45 Is there evidence for limitations to nitrogen mineralization in upper montane tropical forests?

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ABSTRACT

The structure and function of forest ecosystems often change along altitudinal gradients in the tropics, culminating in short-stature, low-productivity cloud forests at the uppermost elevations. Field data and literature values were used to examine patterns in nitrogen mineralization on tropical mountains and to discuss the potential for nitrogen limitation to net primary productivity. Few trends in net nitrogen mineralization within and across elevation gradients in the tropics were found, and rates were generally comparable to those found in tropical forests at low elevations. Gross nitrogen mineralization rates were much higher than net rates, and in Puerto Rico upper montane forests exhibited higher gross nitrogen mineralization than lower elevation forests. Work from Puerto Rico found no effect of short-term anaerobic conditions. In Hawai'i gross nitrogen mineralization increased with substrate age. Ammonium availability was augmented by dissimilatory nitrate reduction to ammonium in montane forests; nitrogen conservation via this pathway exceeded losses via N_2O production. Patterns in nitrogen circulation in upper montane forests in Puerto Rico showed that elfin and palm forests had lower nitrogen use efficiency and a higher proportion of nitrogen mineralized from decomposing litter relative to other forest types, further indicating that rates of nitrogen supply in these forests are considerable. In summary, the data reviewed in this chapter suggest that nitrogen limitation alone cannot explain patterns in the structure and function of tropical montane forest vegetation. Alternative factors are offered that warrant further investigation.

INTRODUCTION

Humid montane tropical forests in general, and montane cloud forests in particular, are often characterized by low net primary productivity, low standing biomass, and short stature relative to lowland tropical forests (Grubb, 1977). Whilst there are many potential mechanisms that can contribute to this, nitrogen limitation has frequently been suggested as an important and probable cause (Tanner *et al.*, 1990, 1992, 1998; Vitousek *et al.*, 1993; Raich *et al.*, 1997; Leuschner *et al.*, 2007; Moser *et al.*, 2007; cf. Soethe *et al.*, 2008a; Benner *et al.*, this volume). The basis for this lies in characteristics of the nitrogen cycle that differ fundamentally from other biogeochemical cycles. Nitrogen inputs to terrestrial ecosystems come primarily from the fixation of atmospheric nitrogen (as opposed to mineral weathering), and its cycling is predominantly controlled by biota that are thought to be highly sensitive to soil temperature, moisture availability, aeration, and nutrient supply rates over short temporal scales. Montane tropical forests are generally cooler than their lower elevation counterparts and often receive high rainfall (Grubb, 1977). Combined, these two factors typically lead to wetter soil conditions, particularly in upper montane forests (Bruijnzeel and Proctor, 1995; Santiago *et al.*, 2000 cf. Schawe *et al.*, this volume), where surface soils can experience periods of oxygen (O_2) depletion (Silver *et al.*, 1999). Depletion of O_2 is linked with temperature and rainfall, with lower temperatures often resulting in slower decomposition rates, higher soil organic matter pools (Silver *et al.*, 1999 Schuur, 2001 Schuur *et al.*, 2001 cf. Roman *et al.*, this volume), and increased water retention, leading in turn to conditions where O_2 consumption can exceed resupply via diffusive transport from the atmosphere (Silver *et al.*, 1999).

Nitrogen cycling is highly dynamic in humid, organic-rich tropical soils, making accurate characterization of patterns in nitrogen availability difficult. Most studies have only measured net rates of soil nitrogen cycling, using a simple analytical

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technique that derives nitrogen availability from the net change in mineral nitrogen (i.e. ammoniumn (NH_4^+) and nitrate (NO_3^-)) pools at two time points, before and after a field or laboratory incubation. A wide range of incubation lengths has been used (24 hours to 40 days). This complicates direct comparisons because nitrogen is likely to be produced or consumed throughout the incubation period, and the termination point is arbitrary with regard to microbial process rates.

Gross rates of soil nitrogen cycling provide a more realistic assessment of the dynamic nature of inorganc nitrogen pools. However, the assumptions of the procedure (principally the lack of internal recycling) are only valid over short time intervals, usually from 6 to 48 hours. Gross nitrogen mineralization and nitrification are determined through isotope pool dilution techniques following ^{15}N additions to the end-product pool (NH_4^+ for gross mineralization and NO_3^- for gross nitrification). The NH_4^+ and NO_3^- pools assessed by this method are those into which the added ^{15}N compounds can diffuse; consequently, these are the pools accessible to plant roots through diffusion (Hart *et al.*, 1994). Comparing rates of carbon mineralization to gross nitrogen transformations has led to the conclusion that nitrogen is being mineralized from labile, nitrogen-rich compounds (Schimel and Bennett, 2004) which is consistent with the enzymatic processes known to directly yield NH_4^+ (Myrold, 1998). The use of isotope tracers can also provide a measure of the fates of nitrogen within the soil (e.g. microbial uptake – termed immobilization, dissimilatory or assimilatory reduction, or storage as organic nitrogen), and when coupled with measurements of ^{15}N uptake by plants and ^{15}N gas emissions it can give a relatively complete picture of internal nitrogen supply and some of the factors affecting supply and loss rates over short time periods (Hart *et al.*, 1994; cf. Soethe *et al.*, 2006).

This study reviews patterns in net and gross soil nitrogen cycling for a series of montane tropical forest elevation gradients. The primary aim was to determine whether patterns of mineral nitrogen supply in soils vary systematically with elevation, redox conditions, or patterns in soil carbon and nitrogen pools. Both net and gross nitrogen mineralization and nitrification measurements are used as indices of nitrogen cycling rates, and the values obtained are compared with other data from montane and lowland tropical forests.

MATERIALS AND METHODS

Study area

This analysis uses a combination of new data and values from the literature. The new data come from a study conducted along a 700-m elevation gradient (350 to 1050 m.a.s.l.) in the Luquillo Experimental Forest (LEF), as part of the Long Term Ecological Research program in Puerto Rico, USA (18° 30′ N, 65° 80′ W). Mean annual temperature ranges from *c.* 26 °C at the lowest elevation to *c.* 19 °C at upper elevations. Annual precipitation ranges from approximately 3500 mm at 350 m elevation to >5000 mm at 1050 m.a.s.l., and is evenly distributed throughout the year (Brown *et al.*, 1983; Weaver, 1994; García-Martino *et al.*, 1996). The cloud-affected zone, which includes tropical montane wet forest (TMW, 650–750 m.a.s.l.), palm forest (750–920 m.a.s.l.), taller cloud forest (820–930 m.a.s.l.), and elfin forest (>900 m.a.s.l.), receives approximately 4500 mm of rainfall annually (García-Martino *et al.*, 1996). Elfin forests are most common on exposed ridges and slopes, and are shorter in stature than the other forests in the research area. The taller cloud forest occurs in swales and on leeward slopes, where the vegetation is taller than in elfin forests (4–9 m vs. 2–3 m, respectively), and has different plant community composition (Brown *et al.*, 1983; Weaver, 1995). The elfin forest receives an estimated additional input via cloud water interception of *c.* 770 mm $year^{-1}$ (Holwerda *et al.*, 2006; cf. Holwerda *et al.*, this volume #29). Soils are classified as clay-rich ultisols (Brown *et al.*, 1983; Roman *et al.*, this volume). Soils are relatively deep and highly weathered, and are rich in exchangeable iron, soil organic matter content, total nitrogen, and extractable phosphorus relative to lower elevation forests. Soil pH (0–10 cm depth) in the elfin zone averages 5.41 (± 0.15) and is significantly higher (less acidic) than in lower elevation forests (Silver *et al.*, 1999). Tree height and some soil nutrient pools (magnesium, potassium) appear to co-vary along the gradient (Roman *et al.*, this volume).

Experimental approach

Twelve 10 × 30 m permanent plots were established in 1994 between ~650 and 970 m.a.s.l., with three replicate plots in each of the four main forest types. Plots were located on ridges and slope positions, where the respective forest types reach their best development (Weaver, 1994). The sites are part of a long-term study to estimate the effects of climate on forest net primary productivity and biogeochemical cycling.

For the determination of net nitrogen mineralization rates and nitrogen pool sizes, three soil samples were collected at 0–10 cm depth in each plot. Samples were split in the laboratory, with one half of each sample being extracted the same day with 2M KCl (Hart *et al.*, 1994). The other half were covered with an air-permeable lid and incubated in the dark at approximately 23 °C for 7 days and then extracted as above. All extracts were frozen for later colorometric analysis of NH_4^+ and $NO_3^- + NO_2$ at the International Institute of Tropical Forestry (IITF) using an Alpkem auto analyzer. Net nitrogen mineralization and nitrification rates were calculated according to Hart *et al.* (1994).

For gross nitrogen cycling rates, five soil samples (0–10 cm depth) were collected from two plots each in the TMW, palm

forest, and elfin forest. Soil samples ($n = 5$ per plot and two replicate 10 × 30 m plots) were also collected from ridge, slope, and valley positions at 350 m elevation in the Bisley Research Watersheds. Samples were express-mailed within 12 hours to the University of California at Berkeley. Upon arrival, samples were split such that half of the samples received $^{15}NH_4SO_4$ at a soil concentration of 0.023 μg g^{-1} (final soil enrichment of 2.4 atom % $^{15}NH_4$), whereas the other half received $^{15}KNO_3$ added at a soil concentration 0.12 μg g^{-1} (final soil enrichment of 12.4 atom % $^{15}NO_3$). Thirty grams of oven-dry equivalent sample from each set of labeled soils were incubated in 225-ml jars under ambient conditions for 0, 6, and 24 hours, and under a dinitrogen (N_2) headspace for 0, 3, 6, and 24 hours. At the end of incubations, the jars were extracted with 150 ml of 2M KCl. Incubations were done at 25 °C. Extracts were prepared for isotope analysis by diffusion (Herman *et al.*, 1995), and nitrogen-isotope ratios were measured using an automated nitrogen-carbon analyzer coupled to an isotope ratio mass spectrometer (ANCA–IRMS). Nitrous oxide was determined by gas chromatography using a ^{63}Ni detector, and nitrogen-gas isotope ratios using a trace gas module coupled to an IRMS. Rates of dissimilatory NO_3^- reduction to NH_4^+ (DNRA) – an anaerobic microbial process that has been shown to rapidly convert NO_3^- to NH_4^+ in some upland soils (Silver *et al.*, 2001, 2005; Pett-Ridge and Firestone, 2005; Pett-Ridge *et al.*, 2006; Templer *et al.*, 2008) – were also measured. DNRA has the potential to conserve nitrogen in ecosystems with high potential NO_3^- losses from denitrification and leaching (Silver *et al.*, 2001). DNRA rates were calculated as the difference in $^{15}NH_4^+$ atom % between sampling periods, multiplied by the mean NH_4^+ pool size during the interval, and corrected for the mean residence time (MRT) of the NH_4^+ pool. This was then divided by the mean $^{15}NO_3^-$ atom % during the interval to account for the isotopic composition of the source pool. To estimate MRT of the $^{15}NH_4^+$ pool, the initial NH_4^+ pool (μg g^{-1}) was divided by the rate of gross consumption using the 0–24-hour interval data from the simultaneous laboratory experiment. The MRT value from the 0–24-hour interval was chosen because it reduced the impact of short-term soil disturbance, and because it was the largest MRT value measured, its use in the DNRA calculation provided the most conservative estimates. Gross mineralization, nitrification, and NH_4^+ and NO_3^- consumption were calculated according to Kirkham and Bartholomew (1954), with means of the 6- and 24-hour incubations reported.

Field litterfall and decomposition experiments were used to estimate patterns in nitrogen cycling in forests along the elevational gradient. Litterfall was collected in five baskets (approximately 0.16 m^2 each) per plot. Baskets were lined with fine mesh and suspended off the ground on 50-cm stakes to avoid contact with the soil surface and perforated at the bottom to allow drainage. Litter was collected every 2 weeks from 1994 to 1999, dried at 65 °C, and sorted into leaves, fruits and flowers, fine wood (<5 cm diameter), and miscellaneous material. Each litter fraction was then redried and weighed. For nutrient analyses, samples were bulked by plot, forest type, and month yielding one nutrient sample per sorting category per forest type per month ($n = 16$ samples per month). Dried and ground samples were analyzed for total carbon and nitrogen using a CE Elantech NC2100 elemental analyzer (Lakewood, NJ). Decomposition of leaf litter was measured over a 2-year period at all the upper montane sites ($n = 12$ plots). Approximately 5 g of dried leaf litter was placed in mesh bags with <1 mm openings. Five bags were collected from each plot after 3, 9, 16, and 24 months. Samples were dried at 65 °C, weighed to determine mass, and redried prior to ashing at 550 °C for 12 hours to determine the amount of mineral contamination. Dried and ground samples were analyzed for total carbon and nitrogen as described above. Examination of the data determined that an exponential relationship best explained patterns in mass loss over time (Wieder and Lang, 1982), and this was used to estimate a decomposition coefficient (k).

Statistical procedures

Statistical analyses were performed using Systat (Wilkinson, 1984). Analysis of variance (ANOVA) was used to determine whether changes in pool sizes or rates occurred among treatments. Data were log-transformed when necessary to meet assumptions for ANOVA. Significant differences were determined as $p < 0.05$ unless noted otherwise.

RESULTS AND DISCUSSION

Net nitrogen transformations in montane and lowland tropical forests

Results from the Puerto Rico elevational gradient and other tropical montane forest transect studies suggest that potential net nitrogen mineralization and nitrification do not generally vary systematically along elevation gradients within or among study sites. In the Luquillo Mountains of Puerto Rico, net nitrogen mineralization rates ranged from −2.1 (± 0.7) to 6.0 (± 5.5) μg g^{-1} day^{-1} and averaged 0.2 (± 0.6) μg g^{-1} day^{-1}. Net nitrification rates exhibited a smaller range (0.0 ± 0.0 to 2.0 ± 1.0 μg g^{-1} day^{-1}) and averaged 0.5 (± 0.2) μg g^{-1} day^{-1}. Neither net nitrogen mineralization nor net nitrification rates followed statistically significant patterns with elevation or forest type (Table 45.1). Although all samples were incubated at laboratory temperatures, rates varied significantly among sites, suggesting that other factors (e.g. organic nitrogen pools, redox potential, pH) are controlling net nitrogen fluxes.

Table 45.1 *Patterns in net nitrogen cycling along an elevation gradient in the Luquillo Experimental Forest, Puerto Rico. Net nitrogen mineralization from field measurements is compared with estimates from the difference between gross nitrogen mineralization and gross ammonium consumption. Upper-case letters identify statistically significant differences among elevations. Lower-case letters identify statistically significant differences between measured and estimated rates. Values are means and standard errors. $p < 0.05$ unless otherwise noted. Short cloud forest is referred to as elfin forest in the text*

Elevation (m)	Forest	Net N mineralization ($\mu g\ g^{-1}\ day^{-1}$)	Net nitrification ($\mu g\ g^{-1}\ day^{-1}$)	Estimated net N mineralization ($\mu g\ g^{-1}\ day^{-1}$)
635	TMW	0.44 ± 0.16	0.84 ± 0.13 AC	
731	TMW	−0.56 ± 0.15	0.23 ± 0.18 B	0.06 ± 0.28 [a]
741	TMW	6.03 ± 5.48	1.98 ± 1.05 A	0.63 ± 0.30
806	Palm	0.37 ± 0.70	1.20 ± 0.53 C	
858	Palm	0.45 ± 0.40	0.75 ± 0.07 D	0.09 ± 0.10
871	Taller cloud	−2.07 ± 0.72	0.00 ± 0.00 BE	
915	Taller cloud	−0.33 ± 0.22	0.00 ± 0.00 BE	
923	Palm	−0.88 ± 0.48	0.25 ± 0.25 BD	0.20 ± 0.06 a
930	Taller cloud	−0.09 ± 0.41	0.28 ± 0.10 DE	
949	Short cloud	−0.57 ± 0.18	0.22 ± 0.11 DE	0.07 ± 0.04 a
967	Short cloud	−0.29 ± 0.28	0.00 ± 0.00 B	
968	Short cloud	−0.22 ± 0.27	0.59 ± 0.22 CD	0.54 ± 0.15 a

[a] $p = 0.085$.

Net nitrogen transformation rates in the LEF were similar to those from other montane systems (Figure 45.1). Few patterns in net nitrogen mineralization or nitrification are discernable with elevation or temperature. Montane forest soils in Costa Rica (Marrs *et al.*, 1988) and Borneo (ultrabasic soils only, Kitayama and Aiba, 2002) showed a linear decrease in net nitrogen mineralization and nitrification with elevation, but in Costa Rica rates were not sensitive to temperature in a laboratory experiment, where high soil moisture and presumably low soil aeration were the primary limiting factors to net nitrogen transformations (Marrs *et al.*, 1988). Similarly, net nitrogen transformations in soils from Colombian cloud forests were insensitive to temperature, but responded positively to drying, again suggesting aeration as a potential controlling mechanism (Cavelier *et al.*, 2000; cf. Leuschner *et al.*, 2007). Vitousek and Matson (1988) reported a range of net nitrogen mineralization rates from 0.8–6.8 $\mu g\ g^{-1}\ day^{-1}$ for lowland tropical forest soils; montane forest ecosystems had somewhat greater net nitrogen immobilization rates (i.e. uptake in microbial biomass), but similar net mineralization potential, with rates ranging from −2.6–6.0 $\mu g\ g^{-1}\ day^{-1}$.

Gross nitrogen mineralization, retention, and loss

In the upper elevations of the LEF, gross nitrogen mineralization rates were considerably higher than net rates and ranged from 19–21 (both ± 5) $\mu g\ g^{-1}\ day^{-1}$ whereas gross nitrification rates ranged from 16 (± 5) to 19 (± 6) $\mu g\ g^{-1}\ day^{-1}$ (Figure 45.2). Gross mineralization and nitrification rates were significantly higher in the upper montane forests (>600 m.a.s.l.) than in lower elevation forest types (*c.* 350 m.a.s.l.) and much of the mineralized nitrogen was consumed, primarily through high gross nitrification rates (Figure 45.2).

Rates of gross nitrogen mineralization in the LEF were similar to rates reported for Hawai'i, the only other tropical montane site having comparable data (Figure 45.3). The Hawaiian data suggest that gross nitrogen mineralization increases with increasing substrate age (Riley and Vitousek, 1995; Hall and Matson, 2003; Figure 45.3). Sites on substrates older than 1 million years had similar gross nitrogen mineralization rates as the Puerto Rican montane soils, which are derived from highly weathered saprolite (Buss *et al.*, 2008). Gross nitrification rates were significantly higher in the montane forests of the LEF than in lower elevation LEF soils, or montane forests in Hawai'i or tropical Australia (Figure 45.4).

Upper montane tropical forest soils often experience periodic reducing conditions (Silver *et al.*, 1999) that can significantly affect microbial nitrogen cycling processes (Silver *et al.*, 2001, 2005; Pett-Ridge *et al.*, 2006). Gross nitrogen mineralization rates were insensitive to short-term anaerobic conditions in both upper and lower elevation Puerto Rican forests. In contrast, rates of dissimilatory NO_3^- reduction to NH_4^+ (DNRA) increased when soils became anoxic in the normally well-drained lower-elevation ridges and in the tropical montane wet forest. In nature, these soils are generally well aerated and experience reducing conditions infrequently. Slope and valley soils at the lower elevation site showed no significant increase in DNRA with

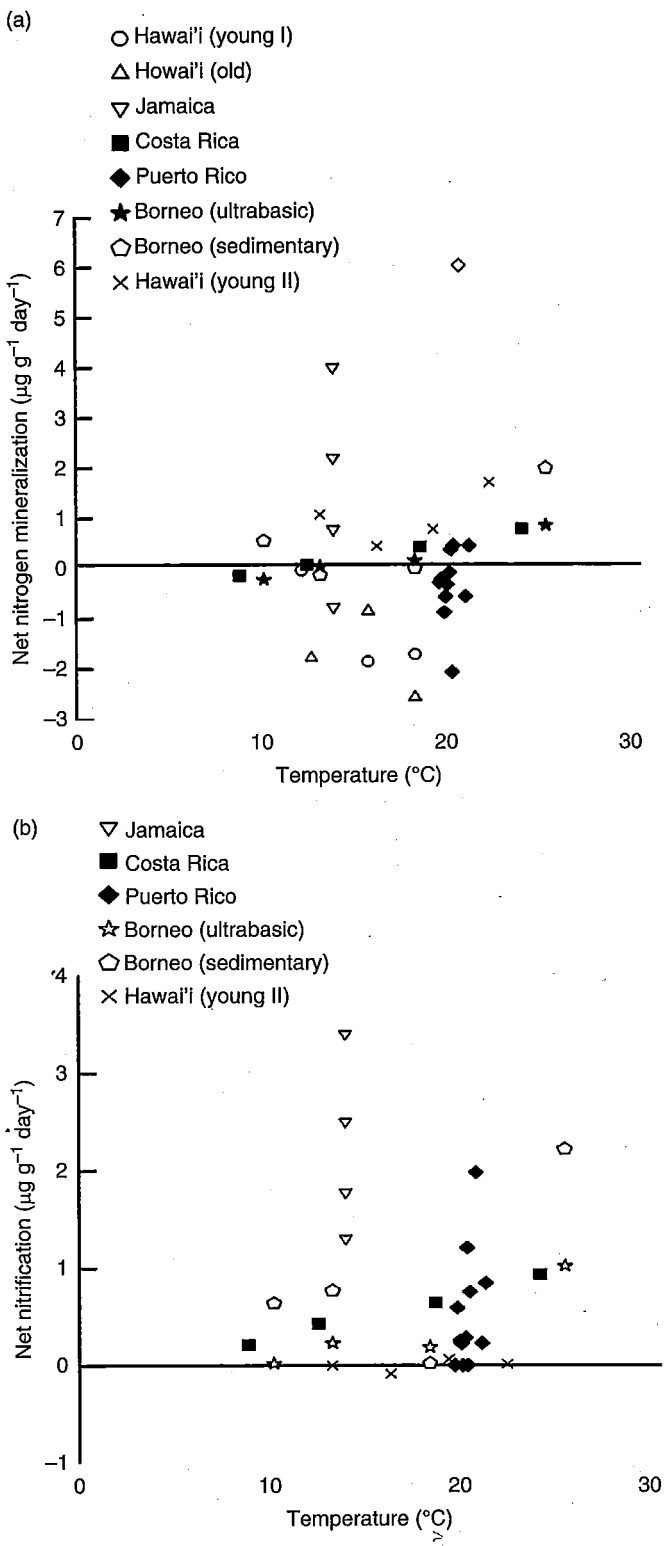

Figure 45.1. Rates of (a) net nitrogen mineralization and (b) nitrification along elevation and temperature gradients on tropical mountains. Data are from: young and old Hawaiian soils I (Vitousek *et al.*, 1988); Jamaica (Tanner, 1977); Costa Rica (Marrs *et al.*, 1988); Puerto Rico (this study); Borneo (Kitayama and Aiba, 2002); and young Hawaiian soil II (Raich *et al.*, 1997).

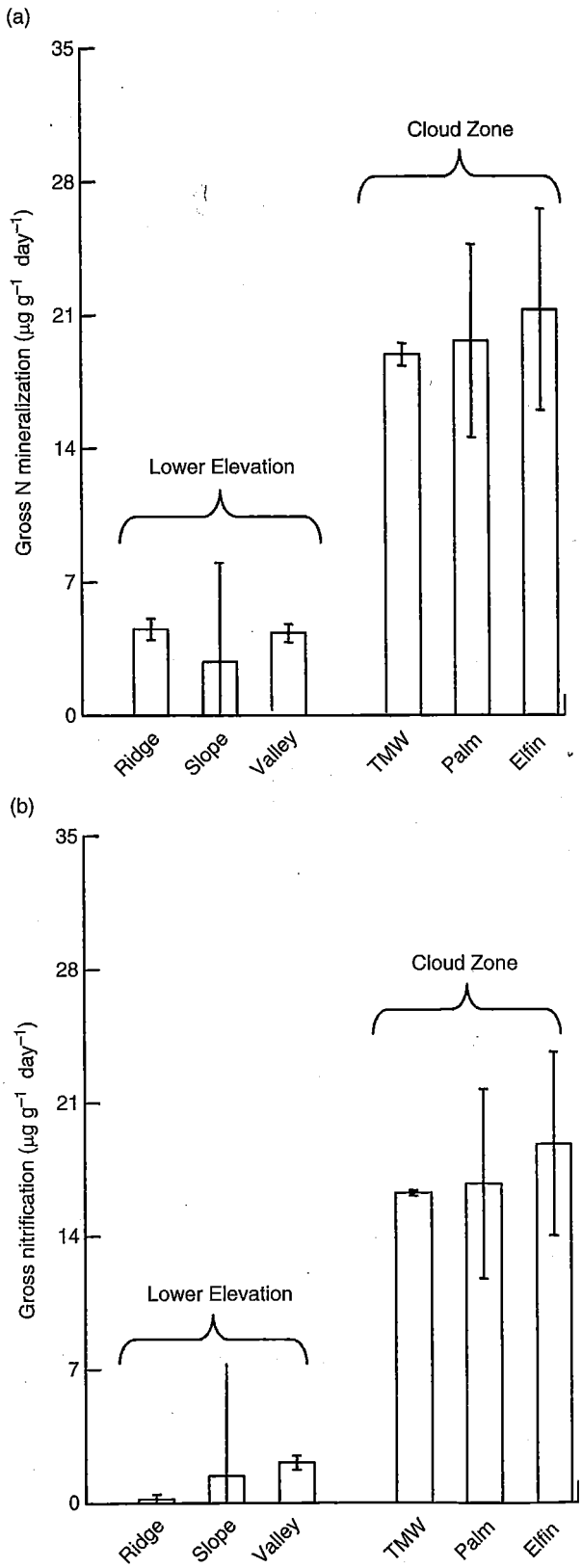

Figure 45.2. Rates of (a) gross mineralization and (b) gross nitrification in low-elevation forests and montane cloud forests in the Luquillo Experimental Forest, Puerto Rico. Values are means and standard errors.

anaerobic conditions, nor did the palm or elfin forest soils (Figure 45.5). These soils are likely to experience frequent low redox potential conditions and may not have been significantly affected by the short-term anaerobiosis imposed during the incubations. Rates of DNRA accounted for approximately 10% of gross mineralization rates. DNRA is also likely to play an important role in decreasing the amount of nitrogen available for N_2O production. Humid tropical forests are the largest natural source of N_2O, a potent greenhouse gas (Lashof and Ahuja, 1990) and catalyst for stratospheric ozone depletion (Cicerone, 1987). Nitrous oxide is produced both via nitrification and denitrification, although denitrification is thought to dominate in perhumid soils (Groffman and Tiedje, 1989). Like DNRA, denitrification is generally thought to be controlled by soil redox conditions, nitrification rates, NO_3^- availability, and labile carbon pools (Tiedje *et al.*, 1982). Nitrous oxide fluxes from LEF soils are high, averaging 34.0 ± 9.6 ng cm^{-2} $hour^{-1}$ (Silver *et al.*, 2001). Rates of DNRA significantly exceeded N_2O fluxes (Figure 45.6), suggesting that DNRA may limit N_2O production by decreasing the NO_3^- available for denitrification (Templer *et al.*, 2008). Denitrification to N_2 is another potential pathway for nitrogen loss under anaerobic conditions (Tiedje *et al.*, 1982). The relative importance of nitrogen loss via N_2 emissions is not well known for montane tropical forests, primarily due to methodological constraints.

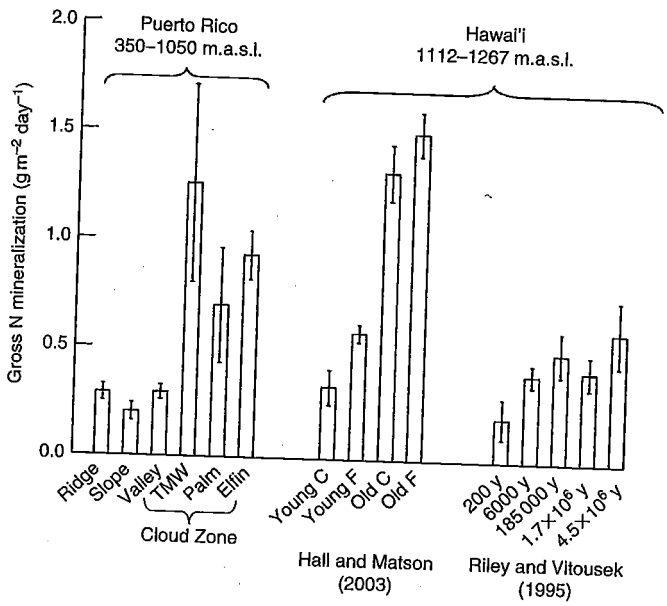

Figure 45.3. Gross mineralization rates in Puerto Rican and Hawaiian montane forest soils. Values are means and standard errors. C, Control; F, fertilized with nitrogen for the Hall and Matson (2003) study; the *x*-axis for Riley and Vitousek (1995) is substrate age.

Patterns of nitrogen circulation

Patterns of nutrient circulation via plant uptake, nutrient use efficiency, and decomposition can provide an indirect index of nutrient availability. Theory would suggest that plants growing in a nutrient-poor soil would cycle those nutrients conservatively and efficiently by maximizing production per unit of nutrient uptake. At the stand level, this can lead to the production of litter with low nutrient quality (due to nutrient resorption prior to senescence), slow decomposition rates, and a positive feedback to low nutrient availability (Vitousek, 1982, 1984; Silver, 1994). In the LEF, leaf litterfall mass, nutrient and chemical content, and the rate of leaf litter decay were measured to determine

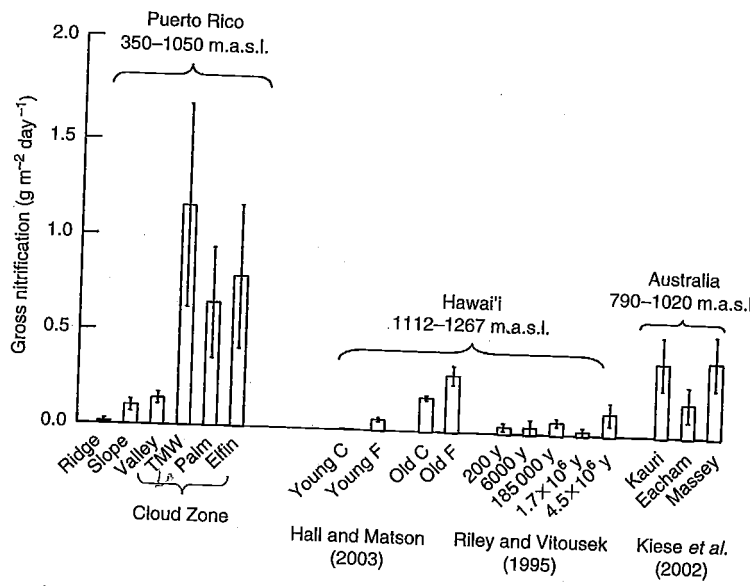

Figure 45.4. Gross nitrification rates in Puerto Rican, Hawaiian, and Australian montane forest soils. Values are means and standard errors. C, Control; F, fertilized with nitrogen for the Hall and Matson (2003) study; the *x*-axis for Riley and Vitousek (1995) is substrate age. The *x*-axis for Kiese *et al.* (2002) refers to site names.

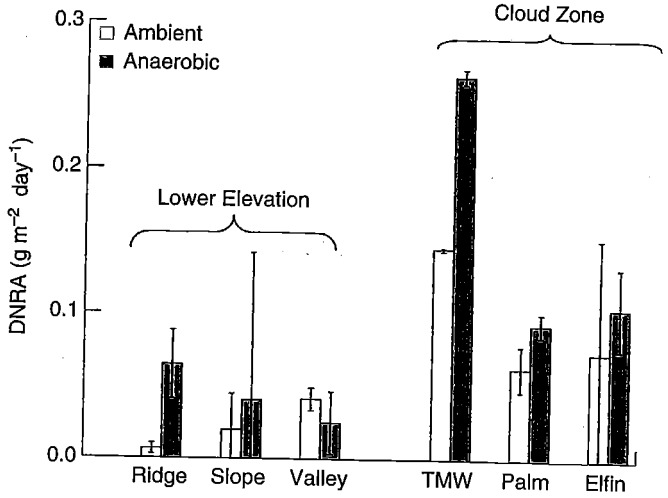

Figure 45.5. The effects of an N_2 headspace on dissimilatory nitrate reduction to ammonium in low-elevation forests and montane cloud forests in the Luquillo Experimental Forest, Puerto Rico. Values are means and standard errors.

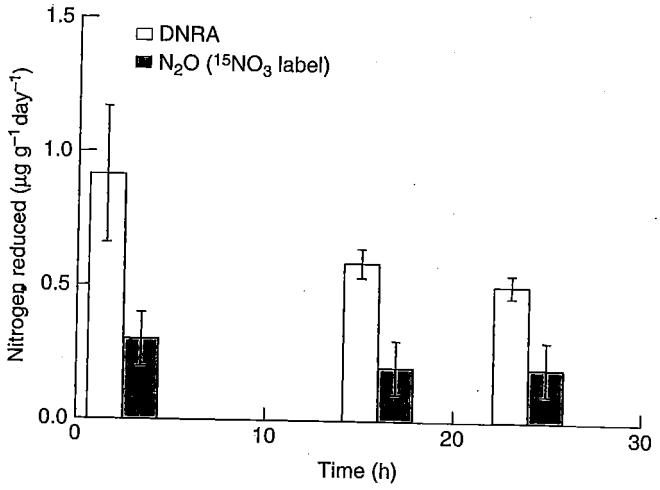

Figure 45.6. Patterns in dissimilatory nitrate reduction to ammonium and nitrous oxide fluxes from montane cloud forests in the Luquillo Experimental Forest, Puerto Rico. Values are means and standard errors.

whether patterns of nutrient circulation through these pools and fluxes appeared to be influenced by nitrogen availability. The amount of nitrogen returned to the forest floor via leaf litterfall was lower in the two cloud forest types relative to palm and montane wet forest (Figure 45.7a). This was due primarily to declining litterfall mass with elevation, not nutrient concentrations. The nitrogen use efficiency value of leaf litterfall (litterfall mass divided by nitrogen content; Vitousek, 1982) was greatest in the tropical montane wet forest (104), followed by the taller cloud forest (92), the elfin forest (82), and the palm forest (78). The low nitrogen use efficiency in the palm forest likely derives from high nitrogen concentrations in leaf tissue of the dominant palm species.

Litter decay rates did not follow the same trend as litter production (Figure 45.7b), and appeared to be related to carbon : nitrogen and lignin : nitrogen ratios in the decomposing material (Figure 45.7c,d). When comparing amounts of nitrogen produced in leaf litterfall annually with amounts released from decomposing leaf tissues, the pattern follows that for nitrogen use efficiency, with the lowest proportion of recycling occurring in the tropical wet forest and the greatest proportion occurring in the palm and elfin forests. This would suggest that in the Luquillo Mountains the higher elevation cloud forests are cycling their nitrogen less conservatively than the tropical montane wet forest, and that nitrogen supply is not likely to be as strongly limiting.

At first glance these results appear to be contradictory. Low nitrogen circulation through the vegetation generally results in poor litter quality, slow decomposition, and low nitrogen mineralization rates. However, in this study, nitrogen supply (as measured by gross N mineralization) did not vary systematically with elevation (Figure 45.3), even though leaf productivity declined at the upper elevations (Figure 45.7a). It is possible that gross nitrogen assays overestimate nitrogen supply, and may not be readily comparable to long-term fluxes of production and decomposition at the ecosystem level. However, there are also other possible explanations. First, gross nitrogen mineralization assays are an index of nitrogen turnover in the microbial pool. The nitrogen derived directly from microbial bodies is probably highly available to plants (through diffusion in the soil), but not directly correlated with nitrogen inputs via leaf litter. Second, not all nitrogen is retained within the ecosystem. Some montane tropical forests have been shown to exhibit high rates of N_2O efflux and denitrification (Keller *et al.*, 1986; Silver *et al.*, 1999; Hall and Matson, 2003) due to high gross nitrogen transformations in soils, fluctuating redox conditions, and abundant labile carbon pools. The humid conditions of the LEF are also likely to lead to considerable nitrogen loss in leachate (McDowell and Asbury, 1994). Nitrogen export via these pathways undoubtedly accounts for some of the mineralized nitrogen not taken up by plants and microbes. Finally, if plants are limited by some other factor that does not directly affect nitrogen mineralization (e.g. high wind stress, low light levels, anaerobic soil conditions), plant demand for nitrogen may be low, inorganic nitrogen supply rates could exceed plant uptake, and overall nitrogen losses could be high.

Does nitrogen supply limit productivity of montane tropical forests?

The results of the present experiments and review of the literature suggest that rates of nitrogen mineralization and nitrification vary within and across tropical mountains, but generally do not decrease systematically with elevation. Rates of mineral nitrogen supply were generally high and not likely to be a limiting factor to

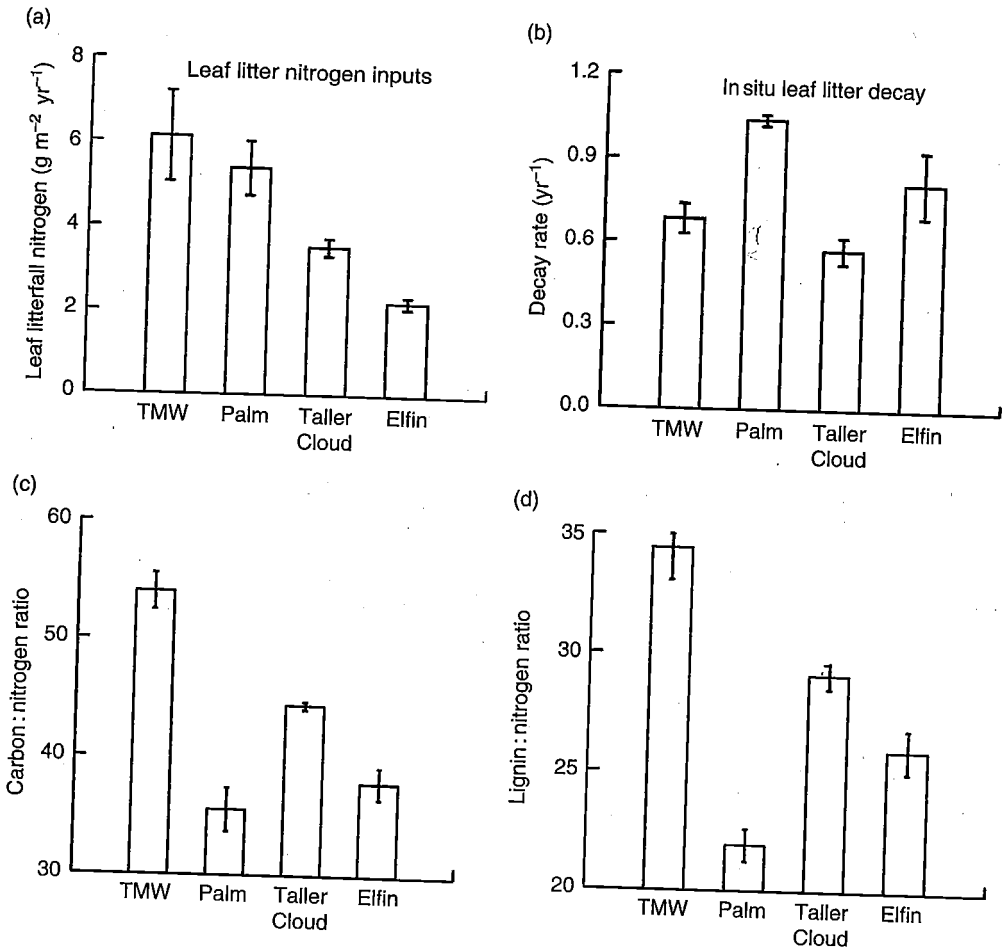

Figure 45.7. (a) Nitrogen content, (b) decomposition rates, (c) carbon-to-nitrogen ratios, and (d) lignin-to-nitrogen ratios for leaf litter from four upper montane forest types in the Luquillo Experimental Forest, Puerto Rico. Values are means and standard errors.

net primary productivity (NPP) in an altitudinal sequence of montane forests in Puerto Rico. Rates of gross nitrogen mineralization in Puerto Rico and Hawai'i were much higher than net rates. Periods of poor aeration did not appear to limit gross nitrogen mineralization, and in some cases stimulated nitrogen conservation via dissimilatory nitrate reduction to ammonium (DNRA). In the Luquillo Experimental Forest, litter quality did not follow a trend with elevation, nor did litter decomposition. The most productive forest along the elevation gradient (tropical montane wet forest) had the highest carbon: nitrogen and lignin: nitrogen ratios in leaf litter (cf. Figure 47.7c, d), exhibited a slower decay rate than the elfin forest, as well as the highest nitrogen use efficiency, and the lowest degree of nitrogen recycling from litter.

These findings suggest that mineral nitrogen supply is unlikely to result in strong nitrogen limitation to NPP in montane tropical forests. However, soil nitrogen mineralization assays are only one index of nitrogen availability and potential limitation. Forest fertilization studies measure growth responses to increased nutrient availability, and constitute a widely accepted approach to assessing nutrient limitation. However, these studies are not without problems either. Most fertilization studies focus only on above-ground tissues (e.g. litterfall and/or stem growth) and do not account for potential shifts in allocation from below- to above-ground processes (cf. Leuschner *et al.*, 2007; Moser *et al.*, 2007; Hertel and Leuschner, this volume), thereby overestimating the degree of nutrient limitation to the biota. Furthermore, the diversity of most tropical forests makes it difficult to determine patterns in species-specific responses to fertilization. Different species may respond differently to nutrient additions, making it difficult to estimate whole ecosystem responses if small plots are used (Tanner *et al.*, 1998).

Nitrogen fertilization studies have been conducted in montane forests in Hawai'i, Jamaica, and Venezuela (summarized in Tanner *et al.*, 1998; Benner *et al.*, this volume). Stem growth increased after nitrogen additions on young volcanic soils in Hawai'i (Vitousek *et al.*, 1993; Raich *et al.*, 1997), but not on older soils (Vitousek and Farrington, 1997), thereby matching the pattern in gross nitrogen supply discussed above. In Jamaica and Venezuela, plant responses to fertilization occurred only after a significant lag time (approximately 2 years). Stem growth

and/or litterfall increased at both sites (Tanner *et al.*, 1990, 1992) suggesting potential nitrogen limitation. Interestingly, net nitrogen mineralization rates in the Jamaican soils were among the highest rates reported for tropical montane forests (Figure 45.1).

Some montane forests clearly do experience nitrogen limitation. It is also possible that other factors could affect nitrogen utilization by plants, even if nitrogen supply rates are adequate, such as poor soil aeration affecting root respiration rates (McGroddy and Silver, 2000) and root uptake capacity (Soethe *et al.*, 2006, 2008b), unfavorable element interactions or specific toxicities (e.g. polyphenols), low light levels, strong winds, or even effects of high ultraviolet radiation, or some combination of these factors (see Benner *et al.*, this volume for further discussion). More detailed studies of the rooting patterns, plant physiology, plant population and community ecology, and biogeochemistry of montane (cloud) forests will help clarify the role of nitrogen and other nutrients in determining the structure and function of these important ecosystems.

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