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Phosphorus and nitrogen retention in five Precambrian shield wetlands

K. J. DEVITO[1,*], P. J. DILLON[2] & B. D. LAZERTE[2]
*[1] Watershed Ecosystems Program, Trent University, Peterborough, Ontario, K9J 7B8, Canada; [2] Dorset Research Centre, Ontario Ministry of the Environment, Dorset, Ontario, P0A 1E0, Canada; (*Present address: Dorset Research Centre, Bellwood Acres Rd., Box 39, Dorset, Ontario, POA 1EO, Canada)*

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Abstract. Phosphorus and nitrogen mass balances of five wetlands (two beaver ponds, two conifer-*Sphagnum* swamps and one sedge fen) situated in three catchments in central Ontario, Canada, were measured. Monthly and annual input-output budgets of total phosphorus (TP), total nitrogen (TN), total organic nitrogen (TON), total inorganic nitrogen (TIN), ammonium ion (NH_4^+-N), nitrate (NO_3^--N) and dissolved organic carbon (DOC) were estimated for the five wetlands during the 1982–83 and 1983–84 water years. Except for the deepest beaver pond (3.2 m) which had annual TP retention of −44% (−0.030 ± 0.015 $g\,m^{-2}\,yr^{-1}$), the wetlands retained < 0.001 to 0.015 $g\,m^{-2}\,yr^{-1}$; however, this was less than 20% of the inputs and the estimated budget uncertainties were equal to or greater than the retention rates. Annual TN retentions ranged from −0.44 to 0.56 $g\,m^{-2}\,yr^{-1}$ (−12 to 4%) but were not significantly different from zero. The wetlands transformed nitrogen by retaining TIN (16 to 80% RT) and exporting an equivalent amount as TON (−7 to 102% RT). The beaver ponds, however, retained NO_3^- while NH_4^+ was passed through or the outputs exceeded the inputs. In contrast, the conifer swamps retained both NH_4^+ and NO_3^-. DOC fluxes into and out of the beaver ponds were equal (−18 and 4% RT) but output from the conifer swamps exceeded input by > 90%. Marked seasonal trends in nutrient retention were observed. Nutrient retention coincided with low stream flow, increased evapotranspiration and biotic uptake during the summer. Net nutrient export occurred during the winter and spring when stream flows were highest and biotic uptake was low.

Introduction

Research on a variety of wetland types has resulted in few generalizations about their effects on nutrient (particularly phosphorus and nitrogen) budgets. Wetlands have been reported to act as sources (Lee et al. 1975; Sloey et al. 1978), sinks (Kuenzler et al. 1980; Verry & Timmons 1982; Yarbro 1983; Peterjohn & Correll 1984; Kadlec 1986) or as transformers of inorganic forms into organic forms (Kemp & Day 1984; Elder 1985) depending on the wetland type, hydrologic condition (Gosselink & Turner 1978;

Bayley et al. 1985) and even the year the work was conducted (Peverly 1982). Reliable nutrient budgets are relatively rare, confounding general conclusions about nutrient dynamics in wetlands (Carter et al. 1979; King 1985).

Wetlands are a common feature on the Canadian Precambrian Sheild. Although wetlands may represent only a small fraction of the total area of any catchment, they are usually located such that much of the runoff and associated nutrients transported through the catchment must pass through them. Uptake, export or transformation of nutrients in the waters that pass through these wetlands may have biological repercussions on downstream aquatic ecosystems.

Beaver (*Castor canadensis*) activity can have a major influence on catchments by creation and maintenance of wetlands. Despite the apparent importance of beaver dams, few studies have quantified their influences on water chemistry. Recently, Naiman & Melillo (1984) and Maret et al. (1987) have suggested that nitrogen and phosphorus are accumulated in beaver ponds.

The primary objective of this study is to evaluate the effects of wetlands on the water chemistry of small headwater streams on the Canadian Shield. A mass balance approach was used to quantify the annual and monthly nutrient retention efficiency of different wetlands within the study area. The budgets were used to test the hypothesis that these freshwater wetlands act as nutrient sinks.

Study site

The wetlands are located in three watersheds that are situated near the southern limit of the Canadian Precambrian Shield (Fig. 1): Harp Lake catchment #4 (Harp 4; 45° 23′ N, 79° 08′ W), Plastic Lake catchment #1 (Plastic 1; 45° 11′ N, 78° 50′ W) and Paint Lake catchment #1 (Paint 1; 45° 13′ N, 78° 55′ W). The largely inpermeable Precambrian metamorphic silicate bedrock is covered with thin basal till, with rock ridges and exposed bedrock common in many areas. The depth of overburden in Harp 4 averages about 1 m, with depths ranging from < 1 m at higher elevation to 10 m near the basin outlet. Surficial deposits in Plastic 1 and Paint 1 are < 1 m. Vegetation in Harp 4 and Paint 1 is deciduous forest (maple and birch) in the dry upland areas and coniferous forest (white cedar, hemlock and balsam fir) in the low-lying areas. Plastic 1 is forested primarily with stands of pine, hemlock and balsam fir. The physiography, geology and geochemistry of the study areas have been detailed by Scheider et al. (1983),

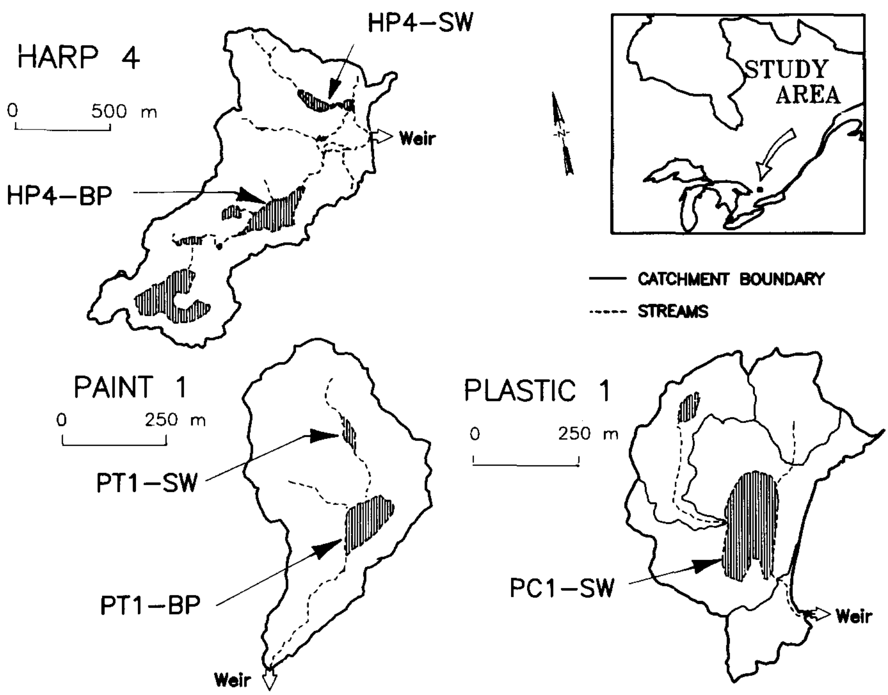

Fig. 1. Location of the study area in the Muskoka-Haliburton area of central Ontario, Canada, showing Harp 4, Plastic 1 and Paint 1 lake subcatchments, microcatchments, streams, and study wetlands. Shaded areas represent wetlands. Pt1-bp = Paint 1 beaver pond (0.83 ha), Pt1-sw = Paint 1 sedge fen (0.10 ha), Hp4-bp = Harp 4 beaver pond (3.8 ha), Hp4-sw = Harp 4 conifer swamp (1.13 ha), Pc1-sw = Plastic 1 conifer swamp (2.12 ha).

Jeffries & Snyder (1983), McDonnell & Taylor (1987), and Shibitani (1988).

Annual precipitation in the area is 0.90–1.10 m with 0.24–0.30 m falling as snow between December 1 and April 10. The mean January air temperature is −10 °C (Scheider et al. 1983). Annual runoff is similar in all three catchments, varying from 0.4 to 0.6 m from year-to-year. Runoff is greatest (50–75% of annual runoff) in March or April in response to snowmelt, and decreases to a minimum from June through September. A secondary peak usually occurs between October and December.

Budgets were measured for two wetlands in the Harp 4 catchment (Fig. 1). The large beaver pond (Hp4–bp; 3.81 ha), is a shallow (1 m), steep-sided, dystrophic pond with floating mats of *Sphagnum spp* and Labrador tea (*Ledum groenlandicum*) along the shore. Beaver activity is sporadic because trappers periodically remove the animals. The pond has three channelized inflows draining 49.1 ha of forested upland containing a large conifer swamp and several beaver ponds. Unchannelized inputs drain 9.0 ha of adjacent uplands. The outflow passes over three smaller dams. Harp 4 conifer swamp (Hp4–sw; 1.13 ha) is a minerotrophic conifer swamp dominated by black spruce (*Picea mariana*) with a shrub layer dominated by *Alnus spp.* A poorly defined *Sphagnum* mat covers the top of the shallow sediments. A hummock-hollow microtopography exists with standing water occurring well into the growing season. One channelized inflow draining a moist conifer-forested lowland (15.1 ha) enters the swamp and unchannelized inputs drain adjacent, steep sloped upland, deciduous forest (11.9 ha).

A large minerotrophic *Sphagnum* - conifer swamp (Pcl–sw; 2.12 ha), occupies the central portion of the Plastic 1 catchment (Fig. 1). The swamp is forested primarily with *P. mariana* and *Thuja occidentalis* with an understory of *Alnus spp.* and black alder (*Ilex verticillata*) and a well-defined ground layer of *Sphagnum*. A hummock-hollow microtopography exists, and pools of standing water persist into the growing season. Two inflows drain 8.8 ha of upland conifer forest. A large portion of adjacent upland (10.0 ha) contributes unchannelized inputs. One outflow drains from the swamp.

The centrally located beaver pond (Pt1–bp; 0.83 ha), in Paint 1 has an average depth of 3.2 m. Floating mats of *Sphagnum* and *Ledum* occur along the shore. A 2 m high beaver dam controls the water outflow at Pt1–09. Two inflows drain 9.0 ha of upland and 8.2 ha of adjacent uplands contribute unchannelized inputs. Paint 1 sedge fen (Pt1–sw; 0.1 ha) occupies a shallow depression in low lying forest floor. The vegetation is dominated by *Carex* spp. A well-defined inflow (4.9 ha) enters the fen. Approximately 1.7 ha of forested upland adjacent to Pt–sw contribute unchannelized inputs.

Methods

Continuous streamflow measurements in each catchment have been made from 1976 at Harp 4 and Paint 1 and from 1979 at Plastic 1 (Locke and Scott 1986). Runoff was assumed to be uniform throughout each catchment and unit areal discharge was estimated for each catchment from the measured outflow discharge. The discharge at each substation was estimated by proration based on the area of the portion of the catchment above that point (Fig. 1, see Plastic 1 for example). Evapotranspiration (ET) was calculated from the difference in the water budget and from mean monthly temperatures using the Thornthwaite (1948) method. Water samples were collected approximately weekly, but the intensity of sampling increased during high flow, principally during snowmelt. During the period November 1982 to May 1984, 41–87 samples were collected from the sites in Plastic 1 and

35–65 samples in Harp 4. 20–74 samples were taken at the streams in Paint 1 from March 1982 to May 1984. Atmospheric decomposition of nutrients directly on the wetlands was estimated by measuring bulk deposition (Dillon et al. 1988). Sampling techniques were described in detail in Locke & Scott (1986) and Locke & de Grosbois (1986).

Total phosphorus (TP), total Kjeldahl nitrogen (TKN), ammonium-nitrogen (NH_4^+-N), nitrate nitrogen (NO_3^--N), and dissolved organic carbon (DOC) were determined as outlined in Ontario Ministry of the Environment (1981). Total organic nitrogen (TON) was calculated by subtracting the NH_4^+-N concentration from TKN, and total inorganic nitrogen (TIN) was calculated by adding NO_3^--N and NH_4^+-N. Total nitrogen (TN) was determined by adding TON and TIN.

Nutrient budgets

A generalized nutrient budget for any wetland can be expressed as: $RT = P + S_i + U - S_o$ where RT is the amount retained in the wetland. The inputs include atmospheric depositon (P), stream inflows (S_i) and ungauged or unchannelized inputs (U) from the area adjacent to the wetland. Inputs from the ungauged areas were estimated by areally prorating the export of nutrients from nearby upland subcatchments with monitored streams. Losses occurred via the outflow stream (S_o). We assumed that no net aerial exchange of nutrients occurred (i.e., by evaporative loss, insect emergence, pollen discharge, etc.) and that regional ground water inputs and outputs were negligible or balanced each other.

Rainfall depth and bulk depositon were measured on an event basis and totalled to give monthly results. Monthly nutrient stream load was estimated by combining continuous measurements of stream discharge with instantaneous estimates of nutrient concentration (Scheider et al. 1979). Annual budgets were determined by addition of monthly budgets for the hydrologic year, June 1 to May 31. The results are expressed as retention (RT) in $\text{mass} . \text{area}^{-1} . \text{time}^{-1}$, where:

$$RT = \frac{\text{total inputs} - \text{total outputs}}{\text{wetland area}}$$

or as % retention where:

$$\%RT = \frac{\text{total inputs (mass.time}^{-1}) - \text{total outputs (mass.time}^{-1})}{\text{total inputs (mass.time}^{-1})} \times 100$$

Error estimates

Estimated errors in monthly loads were used to assess uncertainties associated with the water and nutrient budgets. Work by Scheider et al. (1979) using regional long-term runoff estimates (Pentland 1968) to approximate annual runoff from several Harp Lake subcatchments suggests relatively uniform runoff occurs for the subcatchments in the study area. Fisher and Likens (1973) reported estimates of annual discharge based on watershed area within $\pm 10\%$ of empirical measurements for catchments with similar characteristics, i.e., relatively impermeable bedrock and shallow surficial till. If we assume a relative error for annual runoff estimates of $\pm 10\%$ then the average error associated with monthly stream and ungauged flow can be approximated as $\pm 35\%$ ($SD/\sqrt{n}$; n = 12 months). Precipitation depth is recorded daily from standard guages that stand 1 m above ground with wind shields; thus, instrumentation error is probably about 5% per month (Winter 1981). With a guage density less than 10 km^2/gauge (the gauges were within 1 km of each wetland) and the rainfall patterns in this area errors associated with areal averaging precipitation are probably not greater than 20% per month (Winter 1981). Taking these factors into consideration, errors in estimating monthly precipitation depth are about at $\pm 21\%$. Analytical and sampling error associated with stream and bulk deposition chemistry range from 5 to 10% and are assumed to be $\pm 10\%$ per month.

The magnitude of total error can be approximated by the standard deviation of total error in the nutrient or water budget calculations. As described by Winter (1981) and LaBaugh & Winter (1984), the variance of the total error in budget calculations can be approximated by:

$$S_T^2 = S_P^2 + S_U^2 + \sum_{i=1}^{n} S_{S_i}^2 + S_{S_o}^2$$

where n equals the total number of inflow streams (S_i) and S_T is 1 SD of the total error. Measurement errors in water chemistry and hydrology are or are assumed independent; thus, covariance terms are not included. Variance of the nutrient loading term (a product) can be approximated by (Mood et al. 1974):

$$\text{var}(X, Y) = \bar{X}^2 * S_Y^2 + \bar{Y}^2 * S_X^2 + S_Y^2 * S_X^2$$

This is equivalent to adding the square of the percent errors for both hydrologic and chemical measurements. The estimated variance and SD for

TP, NH_4-N, NO_3-N, TKN and DOC monthly streamloads and bulk deposition loads (a product) are:

$$S^2_{S_i}, S^2_U, S^2_{S_o} = \text{e.g., } U_i^2\,[0.35^2 + 0.10^2 + (0.35^2 * 0.010^2)]$$

$$\therefore S_{S_i}, S_U, S^2_{S_o} = \pm 37\%$$

$$S^2_P = P^2\,[0.21^2 + 0.10^2 + (0.21^2 * .10^2)]$$

$$\therefore S_P = \pm 23\%$$

The variance in TN, TON, TIN loads were determined by summing the variance associated with the parameters used to calculate each. Variance for monthly loads for each component were summed to produce annual values.

Results

Annual budgets

Annual TP and TN retention varied among the five wetlands, ranging from -0.030 to $0.051\,g\,m^{-2}\,yr^{-1}$, and -0.44 to $0.56\,g\,m^{-2}\,yr^{-1}$ for TP and TN respectively (Table 1). The estimated budget uncertainties were largely due to the relatively large inputs and outputs and were equal to or greater than retention estimates (Table 1). The Paint 1 beaver pond was an exception; there was a reported average annual TP retention of -44% ($-0.030 \pm 0.015\,g\,m^{-2}\,yr^{-1}$). The two conifer swamps and the two beaver ponds showed a similar pattern of retaining TIN and exporting an equivalent amount of TON. However, in the beaver ponds only NO_3^--N was retained ($\geqslant 45\%$); NH_4^+-N output was either equal to or greater than input. Both NO_3^--N and NH_4^+-N were retained (RT $> 40\%$) in the two large conifer swamps. The conifer swamps were a major source of TON ($> 50\%$) and DOC ($> 90\%$). As a result of its small size and relatively large input and output of nutrients, the sedge fen had little effect on nutrient fluxes.

Phosphorus and nitrogen retention in the Paint 1 beaver pond, Pt1–bp, and sedge fen, Pt1–sw, were relatively consistent between 1982/83 and 1983/84 water years. Although there is some yearly variation in the % retention, the differences are small compared to the budget uncertainties. The annual percent retention for TP was -43% ($0.026\,g\,m^{-2}$) and -45% ($0.033\,g\,m^{-2}$) and was -4% ($0.15\,g\,m^{-2}$) and -20% ($0.73\,g\,m^{-2}$) for TN in Pt1–bp. In Paint 1 sedge fen the percent retention was 24% ($0.070\,g\,m^{-2}$)

Table 1. Annual nutrient retention ($g\,m^{-2}\,yr^{-1}$) and water budget ($m\,yr^{-1}$) for the 5 study wetlands, (± 1 SD) budget uncertainties for the Harp 4 and Plastic 1 wetlands were measured for 1982–83; budgets and uncertainties for Paint 1 wetlands represent the average of 1982/83 and 1983/84. Negative values for net RT or % RT represents inputs < outputs, positive values represent inputs > outputs.

Budget component	Nutrient ($g\,m^{-2}\,yr^{-1}$)							Water ($m\,yr^{-1}$)
	TP	TN	TON	TIN	NH_4^+-N	NO_3^--N	DOC	
				Harp 4 Beaver Bond				
Stream inputs	0.114 ± 0.013	2.27 ± 0.241	1.72 ± 0.236	0.557 ± 0.057	0.242 ± 0.023	0.316 ± 0.052	50.8 ± 6.0	5.97 ± 0.64
Ungauged	0.004 ± 0.001	0.151 ± 0.018	0.124 ± 0.018	0.027 ± 0.003	0.002 ± 0.001	0.025 ± 0.003	2.02 ± 0.24	1.20 ± 0.162
Precipitation	0.027 ± 0.002	0.979 ± 0.046	0.149 ± 0.037	0.83 ± 0.040	0.315 ± 0.021	0.515 ± 0.034	0.822 ± 0.06	0.992 ± 0.062
Total inputs	0.145 ± 0.013	3.41 ± 0.25	1.99 ± 0.24	1.41 ± 0.070	0.559 ± 0.031	0.856 ± 0.062	53.6 ± 6.0	8.16 ± 0.66
Total outputs	0.135 ± 0.019	3.26 ± 0.36	2.31 ± 0.35	0.947 ± 0.099	0.552 ± 0.063	0.395 ± 0.077	51.4 ± 6.9	7.64 ± 1.03
Net RT	0.010 ± 0.023	0.14 ± 0.044	−0.32 ± 0.42	0.467 ± 0.122	0.007 ± 0.070	0.461 ± 0.099	2.2 ± 9.1	0.52 ± 1.22
% RT	7 ± 16	4 ± 13	−16 ± 21	33 ± 21	1 ± 13	54 ± 12	4 ± 17	6 ± 15
				Paint 1 Beaver Pond				
Stream inputs	0.022 ± 0.003	1.27 ± 0.16	0.859 ± 0.11	0.403 ± 0.114	0.018 ± 0.001	0.397 ± 0.114	19.3 ± 2.2	5.73 ± 0.55
Ungauged	0.021 ± 0.003	1.25 ± 0.12	0.801 ± 0.12	0.446 ± 0.041	0.019 ± 0.002	0.427 ± 0.041	18.5 ± 2.5	5.12 ± 0.65
Precipitation	0.023 ± 0.002	0.994 ± 0.05	0.140 ± 0.041	0.854 ± 0.044	0.339 ± 0.023	0.516 ± 0.037	0.750 ± 0.05	1.12 ± 0.074
Total inputs	0.066 ± 0.005	3.50 ± 0.21	1.80 ± 0.17	1.70 ± 0.13	0.376 ± 0.023	1.34 ± 0.127	38.6 ± 3.3	12.0 ± 0.85
Total outputs	0.095 ± 0.014	3.94 ± 0.53	2.52 ± 0.49	1.43 ± 0.27	0.694 ± 0.13	0.734 ± 0.241	45.6 ± 6.1	11.5 ± 1.45
Net RT	−0.030 ± 0.015	−0.44 ± 0.57	−0.72 ± 0.52	0.27 ± 0.30	−0.318 ± 0.13	0.61 ± 0.272	−7.0 ± 6.9	0.48 ± 1.7
% RT	− 44 ± 23	− 14 ± 16	− 40 ± 29	16 ± 18	− 85 ± 36	45 ± 20	−18 ± 18	4 ± 1.14
				Plastic 1 Conifer Swamp				
Stream inputs	0.008 ± 0.001	0.313 ± 0.028	0.297 ± 0.028	0.016 ± 0.001	0.004 ± 0.001	0.011 ± 0.001	10.4 ± 1.2	2.30 ± 0.24
Ungauged	0.006 ± 0.001	0.222 ± 0.025	0.211 ± 0.025	0.011 ± 0.001	0.005 ± 0.001	0.006 ± 0.001	5.55 ± 0.80	2.63 ± 0.37
Precipitation	0.027 ± 0.002	0.979 ± 0.046	0.149 ± 0.037	0.830 ± 0.040	0.315 ± 0.021	0.515 ± 0.034	0.822 ± 0.06	0.992 ± 0.062
Total inputs	0.042 ± 0.002	1.51 ± 0.059	0.657 ± 0.053	0.857 ± 0.040	0.324 ± 0.021	0.533 ± 0.034	16.8 ± 1.4	5.92 ± 0.44
Total outputs	0.042 ± 0.005	1.50 ± 0.16	1.33 ± 0.16	0.175 ± 0.019	0.017 ± 0.002	0.158 ± 0.019	50.3 ± 6.2	5.48 ± 0.89
Net RT	< 0.001 ± 0.006	0.012 ± 0.17	−0.67 ± 0.17	0.682 ± 0.044	0.307 ± 0.021	0.374 ± 0.039	−33.5 ± 6.4	0.44 ± 0.99
% RT	< 1 ± 14	1 ± 11	−102 ± 26	+80 ± 5	95 ± 6	70 ± 7	−199 ± 38	7 ± 17

Harp 4 Conifer Swamp								
Stream inputs	0.069 ± 0.011	2.02 ± 0.26	1.14 ± 0.18	0.884 ± 0.18	0.015 ± 0.002	0.870 ± 0.178	27.2 ± 3.7	6.35 ± 0.92
Ungauged	0.015 ± 0.002	0.629 ± 0.073	0.517 ± 0.073	0.112 ± 0.013	0.009 ± 0.001	0.102 ± 0.013	8.90 ± 1.2	4.99 ± 0.70
Precipitation	0.027 ± 0.002	0.979 ± 0.046	0.149 ± 0.037	0.830 ± 0.040	0.315 ± 0.021	0.515 ± 0.034	0.822 ± 0.06	0.992 ± 0.062
Total inputs	0.111 ± 0.011	3.63 ± 0.26	1.81 ± 0.20	1.83 ± 0.19	0.339 ± 0.021	1.49 ± 0.182	36.9 ± 3.9	12.3 ± 1.12
Total outputs	0.094 ± 0.014	3.64 ± 0.38	2.75 ± 0.34	0.89 ± 0.18	0.042 ± 0.009	0.85 ± 0.178	71.4 ± 9.8	11.8 ± 1.6
Net RT	0.017 ± 0.018	−0.01 ± 0.46	−0.94 ± 0.39	0.94 ± 0.26	0.297 ± 0.023	0.64 ± 0.255	−34.5 ± 10.5	0.52 ± 1.97
% RT	15 ± 16	<1 ± 13	−52 ± 22	−51 ± 14	88 ± 7	43 ± 17	−94 ± 28	8 ± 16
Paint 1 Sedge Fen								
Stream inputs	0.204 ± 0.031	7.06 ± 0.84	4.86 ± 0.61	2.31 ± 0.58	0.041 ± 0.006	2.27 ± 0.58	117. ± 17.6	24.9 ± 3.3
Ungauged	0.071 ± 0.011	2.45 ± 0.33	1.53 ± 0.25	0.801 ± 0.22	0.014 ± 0.002	0.787 ± 0.22	40.7 ± 5.9	8.60 ± 1.2
Precipitation	0.023 ± 0.001	0.994 ± 0.05	0.140 ± 0.041	0.854 ± 0.045	0.339 ± 0.023	0.516 ± 0.037	0.750 ± 0.05	1.12 ± 0.074
Total inputs	0.297 ± 0.033	10.5 ± 0.90	6.53 ± 0.66	3.96 ± 0.62	0.393 ± 0.025	3.57 ± 0.62	159.00 ± 18.6	34.6 ± 3.5
Total outputs	0.247 ± 0.039	9.94 ± 1.3	6.98 ± 1.0	2.96 ± 1.1	0.260 ± 0.032	2.70 ± 0.69	168.000 ± 25.5	34.1 ± 4.4
Net RT	0.051 ± 0.051	0.56 ± 1.6	−0.45 ± 1.2	1.00 ± 1.06	0.133 ± 0.041	0.870 ± 1.06	−9.00 ± 31.6	0.52 ± 5.6
% RT	17 ± 17	5 ± 15	−7 ± 18	25 ± 27	34 ± 10	24 ± 30	−6 ± 20	2 ± 16

and 10% (0.028 g m^{-2}) for TP and 11% (1.15 g m^{-2}) and −1% (−0.015 g m^{-2}) for TN, respectively. There are two exceptions. In 1983/84, 168% (0.57 g m^{-2}) of the NH_4^--N was released from Pt1–bp compared to 16% (0.07 g m^{-2}) in 1982/83. The release of NH_4^--N balanced the annual TIN budget (−11% RT) for 1982/83 and resulted in an export of TN (−20% RT). In Pt1–sw the TIN was retained as either NO_3^--N or NH_4^+-N depending on the year.

Monthly patterns

Although there were large errors associated with some monthly retention estimates, marked seasonal differences in retention of the nutrients measured were observed in all of the study wetlands. Representative monthly

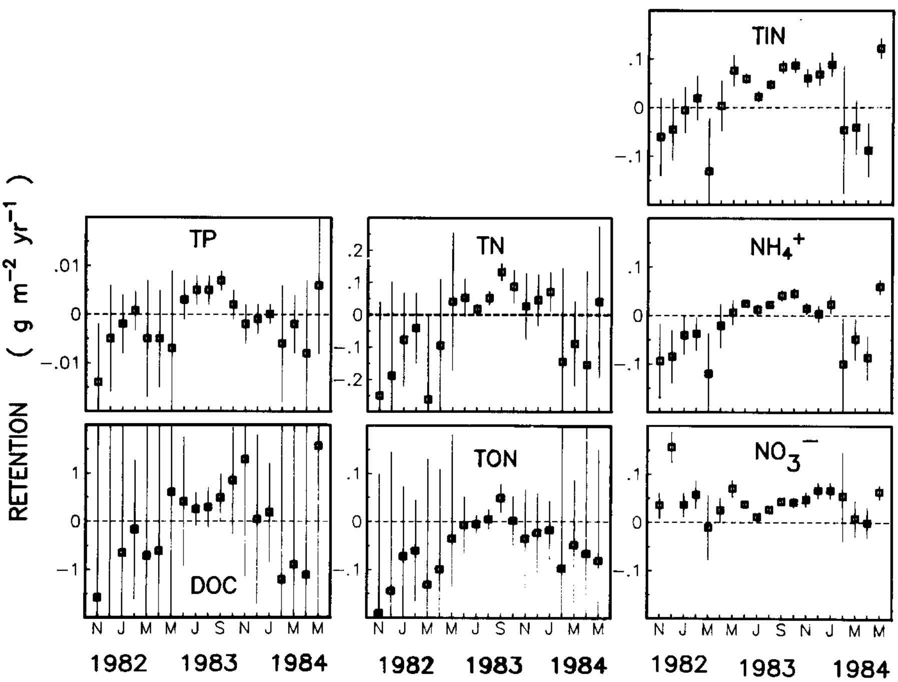

Fig. 2. Monthly nutrient retention ± 1 SD (g.m^{-2}.yr^{-1}) of the Harp 4 beaver pond, November 1982 to May 1984. TP = total phosphorus, TN = total nitrogen, TON = total organic nitrogen, TIN = total inorganic nitrogen, NH_4^+ = ammonium-nitrogen, NO_3^- = nitrate-nitrogen, DOC = dissolved organic carbon. A negative (−ve) represents inputs < outputs and a positive (+ve) represents input > outputs. Note the different y-axis for TP, DOC and TN.

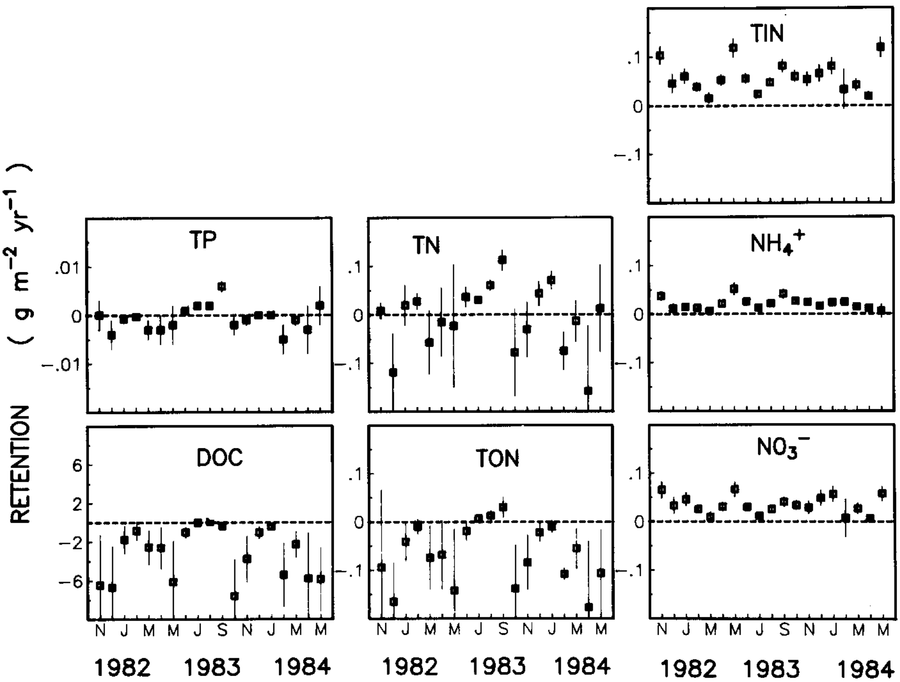

Fig. 3. Monthly nutrient retention ± 1 SD $(g.m^{-2}.yr^{-1})$ of the Plastic 1 conifer swamp, November 1982 to May 1984. Labels as in Fig. 2. Note the different y-axis for TP and DOC.

budgets are shown in Figs. 2 and 3. Nitrate was retained throughout the year. Retention of TP, TON and TN typically occurred in all the wetlands during two or three summer months followed by significant export during a few months in winter and spring. Similar trends were observed for DOC in the beaver ponds. An exception was apparent for the two conifer swamps that showed significant exports of DOC throughout the year. No seasonal pattern was observed for TIN in the conifer swamps because of the net retention of NO_3^--N and NH_4^+-N throughout the year. The marked seasonal trends in NH_4^+-N retention of the beaver ponds correspond to seasonal trends in TIN. The observed differences in annual budgets between the wetlands and among nutrients are reflected in the monthly budgets (Figs. 2 and 3). Annual budgets are primarily a function of the net difference between summer retention and winter and spring export. The annual variation observed in the Paint 1 beaver pond and fen is not as apparent in the monthly budgets as similar seasonal trends were observed for all nutrients in both years.

Discussion

1. Hydrologic budgets

Accurate estimates of hydrologic budgets are essential for reliable nutrient budgets (Winter 1981). However, only precipitation input was independently measured and there may be bias and/or errors associated with prorating unit areal runoff for all the stream and unchannelized inputs. The assumption that areal runoff is uniform over large areas is not new (i.e., Pentland 1968) and has been suggested for use in small catchment studies (Naiman 1982; Fisher & Likens 1973). Runoff within the catchment is directly or indirectly influenced by a number of factors such as soil and rock type, soil depth and vegetation (Ward 1975). The catchments in this study are quite uniform in those respects, so it is reasonable to believe that annual runoff is relatively uniform. Scheider et al. (1983) reported that within a number of subcatchments of varying size near Dorset, Ontario, the variability in total annual discharge was a function of drainage basin area, explaining 98.5 to 99.3% of the variance in total annual discharge.

Over shorter periods (e.g., monthly), the assumption of equal runoff per unit area throughout the catchment may not hold. Because of the very shallow till, small size, and circular shape of Plastic 1 and Paint 1 catchments the hydrologic response of the entire catchment is probably similar to that of the tributaries (Ward 1975). However, in Harp 4 recharge of deeper soils near the basin outlet may occur during the fall and spring following increased precipitation or snowmelt. This seasonal recharge would lead to an underestimation of streamflow in the upper reaches of the catchment. However, the bias may be minimized because stream volumes would probably be underestimated due to the limited recharge areas in the upper reaches. During the summer months discharge originating from the deeper till, ponds and swamps can result in an overestimation of input volume. This overestimate is evident in that several of the small streams regularly become dry during the summer while the outflow still discharges water. However, this represents a minimal contribution to the annual water budget (< 2%). During the summer precipitation inputs dominate the monthly budgets, reducing the effect of such bias.

Groundwater, evapotranspiration and water storage may contribute significantly to the hydrologic budget. Unfortunately, these components were not measured. Although wetlands are often areas of regional groundwater discharge water balance estimates of Harp 4, Plastic 1 and Paint 1 subcatchments based on studies by Scheider et al. (1984), McDonnell & Taylor (1987), Shibitani (1988) and other data (Scheider et al. 1983) suggest there is negligible loss via deep groundwater flow. Most wetlands in this area occupy bedrock depressions. Infiltrating meltwater or precipitation is perched on the largely impermeable bedrock and can result in considerable saturated-unsaturated subsurface (transient groundwater) flow from areas adjacent to the wetlands (McDonnell & Taylor 1987; Shibitani 1988). However, because of the paucity of surficial deposits the hydrologic response of these areas can be approximated by assuming equal runoff for all portions of the subcatchment. The relatively small volume of the wetlands restricts the holding capacity to 2 or 3% of the annual outflow. Although there are large errors associated with determining evapotranspiration (ET) by the budget approach, the values (0.44 to 0.52 m yr^{-1}) are similar to calculated potential evapotranspiration estimates for 1982/83 and 1983/84 (0.467 and 0.476 m yr^{-1}) using the method of Thornthwaite (1948). Due to the errors associated with each component of the water budget, estimates of ET closer than $\pm$15% to the true value are unlikely (Winter 1981).

2. *Nutrient budgets*

Annual budgets

The nutrient budgets suggest that none of the wetlands in this study were very efficient at retaining TP and TN (% RT < $\pm$ 20%), with no rates being significantly greater than estimated budget uncertainties. Within these systems TN was transformed from inorganic forms into organic forms. Kemp & Day (1984) and Elder (1985) found that a Louisiana swamp and floodplain wetlands, respectively, acted as transformers by removing inorganic N and P and exporting organic forms. In contrast, van der Valk et al. (1979) concluded that all types of wetlands act as N and P sinks. These different results may result from seasonal patterns of retention. Many of the wetlands act as only seasonal sinks and large amounts of nutrients are exported during other times of the year (Sloey et al. 1978; Shih et al. 1979; Klopatek 1978; Lee et al. 1975; Kuenzler et al. 1980). From laboratory studies, Richardson (1985) concluded that the annual TP and possibly TN retention capacities of freshwater wetlands are very low. Although Yarbro (1983) reported a net retention of TP in Creeping swamp, North Carolina, the swamp retained particulate and reactive P and exported unreactive (organic) P. Evidence also exists that catchments with wetlands export more organic material than those not containing wetlands (Mulholland & Kuenzler 1979).

Complete annual nutrient budgets for north temperate wetlands are rare. Hemond (1980, 1983) and Verry & Timmons (1982) reported that all forms of N and P were retained in two northern wetlands. Hemond showed that the annual flux of N was small compared to the total N stored in Thoreau's bog. About 69% of the NO_3^--N, 20% of the NH_4^+-N and almost all of the organic N entering the bog was retained. However, Thoreau's bog differs in that it is functionally ombrotrophic. Verry & Timmons (1982) reported a 50% TN and 61% TP retention in a conifer bog in Minnesota. Less organic N (36%) was retained than NO_3^- (86%) and NH_4^+ (69%). No difference in annual retention was found between organic P and orthophosphate.

There are few comparable data for beaver ponds. Maret et al. (1987) found that suspended solids (SS), TP, NO_3^- and TKN accumulated in a Wyoming beaver pond. They attributed TP and TKN retention to trapping of particulates in the pond. This trapping contrasts with the streams on the Canadian Shield that have very low particulate loads even during peak spring runoff (P.J. Dillon, unpub. studies). However, the former study was conducted only during the ice free period and the budgets were calculated from data collected during the last half of spring and the summer. During this time the beaver ponds in the Dorset study area retained all of the nutrients measured. Naiman & Melillo (1984) reported that N was accumulated in the sediments of beaver ponds in a subarctic region of Quebec. However, no difference between the input and output of N was observed; nitrogen fixation was estimated as equivalent to $\sim 5\%$ of the input and this process was assumed to account for the accumulation of N in the sediments of the beaver ponds (Francis et al. 1985). Again, their study was only conducted during the ice-free season. Seasonal variation, inherent uncertainties and the possibility that denitrification rates exceeded 5% of the inputs make extrapolation of these results to an annual budget tenuous.

Seasonal budgets

Seasonal nutrient retention patterns observed in this study are similar to those reported for other different wetland types (van der Valk et al. 1979; Lee et al. 1975; Klopatek 1978; Sloey et al. 1978; Kuenzler et al. 1980; Driscoll et al. 1987). Nutrient retention during the growing season can be attributed to decreased water replacement rates, and increased biotic assimilation and sedimentation. Lower temperatures, reduced biotic assimilation and anoxic conditions under ice cover coupled with high runoff during late fall and spring result in most of the spring nutrient load and that stored during the previous summer being flushed from the wetland (King 1985).

Verry & Timmons (1982) did not observe such seasonal variations in N and P retention in a conifer bog, but found that retention was usually higher during the spring. Runoff in the conifer bog examined does not occur as overland flow. Hydrologic conditions (low hydraulic conductivity, low storage capacity of the surface peat) in the conifer swamps and sedge fen of this study are conducive to saturated overland flow (McDonnell & Taylor 1987). This results in reduced interaction of runoff water and its high nutrient load with the peat during periods of high runoff.

Errors and unmeasured components of the budgets

Uncertainties in nutrient budgets are a function of uncertainties in the hydrologic data and in nutrient concentration measurements. Errors associated with sampling stream and precipitation chemistry are probably minimal (Shih et al. 1979). Both the nutrient and hydrologic loads showed similar temporal patterns, suggesting that uncertainties associated with the budgets are primarily influenced by uncertainties in the water budget (Scheider et al. 1979). This is probably a safe assumption if the portion of the input load originating from ungauged (unchannelized) areas is small and its nutrient concentrations approximate those of adjacent streams (La Baugh & Winter 1984). NH_4^+-N, NO_3^--N and DOC concentrations from lysimeter pits in selected areas of Harp 4 and Plastic 1 subcatchments are generally low and comparable to concentrations observed in waters draining any of the subcatchments upstream of any wetlands (B. LaZerte, unpub. studies) that were used to estimate areal nutrient loads by proration. TP and TKN concentrations were not measured in the lysimeters but are generally low in groundwater as they are in waters draining the upland subcatchments. Estimated loads from the ungauged areas were never the major source of nutrients, generally contributing less than 20% of the total inputs.

Seasonal biases associated with prorating streamflows may contribute to the uncertainties in monthly nutrient budgets. However, the processes described earlier tend to result in underestimation of stream outflow from wetlands during the spring when a net export of nutrients was observed. Conversely, underestimating stream inputs during the summer would have a minimal effect because of the relatively small loadings at this time and the dominance of precipitation inputs.

Although potentially important components of the nutrient budgets were not measured, one can estimate the relative magnitude of some of these components. Allochthonous inputs may represent a major input of nutrients, particularly during the autumn. The forest canopy in the conifer swamps would restrict the lateral movement of forest litter. Using a maximum average litter input of 354 g dry weight . meter wooded shoreline^{-1} . yr^{-1} (Hanlon 1981) and nutrient content of 0.065% TP and 0.987% TN (Lozano 1987), it appears that leaf litter probably supplies little nutrient input, generally representing $< 5\%$ of the total inputs.

Insect emergence probably represents a very small net loss from the beaver ponds. Due to the paucity of standing water within the swamps during the growing season, such losses are insignificant in relation to other components. Naiman & Melillo (1984) reported that insect emergence ($0.1\,g\,N\,m^{-2}$) was not an important component of beaver pond N budgets in Quebec. Using an empirical relationship expressing insect dry weight as a function of TP input (Davies 1980) and TP content of insects (Vallentyne 1952), it was estimated that insect loss represents less than 1% of the TP inputs of Pt1-bp and HP4-bp.

Beaver activity can have a significant influence on a stream ecosystem. Naiman & Melillo (1984) estimated that beavers imported $10.3\,g\,N\,m^{-2}\,yr^{-1}$ into ponds in Quebec. However, it is difficult to estimate the amount of activity in a particular pond because of the periodic removal by trapping and natural predation. A large portion of the woody debris entering a pond is incorporated in the dam structure or the sediments (Naiman et al. 1986). Anoxic conditions in the sediments reduce decomposition rates and nutrients bound in wood remain unavailable for biotic uptake and are subsequently lost to the system. Core samples taken from Harp 4 beaver pond sediments reveal large amounts of undecomposed wood and litter (Devito unpubl. data). Therefore, the amount and quality of this organic material may be of little importance to the nutrient chemistry of waters flowing through beaver ponds.

Nitrogen fixation and denitrification may be important processes in wetlands (Waughman & Bellamy 1980). Small-scale heterogeneity and inherent analytical problems make it difficult to extrapolate and to make quantitative influences of the importance of these processes. However, the relatively good balance between input and output of TN suggests that these processes are probably small compared to hydrologic inputs and outputs. Estimated rates of denitrification for bogs and swamps range from < 0.1 to $2.8\,g\,N\,m^{-2}\,yr^{-1}$ which are similar to estimated rates of nitrogen fixation, $0.07\text{–}2.8\,g\,N\,m^{-2}\,y^{-1}$ (Waugham & Bellamy 1980; Dierberg & Brezonik 1983; Hemond 1983; Engler & Patrick 1974). Nitrogen-fixation by the symbiotic actinomycete in *Alnus* root modules, however, can be very effective in fixing large quantities of nitrogen (Dickinson 1983). Francis et al. (1985) estimated that nitrogen fixation contributed $0.4\text{–}5.1\,g\,N\,m^{-2}\,y^{-1}$ to beaver pond sediments in a subarctic region of the Canadian Shield. They did not estimate denitrification rates. Rates of denitrification in stream sediments range from $0.2\text{–}14.0\,g\,N\,m^{-2}\,y^{-1}$ (Sain et al. 1977, Chatarpaul et al. 1980; Smith & Delaune 1983). Thus, nitrogen fixation and denitrification can be comparable in magnitude to the amounts of TN retained in the wetlands studied here (Table 1).

Conclusions

The importance of various wetlands to the P and N fluxes in small headwater streams on the Canadian Shield was evaluated. The low measured % retention of TP and TN in these Precambrian shield wetlands does not support the hypothesis that freshwater wetlands are major nutrient sinks. Although 4 of 5 of the wetlands retained some of the TP and TN, and the absolute amount could have been significant, the study wetlands had little effect on the TP and TN content of water flowing through them. The dominant processes occurring resulted in the transformation of inorganic forms to organic forms, at least in the case of nitrogen. These systems may function to reduce the export of inorganic N, and possibly P, to downstream aquatic ecosystems.

Some variability in P and N retention was observed between the different wetlands studied. Several more years of data are needed to characterize properly the temporal variation of these ecosystems. Long-term sequestration of the nutrients by soil adsorption and peat and organic sediment accumulation may occur but at a rate too low to be detected in one year due to the inherent uncertainties of the budgets.

Studies conducted entirely during the "ice free" season are common in the literature; however, significant output of TP and TN occurred during the winter "ice cover" period. Collection of data on a year-round basis is essential for determing annual nutrient retention efficiencies.

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References

Bayley SE, Zoltek J, Hermann AJ, Dolan TJ & Tortora L (1985) Experimental manipulation of nutrient and water in a freshwater marsh: Effects on biomass, decomposition, and nutrient accumulation. Limnol. Oceanogr. 30: 500–512

Carter V, Bedinger MS, Novitski RP & Wilen W (1979) Water resources and wetlands. In: Greeson PE, Clark JR & Clark JE (Eds) *Wetland Functions and Values: The State of Our Understanding* (pp. 344–376) Am. Water. Res. Ass., Minneapolis, MN

Chatarpaul L, Robinson JB & Kaushik NK (1980) Effects of tubificid worms on denitrification and nitrification in stream sediment. Can. J. Fish. Aquat. Sci. 37: 656–663

Davies IJ (1980) Relationships between dipteran emergence and phytoplankton production in the Experimental Lakes Area, northwestern Ontario. Can. J. Fish. Aquat. Sci. 37: 523–533

Dickinson CH (1983) Micro-organisms in peatlands. In: Gore AJP (Ed) Ecosystems of the World 4A; Mire: Swamp, Bog, Fen and Moor (pp 225–245) Elsevier Sci. NY

Dierberg FE & Brezonik PL (1983) Nitrogen and phosphorous mass balances in natural and sewage-enriched cypress domes. J. Appl. Ecol. 20: 323–337

Dillon PJ, Lusis M, Reid RA & Yap D (1988) Ten-year trends in sulphate, nitrate and hydrogen deposition in central Ontario. Atmos. Environ. 22: 901–905

Driscoll CT, Wyskowski BJ, Cosentini CC & Smith ME (1987) Processes regulating temporal and longitudinal variations in the chemistry of a low order woodland stream in the Adirondack region of New York. Biogeochem. 3: 225–242

Elder JF (1985) Nitrogen and phosphorous speciation and flux in a large Florida river-wetland system. Water Resour. Res. 21: 724–732

Engler RM & Patrick WH (1974) Nitrate removal from floodwater overlaying flooded soils and sediments. J. Environ. Qual. 3: 409–413

Fisher SG & Likens GE (1973) Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecol. Monogr. 43: 421–439

Francis MM, Naiman RJ & Melillo JM (1985) Nitrogen fixation in subarctic streams influenced by beaver (*Castor canadensis*). Hydrobiol. 121: 193–202

Gosselink JG & Turner RE (1978) The role of hydrology in freshwater wetland ecosystems. In: Good RE, Wightman DF & Simpson RL (Eds) *Freshwater Wetlands* (pp 63–78) Academic Press, NY

Hanlon RDG (1981) Allochthonous plant litter as a source of organic material in an oligotrophic lake (Llyn Frongoch). Hydrobiol. 80: 257–261

Hemond HF (1980) Biogeochemistry of Thoreau's bog, Concord, Massachusetts. Ecol. Monogr. 50: 507–526

Hemond HF (1983) The nitrogen budget of Thoreau's bog. Ecology. 64: 99–109

Jefferies DS & Snyder WR (1983) Geology and geochemistry of the Muskoka-Haliburton study area. Ont. Min. Envir. Data Report. DR 83/2. DRC, Dorset, Ontario

Kadlec JA (1986) Input-output nutrient budgets for small diked marshes. Can. J. Fish. Aquat. Sci. 43: 2009–2016

Kemp GP & Day JW Jr (1984) Nutrient dynamics in a Louisiana swamp receiving agricultural runoff. In: Ewel KC & Odum HT (Eds) *Cypress Swamps* (pp 286–293) University Presses of Florida, Gainsville

King DL (1985) Nutrient cycling in wetlands and possible effects of water level. In: Prinee HH & D'Itri FM (Eds) *Coastal Wetlands* (pp 69–86) Lewis Publ., Chelsea, MI

Klopatek JM (1978) Nutrient dynamics of freshwater riverine marshes and the role of emergent macrophyte. In: Good RE, Wightman DF & Simpson RL (Eds) *Freshwater Wetlands* (pp 195–216) Academic Press, NY

Kuenzler EJ, Mulholland PJ, Yarbro LA & Smock LA (1980) Distributions and budgets of carbon, phosphorous, iron and manganese in a flood plain swamp ecosystem. Water Resour. Res. Inst. North Carolina Report No. 157, Raleigh, NC., 234 p

LaBaugh JW & Winter TC (1984) The impact of uncertainties in hydrologic measurements in phosphorous budgets and empirical models for two Colorado reservoirs. Limnol. Oceanogr. 29: 322–339

Lee GF, Bengly E & Amundson R (1975) Effects of marshes on water quality. In: Hasler AD (Ed) Coupling of Land and Water Systems (pp 105–127) Springer-Verlag, NY

Locke BA & de Grosbois E (1986) Meterological data base for the Muskoka-Haliburton area. Ont. Min. Envir. Data Report DR 86. DRC, Dorset, Ontario

Locke BA & Scott LD (1986) Studies of lakes and watersheds in Muskoka-Haliburton, Ontario: Methodology (1976–1985). Ont. Min. Envir. Data Report DR 86/4. DRC, Dorset, Ontario

Lozano FC (1987) Total amount of elemental content of litter fall on the Harp 4 and Plastic 1 biogeochemical sites. Unpublished data report, Ont. Min. Environ., BGC Report

McDonnell JJ & Taylor CH (1987) Surface and subsurface water contributions during snowmelt in a small Precambrian Shield watershed, Muskoka, Ontario. Atmosphere-Ocean 25: 251–266

Maret JJ, Parker M & Fanny TE (1987) The effect of beaver ponds on the nonpoint source water quality of a stream in southwestern Wyoming. Wat. Res. 21: 263–268

Mood AM, Graybill FA & Boes DC (1974) *Introduction to the theory of statistics* (3rd ed) McGraw-Hill, New York, 504 p

Mulholland PJ & Kuenzler EJ (1979) Organic carbon export from upland and forested wetland watersheds. Limnol. Oceanogr. 24: 960–966

Naiman RJ (1982) Characteristics of sediment and organic carbon export from pristine boreal forest watersheds. Can. J. Fish. Aquat. Sci. 39: 1699–1718

Naiman RJ & Melillo JM (1984) Nitrogen budget of a subarctic stream altered by beaver (*Castor canadensis*). Oecologia 62: 150–155

Naiman RJ, Melillo JM & Hobbie JE (1986) Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). Ecology 67: 1254–1269

Ontario Ministry of the Environment (1981) Handbook of Analytical Methods for Environmental Samples. Ont. Min. Envir., Rexdale, Ontario. 246 p

Pentland RL (1968) Runoff characteristics in the Great Lakes basin. Proc. 11th Conf. Great Lakes Res., 1968: 36. Int. Assoc. Great Lakes Res

Peterjohn WT & Correll DJ (1984) Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest. Ecology 65: 1466–1475

Peverly JH (1982) Stream transport of nutrients through a wetland. J. Environ. Qual. 11: 38–43

Richardson CJ (1985) Mechanisms controlling phosphorous retention capacity in freshwater wetlands. Science 228: 1424–1427

Sain P, Robinson JB, Stammers WN, Kaushik NK & Whitely HR (1977) A laboratory study on the role of stream sediments in nitrogen loss from water. J. Environ. Qual. 6: 274–278

Scheider WA, Moss JJ & Dillon PJ (1979) Measurement and uses of hydraulic and nutrient budgets. In: Lake Restoration: Proceed. Nat. Conf., Aug. 22–24, 1978, Minneapolis, Minnesota (pp 77–83) U.S. EPA 440/5–79–001, Washington

Scheider WA, Cox CM & Scott LD (1983) Hydrological data for lakes and watersheds in the Muskoka-Haliburton study area (1976–1980). Ont. Min. Envir. Data Report Dr 83/6. DRC, Dorset, Ontario

Scheider WA, Logan LA, Belore HS & MacRae CR (1984) Simulation of snowmelt and streamflow during spring runoff in Muskoka-Haliburton, Ontario. Proc. Can. Hydrol. Symp. No. 15, 10–12 June 1984, Quebec (pp 359–380) Quebec

Shibitani R (1988) Meltwater processes and runoff mechanisms in a small Precambrian shield watershed during snowmelt. M.Sc. thesis, Trent University, Peterborough, Ontario. 194 p

Shih SF, Federico AC, Milleson JF & Rosen M (1979) Sampling programs for using upland marsh to improve water quality. Am. Soc. Agric. Engin. (Transact.) 22: 828–833

Sloey WE, Spangler FL & Fetter CW (1978) Management of freshwater wetlands for nutrient assimilation. In: Good RE, Wightman DF & Simpson RL (Eds) *Freshwater Wetlands* (pp 321–340) Academic Press, NY

Smith CG & Delaune RD (1983) Nitrogen loss from freshwater and saline estuarine sediments. J. Environ. Qual. 12: 514–518

Thornthwaite CW (1948) An approach toward a rational classification of climate. Georg. Rev. 33: 55–94

Vallentyne JR (1952) Insect removal of nitrogen and phosphorous compounds from lakes. Ecology 33: 573–577

Van der Valk AG, Davis CB, Barker JL & Beer CE (1979) Natural freshwater wetlands as nitrogen and phosphorous traps for land runoff. In: Greeson PE, Clark JR & Clark JE (Eds) *Wetlands Functions and Values: The State of Our Understanding*, (pp 457–467) Am. Water Resour. Assoc., Minneapolis, MN

Verry ES & Timmons DR (1982) Waterborne nutrient flow through an upland-peatland watershed in Minnesota. Ecology 63: 1456–1467

Ward RC (1975) *Principles of Hydrology*. McGraw-Hill, London, UK, pp 367

Waughman GJ & Bellamy DJ (1980) Nitrogen fixation and the nitrogen balance in peatland ecosystems. Ecology 61: 1185–1198

Winter TC (1981) Uncertainties in estimating the water balance of lakes. Water Res. Bull. 17: 82–115

Yarbro LA (1983) The influence of hydrologic variations on phosphorous cycling and retention in a swamp stream ecosystem. In: Fontaine TD & Bartell SM (Eds) *Dynamics of Logic Ecosystem* (pp 223–245) Ann Arbor Sc., Ann Arbor, MI.