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Substrate, climate, and land use controls over soil N dynamics and N-oxide emissions in Borneo

SHARON J. HALL[1,*], GREGORY P. ASNER[2] and KANEHIRO KITAYAMA[3]

*[1]Environmental Science Program, The Colorado College, Colorado Springs, CO 80903, USA; [2]Department of Global Ecology, Carnegie Institution of Washington, Stanford University, Stanford, CA 94305, USA; [3]Center for Ecological Research, Kyoto University, 509-3 Ohtsuka, Kamitanakami Hirano-cho, Ohtsu, Shiga 520-2113, Japan; *Author for correspondence (e-mail: shall@coloradocollege.edu; phone: +1-719-389-6822; fax: +1-719-227-8229)*

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Abstract. Nitrogen (N) enrichment of tropical ecosystems is likely to increase with rapid industrial and agricultural development, but the ecological consequences of N additions in these systems are not well understood. We measured soil N- oxide emissions and N transformations in primary rain forest ecosystems at four elevations and across two substrate types on Mt. Kinabalu, Borneo, before and after short-term experimental N additions. We also measured N pools and fluxes across a land use gradient of primary forest, burned secondary forest, and fertilized agriculture. Background soil N_2O and NO emissions in primary forest decreased with elevation, and soils derived from sedimentary substrates had larger pools of inorganic N, rates of nitrification, and N-oxide fluxes than ultrabasic soils when there were significant differences between substrate types. N-oxide emissions after N additions and background rates of nitrification were low in all soils derived from ultrabasic substrates compared to sedimentary substrates, even at lowland sites supporting, diverse Dipterocarp forests growing on morphologically similar Oxisols. Rates of potential nitrification were good predictors of N-oxide emissions after N additions. N_2O and NO fluxes were largest at low elevations and on sedimentary-derived soils compared to ultrabasic-derived soils, even at the smallest addition of N, 15 kg N ha^{-1}. Because current methods of soil classification do not explicitly characterize a number of soil chemical properties important to nutrient cycling, the use of soil maps to extrapolate biogeochemical processes to the region or globe may be limited in its accuracy and usefulness. In agricultural systems, management practices were more important than substrate type in controlling N-oxide emissions and soil N cycling. N-oxide fluxes from agricultural fields were more than an order of magnitude greater than from primary forests on the same substrate type and at the same elevation. As primary forests are cleared for intensive agriculture, soil N_2O and NO emissions are likely to far exceed those from the most N-saturated tropical forest ecosystems. This study highlights the inter-dependence of climate, substrate age, N deposition, and land-use practices determining N cycling and N-oxide emissions in humid tropical regions.

Introduction

Tropical ecosystems in southeast (SE) Asia contain 20% of the known terrestrial species of plants and vertebrates and sustain the highest diversity of marine organisms on Earth in less than 4% of the global area (Myers et al. 2000). Nevertheless, extensification of land use for agriculture has cleared over

90% of the region's original vegetation and has caused more than a doubling of nitrogen (N) fertilizer use, biomass burning, and agricultural mechanization in the last several decades (FAO 2001). In addition, rapid industrialization and urbanization in SE Asia is expected to triple the regional emissions and deposition of reactive N-oxide gases between 1990 and 2020 (Galloway et al. 1994; Holland et al. 1997). The combination of increasing fossil fuel use, biomass burning, and N fertilizer use will likely have dramatic consequences for atmospheric composition and biogeochemical cycling in downwind and downstream ecosystems in these ecologically important tropical regions (Vitousek and Matson 1993; Hall et al. 1996; Carpenter et al. 1998; Hall and Matson 1999; Matson et al. 1999).

Despite the rapid rate of development in SE Asia, relatively little is known about the effects of anthropogenic N deposition on tropical soils and the atmosphere. In northern latitude forests of industrialized countries, where the effects of chronic N deposition have been studied most intensively, N-limited forest ecosystems have been shown to store large quantities of added N in plant biomass and soil organic matter (Aber et al. 1998; Tietema et al. 1998). Only after repeated N additions, often after many years, some temperate forests are thought to experience 'N saturation' because they show elevated N losses as nitrate (NO_3^-) in stream water and as gaseous N-oxide emissions from soils above background levels (Ågren and Bosatta 1988; Aber et al. 1998). The timing of N saturation varies between temperate forests depending on the 'N status' of the ecosystem, determined by various factors including land use history, soil type, disturbance, vegetation type, and years and type of nutrient additions.

As atmospheric deposition of pollutants shifts to a more global distribution, however, it is unclear whether the pattern of responses in temperate forests will apply in tropical and subtropical forests as well (Matson et al. 1999; Matson et al. 2002). Whereas primary production in most temperate systems is limited by N (Vitousek and Howarth 1991), phosphorus (P) or other rock-derived nutrients often limit primary production in humid tropical forests growing on highly weathered soils such as Oxisols or Ultisols (Vitousek and Sanford 1986; Cuevas and Medina 1988; Vitousek and Matson 1988; Herbert and Fownes 1995; Vitousek et al. 1997), and N may cycle relatively quickly in these systems (Matson and Vitousek 1990). If N availability is high relative to other elements in humid tropical soils, we might expect the consequences of N deposition to be quite different from that found in N-limited temperate ecosystems (Matson et al. 1999). For example, rather than experiencing a period of N retention, anthropogenic N additions may immediately increase gaseous losses of N as nitrous oxide (N_2O) and nitric oxide (NO) if N availability exceeds biological demand and stimulates the nitrification process (Hall and Matson 1999). However, the extent to which N cycling is accelerated relative to other nutrients has not been explored globally in highly weathered soils such as Oxisols and Ultisols. Although soil order classification by USDA guidelines does not require detailed knowledge of many soil chemical characteristics, orders have

been shown to correlate well with N cycling processes (Matson and Vitousek 1990) and have been used to constrain a few models of terrestrial nutrient cycling (Asner et al. 2000).

N_2O and NO are two gases produced naturally in soils by the microbial processes of nitrification (oxidation of ammonium (NH_4^+) to nitrite (NO_2^-) and nitrate (NO_3^-)) and denitrification (reduction of NO_3^- to N_2O and dinitrogen). Although a number of other factors are important to the release of N_2O and NO from soil surfaces, including soil moisture, carbon, and oxygen availability, an increase in the availability of N as NH_4^+, NO_2^-, or NO_3^- is thought to be a primary driver of soil N-oxide fluxes because these ions are primary substrates used by microorganisms as sources of energy (nitrification) or electron acceptors (denitrification) (Firestone and Davidson 1989; Davidson et al. 2000). N_2O is a stable compound in the troposphere with a long residence time and absorption properties that make it an extremely effective greenhouse gas with a global warming potential nearly 300 times that of CO_2 (IPCC 1996). When injected into the stratosphere, N_2O is transformed by high energy radiation into various N-oxide molecules that can catalyze the destruction of stratospheric ozone. In contrast, NO is a reactive gas in the troposphere with a lifetime of hours to days, and in combination with NO_2 ($NO_2 + NO = NO_x$), NO_x is an important player in tropospheric ozone formation and regional air chemistry (Fowler et al. 1998). Furthermore, NO_x compounds can react with water to become nitric acid, a growing component of acid rain and the primary form of atmospheric N deposition downwind of industrialized areas (Likens et al. 1996).

Concentrations of N_2O and NO_x have been increasing in the atmosphere over the last century due to fossil fuel combustion and fertilized agriculture. Combustion is the largest anthropogenic source of NO_x globally, but in rural areas the agricultural and biomass burning contribution can become large enough to control photochemical ozone episodes (Williams et al. 1992; Lelieveld and Dentener 2000). In contrast, intensive agriculture is the primary source of increasing N_2O concentrations, although variability in this estimate is high (0.6–14.8 Tg N $year^{-1}$; IPCC 1997). Only a few studies have examined soil N-oxide emissions in tropical developing world agriculture, but they suggest that fluxes can be much larger than in temperate systems (Matson et al. 1996; Mosier et al. 1997; Veldkamp and Keller 1997; Matson et al. 1998). Even fewer studies have examined emissions from forest and agricultural systems in SE Asia (Watanabe et al. 2000) or the change in emissions following tropical forest clearing and burning (Keller et al. 1993; Veldkamp et al. 1998; Weitz et al. 1998).

We explored the effects of N additions, land use, elevation, and geologic substrate on the emissions of N_2O and NO_x from soils in humid tropical systems on Mt. Kinabalu, Borneo. In our first experiment, we examined whether soil N-oxide emissions from undisturbed primary forest are predictable based on patterns of soil N availability and turnover. Specifically, we expected that emissions would decrease with increasing elevation and that

emissions would be larger on soils developed from fertile sedimentary substrates compared to those developed from nutrient-poor ultrabasic substrates. Furthermore, we expected that the differences between substrate types would be smallest at higher elevations where cold temperatures and poor soil development limit microbial activity. In our second experiment, we investigated the effects of a range of N additions on N-oxide emissions from both ultrabasic and sedimentary substrates at two different elevations. We expected that emissions following N additions would be highest at low elevation on both substrate types where weathered soils support large, diverse plant communities. In addition, we expected that emissions would vary with N availability, specifically with the activity of nitrifying microorganisms in soils. Last, we examined the effects of land-use change on N-oxide emissions and soil N transformations. We expected that agricultural emissions would not be correlated with substrate type, unlike in the forests, but instead would be related to water and fertilizer management.

Materials and methods

Site description and experimental design

We sampled soils and soil gases in eight permanent primary forest plots at four elevations and two substrate types on a south slope of Mt. Kinabalu in the NE state of Sabah, Borneo (Malaysia) (4095 m elevation, 6°05′N, 116°33′E; Figure 1). All samples were taken in the month of July 2000. Between 1990 and 1995, one 0.1–1 ha plot was established each at 700, 1700, 2700 m, and 3100 m on soils derived from either ultrabasic or sedimentary/granitic substrates of Tertiary origin (>5 million years) as a part of a long term research program to study the ecology of wet tropical mountains (Kitayama et al. 2000). In addition, one 1-ha plot at 1700 m was established in 1995 on a younger sedimentary substrate that is approximately 35,000 year old (Kitayama et al. 2003). All sites are sloped between 11° and 27° and have never been cleared (Table 1). We also sampled soils and gases in three sites at 1700 m that were cleared for agriculture. Two fields (ultrabasic and sedimentary) were burned >5 years earlier. At the time of sampling, the dominant crop type in these fields was fertilized cabbage, a common cash crop grown in the region. In addition, we sampled soils and NO_x emissions from one field at 1700 m on ultrabasic substrates that was recently burned within 2 weeks of sampling (Table 1).

Climate

Mean annual air temperature at sea level in Sabah is fairly constant at 27.5°C with relatively little monthly variability, but temperature declines with elevation on the mountain at an approximate lapse rate of 0.55 °C per 100 m (Table 1). In contrast, mean annual precipitation is highly variable from year to year; however, it remains fairly constant across elevations, ranging from 2509 mm/year^{-1}

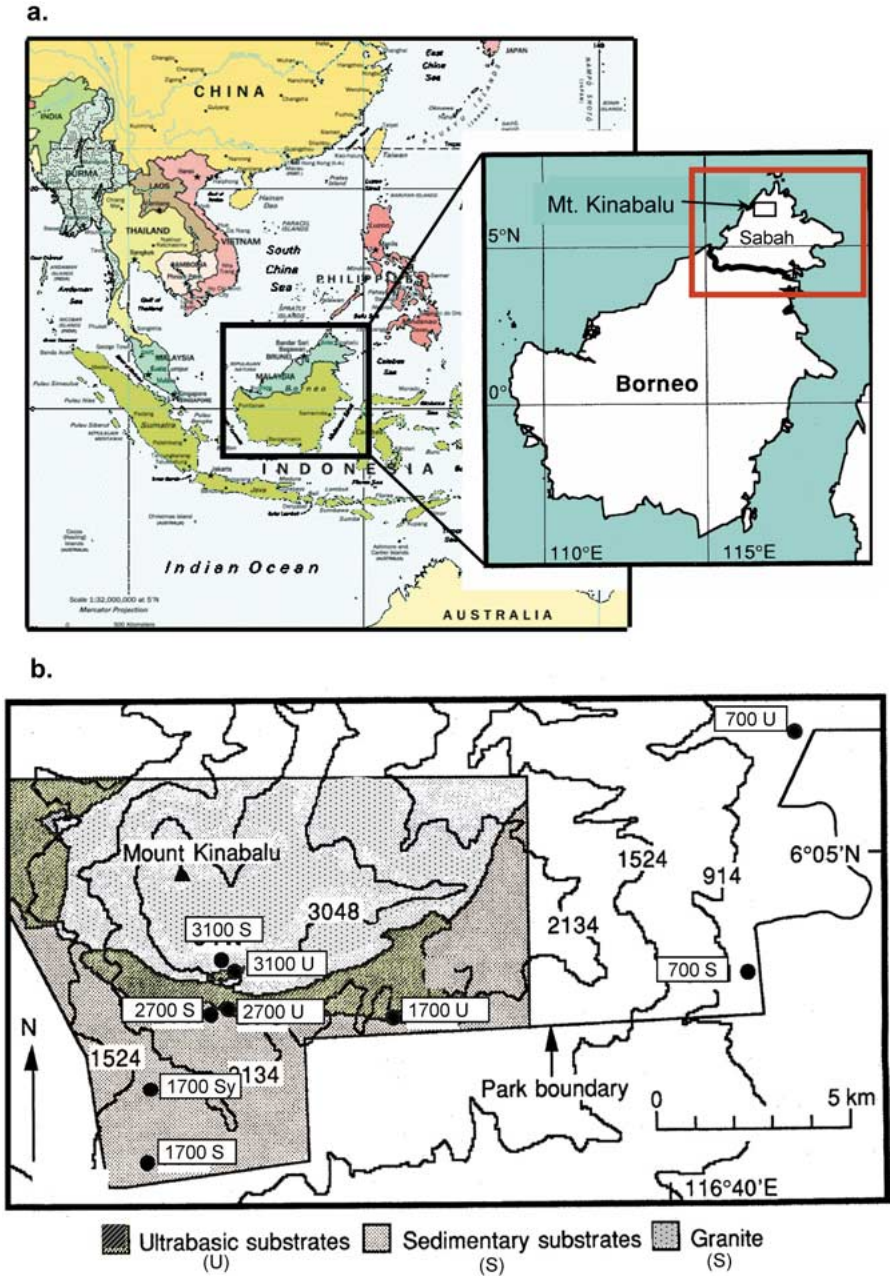

Figure 1. (a) Geographic location of Mt. Kinabalu (6°05′N, 116°33′E) in the Malaysian state of Sabah, Borneo. (b) Geologic substrates and forest sites of Mt. Kinabalu, Borneo. 3100U and 3100S = sites on ultrabasic (U) and sedimentary (S) substrates at 3100 m. 2700, 1700, and 700U/S = ultrabasic/sedimentary substrates at 2700, 1700, and 700 m, respectively. 1700Sy = geologically young sedimentary substrate at 1700 m.

Table 1. Characteristics of the 12 forest and agricultural sites on Mt. Kinabalu, Borneo.

Site (m)	Vegetation type	Exact altitude (m)	Geologic substrate	Age of substrate (Epoch or years)	Soil order	MAT (°C)	MAP (mm)	Slope (°)
Primary forest								
700	Hill dipterocarp rainforest	650	Sedimentary	Tertiary	Oxisol/Ultisol	23.9	2509	19
700	Hill dipterocarp rainforest	700	Ultrabasic	Tertiary	Oxisol/Ultisol	23.7	2509	11
1700	Lower montane rainforest	1560	Sedimentary	Tertiary	Inceptisol/Spodosol	18.9	2714	17
1700	Lower montane rainforest	1860	Ultrabasic	Tertiary	Inceptisol/Spodosol	17.3	2714	24
1700	Lower montane rainforest	1860	Sedimentary	35000	N/D	18.9	2714	15
2700	Upper montane rainforest	2590	Sedimentary	Tertiary	Inceptisol/Spodosol	13.3	2085	20
2700	Upper montane rainforest	2700	Ultrabasic	Tertiary	Inceptisol/Spodosol	12.7	2085	22
3100	Subalpine rainforest	3080	Granite	Tertiary	Inceptisol	10.6	3285	27
3100	Subalpine rainforest	3050	Ultrabasic	Tertiary	Inceptisol	10.7	3285	19
Agricultural								
1700	Fertilized cabbage	1800	Sedimentary	Tertiary	N/D	18	2714	10
1700	Fertilized cabbage	1800	Ultrabasic	Tertiary	N/D	18	2714	10
1700	Burned	1800	Ultrabasic	Tertiary	N/D	18	2714	10

at the lower elevation sites to 2085 mm/year^{-1} at the upper montane sites (Kitayama et al. 1999). Above the cloud belt in the montane zone, the subalpine experiences a slightly wetter environment with a mean annual precipitation of 3285 mm year^{-1}. Seasonality of rainfall in this region is slight, without a clearly distinct dry season. No rain fell over the course of our 2-week sampling period (July 2000).

Vegetation

Vegetation on Kinabalu varies in life-form and stature along the elevation gradient and between substrate types (Aiba and Kitayama 1999). Plant community composition, structure, and species diversity are similar on both substrates at low elevation (dominated by *Dipterocarpaceae*), but a number of plant physiological and ecological properties change with altitude, including primary production, decomposition rate, species diversity, and total soil C and N (Table 2; Aiba and Kitayama 1999).

Geology, substrate age, and soils

Three major substrate types dominate the surface geology of Kinabalu. Below 2700 m, soils are mostly derived from Tertiary deposits of sedimentary rock with interspersed mosaics of ultrabasic, serpentinized periodite. The sedimentary rock consists largely of sandstone and mudstone of the Trusmadi Formation that was deposited in the pelagic basin during the Eocene (38–54 million years ago), folded in the Miocene (5–23 million years ago), and is composed of >50 % SiO_2. Also below 2700 m, ultrabasic rock intruded at depth in the upper Cretaceous and was emplaced by faulting in the Miocene. Ultrabasic rocks are composed of $\leq 45\%$ silica and contain no quartz or feldspar; these substrates on Kinabalu consist of serpentinite and serpentinized peridotite and contain high concentrations of Fe, Mg, Ni, Cr, and Co but are low in Ca, K, and P (41% SiO_2 , 36% MgO and 4% FeO; Jacobson 1970). The geology of the uppermost, 3100 m 'sedimentary' site is actually granite which contains about 60% SiO_2. At 1700 m we also sampled a younger substrate ('Sedimentary Young'; Kitayama et al. 2003) consisting of 90% sedimentary materials (Jacobson 1970) derived from colluvial deposits delivered down from upper elevations in the early Quaternary period (approximately 30,000–40,000 years ago). Soils are currently being classified at each site (R. Wagai and K. Kitayama, personal communication); however, coarse soils maps and visual inspection indicate the lowest elevation sites (700 m) are Ultisols/Oxisols (USDA 2000). Soils in the lower and upper montane zone (1700–2700 m) are organic Spodosol/Inceptisols, and in the upper elevation sites (3100 m) they are weakly-developed Inceptisols (histic Inceptisol on the granite site). Preliminary mineralogical analyses also indicate that the mineral surface area of soils derived from ultrabasic substrates is significantly larger than in sedimentary-derived soils along the elevation gradient (Table 2, R. Wagai, personal communication).

Table 2. Ecosystem processes and properties of nine primary forest sites, modified from Kitayama and Aiba (2002), Kitayama, unpublished data (for the Sed-Y site and bulk density measurements), and R. Wagai, personal communication (pH, soil moisture, mineral surface area). Sed = Sedimentary substrates, Ult = Ultrabasic substrates, Sed-Y = young (35,000 years) sedimentary substrate. ND = No data, NPP = Net primary production. (± SE)

	Elevation (m)								
	700		1700			2700		3100	
	Sed	Ult	Sed	Sed-Y	Ult	Sed	Ult	Granite	Ult
Forest processes and properties									
Forest stature (m)	46.8	65.4	30.0	32.1	22.6	20.6	14.2	15.0	6.1
Aboveground biomass (kg/m^3)	48.1	54.2	28.0	34.9	21.3	29.5	10.8	20.7	1.9
Above ground NPP (g/m^2/year)	1913	1715	1222	1370	813	780	725	816	199
Litterfall (g/m^2/year)	1110	1113	799	900	628	532	594	631	164
Wood increment (g/m^2/year)	803	602	423	470	185	248	131	185	35
Allocation ratio (wood inc./litterfall)	0.7	0.5	0.5	0.5	0.3	0.5	0.2	0.3	0.2
Standing litter (g/m^2)	660	670	680	590	880	530	740	730	370
Decay constant: *k* (litterfall/stnd litter)	1.7	1.7	1.2	ND	0.7	1.0	0.8	0.9	0.4
Mean residence time (year)	0.6	0.6	0.8	ND	1.4	1.0	1.3	1.2	2.3
No. species ≥4.8 cm DBH	163	161	121	ND	43	23	26	24	9
Soil properties: A-horizon									
Soil C (%)	2.9 (0.1)	2.4 (0.2)	4.4 (1.2)	8.1 (0.8)	3.4 (0.3)	17.7 (4.0)	3.5 (0.6)	8.6 (2.1)	3.5 (0.2)
Soil N (%)	0.2 (0.0)	0.2 (0.0)	0.3 (0.1)	0.5 (0.1)	0.3 (0.0)	0.9 (0.2)	0.4 (0.0)	0.6 (0.0)	0.3 (0.0)
Soil C:N	13.8	11.4	13.7	15.2	12.1	19.2	9.9	14.3	13.3
Soil moisture (%)	34.5 (2.3)	27.2 (2.2)	53.7 (5.0)	83.2 (3.9)	59.0 (2.0)	136.5 (10.5)	171.7 (12.3)	74.1 (6.1)	40.0 (2.2)
pH in 0.01 N $CaCl_2$	3.5 (0.0)	4.0 (0.1)	3.4 (0.1)	3.7 (0.1)	4.6 (0.3)	3.1 (0.1)	4.2 (0.2)	3.8 (0.2)	4.4 (0.1)
Bulk density, 0–10 cm (g/cm^3)	1.1	1.0	0.4	0.6	0.7	0.9	0.7	0.5	0.9
Mineral surface area (m^2/g) (organic matter removed by combustion)	31.4 (2.4)	96.7 (6.7)	17.3 (4.3)	43.4 (2.1)	29.6 (2.8)	21.6 (2.9)	24.3 (1.5)	5.2 (0.4)	31.4 (1.6)

N-oxide emissions from primary forest and agricultural soils

Background forest, dose–response, and agricultural studies

At each of the primary forest sites, we measured background soil emissions of N_2O and NO (no fertilization) as well as N-oxide emissions following a dose–response experiment with different concentrations of ammonium nitrate (NH_4NO_3) in water. Paired sedimentary and ultrabasic sites at each elevation were sampled within the same day or on immediately subsequent days. There was no precipitation over the 2-week sampling period, and all gas measurements occurred between 10 am and 6 pm to minimize temperature differences between sites. To measure background N-oxide emissions, six PVC rings were randomly inserted into the soil to a depth of several centimeters in each site. Each ring was >2 m away from one another and served as anchors for the closed-top chambers used for soil N_2O and NO measurements ($N = 6$ replicate chambers). For the dose–response experiment, three blocks of five rings were installed >10 m away from one another within each site at both 700 and 1700 m on ultrabasic and sedimentary substrates ($N = 3$ replicate chambers per treatment). Within each block, rings were placed >1 m apart from one another and received different NH_4NO_3 treatments. Within each ring and around a 5 cm buffer, N in 500 ml of de-ionized water was sprinkled at the rate of 0, 15, 25, 75, and 125 kg N ha^{-1}. N_2O and NO emissions and soil processes from all rings in the dose–response experiment were measured 7 days after fertilization. In the fertilized agricultural fields, six PVC rings were randomly inserted >1 m away from one another ($N = 6$ replicate chambers per site). In the burned field (ultrabasic substrate), six PVC rings were randomly placed >1 m apart from one another and were sampled for gases and soils on the same day as the primary forest site on this substrate (1700U).

Following gas sampling in the dose–response experiments and agricultural fields, three soil cores (0–10 cm depth) were taken from the inside of each ring and composited to examine soil N pools and transformations ($N = 3$ soil samples of 3 cores each; methods described below). Three soil samples of three composited cores were collected from within an area near the rings in the primary forest sites that were sampled for background N cycling. Soils were shipped on ice to the US and refrigerated at 4 °C for up to 4 weeks after soil collection.

Gas collection and analysis

N_2O and NO emissions were measured using techniques described in detail by Matson et al. 1996. Molded PVC chambers were placed over each ring in the soil, and air was sampled from the chamber four times over a 30 min period. Twenty-five milliliters of chamber air and certified N_2O standards were collected in nylon syringes and immediately placed in pre-evacuated, silicone-sealed 10 mL glass Wheaton vials with butyl stoppers. Samples were flown to the US under cabin pressure, and N_2O was analyzed using a gas chromatograph fitted with an electron capture detector (Shimadzu Corp., New York,

NY) and calibrated using certified N_2O standards in the laboratory (Magma Lab, Hawai'i Volcanoes National Park). N_2O flux was calculated as the increase in concentration within each chamber over a 30 min period. Nitric oxide was measured *in situ* at each site within soil chambers using a portable chemiluminescent detector fitted with a CrO_3 filter that converts all NO to NO_2 (LMA-3, Unisearch Associates, Ltd., Canada) NO_2 concentrations were estimated photochemically after its reaction with Luminol solution. Soil NO_2 fluxes were measured occasionally and were always undetectable; hence, all chemiluminescent NO_2 measurements were assumed to be equivalent to measurement of NO. Standard curves were performed in the field several times a day before, during, and after gas sampling using a known concentration of NO standard gas (0.108 ppm NO, Scott-Marrin Co., Riverside, CA). NO fluxes were calculated as the linear slope of the NO concentration in the chamber over a 4 min period.

Mechanisms: soil properties and N dynamics

We measured soil properties and pools of N as well as microbial N transformations to examine whether N cycling in these tropical systems is affected by N additions and if these processes are related to N-oxide emissions.

Soil temperature, moisture, and %WFPS

Gravimetric soil water (subsamples dried 24 h at 105°C) and soil temperature (3 mm depth) were measured in all plots on all sampling dates. Water-filled pore space (WFPS) is thought to be an important factor controlling N-oxide emissions from soil (Firestone and Davidson 1989; Davidson 1993). We calculated WFPS using the equation:

$$\text{WFPS} = \frac{\text{gravimetric moisture} \times \text{soil bulk density}}{1 - (\text{soil bulk density}/\text{particle density})}$$

weighted for percentage organic matter in the top 10 cm of soil in each treatment in all sites. Organic matter (OM) was determined for each site assuming soil C represents 45% of total organic matter (Schlesinger 1997). Particle densities were calculated as 1.3 g m^{-3} for organic matter, 2.9 g m^{-3} for mineral soil at the 700 m sites where Fe-oxide minerals dominate, and 2.65 g m^{-3} for mineral soils at higher elevations (Hall and Matson 2003). Bulk densities of the top 15 cm of soil ranged from 0.43 g m^{-3} (highly organic) at the 1700 m sedimentary site to 1.1 g m^{-3} at the 700 m sedimentary site (Table 2).

Soil inorganic N and net N transformations

We measured exchangeable inorganic N concentrations and net rates of N mineralization and nitrification after each soil collection in both background and dose–response experiments using 2 N KCl extraction and aerobic laboratory incubation methods described in Matson et al. (1996). In the laboratory,

soils were homogenized and sieved. One 10 g subsample from each sample was immediately shaken for 1 min in 50 ml 2 N KCl, set aside for 18–36 h, filtered through pre-leached Whatman No. 1 filters, and then frozen immediately for later analysis. Another 10 g subsample was placed in a small, capped cup and then placed in the dark for 7–10 days at 22°C. After the incubation, soils were extracted as described above. A third subsample was dried at 105°C for 24 h to determine gravimetric moisture content. All KCl extracts were analyzed colorimetrically for NH_4^+-N and NO_3^--N at the University of Colorado using an Alpkem autoanalyzer (OI Analytical, College Station, Texas). Net N mineralization was calculated as the difference between the sum of NH_4^+ and NO_3^- concentrations before and after each incubation. Net nitrification was calculated as the difference between NO_3^- concentrations before and after each incubation.

Nitrification potential assays

We used methods described in Hart et al. (1994) to assess rates of potential nitrification in soils from the primary forest sites. Potential rates estimated with these assays have been used as an index of microbial population size. Ten grams of soil were added to flasks along with 100 ml of a solution containing $(NH_4)_2SO_4$, K_2HPO_4, KH_2PO_4, and adjusted to pH 7.2 (Hart et al. 1994). Blanks of solution without soil were also processed at this time. Soil slurries were shaken vigorously on a mixer to maintain aerobicity for 24 h. At four times within this 24 h period, 5 mL aliquots of soil slurry were removed from the flasks, flocculated with a 0.6 M solution of $MgCl_2$ + $CaCl_2$ to aid in filtration, centrifuged, filtered through pre-leached Whatman No. 43 filters, and frozen until analysis. Extracts were analyzed colorimetrically for NO_3^-. Rates of potential nitrification were determined by using the positive slope of NO_3^- concentrations in soil extracts over the 24 h period.

Statistical analyses

All statistical tests were performed using Statview 5.0 software (SAS 1998). Background nitrification potential data, dose–response NH_4^+ and NO_3^- concentration data, and background, dose–response, and agricultural N-oxide data were transformed to non-zero values and then log-transformed prior to ANOVA and post-hoc Tukey analyses to satisfy linear model assumptions. Data that did not fit parametric assumptions were analyzed using non-parametric tests (Mann–Whitney and Kruskal–Wallis). Due to time, physical, and labor constraints on sampling trace gases in remote tropical forest sites, our replication (and thus statistical power) within plots on the elevation sequence and especially in the dose-response experiment was limited (replicates for elevation sequence = 6 chambers and 3 soils per site; replicate for dose response experiment = 3 blocks of chambers and soil per treatment). Thus, statistical analyses with p-values less than or equal to 0.1 were considered significant (90% confidence).

Results

Primary forest: background N-oxide emissions and soil N dynamics

Both elevation and substrate type separately were important factors in predicting the variability of N_2O and NO emissions from primary forest soils (Figure 2, Table 3). Fluxes generally decreased with elevation, primarily in the sedimentary sites. Sedimentary soils had higher N-oxide fluxes than ultrabasic soils when there were significant differences between substrate types. In particular, N_2O fluxes were significantly higher from the sedimentary-derived Oxisol compared to the ultrabasic-derived Oxisol at 700 m (one-factor ANOVA, 700 m). N_2O and NO fluxes in the ultrabasic site at 700 m were not significantly different from zero (one sample t-test, 700 m). Substrate, however, was not consistently important at all elevations. For example, fluxes at the highest, 3100 m site, were similar and low on both substrate types. N-oxide fluxes between the young and old sedimentary sites were not significantly different from one another (one-factor ANOVA, all sites at 1700 m). Although trends were apparent in the relative magnitude of NO and N_2O emissions (NO > N_2O emissions on sedimentary sites, N_2O > NO on ultrabasic sites), there was no statistically significant difference in the ratio of N_2O/NO across elevations and substrates. Similar to the patterns found in gas fluxes, %WFPS in ultrabasic soils was less variable than in sedimentary soils. Elevation affected %WFPS, but effects of elevation were different for each substrate type (significant interaction term; Figure 3, Table 3). There was no relationship between % soil moisture or %WFPS and fluxes of N_2O, NO, or the ratio of the two.

Elevation and substrate type were also important in predicting variation in inorganic N concentrations and soil N cycling in this study (Figures 3 and 4, Table 3), and the observed patterns are corroborated by previous studies at these sites (Table 4). Nitrate concentrations, net nitrification, NO_3^-/NH_4^+, and potential nitrification were generally higher on sedimentary soils than ultrabasic soils at elevations where there were significant differences between substrate types, and they were lower at 3100 m than at 700 m. Substrate was an important factor in predicting rates of nitrification on the two Oxisols at 700 m (one-factor ANOVA, 700 m) where potential nitrification was larger by an order of magnitude (Figure 4) and net nitrification on sedimentary substrates was more than double than rates on ultrabasic substrates (Figure 3; Table 4).

At 1700 m, NO_3^- concentrations and rates of net and potential nitrification were significantly larger from the young compared to the old sedimentary site (one-factor ANOVA, all sites at 1700 m). The ratio of NO_3^-/NH_4^+ was 1 in young sedimentary substrates and was significantly higher than ratios from either the sedimentary old or ultrabasic substrates ($p < 0.05$; Figure 3). Elevation was the only significant factor correlated to NH_4^+ fluxes, and this was only true in the ultrabasic substrates (substrate × elevation interaction; Figure 3). Rates of N mineralization were highly variable across the elevation gradient. Net N mineralization decreased with elevation faster on ultrabasic

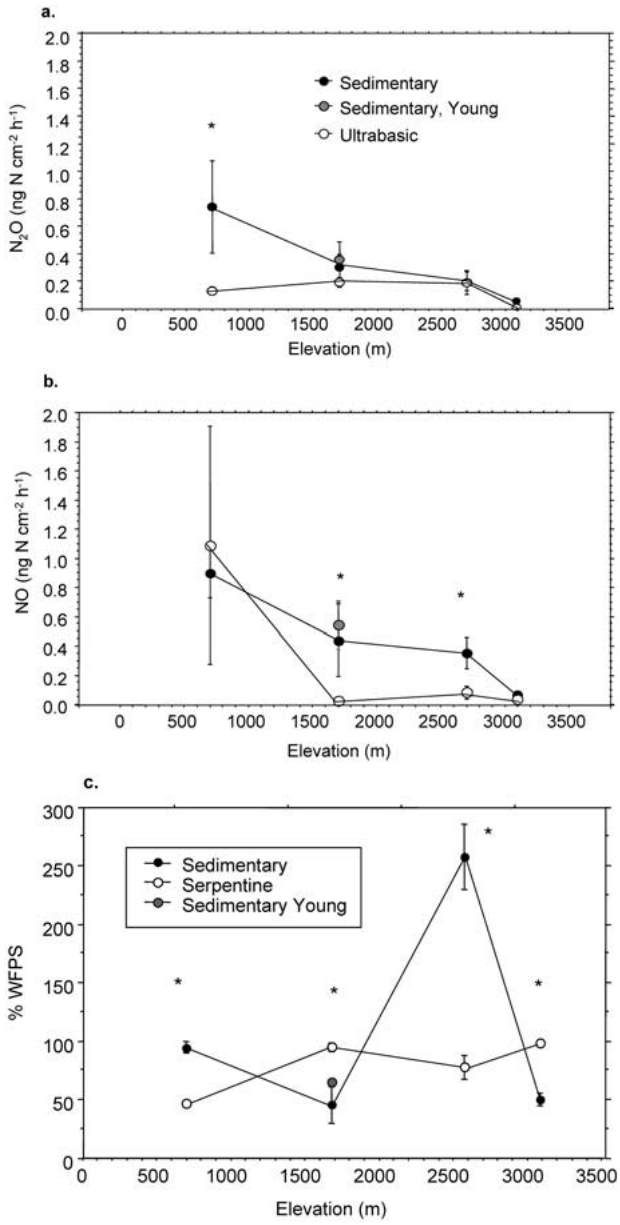

Figure 2. Soil N fluxes and soil properties from primary forest sites on Mt. Kinabalu. (a) N_2O emissions and (b) NO emissions (±SE, $n = 6$ chambers per site.), and (c) WFPS. Soil cores at each site were taken on subsequent days at the same time as gas measurements over a total of 6 days (±SE, 3 composite samples of 3 cores each, 0–15 cm depth). * Represents significant difference ($p < 0.1$) between soil types (old substrates only) within an elevation. Sedimentary young site has a substrate age of approximately 35,000 years.

Table 3. Results of two-factor ANOVA analyses for soil properties and N transformations in old sedimentary and ultrabasic sites along the elevation gradient on Mt. Kinabalu (excludes 1700 m sedimentary young site).

	DF	SS	MS	*F*	*P*
N_2O (ng N cm^{-2} h^{-1})*					
Elevation	3	0.825	0.275	7.17	*0.0006*
Substrate	1	0.267	0.267	6.969	*0.0118*
Elevation × Substrate	3	0.208	0.069	1.808	0.1612
NO (ng N cm^{-2} h^{-1})*					
Elevation	3	0.961	0.32	8.472	*0.0002*
Substrate	1	0.221	0.221	5.838	*0.0203*
Elevation × Substrate	3	0.057	0.019	0.502	0.6832
N_2O/NO (ng N cm^{-2} h^{-1})*					
Elevation	3	1.612	0.537	1.265	0.307
Substrate	1	1.154	1.154	2.716	0.1114
Elevation × Substrate	3	2.396	0.799	1.88	0.1577
NH_4^+ (μg N g^{-1})*					
Elevation	3	0.317	0.106	3.471	*0.0429*
Substrate	1	0.079	0.079	2.592	0.1283
Elevation × Substrate	3	0.313	0.104	3.426	*0.0446*
NO_3^- (μg N g^{-1})					
Elevation	3	178.128	59.376	4.205	*0.024*
Substrate	1	282.967	282.96	20.041	*0.0004*
Elevation × Substrate	3	79.923	26.641	1.887	0.1752
NO_3^-/NH_4^+ (μg N g^{-1})					
Elevation	3	0.165	0.055	2.739	*0.0801*
Substrate	1	0.139	0.139	6.934	*0.0188*
Elevation × Substrate	3	0.073	0.024	1.207	0.3413
Net Nitrification (μg N g^{-1} d^{-1})					
Elevation	3	1.236	0.412	4.761	*0.0159*
Substrate	1	1.933	1.933	22.34	*0.0003*
Elevation × Substrate	3	0.679	0.226	2.616	*0.0893*
Net N mineralization (μg N g^{-1} d^{-1})					
Elevation	3	6.068	2.023	0.617	0.6149
Substrate	1	11.161	11.161	3.402	*0.085*
Elevation × Substrate	3	14.007	4.669	1.423	0.2752
Nitrification potential (μg NO_3^--N g^{-1} d^{-1})*					
Elevation	3	0.014	0.005	12.305	*0.0004*
Substrate	1	0.007	0.007	17.622	*0.001*
Elevation × Substrate	3	0.01	0.003	9.105	*0.0016*
% WFPS					
Elevation	3	39939.1	13313.0	25.701	*< 0.0001*
Substrate	1	5668.72	5668.7	10.944	*0.0052*
Elevation × Substrate	3	50774.9	16924.9	32.674	*< 0.0001*

*Values were log-transformed before statistical analyses.

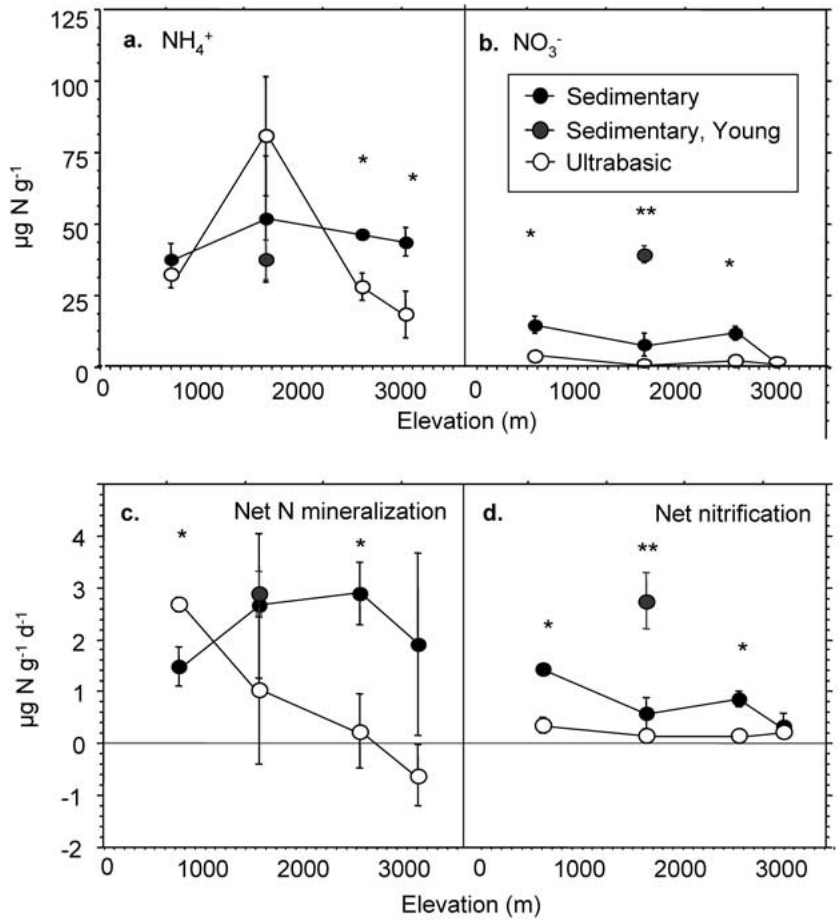

Figure 3. Soil N concentrations and transformations in primary forest sites. Concentrations of soil extractable (a) NH_4^+, (b) NO_3^- and laboratory rates of (c). Net N mineralization and (d). Net nitrification ($\pm$SE, $n = 3$). * Represents significant difference ($p < 0.1$) between soil types (old substrates only) within an elevation. ** Represents significant difference between old and young sedimentary substrate at 1700 m.

compared to sedimentary substrates. In contrast, net nitrification decreased significantly with elevation on the sedimentary but not ultrabasic substrates (Figure 3). Nitrate concentration was a good predictor of net nitrification rates across all elevations and soil types ($r^2 = 0.84$, $p < 0.0001$).

Primary forest: dose–response N addition experiment

Elevation, substrate type, and dose of N were all significant factors responsible for predicting N_2O and NO emissions measured 7 days following a range of N

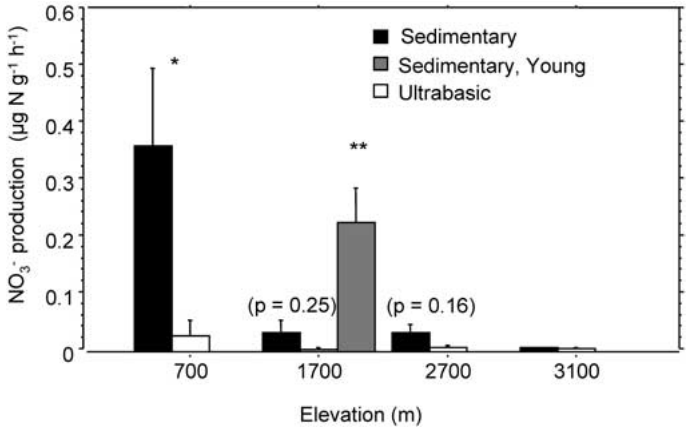

Figure 4. Potential rates of nitrification from soils from primary forest sites as determined from shaken slurries at pH 7.2 (± SE, $n = 3$). * Represents significant difference ($p < 0.1$) between soil types (old substrates only) within an elevation. ** Represents significant difference between old and young sedimentary substrate at 1700 m. One outlier eliminated in 700 m sedimentary site. $N = 2$ composited cores for the 3100 m ultrabasic site.

Table 4. Soil N pools and processes on Mt. Kinabalu measured in previous years, modified from Kitayama and Aiba (2002) and Kitayama et al. (2003) (mean ± SD).

Elevation	Substrate	NH_4^+ (μg N g^{-1})	NO_3^- (μg N g^{-1})	Net N mineralization (μg N g^{-1} day^{-1})	Net nitrification (μg N g^{-1} day^{-1})
700	Sed	0.15 (0.21)*	6.8 (3.18)	1.99 (0.38)*	2.22 (0.41)*
	Ult	0.43 (0.71)	5.7 (4.10)	0.85 (0.27)	1.02 (0.53)
1700	Sed	0.52 (0.83)	7.81 (13.87)*	−0.001 (0.01)	0.02 (0.01)
	Sed-Y	–	–	−0.38 (0.10)	0.83 (0.34)
	Ult	0.74 (1.49)	1.24 (1.16)	0.16 (0.21)	0.19 (0.36)
2700	Sed	0.78 (1.51)	0.24 (0.11)*	−0.13 (0.88)	0.77 (0.22)*
	Ult	0.32 (0.57)	1.86 (1.28)	0.04 (0.14)	0.23 (0.18)
3100	Granite	0.15 (0.22)	2.49 (2.32)*	0.55 (0.14)*	0.64 (0.21)*
	Ult	0.22 (0.34)	0.22 (0.09)	−0.22 (0.04)	0.02 (0.02)

*Significant effect of substrate within an elevation (excluding Sed-Y), $p < 0.05$. Methods: Average N pools were measured using five replicate ion exchange resins sampled five times over 11 months (December–October) in 1997 (40 days incubation each). Net N cycling processes were measured using four composite soils (10 cores each) that were collected in between May 1995 and February 1996 and placed into *in situ* buried bags for 10 days. N cycling processes for the Sed-Y site are averages of four composite buried bag samples (21 day incubation) collected five times from February 1996 to June 2000.

additions (Figure 5, Table 5). N-oxide fluxes were largest at low elevation, from sedimentary substrates, and at doses ≥ 15 kg N ha^{-1}. However, interactions between factors were significant: sedimentary substrates had higher N-oxide

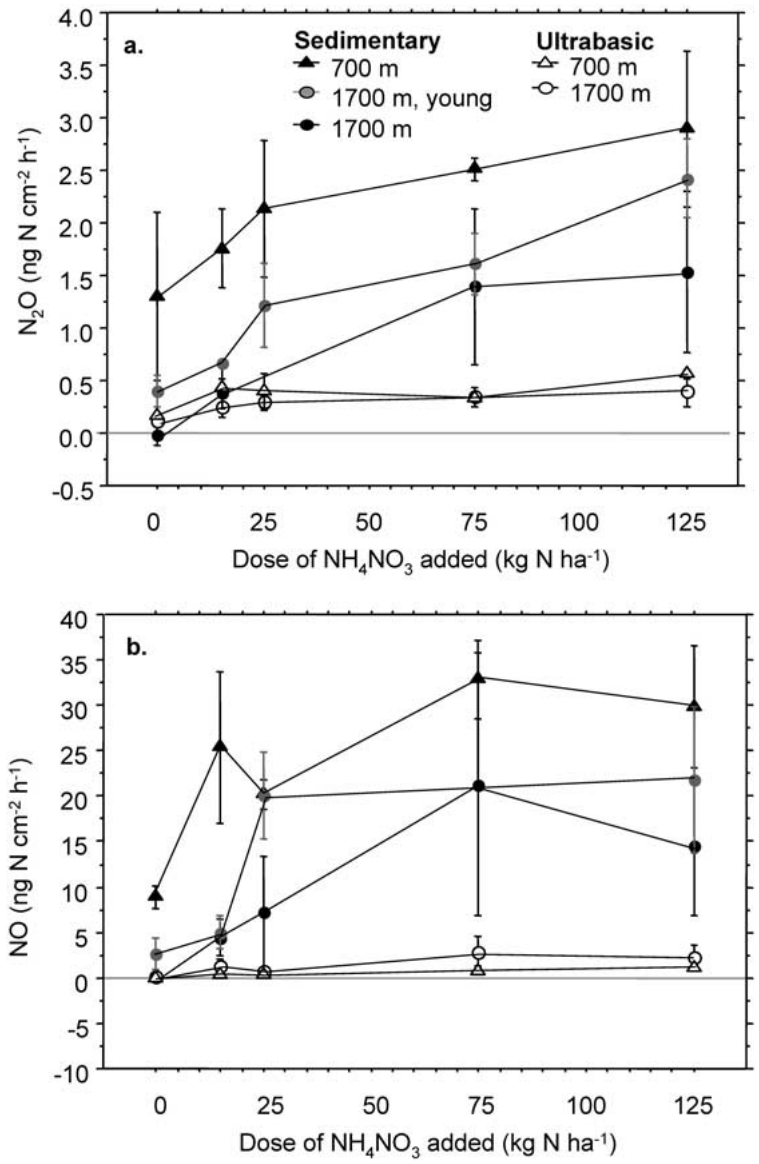

Figure 5. Soil emissions of (a) N_2O and (b) NO, 7 days after a range of N additions ($\pm$ SE, $N = 3$ blocks). Note differences in scale between NO and N_2O.

emissions than ultrabasic substrates at 700 m compared to 1700 m (elevation x substrate), and N_2O emissions were much more sensitive to N additions on sedimentary versus ultrabasic substrates (substrate $\times$ dose of N). N_2O ($p = 0.01$) and NO emissions ($p < 0.01$) following N additions were significantly larger on the sedimentary Oxisol at 700 m compared to the ultrabasic

Table 5. Significant results ($p < 0.1$) from three-factor ANOVA analyses for N-oxide emissions and N transformations in old sedimentary and ultrabasic sites at two elevations (700 and 1700 m) in the N dose-response experiment (excludes 1700 m sedimentary young site). Residual DF = 40, NS = No significance.

	Significant factors
N_2O ($ng\,N\,cm^{-2}\,h^{-1}$)*	Elevation, substrate, dose Elevation × substrate, substrate × dose
NO ($ng\,N\,cm^{-2}\,h^{-1}$)*	Elevation, substrate, dose Elevation × substrate
NH_4^+ ($\mu g\,N\,g^{-1}$)*	Elevation, dose Elevation × substrate
NO_3^- ($\mu g\,N\,g^{-1}$)*	Dose Elevation × substrate, Elevation × dose, substrate × dose Elevation × substrate × dose
Net N mineralization ($\mu g\,N\,g^{-1}\,day^{-1}$)	NS
Net nitrification ($\mu g\,N\,g^{-1}\,day^{-1}$)	Elevation, substrate, dose Elevation × substrate

*Values were log-transformed before statistical analyses.

Oxisol, even at 15 kg $N\,ha^{-1}$, the lowest dose of N (one-factor ANOVA by substrate at 15 kg $N\,ha^{-1}$). At 1700 m, both N_2O ($p < 0.01$) and NO emissions ($p < 0.01$) from young sedimentary substrates were significantly larger than sedimentary old and ultrabasic substrates across treatments ($p < 0.01$; two-factor ANOVA, all sites at 1700 m).

N additions increased NH_4^+ and NO_3^- concentrations in soils (Figure 6). However, substrate type was not equally important across both elevations in predicting inorganic N pools (significant substrate x elevation interaction). NH_4^+ concentrations were generally larger on ultrabasic compared to sedimentary substrates at 1700 m, but not at 700 m. When analyzed separately by elevation and treatment, sedimentary Oxisols at 700 m had higher NH_4^+ and NO_3^- concentrations than ultrabasic Oxisols when differences between substrates were significant (one-factor ANOVA, 700 m by treatment). Similarly at 1700 m, nitrate concentrations were significantly larger from sedimentary young compared to sedimentary old substrates within treatments (Figure 6).

Rates of net N mineralization were extremely variable after N additions across both substrates and elevations (Table 5, Figure 7), but ultrabasic substrates at 700 m had higher rates than sedimentary substrates when there were differences between sites ($p = 0.13$, substrate × elevation interaction). Dose of N had little effect on rates of N mineralization or nitrification except in the sedimentary young site where the relationship was inverse ($p < 0.05$). A combination of substrate and elevation played significant roles in predicting net nitrification in the dose–response experiment. Nitrification rates were highest

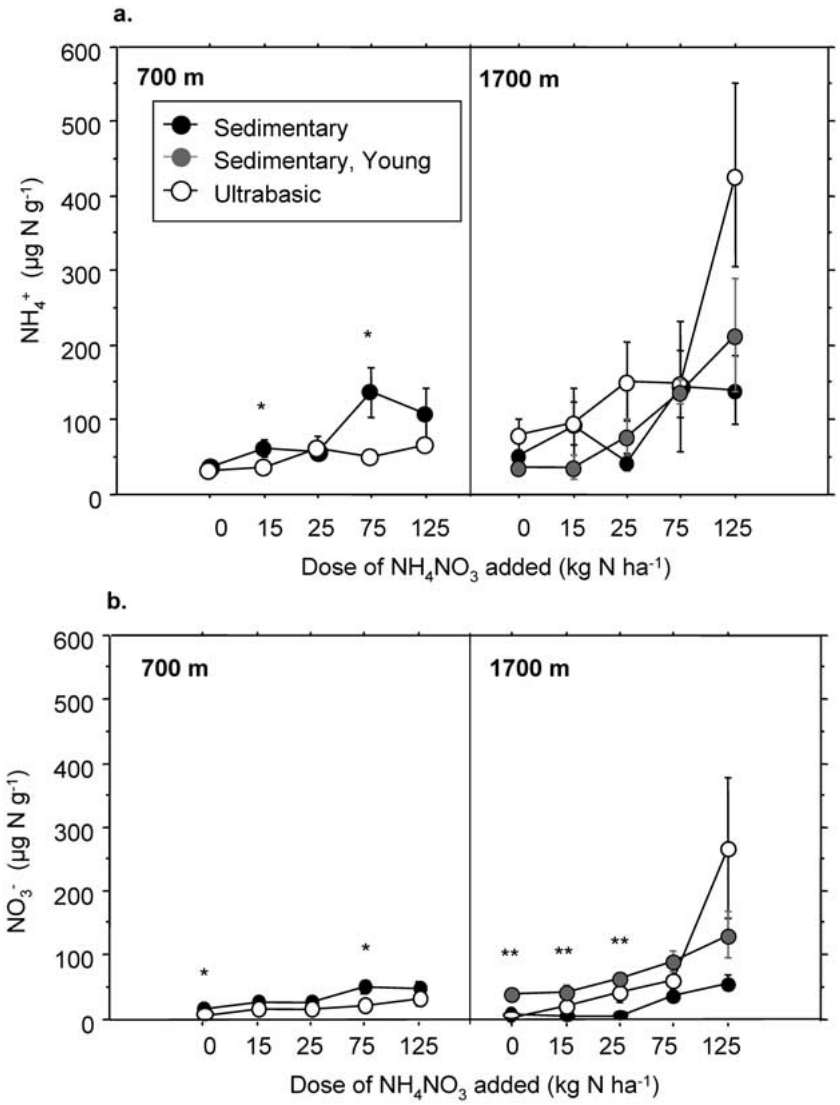

Figure 6. Concentrations of soil (a) NH_4^+ and (b) NO_3^-, 7 days after a range of N additions at 700 m and 1700 m (± SE, $n = 3$ cores). * Represents significant difference ($p < 0.1$) between soil types (old substrates only) within an elevation and treatment. ** Represents significant difference between old and young sedimentary substrate at 1700 m ($p < 0.1$).

from sedimentary substrates and at low elevation at all doses of N. Background potential nitrification (pre-N addition) was a strong predictor of the magnitude of N-oxide emissions following N additions across all doses of N (Figure 8).

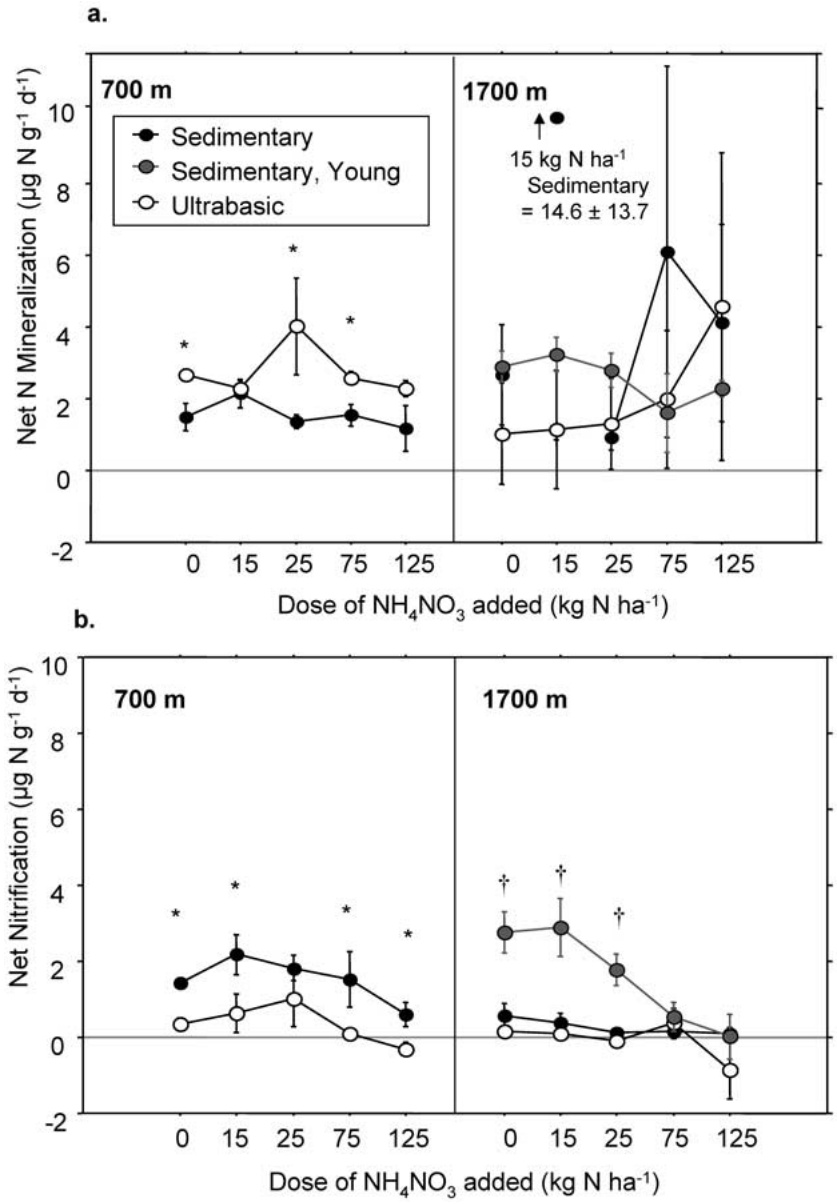

Figure 7. Net rates of (a) N mineralization and (b) nitrification, 7 days after a range of N additions (±SE, $n = 3$ cores). * Represents significant difference ($p < 0.1$) between soil types (old substrates only) within an elevation and treatment using Mann–Whitney Rank non-parametric analyses. † Represents significant differences between sites within a treatment, $p < 0.1$, Kruskal–Wallis non-parametric analyses.

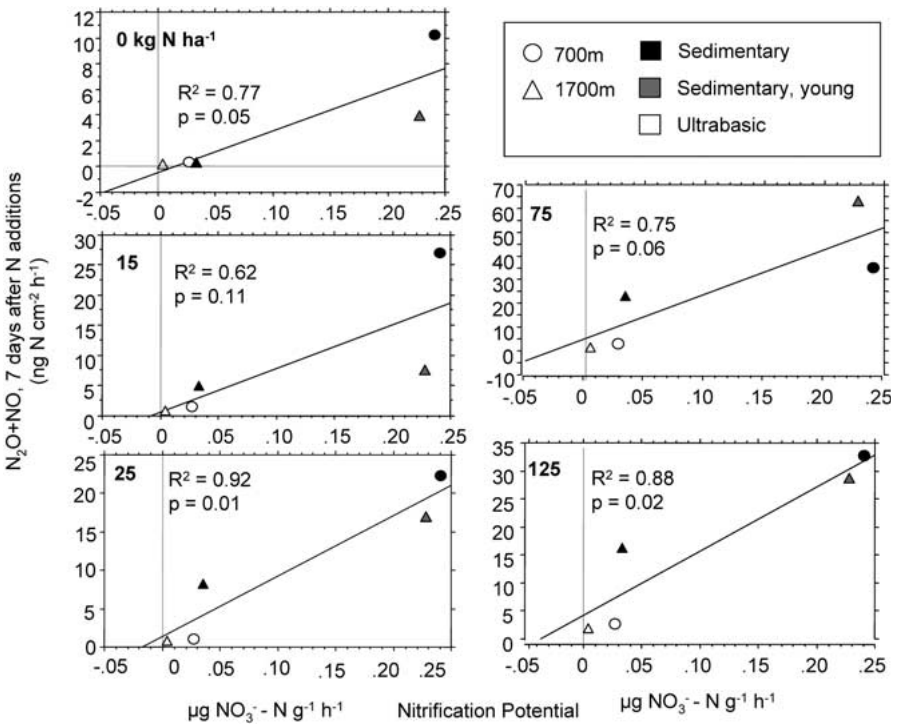

Figure 8. Regression analyses of potential nitrification (prior to N additions) and total soil N-oxide emissions (N_2O + NO) seven days after a range of N additions. Note differences in scale between doses of N.

Table 6. N pools and fluxes (mean ± SE, $N = 3$) and significant results from two-way ANOVA analyses in agricultural fields (substrate × position) and paired forests and agriculture (land use × substrate). Lowercase letters represent significant differences between land use types ($p < 0.1$). In agriculture/forest comparison, S = substrate, L = land use, NS = no significance.

	Agriculture only		Agriculture versus forest	
	Sedimentary	Ultrabasic	Sig. factors	*p*-values
N_2O (ng N cm^{-2} h^{-1})*	16.922a (7.43)	4.45b (1.35)	L, S	<0.0001, 0.041
NO (ng N cm^{-2} h^{-1})*	6.551a (3.16)	83.96a (47.60)	L	0.008
NH_4^+ (µg N g^{-1})*	60.49a (31.48)	30.57a (14.37)	NS	–
NO_3^- (µg N g^{-1})*	7.957a (3.01)	56.80b (35.18)	L, L × S	0.053, 0.020
Net N mineralization (µg N g^{-1} day^{-1})	−2.46a (1.13)	−1.67a (1.31)	L	0.015
Net nitrification (µg N g^{-1} day^{-1})	2.032a (0.96)	0.10a (1.05)	NS	–

*Values were log-transformed before statistical analyses.

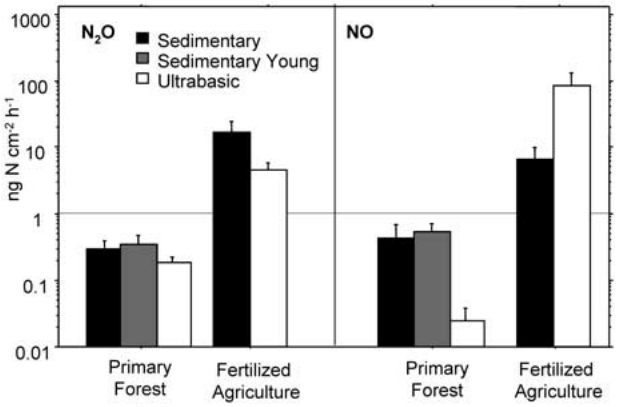

Figure 9. Soil emissions of N_2O and NO from forest and agricultural sites at 1700 m on sedimentary and ultrabasic substrates of Mt. Kinabalu. ($\pm$SE, $N = 6$ chambers per site in forest and agricultural fields). Note that the log scale on the *Y*-axis causes standard errors of large fluxes to appear small.

Land-use change: N-oxide emissions and soil N cycling from burned forest and fertilized agriculture

Substrate was important in predicting emissions of N_2O and concentrations of soil nitrate, but it did not predict variability in NO emissions, ammonium concentrations, or net rates of mineralization and nitrification (Table 6). N-oxide fluxes from agricultural fields were significantly higher than fluxes from primary forest at the same elevation (Figure 9, Table 6). Fluxes of NO in the ultrabasic field were the largest of all sites, reaching 167 ng N cm^{-2} h^{-1}. Soil NO_3^- concentrations from within gas chambers were highly correlated to NO flux ($r^2 = 0.97$, $p < 0.05$), primarily due to high NO_3^- concentrations and fluxes from the ultrabasic agricultural field (Figure 10). Soils in agricultural fields were net sinks for NH_4^+ and NO_3^- (negative net N mineralization) despite high rates of net nitrification compared to forests. Soil moisture was significantly higher from forest compared to fertilized agriculture but did not differ by substrate type.

Average NO emissions and nitrate concentrations increased along a chronosequence of land-use change on ultrabasic substrates at 1700 m, from primary forest, to a 2 week old burned field, to a 3–5 year old agricultural field (Table 7).

Discussion

Soil N cycling in primary tropical forest ecosystems

Soil mineralogy is an important factor to consider when estimating the response of tropical rain forest ecosystems to anthropogenic N deposition. Soils

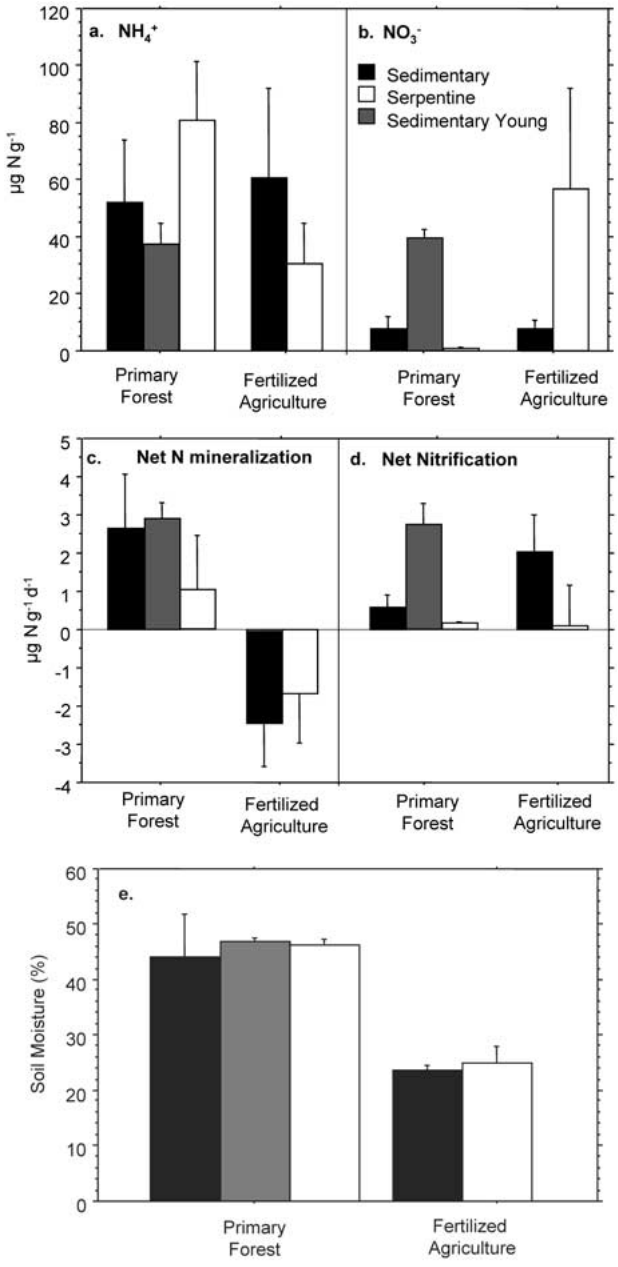

Figure 10. Soil N concentrations and transformations from primary forest and fertilized agricultural sites on both sedimentary and ultrabasic soils at 1700 m. (a) Concentrations of soil NH_4^+ and (b) NO_3^-, (c) net rates of N mineralization and (d) nitrification, and (e) % soil moisture. Agricultural fields were cleared between 1–3 years prior to sampling.

Table 7. Variations in N pools and fluxes (mean ± SE, $N = 6$) by land use at 1700 m on ultrabasic substrates. Lowercase letters represent significant differences between land use types.

	Forest	Burn	Fertilized agriculture
NO ($ng\,N\,cm^{-2}\,h^{-1}$)*	0.025 (0.013) **a**	0.915 (0.357) **a**	83.957 (47.604) **b**
NH_4^+ ($\mu g\,N\,g^{-1}$)*	80.89 (20.793) **a**	109.223 (35.369) **a**	30.565 (14.367) **b**
NO_3^- ($\mu g\,N\,g^{-1}$)*	0.95 (0.127) **a**	9.003 (2.649) **b**	56.802 (35.177) **b**
Net N mineralization ($\mu g\,N\,g^{-1}\,day^{-1}$)	1.03 (1.416)	−2.55 (1.951)	−1.67 (1.314)
Net nitrification ($\mu g\,N\,g^{-1}\,day^{-1}$)	0.15 (0.038)	0.05 (0.047)	0.10 (1.051)
Soil moisture (%)	46.333 (0.992) **a**	49.053 (2.217) **a**	25.038 (2.831) **b**

*Values were log-transformed before statistical analyses.

derived from ultrabasic substrates are known to have high concentrations of heavy metals, low initial P concentrations, high P immobilization potential, and high ratios of Mg/Ca that may limit primary production relative to more fertile soils (Proctor and Woodell 1971; Mansberg and Wentworth 1984; Medina et al. 1994). However, on Mt. Kinabalu, forests at the lowest elevation sites (700 m) are relatively similar in stature, floristics, and soil morphology between ultrabasic and sedimentary substrates. We expected that patterns of N-oxide emissions would follow primary production, with fast cycling in both lowland Oxisols that would decrease up the mountain slope due to the limiting effects of temperature on microbial activity and decomposition. Instead, we found that N-oxide fluxes were small from all ultrabasic substrates, even at low elevations on weathered soils that retain few original primary minerals. This and previous studies at this site over several years show that laboratory rates of net and potential nitrification are also low at the 700 m ultrabasic site despite relatively high rates of net N mineralization (Kitayama et al. 2000) which are clearly sufficient to support diverse, productive rain forest communities. In contrast, low elevation forests on sedimentary Oxisols had high N_2O and NO emissions and supported high N mineralization and potential nitrification rates of similar value to undisturbed humid tropical forests of Brazil and Puerto Rico (<0.01–$2\,\mu g\,NO_3^-\,g^{-1}\,h^{-1}$; Davidson et al. 2000) and Hawai'i (<0.01–$1\,\mu g\,NO_3^-\,g^{-1}\,h^{-1}$; Hall and Matson 1999).

The USDA soil classification system used in this study was developed primarily for field use and thus contains a limited number of laboratory analyses. Therefore, Oxisols and their subdivisions are defined primarily based on cation exchange capacity, fraction of clays and sesquioxides, and thickness of lower mineral horizons (USDA 1998) and do not explicitly consider chemical properties particular to ultrabasic substrates that play important roles in ecosystem functioning. For example, Baillie et al. (2000) found that ultrabasic Oxisols in the Phillipines had significantly higher ratios of Mg/total exchangeable cations and an order of magnitude higher concentrations of Mn, Ni, and Co than morphologically similar fertile, mafic Oxisols of the same

ophiolitic complex. In our study, the concentrations of Mn and Ni were an order of magnitude higher on the ultrabasic compared to sedimentary Oxisols (R. Wagai, personal communication). Furthermore, ultrabasic substrates at all elevations on Kinabalu have larger mineral surface areas compared to sedimentary soils, suggesting that high surface area is a feature of ultrabasic mineralogy under a range of weathering regimes. High surface areas of sesquioxide minerals are known to sequester organic matter (Kaiser and Zech 1998, Kalbitz et al. 2000), and thus may be important in regulating N cycling as well.

Upslope, both substrate and the direct and indirect effects of temperature were responsible for declining soil N_2O and NO emissions. In a reciprocal soil transplant experiment at similar sites, Kitayama et al. (1998) found that soil organic matter quality was more important for net N mineralization in ultrabasic soils across elevations, while temperature was the primary control over nutrient turnover in sedimentary soils. Similarly, our controlled laboratory incubations for net N mineralization showed that soil organic matter quality was high at all elevations on sedimentary substrates, even at the mountain summit, but declined sharply with elevation on ultrabasic substrates. Although additional measurements are needed to confirm these patterns, our data suggest that low temperatures at the mountain summit limit *in situ* NH_4^+ production, nitrification, and denitrification, and are responsible for low N-oxide fluxes from sedimentary substrates in the field, while both soil organic matter quality and temperature are responsible for slow rates of NH_4^+ production and gaseous N losses on ultrabasic substrates. Low litter quality in high elevation ultrabasic soils is thought to be caused directly by high polyphenol concentrations (Bruijnzeel et al. 1993), or by low redox conditions that can solubilize heavy metals and increase their potential toxicity to plants and microorganisms (Baillie et al. 2000). However, in the high elevation ultrabasic sites on Kinabalu, foliar lignin and polyphenol concentrations are relatively low while redox values are high (Kitayama et al. 1998), suggesting that alternative mechanisms are responsible for low litter quality at these sites.

A number of studies in both temperate and tropical ecosystems suggest that nutrient deficiencies, especially of P, limit production on ultrabasic soils more than heavy metal toxicity and may cause litter quality to decline (Medina et al. 1994; Chiarucci 1996; Nagy and Proctor 1997; Chiarucci et al. 1999). Following a detailed examination of P pools and fluxes at these sites, Kitayama and Aiba 2002) determined that plants on sedimentary substrates are able to maintain high net C assimilation at low temperatures by allocating excess P to photosynthetic machinery, while N or P limitation prohibits this photosynthetic adaptation in ultrabasic soils where P is likely resorbed prior to litterfall. Chemoautotrophic nitrification is thought to be more important than heterotrophic nitrification in acid soils like those on Mt. Kinabalu (DeBoer and Kowalchuk 2001). However, if heterotrophic nitrifiers are present and active, differences in C quality due to N and/or P limitation in addition to low NH_4^+ production could be responsible for low nitrification rates on ultrabasic substrates at elevation.

Long-term soil development significantly slowed rates of nitrate production in these tropical forest ecosystems. Background N-oxide emissions from young and old sedimentary substrates at 1700 m were similar to one another and significantly higher than those from ultrabasic substrates, but the population size of nitrifying microorganisms decreased by an order of magnitude on sedimentary substrates with soil age. Laboratory rates of net N mineralization shows that net NH_4^+ production is similar between the two sedimentary soils, so factors other than N availability must limit nitrification in older soils. Control over primary production is thought to shift from N to P limitation over long-term soil development, as available P becomes occluded in mineral complexes with Fe or Al oxides in weathered, acid soils (Walker and Syers 1976; Vitousek and Farrington 1997). A number of experiments in these paired sedimentary sites on Mt. Kinabalu suggest that P may limit microbial N transformations with soil age. Kitayama et al. (2003) found that laboratory P fertilization significantly increased rates of inorganic N consumption in the old sedimentary soils, and litter immobilized higher amounts of labile P (but not N) during decomposition compared to the young sedimentary soils. In addition, higher P resorption efficiencies suggest that P may limit NPP more on these old sedimentary sites compared to younger subtrates. Although P limitation of primary production has been demonstrated in a few tropical forests (Cuevas and Medina 1988; Herbert and Fownes 1995), fewer studies have shown limitation in microbial communities (Cleveland et al. 2002), especially those composed of NH_4^+ and nitrite-oxidizing organisms. For example, nitrification was extremely high in tropical forest ecosystems in Hawai'i, where P was the primary limiting factor to NPP and N uptake by plants (Hall and Matson 1999). Unless P availability affects nitrifiers differently than heterotrophs (N mineralization rates were similar between old and young sedimentary sites), it is likely that other factors were more important than P in limiting rates of nitrification. Although acidity inhibits nitrification in a number of systems, acid-tolerant nitrifiers are now known to be common in N-rich acidic forest soils of Europe and N. America (DeBoer and Kowalchuk 2001) and may be ubiquitous in fertile tropical soils as well. The small difference in pH (3.7 versus 3.4 in $CaCl_2$, Table 2) between young and old sedimentary substrates will not likely limit nitrification directly, but pH in combination with changes in mineralogy (e.g., Fe oxide–P interactions) may play a strong role in limiting these processes over long-term soil development.

The absence of nitrification in soils has been shown to occur in a number of natural and managed ecosystems (Degrange et al. 1998; Ste-Marie and Pare 1999; Page et al. 2002), but the possible mechanisms that limit these processes are often confounding and difficult to identify. In sum, small population sizes of nitrifying microorganisms on ultrabasic soils could be caused directly by soil or plant-derived toxic compounds that inhibit the nitrification process such as heavy metals, polyphenols, or other allelopathic plant products (DeBoer and Kowalchuk 2001). Alternatively, nitrifying microorganisms are thought to be weak competitors for N compared to heterotrophic microbes and plants

(Richards 1987), so populations are likely to be small where N is limiting to NPP. For example, exposed mineral surfaces in ultrabasic soils could also be strong sinks for organic matter that effectively reduce NH_4^+ availability to nitrifiers.

N-oxide emissions after N additions in primary forest ecosystems

Although the variability in N-oxide emissions was high due to limited replication, it is clear that soils at low elevation and derived from sedimentary substrates respond to N additions significantly more than do ultrabasic soils at any elevation. Previous studies in Hawaiian tropical rain forests have shown that the magnitude of N-oxide emissions following N additions are highly correlated to potential nitrification, or the size of the nitrifying community in soils (Hall and Matson 2003). In addition, N-oxide losses were not linear with dose of N in the Hawaiian study, suggesting that initial population size of nitrifiers constrained N-oxide emissions rather than NH_4^+ supply. On Mt. Kinabalu, nitrifier population size was also a strong predictor of N-oxide emissions after N additions, even at the lowest dose of $15\,kg\,N\,ha^{-1}$ (Figure 8), and fluxes were not linear with dose of N or NH_4^+ pools. Nitrifying microorganisms are known to grow slowly in culture (DeBoer and Kowalchuk 2001), and it is unlikely that they would increase their biomass within a week after N additions.

Our study also suggests that NO emissions are a major pathway of loss from tropical rain forest ecosystems and are stimulated by N additions more so than are emissions of N_2O. NO emissions also dominated over N_2O from P-limited tropical rain forests after a similar dose response experiment in the Hawaiian Islands (Hall and Matson 2003). However, N_2O fluxes were nearly an order of magnitude higher than NO fluxes from a long-term fertilized forest in Puerto Rico (Erickson et al. 2001). The ratio of N_2O/NO has been shown to be related to the oxidizing environment in the soil across a number of different sites, where $N_2O/NO \ll 1$ in aerobic soils that are dominated by nitrification, and $N_2O/NO \gg 1$ in wet soils that are dominated by denitrification and where anoxic conditions promote the further reduction of NO to N_2O or N_2 before escaping the soil surface (Davidson 1993). The ratio of N_2O/NO was <1 from soils at most of our sites, which supports the significant correlation we observed between rates of nitrification and N-oxide emissions from soil after N additions.

Effects of land use on N cycling and N-oxide emissions

Agricultural management practices reduce the differences in nutrient cycling between soils derived from different substrate types. Like in many tropical developing countries, land use change in SE Asia often begins with selective

logging of high quality wood products in primary forests, causing significant changes in forest structure and microclimate. Eventually, secondary forests are burned, sometimes unintentionally due to forest drying, and then mineral soils are terraced, tilled, fertilized, and irrigated for crops. In agricultural fields just outside of the boundaries of Kinabalu Park, soils were significantly drier than in forests, probably due to the loss of soil organic matter following burning and warmer temperatures at the exposed soil surface. At the same time, land conversion to agriculture caused high N-oxide fluxes from both substrates, most likely depending on where fertilizer was applied in each field (Matson et al. 1996). Total N-oxide emissions (primarily NO) were higher from ultrabasic fields that were recently fertilized (1 week) compared to sedimentary substrates fertilized a month prior to sampling. This pattern has also been shown in other studies (Matson et al. 1996), emphasizing the importance of agricultural management practices in controlling soil N-oxide emissions.

Anthropogenic N deposition in tropical forests may significantly alter a number of fundamental ecological processes between plants, microbes, and soils, and may contribute to changes in regional and global atmospheric composition. However, the magnitude of N_2O and NO emissions in fertilized agriculture will far outweigh the contribution of N-saturated primary tropical forests to global budgets of these gases. On Mt. Kinabalu, fluxes from fields fertilized 1 week and 1 month prior to sampling were larger than those from the highest N additions in the dose response experiment in primary forests. Hall and Matson (1999) suggested that atmospheric N deposition may increase fluxes of N_2O and NO from tropical forests by 13% and 18% by 2050, respectively, if we assume that approximately the same amount of N will be deposited annually to tropical forests as occurs in temperature forests ($22\,Tg\,year^{-1}$), that tropical forests will be weak sinks for N, and that 2% of that N will be emitted to the atmosphere as N_2O and 1% as NO. The results of our current study suggest that not all low elevation tropical forests growing on highly weathered soils will respond with large N-oxide emissions. However, if nearly 1% of remaining tropical forests are cleared each year for fertilized agriculture worldwide (WRI 1998), the magnitude of N_2O and NO released to the atmosphere from cultivated soils will far exceed the tropical forest contribution.

Conclusions

Human activities are increasing the deposition of reactive N compounds to tropical systems, yet we have limited understanding of the consequences of N enrichment on tropical ecosystem functioning. Our results suggest that N additions will significantly increase N-oxide emissions in soils that have large, active nitrifying microbial populations. Highly weathered soils derived from ultrabasic substrates may support large, diverse rain forest communities but small nitrifier communities, although the mechanisms of microbial limitation

are not well understood. Because current methods of soil classification do not explicitly characterize a number of soil chemical properties important to nutrient cycling, the use of soil maps to extrapolate biogeochemical processes to the region or globe may be limited in its accuracy and usefulness. As primary forests are cleared for intensive agriculture, however, soil N_2O and NO emissions are likely to far exceed those from the most N-saturated tropical forest ecosystems. Wet tropical forests cover 17% of Earth's surface but alone comprise 40% of global net primary production and evapotranspiration (Schlesinger 1997) and contain at least 90% of the known plant and animal species on Earth. Because of their ecological importance, large-scale biogeochemical changes to tropical rain forest ecosystems from N deposition or agricultural intensification will likely have effects at the global scale.

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