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Retention and leaching losses of atmospherically-derived nitrogen in the aggrading coastal watershed of Waquoit Bay, MA

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Abstract. Extensive areas of the eastern United States are being exposed to elevated levels of nitrogen in precipitation, with levels of inorganic N in wet deposition ranging from 5 to over 20 times preindustrial, background levels. This increase in N loading to the terrestrial system, coupled with changes in land use in coastal regions in particular, has dramatically increased the level of nutrient loading from watersheds to the point that coastal waters are today among the most intensely fertilized ecosystems on earth. Studies in upland, aggrading forests have generally found that precipitation N inputs are efficiently sequestered in forest biomass and soil organic matter. However, acidic soils, sandy, porous parent substrates, and chronic inputs of salt spray common to coastal watersheds may all reduce the potential for N sequestration by the terrestrial community.

We assessed the role of coastal forests in the long-term storage and retention of atmospherically-derived N in the watersheds of Waquoit Bay, MA, an increasingly eutrophic estuary on Cape Cod, by measuring precipitation inputs, storage, and lysimeter outputs below the rooting zone in a chronosequence of sites released from agriculture at different times. Calculated annual retention efficiencies were relatively low for an N-limited, aggrading forest (40–62%), and leaching losses did not vary with site age from young pine stands to mature beech forests. Nearly all nitrogen input was retained during summer months except in months with very high rainfall events. Nitrogen was released during the dormant-season in proportion to water flux through the forest floor. The composition of lysimeter output was 76% DON, 11% NO_3^-, and 13% NH_4^+. Total water flux and infiltration appear to be more important determinants of N retention in this sandy, coastal site than in more upland forest ecosystems; sandy systems may inherently have a low N retention efficiency.

Introduction

Intense urbanization and development have occurred on watersheds that adjoin coastal waters over the past few decades. This change in land use has dramatically increased the level of nutrient loading from watersheds to the point that coastal waters are today among the most intensely fertilized ecosystems on earth (Nixon et al. 1986). Nitrogen delivered to coastal waters from adjacent watersheds can lead to the eutrophication of the receiving marine ecosystem, as it is generally considered to be the limiting nutrient for primary production in estuaries (Howarth 1988). Understanding and managing both point and non-point sources of N to coastal receiving waters is a critical management goal for coastal zone protection.

The most obvious and easily quantifiable sources of N to estuaries are trial wastewater. Non-point sources of N, including runoff and leachate from agricultural areas, septic inputs (where present), and precipitation, are more difficult to quantify (Jordan et al. 1986; Jaworski et al. 1992; Fisher & Oppenheimer 1991). The relative dominance and the respective fates of these non-point sources are not well understood. For instance, a percentage of septic N may be denitrified or otherwise attenuated in transit to the receiving estuary (Weiskel & Howes 1992); similarly, fertilizer N may be variably retained as it moves through hydrologically linked ecosystems in the landscape (Correll et al. 1992).

In many regions of the world, the magnitude of N delivered by atmospheric deposition to watersheds may rival these other sources. Extensive areas of the eastern United States are being exposed to elevated levels of nitrogen in precipitation, with levels of inorganic N in wet deposition ranging from 5 to over 20 times preindustrial levels (Shannon & Sisterson 1992; Aber et al. 1993). There are several possible fates for this atmospherically-deposited N in inland forests, including uptake by plant roots and storage in vegetative biomass, immobilization by soil microbes, denitrification that results in a loss of N_2 and N_2O to the atmosphere, sorption of ammonium in the mineral soil, and percolation to groundwater with subsequent delivery to coastal waters. Studies in upland forests have generally found that atmospheric N inputs are efficiently sequestered by young successional forests that are rapidly accumulating biomass in vegetation and soils (Bormann et al. 1977; Vitousek & Reiners 1975; Pearson et al. 1987). Accordingly, groundwater or stream runoff from aggrading upland forests would contribute little to nutrient loading of receiving waters. However, retention of N by terrestrial vegetation may also depend on amounts of anthropogenic nitrogen inputs. The ability of forests to retain N may be saturated in systems receiving high rates of N deposition, with consequent higher levels of N loss by leaching (Nilsson 1986; Ågren & Bosatta 1988; Skeffington & Wilson 1988; Aber et al. 1989).

The situation in coastal ecosystems is less clear. Salt marshes can be sinks for nutrients coming from upland ecosystems, net sources of nutrients, or transformers of inorganic nutrients to organic forms (Valiela et al. 1978; Simpson et al. 1983; Nixon et al. 1986; Craft et al. 1989). Landscape position appears to be critical; riparian and floodplain forests positioned between agricultural areas and receiving waters are generally net sinks for nutrients delivered by runoff (Correll & Weller 1989; Peterjohn & Correll 1984; Brinson et al. 1984; Lowrance et al. 1984; Schlosser & Karr 1981). Soil porosity may also affect the degree of nutrient retention by coastal forest soils and vegetation. Coastal forests developed on coarse, sandy soils may not retain N as efficiently as upland forests (Blood et al. 1989), even without N loading from atmospheric deposition. Leaching of ammonium may also be greater in coastal systems with chronic inputs of sea salt spray (Blood et al. 1989; Duckworth & Cresser 1991). In addition, increasing urbanization decreases forest area and adds wastewater effluent, both of which contribute to increased delivery of N to aquifers. As N loading to coastal systems continues to increase, it is imperative that we understand the role of forest ecosystems in the retention of atmospherically-derived nutrient inputs.

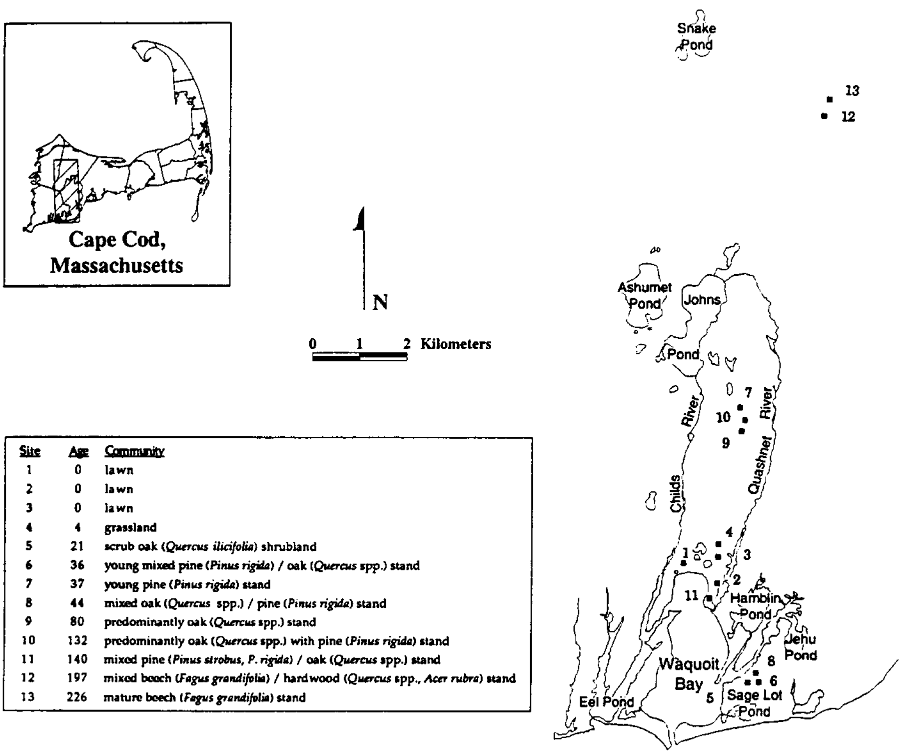
The Waquoit Bay watershed, like most of Cape Cod, has undergone large scale residential development within the last few decades. The rate of growth in housing units in Barnstable County, which includes all of Cape Cod, was 35% between 1980 and 1990, the highest of all mainland Massachusetts counties (Valiela et al. 1992). Increases in urbanization have lead to increases in the production of wastewater and, subsequently, in N loading. Valiela & Costa (1988) attributed the majority of N loading to the estuary to effluent from septic tanks, based on the assumption that virtually all of the N delivered to the watershed by atmospheric deposition would be sequestered by forests that cover the watershed. Like much of New England, vegetation in the watershed represents a mosaic of growing secondary forests of various ages that are recovering from widespread agricultural clearing, and thus are accumulating N in soils and perennial tissues.

In this study, we examined the ability of Cape Cod forests to sequester atmospheric N inputs. We also examined whether retention of precipitation N depends on forest successional status or on seasonality of precipitation and total water flux through the forest floor and soil horizons. Based on paradigms of forest ecosystem function derived from upland forest studies, we expected that younger pine-dominated stands would show lower nutrient losses than older, uncut hardwood-dominated stands. We also predicted that N retention would be higher during the growing season than during dormant seasons, but would be low during large rainfall events in which there was high water flux through the soil due to high soil porosity.

Methods

Location and field sites

The Waquoit Bay watershed is located on the southwestern shore of Cape Cod, Massachusetts (41°34′ N, 70°32′ W). Annual rainfall for the area ranges from about 100 to 130 cm and shows little seasonal variation. The soils of the region are mostly sandy loams of glacial origin with occasional deposits of lacustrine silts and clays (Oldale 1976). The area is primarily drained by infiltration to groundwater as slopes are gentle and there is virtually no surface runoff.



Site	Age	Community
1	0	lawn
2	0	lawn
3	0	lawn
4	4	grassland
5	21	scrub oak (*Quercus ilicifolia*) shrubland
6	36	young mixed pine (*Pinus rigida*) / oak (*Quercus* spp.) stand
7	37	young pine (*Pinus rigida*) stand
8	44	mixed oak (*Quercus* spp.) / pine (*Pinus rigida*) stand
9	80	predominantly oak (*Quercus* spp.) stand
10	132	predominantly oak (*Quercus* spp.) with pine (*Pinus rigida*) stand
11	140	mixed pine (*Pinus strobus, P. rigida*) / oak (*Quercus* spp.) stand
12	197	mixed beech (*Fagus grandifolia*) / hardwood (*Quercus* spp., *Acer rubra*) stand
13	226	mature beech (*Fagus grandifolia*) stand

Fig. 1. Location of the subwatersheds of Waquoit Bay, Massachusetts.

Because different areas within the watershed were released from clearing at different times, stages of the successional sequence ranging from grassland and shrubland to young, pitch pine (*Pinus rigida*)-dominated stands to mixed hardwood forests composed of pitch pine and various oak (*Quercus*) species are present within the watershed boundaries. In 1990, 13 sites were selected in the Waquoit Bay watershed that represents the full successional gradient of the inner Cape (Fig. 1).

Forest inventory and nutrient budgets

The rates at which coastal forests store and retain atmospherically-derived nitrogen was measured by analyzing nutrient contents of vegetation, soils, and the forest floor along the chronosequence. Forest biomass inventories were conducted in 0.1 ha subplots at each site where woody vegetation was present. Diameter and height of all trees in each subplot were measured. Branch, woody stem, and leaf biomass were then estimated using speciesspecific allometric equations (compiled in Tritton & Hornbeck 1982). When possible, allometric equations developed in similar sandy, coastal sites (such as Brookhaven) were chosen. Woody core, twig, and leaf samples were collected from the dominant species at each site for CHN analysis. Three random points were chosen at each site for the analysis of soil organic C and total N content. Three 30 cm cores were taken near each point and composited to yield 3 composite samples/site. Forest floor biomass was measured at each of these points with a 0.25 m^2 quadrat sampler in late August of 1991, when it was assumed that litter accumulation would represent seasonal minima, and thus permanent standing stock. C and N contents of all soil and plant materials were measured with a Perkin-Elmer 2400 CHN analyzer.

Ages of the largest three trees in each subplot were estimated from incremental coring. In the case of pine plots, the oldest core age was assigned to the plot. Although pines may not invade a newly-released plot immediately, we felt that this slight underestimate of plot age would be very small. In oak sites, the age of the oldest oak would be a more serious underestimate of the true plot age, and thus the age of our oldest pine-only site (37 years) was added to these estimates. A similar calculation was made for beech-dominated sites.

Precipitation, throughfall, stemflow and lysimeter collection

Bulk precipitation was collected in vegetation clearings at two sites within the watershed. Bulk precipitation samples for nutrient analysis were collected in six 750 ml, 10.5 cm diameter polyethylene bottles with suspended, screened funnels to exclude insects and other debris. Precipitation volume was measured in calibrated rainfall gauges immediately after each rainfall event. Throughfall samples were collected at all sites with the same type of collectors used for bulk precipitation. At least 10 throughfall collectors at each site were randomly placed so that openings were 0.5 m above the soil surface. Stemflow collectors were made from garden watering hoses cut in half lengthwise. Inner edges of the hoses were wrapped twice around the trunks of 3 randomly chosen trees at each forested site, and nailed and cemented to trunks to ensure continuous contact, with outlets to covered buckets.

Measurements of total wet, dry, and fog/cloud inputs of N to forested ecosystems are difficult, and even the most detailed studies must use models to estimate factors such as canopy capture and gaseous inputs. Bulk deposition collectors or bucket wet/dry collectors may seriously underestimate total N inputs. We thus estimated total N inputs in two different ways. The first method was based on measured N inputs in throughfall. Throughfall inputs have been used to estimate wash-off of dry deposition from canopies, yet differ from true total deposition by the amount of canopy uptake or leaching

(Parker 1983; Friedland et al. 1991). Quantitative estimates of canopy uptake are difficult and have not been made in many cases, although sites that were part of the Integrated Forest Study (IFS) network estimated canopy capture by differences between total inputs and throughfall outputs. Over a wide variety of forest types and N deposition rates, net canopy uptake was estimated as approximately 16% of inputs ($r^2 = 0.89$, Lovett & Lindberg 1993). Thus we adjusted our measured total (DIN + DON) N inputs in throughfall for this average estimate of canopy uptake. Measurements of stemflow demonstrated that it was a minor input (<5%) compared to throughfall, and thus was ignored in the calculation of total input. Low stemflow values have also been observed in similar forests (Qualls & Haines 1991; Eaton et al. 1973); maximum values appear to be in the range of 15% (Lovett et al. 1989). The second method used measured wet-only DIN in precipitation, and was adjusted for an estimate of dry deposition input using the IFS regression between wet-only DIN and total N inputs for low-elevation sites (total inputs = 2.09 × wet-only DIN, $r^2 = 0.91$; Lovett & Lindberg 1993).

Zero-tension lysimeters were used to measure N leaching below the rooting zone. Although more difficult to install than tension lysimeters, zero-tension lysimeters are simpler to maintain in the field and provide a more accurate estimate of soil solution water that is flowing through the soil profile (Hendershot & Courchesne 1991; Jemison & Fox 1992). Zero-tension lysimeters will also more accurately reflect contributions from macropore flow (Joslin et al. 1987; Radulovich & Sollins 1987; Simmons & Baker 1993) and avoid potential adsorption effects suspected of vacuum porous cup samplers (McGuire et al. 1992). Zero-tension lysimeters were constructed from polyethylene funnels, 15 cm in diameter, filled with acid-washed beach sand and connected to a collecting bottle. At each site, two central pits were dug to a depth of 1 m, and at a depth of 50 cm, which was determined to be below the rooting zone of the dominant tree species in even the oldest sites, four small side tunnels, one in each compass direction, were horizontally excavated by hand to a distance of 30 cm from the central pit so that the overlying soil horizons remained undisturbed. The lysimeters were pressed against the top surface of the soil at the end of the tunnels in order to maximize collection efficiency (Radulovich & Sollins 1987). Tygon tubing with valve clips from the collecting bottles were threaded back through tunnels into the central pit and to the surface for leachate collection, and all pits were backfilled with the original soil. The lysimeters were installed in August 1990 and were allowed to equilibrate for 8 months to avoid a high spring N-flush that can result form installation disturbance effects (Shepard et al. 1990).

Collections from throughfall, precipitation, and lysimeter samplers were made after every rainstorm event between April 1991 and December 1992.

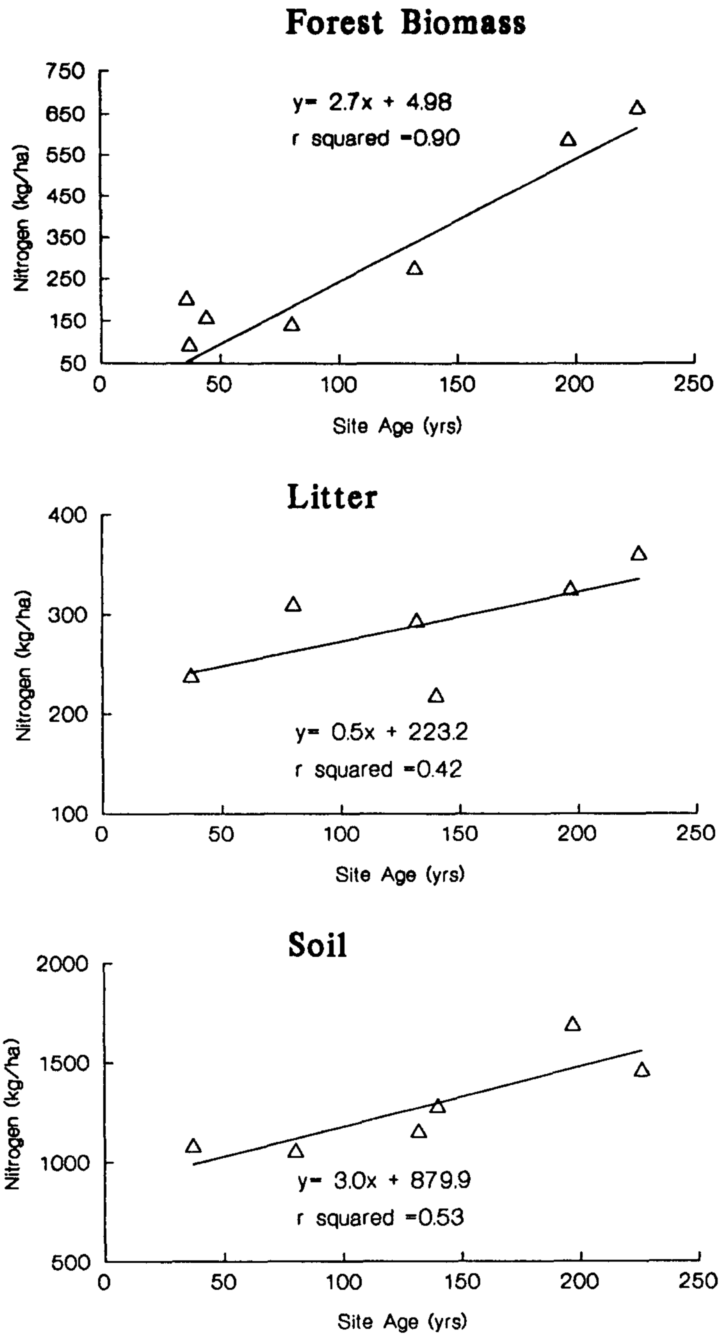


Fig. 2. Total nitrogen contents in different ecosystem components (soil organic matter, forest floor litter, tree aboveground biomass) of the aggrading forests of Waquoit Bay. The calculated regression slopes were used as annual accumulation terms in the overall watershed N budget.

All samples were collected in acid washed 40 ml polypropylene bottles and were immediately transported to the lab for processing. One aliquot of each sample was filtered for DIN analysis and another was left unfiltered for total N analysis. All subsamples were acidified to a pH 4.0–4.5 with 5 N HCl and stored at 5 °C until analysis. The filtered samples were analyzed for DIN (NH_4^+ and NO_3^-) colorimetrically using a Lachat autoanalyzer; the unfiltered samples were analyzed for total nitrogen after persulfate digestion (D'Elia et al. 1977).

Calculation of water flux and nitrogen retention

Because zero-tension lysimeters generally and variably underestimate leachate volumes (Radulovich & Sollins 1987; Vitousek 1983), we calculated water flux from the forest floor to below the rooting zone independently from the lysimeter volumes using a simple tipping bucket type model with a monthly time step, driven by PET, soil water storage capacity, rooting depth and climate data (Fetter 1988). Soil water storage capacity was obtained empirically from soil cores brought to the laboratory, and monthly PET values were estimated with the Penman-Montieth equation (Penman 1948) using daily precipitation and temperature values from the nearby Hatchville weather station. Surface runoff was ignored in this calculation as it is extremely low in the coarse-sandy soils of Cape Cod.

Monthly N retention efficiency was calculated as (N inputs – N outputs)/N inputs. Measured lysimeter total N concentrations were used in conjunction with modeled soil infiltration flux to calculate net losses of N below the rooting zone. Total (DIN + DON) N in throughfall was used to represent N delivered to the surface of the forest floor that was available for uptake by plant roots and soils. This measured throughfall was also close to the midpoint of the two independent total N input estimates; patterns of monthly N retention remained identical when these other input estimates were used.

Results

Total N stored in biomass, soils, and litter increased with stand age (Fig. 2). Least-squares regression of means at each site were used to derive an estimate of annual permanent storage of N over the chronosequence. The accumulation rate of N in soils was slightly higher than that in vegetation, and both were significantly higher than annual accumulation in forest floor litter. Although total N in soils increased with age, total C in soils did not change significantly (Fig. 3a, b), leading to a decrease in soil C:N over the chronosequence (Fig. 3c). This is most likely due to changes in litter quality resulting from the change from pine to hardwood species composition with successional age.

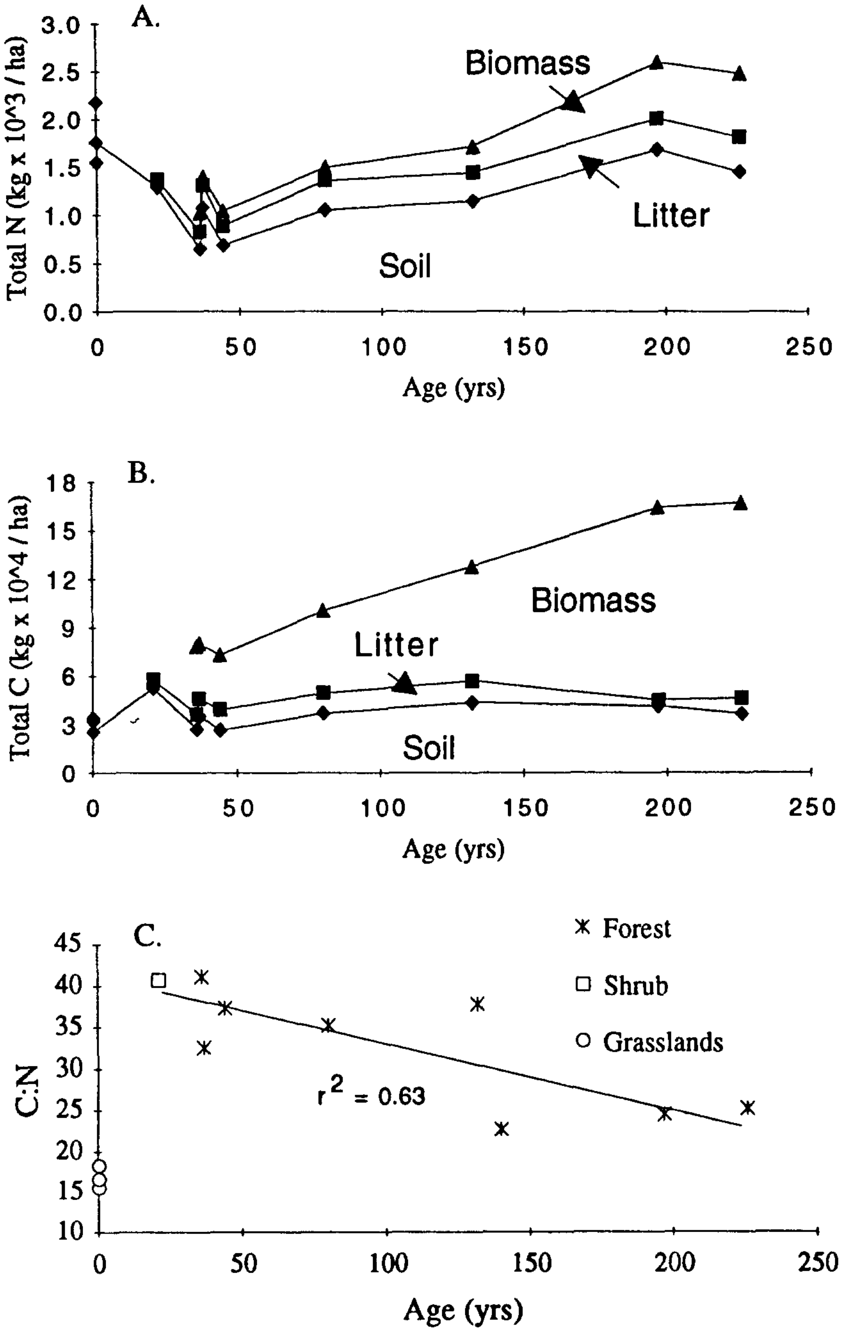


Fig. 3. Accumulation of (A) total N and (B) total C in ecosystem components, and (C) change in soil C:N with stand age in forests, shrublands, and lawns of the Waquoit Bay watershed chronosequence.

Live pitch pine needles averaged 0.83 ± 0.09% N, oak leaves averaged 1.66 ± 0.1% N, and beech leaves averaged 1.93 ± 0.12% N; litter from these species averaged 0.78 ± 0.06, 1.17 ± 0.06, and 1.65 ± 0.13% N, respectively. Total N stored in soils of the lawns was relatively high although total C was not, reflecting a very low soil C:N common to grasslands. Shrubland soil C and N contents were higher than the youngest forest sites, although this may have been due to collection contamination with understory plants and lichens.

There were no statistically significant differences in either N concentrations or total N losses to lysimeters among sites. TN and DIN losses were not related to stand age even when data were grouped by individual events or by seasons (Fig. 4). DIN concentrations were lowest in the youngest sites, particularly in grassland and lawn sites, but this trend was offset by higher DON concentrations at these sites. Thus all sites were combined for calculations of total N leaching losses by season or by year. Averaged over all sites, DIN concentrations were slightly, although not significantly lower during the growing season than during the dormant season. However, TN concentrations were higher during the growing season than during the dormant season ($P = 0.010$) most likely due to decreased water flux to lysimeters during the season of highest evapotranspiration. Although accumulation of leachate in lysimeters was extremely seasonal, with high flow observed primarily in late fall–early spring, concentrations of DIN and TN in lysimeters were not related to precipitation or throughfall volume. Thus calculated leaching losses of N closely followed patterns of modeled water flux to below the rooting zone (Fig. 5a–c), and were also significantly related to amount of precipitation and season. During the dormant season, losses of N were significantly correlated to precipitation volume ($r^2 = 0.42$, $P < 0.03$), yet during summer months, leaching of N only occurred during extreme rainfall events (Fig. 6).

As precipitation passed through the canopy to the forest floor and through to lysimeters, both the concentrations and the forms of N changed (Fig. 7). Precipitation and throughfall measurements are not directly comparable as we only measured DIN in precipitation, yet concentrations and contents of DIN did not differ significantly between precipitation and throughfall. All three components decreased significantly with passage through the forest floor and soils. Concentrations of NH_4^+ and NO_3^- were approximately equal in lysimeter leachates.

Annual DIN inputs via precipitation averaged 4.2 kg N ha^{-1} yr^{-1}, and thus total inputs of N calculated using the IFS wet:dry regression were calculated as 8.4 kg N ha^{-1} yr^{-1}. Total (DIN + DON) N inputs via throughfall were 11.3 kg N ha^{-1} yr^{-1}, and thus total inputs of N calculated using the IFS canopy exchange: throughfall regression were 13.1 kg N ha^{-1} yr^{-1}. Using these input terms, coupled with calculations of N storage and leaching outputs, we

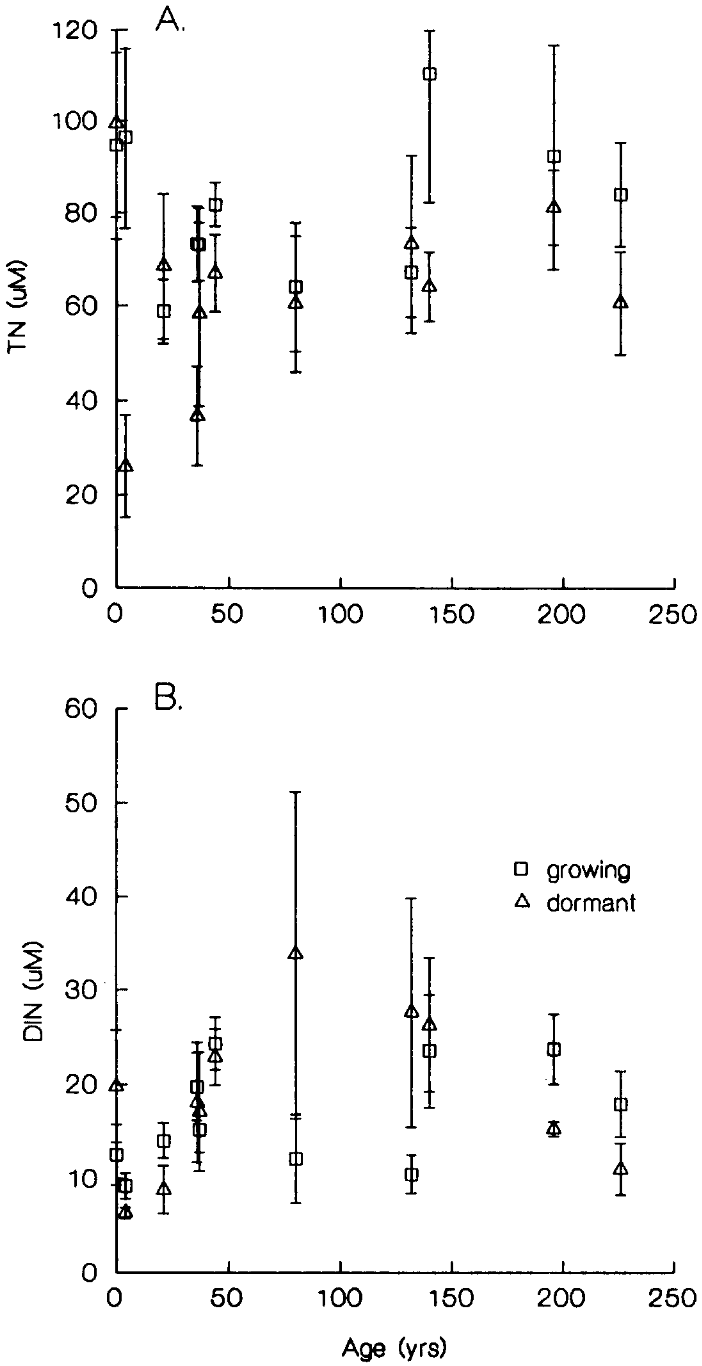


Fig. 4. Concentration of (A) TN and (B) DIN ($NH_4^+ + NO_3^-$) in lysimeters during the growing and dormant seasons over the Waquoit Bay watershed chronosequence.

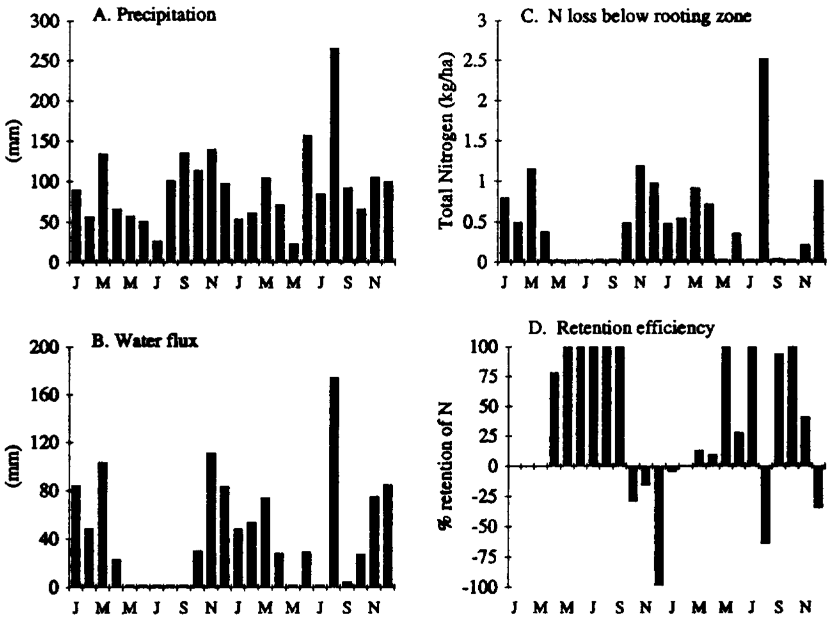


Fig. 5. (A) Monthly precipitation inputs to the watershed, (B) water flux outputs to below the rooting zone, (C) monthly N outputs from below the rooting zone, and (D) retention efficiency (calculated as (total throughfall inputs of N − lysimeter N losses)/throughfall N inputs) in the Waquoit Bay watershed from 1991–1992. Positive values for retention efficiency in (D) indicate that losses to lysimeters were lower than inputs, indicating retention; negative values indicate flushing of N, or that losses to lysimeters were greater than inputs.

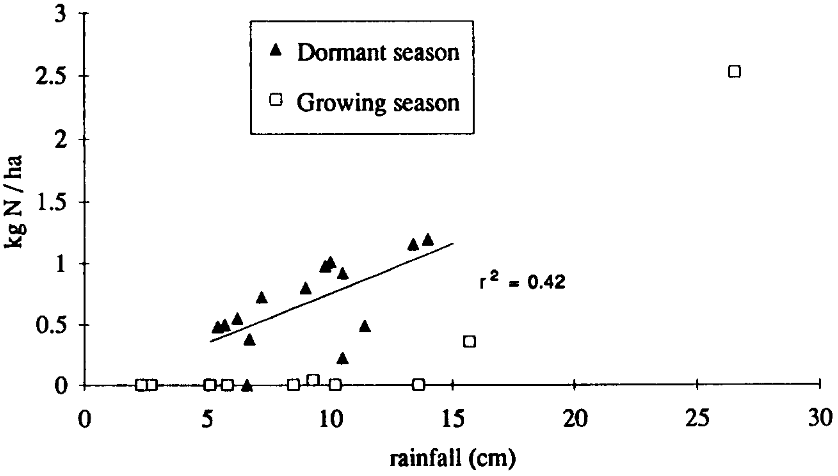


Fig. 6. Nitrogen outputs to lysimeters vs. rainfall, calculated on a monthly basis, in the Waquoit Bay watershed from 1991–1992. The growing season was defined as May–September. The regression is based on dormant season values only.

Table 1. Nitrogen budget ($x \pm$ se) for the Waquoit Bay watershed. Total inputs were calculated using either throughfall (DIN + DON) measurements coupled with estimates of net canopy uptake, or wet-only DIN in precipitation coupled with estimates of dry deposition. Standard errors were calculated using error propagation (Meyer 1975).

	N fluxes (kg N/ha/yr)				
	Throughfall		Precipitation		
	x	(se)	*x*	(se)	Source
Inputs					
Wet-only DIN			4.2	0.2	Measured
Dry			4.2	0.2	Estimated from wet deposition*
Cloud/fog	?				Not measured
N-fixation	<1				Estimated from literature values**
Throughfall	11.3	0.3			Measured
Canopy uptake	1.8				Estimated from literature values***
	13.1	**0.3**	**8.4**	**0.3**	
Storage					
Soil accum.	3.0	0.9			Measured
Litter accum.	0.5	0.3			Measured
Aboveground biomass	2.7	0.4			Measured
Belowground biomass	1.1	0.2			Estimated from aboveground biomass****
	7.3	**1.0**			

Table 1. (continued)

	N fluxes (kg N/ha/yr)				
	Throughfall		Precipitation		
	x	(se)	*x*	(se)	Source
Outputs					
Denitrification	<1				Estimated from literature values****
Loss to lysimeters	5.0	0.6			Measured
	5.0	**0.6**			
Imbalance =	**0.8**	**1.2**			

* Based on IFS regression of dry vs. total N deposition (Lovett & Lindberg 1993)

** Bowden et al. (1991)

*** Based on IFS regression of net canopy uptake vs. throughfall total N (Lovett & Lindberg 1993)

**** Based on ratios determined by Friedland et al. (1991)

***** Gundersen (1991)

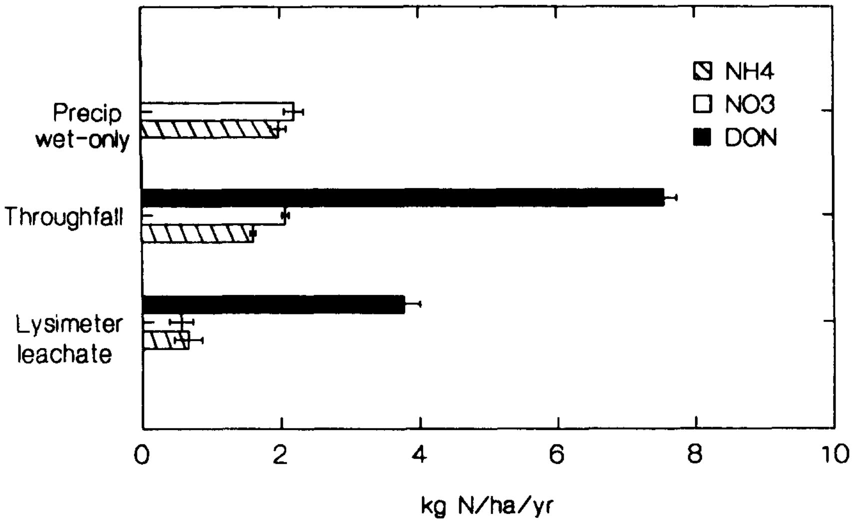


Fig. 7. Annual fluxes of NH_4^+, NO_3^-, and DON in wet-only precipitation, throughfall, and lysimeters.

constructed an N budget for the forested watershed of Waquoit Bay (Table 1). Depending on which estimate of input is used, inputs are either slightly greater (throughfall TN + canopy uptake estimate) or substantially lower (precipitation DIN + dry estimate) than the loss + storage term. This large range in estimates may be caused by the differing assumptions that go into the two regressions. The IFS wet:dry ratio regression was based on low elevation sites only, without significant cloud or fog inputs. Although the Waquoit Bay watershed is at sea level, coastal fog inputs in urban areas, while rarely measured, may be quite high, with N concentrations in urban-influenced coastal fogs significantly greater than mountain cloud water (Kimball et al. 1988). Since these inputs would be reflected in throughfall, we relied on the throughfall calculation in our budget of N for the watershed.

Calculated retention efficiencies of atmospherically-deposited N showed strong seasonal trends (Fig. 5d). Positive net retention generally occurred during the spring and summer, with the exception of August 1992, when total rainfall was exceptionally high. Net negative retention occurred in most fall and winter months, suggesting a release of stored N. Total annual N retention efficiency was 40–62%, using the range of input values for N calculated from either precipitation or throughfall, respectively.

Discussion

Our estimate of N storage within the forests is low compared to many reports from aggrading upland forests (Bormann & Likens 1979; Monk & Day 1988), as would be expected for a coastal sand plain forest. The calculated accumulation rate of 2.7 kg N ha^{-1} yr^{-1} in live trees is similar or lower than rates measured in lodgepole pine stands (Pearson et al. 1987). Accumulation in soil was the greatest sink for N, presumably due to the fact that most N taken up by plants was translocated to leaves which then formed decomposable litter. The watershed's soil C and N pool sizes are much lower than means reported for IFS sites of upland forests generally, but are quite similar to comparable systems, such as Florida slash pine (Van Miegroet et al. 1992).

Total N retention efficiency, calculated as the percentage of N input to the watershed that did not leach past the rooting zone, was 40–62%, using the range of input values for N calculated from either throughfall or precipitation. This range is relatively low compared to efficiencies calculated for more upland forests. For example, Bormann et al. (1977) calculated an 81% retention of total N inputs to the aggrading Hubbard Brook watershed. Estimates of N retention efficiencies for different land uses and vegetative cover types range from 25–100%, with aggrading upland forests at the high end of that range (Swank & Waide 1988; Hinga et al. 1991; Fisher & Oppenheimer 1991; Jaworski et al. 1992; Aber et al. 1993). Conversion of forests to urbanized or agricultural landscapes generally decreases retention efficiencies (Hinga et al. 1991), although Scudlark & Church (1993) estimated an 80% retention efficiency for the partially urbanized Delaware Bay estuary.

Surprisingly, a set of integrated measurements of N dynamics in a series of US forests with varying N deposition rates found little relationship between ecosystem N retention and N deposition (Johnson 1992), perhaps due to differences in forest successional status or soil retention capacities among the sites. However, various authors have suggested that the prospects for forests becoming 'N saturated' from atmospheric N inputs will continue to increase as N levels in deposition remain high, or as 'critical loads' of N deposition are reached (Nilsson 1986; Ågren & Bosatta 1988; Skeffington & Wilson 1988; Aber et al. 1989). Evidence for a relationship between atmospheric N loading and N leaching has come primarily from long-term stream N concentration data and from stream intersite comparisons (Kahl et al. 1993; Driscoll et al. 1989; Murdoch & Stoddard 1992). Results from fertilization experiments that attempt to induce N saturation in forests, or from existing gradients in N deposition, have proved inconsistent. Even after 3 years of chronic N fertilization in the Harvard Forest, retention of N was nearly 100% in all but one high-application pine plot (Aber et al. 1993). Similarly, MacDonald et al. (1992) found no relationship between N inputs and N or cation losses along a gradient of NO_3^- deposition in the Great Lakes region. However, Kahl et al. (1993), using relatively modest fertilizer loading rates of N, was able to induce N saturation in a paired-catchment experiment at the Bear Brook Watershed in Maine (BBWM) as evidenced by elevated stream NO_3^- concentrations. These authors suggested that the BBWM site may have been close to N saturation prior to treatment, however, as soil C:N ratios were relatively low, forest floor N concentrations relatively high, and N retention prior to treatment (50% of N in wet deposition, or 75% of wet + dry deposition) was relatively low compared to other nearby low-elevation sites.

Part of this lack of a correlation between N inputs and N retention may be due to methodological differences among different studies. Studies of ecosystem N budgets have calculated the output, or loss term from zero-tension lysimeters placed below the rooting zone (e.g. this study, Shepard et al. 1990; Russell & Ewel 1985; Radulovich & Sollins 1987), tension lysimeters (e.g. Aber et al. 1993; Friedland et al. 1991; Emmett et al. 1993; Shepard et al. 1990; Mitchell et al. 1992), or, most commonly, from streamwater concentrations (e.g. Likens et al. 1977; Swank & Waide 1988; Kelly 1988; Stottlemyer & Troendle 1992; Kahl et al. 1993). Studies using lysimeters do not always measure DON concentrations in outputs, although these may be significant (Friedland et al. 1991; Qualls & Haines 1991). Streamwater outputs cannot be compared to data from lysimeter outputs, which measure retention processes only within the terrestrial ecosystem, as significant in-stream or riparian processing will occur and may account for the greatest losses of N from the system (Haycock et al. 1993; Correll et al. 1992). For example, under quite high (53 kg N ha^{-1} yr^{-1}) N loading rates in the Netherlands, Tietma & Verstraten (1991) found that denitrification in groundwater accounted for 66% of inputs; it is quite possible that as the ability of many forests to retain N becomes saturated, in-stream or groundwater processing of N may become more important in determining outputs to receiving waters. Correll & Weller (1989) similarly showed the increased importance of denitrification in riparian forests with high N loading from cropland drainage. In addition, Johnson (1992) suggested that fertilization experiments may not accurately simulate pollution-enhanced atmospheric deposition of N, but rather might underestimate N losses. He hypothesized that small, frequent inputs of N via atmospheric deposition would favor nitrification, thereby increasing N leaching and lowering soil retention, whereas fertilization, particularly with NH_4^+, would favor abiotic reactions with humus or clays, and thus increased N retention.

Seasonal patterns of N retention, such as those found in this study, are often seen in ecosystems that exhibit strong seasonality (e.g. Mitchell et al. 1992; Friedland et al. 1991; Shepard et al. 1990; Foster et al. 1989).

Although seasonality of N retention is commonly attributed to plant root activity, we suggest that these patterns may have as much to do with water flux as with patterns of microbial and plant activity. Many studies have found that outputs of nitrate or other ions increased with increasing streamflow, suggesting removal of 'stored' N with increased flow (Jaworski et al. 1992; Kelly 1988; Murdoch & Stoddard 1992; Hill 1993). Seasons of increased biological activity are generally coincident with increased ET and low flow, confounding these two factors. In our study, a net negative retention of N occurred during many months in the dormant season (Fig. 5), as well as during one month of very high rainfall in the summer, which suggest that biological retention of N during the growing season has only a partial role in the retention of N within the terrestrial ecosystem.

Nitrogen saturation has been defined as a level of N input that will no longer increase primary production (Nilsson 1986), or an N input that exceeds the capacity of biota to retain the input (Aber et al. 1989). N saturation is detected when there is increased leaching of NO_3^- (Aber et al. 1989; Gundersen 1991). However, there are several reasons that N leaching could occur, even in N-limited ecosystems. For example, snowmelt runoff may occur without significant interaction with terrestrial plants or soils (Galloway et al. 1987; Rascher et al. 1987), leading to large inputs of N to receiving lakes. Mountainous regions with high percentages of bare rock or thin soil may also exhibit low ecosystem N retention (Baron et al. 1994). Similarly, in highly sandy or porous soils with high infiltration rates, rapid flow of water through the forest floor should be correlated to inefficient removal of N in the B horizon (Joslin et al. 1987), even when vegetation responds to N fertilization, as is true for the forests of the Waquoit Bay watershed (Jordan 1989).

The composition of lysimeter water in this study was 76% DON, 11% NO_3^-, and 13% NH_4^+. This loss via DON is high compared to loss rates found by Friedland et al. (1991), perhaps due to our highly porous soils with low sorption capacities for DON. The relatively high percentage of NH_4^+ leaching seen in this study is also unusual relative to studies in more upland forests, yet in agreement with results found by Woodwell (1979) in a study of the pine barrens vegetation of Long Island that has developed on a similar substrate. High losses of NH_4^+ may stem from low nitrification potentials due to low soil pH, low sorption rates in low organic matter sandy soils with low cation exchange capacity, coastal inputs of salt displacing NH_4^+ from exchange sites (Duckworth & Cresser 1991), and/or the high percolation rates causing the rapid movement of precipitation through soils, bypassing nitrifiers. Certainly all of these factors could explain a low N retention efficiency in many coastal forests, even when the vegetation is N-limited.

We had initially predicted that the retention of atmospherically deposited N would be greatest in the youngest stands and would decrease in the oldest sites. However, leaching losses of N to lysimeters was not related to stand age, and in fact did not vary significantly among sites. It appears that water flux and infiltration may be more important determinants of N retention in this sandy, coastal ecosystem than in more upland sites, again leading to a low N retention efficiency in an aggrading, N-limited site.

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