

Biogeochemical Contributions of Tree Islands to Everglades Wetland Landscape Nitrogen Cycling During Seasonal Inundation

Tiffany G. Troxler^{1*} and Daniel L. Childers²

¹*Southeast Environmental Research Center and Department of Biological Sciences, Florida International University, 11200 SW 8th St, Miami, Florida 33199, USA;* ²*Global Institute of Sustainability and School for Sustainability, Arizona State University, Tempe, Arizona 85287, USA*

ABSTRACT

In the Florida Everglades, tree islands are conspicuous heterogeneous elements in the herbaceous wetland landscape. We characterized the biogeochemical role of a seasonally flooded tree island during wet season inundation, specifically examining hydrologically mediated flows of nitrogen (N) and N retention by the tree island. We estimated ecosystem N standing stocks and fluxes, soil and litter N transformation rates, and hydrologic fluxes of N to quantify the net ecosystem N mass flux. Results showed that hydrologic sources of N were dominated by surface water loads of nitrate (NO₃) and ammonium (NH₄). Nitrate immobilization by soils and surficial leaf litter was an important sink for surface water dissolved inorganic N (DIN). We estimated that the net annual DIN retention by a seasonally flooded tree island was $20.5 \pm 5.0 \text{ g m}^{-2}$ during wet season inundation. Based on the

estimated tree island surface water DIN loading rate, a seasonally flooded tree island retained 76% of imported DIN. As such, seasonally flooded tree islands have the potential to retain 55% of DIN entering the marsh landscape via upstream canal overland flow in the wet season. By increasing reactive surface area and DOC availability, we suggest that tree islands promote convergence of elements that enhance DIN retention. Tree islands of this region are thus important components of landscape-scale restoration efforts that seek to reduce sources of anthropogenic DIN to downstream estuaries.

Key words: ecosystem budget; gross mineralization; gross nitrification; denitrification; nitrogen fixation; plant uptake; landscape heterogeneity.

Received 23 September 2008; accepted 6 October 2009;
published online 24 November 2009

Author contributions: TGT conceived of and designed study, performed research, analyzed data, contributed new methods/models, and wrote article. DLC assisted in conceiving of the design, performing the research, writing the article, and supported the research.

*Corresponding author; e-mail: troxler@fiu.edu

INTRODUCTION

Biogeochemical fluxes of heterogeneous elements within landscapes have received considerable scientific attention because these areas are often “hot spots” of biogeochemical activity (McClain and others 2003; Ensign and Doyle 2005; Mitchell and

Branfireun 2005; Duval and Hill 2007; Gribsholt and others 2007; Lewis and others 2007; Boomer and Bedford 2008; Harms and Grimm 2008; Hester and Doyle 2008). However, biogeochemical research, often focusing on nutrient inputs and outputs alone, tends to conceptualize landscapes as homogeneous units, overlooking the biogeochemical contributions of heterogeneous elements. As a consequence, sites of important biogeochemical fluxes may not be adequately characterized. Landscapes that include both terrestrial and aquatic ecosystems are of particular interest because the terrestrial–aquatic interface is identified as an area where nutrient fluxes converge and occur at maximum rates relative to the overall landscape (Kemp and others 1982; McClain and others 2003). As human activities increase nitrogen (N) deposition, alter hydrologic cycles, and modify land cover in watersheds across the globe, increased N loading results in eutrophication of downstream coastal ecosystems (Vitousek and others 1997; Corredor and others 1999; Downing and others 1999). As such, it is critically important to understand how spatial variability of biogeochemical fluxes and nutrient retention in heterogeneous watershed landscapes influences water quality and nutrient loading, as they are inextricably linked (Burt and Pinay 2005).

In the Florida Everglades, tree islands are conspicuous heterogeneous elements of the landscape. Tree islands appear to concentrate large quantities of phosphorus (P) as shown by high soil P concentrations (Orem and others 2002; Wetzel and others 2005, 2008). This function has likely been compromised because up to 60% of tree islands that once existed have been lost since the 1940s (Patterson and Finck 1999). Phosphorus enrichment of Everglades surface water is of concern because P loading has been documented to dramatically change the ecological structure and function of Everglades wetland communities (Newman and others 1996; McCormick and others 2001; Gaiser and others 2005). Phytoplankton bioassays show N limitation in the western region of downstream Florida Bay (Tomas and others 1999). The loss of tree islands is a prime example of the degradation of the Everglades (Sklar and van der Valk 2002), yet the biogeochemical significance of these landscape components has not been characterized.

In wetland landscapes, seasonally flooded forests have been shown to play an important role in retaining surface and subsurface hydrologic sources of N (Correll and others 1992; Hopkinson 1992; Hedin and others 1998). For example, the vegetation and hydrology typical of seasonally flooded tree

islands influences variation of available oxygen in soils but also promotes large carbon (C) stocks relative to the herbaceous marsh landscape (Troxler Gann and others 2005). Thus, mechanisms for N retention and removal can occur by: (1) plant uptake and subsequent accumulation of organic matter, (2) microbial immobilization, and (3) coupled nitrification–denitrification. In a biogeochemical comparison of tree islands with the adjacent herbaceous marshes, we found that tree islands had significantly higher soil bulk P and N content and lower inorganic N in soil porewater (Troxler Gann and others 2005). In this study, we hypothesized that tree islands in the southern Everglades promote greater landscape retention of dissolved inorganic N [DIN: ammonium (NH_4) and nitrate (NO_3)] relative to the marsh system in general. Here, we present a wet season, mass N balance for a seasonally flooded, bayhead tree island to quantify: (1) net ecosystem mass N flux and (2) contribution to whole-landscape N retention. Specifically, we quantified N stocks in plants, soils and water, rates of mineralization, nitrification, NH_4 and NO_3 immobilization, N fixation and denitrification, and hydrologic imports of DIN. We focused our investigation on wet season processes as wetland inundation from an upstream canal is the main source of water (and nutrients) to this system throughout the year.

METHODS

Study Site

The study was conducted in the Everglades National Park Panhandle, also referred to as the C-111 Basin, in the southern Everglades, Florida, USA (Figure 1). Specifically, these are bayhead, fixed tree islands with similar tree island types common throughout the study area (Meeder and others 1996). Tree islands in this area are characterized by peat soils overlying a carbonate substrate, seasonal flooding, and vegetation cover dominated by *Chrysobalanus icaco*, a tropical non-nitrogen-fixing evergreen (cocoplum; Troxler Gann and others 2005). They are typically less than 0.25 ha in size, elliptical in shape, and are aligned with their longer axis parallel to the south–southeast direction of flow. The wetland landscape surrounding these tree islands is dominated by short-hydroperiod sawgrass (*Cladium jamaicense*) marsh with carbonate-derived (marl) soils. Thus, the islands in the study area presumably developed via paludification (Anderson and others 2003a, b). The tree island utilized in this research was part of a larger experiment where long-term measurements of

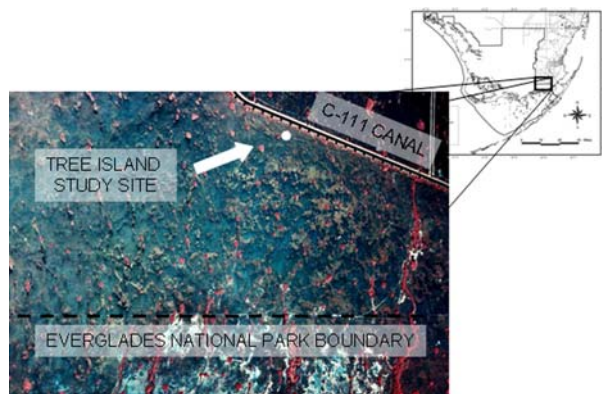


Figure 1. Map of the southern Everglades study area in the C-111 Basin. Tree Island is highlighted with a white circle. The hatched line represents the northern boundary of Everglades National Park.

ecosystem parameters have been made on eight similar islands since 1999 (Troxler Gann and others 2005). Data reported in this study are based on a 6-month wet season period in 2004 (July–December), with 5 months of overland sheetflow. Sheetflow is dominated by overbank outflows from the C-111 canal just to the north (Figure 1). When overland flows cease to occur, advective surface water flows do not occur, and there is little surface water hydrologic connection with the wetland marsh surrounding the tree islands.

Determination of Plant Community Intrasystem Fluxes and N Demand

Litterfall Collection and Turnover

We used litterfall deposition data to estimate plant N cycling, N uptake, and N accumulation in soils. Litterfall was collected monthly (August 1999–July 2004) from 10 0.5-m² traps, and we used estimates of annual litterfall production averaged over this period. Leaf turnover occurs approximately annually for the dominant evergreen species of this tree island, and thus we used values from the year previous to the 2004 wet season period of study (Troxler Gann and others 2005). Litter collected from each trap was dried to constant weight at 70°C, sorted into leaves (by species), wood, reproductive parts, and miscellaneous parts, and weighed. A representative sample of mature green leaves from the species most commonly represented in each month's litterfall samples was also collected monthly, and used in our budget estimates as described below.

In August 2004, we determined standing stocks of litter and litter turnover rates by collecting

standing litter from 10 0.5-m² quadrats (excluding large woody debris > 2.5 cm in diameter) from the soil surface ($k_t = L/X_{ss}$; the ratio of annual litterfall to standing litter; Nye 1966). Standing litter was sorted into leaf, wood, reproductive, and miscellaneous components, dried to constant weight at 70°C, and weighed.

Tree Island Leaf and Litterfall Nutrient Analyses

Subsamples from each component were compiled, ground to a homogeneous powder (<500 μm), and analyzed for N. Live leaf, litterfall, and standing litter samples were analyzed for N with a Carlo Erba elemental analyzer. Nitrogen content of litterfall and green leaves collected in August, December, and April (2003–2004) was used to calculate nutrient resorption efficiency (% nutrients withdrawn upon senescence of leaves; Chapin and van Cleve 1989).

Plant Community N Demand

We estimated plant community N uptake using N data obtained from live leaves and litterfall, and rates of litterfall production, decomposition, and peat accumulation. Specifically, we used a mass balance approach where the plant N requirement in excess of that available through internal recycling, leaching, and potential remineralization was that obtained from some other source (that is, N input from marsh surface or subsurface water). In the calculation of these parameters, we assumed that N concentration of plant tissues was supported by uptake of inorganic N (DIN: NH₄ + NO₃), and thus TN and DIN were comparable plant-mediated fluxes. First, we quantified the annual N biomass standing crop based on annual litterfall production and nutrient content of live leaves of *C. icaco* (the dominant species), co-dominant species, wood, and reproductive components. Second, we estimated the N flux to the forest floor by litterfall using the nutrient content of each litterfall component (less miscellaneous). Third, we estimated potential N leaching from this litterfall using annual litterfall production values and rates of tree island *C. icaco* litter decomposition (that is, fraction of mass loss after 2 weeks decomposition, 11% for *C. icaco*, Troxler and Childers 2009; assumed 11% for co-dominant species, 0% for wood, and 20% for the reproductive component). Fourth, we estimated the N accumulation in the detrital soil pool (peat) as the product of peat accumulation rate (2 mm y⁻¹; based on value for peat marshes from Craft and Richardson 1993), N concentration of litterfall, and bulk density of 0.28 g cm⁻³ (Troxler Gann and

others 2005). We used N concentration of litterfall to estimate the portion of accumulated peat that was derived solely from plant N. We calculated N accumulation in peat in this way because total N of soil would necessarily include parameters we either measured directly or otherwise estimated. Fifth, we determined the input of N via potential remineralization as the fraction of mass loss after an additional 10 months of decomposition [(N in litterfall – N leached) – N accumulation], verified with experimental results (Troxler and Childers 2009). Finally, we estimated internal cycling with N resorption (leaf standing crop * nutrient resorption efficiency). We estimated plant community N demand, the amount of “new” or allochthonous N required for primary production of community fine (leaves, twigs, and fruits) biomass, as: biomass standing crop N – recycled N – leached N – remineralized N.

Hydrologic Fluxes

Subsurface Hydrologic Fluxes

In 2004, we installed nine piezometer clusters of known elevations (relative to mean sea level and surveyed with a Leica™ Totals Station, Figure 2) to quantify horizontal and vertical groundwater and N fluxes (Fetter 1994). Piezometers were constructed of 5.1 cm inner diameter PVC pipe and were slotted at the bottom over a 10-cm length. This slotted section was covered with nylon, and each piezometer was capped at the bottom. We installed the piezometers using a 10-cm inner diameter corer constructed of PVC and fitted with a saw blade. After coring the peat, the soil was removed and the piezometer placed into the center of the hole (~20 cm). We then filled the rest of the annulus with Sakrete™ cement. Piezometer clusters were installed in both edge and interior locations (Figure 2). In edge clusters, we installed piezometers at both shallow (30 cm) and groundwater (to the limestone surface; 50–60 cm) depths. In interior clusters, we installed piezometers at three depths: shallow (30 cm), deep (50 cm), and groundwater (to limestone surface; 60–90 cm). The limestone was consistently deeper within the interior of the tree island than on the edge of the tree island (immediately adjacent to the surrounding marsh). Piezometers installed to the limestone surface were of variable depth as the limestone was not flat.

Water depth (cm) was measured monthly in each piezometer to calculate hydraulic head (h_x).

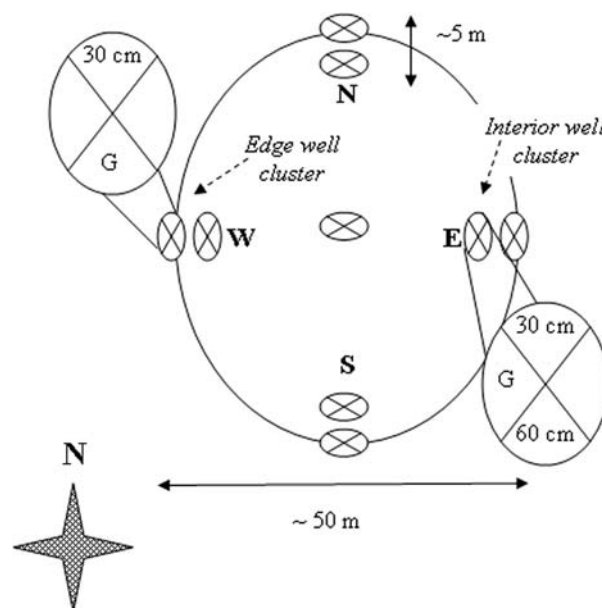


Figure 2. Plan view of tree island piezometer design. Each piezometer cluster (oval with hatch mark) represents piezometers installed at two (edge clusters) and three depths (interior clusters). Piezometer clusters are identified by ordinal direction (N, S, W, and E). The long axis of each oval depicting interior clusters is oriented parallel to the location of shallow (30-cm depth) and deep (installed 60 cm depth) piezometers with the groundwater (G) piezometer installed at an approximately equal distance between the two shallower piezometers to a depth of 60–90 cm. The piezometers in the edge clusters have a similar design with shallow and groundwater (installed at 50–60-cm depth) piezometers only.

These hydraulic head values were used to calculate Darcy’s groundwater flux (q ; m wet season^{-1}):

$$q = \frac{Q}{A} = \frac{K(h_1 - h_2)}{\Delta l},$$

where Q/A is the volumetric flow rate Q (l d^{-1}) per unit cross-sectional area [A , the product of the piezometer length (30 cm) and the piezometer diameter; in m^2], K is hydraulic conductivity (cm s^{-1}), and $(h_1 - h_2)/\Delta l$ [hydraulic gradient; length (l)] is the hydraulic gradient (Fetter 1994). Values of hydraulic conductivity were determined using Hvorslev’s slug tests following the equation:

$$K = \frac{A}{F} \frac{1}{t_2 - t_1} \ln \frac{H_1}{H_2},$$

where K is the hydraulic conductivity, A the cross-sectional area of the piezometer, F a shape factor, and H_1 and H_2 the water levels at t_1 and t_2 (Fetter 1994). We calculated K utilizing a shape factor for a cased hole, where soil is flush with the bottom of the piezometer ($F = 11 \cdot R/2$) and R is the radius of

the piezometer. A peristaltic pump was used to evacuate piezometers (remove the slug), and water level return was determined using a pressure transducer. Voltage and time were plotted on a log scale, and t_1 , H_1 , t_2 , and H_2 were recorded.

Wet season subsurface mass flux (assuming advective flux is the main transport mechanism; Schwartz and Zhang 2003) was calculated following the equation:

$$J_{\text{adv}} = nCv,$$

where J_{adv} is the mass flux (g m^{-2} wet season $^{-1}$), n the porosity of the peat (approximated as 0.85 based on the fraction of soil moisture in this saturated peat; Troxler Gann and others 2005), C the concentration of NO_3 or NH_4 ($\mu\text{mol l}^{-1}$), and v the groundwater velocity vector ($q n^{-1}$; see above). Nutrient concentrations were obtained from average concentrations of NO_3 and NH_4 in interstitial porewater as described below. Mass fluxes across the tree island-marsh boundary (between shallow piezometers of island-edge and island-interior piezometer clusters) were averaged over wet season months (August-December) to estimate potential contribution of a subsurface hydrologic source of DIN ($\text{NO}_3 + \text{NH}_4$). This condition, the interface between tree island-edge and tree island-interior piezometer clusters defined the boundary for the ecosystem N model.

Surface Hydrologic Fluxes

We estimated mass fluxes of DIN to the tree island and through the marsh landscape to differentiate surface water contributions of N between our focal ecosystem—tree islands—and the marsh landscape. We estimated tree island and marsh surface water discharge using two methods to cross-validate estimates based on calculations using: 1) instantaneous measurements and 2) basin overland flow. For estimates based on instantaneous measurements, upstream discharge (l d^{-1}) was the product of instantaneous flow rates (cm s^{-1}), water levels (cm), and cross-sectional distance just upstream of the tree island or marsh, respectively. We measured water flow bimonthly upstream of the tree island using fluorescein dye as a visible tracer. To obtain tree island water levels, measurements were conducted monthly at a fixed datum located at the lowest observed topographic position within the island, avoiding tree tip-ups. We generated a continuous record of daily water levels for the tree island by relating these monthly point measures to a continuous water level recorder from a nearby USGS marsh groundwater sampling station (CVNR3) using

simple linear regression (Troxler Gann and others 2005). This USGS station was also used to determine marsh surface water levels. For estimates based on overland flow, we determined upstream discharge into the C-111 Basin as the difference between control structure inflows and outflows (that is, the difference as estimated discharge into the study area using stations S197 and S18C maintained by the South Florida Water Management District; DBHY-DRO, www.sfwmd.gov). Total surface water input (m wet season^{-1}) estimated from both upstream discharge methods was then calculated as the product of discharge (l d^{-1}) and island hydroperiod days month $^{-1}$ (d wet season^{-1}), divided by tree island or equivalent marsh area ($1,674 \text{ m}^2$). We used the average difference between daily marsh and tree island water levels as described above, calculated for each month, to obtain a “multiplier” that accounted for lower water levels in (and thus lower discharge to) the tree island throughout the wet season.

Mass fluxes of DIN for both tree island and marsh were determined from the product of the bi-monthly surface water input estimated for either tree island or marsh and marsh surface water concentration, summed over the 6-month period (g m^{-2} wet season $^{-1}$). Monthly water quality data for NO_3 and NH_4 were obtained from nearby monitoring stations associated with the Florida Coastal Everglades LTER Program (site TS/Ph-4 and 5; <http://fcelter.fiu.edu>). These stations were located at upstream and downstream sites relative to the tree island. Using data from the National Atmospheric Deposition Program (NADP) for the 2004 wet season (July-December) from the Everglades National Park station (F-11), we estimated atmospheric DIN deposition rate to be 0.65 g m^{-2} wet season $^{-1}$.

Soil Nitrogen Characterization

In July 2004, we collected duplicate soil cores to limestone depth ($\sim 50\text{-cm}$ length) in 3 locations near west, east, and central interior piezometer clusters. Cores were extracted with a 2.4-cm inner diameter PVC tube with a thin sleeve ($\sim 5\text{-mm}$ thickness). The tube was fitted with a razor blade to minimize peat compaction. Each core was sectioned into 4-cm increment subsections, and each subsection analyzed separately for each core. The first core was used to determine inorganic nutrient concentrations from KCl soil extractions ($n = 3$ of each depth increment). The samples were homogenized and approximately 17 ml samples were extracted in 25 ml of 2 M KCl. Samples were centrifuged at ambient temperature, and filtered

through Supor™ 0.45- μm membrane filters. Filtered samples were analyzed for NH_4 and NO_3 on a three-channel auto-analyzer (Technicon model). The second core was split length-wise. We removed roots from each section, and two subsamples were dried to a constant weight at 70°C . One subsample was used to determine moisture content ($\text{g wet} - \text{g dry}/\text{g dry}$) and then ashed at 500°C for 4 h to determine organic matter content. The second subsample ($n = 3$) was analyzed for TC and TN with a Carlo Erba elemental analyzer, and for N and C stable isotopic composition on a Finnigan Delta C isotope ratio mass spectrometer (Thermo Fisher Scientific Inc., Waltham, MA, USA) in a continuous flow mode with an elemental analyzer.

We measured interstitial water concentrations during the wet season of 2004 by extracting porewater using “sippers” (aquarium air stones equipped with fine Tygon® tubing and sealed with teflon tape; Dailey 2000) placed 10 cm into the soil. Porewater was sampled using a 120-ml syringe and filtered through Whatman GF/F filters. Filtered samples were then analyzed for NH_4 and NO_3 concentration on a four-channel auto-analyzer (Alpkem model RFA 300). Tree island surface water was collected in August, October, and December for determination of NH_4 and NO_3 concentrations with analytical methods as described above.

N characterization of Soil, Surficial Litter, and Surface Water Pools

We estimated the mass (g) of DIN in standing surface water m^{-2} as the product of DIN surface water concentration and the average volume of water m^{-2} , respectively ($n = 3$). Nitrogen in surficial litter (standing litter) was determined as the product of the standing litter mass (obtained from standing litter collections as described above) and N concentration of each standing litter fraction, and summed to obtain surficial litter g N m^{-2} . We estimated the dry mass standing stock of organic N in soils using the soil N content and the dry weight of soil per m^2 of tree island ($n = 3$). We calculated the mass of KCl-extractable N, and interstitial porewater DIN based on soil porosity ($n = 3$, respectively).

Nitrogen Transformation Rates

We utilized the N isotope pool dilution technique to quantify rates of N mineralization, nitrification, and N immobilization (DIN production, transformation, and consumption, respectively; Brooks and others 1989; Davidson and others 1990) and a standard acetylene reduction assay to calculate

rates of asymbiotic nitrogen fixation and denitrification (Gordon and others 1986).

To determine gross mineralization rates, soil cores were collected at four locations in close proximity to piezometer clusters. Peat cores were collected to 20-cm depth, removing the surficial litter layer before coring, capped at the bottom, and sealed from the atmosphere with Parafilm™. Ambient water was collected along with peat soils. Cores were stored in a cooler with ambient water until processing (<24 h). Just before processing, water from the tops of the cores was replaced with additional ambient water to simulate in situ field conditions. We used an initial pilot study to test appropriate incubation times. Soil cores were incubated for 0, 12, 24, and 48 h at room temperature. All incubation times produced similar recovery efficiencies, but to prevent possible organic matter breakdown with a longer incubation, we used a 24 h incubation time as T_i (end of the incubation) for our rate determinations.

Cores were constructed of 5.1-cm inner diameter, clear PVC tube, cut into 40-cm lengths. Injection ports were drilled at 1-cm intervals along the bottom 20-cm length of each tube, and filled with silicone. Injection ports were used to deliver an isotopic tracer solution of $10 \mu\text{mol l}^{-1}$, 30 at.% $^{15}\text{NH}_4\text{SO}_4$ with 1 cc syringes. The injection ports allowed even distribution of the tracer throughout the soil core. After incubation, soils were extruded from cores into plastic bags containing 240 ml of 2 M KCl. Bags were shaken for one hour on a rotary shaker and centrifuged at 5,600 rpm for 10 min. Soil extracts were slowly poured off into 120 ml, acid washed syringes, and filtered through Supor™ 0.45- μm membrane filters into Whirlpak™ bags. Subsamples were collected for inorganic nutrient analyses. Both samples for nutrient and isotope analyses were stored frozen until processing. Rates of mineralization were calculated using the model of Wessel and Tietema (1992).

To determine gross nitrification rates, we used a similar procedure. Here, soil cores were 20 cm in length, and injection ports covered an 8-cm length of each core. The injection solution was $10 \mu\text{mol l}^{-1}$, at.% K^{15}NO_3 . Here, we used incubation times of 0, 1, 2, and 4 h, and a 2-h incubation time as T_i for our rate determinations. Two subsamples were extracted separately (0–4 and 4–8 cm) in 60 ml KCl. Soil NO_3 fluxes below 8-cm depth were considered negligible due to the low redox conditions at 10-cm depth (Troxler Gann and others 2005).

We used the diffusion method of Brooks and others (1989) to determine ^{15}N of soil extracts. Production and consumption rates for NH_4 and

NO_3 ($\text{mmol m}^{-2} \text{h}^{-1}$) were averaged for two monthly sampling periods (October and November 2004) to estimate wet season values (g m^{-2} wet season $^{-1}$).

Nitrogen fixation and denitrification rates were determined to 10-cm soil depth and in surface litter of five cores collected in close proximity to piezometer clusters following Gordon and others (1986). Cores were separated into 2-cm subsections. Nitrogen fixation and denitrification were determined simultaneously on headspace gas. Approximately 3-ml samples were placed in 20-ml gas vials that were purged with N_2 . Each vial was capped with a butyl-rubber septum and sealed with an aluminum crimp. A 2-ml sample was extracted from the head space of each vial with a gas tight syringe, and 2 ml of acetylene (~ 10 at.%) was injected into each vial. The vials were incubated in the dark for 44 h (the incubation time was determined from a trial where several incubation lengths were assessed). Samples were analyzed on a gas chromatograph (model HP 5890 Series II) affixed to a headspace sampler (Model HP 7694) with a Poropak Q column. Headspace was sampled for analysis of both ethylene and N_2O . A conversion of 1:3 was used to relate acetylene reduced to ethylene with nitrogen fixed (Hardy and others 1968). Nitrogen fixation and denitrification rates were calculated as the product of the mass of each component (soil and proportions of new, old, and wood fractions of standing litter; g m^{-2}) and the hourly flux of N ($\text{nmol g}^{-1} \text{h}^{-1}$) and the components were summed for the respective rate. Fluxes below 10-cm soil depth were considered negligible.

Isotopic analyses of diffusion filters were conducted at the University of California, Davis Stable Isotope Laboratory. Samples were analyzed using an elemental analyzer coupled with an isotope ratio mass spectrometer. For $\delta^{15}\text{N}$, the stable isotopic ratio was calculated using standard δ notation where: $\delta^{15}\text{N} = (R_{\text{sample}}/R_{\text{standard}} - 1) * 1000$ versus air. R is the ratio of $^{15}\text{N}/^{14}\text{N}$ of the sample and standard (Martinelli and others 1999).

Synthesis

We determined net nitrogen flux through our experimental tree island utilizing results from the N transformation studies in conjunction with surface water and tree island–island-edge groundwater fluxes, biomass N pools and N fluxes. All soil pools and fluxes were normalized to a 20-cm soil depth (considered the active biogeochemical layer for N cycling beyond which soils become very reducing and the mass of fine roots declines). With the tree

island–marsh interface as our boundary, our N budget followed the general form:

$$\text{Imports} - \Delta \text{Storage} = \text{Exports}$$

where Imports = $[N_{\text{dep}} + N_{\text{sw}} + N_{\text{ssw}}]$, Δ Storage = $[(N_{\text{uptake}} + N_{\text{NH4imm}} + N_{\text{NO3imm}} + N_{\text{denit}}) - (N_{\text{min}} + N_{\text{nit}} + N_{\text{fix}})]$, and Exports = N_{flux}

Here, N_{min} is gross mineralization, N_{nit} the gross nitrification, N_{fix} the N fixation in the soil and litter layers, N_{dep} the N as atmospheric deposition, N_{sw} the net surface water inputs of DIN, N_{ssw} the net subsurface water inputs of DIN, N_{NH4imm} the NH_4 consumption, N_{NO3imm} the NO_3 consumption, N_{denit} the denitrification in the soil and litter layers, N_{uptake} the plant community N demand, and N_{flux} the net ecosystem N flux. All units are in g m^{-2} wet season $^{-1}$. Standard errors were propagated to calculate a standard error value for budget estimates.

RESULTS

Biomass N Pools and Plant Community Intrasystem N Fluxes

We calculated N standing stocks (g N m^{-2}) and fluxes ($\text{g N m}^{-2} \text{y}^{-1}$) of plant-mediated components of the tree island (Figure 3). Biomass standing crop was the largest annual stock, a function of relatively high live leaf N concentrations (Figure 3A). More than half of that pool was lost within a year through biomass senescence (litterfall production; Figure 3B), with a portion recouped by leaf litter leaching after 2 weeks decomposition (Figure 3C). A much larger portion of N in litterfall was accumulated as peat within 1 year, based on a rate of 2 mm y^{-1} (Figure 3D). Subsequently, through slow decomposition of more recalcitrant materials, a small portion of N is further remineralized within a year, becoming available for plant uptake (Figure 3E). About 40% N is resorbed by plant tissues before biomass senescence, representing the largest source of plant-mediated available N (Figure 3F). Notably, the value for N accumulated as peat (Figure 3G) approximated the value of plant N demand (uptake) of $3.96 \pm 0.43 \text{ g N m}^{-2} \text{y}^{-1}$.

Although leaf turnover for *C. icaco*, the dominant species, occurs through the year (Troxler Gann and others 2005), we report annual values as previous work demonstrated most plant growth of *C. icaco* was during the wet season (Gann 2001). Thus, annual litterfall represents seasonal plant uptake of N. Furthermore, leaf deposition for co-dominant species is highest in the dry season reflecting their dry deciduous physiology (Troxler Gann and others

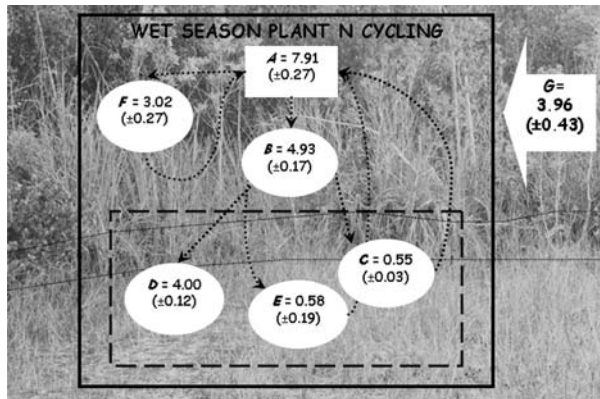


Figure 3. Plant biomass N pool (g m^{-2}) and intrasystem N fluxes ($\text{g m}^{-2} \text{ season}^{-1}$). Biomass standing crop (**A**) approximates the minimum N requirement to maintain that pool and provides the basis of our estimation of plant N demand (*large arrow*). Litterfall N (**B**) is estimated from N content and mass of litterfall. The sum of N derived from leaf leachate (**C**; after 2 weeks decomposition). N accumulation in recently deposited peat (**D**), and the value of N leached, are incorporated to estimate the value of remineralized N derived from more recalcitrant organic N (**E**). The internal recycling rate (**F**) of N is determined from percent nutrient resorption efficiency of dominant (*C. icaco*) and co-dominant species groups. Plant N demand (**G**) is an allochthonous source of N required to maintain the biomass standing crop.

2005). Based on dry season leaf drop, we assumed that most growth for co-dominant species was also highest in the wet season. Previously reported values for parameters used to derive this value of plant community N demand are provided in Troxler Gann and others (2005) and Troxler and Childers (2006).

Hydrologic Fluxes

Hydraulic conductivity values varied with tree island soil depth and soil type (that is, island versus marsh). Island hydraulic conductivity values decreased with depth, and ranged from 5×10^{-2} to $7 \times 10^{-4} \text{ cm s}^{-1}$. Marl soils from the marsh landscape had the lowest conductivity values ($3\text{--}6 \times 10^{-4} \text{ cm s}^{-1}$). Hydrologic fluxes between shallow piezometers of edge and interior clusters indicated horizontal discharge (Q ; imports) to tree islands, averaging $8.10 \pm 2.18 \text{ l d}^{-1}$ ($n = 4$) to the tree island water budget across the tree island–marsh boundary at 30-cm depth. We found higher fluxes across this boundary parallel to surface water flow direction (W and E; Figure 2). Averaging these flux values only ($n = 2$), the rate of subsurface import increased to $13.92 \pm 1.87 \text{ l d}^{-1}$. Similarly, hori-

zontal groundwater inputs (q) averaged $0.529 \pm 0.230 \text{ m season}^{-1}$ for all edge–interior piezometers, and $0.910 \pm 0.122 \text{ m season}^{-1}$ averaging piezometers parallel to flow. As we only considered fluxes that occurred across the tree island–marsh boundary as parameters to be included in our N budget, subsurface hydrologic data for other piezometers are reported elsewhere, and not included in this study (see Gann 2005). Horizontal mass fluxes of NO_3 and NH_4 averaged across all four locations were 0.003 ± 0.001 and $0.057 \pm 0.025 \text{ g m}^{-2} \text{ season}^{-1}$, respectively. If primary inputs are considered to occur along flowpaths parallel to the island edge (aligned with surface water flow), horizontal mass fluxes of NO_3 and NH_4 were 0.005 ± 0.001 and $0.100 \pm 0.013 \text{ g m}^{-2} \text{ season}^{-1}$, respectively.

Wet season surface water input was approximately three orders of magnitude greater than subsurface water input. Calculating surface water inputs based on C-111 overland flow yielded lower values that were within the standard error estimates of values based on instantaneous measurements. We used surface water input values based on C-111 overland flow because the variability as standard error was considerably constrained. Average daily discharge based on C-111 overland flow averaged across months ($n = 5$) was $3008.5 \pm 589.5 \text{ m}^3 \text{ d}^{-1}$. Average surface water input was $269.6 \pm 52.8 \text{ m wet season}^{-1}$. Intraseasonal variability in NO_3 loads varied from 1.1 g m^{-2} in December to 7.2 g m^{-2} in November. Similarly, intraseasonal variability in NH_4 loads was more muted where early wet season months were twice the loading rate of late wet season months. Average surface water NO_3 and NH_4 fluxes to the tree island were 22.5 ± 6.5 and $4.26 \pm 0.65 \text{ g m}^{-2} \text{ wet season}^{-1}$, respectively, with a wet season DIN loading rate of $26.8 \pm 6.5 \text{ g m}^{-2}$ (Figure 4).

N Characterization of Soil, Surface Water, and Surficial Litter Pools

Soil N concentrations in interstitial porewater and KCl extracts were low. Average porewater interstitial concentrations of NO_3 and NH_4 were 0.38 ± 0.12 and $7.74 \pm 0.08 \mu\text{mol l}^{-1}$, respectively. Interstitial DIN averaged $0.001 \pm 0.0003 \text{ g N m}^{-2}$. KCl-extractable soil N concentrations (providing an estimate of interstitial + adsorbed nutrient content) averaged 3.40 ± 0.81 and $39.5 \pm 2.5 \mu\text{g g}^{-1}$ soil, respectively, thus totaling $2.40 \pm 0.15 \text{ g DIN m}^{-2}$ (Figure 4). Soil total N and C averaged 1.88 ± 0.24 and $36.74 \pm 1.59\%$. Soil N mass was estimated to 20-cm depth, and was $1056 \pm 135 \text{ g N m}^{-2}$. The

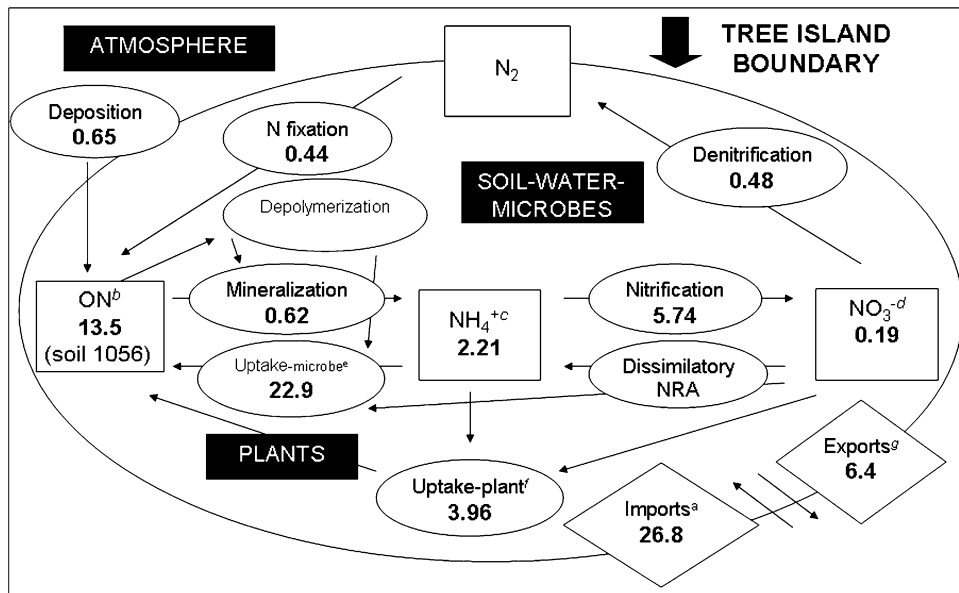


Figure 4. Tree island N balance with N process rates and pools for a seasonally flooded tree island during wet season inundation. The difference between total DIN imports (26.8 g N m^{-2}) and the change in storage (20.5 g m^{-2}) derived from our parameter estimates provides an estimated DIN export of 6.4 g m^{-2} . The tree island boundary sets the boundary conditions for the N budget. See text for standard error values.

^aThe sum of surface and subsurface hydrologic imports of DIN; ^bOrganic nitrogen: the sum of biomass standing crop and surficial leaf litter N; ^cKCl-extractable N in soil; ^dThe sum of NO_3 and NH_4 consumption; ^ePlant N demand; ^fTree island DIN imports minus tree island ecosystem retention

variability in this estimate was driven by variability in N concentrations. The variation in the surface water DIN pool was also driven by variation in N concentration (NH_4 : 1.158 ± 0.322 and NO_3 : $0.150 \pm 0.042 \mu\text{mol l}^{-1}$) and was $0.003 \pm 0.001 \text{ g N m}^{-2}$. Surface water DIN is incorporated as a surface water import whereas stocks for standing litter, soil organic N, and KCl-extractable N are representative of longer time scales (> period of seasonal inundation) and not incorporated into the value for plant community DIN uptake. Values for fresh leaf, decomposed leaf, and wood surficial litter were 50 ± 4.5 , 463 ± 49 , and $309 \pm 31 \text{ g m}^{-2}$, respectively. Nitrogen concentrations for each litter fraction were 1.20 ± 0.09 , 0.62 ± 0.04 , and $0.63 \pm 0.13 \%$ N. Thus, standing litter fractions contained 0.31 ± 0.003 , 5.54 ± 0.07 , and $1.95 \pm 0.09 \text{ g N m}^{-2}$, respectively. Normalizing for the rate of litter turnover, the total mass of organic N contained within standing litter was $5.59 \pm 0.11 \text{ g N m}^{-2}$ (Figure 4).

N Transformation Rates

We extrapolated hourly fluxes for gross NH_4 and NO_3 production and consumption to annual rates per unit area (m^{-2}) based on core surface area. Spatial variability within the tree island was lower than monthly temporal variability. Average gross NH_4 production and consumption rates were 0.010 ± 0.004 and $0.014 \pm 0.004 \text{ mmol m}^{-2} \text{ h}^{-1}$. Scaled to a per unit area basis, gross NH_4 production and consumption rates averaged 0.62 ± 0.23

and $0.82 \pm 0.23 \text{ g m}^{-2} \text{ season}^{-1}$ (Figure 4). This corresponded to a net NH_4 consumption of $0.20 \pm 0.33 \text{ g m}^{-2} \text{ season}^{-1}$. Gross NO_3 production and consumption rates for 0–4 and 4–8 cm depths were summed for each month and then averaged. Gross NO_3 production and consumption rates averaged 0.095 ± 0.076 and $0.36 \pm 0.03 \text{ mmol m}^{-2} \text{ h}^{-1}$. Scaled to a per unit area basis, gross NO_3 production and consumption rates averaged 5.74 ± 4.60 and $22.04 \pm 1.54 \text{ g m}^{-2} \text{ season}^{-1}$ (Figure 4). Thus, there was a net NO_3 consumption of $16.30 \pm 4.85 \text{ g m}^{-2} \text{ season}^{-1}$. Although gross NH_4 production approximated consumption rates, NO_3 consumption was about twice NO_3 production. Annual values for NH_4 and NO_3 production and consumption thus yielded a net soil DIN consumption of $16.50 \pm 4.93 \text{ g m}^{-2} \text{ season}^{-1}$, with the least variability in the process driving net N retention (NO_3 consumption).

We also estimated hourly fluxes and annual rates of denitrification and N_2 fixation per unit area (m^{-2}). We calculated rates for soil (0–10 cm depth) and leaves (recently senesced and decomposed) and wood of standing (surficial) litter. We found no N_2O production from any soil depth with only one exception. One soil core collected from the upstream end of the island (north) produced N_2O at depths below 6 cm, but these values were not used as no other soil samples produced N_2O . However, standing litter collected from the soil surface had low rates of N_2O production. Fresh leaf litter, decomposed leaf litter, and wood produced 5.2 ± 2.9 , 3.9 ± 3.1 , and $6.3 \pm 1.3 \text{ nmol g}^{-1} \text{ h}^{-1} \text{ N}_2\text{O}$.

Based on biomass proportions (described above), the wood and decomposed leaf litter fractions had the highest denitrification rates per unit area, whereas rates for fresh material were considerably less. Denitrification rates of fresh, decomposed, and woody litter were thus 0.032 ± 0.016 , 0.217 ± 0.174 , and 0.234 ± 0.057 g N m⁻² season⁻¹, respectively. Summing these values, total denitrification was 0.48 ± 0.05 g m⁻² (Figure 4). For N fixation rates, we also separated out litter fractions and soil. We found that standing litter had higher rates of N fixation than soil subsections, and that fresh litter had the highest N fixation rates. Average N fixation rates for fresh, decomposed and wood litter fractions were 8.85 ± 3.91 , 6.93 ± 2.40 , and 1.35 ± 0.75 nmol g⁻¹ h⁻¹, respectively. Average soil N fixation rates were 0.320 ± 0.05 nmol g⁻¹ h⁻¹ averaged over the top 10 cm of surface soil. However, based on mass per unit area, soil had the highest rates of N fixation, whereas the decomposing litter fraction had higher rates than fresh litter, followed by the lowest N fixation rates for wood (0.290 ± 0.043 , 0.117 ± 0.040 , 0.016 ± 0.007 , and 0.015 ± 0.008 g N m⁻² season⁻¹, respectively). These components summed yielded an N fixation rate of 0.44 ± 0.01 g m⁻² season⁻¹ (Figure 4). Combining N fixation and denitrification rates for soil and litter components, we found a net atmospheric N loss of 0.04 ± 0.05 g m⁻² season⁻¹.

Net Ecosystem N Flux

Utilizing the estimates of total net soil inorganic N produced and consumed and total N fixation and denitrification rates, we estimated the total net N assimilated by the tree island as 16.54 ± 4.93 g m⁻² season⁻¹. Consumption exceeded production in these incubations, suggesting the potential for a complete turnover of the readily mineralized N. Given this, the N that tree island plants take up for new production must be obtained from allochthonous sources, because it apparently cannot be generated by soil N mineralization or nitrification alone. Thus, we added the value of net N consumption by the soil complex to the value of net plant uptake. This yielded a value of net ecosystem N consumption of 20.5 ± 4.95 g m⁻² season⁻¹ in a typical seasonally flooded tree island.

We utilized these values of net island N retention to estimate tree island biogeochemical contributions to landscape N retention in our study area, and the efficiency by which the study island retained allochthonous DIN. DIN hydrologic imports into the tree island, the sum of surface and subsurface water N inputs for both NO₃ and NH₄,

and atmospheric DIN deposition, were 26.9 ± 6.5 g DIN m⁻² season⁻¹. Assuming that DIN hydrologic imports are efficiently utilized for plant N uptake, interception should reduce the mass of N flowing through a given m⁻² area of tree island to 6.4 ± 8.1 g season⁻¹ (Figure 4), with the tree island retaining approximately 76% of imported DIN.

DISCUSSION

Heterogeneity in landscapes has taken a primary role in studies of large-scale biogeochemical fluxes, predominantly focusing on heterogeneous components within riparian watersheds (Hedin and others 1998; McClain and others 2003; Gribsholt and others 2007; Harms and Grimm 2008). Quantifying biogeochemical transformations in the landscape has long been a focus of wetland and coastal research, particularly regarding the quality of water delivered to downstream systems (Peterjohn and Correll 1984; Correll and others 1992). Many such studies evaluate this role of a wetland as the difference between inputs and outputs of nutrients (Jaworski and others 1992; Mortazavi and others 2000; Sutula and others 2001). Although these are important studies, they do not elucidate the sites of important biogeochemical transformations. More recently, this focus has broadened to include studies of the importance of various components, inherent to the ecosystem or landscape of interest, in a range of systems. These studies include those of geomorphic features (Hester and Doyle 2008), flow baffles (Ensign and Doyle 2005), upland-peatland ecotones (Mitchell and Branfireun 2005; Boomer and Bedford 2008), seepage banks (Duval and Hill 2007), points of flow path confluence (Hedin and others 1998; Lewis and others 2007; Dent and others 2007), leaf litter (Sobczak and others 2003; Ashkenas and others 2004), and microbial biofilms (Mullholland and others 2000; Mullholland 2004). The focus of these studies is where, and how, heterogeneity increases the reactive rate or surface area by which nutrient processing can occur. A unifying feature among these fields and research directions is that hydrology connects biogeochemical processes in the landscape (Burt and Pinay 2005). In heterogeneous landscapes, research that identifies how hydrologic connectivity actuates nutrient processing by heterogeneous components will help to identify, protect, and restore these points of confluence that enhance nutrient retention. In this study, we present evidence for how a seasonally flooded tree island enhances nutrient

retention in a southern Everglades short-hydroperiod marsh during wet season inundation.

Nitrogen and the “Reactive” Tree Island Ecosystem

Total tree island ecosystem N (sum of pools) was approximately 1.5 kg m^{-2} with most stored as organic N in peat. Most N stored in peat likely does not contribute to short-term (that is, wet season) N cycling, except perhaps with intermittent precipitation events at the onset of the wet season that may promote DON infiltration through peat soils (Stutter and others 2007). Water table fluctuations that aerate surface soils may also increase nitrate concentrations, and with infiltration, increase denitrification rates (Hefting and others 2004). However, peats generally remain saturated throughout the year despite seasonal water level fluctuations (Troxler Gann and others 2005). Thus, during wet season inundation, most of the available N necessary to meet the minimum requirement to maintain live biomass was from allochthonous sources. These points do not preclude that a better approximation of N cycling and overall N flux should include dry season N processes to develop annual estimates. Furthermore, hydrologic losses of organic N were not considered in this study. Although DON may be mobilized at the onset of the wet season as mentioned, we did not quantify measurable subsurface lateral export of soil water from the tree island. It is not known whether surface water export of DON is an important flux, however, DON in marsh waters are considerably lower than tree island surface water, and decline in marsh waters further downstream. It is plausible that photochemical oxidation contributes to low DON concentrations in this carbonate, short-hydroperiod marsh (Miller and Zepp 1995). Additionally, in general, particulate materials are absent in Everglades wetlands except for flocculent matter that occurs as bed load in long hydroperiod sloughs (Noe and others 2001).

Plant uptake, and to a large extent, microbial assimilation of N, mediated N retention by this tree island. Overall, DIN immobilization by the tree island could be attributed to microbial assimilation, specifically NO_3 immobilization. DIN assimilation by shallow sediments and microbial communities associated with leaf litter and biofilms is well documented for wetland and aquatic systems (Qualls 1984; Rivera-Monroy and Twilley 1995; Tank and others 2000; Anderson and others 2003a, b; Ashkenas and others 2004; Mullholland 2004; Ensign and Doyle 2005). Although our intent was

to examine soil N transformation rates independently of the surface litter, it is likely that other organic materials (that is, fine benthic organic matter, bulk leaf litter, roots) that increased the reactive surface area of surficial soils contributed to the net DIN consumption we observed. The Everglades peat can provide a highly conductive medium for solute transport when it is saturated (Harvey and others 2005), and the tree island of this study has peat soils of relatively high conductivity that are also slightly elevated above the marsh surface. Here, the organic matter complex that includes soil, fine benthic materials, roots, and leaf litter, maximizes the potential for litter/soil-water column exchange of nutrients and emerges as a point of confluence for nutrient retention when intercepting surface water flowing through the marsh landscape.

In tree islands typical of those of this study area, the influx of leaf litter of high C:N ratio, and considerable cover of standing litter, produces tannic, DOC-rich surface water ($20.5 \pm 2.7 \text{ mg l}^{-1}$) that is twice the concentration found in marsh surface water ($9.1 \pm 0.1 \text{ mg l}^{-1}$; Troxler Gann and others 2005). Thus, leaf leachate may also contribute to the high microbial assimilation of NO_3 we found in this tree island ecosystem. In a Catskill Mountain stream, bioavailable DOC (leaf leachate) stimulated microbial assimilation of NO_3 over N loss to denitrification (Sobczak and others 2003). Rivera-Monroy and Twilley (1995) identified a high C:N ratio of soil and *Rhizophora mangle* litter as the key feature promoting microbial assimilation of NO_3 over denitrification in a tropical mangrove system. Here, denitrification rates were similarly low in soil cores of a basin mangrove community despite enrichment with $^{15}\text{N-NO}_3$ ($1.9\text{--}4.5 \text{ } \mu\text{mol N}_2\text{O m}^{-2} \text{ h}^{-1}$). In our study, denitrification rates determined by acetylene reduction of leaf litter ranged from $0.26\text{--}1.94 \text{ } \mu\text{mol N}_2\text{O m}^{-2} \text{ h}^{-1}$ with rates from soils negligible. In mangrove systems, high DOC has been suggested to inhibit the activity of nitrifying bacteria and low rates of nitrification have generally been reported (see Rivera-Monroy and Twilley 1995). Thus, mechanisms for NO_3 assimilation by microbes are likely similar as both basin mangroves and the peat-based tree island of this study have litter and soils of similar quality. However, although in situ nitrification rates may be constrained by high DOC and relatively low redox potential, the influx of NH_4 via surface water may fuel nitrification rates.

Although there is good support for NO_3 retention in the tree island in the study (including low variation in our estimates), uncertainties remain about

the contribution of the various possible mechanisms by which this occurs (that is, microbial assimilation, denitrification, DNRA). However, given that the potential for denitrification was not detected except for a single sample, denitrification does not appear to be a significant process during wet season inundation. Changes in leaf litter production (or decomposition), and hydrology (hydroperiod, water level, or flow rate) with landscape-scale hydrologic modifications would likely influence the relative importance of microbial immobilization of NO_3 to denitrification in the N budget of the tree island ecosystem. It is also important to note however that some laboratory techniques for estimating N process rates (that is, acetylene reduction) do have methodological limitations (that is, also blocks nitrification) that should be taken into consideration when applying to large-scale estimates such as those we have developed here.

Further uncertainties around final estimates of tree island N retention and retention efficiency were mostly a function of variability in NO_3 production and DIN import, respectively. Although NO_3 production estimates were difficult to constrain due to spatial variability in the measurements, cross-validating DIN import estimates based on two calculation methods was a valuable means of reducing error in the value of N retention efficiency. Although the rate of N retention per se is not a function of DIN imports, the efficiency of retention is another important measure of the relative biogeochemical contribution of tree islands to N cycling in the landscape.

Landscape Contribution of Heterogeneous Components

By influencing the biogeochemical properties that promote inorganic N retention, the tree island examined in this study provided evidence that these heterogeneous components of the landscape are net sinks for surface and subsurface water DIN. In this study, tree islands promoted convergence of elements by increasing reactive surface area of surface soils and modifying the availability of DOC that enhances NO_3 retention. Thus, tree islands have the potential for retention of N at a higher rate relative to the overall landscape. We estimated this potential using DIN input to and output from our study area. Total DIN input to and output from the study area was 36.9 ± 8.7 and 19.7 ± 4.2 g DIN m^{-2} wet season⁻¹, respectively, with a net landscape retention of 17.1 ± 9.6 g DIN m^{-2} wet season⁻¹. If tree islands act efficiently to retain DIN as we show, tree islands can retain 55% of that DIN which enters the

southern Everglades marsh landscape via canal overland flow of surface water.

Wet season periphyton N uptake would also contribute to landscape N uptake, but at unknown rates relative to tree islands. Estimates based on biomass and a short-term NO_3 tracer experiment suggest wet season periphyton N uptake ranges from 44 to 60 g N m^{-2} (Iwaniec and others 2006; Wozniak 2006). However, periphyton has been shown to have considerably high N fixation rates that in some cases accounts for 88% of its N requirement (Rejmankova and Komarkova 2000). Furthermore, periphyton net production often approximates respiration suggesting the potential for high N turnover in the water column (Iwaniec and others 2006). Notably, N fixation has been implicated as contributing to residual N of a watershed mass balance for our study area (Sutula and others 2001). Thus, although our ability to assess the net N retention of the study tree island during wet season inundation and contributions to biogeochemical cycling of N were well supported, estimates that scale the relative importance of heterogeneous landscape components like tree islands will require better estimates of other components at similar spatial and temporal scales. Nonetheless, this study demonstrates the important role of tree islands in seasonal N retention.

Other studies that quantify nutrient retention associated with heterogeneous components are reported for a range of systems, and at various scales, showing significant contributions to landscape nutrient cycling. For example, at the microscale (< 1 m^2), in-stream NO_3 retention associated with microbes colonizing leaf detritus was 20% of that which entered the stream annually (Mullholland 2004). On the mesoscale (1–100 m^2), experimental manipulations removing coarse woody debris (CWD) and adding flow baffles in blackwater streams showed an 88% decrease and over two orders of magnitude increase in NH_4 uptake (Ensign and Doyle 2005). These results were attributed to changes in in-channel transient storage, and in the case of CWD, decreased reactive time with microbial biofilms. At the macroscale (> 100 m^2), DIN retention associated with forested headwater catchments was 93–97% of inputs relative to urbanized catchments, due to greater forest cover and less impervious surface (Wollheim and others 2005). Thus, natural variation in landscape components in conjunction with landscape hydrologic connectivity is an important feature of large-scale biogeochemical cycling regardless of the physical or biological factors that characterize these heterogeneous attributes of a system.

The N model presented here provided important information about the N retention of seasonally flooded tree islands, and would be valuable for application in wetland landscapes with similar forest-marsh mosaics (for example, Ellery and others 1993; Ponce and Cunha 1993; Langstroth 2001) or other notable heterogeneous components. As the restoration of Everglades freshwater marshes enhances hydrological connectivity and strives to increase the cover of tree islands throughout the system, the biogeochemical contribution of tree islands to landscape nutrient cycling may be further enhanced.

ACKNOWLEDGMENTS

This work would not have been possible without the contributions of several colleagues. I. Anderson and B. Neikirk of the Virginia Institute of Marine Sciences were patient and accommodating enough to share and demonstrate the techniques of isotope N pool dilution. L. Scinto of Florida International University greatly facilitated denitrification and N fixation studies. D. Rondeau, J. Mahoney, T. Grahl, G. Losada and A. Wood of the Wetland Ecosystem Ecology lab helped greatly with field and laboratory work. We also appreciate the thoughtful and detailed comments provided by two anonymous reviewers and Dr. Stephen Davis on an earlier draft of the manuscript. This work was also supported by a FIU University Graduate School Dissertation Year Award, the South Florida Water Management District and the National Science Foundation through its support of the FCE LTER Program (DEB-9910514).

REFERENCES

- Anderson IC, McGlathery KJ, Tyler AC. 2003a. Microbial mediation of 'reactive' nitrogen transformations in a temperate lagoon. *Mar Ecol Prog Ser* 246:73–84.
- Anderson RL, Foster DR, Motzkin G. 2003b. Integrating lateral expansion into models of peatland development in temperate New England. *J Ecol* 91:68–76.
- Ashkenas LR, Johnson SL, Gregory SV, Tank JL, Wollheim WM. 2004. A stable isotope tracer study of nitrogen uptake and transformation in an old-growth forest stream. *Ecology* 85:1725–39.
- Boomer KMB, Bedford BL. 2008. Influence of nested groundwater systems on reduction-oxidation and alkalinity gradients with implications for plant nutrient availability in four New York fens. *J Hydrol* 351:107–25.
- Brooks PD, Stark JM, McInteer BB, Preston T. 1989. Diffusion method to prepare soil extracts for automated nitrogen-15 analysis. *Soil Sci Soc Am J* 53:1707–11.
- Burt TP, Pinay G. 2005. Linking hydrology and biogeochemistry in complex landscapes. *Prog Phys Geogr* 29:297–316.
- Chapin FS, van Cleve K. 1989. Approaches to studying nutrient uptake, use and loss in plants. In: Pearcy RW, Ehleringer JR, Mooney HA, Rundel PW, Eds. *Plant physiological ecology, field methods and instrumentation*. New York (NY): Chapman and Hall. p 185–207.
- Corredor JE, Howarth RW, Twilley RR, Morell JM. 1999. Nitrogen cycling and anthropogenic impact in the tropical interamerican seas. *Biogeochemistry* 46:163–78.
- Correll DL, Jordan TE, Piezometerer DE. 1992. Nutrient flux in a landscape: effects of coastal land use and terrestrial community mosaic on nutrient transport to coastal waters. *Estuaries* 15:431–42.
- Craft CB, Richardson CJ. 1993. Peat accretion and N, P, and organic C accumulation in nutrient-enriched and unenriched Everglades peatlands. *Ecol Appl* 3:446–58.
- Dailey SK. 2000. Phosphorus enrichment effects on interactions among the ecosystem components in a long-hydroperiod oligotrophic marsh in Everglades National Park. Ph.D. Dissertation, Florida International University, Miami, FL, p 118.
- Davidson EA, Stark JM, Firestone MK. 1990. Microbial production and consumption of nitrate in an annual grassland. *Ecology* 71:1968–75.
- Dent CL, Grimm NB, Marti E, Edmonds JW, Henry JC, Welter JR. 2007. Variability in surface-subsurface hydrologic interactions and implications for nutrient retention in an arid-land stream. *J Geophys Res* 112:G04004.
- Downing JA, McClain M, Twilley R, Melack JM, Elser J, Rabalais NN, Lewis WM, Turner RE, Corredor J, Soto D, Yanez-Arancibia A, Kopaska JA, Howarth RW. 1999. The impact of accelerating land-use change on the N cycle of tropical aquatic ecosystems: current conditions and projected changes. *Biogeochemistry* 46:109–48.
- Duval TP, Hill AR. 2007. Influence of base flow stream bank seepage on riparian zone nitrogen biogeochemistry. *Biogeochemistry* 85:185–99.
- Ensign SH, Doyle MW. 2005. In-channel transient storage and associated nutrient retention: Evidence from experimental manipulations. *Limnol Oceanogr* 50:1740–51.
- Ellery W, Ellery K, McCarthy T. 1993. Plant distributions in islands of the Okavango Delta, Botswana: determinants and feedback interactions. *Afr J Ecol* 31:118–34.
- Fetter CW. 1994. *Applied hydrogeology*. Upper Saddle River (NJ): Prentice Hall. p 488.
- Gaiser EE, Trexler JC, Richards JH, Childers DL, Lee D, Edwards AL, Scinto LJ, Noe GB, Jones RD. 2005. Cascading ecological effects of low-level phosphorus enrichment in the Florida Everglades. *J Environ Qual* 34:717–23.
- Gann TGT. 2001. Investigating tree island community response to increased water flow on seasonally flooded tree islands in the southern Everglades. M.S. Thesis, Florida International University, Miami, FL, p 113.
- Gann TGT. 2005. Ecosystem responses to hydrologic change and mechanisms of nitrogen sequestration in seasonally flooded tree islands of the southern Everglades. Ph.D. Dissertation, Florida International University, Miami, FL, p 137.
- Gordon AS, Cooper WJ, Scheidt DJ. 1986. Denitrification in marl and peat sediments in the Everglades. *Appl Environ Microbiol* 52:987–91.
- Gribsholt B, Struyf E, Tramper A, DeBrabandere L, Brion N, van Damme S, Meire P, Dehairs F, Middelburg JJ, Boschker HTS. 2007. Nitrogen assimilation and short term retention in a

- nutrient-rich tidal freshwater marsh—a whole ecosystem 15 N enrichment study. *Biogeosciences* 4:11–26.
- Hardy RWF, Holsten RD, Jackson EK, Burns RC. 1968. The acetylene-ethylene assay for N₂ fixation: laboratory and field evaluation. *Plant Physiol* 43:1185–207.
- Harms TK, Grimm NB. 2008. Hot spots and hot moments of carbon and nitrogen dynamics in a semiarid riparian zone. *J Geophys Res* 113:G01020.
- Harvey JW, Saiers JE, Newlin JT. 2005. Solute transport and storage mechanisms in wetlands of the Everglades, south Florida. *Water Resour J* 41:W05009.
- Hedin LO, von Fischer JC, Ostrom N, Kennedy BP, Brown MG, Robertson GP. 1998. Thermodynamic constraints on nitrogen transformations and other biogeochemical processes at soil-stream interfaces. *Ecology* 79:684–703.
- Hefting M, Clement JC, Downrick D, Cosandey AC, Bernal S, Cimpian C, Tatur A, Burt TP, Pinay G. 2004. Water table elevation control on soil nitrogen cycling in riparian wetlands along a European climatic gradient. *Biogeochemistry* 67:113–34.
- Hester ET, Doyle MW. 2008. In-stream geomorphic structures as drivers of hyporheic exchange. *Water Resour Res* 44:1–17.
- Hopkinson CS. 1992. A comparison of ecosystem dynamics in freshwater wetlands. *Estuaries* 15:549–62.
- Iwaniec DM, Childers DL, Rondeau DR, Madden CJ, Saunders C. 2006. Effects of hydrologic and water quality drivers on periphyton dynamics in the southern Everglades. *Hydrobiologia* 569:223–35.
- Jaworski NA, Groffman PM, Keller AA, Prager JC. 1992. A watershed nitrogen and phosphorus balance: the upper Potomac River Basin. *Estuaries* 15:83–95.
- Kemp WM, Wetzel RL, Boynton WR, D'Elia CF, Stevenson JC. 1982. Nitrogen cycling concepts and estuarine interfaces: some current concepts and research directions. In: Kennedy V, Ed. *Estuarine comparisons*. New York (NY): Academic Press. p 209–30.
- Langstroth P. 2001. Forested islands in an Amazonian savanna of northeastern Bolivia (revised version). Doctoral Dissertation. University of Madison, WI, USA.
- Lewis DB, Grimm NB, Harms TK, Schade JD. 2007. Subsystems, flowpaths, and the spatial variability of nitrogen in a fluvial ecosystem. *Landsc Ecol* 22:911–24.
- McClain ME, Boyer EW, Dent CL, Gergel SE, Grimm NB, Groffman PM, Hart SC, Harvey JW, Johnston CA, Mayorga E, McDowell WH, Pinay G. 2003. Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. *Ecosystems* 6:301–12.
- McCormick PV, O'Dell MB, Shuford RB. 2001. Periphyton responses to experimental phosphorus enrichment in a subtropical wetland. *Aquat Bot* 71:119–39.
- Martinelli LA, Piccolo MC, Townsend AR, Vitousek PM, Cuevas E, McDowell WH, Robertson GP, Santos OC, Treseder K. 1999. Nitrogen stable isotopic composition of leaves and soil: tropical versus temperate forests. *Biogeochemistry* 46:45–65.
- Meeder JF, Ross MS, Telesnicki G, Ruiz PL, Sah JP. 1996. Vegetation analysis in the C-111/Taylor Slough basin. Final Report. Florida International University, Miami, FL.
- Miller WL, Zepp RG. 1995. Photochemical production of dissolved inorganic carbon from terrestrial organic matter: significance to the oceanic organic carbon cycle. *Geophys Res Lett* 22:417–20.
- Mitchell CPJ, Branfireun BA. 2005. Hydrogeomorphic controls on reduction–oxidation conditions across boreal upland–peatland interfaces. *Ecosystems* 8:731–47.
- Mortazavi B, Iverson RL, Huang W, Graham Lewis F, Caffrey JM. 2000. Nitrogen budget of Apalachicola Bay, a bar-built estuary in the northeastern Gulf of Mexico. *Mar Ecol Progr Ser* 195: 1–14.
- Mullholland PJ, Tank JL, Sanzone DM, Wollheim WM, Peterson BP, Webster JR, Meyer JL. 2000. Nitrogen cycling in a forest stream determined by a ¹⁵N tracer addition. *Ecol Monogr* 70:471–93.
- Mullholland PJ. 2004. The importance of in-stream uptake for regulating stream concentrations and outputs of N and P from a forested watershed: evidence from long-term chemistry records for Walker Branch Watershed. *Biogeochemistry* 70:403–26.
- Newman S, Grace JB, Koebel JW. 1996. Effects of nutrients and hydroperiod on *Typha*, *Cladium*, and *Eleocharis*: implications for Everglades restoration. *Ecol Appl* 6:774–83.
- Noe GB, Childers DL, Jones RD. 2001. Phosphorus biogeochemistry and the impact of phosphorus enrichment: why is the Everglades so unique? *Ecosystems* 4:603–24.
- Nye PH. 1966. Organic matter and nutrient cycles under moist tropical forests. *Plant Soil* 13:333–46.
- Orem WH, Willard DA, Lerch HE, Bates AL, Boylan A, Comm M. 2002. Nutrient geochemistry of sediments from two tree islands in water conservation area 3B, the Everglades, Florida. In: Sklar FH, van der Valk A, Eds. *Tree islands of the Everglades*. Boston (MA): Kluwer Academic Publishers. p 153–86.
- Patterson K, Finck R. 1999. Tree islands of the WCA3 aerial photointerpretation and trend analysis: project summary report. St. Petersburg (FL): Geonex Corporation. Report to the South Florida Water Management District.
- Peterjohn WT, Correll DL. 1984. Nutrient dynamics in an agricultural watershed observations on the role of a riparian forest. *Ecology* 65:1466–75.
- Ponce V, Cunha C. 1993. Vegetated earthmounds in tropical savannas of Central Brazil: a synthesis with special reference to the Pantanal do Mato Grosso. *Journal of Biogeography* 20:219–25.
- Qualls RG. 1984. The role of leaf litter nitrogen immobilization in the nitrogen budget of a swamp stream. *J Environ Qual* 13:640–4.
- Rejmankova E, Komarkova J. 2000. A function of cyanobacterial mats in phosphorus-limited tropical wetlands. *Hydrobiologia* 431:135–53.
- Rivera-Monroy VH, Twilley RR. 1995. The relative role of denitrification and immobilization in the fate of inorganic nitrogen in mangrove sediments (Terminos Lagoon, Mexico). *Limnol Oceanogr* 41:284–96.
- Schwartz FW, Zhang H. 2003. *Fundamentals of groundwater*. John Wiley and Sons Inc., Hoboken, NJ, USA. 592 p.
- Sklar FH, van der Valk A. 2002. Tree islands of the Everglades: an overview. In: Sklar FH, van der Valk A, Eds. *Tree islands of the Everglades*. Boston (MA): Kluwer Academic Publishers. p 1–18.
- Sobczak WV, Findlay S, Dye S. 2003. Relationships between DOC bioavailability and nitrate removal in an upland stream: an experimental approach. *Biogeochemistry* 62:309–27.
- Stutter MI, Lumson DG, Thoss V. 2007. Physico-chemical and biological controls on dissolved organic matter in peat aggregate columns. *Eur J Soil Sci* 58:646–57.

- Sutula M, Day JW, Cable J, Rudnick D. 2001. Hydrological and nutrient budgets of freshwater and estuarine wetlands of Taylor Slough in Southern Everglades, Florida (USA). *Biogeochemistry* 56:287–310.
- Tank JL, Meyer JL, Sanzone DM, Mullholland PJ, Webster JR, Peterson BJ, Wollheim WM, Leonard NE. 2000. Analysis of nitrogen cycling in a forest stream during autumn using a ^{15}N -tracer addition. *Limnol Oceanogr* 45:1013–29.
- Tomas CR, Bendis B, Johns K. 1999. Role of nutrients in regulating plankton blooms in Florida Bay. In Kumpf H, Steidinger K, Sherman K, Eds. *The Gulf of Mexico large marine ecosystem: assessment, sustainability, and management*. Malden, MA: Blackwell Science. p 323–37.
- Troxler TG, Childers DL. 2009. Litter decomposition promotes differential feedbacks in an oligotrophic southern Everglades wetland. *Plant Ecol* 200:69–82.
- Troxler Gann TG, Childers DL, Rondeau DN. 2005. Ecosystem structure and hydrologic features of tree islands in the southern Everglades. *For Ecol Manag* 214:11–27.
- Troxler TG, Childers DL. 2006. Relationships between hydrology and soils describe vegetation patterns in seasonally flooded tree islands of the southern Everglades, Florida. *Plant Soil* 279:271–86.
- Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG. 1997. Human alteration of the global nitrogen cycle: sources and consequences. *Ecol Appl* 7:727–50.
- Wessel WW, Tietema A. 1992. Calculating gross N transformation rates of ^{15}N pool dilution experiments with acid forest litter: analytical and numerical approaches. *Soil Biol Biochem* 24:931–42.
- Wetzel PR, van der Valk AG, Newman S, Gawlik DE, Troxler Gann T, Coronado-Molina CA, Childers DL, Sklar FH. 2005. Nutrient redistribution key to maintaining tree islands in the Florida Everglades. *Front Ecol Environ* 3:370–6.
- Wetzel PR, van der Valk AG, Newman S, Coronado-Molina CA, Troxler-Gann TG, Childers DL, Orem WH, Sklar FH. 2008. Heterogeneity of phosphorus distribution in a patterned landscape, the Florida Everglades. *Plant Ecol* 200:83–90.
- Wollheim WM, Pellerin BA, Vorosmarty CJ, Hopkinson CS. 2005. N retention in urbanizing headwater catchments. *Ecosystems* 8:871–84.
- Wozniak JR. 2006. Quantifying nitrogen cycling rates in freshwater marshes of the southern Everglades using ^{15}N tracer techniques. Ph.D. Dissertation, Florida International University.