whereas other changes may be detrimental, causing species replacement in the forage base for beaver (conversion of riparian forests from aspen to spruce) and the abandonment of ponds by beaver.

The three main results from this study, the accumulation, availability, and the translocation of ions and nutrients, are not unique to beaver. These activities are found in a wide variety of mammals, arthropods, and nematodes (Anderson 1987*a*). Under certain conditions moose (*Alces alces*) foraging on deciduous plants can shift the boreal forest community towards conifers (e.g., spruce: *Picea glauca, Picea mariana*), which produce a low quality litter. Over several decades, this shift affects soil formation and nitrogen cycling, which ultimately affects the productivity of the spruce, longer term plant succession in the forest, and the population dynamics of the moose (Pastor et al. 1988, 1993, McInnes et al. 1992, Pastor and Naiman 1992). Likewise, foraging by arthropods and nematodes on roots (Andersen 1987*a*), foraging by bush elephant (*Loxodonta africana*) on acacia (*Acacia*) trees in Africa (Laws 1970, Hatton and Smart 1984), grazing by mammals on the Serengeti grasslands (McNaughton et al. 1988), foraging by snow geese (*Anser caerulescens*) in subarctic salt marshes (Cargill and Jefferies 1984, Jefferies 1988), and burrowing and foraging by prairie dog (*Cynomys*) and pocket gopher (*Geomys bursarius*) in North America (Huntly and Inouye 1988, Whicker and Detling 1988, Holland and Detling 1990) affect vegetative cover, productivity, and the accumulation and availability of soil nutrients.

Translation of ions and nutrients from vegetation to the soils is also mediated by a wide variety of other animals. For example, grazing and browsing mammals will directly transfer 30–60% (occasionally ranging up to 95%) of the annual primary production back to the soil as feces (McNaughton and Georgiadis 1986). However, the greatest direct translocation of ions and nutrients may be affected by the burrowing of fossorial rodents. In natural settings free-living gopher and ground squirrel move 10 000 to 90 000 $kg \cdot ha^{-1} \cdot yr^{-1}$ of subsurface soil to the surface (Taylor 1935, Thorp 1949, Andersen 1987*b*) where the combination of nutrients and the physical mixing process result in productive plant communities (Huntley and Inouye 1988). Early in this century in the western United States, nearly 25% of the mammalian species were fossorial rodents estimated to represent nearly one-half of the total number of mammals (Grinnell 1923). Beaver do not transfer large amounts of ions and nutrients directly from the vegetation to the soils (or vice versa) but through manipulations of the hydrologic regime they do have strong indirect effects on translocation, accumulation, and availability.

Beaver are just one example of how animals affect the basic elemental cycles upon which the development and maintenance of trophic and successional pathways depend. Inherent in this example is the fact that beaver populations are temporally variable in a dramatic cycle, producing a rich array of heterogeneous habitat within drainage networks. Habitat created by beaver becomes a shifting mosaic of environmental conditions dependent upon patch age and size, successional status, substrate, hydrologic characteristics, and resource inputs, which together provide for the long-term environmental vitality of drainage networks.

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