WATER RESOURCES RESEARCH, VOL. 29, NO. 8, PAGES 2675–2685, AUGUST 1993

The Influence of Hydrologic Conditions and Peat Oxia on the Phosphorus and Nitrogen Dynamics of a Conifer Swamp

KEVIN J. DEVITO[1]

Watershed Ecosystems Program, Trent University, Peterborough, Ontario, Canada

PETER J. DILLON

Dorset Research Centre, Ontario Ministry of the Environment, Dorset, Canada

A mass balance approach was used to determine the factors influencing phosphorus and nitrogen dynamics in wetlands common to headwater catchments of the Precambrian Shield. The relationships of runoff, water level, water temperature, and anoxia to the annual and seasonal total phosphorus (TP) and total nitrogen (TN) retentions of a headwater *Sphagnum*-conifer swamp during 1987–1988 were examined. Annual retentions of TP (4%) and TN (10%) were low in the swamp. On an annual basis, inputs exceeded outputs of total reactive P, NO_3-N, and NH_4-N and outputs exceeded inputs of total unreactive P and total organic N. Seasonal trends in P and N retention were inversely correlated with runoff. Positive monthly retention coincided with low runoff and increased biotic assimilation during the growing season. Water table drawdown during the summer was associated with peat aeration and increased levels of P and N in surface and pore water. High levels of P and N in the swamp surface water during the fall and winter were coupled with increased runoff, saturated overland flow, and potentially low biotic assimilation resulting in a net release of TP and TN. Large flow through of waterborne inputs and flushing of regenerated P and N occurred during peak snowmelt runoff resulting in low annual retention.

INTRODUCTION

Phosphorus (P) and nitrogen (N) export from headwater catchments is an important source of nutrients to downstream surface waters [*Schindler et al.*, 1976]. Sedge fens and conifer swamps are typical of central Ontario wetlands occupying small, headwater basins of the low boreal region of the Precambrian Shield [*Zoltai and Pollett*, 1983]. Such wetlands often are situated at or near the interface between the terrestrial and aquatic ecosystems and may have a large influence on the hydrologic and nutrient dynamics of these catchments [*Hill*, 1991; *Pierson and Taylor*, 1985].

Despite their importance, few data related to P and N dynamics of wetlands on the Precambrian Shield exist. The available information suggests that wetlands in this region exhibit variable nutrient retention efficiencies. *Devito et al.* [1989] reported low total phosphorus (TP) and total nitrogen (TN) retention in a number of headwater wetlands in central Ontario. *Devito et al.* [1989] measured a net retention of inorganic N and a net release of organic N, but no analysis of the forms of P were reported. *Verry and Timmons* [1982] and *Urban and Eisenreich* [1988] measured net retention of N and P in a forested Minnesota bog. *Bayley et al.* [1987] reported net retention of nitrate in a *Sphagnum* peatland in northwestern Ontario, but TN was not reported.

Seasonal variations in P and N retention in a number of wetlands on the Precambrian Shield were described by *Devito et al.* [1989]. Annual retention of TP and TN within the wetlands was the difference between positive retention during the "ice free" season and negative retention during winter and spring. Seasonal dynamics have been reported in other wetlands with export of nutrients occurring only during certain times of the year [*Elder*, 1985]. This suggests that nutrient flux and transformation may be controlled by seasonal variations in hydrologic fluctuations and/or temperature-related biotic assimilation.

There is evidence that hydrologic and biogeochemical processes influence nutrient export and cycling in wetlands. Water acts as a vehicle for export, and the loss of dissolved and particulate substances has been related to the magnitude of runoff, water retention time and water flow pathways in both aquatic and terrestrial ecosystems [*Hill*, 1991; *Klein*, 1981; *Richardson and Marshall*, 1986]. The hydrologic mobility of P and N may be controlled by homeostatic processes in the peat or surface water which may either limit or enhance the transformation and mobility of nutrients in solution [*Richardson and Marshall*, 1986; *Bowden*, 1987; *Hill*, 1988]. Anoxic environments in saturated sediments are important sites for the transformation and retention of P and N in wetlands [*Gorham et al.*, 1984]. Knowledge of the interaction of hydrology, peat redox, and homeostatic processes and how these vary seasonally is necessary to develop reliable generalizations about the role of small wetlands in the nutrient dynamics in headwater catchments.

We examine the influences of runoff magnitude and water table fluctuation and peat redox processes on phosphorus and nitrogen dynamics in a *Sphagnum*-conifer swamp. This quantitative information is needed to generalize about the role of wetlands in nutrient transport and retention in small headwater Precambrian catchments. The magnitude of runoff, water residence time, and water level fluctuations of the swamp were examined in relation to annual and seasonal patterns of TP and TN export and retention. Physical and chemical parameters and nutrient concentrations of water in

[1]Now at Department of Geography, York University, North York, Ontario, Canada.

Paper number 93WR00622.
0043-1397/93/93WR-00622$05.00

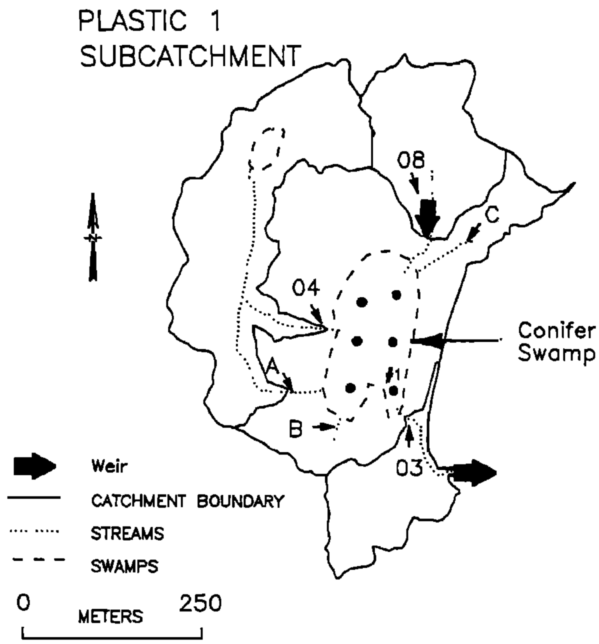

Fig. 1. Plastic Lake subcatchment 1 showing the location of stream sampling locations (numbers and letters), conifer swamp (Pc1-sw), and location of swamp water sampling sites (solid circles).

the swamp were measured through the 1987/1988 year to determine the relationship between redox potential and the form and availability of P and N and its influence on annual and seasonal retention of these nutrients.

STUDY AREA

The conifer swamp (Pc1-sw) is in Plastic Lake subcatchment 1 (45°11'N, 78°50'W), central Ontario. The mean annual January and July air temperatures are −11.0° and 17.7°C, respectively. The area receives 900–1100 mm yr^{-1} of precipitation with 240–300 mm falling as snow. Each month during the period of snow cover some precipitation falls as rain. The long-term annual runoff is 400–600 mm yr^{-1}. A more detailed description of the climate, physiography, geology, and geochemistry of the area have been reported by *LaZerte and Dillon* [1984], *Devito et al.* [1989], *Scheider et al.* [1983], and *Wels and Devito* [1989].

The peat deposits (0.5–5.0 m of peat), overlaying shallow layers of clay and sand, occupy a bedrock depression in the center of the subcatchment (Figure 1). Well-decomposed peat extends to within 20–30 cm of surface. The bulk density of the top 20 cm of peat in the depressions ranges from 0.02 to 0.11 g/cm^3, and the top 30 cm of the mounds 0.00 (hollow spaces) to 0.09 g/cm^3. The swamp is forested primarily with white cedar (*Thuja occidentalis*) and black spruce (*Picea mariana*) with lesser amounts of balsam fir (*Abies balsamifer*), white pine (*Pinus strobus*), *Larix laricina*, birch (*Betula* spp.), and maple (*Acer* spp.). An understory of *Alnus* spp. and black alder (*Ilex verticillata*) exists, with shrubs dominating in the open areas. There is a well-defined ground layer of *Sphagnum*. A mound-depression microtopography exists, with pools of standing water present well into the growing season.

Four intermittent channelized inflows enter the swamp (Figure 1). Pc1-08 and Pc1-C drain small, primarily conifer forest upland microcatchments. Pc1-04 and Pc1-A originate from a small bog and flow through moderately sloped, conifer-forested uplands. A large portion of the watershed (9.9 ha) consisting of moderately sloping, conifer-forested uplands contributes unchannelized inputs. The outlet, Pc1-03, is an ephemeral stream originating at the southeast corner of the swamp. The depth of overburden surrounding the swamp ranges from zero to about 1 m.

METHODS

Precipitation depths and air temperature data were obtained from meteorological stations located within 1 km of the wetland [*Locke and de Grosbois*, 1986]. Stream discharge at the mouth of Pc1 catchment and at Pc1-08 subcatchment has been continuously monitored at 90° V notch weirs [*Locke and Scott*, 1986]. Instantaneous discharges of the other inflow streams were measured at least once a week, but more frequently (often daily) during peak flow. Mean daily discharge was calculated by linear integration of instantaneous discharge measurements [*Scheider et al.*, 1979]. Discharge at the swamp outflow and ungauged runoff from adjacent uplands were estimated by prorating unit area runoff at the mouth of Pc1 and Pc1-08, respectively. Water levels in Pc1 conifer swamp were monitored daily to weekly in six locations, the frequency determined according to discharge (Figure 1). Surface water velocities within the swamp were determined by timing the velocity of a small float.

Precipitation, stream, and swamp water sampling were carried out as described by *Locke and Scott* [1986]. Prior to the 1987/1988 water year, water samples were collected one to three times per week depending on the time of year. During the 1987/1988 water year, water samples were collected three to seven times a week depending on runoff. Subsurface water was sampled from wells at sites 1–6. Initially, tubing was inserted vertically 20–30 cm into the *Sphagnum* and peat. Pore water was drawn up by suction with a syringe. This method greatly reduced the amount of water that could be sampled. By July 1987 the sampler was inserted into polyvinyl chloride wells, which were inserted 0.5 m into the peat, and water was removed from the bottom of the well. The standpipes had holes cut in the sides extending from 0.20 to 0.50 m below the surface of the *Sphagnum* peat mat. To determine spatial variability, sites 2–5 were sampled approximately monthly.

Total phosphorus (TP), total Kjeldahl nitrogen (TKN), ammonium-nitrogen (NH_4-N), nitrate/nitrite nitrogen (NO_3-N), and chloride (Cl) were determined as outlined by the *Ontario Ministry of the Environment* [1981]. Total reactive phosphorus was determined as outlined by *Stainton et al.* [1977]. The platinum/calomel electrode used for determining oxidative reduction potential (ORP) was standardized with Zobell solution [*Zobell*, 1946]. The calomel electrode potential (EM) was converted to the standard hydrogen potential (EH) and corrected for temperature (T) using the equation of *Skoog and West* [1976], where $EH = EM + 223 + 0.76T$ (°C). Total organic nitrogen (TON) was calculated as TKN − NH_4, total unreactive P (TUP) as TP − TRP, and total nitrogen (TN) as TKN + NO_3.

TABLE 1. Seasonal and Annual Water and Chloride Balance for Plastic 1 Conifer Swamp for the 1987/1988 Hydrologic Year

	Input			Output		Evapotranspiration	
	Streamflow	Ungauged Runoff	Precipitation	Streamflow	Change in Storage	Balance (In − Out)	Computed From *Thornthwaite* [1948]
				Water, mm			
Summer	9 ± 1	38 ± 11	182 ± 22	40 ± 7	−220 ± 110	409 ± 113	275
Fall	82 ± 6	202 ± 53	235 ± 30	217 ± 33	+213 ± 107	89 ± 127	100
Winter	280 ± 13	719 ± 143	301 ± 37	1082 ± 127	−15 ± 7	233 ± 195	0
Spring	924 ± 49	1651 ± 370	205 ± 25	2973 ± 420	−11 ± 6	−182 ± 562	86
Annual	1295 ± 51	2610 ± 400	923 ± 58	4312 ± 440	−33 ± 17	549 ± 600	461
				Chloride, mg/m²			
Summer	<0.01 ± <0.01	0.01 ± 0.01	0.03 ± <0.01	0.03 ± 0.01	···	0.01 ± 0.01	
Fall	0.08 ± 0.01	0.26 ± 0.09	0.05 ± 0.01	0.28 ± 0.07	···	0.11 ± 0.11	
Winter	0.19 ± 0.01	0.65 ± 0.24	0.08 ± 0.01	0.95 ± 0.19	···	−0.03 ± 0.31	
Spring	0.42 ± 0.03	0.83 ± 0.30	0.04 ± 0.01	1.36 ± 0.31	···	−0.07 ± 0.43	
Annual	0.69 ± 0.03	1.75 ± 0.39	0.20 ± 0.02	2.62 ± 0.37	···	0.02 ± 0.54	

Values are plus or minus one standard deviation. A negative balance represents inputs are less than outputs, and a positive value represents inputs are greater than outputs.

Water and Nutrient Budgets

A general water budget equation for the swamp is

$$P + U_i + \sum^{n} S_i - \mathrm{ET} - S_o \pm \Delta W = 0 \pm e \qquad (1)$$

All runoff from the base of each microcatchment was assumed to be streamflow. Inputs include stream inflows (S_i), precipitation depth (P) and ungauged runoff (U_i). Both subsurface and diffuse surface flow from ungauged areas adjacent to the pond were combined into ungauged runoff. Outputs include outflow (S_o), evapotranspiration (ET) and change in water storage (W). The inputs should balance the outputs plus or minus measurement error (e). In determining water storage the flooded area of the wetland was assumed to be constant with depth. For change in volume below the peat surface a specific yield of 0.5 was assumed. The top 20 cm of peat have a bulk density of <0.10 g/cm³. Peat with bulk densities <0.09 g/cm³ has been reported to have specific yields >0.45 [*Boelter and Verry*, 1977]. Potential evapotranspiration (PET) was estimated from *Thornthwaite*'s [1948] equation. Deep groundwater inputs and outputs are negligible (K. J. Devito, unpublished data, 1992).

Waterborne nutrient retention (RT) was calculated from inputs which include bulk atmospheric deposition (P_i), stream inflow (S_i), and unchannelized or ungauged inflows (U_i). Outputs are via stream outflow (S_o):

$$P_i + \sum^{n} S_i + U_i - S_o = \mathrm{RT} \pm e \qquad (2)$$

Wet precipitation and dry deposition are incorporated into P_i. Gas fluxes (e.g., denitrification) and weathering inputs are not included; thus this study measures only the waterborne nutrient budgets.

Atmospheric deposition (mass per square meter) was calculated as described by *Locke and de Grosbois* [1986]. Reactive phosphorus measurements in bulk deposition were previously determined to be 34% of the TP deposition [*Dillon and Reid*, 1981].

Stream load was determined by integrating the estimated daily average discharge (liters per second) over time and multiplying the total volume of water by the nutrient concentration at the midpoint of the time interval [*Scheider et al.*, 1979]. Nutrient loads from adjacent ungauged areas were determined from the mean monthly, volume-weighted concentration of nearby upland streams multiplied by the prorated monthly runoff volume. Annual budgets were determined by addition of the monthly budgets for the hydrologic year June 1 to May 31. Seasonal budgets were determined by addition of the months June–August (summer), September–November (fall), December–February (winter), and March–May (spring).

Absolute retention (RT) was calculated as RT = (total input − total output)/(swamp area); percent retention (%RT) as %RT = ((total input − total output)/total inputs) × 100.

Error Estimates

The variance of water and chemical budgets was calculated from the sum of squares error [*Winter*, 1981]:

$$S_T^2 = S_P^2 + S_U^2 + \sum^{n} S_{si}^2 + S_E^2 + S_{SO}^2 + S_{\Delta W}^2 \qquad (3)$$

where n equals the number of inflow streams (S_i) and S_T is the standard deviation of the total monthly water budget. To obtain S_T^2, total monthly water volumes were multiplied by their associated fractional error (CV) and then squared and summed. The variance of all products in this study was approximated as [*Mood et al.*, 1974]:

$$\mathrm{Var}\,(X,\ Y) \simeq u_x^2\ \mathrm{Var}\,(Y) + u_y^2\ \mathrm{Var}\,(X) + \mathrm{Var}\,(Y)\ \mathrm{Var}\,(X) \qquad (4)$$

Calculation of standard deviation estimates and measured or literature estimates of CVs associated with analytical and sampling error to determining budget inputs and outputs are outlined by *Devito* [1989].

RESULTS

Water and Waterborne Nutrient Budgets

Annual inputs and outputs of water and chloride for 1987/1988 roughly balanced using only runoff and precipitation components (Table 1). Estimated ET by budget difference was 20% greater than PET estimates. On an annual basis, the major input was runoff. Precipitation contributed

TABLE 2. Plastic 1 Conifer Swamp Phosphorus Input, Output, and Retention for the 1987/1988 Hydrologic Year

Phosphorus Form	Input, mg P m^{-2}: Streamflow	Input: Ungauged Runoff	Input: Precipitation	Input: Total	Output in Streamflow, mg P m^{-2}	Retention: Absolute (In − Out), mg P m^{-2}	Retention: Relative, %
			Total Reactive Phosphorus				
Summer	<0.1 ± <0.1	<0.1 ± <0.1	1.8 ± 0.7	1.8 ± 0.7	0.1 ± <0.1	1.7 ± 0.7	94
Fall	0.1 ± <0.1	0.2 ± 0.1	1.2 ± 0.4	1.5 ± 0.5	0.2 ± 0.1	1.3 ± 0.5	87
Winter	0.3 ± <0.1	0.7 ± 0.4	0.9 ± 0.3	1.9 ± 0.5	1.1 ± 0.2	0.8 ± 0.5	42
Spring	0.7 ± 0.1	1.2 ± 0.8	1.5 ± 0.5	3.4 ± 0.9	2.6 ± 0.5	0.8 ± 1.0	24
Annual	1.1 ± 0.1	2.1 ± 0.8	5.4 ± 1.0	8.6 ± 1.3	4.0 ± 0.6	4.6 ± 1.4	53
			Total Unreactive Phosphorus				
Summer	<0.1 ± <0.1	0.1 ± <0.1	3.9 ± 1.0	4.0 ± 1.0	0.6 ± 0.1	3.4 ± 1.0	85
Fall	0.3 ± <0.1	0.9 ± 0.5	2.6 ± 0.7	3.8 ± 0.8	1.5 ± 0.3	2.3 ± 0.9	61
Winter	0.6 ± 0.1	1.6 ± 1.3	1.9 ± 0.5	4.1 ± 1.4	5.6 ± 0.9	−1.5 ± 1.7	−37
Spring	2.5 ± 0.3	3.4 ± 3.1	3.1 ± 0.8	9.0 ± 3.2	16.4 ± 2.8	−7.4 ± 4.2	−82
Annual	3.4 ± 0.3	6.0 ± 3.4	11.5 ± 1.6	20.9 ± 3.8	24.1 ± 2.9	−3.2 ± 4.8	−15
			Total Phosphorus				
Summer	<0.1 ± <0.1	0.1 ± <0.1	5.7 ± 0.8	5.8 ± 0.8	0.6 ± 0.1	5.2 ± 0.8	90
Fall	0.4 ± <0.1	1.0 ± 0.5	3.8 ± 0.5	5.2 ± 0.7	1.8 ± 0.3	3.4 ± 0.8	65
Winter	0.8 ± 0.1	2.3 ± 1.3	2.7 ± 0.4	5.8 ± 1.3	6.7 ± 0.8	−0.9 ± 1.6	−16
Spring	3.1 ± 0.3	4.8 ± 3.0	4.5 ± 0.6	12.4 ± 3.1	19.0 ± 2.7	−6.6 ± 4.1	−53
Annual	4.3 ± 0.3	8.2 ± 3.3	16.7 ± 1.2	29.2 ± 3.5	28.1 ± 2.9	1.1 ± 4.5	4

Values are estimates plus or minus one standard deviation.

<20%. ET and change in storage were minor components representing ≤10 and <1% of the total outputs, respectively. The relative contribution of each budget component varied seasonally. Positive retention of water and Cl occurred during the summer and winter, and negative retention occurred during the spring (Table 1). Precipitation, ET, and change in storage were dominant components of the summer budget. Runoff increased in importance and represented the major input and output during the spring months.

In 1987/1988, annual retentions of TP and TN were low with absolute retentions less than the budget uncertainties (Tables 2 and 3). The swamp transformed N and P by retaining TRP (53%), NH_4-N (89%), and NO_3-N (51%) with a concomitant release of organic N (−79%) and unreactive P (−15%).

Seasonal trends in nutrient retention were observed in Pc1-sw (Tables 2 and 3). TUP, TP, and TN were retained during the summer and released during the winter and spring. A negative retention of TON was observed throughout much of the year. TON was retained only during the summer when outflows were low or ceased. TRP, NH_4-N, and NO_3-N were retained throughout the year, but lower absolute and relative retention occurred during the spring.

The absolute input and output of nutrients varied seasonally (Table 4). The majority of the runoff and flux of TP and TN occurred during the winter and early spring and was primarily confined to only a few rain and snowmelt events. Ninety-four percent of the runoff and greater than 60% of N and P inputs and 85% of the outputs occurred from December 1, 1987, to May 31, 1988. During April 1988, 23–28% of the annual inputs and 38–47% of the annual outputs of TP and TN occurred.

Swamp Hydrology

The outflow hydrograph and water table (WT) elevation from March 1987 to May 1988 are shown in Figure 2. There was no outflow during the summer, and peak discharge occurred during snowmelt in March or April. Discharge peaks in late fall and winter were a result of snowmelt associated with rain, where much of the accumulated snow pack was lost.

Water levels varied seasonally in response to rainfall, evapotranspiration, and upland runoff, with peaks in water level coinciding with peak outflow (Figure 2). The water level relative to the surface appeared to follow the elevation of the surface peat, and the depth of standing water above the peat surface was similar at each sample site [*Devito*, 1989; also unpublished data, 1987, 1988]. The surface peat of the entire swamp was saturated with 10–15 cm of water from October to June. The water level fell below the surface from late June to late October, reaching a maximum depth of 45 cm in September 1987. The water level responded rapidly to increases in upland runoff with up to 40 cm of standing water during peak snowmelt.

Assuming maximum storage of 35 cm, the nutrient flushing rate (swamp volume/outflow volume) for 1987/1988 averaged 30 days over the year (Table 4). The flushing rate of nutrients varied seasonally with discharge, being 247 days for summer/fall and 16 days for winter/spring. During peak spring melt, April 7, 1988, the flushing rate was less than 1 day. An average residence time of 2 days was determined by LiBr tracing in Pc1-sw during the recession of the 1987 snowmelt [*Wels and Devito*, 1989]. The outflow discharge at the time of the tracer experiment was about one third (15–20 L/s) that of peak discharges (50–60 L/s).

The LiBr tracing suggests that movement of water through the swamp is an integration of surface flow via various pathways and subsurface flow through shallow peat [*Wels and Devito*, 1989]. Although lateral dispersion of waters from the Pc1-08 tributary occurred, it was limited, and water preferentially flowed along the east side (lagg) of the swamp. During peak snowmelt, movement of surface water was

TABLE 3. Plastic 1 Conifer Swamp Waterborne Nitrogen Input, Output, and Retention for the 1987/1988 Hydrologic Year

Nitrogen Form	Input, g N m^{-2}				Output in Streamflow, g N m^{-2}	Retention	
	Streamflow	Ungauged Runoff	Precipitation	Total		Absolute (In − Out), g N m^{-2}	Relative, %
			NH_4-N				
Summer	<0.01 ± 0.01	<0.01 ± 0.01	0.07 ± 0.01	0.07 ± 0.01	0.00	0.07 ± 0.01	100
Fall	<0.01 ± <0.01	<0.01 ± <0.01	0.09 ± 0.01	0.09 ± 0.01	<0.01 ± <0.01	0.09 ± 0.01	99
Winter	<0.01 ± <0.01	<0.01 ± <0.01	0.09 ± 0.01	0.09 ± 0.01	0.01 ± <0.01	0.08 ± 0.01	89
Spring	0.01 ± <0.01	0.01 ± <0.01	0.10 ± 0.01	0.12 ± 0.01	0.03 ± 0.02	0.09 ± 0.02	75
Annual	0.01 ± 0.01	0.01 ± 0.01	0.35 ± 0.02	0.37 ± 0.02	0.04 ± 0.02	0.33 ± 0.03	89
			NO_3-N				
Summer	<0.01 ± <0.01	<0.01 ± <0.01	0.09 ± 0.01	0.09 ± 0.01	<0.01 ± <0.01	0.09 ± 0.01	100
Fall	<0.01 ± <0.01	0.01 ± 0.01	0.15 ± 0.02	0.16 ± 0.02	0.08 ± 0.01	0.08 ± 0.02	50
Winter	<0.01 ± <0.01	0.01 ± <0.01	0.20 ± 0.02	0.21 ± 0.02	0.10 ± 0.01	0.11 ± 0.03	52
Spring	0.01 ± <0.01	0.03 ± 0.02	0.14 ± 0.02	0.18 ± 0.03	0.13 ± 0.06	0.05 ± 0.07	28
Annual	0.01 ± 0.01	0.05 ± 0.02	0.58 ± 0.04	0.64 ± 0.04	0.31 ± 0.07	0.33 ± 0.08	51
			Total Organic Nitrogen				
Summer	<0.01 ± <0.01	<0.01 ± <0.01	0.06 ± 0.02	0.06 ± 0.02	0.02 ± <0.01	0.04 ± 0.02	67
Fall	0.01 ± <0.01	0.03 ± 0.01	0.02 ± 0.02	0.06 ± 0.02	0.10 ± 0.02	−0.04 ± 0.03	−67
Winter	0.04 ± <0.01	0.10 ± 0.04	0.03 ± 0.02	0.17 ± 0.05	0.31 ± 0.04	−0.14 ± 0.06	−82
Spring	0.10 ± 0.01	0.20 ± 0.10	0.04 ± 0.02	0.34 ± 0.11	0.68 ± 0.09	−0.34 ± 0.14	−100
Annual	0.15 ± 0.01	0.33 ± 0.11	0.15 ± 0.04	0.63 ± 0.12	1.11 ± 0.10	−0.48 ± 0.16	−76
			Total Nitrogen				
Summer	<0.01 ± <0.01	<0.01 ± <0.01	0.22 ± 0.02	0.22 ± 0.02	0.02 ± <0.01	0.20 ± 0.02	91
Fall	0.01 ± <0.01	0.03 ± 0.01	0.26 ± 0.02	0.30 ± 0.03	0.18 ± 0.02	0.12 ± 0.03	40
Winter	0.04 ± <0.01	0.12 ± 0.04	0.33 ± 0.03	0.49 ± 0.05	0.42 ± 0.04	0.07 ± 0.07	14
Spring	0.12 ± 0.01	0.23 ± 0.11	0.28 ± 0.03	0.63 ± 0.11	0.85 ± 0.11	−0.22 ± 0.16	−35
Annual	0.17 ± 0.01	0.38 ± 0.11	1.09 ± 0.05	1.64 ± 0.13	1.47 ± 0.12	0.17 ± 0.18	10

Values are estimates plus or minus one standard deviation.

visible, primarily at the lagg. Surface flow over ice and through mounds (macropores) was observed. The velocity of surface water passing through the depressions in site 1 was 20 and 24 cm/s on April 5 and 7, 1988, respectively. Surface water velocities exceeding 1 cm/s occurred at all sample sites during the 1987 and 1988 spring melt. *Wels and Devito* [1989] estimated average water velocities of 0.27 cm/s during the recession of 1987 spring melt.

Swamp Chemistry

Temperatures of the surface and interstitial water varied seasonally, with maximum temperature in excess of 20°C in the summer, 1°C in the winter. The temperature of the peat water remained about 1°–2°C warmer than the surface water through the winter and was similar to the surface water during spring melt.

TABLE 4. Runoff, Nutrient Flushing Rate, and Phosphorus and Nitrogen Export and Import From Plastic 1 Conifer Swamp for the 1987/1988 Hydrologic Year

	Period						
	Annual 1987/1988	Summer and Fall	Winter and Spring	April 1988	April 1–10, 1988	Dec. 10–16, 1987	Jan. 31 to Feb. 6, 1988
Number of days	365	183	182	30	10	7	7
Runoff, 10^6 L	95	6 (6%)	89 (94%)	50 (53%)	30 (32%)	6 (6%)	6 (6%)
Nutrient flushing rate, days	30	247	16	5	3	10	9
			Total Phosphorus, g				
Export	617	53 (9%)	564 (91%)	291 (47%)	186 (30%)	33 (5%)	55 (9%)
Import	645	243 (38%)	402 (62%)	181 (28%)	...	...	...
			Total Nitrogen, kg				
Export	32	4 (13%)	28 (88%)	12 (38%)	9 (28%)	2 (6%)	3 (9%)
Import	36	12 (33%)	24 (67%)	8 (23%)	...	...	...

Values in parentheses represent percent of annual total.

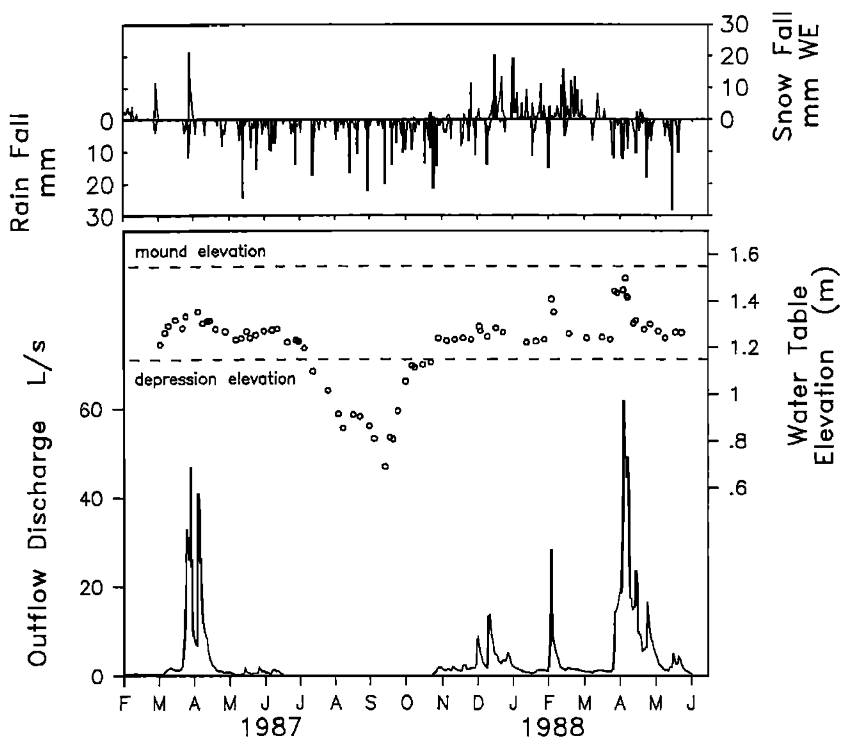

Fig. 2. Daily rain and snowfall depths, swamp outflow discharge, and water level elevation at swamp site 1, for March 1, 1987, to May 31, 1988.

The chemistry of the surface and subsurface (well) water varied with water table fluctuations and runoff through the year. Stratification is apparent in the dissolved oxygen (DO) and ORP profiles (Figure 3). DO concentrations and ORP remained low in peat interstitial water through much of the year. Sporadic increases in ORP and DO occurred through the summer, in association with rainfall events during periods when the peat was exposed to air, and with increased runoff in the fall and during the spring melt. The surface water generally remained oxygenated when significant outflow discharge occurred. DO concentrations dropped to levels below 2 mg/L as surface water fell and stagnated during summer and in late March.

Temporal variations in P and N concentrations and vari-

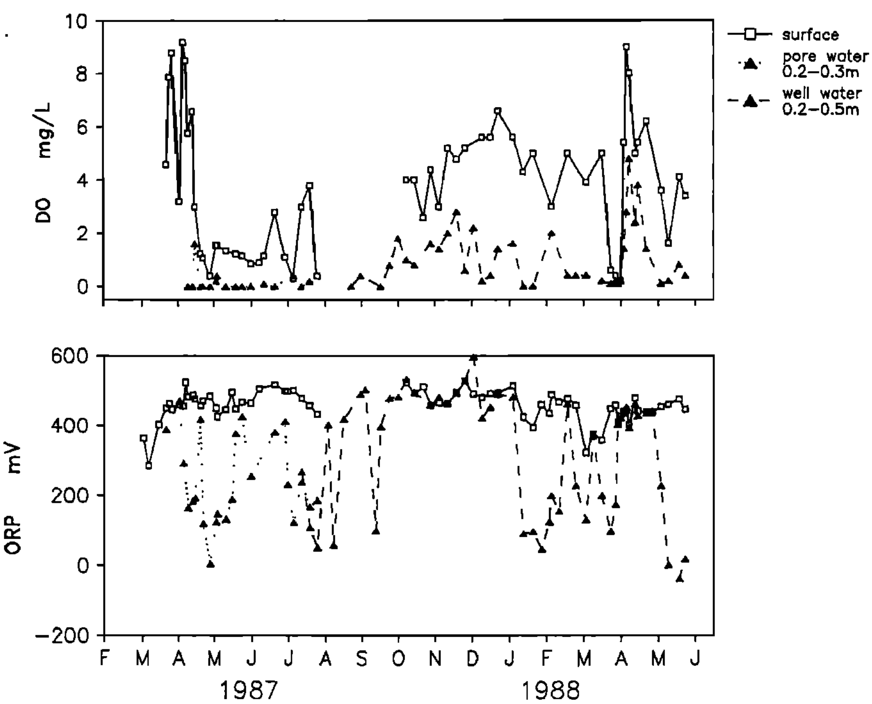

Fig. 3. Temporal variation in (top) dissolved oxygen concentration (DO) and (bottom) oxidative reduction potential (ORP) of surface and peat pore or well water at swamp site 1 for March 1, 1987 to May 31, 1988.

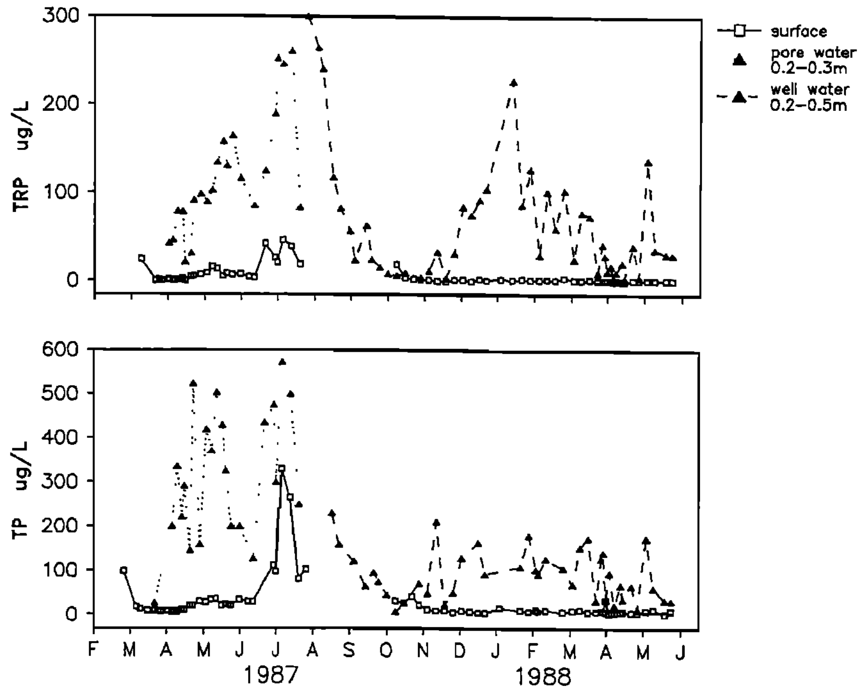

Fig. 4. Temporal variation in (top) total reactive phosphorus (TRP) and (bottom) total phosphorus (TP) of surface and peat pore or well water at swamp site 1 for March 1, 1987 to May 31, 1988.

ation between depths generally followed those observed for temperature, DO, and ORP profiles (Figures 4 and 5). TP and TN concentrations were higher in the interstitial water than the surface. TRP was the dominant form of TP in the well water, and TUP (not shown) was the dominant form in the surface water (Figure 4). TRP and TP concentrations of the peat pore water showed large temporal variability, increasing with reductions in DO during the summer and winter. A large increase in TP and TRP occurred in early summer as the water table dropped below the peat surface. TRP and TP concentrations declined to surface values with a rise in water table and increased runoff during the fall and during spring snowmelt. Surface concentrations of TRP remained near detection limit for most of the year, with some increase in late summer. TP concentrations remained relatively constant through most of the year, with a large increase during the summer, as the water table fell to the peat surface.

TON was the primary form of TN in both the surface and well water (Figure 5). TON in the interstitial and surface water showed similar temporal variations to TP. NH_4-N concentrations increased to about 200–300 μg/L with anoxic conditions during the early summer and winter, with lower concentrations following increased runoff in the fall and spring. Very high NH_4-N concentrations (>1000 μg/L) occurred in the peat pore water as the water table dropped during the summer. The NH_4-N concentration of the surface water remained near detection level for much of the year, as expected with aerobic conditions. A large increase in concentration occurred in early summer and in October as the water table rose to and above the surface. NO_3-N concentrations in the well water were low, with some increase during periods of higher runoff in the fall and spring. NO_3-N concentrations of >500 μg/L occurred during the summer drawdown. Surface water concentrations showed marked seasonal variations. Concentrations remained near detection limit through the summer and increased to >500 μg/L during the fall following the water table drawdown. NO_3-N concentrations remained around 150 μg/L through the winter, with peak concentrations associated with the ascending limb of outflow storm hydrographs.

The concentration of the wetland outflow followed that of the surface water at site 1. The marked seasonal patterns in P and N concentrations observed in the outflow were not observed in the inflows (i.e., Pc1-08). TP, NO_3-N, and TON concentrations of the inflows did not exceed 8, 100, and 200 μg/L, respectively, during the fall.

Monthly Retention in Relation to ORP and Discharge

There is a strong inverse relationship between monthly retention of TP and TN and outflow runoff ($r = -0.91$ and -0.95) for March 1987 to May 1988. The scatter of data in the relationship between monthly TP and TN retention and runoff was relatively small for the years 1984/1985 to 1987/1988 (Figure 6). The relationship is not linear. The decrease in retention with runoff occurs at a greater rate to about 600 mm month^{-1}, with lower rate of change for higher runoff magnitudes. There is a very weak relationship between mean monthly temperature and TP and TN retention ($r = 0.66$ and 0.48). Highly reducing conditions occurred sporadically and, therefore, there appears to be no relationship between TP and TN retention and mean ORP ($r = -0.09$ and -0.17). A significant correlation was observed between TP and TN retention and mean monthly DO concentration ($r = -0.723$ and -0.573). The linear relationship between mean DO and TP and TN retention was primarily due to an observed relationship between mean DO and runoff ($r = 0.635$).

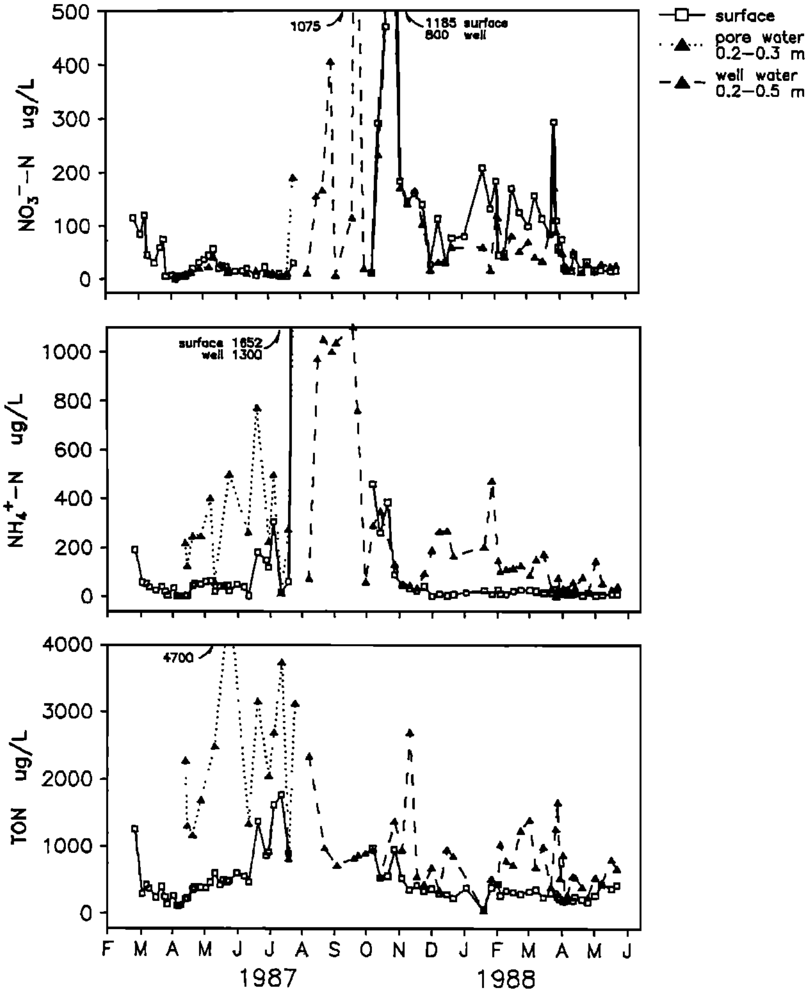

Fig. 5. Temporal variation in (top) nitrate-nitrite nitrogen (NO_3-N), (middle) ammonium nitrogen (NH_4-N), and (bottom) total organic nitrogen (TON) concentrations of surface and peat pore or well water at swamp site 1 for March 1, 1987 to May 31, 1988.

DISCUSSION

Annual Budgets

The results presented here help to clarify the relative importance of conifer swamps to the water chemistry of small headwater streams of the Precambrian Shield. Low annual TP and TN retention in Pc1 swamp is a long-term phenomenon. No significant retention was observed for 5 years (1983/1984 to 1987/1988 [*Devito et al.*, 1989; *Devito*, 1989]). It appears that cycling of N and P within the swamp has reached steady state [*Koerselman et al.*, 1990], or the retention rate may be too low to be detected when compared to the large influxes and effluxes.

The primary role of the conifer swamp is to transform inorganic forms of N and P into organic forms which are subsequently transported downstream. Very low annual retention, and net transformation of inorganic to organic TP and TN have been reported in freshwater wetlands from a wide geographical distribution [*Elder*, 1985; *Hill*, 1991; *Koerselman et al.*, 1990]. This contrasts with the high retention efficiency of P and N in bogs or poor fens which receive little upland runoff and where atmospheric deposition dominates the total inputs [*Hemond*, 1983; *Verry and Timmons*, 1982].

The water volume and chemistry of unchannelized runoff from hillslopes adjacent to the swamp were not measured directly, and uncertainties in ungauged estimates can bias interpretation of budget estimates. Recent analysis of groundwater flow confirms that deep groundwater inputs are minimal. The runoff coefficients for the Pc1-08 subcatchment were the same as the entire Pc1 catchment [*Devito*, 1989]. Using unit area runoff estimates for the ungauged area resulted in good water and Cl balances. The greatest errors would be associated with estimating the chemistry. Concentrations varied between measured sites and are reflected in the relatively high uncertainty of the ungauged estimates. The N chemistry of soil water extracted by lysimeters in the Pc1-08 subcatchment was similar to stream chemistry, particularly during peak runoff when most of the water and nutrient transport occurs (B. LaZerte, unpublished data, 1988). Due to the dominance of precipitation inputs of inorganic nitrogen (>90%), large uncertainties in ungauged inputs have little impact. Estimates of inputs from ungauged areas represented 30, 28, 52, and 23% of the TUP, TP, TON, and TN inputs to the swamp, respectively. Doubling the estimated ungauged inputs would result in a rough balance of TUP and TON and a positive retention of TP and TN in

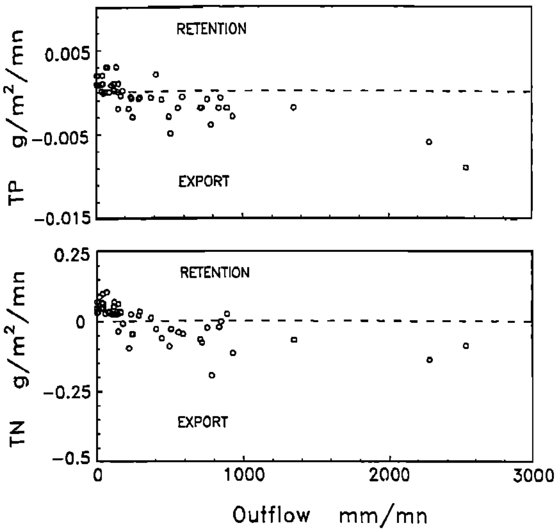

Fig. 6. Monthly total phosphorus (TP) and total nitrogen (TN) retention versus outflow runoff of Plastic 1 swamp from June 1984 to May 1988. All budgets calculated by prorating unit runoff (see text).

excess of budget uncertainties. However, TUP and TON concentrations are low in mineral upland soils. Halving the ungauged inputs would result in the observed net release of TUP and TON and balance of TP and TN.

Factors Influencing Seasonal Nutrient Retention

The seasonal, and thus annual, retentions of P and N in the swamp are controlled by hydrologic variables, particularly runoff magnitude, nutrient flushing rate, the occurrence of saturated overland flow (SOF), and the interaction between hydrologic conditions and nutrient assimilation by vegetation, and regeneration rates of P and N via decomposition and leaching of organic sediments.

Gross export and absolute retention of P and N within Pc1 swamp were controlled by seasonal variations in runoff. Outflow concentrations varied by an order of magnitude at low flow but remained relatively constant with increases in outflow discharge greater than 5 L/s [*Devito*, 1989]. In contrast, discharge varied over 4 orders of magnitude; thus P and N export were directly proportional to stream discharge. NO_3-N was an exception. Elevated NO_3-N concentrations occurred on the ascending limb of hydrograph peaks, and NO_3-N export was also directly related to runoff. Increased gross export of elements as discharge increases has been widely reported [*Klein*, 1981; *Hill*, 1988].

Episodic events are important in the annual retention and transport of P and N in the study swamp. Accumulation of precipitation within the snowpack redistributed precipitation of several months into three hydrologic events in which greater than 40% of the annual P and N inputs and outputs to the swamp occurred. High nutrient flushing rates and potentially high rates of saturation overland flow (SOF) restrict nutrient removal from the water to instantaneous reactions and result in low retention of nutrients. Greater than 50% of the annual water and nutrient yield from temperate and boreal catchments has also been reported to occur during episodic storms or snowmelt [*Pierson and Taylor*, 1985; *Scheider et al.*, 1983; *Schindler et al.*, 1976].

An important consideration is the timing of nutrient cycling processes relative to variations in runoff and nutrient transport. The amount of nutrients assimilated by plants and regenerated from peat often exceeds the amount of nutrients that flow in or out of wetlands [*Bowden*, 1987]. Plant uptake was not measured in Plastic swamp, but uptake of 3 g N m^{-2} yr^{-1} was reported in a black spruce bog in Minnesota [*Urban and Eisenreich*, 1988]. Assuming a P:N ratio of about 1:20, P uptake would be about 0.15 g P m^{-2} yr^{-1}. Estimated uptake rates exceed the annual TN and TP inputs to Plastic swamp. Microbes also rapidly assimilate P and N and may limit the amount of available (nonrefractory) P and N in surface waters [*Richardson and Marshall*, 1986; *Urban and Eisenreich*, 1988]. The low surface concentrations and high retention efficiencies suggest that biotic assimilation controls inorganic P and N retention in the swamp.

High nutrient flushing rates and SOF coupled with low temperatures during the winter and spring result in lower annual (51–89%) retention efficiencies than would be estimated using only growing season estimates (>80%). Periods of high assimilation occur when nutrient transport is low and contribute little to the annual nutrient flux of the swamp. The majority of the annual runoff, inputs, and outputs occurred from late fall to spring when the retention efficiency of inorganic N and P was relatively low. During April there was no net retention of inorganic N and P. Inorganic N and P inputs during April and the two winter storm events ranged from 10 to 60% of integrated annual estimates of potential plant uptake (8 mg N m^{-2} d^{-1} and 0.5 mg P m^{-2} d^{-1}). Seasonal estimates of plant uptake of Shield wetlands are not available, but integrated annual estimates would overestimate actual plant uptake rates during winter and early spring. P and N inputs rates probably exceed plant and microbial uptake during spring melt and storm events when a large portion of annual inputs enter the wetland. In addition, increased water depths and preferential flow along specific channels also occurred during periods of high runoff and nutrient input [*Wels and Devito*, 1989]. The hydrologic conditions in the swamp reduce the interaction of nutrients with peat and biota, further limiting nutrient uptake [*Hill*, 1988].

The efficient annual retention of inorganic N and P was balanced by net export of organic N and P resulting in low annual TN and TP retention. Regeneration of organic P and N within the swamp buffered the outflow TP and TN concentration from dilution by increased runoff, resulting in the direct relationship between TN and TP retention and runoff. Net retention of organic N and P occurred during the summer when evapotranspiration exceeded rainfall in the swamp, causing outflow cessation. Twice as much TON and TUP was removed from the swamp as entered during high runoff in spring. Reductions in concentrations of organic N and P in surface waters and large export during periods of greatest standing water, and surface water velocities suggest that SOF is an important export pathway in Plastic swamp. SOF has been reported to be a major export pathway of elements from other minerotrophic wetlands during peak runoff [*Pierson and Taylor*, 1985; *Kadlec et al.*, 1981].

The probable sources of organic P and N are the sediments and vegetation which represent the largest pools of P and N in most wetlands [*Bowden*, 1987]. Although direct measurements of mineralization were not made, increased concentrations of dissolved organic carbon are associated with organic decomposition and were observed with increases in surface N and P concentrations during the summer and winter [*Devito*, 1989]. Nitrogen and P mineralization can occur in both aerobic and anaerobic sediments [*Urban and Eisenreich*, 1988; *Richardson and Marshall*, 1986] as well as during the winter [*Hill and Shackleton*, 1989], providing a source of N and P to outflow. Translocation of nutrient from sediments and plant senescence during the fall may account for some of the increase in surface water concentrations and export of organic N and P [*Bowden*, 1987; *Richardson and Marshall*, 1986].

Anoxic processes associated with increased water levels are important in immobilizing and regenerating nutrients in wetlands [*Gorham et al.*, 1984; *Richardson and Marshall*, 1986]. Elevated concentrations of pore water TRP and NH_4-N suggest anaerobic mineralization is occurring and diffusive flux from deeper peats may be an important source to surface waters. Low NO_3-N concentration in the pore water suggests dissimilatory reduction occurs at depth through much of the year. However, low oxygen tension in the surface water occurred only in late winter and early summer as runoff and water levels decreased and water stagnated in depressions. Although the concentration of TRP, NH_4-N, and TON increased in the surface water, the total flux of P and N during these periods was small relative to the annual fluxes.

Surface water concentrations and relative retention efficiencies of NH_4-N, NO_3-N, and TRP suggest that aerobic processes are important in controlling the hydrologic flux of nutrients in Plastic swamp. During higher runoff and nutrient transport, only a small proportion of the water flowing through the peat makes contact with deeper peats where anoxic conditions persists [*Wels and Devito*, 1989]. Anoxic conditions were not maintained for extended periods in the surface water, as oxygenation of the surface waters occurred periodically throughout the year in association with peak water levels and increased surface water velocities. *Sparling* [1966] reported increases in DO concentration and declines in reduced forms of N in the surface water, to a depth of 20 cm, with increasing flow in a number of wetlands in central Ontario. Dissolved oxygen saturation occurred at surface water velocities of 1 cm/s. Oxygenated surface peats may be common in small valley wetlands which receive large water volume from surrounding hillslopes.

Summer drawdown of the water table, resulting in aeration of the peat, had a large influence on the regeneration and concentration of P and N in the surface water and outflow. There are few data available on the influence of water table fluctuations on mineralization and nutrient dynamics of unperturbed northern peatlands, but peat decomposition is stimulated by the warmer temperatures and aeration of peat following wetland drainage [*Lieffers*, 1988]. Large export of elements following water table drawdown during the summer or drought conditions has been observed in other wetlands [*Bayley et al.*, 1987; *Van dam*, 1988].

The periodicity and amplitude of water table fluctuations are a function of the source and magnitude of water inputs (i.e., precipitation) and vary between wetlands and between years. At Pc1-sw, the annual variations in water table fluctuations were not measured; however, during summers with little precipitation, elevated NO_3-N, TON, TP, and DOC concentrations were observed during the fall when outflow runoff commenced [*LaZerte and Dillon*, 1984; also unpublished data, 1981–1988]. This was not observed following summers with ample precipitation. However, little annual variation in TP and TN retention was observed over the past 5 years [*Devito*, 1989]. It is unclear how important water table drawdown is to the long-term dynamics of P and N in this swamp.

Variations in nutrient retention efficiencies between wetlands reflect differences in the hydrology which determine both the magnitude and rate of nutrient transport as well as influence the biogeochemistry of a system. This work shows that characterizing how biotic and geochemical cycling vary temporally with the magnitude of hydrologic fluctuations in conjunction with a budget approach is needed to develop reliable generalizations of the influence of wetlands on the Precambrian Shield landscape.

Acknowledgments. We thank B. Anthony, A. Bently, D. Elliot, B. Ferguson, and G. Little for help with field and lab work, and the staff at the Dorset Research Centre and Trent University. We thank A. Hill and B. LaZerte and two anonymous reviewer for comments on early drafts of this manuscript. Funding for this research came principally from the Natural Science and Engineering Research Council (NSERC), as a postgraduate scholarship, and as a grant from the Dorset Research Centre, Ontario Ministry of Environment (MOE).

REFERENCES

Bayley, S. E., D. H. Vitt, R. W. Newbury, K. G. Beaty, R. Behr, and C. Miller, Experimental acidification of a *Sphagnum*-dominated peatland: First year results, *Can. J. Fish. Aquat. Sci.*, *44*, 194–205, 1987.

Boelter, D. H., and E. S. Verry, Peatland and water, *Gen. Tech. Rep. NC-31*, 22 pp., Forest Serv., U.S. Dep. of Agric., Washington, D. C., 1977.

Bowden, W. B., The biogeochemistry of nitrogen in freshwater wetlands, *Biogeochemistry*, *4*, 313–348, 1987.

Devito, K. J., Waterborne phosphorus and nitrogen retention in some Precambrian Shield wetlands: Role of hydrology and oxidation-reduction potential, M.Sc. thesis, 256 pp., Trent Univ., Peterborough, Ont., Canada, 1989.

Devito, K. J., P. J. Dillon, and B. D. LaZerte, Phosphorus and nitrogen retention in five Precambrian Shield wetlands, *Biogeochemistry*, *8*, 185–204, 1989.

Dillon, P. J., and R. A. Reid, Input of biologically available phosphorus by precipitation to Precambrian lakes, in *Atmospheric Pollutants in Natural Waters*, edited by S. Eisenreich, pp. 183–198, Butterworth, Stoneham, Mass., 1981.

Elder, J. F., Nitrogen and phosphorus speciation and flux in a large Florida river-wetland system, *Water Resour. Res.*, *21*, 724–732, 1985.

Gorham, E., S. E. Bayley, and D. W. Schindler, Ecological effects of acid deposition upon peatland: A neglected field in "acid-rain" research, *Can. J. Fish. Aquat. Sci.*, *41*, 1256–1268, 1984.

Hemond, H. F., The nitrogen budget of Thoreau's bog, *Ecology*, *64*, 99–109, 1983.

Hill, A. R., Factors influencing nitrate depletion in a rural stream, *Hydrobiologia*, *169*, 111–122, 1988.

Hill, A. R., A ground water nitrogen budget for a headwater swamp in an area of permanent ground water discharge, *Biogeochemistry*, *14*, 209–224, 1991.

Hill, A. R., and M. Shackleton, Soil N mineralization and nitrification in relation to nitrogen solution chemistry in a small forested watershed, *Biogeochemistry*, *8*, 167–184, 1989.

Kadlec, R. H., D. E. Hammer, I.-S. Nam, and J. O. Wilkes, The hydrology of overland flow in wetlands, *Chem. Eng. Commun.*, *9*, 331–344, 1981.

Klein, M., Dissolved material transport—The flushing effect in surface and subsurface flow, *Earth Surf. Processes Landforms*, *6*, 173–178, 1981.

Koerselman, W., S. A. Bakker, and M. Blom, Nitrogen, phosphorus and potassium budgets for two small fens surrounded by heavily fertilized pastures, *J. Ecol.*, *78*, 428–442, 1990.

LaZerte, B. D., and P. J. Dillon, Relative importance of anthropogenic versus natural sources of acidity in lakes and streams of central Ontario, *Can. J. Fish. Aquat. Sci.*, *41*, 1664–1677, 1984.

Lieffers, V. J., *Sphagnum* and cellulose decomposition in drained and natural areas of an Alberta peatland, *Can. J. Soil Sci.*, *68*, 755–761, 1988.

Locke, B. A., and E. de Grosbois, Meteorological data base for the Muskoka-Haliburton area, data report, Ont. Minist. of the Environ., Toronto, 1986.

Locke, B. A., and L. D. Scott, Studies of lakes and watersheds in Muskoka-Haliburton, Ontario: Methodology (1976–1985), *Data Rep. DR 86/4*, Ont. Minist. of the Environ., Toronto, 1986.

Mood, A. M., F. A. Graybill, and D. C. Boes, *Introduction to the Theory of Statistics*, 564 pp., McGraw-Hill, New York, 1974.

Ontario Ministry of the Environment, Outlines of analytical methods, report, 246 pp., Water Res. Branch, Rexdale, 1981.

Pierson, D. C., and C. H. Taylor, Influence of snow cover development and ground freezing on cation loss from a wetland watershed during spring runoff, *Can. J. Fish Aquat. Sci.*, *42*, 1979–1985, 1985.

Richardson, C. J., and P. E. Marshall, Processes controlling movement, storage, and export of phosphorus in a fen peatland, *Ecol. Monogr.*, *56*, 279–302, 1986.

Scheider, W. A., J. J. Moss, and P. J. Dillon, Measurement and uses of hydraulic and nutrient budgets, in Restoration: Proceedings of a National Conference, August 22–24, 1978, Minneapolis, Minnesota, *Rep. EPA 440/5-79-001*, pp. 77–83, Environ. Prot. Agency, Washington, D. C., 1979.

Scheider, W. A., C. M. Cox, and C. D. Scott, Hydrological data for lakes and watersheds in the Muskoka-Haliburton study area (1976–1980), *Data Rep. DR 83/6*, Ont. Minist. of the Environ., Toronto, 1983.

Schindler, D. W., R. W. Newbury, K. G. Beaty, and P. Campbell, Natural water and chemical budgets for a small Precambrian lake basin in central Canada, *J. Fish. Res. Board Can.*, *33*, 2526–2543, 1976.

Skoog, D. A., and D. M. West, *Fundamentals of Analytical Chemistry*, 804 pp., Holt, Rinehart and Winston, New York, 1976.

Sparling, J. H., Studies on the relation between water movement and water chemistry in mires, *Can. J. Bot.*, *44*, 747–758, 1966.

Stainton, M. P., M. J. Capel, and F. A. J. Armstrong, The chemical analysis of fresh water, *Misc. Spec. Publ. 25*, 119 pp., Dep. of Environ., Fish. and Mar. Serv., Winnipeg, Manit., Canada, 1977.

Thornthwaite, C. W., An approach toward a rational classification of climate, *Geogr. Rev.*, *33*, 55–94, 1948.

Urban, N. R., and S. J. Eisenreich, Nitrogen cycling in a forested Minnesota bog, *Can. J. Bot.*, *66*, 435–449, 1988.

Van dam, H., Acidification of three moorland pools in the Netherlands by acid precipitation and extreme drought periods over seven decades, *Freshwater Biol.*, *20*, 157–176, 1988.

Verry, E. S., and D. R. Timmons, Waterborne nutrient flow through an upland-peatland watershed in Minnesota, *Ecology*, *63*, 1456–1467, 1982.

Wels, C., and K. J. Devito, Tracing of flow paths in a conifer swamp, *in* Ontario wetlands: Inertia or momentum, edited by M. J. Bardecki and N. Patterson, report, pp. 293–299, Fed. of Ont. Naturalists, Don Mills, 1989.

Winter, T. C., Uncertainties in estimating the water balance of lakes, *Water Resour. Bull.*, *17*, 82–115, 1981.

Zobell, C. E., Studies on redox potential of marine sediments, *Bull. Am. Assoc. Petrol. Geol.*, *30*, 477–513, 1946.

Zoltai, S. C., and F. C. Pollett, Wetlands in Canada: Their classification, distribution and use, in *Ecosystems of the World*, vol. 4B, *Mires: Swamp, Bog, Fen, and Moor*, edited by A. J. P. Gore, pp. 245–268, Elsevier Science, New York, 1983.

K. J. Devito, Department of Geography, York University, 4700 Keele Street, North York, Ontario, Canada M3J 1P3.

P. J. Dillon, Dorset Research Centre, Ontario Ministry of the Environment, P. O. Box 39, Dorset, Ontario, Canada P0A 1E0.

(Received July 31, 1992;
revised February 2, 1993;
accepted March 10, 1993.)