The effects of gap disturbance on nitrogen cycling and retention in late-successional northern hardwood–hemlock forests

Article *in* Biogeochemistry · March 2008

DOI: 10.1007/s10533-008-9180-0

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SYNTHESIS AND EMERGING IDEAS

The effects of gap disturbance on nitrogen cycling and retention in late-successional northern hardwood–hemlock forests

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Received: 27 June 2007 / Accepted: 9 January 2008

Abstract Late-successional forests in the upper Great Lakes region are susceptible to nitrogen (N) saturation and subsequent nitrate (NO_3^-) leaching loss. Endemic wind disturbances (i.e., treefall gaps) alter tree uptake and soil N dynamics; and, gaps are particular susceptible to NO_3^- leaching loss. Inorganic N was measured throughout two snow-free periods in throughfall, forest floor leachates, and mineral soil leachates in gaps (300–2,000 m^2, 6–9 years old), gap-edges, and closed forest plots in late-successional northern hardwood, hemlock, and northern hardwood–hemlock stands. Differences in forest water inorganic N among gaps, edges, and closed forest plots were consistent across these cover types: NO_3^- inputs in throughfall were significantly greater in undisturbed forest plots compared with gaps and edges; forest floor leachate NO_3^- was significantly greater in gaps compared to edges and closed forest plots; and soil leachate NO_3^- was significantly greater in gaps compared to the closed forest. Significant differences in forest water ammonium and pH were not detected. Compared to suspected N-saturated forests with high soil NO_3^- leaching, undisturbed forest plots in these late-successional forests are not losing NO_3^- (net annual gain of 2.8 kg ha^{-1}) and are likely not N-saturated. Net annual NO_3^- losses were observed in gaps (1.3 kg ha^{-1}) and gap-edges (0.2 kg ha^{-1}), but we suspect these N leaching losses are a result of decreased plant uptake and increased soil N mineralization associated with disturbance, and not N-saturation.

Keywords Forest gap · Forest floor leachate · Nitrate · Soil leachate · Throughfall

Introduction

Biogeochemical cycling in late-successional forests is broadly described by theories such as the “nutrient retention hypothesis” (Vitousek and Reiners 1975; Gorham et al. 1979) and the “nitrogen saturation hypothesis” (Agren and Bosatta 1988; Aber et al. 1989). The “nutrient retention hypothesis” predicts that unpolluted late-successional forests should exhibit minimal biotic nutrient retention relative to that occurring in rapidly growing mid-successional forests. Net ecosystem production is expected to be negligible in these forests; demands on nutrients supplied from the atmosphere or weathering should also be negligible, resulting in little or no overall retention of nutrients. Late-successional forests are viewed as

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nutrient-rich relative to biologic demands and poor at retaining added nutrients (i.e., "leaky"). The "nitrogen (N) saturation hypothesis" recognizes increased anthropogenic N deposition, and is summarized by long-term removal of N limitations on biotic activity with corresponding decreases in N retention capacity. Most temperate forests remain N limited, but in an increasing number of forests, N availability is in excess of N retention (Aber et al. 1995; Dise and Wright 1995; Gundersen et al. 2006). Fenn et al. (1998) combined components from these hypotheses to describe late-successional forest N cycling as follows. As forests age, plant N demand diminishes, allowing N to accumulate in soil and litter. If biotic N demand is low, net N mineralization and nitrification can produce large amounts of leachable nitrate (NO_3^-). Atmospheric N deposition contributes to sustained leaching losses from these forests.

Late-succesional forests are especially important for indicating ecological effects of N-saturation (Hedin et al. 1995). These forests have properties associated with forests prone to N-saturation, such as, low net primary production, low N uptake by trees, high soil N reserves, and low soil C/N ratios (e.g., Van Miegroet et al. 1992). Forests in the upper Great Lakes region have additional characteristics that favor their potential to be N-saturated. These forests have short growing seasons, 90–120 days (Phillips and McCulloch 1972), and much of the total N flux activity can occur during early snowmelt periods (Scharenbroch and Bockheim 2007), both favoring reduced plant N uptake. Wet annual NO_3^- deposition in Houghton County, upper Michigan, USA, (north-central Great Lakes) increased from 7.3 kg ha^{-1} in 1996 to 11.1 kg ha^{-1} in 2005 (NADP 2007); exceeding the N deposition threshold (10 kg N ha^{-1}) for NO_3^- leaching proposed by Gundersen et al. (2006). Nitrogen saturation has been inferred from high levels of NO_3^- leaching in mixed hardwood stands in the nearby Turkey Lakes Watershed in Ontario, Canada (northcentral Great Lakes) (Foster et al. 1989; Van Miegroet et al. 1992).

Endemic wind disturbances are essential in creating the patchiness or the "shifting mosaic" of northern hardwood–hemlock ecosystems of the upper Great Lakes region (Pastor and Broschart 1990; Frelich and Lorimer 1991; Frelich et al. 1993; Davis et al. 1998; Woods 2000). Small, single-tree windthrow gaps in these forests range from 10 s to 100 s m^2 in area and remove 5 to 20% of canopy trees per decade (Tyrrell and Crow 1994; Dahir and Lorimer 1996; Goodburn and Lorimer 1999). Catastrophic blowdowns (killing >90% of canopy trees over 10 s–1,000 s of ha) associated with tornados and down-bursts, occur, but are rare (return times of one to several millennia) (Canham and Loucks 1984; Frelich and Lorimer 1991). Intermediate wind disturbances (single events removing 10–50% of canopy trees, opening gaps of 100 s–1,000 s m^2, and returning on century intervals) are also present in these forests (Frelich and Lorimer 1991; Woods 2004). The effects of intermediate-sized gaps remain substantially undocumented (Seymour et al. 2002), and in this study, we focus on these disturbances (200–3,000 m^2 and 6–9 years old).

Changes in N uptake, microclimate (e.g., increased radiation, temperature, and moisture), and substrate associated with gaps impart significant influence on forest N dynamics. In general, increased organic matter decomposition and N mineralization and reduced root N uptake tends to favor leaching of inorganic N in gaps relative to the undisturbed closed forest (e.g., Mladenoff 1987; Parsons et al. 1994a, 1994b; Brumme 1995; Zhang and Zak 1995; Denslow et al. 1998). Elevated soil N leaching response in gaps has been observed for up to 7 years (Prescott et al. 2003). Nitrogen leaching has been measured across different gap sizes (0.1–10 ha and 20–30 m diameter and, respectively); although significant differences were not observed among these gap sizes (Prescott et al. 2003; Ritter et al. 2005).

Nutrient retention is dependent upon the balance between inputs (atmospheric deposition, gas adsorption/fixation), transformations (mineral weathering, mineralization of soil organic matter), and outputs (soil leaching and volatilization) (Bruijnzeel 1991; Lesack and Melack 1996). Excessive leaching loss of NO_3^- is considered the cardinal sign of an N-saturated forest (Fenn et al. 1998). But, NO_3^- leaching on its own does not necessarily indicate N-saturation, and as previously described, could also be short-term response to disturbance. Other indicators that have been used to indicate N-saturation include increased N deposition (Johnson and Lindberg 1992), increased N mineralization and nitrification (Foster et al. 1989), high soil N accumulation with decreased soil C/N ratios (McNulty et al. 1991; Aber 1992), and increased NO_3^-/NH_4^+ ratios in drainage waters (Hedin et al. 1995). Gundersen et al. (2006) suggest NO_3^-

leaching occurs when N deposition and net mineralization (soil N flux density) exceeds plant demand; and, the imbalance of supply and demand starts at a threshold of 100 kg N ha^{-1}. Indicators, thresholds, and flux input–output balances can be used to relate information of potential N losses associated with gaps to examine hypotheses governing biogeochemical cycling in late-successional forests.

The goal of this study was to examine forest water N dynamics in late-successional forests in the upper Great Lakes region, USA. Inorganic N fluxes in throughfall (tf), forest floor leachates (ffl), and mineral soil leachates (sl) were measured for two consecutive growing seasons (defined as the snow-free period between June and September) in gaps (300–2,000 m^2, 6–9 years), gap-edges, and the adjacent undisturbed forest in three different forest cover types (northern hardwood, hemlock, and hardwood–hemlock). In this study, we test two general hypotheses: (1) undisturbed forest plots in these late-successional forests will exhibit net inorganic N retention, and thus are likely not N-saturated; (2) inorganic N loss will occur in gaps and gap-edges, and the N loss will likely be in response to the disturbance event, and not N-saturation.

Materials and methods

Site description

The term late-successional in this study refers to forests with overstory trees that are ecologically mature (c.a. 100+ years old) and a disturbance regime that is mostly natural (i.e., negligible unnatural disturbances such as logging, roading and clearing). This research was carried out in the Porcupine Mountains Wilderness State Park (PMWSP) (46°N and 89°W) and the Huron Mountain Reserve Area (HMRA) (46°N and 87°W). Forest stands in the PMWSP and HMRA are composed of sugar maple (*Acer saccharum* Marsh.) and eastern hemlock (*Tsuga canadensis* Linn.) with lesser amounts of yellow birch (*Betula alleghaniensis* Britt.), red maple (*Acer rubrum* Linn.), and basswood (*Tilia americana* Linn.) (Curtis 1959). Basal areas of these stands ranged from 28 to 69 m^2 ha^{-1} (Table 1). According to Frelich and Lorimer (1991), the average canopy residence time of a tree in these forests is 145–175 years. The Porcupine and Huron Mountains have a humid cold climate with no dry seasons and cool, short summers. They have low potential evapotranspiration rates, and the frost-free period ranges from 90 to 120 days (Phillips and McCulloch 1972). Annual precipitation averages 800–900 mm (NOAA 2007). The average monthly temperatures near Lake Superior range from −7.8°C in January to 19.4°C in July (NOAA 2007). The soil temperature and moisture regimes are frigid and udic, respectively. Spodosols are common in the Huron and Porcupine Mountains (e.g., Typic and Alfic Haplorthods) (Bockheim 2003). Soils at each of nine sites were described to the US Soil Taxonomic subgroup: Alfic and Typic Fragiorthods, Typic Haplorthods, and Lithic and Typic Udorthents (Table 1) (USDA NRCS 2006). The depth of the forest floor in these forests ranged from 3.6 to 8.2 cm (Table 1, Fig 1).

Five gaps in the PMWSP and four in the HMRA were selected using the criteria of Runkle (1992), Tyrrell and Crow (1994), and McClure et al. (2000) (Table 1). At each of these locations, we installed one 10-m diameter circular plot in the each gap center, along the gap edge, and within the closed canopy. Gaps were intermediate in size (300–2,000 m^2), open but relatively old (6–9 years) (Table 1). Percent canopy cover, measured with a spherical densitometer at gap center, in gaps ranged from 55% to 75% (Table 1). Woody regeneration, with an inverted spherical densitometer at gap center, in gaps ranged from 10% to 60% ground cover (Table 1). The edge plot was located at a random azimuth out from the gap center in line with edge tree boles and under edge tree canopies. We recognize directional microclimate variability in gaps (i.e., gap rainfall may vary with wind direction), but randomly choose our transect azimuth as in Runkle (1992). The forest plot was located at a random distance from gap center, at least one and a half tree heights within the contiguous forest. Specific plot characteristics and a more detailed site description are provided in Scharenbroch and Bockheim (2007).

Forest water fluxes

Throughfall (tf) was collected July through September, 2006, in each gap, edge, and forest plot. Because of the remoteness of the sites, we limited our sampling to monthly, wet-only collections; so, tf included wet and

Table 1 Research plots in late-successional forests of the Huron Mountain Reserve Area (HMRA) and Porcupine Mountain Wilderness State Park (PMWSP), upper MI, USA

Plot	Location	Latitude (°N)	Longitude (°W)	Soil subgroup	Forest floor depth (cm)	Forest cover type	Canopy density (% cover)	Forest basal area (m^2 ha^{-1})	Woody regeneration (% cover)	Gap creating trees (species #)[a]	Gap area (m^2)	Extended area (m^2)[b]	Gap age (year)
H1	Mountain Lake (HMC)	46°52′12.8″	87°53′86.8″	Typic Haplorthod	5.2	Northern hardwood	75	40	15	MH (5)	324	1,022	6
H10	Compound (HMC)	46°31′50.1″	87°53′14.9″	Typic Udorthent	7.5	Hemlock	65	65	25	HE (9) YB (2)	1,438	3,419	9
H8[c]	Trout Lake (HMC)	46°51′19.1″	87°53′47.2″	Alfic Fragiorthod	3.6	N. hardwood–hemlock	60	40	40	HE (5) MH (2)	691	1,800	8
H9[c]	Fortress (HMC)	46°52′50.8″	87°53′34.0″	Lithic Udorthent	8.2	N. hardwood–hemlock	55	69	10	HE (9) MH (4)	502	3,768	9
P10	Lily Pond Trail (PMWSP)	46°44′06.9″	89°45′44.9″	Typic Fragiorthod	7.7	Northern hardwood	60	32	50	MH (4) YB (1)	301	816	6
P11	Trap Falls (PMWSP)	46°47′57.7″	89°41′22.8″	Alfic Fragiorthod	7.0	Hemlock	65	53	60	HE (3)	518	1,884	6
P6	Pinkerton Trail (PMWSP)	46°44′18.5″	89°53′40.7″	Alfic Fragiorthod	5.8	N. hardwood–hemlock	60	45	30	MH (4) HE (3)	1,890	3,149	9
P7[c]	Deeryard (PMWSP)	46°43′38.5″	89°40′10.5″	Typic Fragiudalf	8.7	Hemlock	70	65	50	HE (7)	829	2,207	7
P9[c]	Little Carp River (PMWSP)	46°49′25.1″	89°49′02.0″	Typic Haplorthod	5.3	Northern hardwood	70	28	60	MH (4)	528	1,140	6

[a] MH is *Acer saccharum*; HE is *Tsuga canadensis*; YB is *Betula alleghaniensis*

[b] Gap area is the area of canopy hole and extended gap area extends to the stems of edge trees

[c] In-situ solar radiation, air temperature, soil temperature, and soil moisture measured on this plot

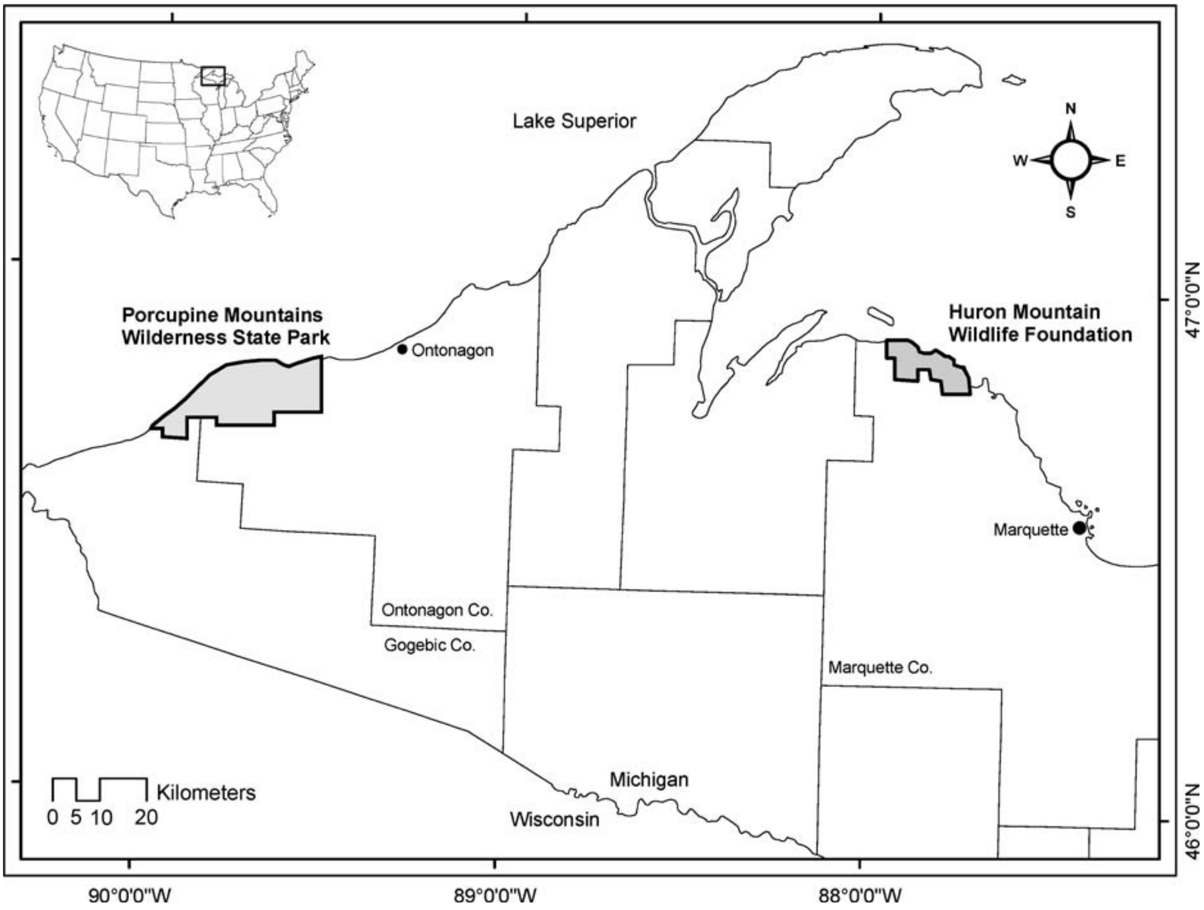

Fig. 1 Location of the study areas in the Huron Mountain Reserve Area (HMRA) and Porcupine Mountain Wilderness State Park (PMWSP), upper MI, USA

dry deposition. We recognize the potential for N to change forms while sitting in tf collectors. Michalzik et al. (1997) found mineralization of organic N to ammonium (NH_4^+) can occur with time (up to 4 weeks) in tf collectors, but they also suggested that dissolved N may be relatively stable in this time period. Throughfall collectors consisted of 4-l polyethylene bottles with 19.5-cm polyethylene mesh-lined funnels held 1.5-m above the forest floor on permanent posts (Eaton et al. 1973). Two tf collectors were randomly placed on the plot at a distance of at least 1-m from eachother. Data was carefully examined for abnormalities and a mean for each plot was calculated for statistical analyses. Because tf could only be measured three times throughout the study, replicated twice per plot, and collected monthly; the conclusions we make regarding tf are relative and should be interpreted in a tentative manner.

Forest floor leachate (ffl) was collected throughout the 2005 and 2006 growing seasons (June through September) using zero tension samplers (5-cm wide by 30-cm long) placed horizontally under the forest floor (Jordan 1968). The forest floor was carefully removed and placed atop the mesh-lined PVC collector. An adjacent hole (c.a., 0.5 m^3) was dug to house a 1-l polyethylene bottle, in which the ffl drained for sample collection. A plot mean was calculated from three ffl collectors, randomly located at least 1-m from eachother.

Soil leachate (sl) was collected throughout the 2005 and 2006 growing seasons (June through September) using ceramic porous-cup suction water samplers (Soil Moisture Equipment Corporation), at a pressure of −65 kPa, and installed to a depth of 50 cm within the soil profile. Soil profiles were examined on each plot and roots were mostly confined to the upper 50 cm, so the soil water collected in samplers represented water leached below the effective rooting volume. Samplers were installed with a 5-cm bucket auger, and the holes were backfilled with soil material corresponding to excavated horizon. A plot mean was calculated from three samplers, randomly located no closer than 1-m from eachother.

Following collection, water samples were stored on ice during transport to the laboratory. Prior to analyses, samples were filtered through quantitative filters (Fisherbrand Q2). Solution pH values were determined in the laboratory using a pH-EC meter (Oakton pH/CON 510 Series). The concentrations of NH_4^+ in the filtered extracts were determined colorimetrically with absorbance readings on a microplate reader at 650 nm (Sims et al. 1995; Drinkwater et al. 1996). Nitrate concentrations in filtered extracts were measured by reducing NO_3^- to nitrite (NO_2^-) and then NH_4^+ with Devarda's alloy and H_2SO_4, and subsequent colorimetric analyses of NH_4^+ (Sims et al. 1995; Drinkwater et al. 1996). Throughfall and ffl volumes were recorded in the field during collection. Total flux of inorganic N in tf and ffl was calculated by multiplying the concentration by the water volume for each collection interval; this product was summed over all intervals for growing season flux.

We recognize dissolved organic N is an important component of total forest water N flux (e.g., Hedin et al. 1995), but due to limited resources we were unable to measure this N pool. Our focus on inorganic N is justified, as the NO_3^- anion is highly mobile, a major forest water constituent, and responds to changes in forest N input, biotic N uptake, and N mineralization processes (Gundersen et al. 2006). The inclusion of NH_4^+ details the impacts of gaps on a N-cation in forest water fluxes.

Drainage flux estimates with WATBAL

The monthly soil water drainage flux throughout 2006 from the effective rooting zone (0–50 cm) was estimated using the one-dimensional water balance model, WATBAL (Starr 1999; Ritter et al. 2005). WATBAL is based on the simple water balance equation where precipitation inputs equal the sum of evapotranspiration, soil water drainage, and changes in soil water storage, and uses end-of-the-month accounting. The model is driven by monthly mean air temperature, precipitation, and a number of site, stand, and soil parameters. A detailed explanation of the model and parameters is provided in Ritter et al. (2005).

Mean monthly air temperature, incoming solar radiation, soil temperature, and soil moisture content in four gaps and four adjacent forest plots were measured directly with temperature sensors, pyranometers, and tensiometers (Onset Computer Corporation 2003) (Table 1). Our direct microclimate measurements as well as the NOAA database (NOAA 2007) were used for WATBAL inputs. Means of gap and forest plot measurements were used for estimations of edge plot microclimate. To optimize the canopy coefficient value (K_c) we compared WATBAL simulated potential evapotranspiration with independent estimates of potential evapotranspiration (Phillips and McCulloch 1972; Palik and Pregitzer 1992). For the period, July through September, 2006, we used in-situ tf measurements for precipitation in gaps, edges, and forest plots. Throughfall samples in June 2006 were not available, so we estimated them by using ratios of gap to forest or edge tf from July and the NOAA precipitation database (Ritter et al. 2005; NOAA 2007). During the dormant season (October through May) incident precipitation in gap, edge, and forest plots was equal to the monthly precipitation values attained from the NOAA database (NOAA 2007).

In-situ measurements of soil moisture were used to calibrate the model (Fig. 2). We found significant agreement between our field measurements and model calculations for soil moisture content ($P < 0.0001$, R^2 values of 0.96). The model calculations of soil moisture contents underestimated field moisture contents during the growing season. We suspect this limitation is due to the model's inability to incorporate a value for soil moisture permanent wilting point. Sensitivity analyses were performed on the model and incoming precipitation was the parameter with most influence. Other parameters such as monthly mean air temperature, canopy coefficient, etc. had relatively minimal impact on the modeled soil leachate.

Monthly NO_3^- leaching losses were calculated as the product of the monthly average sl-NO_3^- concentration and the simulated monthly soil water flux. As in Ritter et al. (2005), when soil solution was not available (i.e., the dormant season), concentration values in the previous or following sampling period, whichever lower, were used as estimates. In periods

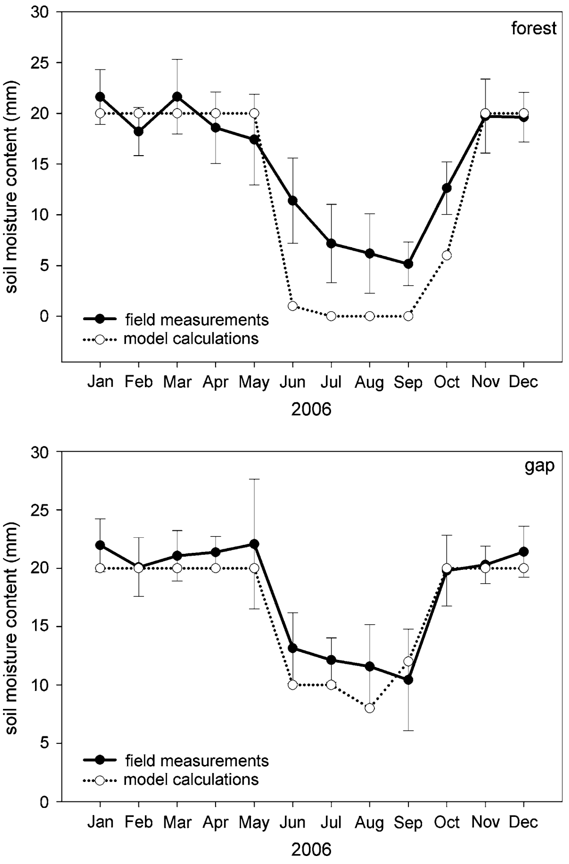

Fig. 2 Soil moisture contents in forest and gaps as measured in the field and as estimated for monthly intervals by the WATBAL model. Field measurements calculated from four gaps and four adjacent forest plots (sites H8, H9, P7, and P9, see Table 1). Error bars are the standard error of means. $N = 8$

when the soil solution was sampled but the modeled drainage flux was zero, it was assumed that the soil moisture store was sampled and that NO_3^- leaching was zero (Ritter et al. 2005). During the dormant season, sl-volumes tend to be high and N concentrations lower (Likens and Bormann 1995); thus, our model extrapolations likely overestimate the total dormant season inorganic N flux. Consequently, our results should be interpreted as potential maximum inorganic N leaching losses.

Statistical analyses

The experimental design was a randomized block with three treatments (forest, edge, and gap) for each of nine locations. To test the treatment effects we used one-way analysis of variance with Tukey-Kramer HSD and Student's *t* tests (SAS 2005). Principal component analyses were used to examine relationships in the multivariate dataset (SAS 2005). Unbiased analyses on correlations were performed and the components were not rotated. Multivariate correlations and Pearson's correlation coefficients were used to identify significant relationships among variables and principal components, and examine treatment interactions. Statistical differences are reported at the $P \leq 0.05$ probability level. Percentage changes were used to discuss data from gaps, edges, and forested plots. For these comparisons the base was the undisturbed forest, or if gap and edge plots were compared, the base was the edge.

Preliminary analyses were performed using standard least squares approach to determine the impacts of grouping data from two sites (i.e., the Huron vs. Porcupine Mountains), different forest cover types (i.e., hardwood or hemlock dominated, or a mixture of hardwood and hemlock), varying gap sizes (i.e., 300–550, 550–850, and >850 m^2), different soil types (i.e., Haplorthod, Fragiorthod/Fragiudalf, and Udorthent), and across sampling dates (SAS 2005). These preliminary analyses revealed that the treatment effects by site, gap size, and soil type were orderly, and significant treatment interactions were not detected ($P \geq 0.11$). Higher order treatment interactions (e.g., treatment*site*cover) were also examined and found to be not significant ($P \geq 0.63$).

Results and discussion

Justification for examining treatment effects across cover types

To discuss forest water N fluxes in broader terms relating to gaps in these mosaic northern hardwood–hemlock forests, inorganic N data from northern hardwood (NH), northern hardwood–hemlock (NH–HE), and hemlock (HE) forest cover types were pooled (Table 2). This is justifiable, as treatment*cover or treatment*time interactions were not detected in the present study for inorganic N in tf, ffl, and sl ($P > 0.06$) (Fig. 3). In addition, treatment*cover type interactions ($P > 0.17$) were not significant for N mineralization and other soil chemical and biological properties in these mosaic forests (Scharenbroch and Bockheim 2007).

Table 2 Volume, pH, and inorganic N in throughfall, forest floor leachate, and soil leachate from gap, edge, and forest plots throughout the 2005 and 2006 growing seasons (June through September) in late-successional northern hardwood–hemlock forests of the upper Great Lakes region, USA

Biogeochemical water flux		Edge		Forest		Gap		*P*-value
		Mean	SE	Mean	SE	Mean	SE	
2005								
Volume	Floor (mm)	79.80	15.00 b	51.80	10.01 b	120.02	19.04 a	0.017
pH	Floor	5.33	0.15 a	5.39	0.18 a	5.58	0.14 a	0.285
	Soil	6.27	0.16 a	6.16	0.25 a	6.16	0.13 a	0.475
NH_4^+	Floor (kg ha^{-1})	0.53	0.12 a	0.71	0.11 a	1.01	0.14 a	0.292
	Soil (mg l^{-1})	0.03	0.00 a	0.03	0.00 a	0.03	0.00 a	0.431
NO_3^-	Floor (kg ha^{-1})	6.01	1.10 b	4.44	0.72 b	9.45	1.60 a	0.027
	Soil (mg l^{-1})	0.19	0.05 ab	0.16	0.05 b	0.25	0.03 a	0.014
2006								
Volume	Canopy (mm)	117.02	16.00 b	102.04	12.03 b	176.03	23.01 a	0.023
	Floor (mm)	44.70	8.70 b	42.71	10.04 b	102.00	20.02 a	0.024
	Soil (mm)	25.00	–	24.93	–	39.30	–	–
pH	Canopy	5.59	0.11 a	5.58	0.11 a	5.53	0.14 a	0.651
	Floor	5.39	0.09 a	5.31	0.09 a	5.38	0.09 a	0.437
	Soil	5.74	0.09 a	5.70	0.10 a	5.59	0.09 a	0.276
NH_4^+	Canopy (kg ha^{-1})	0.50	0.07 a	0.64	0.11 a	0.53	0.05 a	0.366
	Floor (kg ha^{-1})	0.53	0.10 a	0.59	0.19 a	0.87	0.18 a	0.399
	Soil (mg l^{-1})	0.02	0.00 a	0.02	0.00 a	0.02	0.00 a	0.592
NO_3^-	Canopy (kg ha^{-1})	2.89	0.43 b	4.21	0.63 a	2.95	0.39 b	0.012
	Floor (kg ha^{-1})	2.69	0.49 b	2.38	0.40 b	5.37	1.10 a	0.005
	Soil (mg l^{-1})	0.17	0.03 ab	0.16	0.03 b	0.21	0.03 a	0.005

[a] Soil drainage volume estimated from WATBAL. Values are growing season means for concentrationsand totals for volumes and ion fluxes (five dates in 06/15/05 to 10/08/05, four dates in 05/23/06 to09/16/06, three dates 07/02/06 to 09/16/06 for throughfall). Unique letters show significant difference atthe $P \leq 0.05$ level using Tukey's test. *P*-values show significance of treatment effect with ANOVA. $N = 27$

Furthermore, groupings established from principal component analyses differentiated by 11 forest water flux variables demonstrate that treatment effects ($P < 0.0001$ using MANOVA) were orderly across cover types (Fig. 4). The first and second components accounted for 30.8% and 20.2% of the variation, respectively. Positive coefficients for the first component explained significant ($P < 0.05$, $R^2 > 0.60$) variation in tf-NH_4^+, tf-NO_3^-, ffl-NH_4^+, ffl-NO_3^-, and decreased tf-volumes and ffl-volumes (Fig. 4). The second component accounted for significant ($P < 0.05$, $R^2 > 0.60$) variation in sl-NH_4^+, sl-NO_3^-; and, decreased ffl-NH_4^+ and ffl-NO_3^- (Fig. 4). The first component separated forest and gap plots, with forest plots corresponding to positive coefficients (higher tf- and ffl-NH_4^+ and NO_3^-, and decreased tf- and ffl-volumes). Gap plots tended to be more positively correlated with PC2 (increased sl-NH_4^+ and sl-NO_3^-), and forest plots tended to be negatively correlated with PC2 (decreased sl-NH_4^+ and sl-NO_3^-). Principal components on edge plots tended to be neutral, indicating that properties of forest water transfers in edges fall between extremes of gaps and closed forest plots.

Forest water and N flux treatment effects across cover type

During July through September, 2006, tf hydrologic flux (volume in mm) was significantly greater in gaps vs. forest (73%) and edge (51%) plots (Fig. 3). The

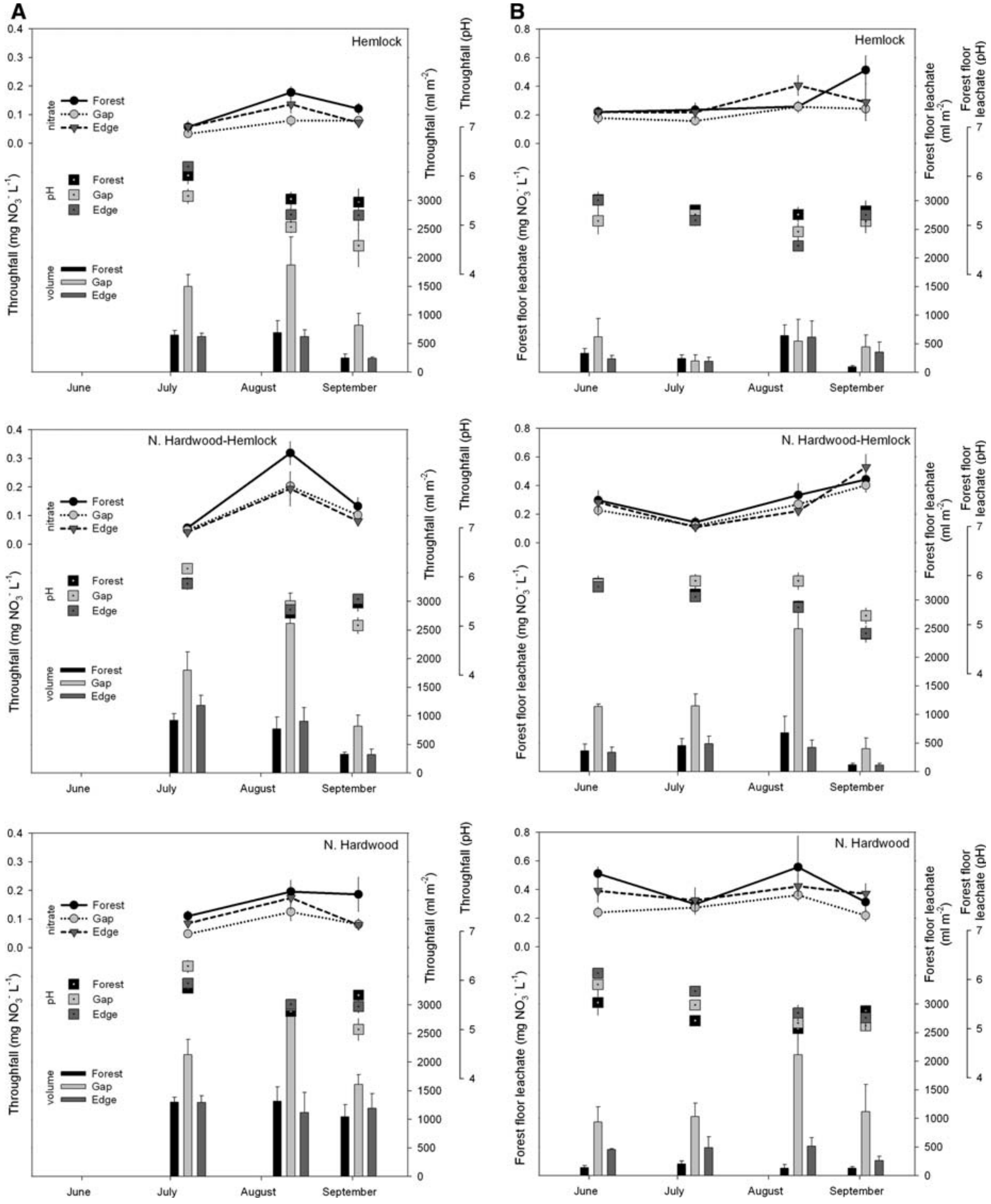

Fig. 3 Flux volume, pH, and nitrate in (**a**) throughfall, (**b**) forest floor leachate, and (**c**) soil leachate in gap, edge, and forest plots throughout the 2006 growing season in late-successional hemlock, northern hardwood–hemlock, and northern hardwood forests of the upper Great Lakes region, USA. Treatments (gap, edge, and forest), cover types (northern hardwood, northern hardwood–hemlock, and hemlock); dates (2006 only, 5/23–6/15/06, 6/16–7/28, 7/29–8/24, 8/25–9/16/06). Treatment*cover and treatment*date interactions $P > 0.0553$ for nitrate in these forest water fluxes. Treatment*cover and treatment*date interactions $P < 0.0023$ for throughfall and forest floor leachate pH. $N = 27$

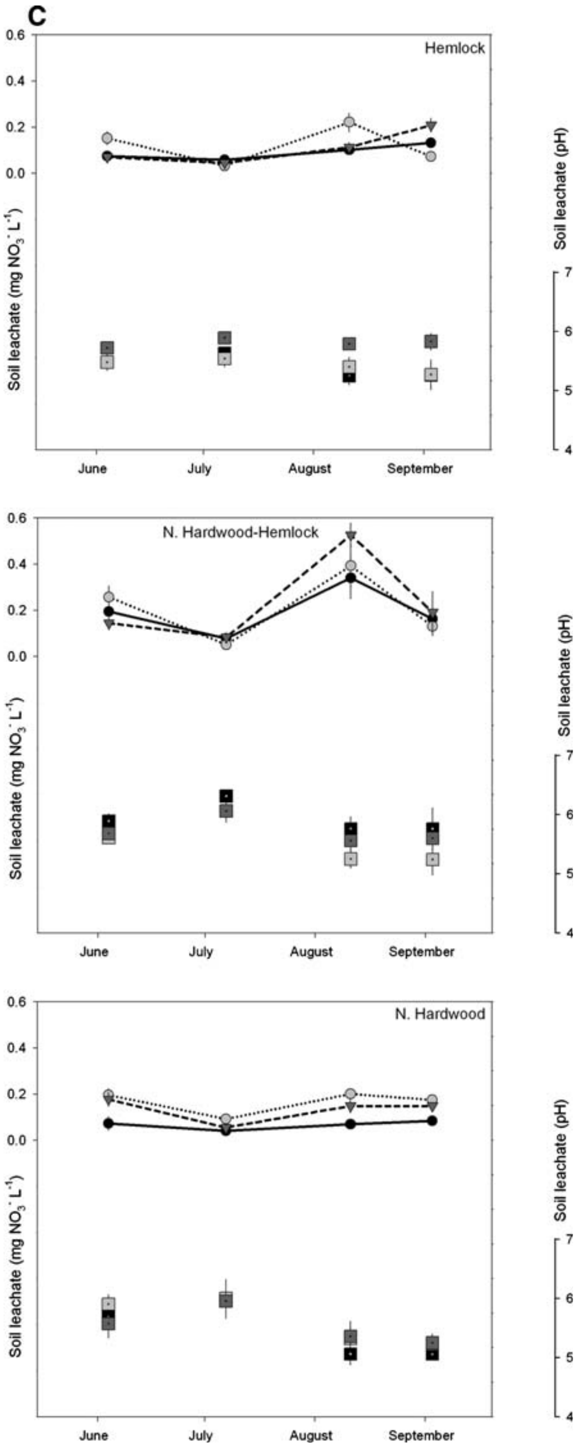

Fig. 3 continued

concentration of tf-NO$_3^-$ tended to increase from July to August and decrease from August to September (Fig. 3). Total NO$_3^-$ flux in tf was significantly less in gaps (30%) and edge (31%) plots compared to forest plots (Table 2). Significant differences among gaps, edges, and forest plots for tf-NH$_4^+$ or tf-pH were not detected (Table 2).

These results are consistent with consensus that canopies tend to enhance nutrient concentrations of incident precipitation (Parker 1983; Lindberg and Owens 1993). The amounts of tf inorganic N in forest gaps (3.5 kg ha^{-1}), edges (3.4 kg ha^{-1}) and closed forest plots (4.9 kg ha^{-1}), July through September, were within range of annual tf fluxes for northern hardwood forests in upper Michigan (9.9 kg ha^{-1} year^{-1}) (MacDonald et al. 1992) and at Hubbard Brook Experimental Forest in New Hampshire (10.6 and 1.8 kg ha^{-1} for tf and incident precipitation, respectively) (Eaton et al. 1973). There is a strong negative relation in tf concentrations with the amount of precipitation (e.g., Lindberg et al. 1979). Total nutrient deposition, on the other hand, is positively related to precipitation amounts (Parker 1983). Differences in tf concentration rather than water flux accounted for main differences in the total tf-NO$_3^-$ flux. Nitrate flux in tf was greater under the contiguous forest compared to gaps, even though the hydrologic volume input was significantly greater in gaps compared to the closed forest. It should be noted that dissolved organic N typically accounts for a large component of total dissolved N in tf (e.g., Hedin et al. 1995), but our results represent only inorganic N contribution.

The total growing season ffl-hydrologic flux volume (2005 and 2006, respectively) was significantly greater in gaps compared to forest (131% and 73%) and edge (50% and 51%) plots (Table 2). Concentrations of ffl-NO$_3^-$ were significantly less in gaps than in forest plots (Fig. 3). Inorganic N concentrations in ffl ranged from 0.1 to 0.5 mg NO$_3^-$ l^{-1} and 0.01 to 0.1 mg NH$_4^+$ l^{-1}, and were greater, but within range of those observed in uncut mature deciduous forests in the Appalachian Mountains, USA (0.083 mg NO$_3^-$ l^{-1} and 0.032 mg NH$_4^+$ l^{-1}) (Qualls et al. 2000). Total hydrologic flux of ffl-NO$_3^-$ over the two growing seasons (2005 and 2006, respectively) was significantly greater in gaps compared to forest (113% and 126%) and edge (51% and 100%) plots. Differences in total ffl-NO$_3^-$ flux were due to the volume and not the ion concentration. Forest floor leachate ion flux is related to seasonal changes in hydrologic conditions and microbial activity (e.g., McDowell and Likens 1988). Similar

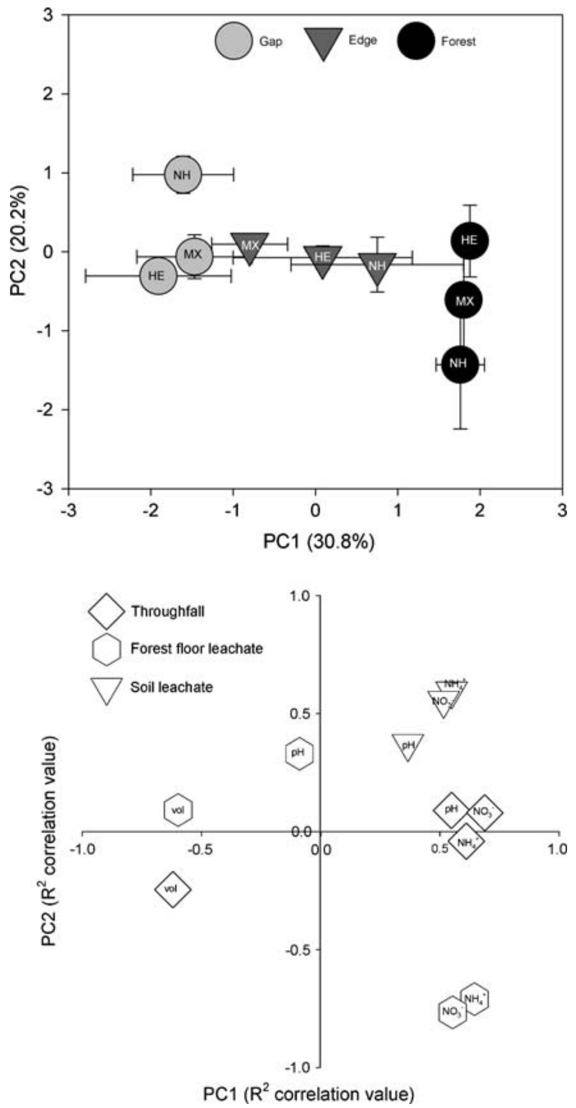

Fig. 4 Principal components and loadings for forest water transfers in gap, edge, and forest plots throughout the 2006 growing season in late-successional northern hardwood–hemlock forests of the upper Great Lakes region, USA. Principal component analyses were performed on 2006 growing season means. $N = 27$

to tf, ffl-NH_4^+ concentrations and ffl-pH values were not significantly different among gap, edge, and forest plots (Table 2).

Throughout both growing seasons (2005 and 2006, respectively) mineral sl-NO_3^- concentrations were significantly greater (56% and 31%) in gaps compared to forest plots (Table 2). In both years, edge plot sl-NO_3^- was greater than in forest plots but less than in gaps (Table 2). Seasonal mean values of sl-NH_4^+ and sl-pH were not significantly different among gaps, edges, and forests (Table 2). Ammonium is absorbed on the soil cation exchange complex, so it is reasonable that sl-NH_4^+ flux was not impacted by gaps. Soil acidification often occurs with NO_3^- leaching and nitrification (Gundersen and Rasmussen 1990). Soil leachate-pH, as well as soil pH (Scharenbroch and Bockheim 2007), was not significantly different among gaps, edges, and forest plots; thus, it is unlikely gap disturbances have a role in acidification of these forest soils through NO_3^- leaching or increased nitrification.

Concentrations of sl-NO_3^- were cyclic throughout the growing seasons, with peaks in June and August (Fig. 3). These peaks coincide with increased N mineralization in gaps during the early and later portions of the growing season (Scharenbroch and Bockheim 2007). Mean gap sl-NO_3^- concentrations in 2005 and 2006, respectively, (0.21–0.25 mg NO_3^- l^{-1}) were similar to NO_3^- leaching concentrations observed in vegetation-removed-trenched plots in maple-beech forests in New Hampshire and Indiana (0.11–0.22 mg NO_3^- l^{-1}) (Vitousek et al. 1979).

Nitrate retention capacity of gaps, edges, and forests

When comparing NO_3^- inputs in tf and outputs in sl, net annual losses of NO_3^- occurred for gaps (-1.3 kg ha^{-1}) and gap edges (-0.2 kg ha^{-1}), and net annual gains occurred for forest plots (+2.8 kg ha^{-1}) (Fig. 5). Nitrate losses tended to be greatest prior to and immediately following the growing season, and early spring (2.8–3.5 kg ha^{-1} for gaps) losses far outweighed autumn (0.3 kg ha^{-1} for gaps) NO_3^- losses. In cold, snow-melt systems, much of the total annual N flux can occur during early snow-melt periods (Foster et al. 1989; Campbell et al. 1995; Williams et al. 1996; Brooks et al. 1998). As previously mentioned our model extrapolations likely overestimate the total dormant season N flux, so our results should be interpreted as maximum inorganic N losses.

Annual tf-NO_3^- inputs in N-saturated, mature sugar maple forests of the Turkey Lakes Watershed, Ontario ranged from 7.0 to 7.7 kg ha^{-1}, and soil leachate NO_3^- outputs ranged from 17.9 to 23.6 kg ha^{-1} (Foster et al. 1989; Johnson and Lindberg 1992). In comparison, undisturbed forest plots in these late-successional northern hardwood–hemlock forests had modeled

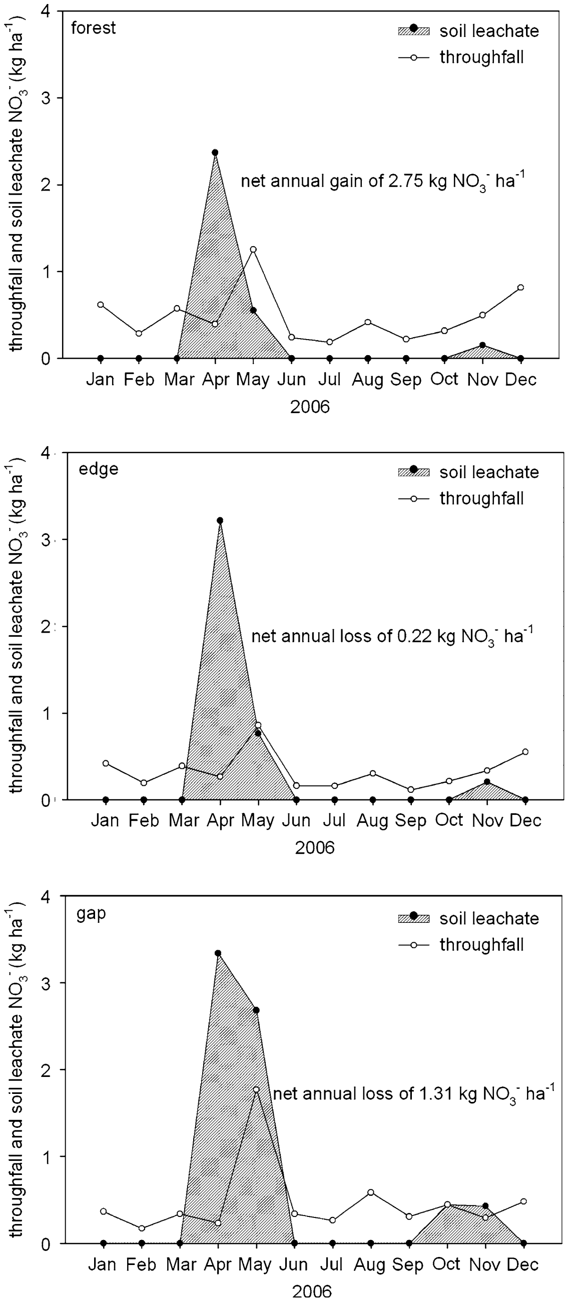

Fig. 5 Nitrate inputs in throughfall and outputs in soil leachates in gap, edge, and forest plots throughout 2006 in late-successional northern hardwood–hemlock forests of the upper Great Lakes region, USA. Values are monthly modeled response using WATBAL

annual tf-NO_3^- inputs of 5.8 kg ha^{-1} $year^{-1}$ and sl-NO_3^- outputs of 3.1 kg ha^{-1} $year^{-1}$ (Fig. 5). Pristine "non-leaky" forests have NO_3^-/NH_4^+ ratios of less than one in discharge waters; and, ratios exceeding 8 in drainage waters have been associated with "leaky" forests with high N deposition in the eastern United States (Hedin et al. 1995). The sl-NO_3^-/NH_4^+ ratios in our late-successional northern hardwood–hemlock forests were 6.5 for forest plots, 7.0 for edge plots, and 9.4 for gap plots (Table 2). Increased nitrification is also indicative of N-saturation, and nitrification rates were high in forests of the Turkey Lakes Watershed (112.9 kg ha^{-1}, May through October) (Foster et al. 1989). Increased N mineralization rates in the Turkey Lakes forests were the primary cause of high soil N leaching (Foster et al. 1989). In comparison, potential nitrification rates in these northern hardwood–hemlock forests were about five times lower (20 kg ha^{-1}, June through October) (Scharenbroch and Bockheim 2007).

Thresholds proposed by Gundersen et al. (2006) indicative of "leaky" systems with elevated NO_3^- leaching (and potential N-saturation) include: 1.0 mg NO_3^- l^{-1} in soil leachate output, 10 kg N ha^{-1} $year^{-1}$ of deposition input, and a soil flux density (N deposition plus soil N mineralization) greater than 100 kg inorganic N ha^{-1} $year^{-1}$. In comparison, undisturbed forest plots in our study had sl-NO_3^- concentrations of 0.16 and 0.19 mg NO_3^- L^{-1} in 2005 and 2006 (Table 2), total tf-NO_3^- 2006 input of 5.8 kg ha^{-1} (Fig. 5), and total 2006 soil flux density of 45.8 kg inorganic N ha^{-1}. Annual net N mineralization on these same forest plots in 2006 was 40 kg ha^{-1} (Scharenbroch and Bockheim 2007). Ammonium contributions in throughfall were relatively minimal (Table 2), and not included in the calculation of soil flux density. In gap-edges, sl-NO_3^- concentrations were 0.19 and 0.17 mg l^{-1} in 2005 and 2006 (Table 2) and the 2006 annual tf-NO_3^- input was 4.0 kg ha^{-1} (Fig. 5). Gap sl-NO_3^- concentration was 0.25 and 0.21 mg l^{-1} in 2005 and 2006 (Table 2) and tf-NO_3^- input was 5.6 kg ha^{-1} (Fig. 5), both well below the thresholds proposed by Gundersen et al. (2006). Soil flux densities in gaps and gap-edges (75.6 and 84.0 kg inorganic N ha^{-1}, respectively) (gap and edge Nmineralization was 70 and 80 kg ha^{-1} in Scharenbroch and Bockheim 2007) approached, but were still below thresholds described in Gundersen et al. (2006) for the combined deposition and mineralization flux.

Gaps and gap-edges in these late-successional northern hardwood–hemlock forests are characterized by periods of amplified N loss. The response of this endemic disturbance would tend towards stage 1 of the Aber N-saturation model (Aber et al. 1989); but, we suspect the N loss in gaps is directly linked to reduced uptake with vegetation removal and increased N mineralization in response to gap microclimate (Scharenbroch and Bockheim 2007), and not N-saturation. Studies from European beech stands in high deposition areas report NO_3^- in seepage waters in gaps above 11.3 mg l^{-1}, which is the threshold for drinking water quality (Bauhus and Bartsch 1995; Ritter et al. 2005; Ritter and Vesterdal 2006). Soil leachate NO_3^- concentrations in our gaps and edges were two magnitudes of order lower (0.17–0.25 mg l^{-1}). Clear-cut studies suggest the peak N loss period to be 2 to 3 after the cutting with a return to pre-cut levels after 5 years (Gundersen et al. 2006). Although minimal, our results show that N loss in these gaps, 6–9 years old, is significant relative to the closed forest. Likewise, Prescott et al. (2003) found gaps in Canadian spruce-fir forests still had significant N loss 7 years after disturbance.

Our results indicate it is unlikely that undisturbed forest plots in these late-successional forests are N-saturated. Further support for this suggestion is provided in that, even in the most sensitive areas to N-saturation (i.e., gaps), we did not find sufficient evidence to suggest N-saturation. Intermediate gap disturbances are expected to represent 10 to 50% of stand area (Woods 2004). In two hypothetical 1,000 ha forests, with 10% and 50% of the area occupied by intermediate gaps, the net NO_3^- balance would be +1.4 Mg NO_3^- (+2.8 kg ha^{-1} * 500 ha − 1.3 kg ha^{-1} * 500 ha^{-1}) and +2.3 Mg NO_3^- (+2.8 kg ha^{-1} * 900 ha −1.3 kg ha^{-1} * 100 ha^{-1}). Even if these intermediate-sized gap disturbances represent larger spatial components of a current stand, N loss from these gaps seems temporally limited through the actual time gaps remain open and by the return interval of intermediate wind disturbance, which is suspected to return on century intervals (Woods 2004).

Nitrogen saturation in these forests may be subdued, relative to the nearby N-saturated Turkey Lakes Watershed (Foster et al. 1989; Johnson and Lindberg 1992), due to soil N retention and microbial immobilization (Fenn et al. 1998). In a Michigan northern hardwood forest, Zak et al. (1990) found microbial N immobilization in the early spring to be a larger sink than plant uptake, potentially lessening N losses from the system. Under snow-cover, dormant season microbial N activity and biomass can be significant (Williams et al. 1996; Brooks et al. 1998). High rates of potential microbial N immobilization (1.5–2.5 kg N ha^{-1} day^{-1}) were directly observed in the early growing seasons (May and June) of these late-successional forests (Scharenbroch and Bockheim 2007).

Conclusion

Differences in forest water inorganic N among gaps, edges, and closed forest plots were consistent across cover types in these late-successional northern hardwood–hemlock forests. Throughfall NO_3^- inputs were significantly greater in undisturbed forest plots compared with gaps and edges. Nitrate in forest floor leachates were significantly greater in gaps compared to edges and closed forest plots. Nitrate in soil leachates were significantly greater in gaps compared to closed forest plots. A net annual gain of NO_3^- was measured in the closed forest and a net annual NO_3^- loss measured in gaps and gap-edges. We did not find sufficient support for N-saturation in undisturbed forest plots, gap-edge plots, or gap plots in these late-successional northern hardwood–hemlock forests. Our results are relevant for ecosystem process understanding (i.e., endemic disturbances and N retention); and, these late-successional forests have particular value as reference benchmarks for comparing forests subjected to pollution and manipulation.

Acknowledgements The authors gratefully acknowledge financial support from United States Department of Agriculture, Cooperative State Research, Education and Extension Service, McIntire-Stennis. We thank Nick Balster, Craig Lorimer, Birl Lowery, Cynthia Stiles, Jun Zhu, three anonymous reviewers, and the associate editor (Per Gundersen) for advice on preparing and revising this manuscript. Permission to work in the Huron Mountains was granted by Kerry Woods, Director of Research, on behalf of the Huron Mountain Wildlife Foundation and Club. We also thank Robert Sprague, Park Manager of the Porcupine Mountains Wilderness State Park for his consent and technical assistance in the Porcupine Mountains.

References

Aber JD (1992) Nitrogen cycling and nitrogen saturation in temperate forest ecosystems. Trends Ecol Evol 7:220–223

Aber JD, Nadelhoffer KJ, Steudler P, Melillo JM (1989) Nitrogen saturation in northern forest ecosystems. BioScience 3:378–386

Aber JD, Magill A, McNulty SG, Boone RD, Nadelhoffer KJ, Downs M, Hallett R (1995) Forest biogeochemistry and primary production altered by nitrogen saturation. Water Air Soil Pollut 85:1665–1670

Agren GI, Bosatta E (1988) Nitrogen saturation of the terrestrial ecosystem. Environ Pollut 54:185–197

Bauhus J, Bartsch N (1995) Mechanisms for carbon and nutrient release and retention in beech forest gaps. I. Microclimate, water balance and seepage water chemistry. Plant Soil 168–169:579–584

Bockheim JG (2003) Genesis of bisequal soils on acidic drift in the Upper Great Lakes region, USA. Soil Sci Soc Am J 67:612–619

Brooks P, Williams MW, Schmidt SK (1998) Inorganic nitrogen and microbial biomass dynamics before and during spring snowmelt. Biogeochemistry 43:1–15

Bruijnzeel LA (1991) Nutrient input-outpur budgets of tropical forest ecosystems: a review. J Trop Ecol 7:1–24

Brumme R (1995) Mechanisms of carbon and nutrient release and retention in beech forest gaps. Plant Soil 168–169:593–600

Campbell DH, Clow DW, Ingersoll GP, Mast MA, Spahr NE, Turk JT (1995) Processes controlling the chemistry of two snowmelt-dominated streams in the Rocky Mountains. Water Resour Res 31:2811–2821

Canham CD, Loucks OL (1984) Catastrophic wind-throw in the presettlement forests of Wisconsin. Ecology 65:803–809

Curtis JT (1959) The vegetation of Wisconsin. University of Wisconsin Press, Madison

Dahir SE, Lorimer CG (1996) Variation in canopy gap formation among developmental stages of northern hardwood stands. Can J For Res 26:1875–1892

Davis MR, Calcote RR, Sugita S, Takahura H (1998) Patch invasion and origin of a hemlock-hardwoods forest mosaic. Ecology 79:2641–2659

Denslow JS, Ellison AM, Sanford RE (1998) Treefall gap size effects on above- and below-ground processes in a tropical wet forest. J Ecol 86:597–609

Dise NB, Wright RF (1995) Nitrogen leaching from European forests in relation to nitrogen deposition. For Ecol Manage 71:153–161

Drinkwater LE, Cambardella CA, Reeder J, Rice CW (1996) Potentially mineralizable nitrogen as an indicator of biologically active soil nitrogen. In: Doran JW, Jones AJ (eds) Methods for assessing soil quality. Soil Sci Soc, Madison

Eaton JS, Likens GE, Bormann FH (1973) Throughfall and stemflow chemistry in a northern hardwood forest. J Ecol 61:495–508

Fenn ME, Poth MA, Aber JD, Baron JS, Bormann BT, Johnson DW, Lemly AD, McNulty SG, Ryan DF, Stottlemyer R (1998) Nitrogen excess in North American ecosystems: predisposing factors, ecosystem responses, and management strategies. Ecol Appl 8:705–733

Foster NW, Nicolson JA, Hazlett PW (1989) Temporal variation in nitrate and nutrient cations in drainage waters from a deciduous forest. J Environ Qual 18:238–244

Frelich LE, Lorimer CG (1991) Natural disturbance regimes in hemlock-hardwood forests of the upper Great Lakes region. Ecol Monogr 61:145–161

Frelich LE, Calcote RR, Davis MB (1993) Patch formation and maintenance in an old-growth hemlock hardwood forest. Ecology 74:513–527

Goodburn JM, Lorimer CG (1999) Population structure in old-growth and managed northern hardwoods: an examination of the balanced diameter distribution concept. For Ecol Manage 118:11–29

Gorham E, Vitousek PM, Reiners WA (1979) The regulation of chemical budgets over the course of terrestrial ecosystem succession. Ann Rev Ecol Syst 10:53–84

Gundersen P, Rasmussen L (1990) Nitrification in forest soils: effects of nitrogen deposition on soil acidification and aluminium release. Rev Environ Contam Toxicol 13:1–45

Gundersen P, Schmidt IK, Raulund-Ramussen K (2006) Leaching of nitrate from temperate forests – effects of air pollution and forest management. Environ Rev 14:1–57

Hedin LO, Armesto JJ, Johnson AH (1995) Patterns of nutrient loss from unpolluted, old-growth temperate forests: evaluation of biogeochemical theory. Ecology 76:493–509

Johnson DW, Lindberg SE (1992) Atmospheric deposition and forest nutrient cycling. Ecological Studies Series 91, Springer-Verlag, New York

Jordan CF (1968) A simple, tension-free lysimeter. Soil Sci 105:81–86

Lesack LFW, Melack JM (1996) Mass balance of major solutes in a rainforest catchments in the Central Amazon: implications for nutrient budgets in tropical rainforests. Biogeochemistry 32:115–142

Likens GE, Bormann FH (1995) Biogeochemistry of a forested ecosystem. Springer-Verlag, New York

Lindberg SE, Owens JG (1993) Throughfall studies of deposition to forest edges and gaps in montane ecosystems. Biogeochemistry 19:173–194

Lindberg SE, Hariss RC, Turner RR, Shriner DS, Huff DD (1979) Mechanisms and rates of atmospheric deposition of selected trace elements and sulfate to a deciduous forest watershed. Oak Ridge National Lab Environmental Sciences Division Publ. No. 1299 ORNL/TM 6674

MacDonald NW, Burton AJ, Liechty HO, Witter JA, Pregitzer KS, Mroz GD, Richter DD (1992) Ion leaching in forest ecosystems along a Great Lakes air pollution gradient. J Environ Qual 21:614–623

McClure JW, Lee TD, Leak WB (2000) Gap capture in northern hardwoods: patterns of establishment an height growth in four species. For Ecol Manage 127:181–189

McDowell WH, Likens GE (1988) Origin, composition, and flux of dissolved organic carbon in the Hubbard Brook Valley. Ecol Monogr 58:177–195

McNulty SG, Aber JD, Boone RD (1991) Spatial changes in forest floor and foliar chemistry of spruce-fir forests across New England. Biogeochemistry 14:13–29

Michalzik B, Dorsch T, Matzner E (1997) Stability of dissolved organic nitrogen and mineral nitrogen in bulk precipitation and throughfall. Z Pflanzenernährung Bodenkunde 160:433–434

Mladenoff DJ (1987) Dynamics of nitrogen mineralization and nitrification in hemlock and hardwood treefall gaps. Ecology 68:1171–1180

National Atmospheric Deposition Program (NADP) (2007) Annual data summary for Houghton County, Chassel station MI99, http://www.nadp.sws.uiuc.edu/sites/siteinfo.asp?net=NTN&id=MI99, 12 Apr 2007

National Oceanic and Atmospheric Administration (NOAA) (2007) Climatological data national summary. Environmental Data Service National Climatic Center, North Carolina. Big Bay 8 NW at 46°53’N and 87°52’W and Ontonagon 6 SE at 46°50’N and 89°12’W, http://www.ncdc.noaa.gov/oa/climate/stationlocator.html, 03 Feb 2007

Oakton pH/CON 510 Series Multiparameter Meters, Fisher Scientific

Onset Computer Corporation (2003) Pocasset, Massachusetts

Palik BJ, Pregitzer KS (1992) A comparison of pre-settlement and present-day forests on two big tooth aspen-dominated landscapes in northern lower Michigan. Am Midl Nat 127:327–338

Parker GG (1983) Throughfall and stemflow in the forest nutrient cycle. Adv Ecol Res 13:57–133

Parsons WFJ, Knight DH, Miller SL (1994a) Root gap dynamics and forest disturbance theory in lodgepole pine forests: nitrogen transformations in gaps of different size. Ecol Appl 4:354–362

Parsons WFJ, Knight DH, Miller SL (1994b) Root gap dynamics in lodgepole pine forests: ectomycorrhizal and nonmycorrhizal fine root activity after experimental gap formation. Can J For Res 24:1531–1538

Pastor J, Broschat M (1990) The spatial pattern of a northern confier hardwood landscape. Landsc Ecol 4:55–68

Phillips DW, McCulloch JAW (1972) The climate of the Great Lakes Basin. Climatological Studies Number 20. Atmospheric Environment Service Environment Canada, Toronto

Prescott CE, Hope GD, Blevins LL (2003) Effect of gap size on litter decomposition and soil nitrate concentrations in a high-elevation spruce-fir forest. Can J For Res 33:2210–2220

Qualls RG, Haines BL, Swank WT, Tyler SW (2000) Soluble organic and inorganic nutrient fluxes in clearcut and mature deciduous forests. Soil Sci Soc Am J 64:1068–1077

Ritter E, Vesterdal L (2006) Gap formation in Danish beech (*Fagus sylvatica* L.) forests of low management intensity: soil moisture and nitrate in soil solution. Eur J For Res 125:139–150

Ritter E, Starr M, Vesterdal L (2005) Losses of nitrate from gaps of different sizes in a managed beech (Fagus sylvatica) forest. Can J For Res 35:308–319

Runkle JR (1992) Guidelines and sample protocol for sampling forest gaps. General Techniques Reproduction PNW GTR 283 U.S. Department of Agriculture, Forest Service, Pacific Northwest Resource Station

SAS Institute (2005) JMP Ver 6. SAS Institute Inc. North Carolina

Scharenbroch BC, Bockheim JG (2007) Impacts of forest gaps on soil properties and processes in old growth northern hardwood-hemlock forests. Plant Soil 294:219–233

Seymour RS, White AS, deMaynadier PG (2002) Natural disturbance regimes in northeastern North America: evaluating silvicultural systems using natural scales and frequencies. For Ecol Manage 155:357–367

Sims GK, Ellsworth TR, Mulvaney RL (1995) Microscale determination of inorganic nitrogen in water and soil extracts. Commun Soil Sci Plant Anal 26:303–316

Soil Moisture Corportation (2007) Soil water sampler #1900. Goleta, California, USA

Starr M (1999) WATBAL: a model for estimating monthly water balance components, including soil water fluxes. In: Kleemola S, Forsius M (eds) 8th annual report 1999 UN ECE ICP integrated monitoring, the Finnish environment 325, Finnish Environment Institute, Helsinki, Finland, pp 31–35

Tyrrell LE, Crow TR (1994) Structural characteristics of old-growth hemlock-hardwood forests in relation to age. Ecology 75:370–386

United States Department of Agriculture, National Resources Conservation Service (USDA NRCS) (2006) Keys to soil taxonomy, 10th edn. National Cooperative Soil Survey, Madison, WI

Van Miegroet H, Cole DW, Foster NW (1992) Nitrogen chemistry, deposition, and cycling in forests: summary and conclusions. In: Johnson DW, Lindberg SE (eds) Atmospheric deposition and forest nutrient cycling. Ecological Studies 91, Springer-Verlag, New York

Vitousek PM, Reiners WA (1975) Ecosystem succession and nutrient retention: a hypothesis. BioScience 25:376–381

Vitousek PM, Gosz JR, Grier CC, Melillo JM, Reiners WA, Todd RL (1979) Nitrate losses from disturbed ecosystems. Science 204:469–474

Williams MW, Brooks PD, Moiser A, Tonnessen KA (1996) Mineral nitrogen transformations in and under seasonal snow in high-elevation catchment in the Rocky Mountains, United States. Water Resour Res 32:3161–3171

Woods KD (2000) Long-term change and spatial pattern in a late-successional hemlock-northern hardwood forest. J Ecol 88:267–282

Woods KD (2004) Intermediate disturbance in a late-successional hemlock-northern hardwood forest. J Ecol 92:464–476

Zak DR, Groffmann PM, Pregitzer KS, Christensen S, Tiedje JM (1990) The vernal dam: plant-microbe competition for nitrogen in northern hardwood forests. Ecology 71:651–656

Zhang Q, Zak JC (1995) Effects of gap size on litter decomposition and microbial activity in a subtropical forest. Ecology 76:2196–2204