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A nitrogen budget for late-successional hillslope tabonuco forest, Puerto Rico

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Abstract. Nitrogen budgets of late successional forested stands and watersheds provide baseline data against which the effects of small- and large-scale disturbances may be measured. Using previously published data and supplemental new data on gaseous N loss, we construct a N budget for hillslope tabonuco forest (HTF) stands in Puerto Rico. HTF stands are subject to frequent hurricanes and landslides; here, we focus on N fluxes in the late phase of inter-disturbance forest development. N inputs from atmospheric deposition (4–6 kg N/ha/yr) are exceeded by N outputs from groundwater, gaseous N loss, and particulate N loss (6.3–15.7 kg N/ha/yr). Late-successional HTF stands also sequester N in their aggrading biomass (8 kg N/ha/yr), creating a total budget imbalance of 8.3–19.7 kg N/ha/yr. We surmise that this imbalance may be accounted for by unmeasured inputs from above- and belowground N-fixation and/or slow depletion of the large N pool in soil organic matter. Spatial and temporal variability, especially that associated with gaseous exchange and soil organic matter N-mineralization, constrain the reliability of this N budget.

Introduction

Nutrient budgets of forest ecosystems are frequently characterized by an imbalance between inputs and outputs. A prime example of this phenomenon is the so-called "missing N" which refers to a gap between measured or calculated N inputs and measured or calculated N outputs (Bormann et al. 1977; Bruijnzeel 1991; Driscoll in prep.; Likens et al. 1977; McDowell & Asbury 1994). The literature is replete with examples in which N input estimates are insufficient to account for system outputs and net N sequestration in biomass (e.g. Bormann et al. 1977; Likens et al. 1977; Jordan et al. 1982; McDowell & Asbury 1994). Various researchers have hypothesized that N imbalances may be accounted for by N-fixation (Bormann et al. 1977; Bormann et al. 1993; Likens et al. 1977), unmeasured allocthonous inputs (Zarin & Johnson

1995), systematic or random errors of commission and/or omission in internal N flux measurements (Bruijnzeel 1991), and errors in the general assumption of a steady-state soil organic matter (SOM) N reservoir. Yet there are few locales where these alternative hypotheses have been addressed.

Nitrogen budgets of varying complexity have been developed for both tropical and temperate forests (e.g. Adams & Attiwill 1992; Bellias & Roda 1991; Bormann et al. 1977; Fischer et al. 1996; Friedland et al. 1991; Johnson et al. 1991; Likens et al 1977; McDowell & Asbury 1994; Mitchell et al. 1996; Mitchell et al. 1992; Monk & Day 1988; Sollins et al. 1980; Triska et al. 1984). However, most studies do not sufficiently examine all N cycle components necessary to accurately determine whether N inputs are sufficient to account for exports plus net forest growth. Bruijnzeel (1991) compared N budgets for many lowland and montane tropical forests on the basis of precipitation inputs and losses in drainage water only. For many sites, including two in Puerto Rico, he found that N outputs via drainage were considerably higher than N inputs in precipitation; other tropical sites had opposite results with inputs exceeding outputs (Bruijnzeel 1991). However, Brunijzeel's synthesis includes no data on either gaseous exchange of N or net sequestration of N in biomass. McDowell & Asbury (1994) constructed input-output budgets for 3 watersheds in Puerto Rico, and concluded that when biomass accumulation is included, net unmeasured inputs of N are large (8 to 16 kg N/ha/yr).

Here, we develop a N budget for late-successional hillslope *tabonuco* forest (HTF) stands in the Luquillo Experimental Forest (LEF), Puerto Rico. We have two objectives for this undertaking: first, to quantify imbalances in the N budget of HTF stands; second, to explicitly identify gaps for future investigations of the N cycle in the LEF. We limit our analysis to hillslope stands (Figure 1) because riparian and floodplain areas are characterized by distinctly different nitrogen dynamics (McDowell et al. 1992). Similarly, our analysis is limited to late-successional stands, because younger stands are characterized by significantly different nitrogen cycling regimes (Perry 1994). Earlier input-output calculations by McDowell and Asbury (1994) indicated that measured N deposition was insufficient to account for streamflow output + net biotic uptake integrated across a watershed in the tabonuco forest zone (300-600 masl); they estimated a catchment-level N imbalance of approximately 8.3 kg N/ha/yr.

In this paper, we characterize the N budget of late-successional HTF stands in terms of internal fluxes (above-and belowground litterfall, decomposition, net mineralization and throughfall) in addition to external inputs, outputs and biomass accumulation. Characterization of internal fluxes permits us to explicitly identify potential mechanisms which could account for imbalances in the input-output budget.

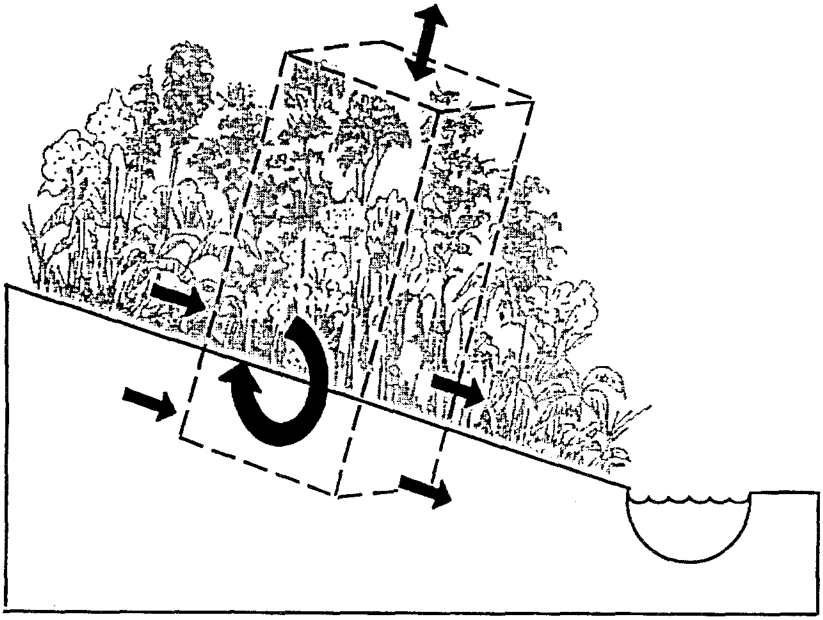

Figure 1. Idealized illustration of hillslope *tabonuco* forest (HTF). Dashed lines illustrate that the unit of analysis for our synthesis is a generic HTF stand. Arrows represent gaseous and aqueous flux (above- and belowground), and within-stand cycling and uptake.

Methods

Our analysis is based primarily on previously published data from studies conducted in late successional HTF stands throughout the LEF. We also include new data on gaseous N loss for HTF stands in three different LEF watersheds. In this section, we provide a summary of the estimates in Table 1; calculations are presented in Appendix I. Error ranges presented represent multiple years or studies; no attempt was made to incorporate or propagate the error estimates of individual measurements. Our unit of study is a hypothetical HTF stand (Figure 1). The HTF occupies a large percentage of the total landscape in the *tabonuco* forest (approximately 65% in the Bisley watershed; Scatena & Lugo 1995). We draw on data for this forest type from a number of locations; most of the data come from the Bisley and El Verde sites, both of which have been the subject of long-term ecological and biogeochemical investigations (see Brown et al. 1983; Walker et al. 1991, 1996; Holdridge 1967).

External inputs

Atmospheric deposition, geological weathering, and N-fixation are the principal potential sources of external N input to forest ecosystems. The N content of bulk precipitation for the HTF was estimated as the sum of measured NO_3-N and NH_4-N concentrations (McDowell et al. 1990) and an estimate of dissolved organic nitrogen (DON). Inputs of dissolved organic nitrogen (DON) have not been quantified for any HTF locations, but an estimate of DON was generated using DOC:DON ratios for precipitation at La Selva, Costa Rica (Eklund et al. 1997) and measured DOC inputs in HTF rain (McDowell et al. 1990). Bedrock N content has not been measured at any HTF locations; however, N concentrations have been measured to 6 m (Scatena, pers. comm.), a depth which greatly exceeds that of the HTF rooting zone (< 1 m). Edmisten (1970) report elevated rates of N-fixation for specific species of trees and epiphytes with high N-fixation potential. However, there are no published data for spatially-integrated average levels of N-fixation above- or belowground in HTF stands. Numerous authors have suggested that N-fixation may be an important source of "missing N"; we address the circumstantial evidence surrounding that hypothesis in the Discussion.

Outflows

Aqueous export and gaseous losses are the principal pathways for N loss from HTF ecosystems. We assume that concentrations of N entering the system in lateral subterranean flow are the same as those in lateral flow leaving the site. Although we assume that the concentration is constant, total water flux increases and hence there is a net loss of N from the plot proportional to runoff generation in the plot. Nitrogen flux from groundwater was calculated as the product of annual basin-wide runoff for the HTF (García-Martinó et al. 1996, McDowell & Asbury 1994) and total N concentrations in shallow subterranean groundwater of the HTF area in the Bisley watershed (McDowell et al. 1992). We use groundwater instead of streamwater N concentrations to estimate inorganic aqueous export in order to avoid the potentially confounding effects of riparian and in-stream N processing. Although riparian zones can alter hydrologic estimates of runoff generation due to increased evapotranspiration, they only occupy 7% of the watershed area (Scatena & Lugo 1995) and therefore do not have a significant impact on water balance in this system. Other potential complications, such as temporal variation in subterranean groundwater concentrations, do not significantly impact our estimate due to the lack of seasonal variability in groundwater in the HTF (McDowell et al. 1992). Annual particulate organic N export for a single HTF watershed averaged over a three-year period was used as an estimate of particulate N

Table 1. Fluxes of nitrogen (kg/ha/yr) in a hillslope tabonuco forest, Puerto Rico. Data reported as ranges of published values. Calculations are included in Appendix I.

	External Input	Outflows	Biomass Accumulation	Internal Flux
Precipitation[1]	4			
Dry Deposition	0–2[a]			
Geological Weathering	0[b]			
Nitrogen Fixation	?			
Total Inputs	4–6 + ?			
Groundwater[2,3]		5–11		
Particulate Organic N Losses[3]		0.3–0.7		
Gaseous N Losses[4,5]		1–4		
Total Outputs		6.3–15.7		
Aboveground Biomass Accumulation[6,7,8]			6	
Belowground Biomass Accumulation[6,7,8]			2	
Total Biomass Accumulation			8	
Whole Tree Mortality[6,9]				18
Coarse Woody Debris (Branchfall)[6,10]				6
Coarse Root Turnover[6,10]				1
Fine Litterfall[7,11]				101–103
Fine Root Turnover[6,12,13]				17
Net Throughfall[1,14,15]				3
Total N Uptake Requirement			154–156[c]	

[1]McDowell et al. 1990; [2]McDowell et al. 1992; [3]McDowell & Asbury 1994; [4]Erickson in prep.; [5]Data this study (Appendix II); [6]Scatena et al. 1993; [7]Weaver & Murphy 1990; [8]Crow 1980; [9]Lugo & Scatena 1996; [10]Vogt et al. 1996; [11]Lodge et al. 1991; [12]Silver & Vogt 1993; [13]Vogt et al. 1995; [14]McDowell 1998; [15]Scatena 1990.

[a]Estimates potential range based on dry deposition rates at other sites.

[b]Estimate based on basin geologic characteristics.

[c]Total N uptake requirement equals biomass accumulation + internal flux.

losses (McDowell & Asbury 1994). We reasoned that overall loss of particulate N from the basin was the best estimate of loss from HTF; we do not have the detailed plot-level studies of particulate N transport that would be needed to improve this estimate. Nitrous-oxide (N_2O) and nitric-oxide (NO) production rates were measured for three watersheds within the HTF zone (Erickson et al. in prep.; see Appendix II). We used acetylene inhibition of N_2 production to determine the ratio of N_2 to N_2O for the three watersheds

(Appendix II). We use this ratio as the basis for calculating total gaseous N loss from Erickson et al.'s (in prep.) measurements of N_2O production. NH_3 volatilization has not been measured in the LEF, but is generally considered to be small in forested ecosystems where NH_3 concentrations in ambient air are below the compensation point of 0.8 ppb (Langford & Fehsenfeld 1992) and soils are acidic.

Biomass accumulation

Principal reservoirs for N are aboveground biomass, root biomass, forest floor and soil organic matter (SOM). Nitrogen storage in aboveground biomass and roots in HTF stands is reported in Scatena et al. (1993). Nitrogen storage in forest floor and soils (0–60 cm) for the same locations are reported by Silver et al. (1994).

Following Scatena et al. (1993) we used Crow's (1980) estimates of aboveground woody biomass accumulation and Scatena et al.'s (1993) average aboveground woody biomass N concentrations to calculate net aboveground N sequestration for HTF. Biomass accumulation was estimated during an inter-hurricane period over the course of a 30-year period (Crow 1980). Recent data from Scatena et al. (1996) on hurricane damaged areas suggest this pre-hurricane estimate is still accurate. Because we know of no data on net accumulation of coarse root biomass in HTF we assumed an equal ratio of net accumulation to standing biomass for aboveground woody biomass and coarse root biomass to calculate a net belowground accumulation estimate. We then used the average coarse root N concentration (Scatena et al. 1993) to calculate an estimate of net N sequestration in coarse roots. We developed this N budget with the assumption that foliar, fine root, forest floor and SOM N reservoirs have reached steady-state conditions. Consequences of deviations from steady state are evaluated in the Discussion and Conclusion Sections.

Internal fluxes

We consider above- and belowground litterfall, litter decomposition, net SOM mineralization and net throughfall (total throughfall minus precipitation) to be the principal internal N fluxes in HTF stands. Ecosystem scientists in the LEF and elsewhere have adhered to an operational distinction between litterfall decomposition and net SOM mineralization. Although SOM mineralization is clearly part of the litterfall decomposition process, we maintain this operational distinction wherein N flux from leaf litter is accounted for as decomposition and N flux from SOM is estimated by determining potential net mineralization rates.

Aboveground litterfall includes leaves, fine wood < 1 cm diameter, and reproductive parts (Lodge et al. 1991; Weaver & Murphy 1990) in addition to coarse woody debris 1–6 cm diameter (Vogt et al. 1996). We used litterfall biomass reported in the references cited and multiplied these values by N concentrations given therein or in Scatena et al. (1993) to calculate N flux. Also included here is an estimate of N flux associated with whole tree mortality, which includes both above- and belowground components (Lugo & Scatena 1996; Scatena et al. 1993). We recognize that dead trees may remain standing for long periods and that net N immobilization rather than net N release characterizes early phases of dead wood decomposition. Nonetheless, the long-term fate of N sequestered in dead wood is solubilization (and subsequent uptake or loss) or transfer to the SOM N pool.

Belowground litterfall refers primarily to fine root turnover compiled from data reported in Scatena et al. (1993) and Silver & Vogt (1993). Because we do not have an estimate of fine root turnover under control or ambient conditions for HTF, we used a standard technique to generate this estimate. Fine root turnover was calculated following the method of McClaugherty et al. (1982) as the difference between annual maximum and minimum for dead root biomass (Silver & Vogt 1993) with N content of fine roots taken from Scatena et al. (1993; Table 1). Because we know of no data on belowground coarse root turnover, we estimate belowground coarse root turnover by assuming an equal ratio of aboveground coarse woody debris (branchfall) to aboveground woody biomass and coarse root biomass to calculate a turnover rate for coarse roots (Scatena et al. 1993; Vogt et al. 1996). We then used the average coarse root N concentration (Scatena et al. 1993) to calculate an estimate of N flux from this process. Live root N concentrations are used for estimating coarse and fine root turnover, therefore, retranslocation of N prior to senescence is included in these estimates. The belowground component of whole tree mortality was estimated by applying stem mortality rates (Lugo & Scatena 1996) to large coarse root biomass (Scatena et al. 1993).

Decomposition rates and associated net N releases from aboveground litterfall (Table 2) are derived from data presented by Weaver & Murphy (1990), Lodge et al. (1991), Vogt et al. (1996), Zimmerman et al. (1995), and Zou et al. (1995). Vogt et al. (1996) report rates of decomposition for coarse woody debris (1–6 cm diameter), and rates for large woody debris (Zimmerman et al. 1995) were used to estimate above- and belowground whole tree decay. Analogous data from fine root decay are provided by Silver & Vogt (1993) using *in situ* methods.

Data on N immobilization – mineralization rates during decomposition are lacking for most HTF plant tissue types. We used decay constants from mass loss and assumed that N loss was linearly proportional to mass loss. We recognize that this assumption is not valid particularly during the first stages of decomposition when N is immobilized. Zou et al. (1995) report rates of mass loss for decomposing leaf litter at 75.8% yr^{-1}, but their data on N loss from this litter translate into a N loss rate of approximately 50% during the first year of decomposition. We recognize that different plant tissues will immobilize and mineralize N at different rates, however litter types with the largest N contribution, such as fine litterfall and leaffall, also decompose the most rapidly. In addition, our estimates of litter turnover do not explicitly include N release from litter that fell during previous years. Because we are most interested here in the total annual N input from litterfall to the forest floor, which includes litterfall from previous years, we estimate N loss using mass loss decay constants without any adjustment for the initial immobilization phase.

Net mineralization of N from SOM was estimated using data from Steudler et al. (1991), Bowden et al. (1992), and Silver et al. (1994). Soil samples were taken from reference and hurricane plots from 0 to 2 cm depth and net mineralization rates were calculated as the net change in soil nitrate and ammonium concentrations over a seven-day period (Stuedler et al. 1991). Silver et al. (1994) report HTF SOM as 154 mg/ha from 0 to 60 cm depth. According to Bowden et al. (1992) soils from 0 to 10 cm in depth exhibited high rates of potential net N mineralization (average 14.3 μg N/ g soil/ day) while soils from 35 to 100 cm depth exhibited virtually no potential for net mineralization. We assume that $>$ 95% of net N mineralization is occurring in the top 10 cm of soil where organic matter inputs are continual, and atmospheric inputs of water and oxygen are at a maximum. Silver et al. (1994) report percent organic matter and bulk densities for 3 soil depths (0–10 cm, 10–35 cm, and 35–60 cm); therefore, we can accurately determine the percentage of SOM present in the top 10 cm of soil for the Bisley forest and subsequently calculate net N mineralization as a function of available SOM (Table 2).

McDowell (1998) measured throughfall N flux (NH_4-N and NO_3-N) for El Verde; we estimate DON in throughfall by using the ratio of DOC:DON generated by Qualls & Haines (1991) and Qualls et al. (1991), and DOC concentrations from McDowell (1998). Net N transfer to the forest floor was estimated as the difference between canopy throughfall and precipitation. The quantity of annual canopy throughfall is relatively uniform through the HTF, approximately 59% of incoming precipitation (Scatena 1990); throughfall chemistry is only available for the El Verde site. Total annual watershed stemflow is reported in Scatena (1990). Some data suggest that N content in

Table 2. Decomposition and mineralization data for hillslope tabonuco forest, Puerto Rico. All input and decomposition values are reported in kg N/ha/yr and rounded to the nearest whole number. We applied the decay constant from mass loss (k) to N loss. Errors inherent in this assumption and our justification for making it are discussed in the Internal Fluxes portion of the Methods section.

	Total Input	Decomposition	k (yr^{-1})
Fine Litterfall[1,2]	101–103	78–80	0.78
Coarse Woody Debris (Branchfall)[3,4]	6	4	0.69
Fine Root Turnover[3,5,6]	17	7	0.40
Aboveground Tree Mortality[3,7]	13	1	0.10
Belowground Coarse Root Mortality[3,7]	5	1	0.10
Soil N Mineralization Estimate[8,9,10]		46–178	

[1]Lodge et al. 1991; [2]Weaver & Murphy 1990; [3]Scatena et al. 1993; [4]Vogt et al. 1996; [5]Silver & Vogt 1993; [6]Vogt et al. 1995;[7]Lugo & Scatena 1996; [8]Stuedler et al. 1991; [9]Silver et al. 1994; [10]Bowden et al. 1992.

stemflow is similar to throughfall (Edmisten 1970), but complete data on N content of stemflow are not available and thus are not included in our analysis.

Results and discussion

Results of our data analyses are summarized in Tables 1 and 2; we present a graphic illustration of the HTF N budget in Figure 2. Below we discuss these results and some of their implications.

External inputs

Bulk precipitation measurements for NH_4-N and NO_3-N (2 kg N/ha/yr) include wet deposition plus an unknown fraction of dry deposition. The inclusion of an estimate of DON in precipitation (2 kg/ha/yr) using DOC:DON ratios for rainfall in Costa Rica (8.2:1; Eklund et al. 1997) increased total precipitation N inputs two-fold. Dry deposition data were not available for any HTF stands. Estimates of throughfall suggest a minimal input of marine aerosols from dry deposition (McDowell 1998); however this does not necessarily translate into low levels of gaseous dry deposition of N. Lovett & Lindberg (1993) report N deposition data for 11 forests around the U.S. and one in Europe with dry deposition ranging from 39% to 56% of total N deposition. Based on the potential of long-range pollution transport to the LEF (McDowell et al.1990), precipitation inputs reported here could conceivably increase by 2 kg N/ha/yr with the inclusion of dry deposition.

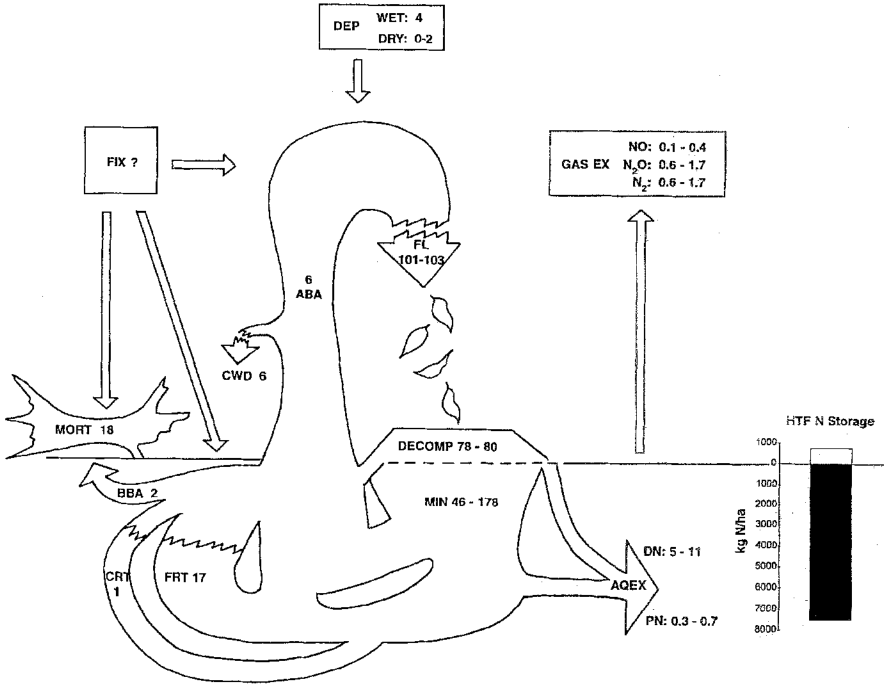

Figure 2. A model of the HTF N cycle. FIX – N-fixation, DEP – bulk deposition, GAS EX – gaseous, N export, FL – fine litterfall, ABA – aboveground biomass accumulation, CWD – coarse woody debris, MORT – above + belowground mortality, BBA – belowground biomass accumulation, CRT – coarse root turnover, FRT – fine root turnover, DECOMP – decomposition, MIN – net SOM mineralization, AQEX – aquesous export (groundwater + particulate organic N). All values are in kg N/ha/yr except for the accompanying bar graph, which illustrates HTF N pools (kg N/ha). Aboveground pools (empty bar) include forest floor (84 kg N/ha), understory vegetation (56 kg N/ha), woody tissue (506 kg N/ha) and foliage 108 kg N/ha); belowground pools (solid bar) include SOM (7250 kg N/ha), fine roots (35 kg N/ha) and coarse roots (203 kg N/ha).

Nitrogen inputs from geological weathering were not available for HTF stands. Some sedimentary rocks contain up to 0.4 percent N due to the incorporation of organic material into the rock matrix and their weathering can be an important N flux in some ecosystems (Dahlgren et al. 1994). However, volcaniclastic bedrock underlying the HTF probably contains little N, so weathering contribution is likely minimal. Measured N concentrations from 1–5 m depth in an HTF soil profile were always < 0.02 percent; below 5 m, N was undetectable (F.N. Scatena, pers. comm.).

Nitrogen fixation may be an important input of N into the HTF ecosystem. Edmisten (1970) reported the presence of several species of N-fixing bacteria and blue-green algae in HTF. To date no research has been published on the spatially-integrated rates of N-fixation in the canopy or forest floor for the HTF or other forest zones in Puerto Rico.

In most terrestrial ecosystems inputs from N-fixation are between 1 and 10 kg N/ha/yr (Cushon & Feller 1989; Perry 1994). However, levels of N-fixation are highly dependent on both plant and animal species composition. Several ecosystem types ranging from grasses to coniferous forests have exhibited high levels of potential N-fixation (50 to 150 kg/ha/yr) even without the presence of symbiotic N-fixing species (Bormann et al. 1993; Perry 1987; Stevenson 1986). Canopy lichens may contain N-fixing cyanobacteria that are capable in some cases of fixing large amounts of N (1.5 to 9 kg/ha/yr) in tropical forests (Forman 1975). Termites, which are very common in the LEF, may also be a host organism for N-fixing bacteria especially in tropical environments (Breznak & Brill 1973; Martius 1994; Perry 1994). Elevated rates of N-fixation are associated with primary succession and early pedogenesis. For the first 191 years of soil development on new volcanic substrates in Hawaii, N-fixation averaged 22 kg N/ha/yr (Vitousek et al. 1983). Hurricanes and landslides occur frequently in the LEF (Scatena & Lugo 1995); the latter disturbance is especially likely to trigger elevated rates of N-fixation (Zarin & Johnson 1995).

Outflows

We calculated a range for groundwater export (5–11 kg/ha/yr) which is similar to, though somewhat higher than, that of streamwater export found for a single HTF watershed by McDowell & Asbury (1994). Particulate organic N losses (0.3–0.7 kg N/ha/y)are also included to account for export due to surface erosion and runoff, but are considerably smaller than losses due to groundwater export.

Losses of nitrogen oxide (N_2O and NO; 0.6–1.7 kg N/ha/yr and 0.1–0.4 kg N/ha/yr, respectively) were measured for 3 late-successional HTF sites (Erickson in prep; see Appendix 2). While N_2 losses were not measured directly, we estimated losses of N_2 from these sites using the acetylene (C_2H_2) inhibition assay (Mosier & Klemedtsson, 1994; see Appendix 2). This assay relies upon the observation that, at high concentrations, C_2H_2 blocks the reduction of N_2O to N_2 during the process of denitrification. We followed the approach of Parsons et al. (1993) using intact soil cores. Randomly selected fresh soil cores were incubated for several hours with and without C_2H_2. We estimate the ratio of about 1:1 N_2 to N_2O by comparing the amount of N_2O produced under C_2H_2 to N_2O produced by control cores. Using this ratio, and assuming that all N_2O flux observed by Erickson et al. (in prep.) was due to denitrification, we calculate total gaseous N flux for HTF as 1–4 kg N/ha/yr. Other studies in HTF (Bowden et al.1992; Keller et al. 1986; and Stuedler et al. 1991) report N_2O fluxes similar to those of Erickson et al. (in prep); however, they do not include any losses of N as N_2 directly. Furthermore, Erickson et al. (in prep) include improved spatial replication and account for seasonal variation with their sampling strategy. The ranges we report in this budget are for N losses from NO, N_2O and N_2 calculated from the data of Erickson et al. (in prep.) and do not include data reported in previous studies. We note that NO emissions from the forest floor represent a maximum NO loss from the system. Kaplan et al. (1988) and Bakwin et al. (1990) observed that in Amazonian forests some or all of the NO produced at the soil surface could be recycled to the forest vegetation after chemical reaction to NO_2 and deposition on forest surfaces.

Biomass accumulation

Based on estimates of net accumulation of woody biomass, we know that the above- and belowground biomass pools are not in steady-state but rather there is a net sequestration of approximately 8 kg N/ha/y into the biomass pool annually. This calculation is based on long-term average biomass accumulation rates and a one-time measurement of plant tissue N concentrations. As such, we cannot specifically determine the actual N sequestration rate for any given year. The temporal dynamics of N accumulation in biomass are complex because, following catastrophic disturbance, N in aboveground biomass approaches pre-disturbance levels faster than the biomass itself (Scatena et al. 1996; Zarin & Johnson 1995). During succession, C:N ratios increase as the ratio of woody to nonwoody tissue increases. This proportional dilution of the biomass N pool implies that the curve of biomass N accumulation reaches its asymptote earlier than the asymptote for biomass accumulation itself is reached. Consequently, our method of calculating N accumulation in biomass sets an upper bound.

Internal fluxes

Annual above- and belowground litterfall turnover rates are quite high relative to other N fluxes (Table 1). These intrasystem processes supply the evergreen forest with much of the N necessary for plant growth and maintenance. Fine litter inputs (101–103 kg N/ha/yr) are the largest aboveground input of N to the forest floor. Compared to the external inputs and outflows, other forms of aboveground litter (branchfall and aboveground whole tree mortality) also provide a considerable amount of N to the forest floor annually (6 and 13 kg N/ha/yr, respectively). Some overlap may occur between these two measures because aboveground whole tree mortality may include some portion of branchfall. Belowground fine root turnover (17 kg N/ha/yr), coarse root turnover (1 kg/ha/yr) and belowground whole tree mortality (5 kg N/ha/yr) cycle considerably less N than their aboveground counterparts. However, these belowground sources are still significant relative to other N fluxes.

Decomposition rates for aboveground fine litter (78–80 kg N/ha/yr) are quite high relative to decay rates of fine roots and larger debris associated with whole tree mortality (Table 2; Silver & Vogt 1993; Vogt et al. 1996; Weaver & Murphy 1990; Zimmerman et al. 1995; Zou et al. 1995). The rapid decay rates reported here and the relatively large amount of net SOM-N mineralization suggest that cycling of N, especially from fine litter, occurs quite rapidly within this tropical forest system (Table 2).

Conclusions

Measured external inputs and outputs to the hillslope *tabonuco* forest are not balanced: inputs from precipitation (4 kg N/ha/yr) and geological weathering (~0 kg N/ha/yr) are considerably less than outputs from the system through groundwater (5–11 kg N/ha/yr), particulate organic N export (0.3–0.7 kg/ha/yr) and gaseous N loss (1–4 kg N/ha/yr). The long-term accretion in living biomass both aboveground and belowground sequesters up to 8 kg N/ha/yr in the hillslope forest, and this N must be supplied from additional unmeasured inputs or a change in N storage in SOM. Therefore, even with the inclusion of additional N from dry deposition (up to 2 kg/ha/yr), we have a considerable budgetary imbalance (8.3–19.7 kg N/ha/yr). It is unlikely that such a large imbalance is simply due to error associated with budget generation. Our inclusion of gaseous N loss and belowground biomass accumulation lead to a larger imbalance than the catchment-scale N deficit reported by McDowell and Asbury (1994).

There are several possible sources of this "missing N" (Bormann et al. 1977; Likens et al. 1977). First, while we assume that the SOM pool is in steady state, small and unmeasurable deviations from steady state within this large pool (7250 kg N/ha) could lead to large inputs of available N. Nitrogen could be surreptitiously supplied to the system either through an increase in soil mineralization or through a change in soil C:N ratios. A 1% increase in the soil C:N ratio over a ten-year period could provide over 7 kg/ha/yr of additional N to the system, which would account for much of the N budget imbalance. Johnson et al. (1995) have reported a >1 percent per year net loss of carbon from the solum in an undisturbed late-successional northern hardwoods watershed, an indication that the prevalent assumption of a steady-state SOM pool may be unwarranted. Based on the size of the HTF SOM-N pool, an annual drawdown of ~0.1 percent of the SOM-N could account for most of our estimated N imbalance.

The size of our estimated imbalance between known inputs and outputs plus system accretion requirements is large relative to the actual input and output measurements. Since N-fixation may be actively occurring within the HTF (Edmisten 1970), unmeasured N-fixation is likely to account for some portion of our N imbalance. The lack of analyses of above- and belowground N-fixation and limitations inherent in published measurements of internal solum N fluxes in HTFs constrain our ability to do more than speculate about the potential contributions of N-fixation and net SOM-N mineralization to the N cycle of this forest type.

Finally, we cannot exclude the impacts of experimental error due to interannual variability in individual fluxes. We have compiled data collected over a number of years at several HTF sites, thereby enhancing the potential for error. Principal limitations of the flux measurements are largely related to the spatial heterogeneity and temporal variability inherent in these processes (Robertson et al. 1988).

Spatial heterogeneity

Microsite variability within HTF stands may lead to significant differences in estimations of gaseous exchange and net mineralization. Robertson et al. (1988) determined that, within a Michigan forest, the spatial heterogeneity of N flux processes (denitrification, nitrification, and mineralization) was complex and dependent upon surface topography. For tropical dry forests various aspects of the N cycle have also been found to be affected by topography and microsite variability (Roy & Singh 1994, 1995; Raghubanshi 1992). Topographic variability led to heterogeneous aboveground litter accumulation and fine root production, causing alterations in net mineralization rates and net primary productivity (Roy & Singh 1994; 1995). Nitrogen mineralization and nitrification were found to decrease along a topographic gradient in Michigan forests (Raghubanshi 1992), and Silver et al. (1994) report that other soil characteristics vary along a topographic gradient at the Bisley watershed. We expect that the highly complex and varied surface topography of HTF ecosystems also produces microsite variability in N flux rates, as it does in the riparian zones of the Luquillo Forest (McDowell et al. 1992; Bowden et al. 1992).

Temporal variability

The LEF is heavily influenced by hurricanes with 83 percent of the landscape being affected each century (Lugo & Scatena 1996). Although hurricanes are the most extensive disturbance in the LEF, landslides and tree fall gaps affect the forest as well, with landslides having a recurrence interval of 3,000 to

10,000 years, affecting 3 percent of the landscape each century (Walker et al. 1996). Increased N inputs resulting from large scale disturbance may in fact be offset by the increased N requirements of forest regeneration in the LEF. Aboveground N pools in biomass following Hurricane Hugo in 1989 decreased initially but returned to pre-hurricane levels within 48 months due to the rapid growth rates of regenerating vegetation (7–10 times the growth rate of mature forest) and the high N content of new wood and herbaceous plants (Scatena et al. 1996). Following harvest and hurricane disturbances, Silver et al. (1996) found that belowground stocks of NO_3 and NH_4 were altered, but effects were short-term and the system returned to pre-disturbance levels within one year. McDowell et al. (1996) report that inorganic N concentration in groundwater also returned to pre-hurricane levels in HTF within 1–2 yrs. after the disturbance. Temporal variability in biomass C:N ratios associated with successional development also contributes to changes in N cycling rates as detrital inputs to the SOM pool increasingly reflect the high C:N ratios characteristic of woody debris. Although disturbances may produce major alterations in forest composition and structure, the overall nitrogen economy appears both resistant and resilient to disturbance.

Directions for future research

Development of this N budget has led us to identify several key areas for future investigations. (1) Nitrogen fixation has not been studied on a large scale within the natural forest system in either canopy or soil environments and may be a significant source of N to this system. What is the magnitude, distribution, and spatial and temporal variability in N-fixation in the tabonuco forest? (2) Nitrogen within HTF stands appears to be cycled through decomposition and biotic uptake with internal fluxes considerably larger than losses. Are the SOM and forest floor pools really in steady-state? (3) Temporal variability may be high for mineralization and gaseous exchange based on the disturbance regime of the watershed; however, nitrogen reserves above- and belowground appear to stabilize quickly. How are the impacts of large (hurricanes and landslides) and small (treefall gaps) disturbances on these N processes distributed within affected HTF stands? (4) Spatial and temporal variability may lead to misinterpretations especially with respect to mineralization and gas exchange rates. What spatial and temporal scales of analysis are required to accurately represent these processes in stand and catchment-level nutrient budget analyses?

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Appendix I

Values reported here and in Table 1 have been rounded to reflect our best estimate of precision.

1. **Precipitation = 4 kg N/ha/yr**
   NO_3-N + NH_4-N in bulk precipitation for El Verde = 1.95 kg N/ha/yr (McDowell et al. 1990)
   DON:DOC Ratio in precipitation at La Selva, Costa Rica = 1:8.2 (Eklund et al. 1997)
   DOC in precipitation at El Verde = 19.1 kg/ha/yr (McDowell et al. 1990)
   DON in precipitation at El Verde using ratio = 2.3 kg N/ha/yr
      N Flux = 1.95 + 2.3 = 4.25 kg N/ha/yr

2. **Groundwater = 5–11 kg N/ha/yr**
   Basin-wide runoff (Toronja) = 1750 mm/yr (McDowell & Asbury 1994)
   Basin-wide runoff (Bisley) = 1776 mm/yr (Scatena pers. comm.)
   Average basin-wide runoff (Tabonuco Forest Zone) = 1830 mm/yr (García-Martinó et al. 1996)
   Groundwater TDN concentration for Bisley slope = 0.3–0.6 g N/m^3 McDowell et al. 1992)
   Minimum N Flux from GW = 1750 mm/yr * 0.3 g N/m^3 = 5.3 kg N/ha/yr
   Maximum N Flux from GW = 1830 mm/yr * 0.6 g N/m^3 = 11.0 kg N/ha/yr
      N Flux - 5.3–11.0 kg N/ha/yr

3. **Particulate Organic N Export = 0.3–0.7 kg N/ha/yr**
   Range of basin-wide stream export for Toronja watershed for 3 years
      (McDowell & Asbury 1994)

4. **Denitrification = 1–4 kg N/ha/yr**
   N_2O and NO data from Erickson et al. in prep. for HTF
   El Verde N_2O = 0.75 ng N/cm^2/h; NO = 0.11 ng N/cm^2/h

Mameyes N_2O = 0.64 ng N/cm^2/h; NO = 0.14 ng N/cm^2/h
SSabana N_2O = 1.93 ng N/cm^2/h; NO = 0.40 ng N/cm^2/h
N_2 Ratio for HTF = 1:1 (this paper; Appendix II)
Minimum N Flux from N_2O and N_2 = 0.6 kg N/ha/yr * 2 = 1.2 kg N/ha/yr
Maximum N Flux from N_2O and N_2 = 1.7 kg N/ha/yr * 2 = 3.4 kg N/ha/yr
Minimum N Flux (N_2O, N_2 and NO) = 1.2 kg N/ha/yr + 0.10 kg N/ha/yr = 1.3 kg N/ha/yr
Maximum N Flux (N_2O, N_2 and NO) = 3.4 kg N/ha/yr + 0.35 kg N/ha/yr = 3.75 kg N/ha/yr
N Flux = 1.3–3.75 kg N/ha/yr

5. **Aboveground Biomass Accumulation = 6 kg N/ha/yr**

Net woody production Tabonuco Forest = 2268 kg/ha/yr (Crow 1980; Weaver & Murphy 1990)
Total N Bisley slope (aboveground vegetation) = 2.82 mg N/g biomass (Scatena et al. 1993)
N flux = 2268 kg/ha/yr * 0.00282 g/g = 6.4 kg N/ha/yr

6. **Belowground Biomass (Coarse Roots) Accumulation = 2 kg N/ha/yr**

Above biomass/net woody production = Below biomass/below woody production
Below biomass (coarse roots) = 65681 kg/ha (Scatena et al. 1993)
Above biomass (leaves, branches, bark, bole) = 224841 kg/ha (Scatena et al. 1993)
Net woody production = 2268 kg/ha/yr (Crow 1980; Weaver & Murphy 1990)
Below production = (73558 * 2268) / 224841 = 742 kg/ha/yr
Total N for Bisley slope (coarse roots) = 0.0031 g N/ g biomass (Scatena et al. 1993)
N flux = 0.0031 g/g * 742 kg/ha/yr = 2.4 N/ha/yr

7. **Aboveground Fine Litterfall Turnover = 101–103 kg N/ha/yr**

Bisley watershed mean annual nutrient input from total fine litterfall (Lodge et al. 1991)
Litterfall biomass = 9697 kg/ha/yr (Lodge et al. 1991)
Leaf biomass = 1.29 g/m^2/day; Leaf N content = 12.6 mg/g
Fine wood biomass = 0.55 g/m^2/day; Fine wood N content = 8.6 mg/g
Misc. fine litter biomass = 0.54 g/m^2/day; Misc. fine litter N content = 13.4 mg/g
N Flux = (1.29 g/m^2/day * 0.0126g/g) + (0.55 g/m^2/day * 0.0085g/g) + (0.54 g/m^2/day * 0.0134g/g) = 102.9 kg N/ha/yr
Litterfall biomass = 8748 kg/ha/yr (Weaver & Murphy 1990)
Avg N content = 0.0115 g N/g (Lodge et al. 1991)
N Flux = 8748 kg/ha/yr * 0.0115 g N/g = 100.6 kg N/ha/yr
N Flux = 100.6–102.9 kg N/ha/yr

8. **Fine Root Turnover = 17 kg N/ha/yr**

Maximum Dead Root Biomass = 175 g/m^2 (Silver & Vogt 1993)
Minimum Dead Root Biomass = 75 g/m^2 (Silver & Vogt 1993)
Annual Difference = 1000 kg/ha/yr
Total N Fine Roots = 0.017 g/g (Scatena et al. 1993)
N Flux = 1000 kg/ha/yr * 0.017 g N/g biomass = 17.0 kg N/ha/yr

9. Coarse Woody Debris – Branchfall (1–6 cm) = 6 kg N/ha/yr

Bisley coarse woody debris inputs for decomposition = 1200 kg/ha/yr (Vogt et al. 1996)
Total N Branches = 127.2 kg $N_{branches}$/ha ÷ 25492.3 kg $N_{biomass}$/ha = 0.00499 g N/g (Scatena et al. 1993)
N Flux = 1200 kg/ha/yr * 0.00499 g N/g = 6.0 kg N/ha/yr

10. Coarse Root Turnover = 1 kg N/ha/yr

Aboveground biomass/coarse woody debris Input = Coarse root biomass/coarse root turnover
Aboveground coarse woody debris = 1200 kg/ha/yr (Vogt et al. 1996)
Aboveground woody biomass = 217729 kg/ha (Scatena et al. 1993)
Coarse root biomass = 73558 kg/ha (Scatena et al. 1993)
Coarse root turnover = (73558 * 1200) / 217729 = 405.4 kg/ha/yr
Total N coarse roots = 0.0031 g N/g biomass (Scatena et al. 1993)
N Flux = 405.4 kg/ha/yr * 0.0031 g N/g = 1.25 kg N/ha/yr

11. Whole Tree Mortality = 18 kg N/ha/yr

Background aboveground biomass turnover for slopes = 2.0%/yr (Lugo & Scatena 1996)
Total aboveground biomass for Bisley = 229,616 kg/ha (Scatena et al. 1993)
Annual aboveground mortality = 2.0%/yr * 229,616 kg/ha = 4592 kg/ha/yr
Average N concentration of stems for Bisley slope forest = 2.82 ng N/g biomass (Scatena et al. 1993)
N Flux for aboveground = 4592 kg/ha/yr * 0.00282 g N/g = 12.9 kg N/ha/yr

Assume Belowground mortality ~ Aboveground mortality
Average annual belowground mortality = 2.0% (Lugo & Scatena 1996)
Coarse root biomass Bisley = 73,558 kg/ha (Scatena et al. 1993)
Belowground mortality = 2.0%/yr * 73,558 kg/ha = 1471 kg/ha/yr
N concentration of live coarse roots = 3.1 mg N/g biomass (Scatena et al. 1993)
N Flux for Belowground = 1471 kg/ha/yr * 0.0031 g N/g = 4.6 kg N/ha/yr
N Flux = aboveground mortality + belowground mortality
N Flux = 12.9 kg N/ha/yr + 4.6 kg N/ha/yr = 17.5 kg N/ha/yr

13. Net Throughfall = 3 kg N/ha/yr

Total throughfall at El Verde (NH_4 + NO_3) = 3.5 kg N/ha/yr (McDowell in press)
Ratio of DOC: DON in throughfall = 35–41 (Qualls et al. 1991, Qualls & Haines 1991)
DOC in throughfall at El Verde = 127 kg/ha/yr (McDowell in press)
DON in throughfall at El Verde using ration = 3.1–3.6 kg N/ha/yr
Total N in precipitation = 4 kg N/ha/yr
Minimum N Flux = 3.5 kg N/ha/yr + 3.1 kg N/ha/yr – 4 kg N/ha/yr = 2.6 kg N/ha/yr
Maximum N Flux = 3.5 kg N/ha/yr + 3.6 kg N/ha/yr – 4 kg N/ha/yr = 3.1 kg N/ha/yr
N Flux = 2.6–3.1 kg N/ha/yr

14. Mineralization Rates = 46–178 kg N/ha/yr

Average net mineralization (0–2 cm) for reference plots = 2.6 μg N/g OM/day (Stuedler et al. 1991)

Average net mineralization (0–2 cm) for hurricane plots = 10.1 μg N/g OM/day (Stuedler et al. 1991)
We assume >95% occurs from 0 to 10 cm soil (Bowden et al. 1992)
Total soil organic matter = 154 Mg/ha (0 to 60 cm) (Silver et al. 1994)
Bulk density 0 to 10 cm depth = 0.68 g/cm^3
0 to 10 cm = 7.1% OM
Organic matter (0–10 cm) = 0.071 g OM/g soil * 0.68 g soil/cm^3 * 10 cm = 48280 kg OM/ha
Reference Net Mineralization = 2.6 μg N/g OM/day * 48280 kg OM/ha = 46 kg N/ha/yr
Hurricane Net Mineralization = 10.1 μg N/g OM/day * 48280 kg OM/ha = 178 kg N/ha/yr
N Flux = 46–178 kg N/ha/yr

Pool Size

1. **Forest Floor = 84 kg/ha**
   Forest floor biomass = 7000 kg/ha (Silver et al. 1994)
   Total N Bisley slope forest = 12 mg/g = 0.012 g N/g
   Forest floor N = 7000 kg/ha * 0.012 g N/g = 84 kg N/ha

2. **Soil Organic Matter 0 to 60 cm = 7250 kg N/ha**
   Silver et al. 1994

3. **Aboveground Biomass = 670 kg N/ha**
   Bisley watershed (Scatena et al. 1993)
   N content kg N/ha
   Leaves = 108.2; Branches = 127.2; Bole = 353.8; Bark = 24.8
   Understory Palms = 44.6; Saplings = 4.4; Herbs = 4.6; Ferns = 2.2
   Total aboveground biomass N pool = 669.8 kg N/ha

4. **Belowground Biomass = 237 kg N/ha**
   Coarse roots > 0.5 cm = 202.7 kg N/ha (Scatena et al. 1993)
   Fine roots < 0.5 cm = 34.6 kg N/ha (Scatena et al. 1993)
   Total belowground biomass N pool = 237.3 kg N/ha

Appendix II

Methods for N_2O and NO Measurements

Soil-atmosphere N_2O and NO flux measurements were made at three study areas for late successional *tabonuco* forest (El Verde, Mameyes, and Sabana; Erickson et al. in prep.). Erickson et al. (in prep.) followed the static vented chamber approach for N_2O and the dynamic open vented chamber approach for NO (Keller and Reiners 1994). Eight chambers for N_2O and 4 chambers for NO were analyzed for each sampling date. The Mameyes and Sabana sites were sampled 12 times for N_2O and 11 times for NO over one year. The El Verde site was sampled 6 times over slightly more than one year. N_2O was collected in 20 mL nylon syringes and analyzed using electron capture gas chromatography within 24 hours of sample collection.

NO was analyzed in the field using a portable chemiluminescent detector (Scintrex LMA-3) following the methods of Veldkamp and Keller (1997). N_2O and NO fluxes were calculated from the linear increase of concentration over time.

Measurement of the ratio of N_2 to N_2O

The ratio of N_2 to N_2O produced by dentrification was estimated based on assays conducted in January 1997 using the same study sites as Erickson et al. (in prep) and the acetylene (C_2H_2) inhibition technique (Mosier and Kelmedtsson 1994) following the approach of Parsons et al. (1993). Sixteen soil cores (PVC pipe, 10 cm length × 5 cm diameter) were sampled randomly along a transect at each site. Cores with greater than 10% volume compaction were discarded and replaced. Eight cores were randomly selected for each of the C_2H_2 or control treatments. Cores were placed in 1L vacuum sealed canning jars immediately following field collection. Jars were evacuated and allowed to refill 4 times. For the C_2H_2 cores jars were evacuated and refilled 3 times. Following the fourth evacuation, 100 mls C_2H_2 (generated from CaC_2) was added prior to admitting air to jar. Cores were incubated for 4 hours and then the air exchange procedure was repeated including the addition of acetylene.

We sampled jars to determine instantaneous rates of N_2O production. Sampling was performed four times (0, 10, 20, and 30 min) following the second air exchange using 20 ml nylon syringes. Air (20 ml) was replaced into each jar following sampling. Samples were analyzed using electron capture gas chromatography (Veldkamp and Keller 1997). Following each experiment, soils were removed from the PVC sleeves and weighted for both wet and dry (105 °C; 48 hours) weight. N_2 to N_2O ratios ($R_{N_2:N_2O}$) were calculated from the production of N_2O in the treated and control cores according to the formula:

$$R_{N_2:N_2O} = (F_{C_2H_2} - F_{control})/F_{control}$$

where $F_{C_2H_2}$ and $F_{control}$ are the production rates (on a dry weight of soil basis of N_2O under C_2H_2 and control conditions respectively.

Our calculation assumes that all N_2O produced in the control cores was produced by the process of denitrification. The presence of C_2H_2 would inhibit nitrification-derived N_2O production (Mosier and Kelmedtsson 1994) in treated cores. However, there may be nitrification-produced N_2O in the control cores. Greater propertions of nitrification-produced N_2O in the control cores would cause us to underestimate $R_{N_2:N_2O}$. Therefore, our estimates for $R_{N_2:N_2O}$ are conservative.

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