

Nitrogen aboveground turnover and soil stocks to 8 m depth in primary and selectively logged forest in southern Amazonia

TED R. FELDPAUSCH*†, EDUARDO G. COUTO‡, LUIZ CARLOS RODRIGUES‡, DANIELA PAULETTO§, MARK S. JOHNSON¶, TIMOTHY J. FAHEY||, JOHANNES LEHMANN† and SUSAN J. RIHA*

*Department of Earth and Atmospheric Sciences, Cornell University, Ithaca, NY, USA, †Department of Crop and Soil Sciences, Cornell University, Ithaca, NY, USA, ‡Departamento de Agronomia, Universidade Federal de Mato Grosso, Cuiabá, Mato Grosso, Brazil, §Coordenação de Pesquisas em Silvicultura Tropical, Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil, ¶Institute for Resources, Environment and Sustainability and Department of Earth and Ocean Sciences, University of British Columbia, Vancouver, BC, Canada, ||Department of Natural Resources, Cornell University, Ithaca, NY, USA

Abstract

Extensive areas of Amazonia undergo selective logging, modifying forest structure and nutrient cycles. Anthropogenic-accelerated rates of nitrogen (N) turnover could increase N loss and affect regeneration, carbon sequestration and timber production. We quantified leaf area reduction, canopy opening and downed biomass and resultant N flux from reduced impact logging (RIL) activities. We compared canopy reduction, surface soil moisture and nitrate to 8 m depth between logged gaps and intact primary forest to determine if logging activities increase subsoil nitrate. To test long-term logging effects, we evaluated surface N stocks along a 12-year postlogging chronosequence. At the harvest rate of 2.6 trees ha⁻¹, total N additions in logging gaps, including leaves and wood from felled crowns (24.8 kg N ha⁻¹) and other killed trees (41.9 kg N ha⁻¹), accounted for over 80% of the total N addition to aboveground necromass from all logging activities (81.9 kg N ha⁻¹). Despite this N turnover by logging, belowground nitrate storage to 8 m depth did not differ between logging gaps and primary forest at the low harvest rate and disturbance intensity of this study. Soil water depletion also did not differ between gaps and primary forest over 1 year, indicating the impact on belowground inorganic N was low. Compared with primary forest, nitrate concentrations to 8 m depth in logging gaps were only significantly higher at 60–100 cm, suggesting some N redistribution beyond the bulk of the fine roots in logging gaps. Extrapolated to the Amazon Basin scale, we provide a conservative estimate that logging damage and bole export under RIL would turn over 0.14 ± 0.07 to 0.23 ± 0.12 Tg N yr⁻¹ based on 1999–2002 selective logging rates. Greater damage during conventional selective logging would cause higher N turnover throughout the Amazon Basin than our results based on RIL.

Keywords: Amazon, Brazil, coarse woody debris (CWD), deforestation, forest certification, LAI, reduced-impact logging (RIL), selective logging, soil moisture, soil nitrate, subsoil

Received 2 June 2009 and accepted 10 July 2009

Introduction

Landscape-scale acceleration of nitrogen (N) turnover is occurring throughout the Amazon Basin as a result of selective logging through forest damage, soil disturbance, and generation of woody debris. Estimates of

selective logging in Amazonia (Asner *et al.*, 2005) indicate that the extent may be higher than previously estimated (Nepstad *et al.*, 1999), with the area affected by selective logging nearly equal or exceeding the area deforested annually (12 075–19 823 km² logged yr⁻¹). Despite the scale of selective logging and potential implications for forest productivity and carbon sequestration in these globally important forests, few data exist to evaluate changes caused by N turnover following logging. Shifts in climate patterns have potentially resulted in basin-wide reductions in rainfall and rising

Correspondence: Ted R. Feldpausch, Earth and Biosphere Institute, Ecology and Global Change, School of Geography, University of Leeds, Leeds LS2 9JT, UK, tel. + 44 113 343 3381, fax + 44 113 343 3308, e-mail: T.R.Feldpausch@leeds.ac.uk

temperatures (Malhi *et al.*, 2008), which in turn could increase forest drying, fire probability, and N loss. Anthropogenic-accelerated rates of N turnover through selective logging could further increase N loss on these highly weathered and nutrient deficient soils, affecting landscape-scale forest regeneration, carbon sequestration, and timber production.

N is readily lost following forest disturbance on the highly weathered Oxisols and Ultisols of lowland *terra firme* Amazonian forest (Buschbacher *et al.*, 1988; Fernandes *et al.*, 1997; Schroth *et al.*, 1999; Markewitz *et al.*, 2004). The susceptibility of N loss following disturbance stems primarily from gaseous emissions during fire and from denitrification and leaching of nitrate (NO_3^-) anions. Rapid land-cover and land-use change in high rainfall regions in Amazonia, with a corresponding reduction in N uptake and storage capacity in the aboveground biomass that replaces primary forest, could substantially affect regional soil N pools.

Reduced-impact logging (RIL) is a technique that attempts to lessen the overall effect of intensive logging. Relative to conventional selective logging methods, RIL conserves carbon by damaging fewer trees and disturbing less forest surface area (Johns *et al.*, 1996; Pinard & Putz, 1996; Pereira *et al.*, 2002; Feldpausch *et al.*, 2005). However, gap formation, whether by selective logging or natural tree fall in undisturbed primary forest, results in canopy damage (Johns *et al.*, 1996; Webb, 1997; Asner *et al.*, 2004), generation of woody debris (Keller *et al.*, 2004c), and modification of soil and microclimatic conditions such as irradiance, humidity, through-fall, temperature, and soil moisture (Sluiter & Smit, 2001). Gap size has a strong influence on microclimatic variables, with lower soil moisture during the dry season in large gaps (>1280 m²) and higher soil moisture in small gaps (<210 m²) than undisturbed forest (Sluiter & Smit, 2001). Coarse woody debris (CWD) in moist Amazonian primary forest comprises 6–18% of the aboveground biomass (Chambers *et al.*, 2000; Gerwing, 2002; Keller *et al.*, 2004c), increasing by 35–43% above background levels following RIL (Keller *et al.*, 2004c). Mineralization of nutrient-rich litter may be rapid following disturbance, with respiration from fallen and standing CWD averaging 5.7 Mg C ha⁻¹ yr⁻¹ (Rice *et al.*, 2004); one-half of the N stocks of CWD have been shown to leach from fresh fine litter within 3–6 months after logging (Olander *et al.*, 2005). Changes in surface soil nutrients such as N and P during logging are rapid in the most severely disturbed areas such as roads and log decks (Ivo *et al.*, 1996; Olander *et al.*, 2005), and the changes can persist for many years following logging (McNabb *et al.*, 1997). However, the effect of logging on the translocation of N from surface to deep soil layers remains unknown. Attempts to quantify the N flux due

to selective logging have frequently ended at <1 m soil depth because of the difficulty and time required to bore to greater depths. Furthermore, many studies report total N rather than NO_3^- -N, whereas NO_3^- has a higher potential of being lost from the system by deep leaching. Nitrate leaching to the subsoil could represent a permanent loss from the system in the absence of deep root uptake. Although deep rooting has been reported for Amazonian trees (Nepstad *et al.*, 1994; Hodnett *et al.*, 1996), following gap formation a 'root gap' may be formed, reducing this potential N retention mechanism. The aboveground canopy gap could increase rainfall penetration to the ground, increase surface temperatures, and add N from logging damage. The root gap may result in lower water depletion, reduced nutrient uptake, and N turnover following root mortality, during which time nitrate leaching may occur. Excessive N leaching to depth in the absence of uptake by roots could negatively affect forest regeneration and prolong the regeneration time to the next timber harvest.

We quantified how logging accelerates N turnover and determined if logging-induced changes in forest structure could result in the accumulation of N in the subsoil, potentially beyond the active root zone. Our objectives were to (1) quantify changes in canopy structure and N additions to the soil as foliage and woody slash following reduced-impact logging; (2) evaluate whether surface soil water depletion in logging gaps differs from undisturbed primary forest; and (3) determine if there is a relationship between N addition via foliage and wood, and N accumulation as nitrate in the subsoil. The results of N turnover following forest disturbance have Amazon Basin-wide implications for forest productivity, carbon sequestration, and the sustainability of timber harvesting.

Materials and methods

Study site

The study was conducted in Fazenda Rohsamar in southern Amazonia, a 25 000 ha forest managed by Rohden Indústria Lígnea Ltda (S10°28'W058°30'). The forest lies adjacent to Rio Juruena in the northwestern region of the state of Mato Grosso in the municipality of Juruena, Brazil. The regional climate is tropical humid, with 2200 mm of annual rainfall, a 4 month dry season (July–October) when precipitation drops to <100 mm month⁻¹ and a mean annual temperature of 24.8 °C (IBGE 2005). The soils, predominantly dystrophic acidic Oxisols and Ultisols, are classified as Kandistults and Haplustoxes according to USDA classifications (Soil Survey Staff, 1999) and as Acrisols and Ferralsols according to UN FAO classifications

(FAO-UNESCO, 1987). The vegetation is closed canopy forest with an average of 276 Mg ha⁻¹ dry biomass and 516 trees ha⁻¹ ≥ 10 cm DBH (diameter at breast height, 1.3 m height or above prop-roots or buttresses) (Feldpausch *et al.*, 2006). This research is part of the Large-scale Biosphere Atmosphere Experiment in Amazonia (e.g. Roberts *et al.*, 2003; Davidson & Artaxo, 2004; Keller *et al.*, 2004a).

The 25 000 ha forest was divided into 20 ~ 1200 ha management and unlogged control units. Logging began in 1992 using conventional selective logging methods and continued through 2002 with some improvements to reduce forest damage during road building and logging. Rohden Indústria was certified by the Forest Stewardship Council (FSC) in 2003 for certified timber. This study focuses on Block 5, a ~ 1400 ha area logged using RIL practices during July–September, 2003.

According to FSC guidelines, measures are taken to reduce collateral forest damage. Before logging, a 100% forest survey of commercial timber trees is conducted and low-lying areas and streams are mapped to facilitate the planning of roads, log consolidation decks, and skidder extraction pathways. During logging, directional felling is employed by selecting the tree fall-path least likely to damage surrounding trees. Rubber-tire skidders with a winch are used to move logs to consolidation log decks.

Leaf area reduction, canopy opening, and gap size

To calculate the canopy N input from logging damage, we estimated changes in canopy openness and leaf area reduction using two methods. Areas of intact primary forest ($n = 50$) were compared with nearby areas of the forest that were logged [logging gaps ($n = 54$), roads ($n = 11$), skid trails ($n = 12$) and log decks ($n = 9$)] and changes in canopy cover and leaf area index (LAI) computed as the difference between intact forest and the respective damage category. Logging gap measurements were made only in gaps formed by the harvest of single trees. We developed and evaluated two methods to quantify leaf reduction relative to primary forest and consequent N addition to the soil in disturbed areas, including gaps, skid trails, roads, and log decks.

Method 1 (LAI reduction in contiguous canopy opening): we measured the contiguous canopy opening to compute the area of canopy losing leaves above logging gaps and log decks using the 'center-point' system (adapted from Runkle, 1992), a system of summing the area of six triangles based on the distance from the center to the edge of the gap. The edge of gaps was defined as the outline of the remaining canopies (Runkle, 1982). Leaf loss for logging gaps and log decks was

computed from the canopy opening area (m²) and LAI (m² leaf m⁻² ground) as the difference in LAI measured in each category *relative* to estimates in adjacent undisturbed primary forest (i.e. reduction in LAI above gaps relative to mean LAI: 3.7 ± 0.2 in adjacent undisturbed forest). Canopy images were taken in each of the disturbance categories (e.g. logging gaps, roads) in Block 5 and in adjacent patches undisturbed by logging with a fisheye lens (Sigma 8 mm/F4) attached to a digital camera (Nikon D70) on a tripod at ~ 150 cm height. This setup crops the sides of the hemispheric image, giving an incomplete circular image. To resolve this restriction, we shot a second image perpendicular to the first and digitally joined the paired images using ADOBE PHOTOSHOP[®], thereby creating a complete 180° image. Canopy openness and LAI were calculated using the software GAP LIGHT ANALYZER (Frazer *et al.*, 1999), which uses inverse gap fraction analysis to calculate LAI (Norman & Campbell, 1989). The analysis assumes diffuse light conditions so we restricted our measurements to times of uniform cloud cover or late afternoon.

Method 2 (allometric basis): This method was based entirely on allometry, where we used an allometric equation to estimate leaf area lost from the DBH of trees harvested or killed, those trees crushed prone or with their stems severed by logging activities. Stems receiving partial canopy damage were not included in the analysis. Leaf area of all trees harvested or killed by logging activities and tree fall was calculated using an equation developed in central Amazonia from 50 harvested trees that relates DBH to leaf area ($R_{\text{adj}}^2 = 0.65$) (Chambers *et al.*, 2004)

$$\log(\text{leaf area}) = 4.22\log(\text{DBH}) - 0.918[\log(\text{DBH})]^2 - 2.21.$$

Leaf area loss values estimated from the two methods were scaled based on harvest rate and disturbance transects (Feldpausch *et al.*, 2005) to estimate canopy and leaf area reduction on a per hectare basis for each damage class (e.g. logging gaps, skid trails, etc.). For log decks and roads, where it was impossible to measure the diameter of trees felled or severed for Method 2, we applied the diameter size–class distribution from adjacent undisturbed forest to estimate the number and diameter of trees killed in log decks and roads based on the area affected.

N additions in gaps, roads, log decks and skid trails

To estimate N flush to the soil from leaves, wood, and the logged crown, we used the leaf loss values based on the two methods above and the biomass flux in wood caused by logging damage for the logging block

(Feldpausch *et al.*, 2005). In that damage analysis of the biomass flux in boles and branch turnover following RIL, we quantified forest damage from all logging activities in Block 5, including damage caused by road and log deck construction, tree-fall in gaps, and trees crushed by skidder movement within the forest. The total area (100% area surveyed) disturbed by road and deck construction was directly measured in Block 5 by ground-based measurements. Stand diameter tables developed from the surrounding forest (Feldpausch *et al.*, 2005) were then applied to estimate the number of trees killed by road and deck construction. To estimate damage and tree mortality in logging gaps and skid trails, all trees damaged were measured in 54 logging gaps and in 12 independent skid trails (total of 1100 m of skid trail). To determine the percent of the forest disturbed by skid trails and logging gaps and scale measurements to the entire block, we measured 7800 m of disturbance line-intercept transects, where disturbance encountered along the transect was defined as evidence of logging activity. The mass of individual trees (kg) killed during logging activities was calculated based on the allometric equation from Brown (1997), with DBH as the predictor of dry biomass. This equation was developed from harvesting 170 trees with a DBH range of 5–148 cm ($R^2 = 0.84$)

$$\text{tree biomass} = 42.69 - 12.80(\text{DBH}) + 1.24(\text{DBH})^2.$$

The total crown mass (kg) of each logged tree was calculated from DBH using a crown allometric equation developed in central Amazonia ($R_{\text{adj}}^2 = 0.88$) (Chambers *et al.*, 2001)

$$\begin{aligned} \ln(\text{crown mass}) = & 0.235 - 1.713 \ln(\text{DBH}) \\ & + 1.588 [\ln(\text{DBH})]^2 \\ & - 0.183 [\ln(\text{DBH})]^3. \end{aligned}$$

Crown wood mass (kg) was calculated as the difference of the total crown mass and leaf mass. Bole mass of individual trees was computed as the difference between total mass and crown mass.

The reduction in leaf area in gaps and other disturbed areas based on the two methods were converted to leaf mass (kg) to estimate N addition to the soil following logging based on published values from Amazonia of mean specific leaf area (SLA: leaf area per unit leaf mass) ($85.1 \text{ cm}^2 \text{ g}^{-1}$) and leaf N concentrations (16.9 g N kg^{-1}) (Thompson *et al.*, 1992; Reich *et al.*, 1995; Martinelli *et al.*, 2000; Olander *et al.*, 2005). These values were then multiplied by the disturbance rates to give N turnover for each type of activity (e.g. gap, skid trail) on a per hectare basis. N additions from wood (e.g.

severed boles and fallen crowns) to the soil were calculated from wood flux estimates for the same forest (Feldpausch *et al.*, 2005) using mean N concentrations for crowns and boles from *terra firme* Amazonian forests (Martinelli *et al.*, 2000).

To estimate total N-turnover at the Amazon Basin-level due to logging, we multiplied our total N turnover estimates (kg N ha^{-1}) from all logging activities by the estimated area annually selectively logged (Asner *et al.*, 2005). Uncertainties in N concentration and logging damage in scaling results from individual tree measurements were propagated as $\sqrt{(\text{error}_1)^2 + \dots + (\text{error}_n)^2}$, where *error* represents the absolute (δx) or relative error ($\delta x/x$) for addition and subtraction or multiplication and division, respectively.

Soil chemical and physical properties

Nitrate accumulation in the subsoil 1 year following RIL was measured by a stratified random soil sampling scheme, where sample locations were randomly selected from stratified regions of the ~ 1400 ha Block 5 to account for local scale soil variability. We collected soil samples to 8 m depth in nine gaps formed by single tree removal and nine areas of undisturbed primary forest. Areas of undisturbed forest were confined to patches of forest within Block 5 that were protected from logging. Three areas were sampled to shallower depths when we were unable to bore to deeper depths. Soil samples were collected from below the fallen crown of the logged tree within each gap and in undisturbed forest using an Edelman auger extendible to 8 m at the following depth increments: 0–20, 20–40, 40–60, 60–100, and 50 cm increments thereafter to 8 m. Soil samples were stored in bags in a cooler with ice in the field. Soil mineral N was extracted the following day with 1 N KCl, the sample then filtered and analyzed by cadmium reduction. Nitrate (NO_3^-) was measured on a spectrophotometer (GENESYS 5) at the *Universidade Federal de Mato Grosso*, Cuiabá, Brazil. Soil NO_3^- was calculated by converting solution content to adjusted volume based on soil water content and soil bulk density (BD) measured to 8 m depth. To determine soil water content, 40–50 g of soil was taken from the same original sample, weighed wet, dried for 48 h at 105°C to constant weight and reweighed.

To determine the long-term effect of logging on total soil N in surface soils, we sampled soil in undisturbed forest and a chronosequence of blocks logged 2, 6–7, and 11–12 years ago. In four randomly selected areas in each of the four blocks we formed five samples representing both 0–10 and 10–20 cm depth. Each sample was formed by compositing five subsamples for each soil

sample. This resulted in 20 samples for each depth for each of the four blocks comprising the time-since-logging chronosequence. The samples were analyzed for total N by the Kjeldahl method (Silva, 1999) at the *Instituto Nacional de Pesquisas da Amazonia* in Manaus, Brazil.

Soil chemical and physical properties were measured in the intact 8 m deep forest samples. The soil was air-dried, screened through a 2 mm stainless-steel sieve and analyzed according to methods described by EMBRAPA (Silva, 1999). Total organic carbon (OC) content was determined chromatographically after dry combustion at 1400°C with a total carbon analyzer (Jena Analytik AG, Jena, Germany). Because carbonates were not present in the acidic soils of the study site the total carbon measured was equivalent to OC. Exchangeable Ca, Mg and Al were extracted with 1 M KCl and determined by atomic absorption (Ca and Mg) and titration (Al). Mehlich extractable P was determined by colorimetry. The pH was determined using a glass electrode in deionized water (pH_w) in a 1:2.5 weight-to-volume ratio. Cation exchange capacity (CEC) was determined as the sum of cations after adjusting the soil solution to pH 7. Soil BD was measured to 8 m depth. Surface BD (0–100 cm depth) was based on volumetric soil samples. Deeper depths were measured by collecting a known soil sample volume using an Edelman auger integrated over 100 cm depth increments. BD was computed as the dry weight of soil per measured soil volume extracted by soil rings for surface samples and auger from each depth increment. Soil from each depth was analyzed for percent sand, silt, and clay. Particle size distribution was determined using the densimeter method. Owing to high clay concentrations typical of Oxisol soils, samples were placed in a 1:1 solution of 1 N sodium hydroxide (NaOH) and sodium hexametaphosphate ($(\text{NaPO}_3)_6$) and placed on a slow shaker for 16 h to disperse clay aggregates before densimetry.

Time domain reflectometry (TDR) access tubes (TRIME, 2000) were installed to 70 cm depth into the nine logging gaps and nine areas of intact forest sampled for nitrate. Volumetric soil water content (θ , percent water) was measured over 1 year. The TDR system consists of a 20 cm probe covered by four sets of spring-mounted wave guides. The cylindrical probe is inserted into plastic tubes permanently installed into the soil, where the wave guides make contact with the tube wall. Soil θ was measured monthly or bimonthly by taking two measurements per depth (second measurement perpendicular to the first to account for the elliptical area sampled by the probe) at 10, 20, 40, 60 cm depth, providing data to 70 cm depth. Soil θ was computed by the probe based on a factory calibration curve

since soil properties were within the applicable range. Soil water storage was calculated by multiplying θ by the 20 cm measured by the probe for each depth. To account for potential differences in soil texture, the field capacity for the soils of each individual tube (rather than site average) was measured as the maximum soil recharge at the peak of the rainy season. Mean monthly soil water depletion was calculated as the depletion (mm) of soil water from maximum soil recharge (field capacity) during the wet season. Rainfall was measured by a tipping-bucket rain gauge placed in a clearing within 3 km from all sample sites in Block 5. Soil moisture was measured from August 2004 to August 2005. Soil nitrate, LAI and logging damage measurements took place during the dry season 1-year following logging.

Differences between gaps and intact forest for soil water depletion, soil nitrate concentration, and storage and soil texture were analyzed by depth using a general linear model from the statistical software MINITAB (Minitab, 2000). In the presence of statistically significant differences ($P < 0.10$), we used a Tukey multiple comparison test with the same error rate to determine which depths differed significantly.

Results

Forest disturbance and canopy reduction

Logging gaps constituted the greatest percent of forest area disturbed by RIL (10%), followed by skid trails (6%). Roads and log decks together accounted for disturbance of 1% of the total forest surface area (Fig. 1). Canopy openness, measured as the percent of the canopy unobstructed by leaves above 1.5 m in hemispheric images, was significantly greater above roads, logging gaps, and log decks (increasing order of openness) compared with undisturbed forest (Fig. 1). Since logging gaps constituted the greatest surface area disturbance from selective logging, we focused our efforts and analysis on gaps to quantify N turnover and potential loss to the subsoil.

An average 2.6 trees were harvested per hectare under RIL in Block 5. The mean canopy opening created from single tree-fall (canopy removal of the logged tree in addition to damage to surrounding trees during tree-fall and harvest operations) was $202.1 \pm 12.5 \text{ m}^2$ (Table 1). Vegetation colonizing the logging gaps remained <2 m height after 1 year. Log decks created a larger canopy opening than logging gaps, but were infrequent compared with logging gaps (Fig. 1). The LAI of intact primary forest was 3.7 ± 0.2 , with logging damage reducing LAI above skid trails, logging gaps, roads, and log decks by 0, 1.3, 1.5,

$2.0\text{ m}^2\text{ leaf m}^2\text{ ground}^{-1}$, respectively. The LAI value for intact forest was low because all measurements were taken during the dry season when some trees lose some or all of their leaves. Based on the two methods to estimate foliar loss, the mean leaf loss

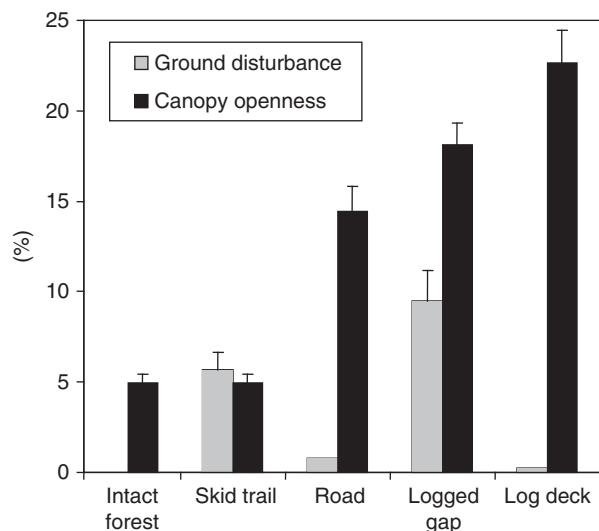


Fig. 1 Frequency of total ground disturbance defined as presence of logging activity and mean canopy openness for intact forest, skid trails, roads, logged gaps, and log decks immediately following selective logging. Disturbance was measured along $n = 26$ line intercept transects totaling 7800 m in Fazenda Rohsamar, southern Amazonia, MT Brazil. Error bars indicate standard error (for road and log decks, 100% of the area inventoried).

for logging gaps ranged from 79 to 85 kg ha^{-1} forest (Table 1).

N additions to soil from logging activities

Mean foliar N flux estimated for trees killed or severed by tree-fall and crown loss, skid trails, and construction of roads and log decks resulted in an addition of $1.3\text{--}1.4\text{ kg N ha}^{-1}\text{-forest}$ to the soil surface based on estimates from the two leaf loss methods (Table 1). N addition from leaves in gaps ranged from 25.4 based on the allometric Method 2 to estimate leaf loss to $27.2\text{ kg N ha}^{-1}\text{-gap}$ based on the contiguous gap Method 1 on a per hectare of gap basis. Estimates of N inputs by leaves from all logging activities were slightly higher when calculated based on the LAI reduction Method 1 than on the allometric tree mortality Method 2 basis. Approximately 74% of the foliar N flux in logging gaps (1.3 kg N ha^{-1}) was from the crown of the logged tree (Table 2), with the remainder from the average of 25 trees $\geq 10\text{ cm DBH}$ crushed or severed in each gap by tree-felling and within-gap skidder movement. At the stand level, N additions from leaf loss from logging gaps accounted for over 89% of the total foliar N additions from all logging activities. Because of their larger size, individual log decks contributed 2.2 times more N than individual logging gaps, but only covered about 0.2% of the total logged area compared with 10% for logging gaps.

N additions from wood flux accounted for a much higher percent of the total N additions to the soil surface

Table 1 Leaf mass, area and nitrogen flush estimated from method (1) LAI reduction relative to intact primary forest and the contiguous canopy gap, (2) an allometric equation to estimate leaf loss for stems severed or crush by logging activities in gaps, log decks, skid trails, and roads in Block 5 logged at a rate of 2.6 trees ha^{-1} in Fazenda Rohsamar, southern Amazonia, MT Brazil

	Logged gaps	Log decks	Skid trails	Road	Total
$n =$	54	9	12(1100 m)	100%	–
No. canopy openings per ha (gaps ha^{-1})	2.6	0.06	–	–	–
<i>(1) LAI reduction + contiguous canopy opening basis*</i>					
LAI reduction from primary forest values	1.3	2.0	0	1.5	–
Leaf loss per ha forest ($\text{kg ha}^{-1}\text{-forest}$)†	84.8	5.5	0	14.9	90.3
Nitrogen per ha forest ($\text{kg N ha}^{-1}\text{-forest}$)	1.4	0.09	0	0.3	1.5
Nitrogen per ha gap or deck ($\text{kg N ha}^{-1}\text{-gap or deck}$)	27.2	41.8	–	–	–
<i>(2) Allometric tree mortality basis</i>					
Stems killed per ha forest ($\text{stems ha}^{-1}\text{-forest}$)	27.6	1.1	12	4.3	45
Leaf loss per ha forest ($\text{kg ha}^{-1}\text{-forest}$)†	79.1	1.1	5.0	4.2	89.4
Nitrogen per ha forest ($\text{kg N ha}^{-1}\text{-forest}$)	1.3	0.02	0.08	0.07	1.5
Nitrogen per ha gap or deck ($\text{kg N ha}^{-1}\text{-gap or deck}$)	25.4	9.8	–	–	–

*Canopy gap defined as the actual projected canopy as outlined by the remaining canopies (Runkle, 1982).

†From mean specific leaf area estimates.

LAI, leaf area index.

Table 2 Nitrogen stocks in trees and palms (>10 cm DBH) in primary forest and mean nitrogen returned to the soil surface as necromass by logging activities and exported from the site in boles in the same forest logged at a rate of 2.6 trees ha⁻¹ in Fazenda Rohsamar, southern Amazonia, MT Brazil

	Nitrogen (kg ha ⁻¹)				Percent of total		
	Foliage*	Crown†	Bole‡	Total	Foliage	Wood	Total
Undisturbed primary forest‡	77.4	579.8	706.2	1363.4			
Logged forest – necromass							
Gap – trees killed by harvesting operations	0.34	18.5	23.0	41.9	22.8	51.6	51.1
Gap-residual crown of logged tree	0.99	23.8		24.8	65.8	29.6	30.3
Log decks	0.02	0.8	1.0	1.9	1.2	2.3	2.3
Skid trails	0.08	2.5	3.1	5.7	5.6	7.0	7.0
Roads	0.07	3.4	4.2	7.6	4.7	9.4	9.3
Total necromass	1.51	49.0	31.4	81.9	100	100	100
Logged forest – export in boles§			31.8				

*Based on an allometric equation to estimate leaf area (Chambers *et al.*, 2004) and mean DBH and number of trees crushed or severed by logging activities (Feldpausch *et al.*, 2005).

†Based on an allometric equation to estimate crown and bole mass (Chambers *et al.*, 2001). Wood crown mass calculated as total crown mass minus foliar mass.

‡Primary forest biomass estimated by Feldpausch *et al.* (2005).

§Bole of the logged tree exported from the forest; nitrogen stocks based on the mean DBH of logged trees. DBH, diameter at breast height.

than additions from leaves (Table 2). The greatest N addition from wood flux occurred in logging gaps as slash and trees killed by tree-fall, over 80% of the total N inputs in wood flux, since skid trails, roads, and log decks were relatively infrequent on a per hectare basis. Total N additions in aboveground necromass from all logging activities (81.9 kg N ha⁻¹) and N export in boles (31.8 kg N ha⁻¹) represented 6% and 2%, respectively, of the total prelogging aboveground N in trees and palms \geq 10 cm DBH for the entire 1400 ha block.

Surface and subsoil nitrate following selective logging

Compared to intact forest, nitrate concentrations in logging gaps were only significantly higher in the 60–100 cm depth of the 8 m deep profile (Fig. 2). Of the nine nitrate soil profiles for logging gaps, there was one profile with high nitrate concentrations at 60–100 cm depth, with nitrate concentrations five to eight times greater than the mean for those depths. To test the effect of this high profile on the statistical analysis, analyses were performed with and without the high nitrate profile. Because removal of the high profile still resulted in a statistical difference at 60–100 cm depth between intact forest and logging gaps ($P < 0.10$), further analyses were conducted with the profile included. Variability in the nitrate concentrations (expressed by the standard deviation) was greater in the upper 1 m, four times greater than >1–8 m depth. Total nitrate storage to 8 m depth varied from 148 to 1649 kg for each sample

location, with mean nitrate storage not significantly different between logging gaps (742.3 \pm 126.7) and undisturbed forest (635.6 \pm 152.5 kg ha⁻¹) (Fig. 3).

N stocks in a logging chronosequence

To determine the long-term effects of selective logging on surface N stocks, we examined a 12-year time-after-logging chronosequence in the same forest. Based on the chronosequence, there was no increase 2 years after logging in soil total N concentrations and storage to 10 cm depth (1300–1500 kg N ha⁻¹) (Fig. 4). Soil N stocks at 10–20 cm depth were also unaffected by logging. After 6–12 years following logging, total soil N to 0.2 m depth did not differ from undisturbed forest values.

Soil physical properties and soil water depletion

Soil texture to 8 m depth averaged 31–46% sand, 15–31% silt, and 31–43% clay (Table 3). Clay and sand content were frequently greater near the surface. Mean gravimetric soil water at the time of nitrate sampling ranged from 22% at the surface to 40% at 8 m. There was no relationship between soil texture and nitrate storage to 8 m. Mean annual volumetric θ in the surface 70 cm in logging gaps and undisturbed primary forest ranged from 15% to 45% from the dry to the wet season. The soils in logging gaps and intact forest were fully recharged to field capacity in April and March, 265 and 297 mm storage to 70 cm depth, respectively, and

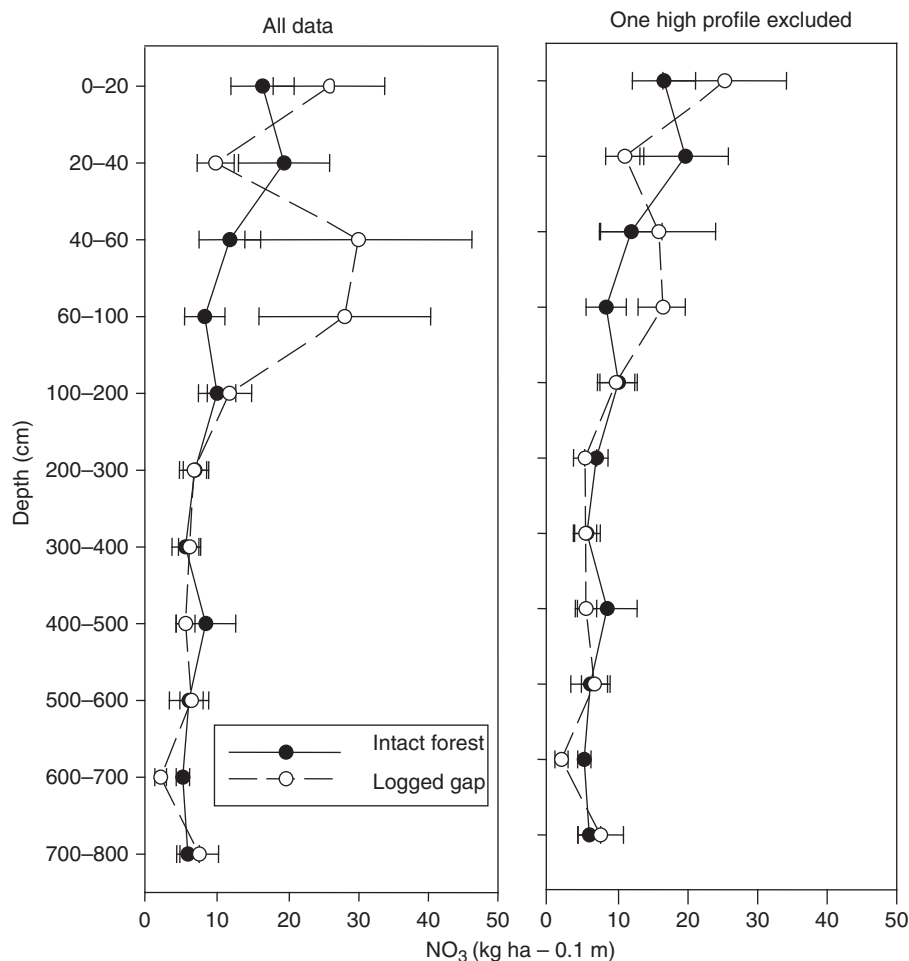


Fig. 2 Mean nitrate ($\text{kg ha}^{-1}\text{-0.1 m}$) to 8 m depth in intact forest ($n = 3\text{-}3\text{ m}$ and $n = 9\text{-}8\text{ m}$) and logged gaps ($n = 9\text{-}8\text{ m}$) for all data and with one high profile removed 1 year following logging in Fazenda Rohsamar, southern Amazonia, MT Brazil. Bars indicate standard error. Significant nitrate differences were present only at 60–100 cm depth, with and without the high profile ($P < 0.10$).

depleted by about 150 mm water in July, August, and September during the dry season (Fig. 5). There was no difference in mean annual soil water depletion to 70 cm depth between logging gaps and intact forest.

Discussion

Logging and gap formation

The observed total ground disturbance (16%) from all logging activities following logging was within the range for other RIL operations at comparable or higher harvest rates and below the range for conventional logging (Feldpausch *et al.*, 2005). These findings place interpretation of our N results within the context of typical RIL logging operations in the Amazon Basin, where ground disturbance from logging reportedly ranges from 10% to 23% for RIL, as compared with

20–55% ground disturbance for conventional logging (Jonkers, 1987; Hendrison, 1990; Johns *et al.*, 1996; Kammesheidt *et al.*, 2001; Pereira *et al.*, 2002; Asner *et al.*, 2004). The logging rate of 2.6 trees ha^{-1} in this study is intermediate of other RIL logging operations in Amazonia (1.1–4.5 trees ha^{-1}) (Johns *et al.*, 1996; Pereira *et al.*, 2002; Asner *et al.*, 2004; Feldpausch *et al.*, 2005). The mean logging gap area (202 m^2) in our study is comparable to natural gap openings, to the lower end of most experimental artificial gap formation studies, and to single-tree gaps formed by logging (Johns *et al.*, 1996; Brouwer, 2001). Based on these results, we expect nutrient and water dynamics and plant colonization to follow similar dynamics as natural gaps in primary forests, with the exception of skidder disturbance of the soil and removal of the timber bole.

The relatively small felling gap size in the logged forest of our study probably played a large role in

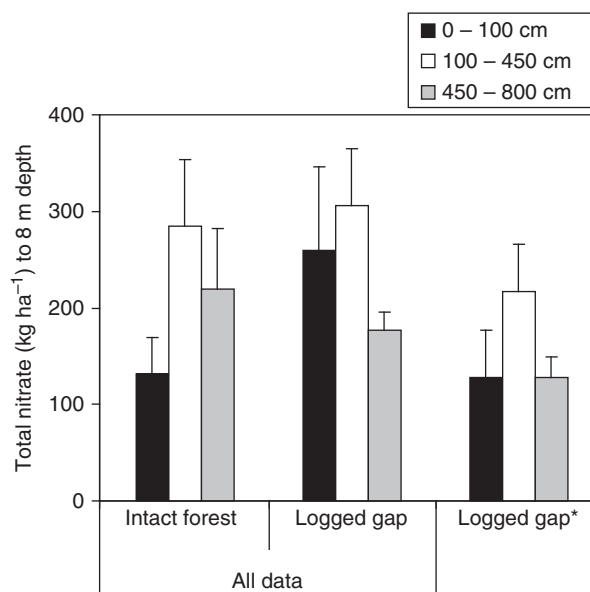


Fig. 3 Mean total nitrate (kg ha^{-1}) to 8 m depth in intact forest ($n = 3-3$ m and $n = 9-8$ m) and logged gaps ($n = 9-8$ m) for all data and with one high profile removed in Fazenda Rohsamar, southern Amazonia, MT Brazil. *One 8 m deep profile with high values excluded. Bars indicate standard error.

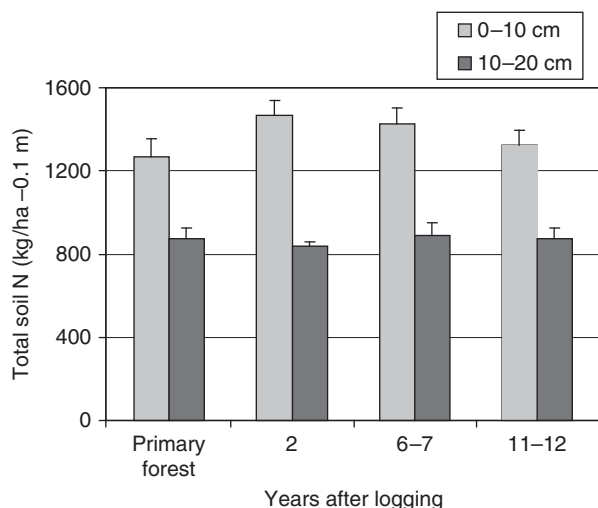


Fig. 4 Mean total soil nitrogen storage to 10 and 20 cm depth (kg ha^{-1} –0.1 m) in primary forest ($n = 20$) and three selectively logged blocks 2–12 years after logging ($n = 20$ per year category) in Fazenda Rohsamar, southern Amazonia, MT Brazil. Bars indicate standard error.

producing similar soil nitrate storage and surface soil water depletion between gaps and intact forest. We found no difference in soil water depletion between logging gaps and intact forest over the second year following logging, despite the leaf area reduction fol-

lowing canopy damage by falling trees, the death of a dominant or emergent tree by logging and subsequent reduction in soil water uptake in the gap as a potential root gap was formed. These findings suggest that near-surface nitrate uptake may have been similar between 1-year-old felling gaps and intact forest since gap edge trees may have recovered the water uptake potential lost by the harvested stem for water depletion to 70 cm depth.

N additions to the soil surface

The largest logging-related N additions to the soil surface on a stand basis were associated with logging gaps. We estimated each tree logged would add 25.7 kg N to the forest floor as leaves, branch and the logged crown, this being comprised of 16.1 kg N from tree mortality caused by falling logged trees and within-gap skidder movement and 9.5 kg N from the residual crown of the tree logged (values scaled to hectare-basis from Table 2). Our estimate of soil N additions from canopies using LAI reduction gap opening- and allometric-based methods to estimate leaf area was 79–85 kg leaf ha^{-1} forest, with leaf loss estimated from the LAI reduction-based method slightly higher than the allometric method (Table 1). Estimates of leaf loss based on the LAI reduction method were probably greater because this method included liana leaf loss and partially damaged canopies for trees not killed at the edges of the gap. The allometric method, where leaf loss was based on diameter, included only trees crushed prone or having their stem severed from tree-fall and not trees receiving partial crown damage. Leaf loss based on the LAI reduction and allometric basis differed by only around 6 kg ha^{-1} , indicating the two methods provide an accurate estimate of N flush following damage. Measuring the DBH of individual stems killed by logging activities under the allometric method is labor intensive, while LAI and contiguous canopy measurements are rapid. Estimates based on the LAI reduction Method 1 are therefore less time intensive and more comprehensive of N turnover.

A study in eastern Amazonia estimated N addition only from leaves of the crown of the tree logged (Olander *et al.*, 2005). In that study, each crown left in gaps following logging added 0.13 kg N as leaves per gap. We showed that over 50% of the total N inputs from all damage came from trees killed in logging gaps. Our estimate of N addition from leaves in gaps, which included both leaves of the crown of the logged tree in addition to N additions as leaves from surrounding trees damaged by tree-fall, was 0.51 kg N per gap, 3.9 times greater when including N flush from damaged trees (Table 2). The N addition in logging gaps of our

Table 3 Soil chemical and physical properties (mean \pm SE) to 8 m depth in intact primary forest in Fazenda Rohsamar, southern Amazonia, MT, Brazil*

Depth (cm)	C (g kg ⁻¹)	P (mg kg ⁻¹)	K (mg kg ⁻¹)	pH _w	CEC (cmol _(c) kg ⁻¹)	Bulk Density (g cm ⁻³)	Sand (%)	Silt (%)	Clay (%)
0–20	9.72 \pm 1.00	0.38 \pm 0.11	31.69 \pm 8.12	4.58 \pm 0.09	2.10 \pm 0.88	1.20 \pm 0.09	40.3 \pm 34.8	18.2 \pm 10.9	41.6 \pm 31.8
20–40	6.66 \pm 0.60	0.21 \pm 0.06	27.23 \pm 7.43	4.64 \pm 0.06	1.15 \pm 0.11	1.24 \pm 0.07	42.8 \pm 30.1	14.7 \pm 9.4	42.6 \pm 27.3
40–60	5.49 \pm 0.75	0.12 \pm 0.05	22.46 \pm 6.76	4.75 \pm 0.09	1.23 \pm 0.13	1.20 \pm 0.07	44.3 \pm 23.7	14.7 \pm 6.5	41.1 \pm 21.4
60–100	4.02 \pm 0.70	0.08 \pm 0.06	17.85 \pm 5.66	4.97 \pm 0.06	1.20 \pm 0.15	1.18 \pm 0.06	42.3 \pm 19.8	14.8 \pm 4.4	42.8 \pm 18.9
100–200	2.06 \pm 0.28	0.37 \pm 0.22	13.85 \pm 3.27	5.25 \pm 0.10	1.32 \pm 0.14	1.18 \pm 0.05	45.8 \pm 19.1	18.6 \pm 6.8	35.5 \pm 16.1
200–300	0.99 \pm 0.16	1.07 \pm 0.42	17.85 \pm 4.68	5.46 \pm 0.12	1.36 \pm 0.20	1.16 \pm 0.07	40.1 \pm 21.7	29.1 \pm 16.3	30.8 \pm 14.5
300–400	0.67 \pm 0.16	0.36 \pm 0.19	20.17 \pm 5.23	5.49 \pm 0.11	1.58 \pm 0.19	1.10 \pm 0.04	43.4 \pm 24.1	18.8 \pm 9.5	38.1 \pm 15.0
400–500	0.39 \pm 0.04	0.03 \pm 0.02	9.50 \pm 2.95	5.32 \pm 0.09	1.77 \pm 0.24	1.09 \pm 0.05	40.9 \pm 23.6	24 \pm 10.3	35.1 \pm 13.3
500–600	0.44 \pm 0.05	0.10 \pm 0.04	10.63 \pm 2.63	5.31 \pm 0.09	1.74 \pm 0.21	1.11 \pm 0.06	40.6 \pm 21.4	25.6 \pm 6.6	33.8 \pm 14.8
600–700	0.43 \pm 0.03	0.15 \pm 0.05	13.75 \pm 3.57	5.28 \pm 0.08	1.72 \pm 0.24	1.12 \pm 0.08	30.8 \pm 20.0	31.4 \pm 6.9	37.8 \pm 14.1
700–800	0.57 \pm 0.10	0.13 \pm 0.04	17.25 \pm 4.47	5.22 \pm 0.09	2.48 \pm 0.66	1.12 \pm 0.08	34.2 \pm 20.5	27.7 \pm 3.0	38.0 \pm 19.4

*Extractable P, K, Ca and Mg. Soil pH is in deionized water (pH_w) in a 1 : 2.5 weight-to-volume ratio. CEC is cation exchange capacity by the sum of cations at pH 7.

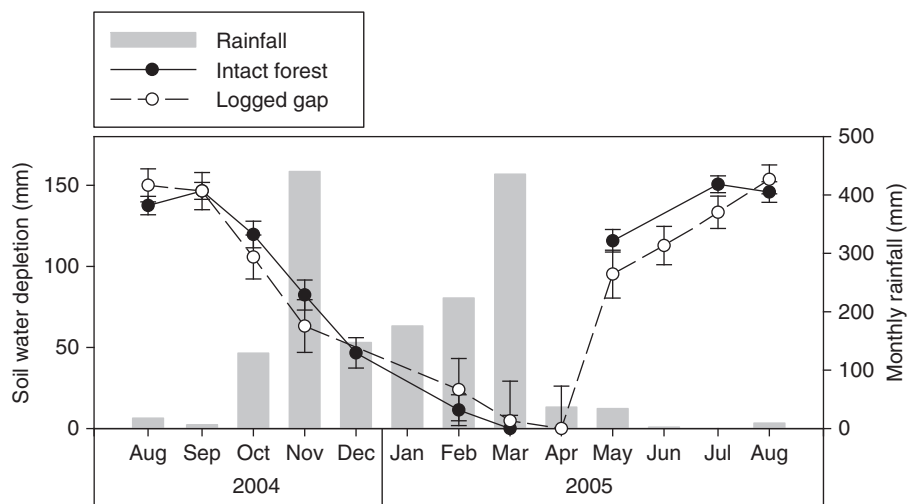


Fig. 5 Mean soil water depletion (mm) (depletion of soil water from maximum soil recharge during the wet season) to 70 cm depth in intact forest ($n = 9$) and logged gaps ($n = 9$) 1 year after logging in Fazenda Rohsamar in southern Amazonia, Brazil. Precipitation measured on site.

study increased to 16.3 kg N gap⁻¹ when also including wood additions from crowns and tree-fall. N inputs from road and log deck construction and skid trails together on a per hectare basis represented about 19% of the total N addition to the soil in leaves and wood, further increasing total N turnover compared with measuring N leaf flush in gaps alone.

Soil nitrate under gaps and undisturbed forest

Our results show there is substantial nitrate storage to 8 m depth in undisturbed primary forest and that nitrate concentrations vary considerably by depth. The small N additional from logging damage, relative to the large pre-existing below ground storage, only affected

the top 1 m. Few studies in lowland tropical rain forest have measured nitrate following logging, and none, to our knowledge, to great depth. Shallower sampling (≤ 15 cm) in gaps indicated that nitrate concentrations fluctuate seasonally, although results comparing gaps with undisturbed forest are inconsistent. For example, in a study in Costa Rica Denslow *et al.* (1998) found higher nitrate concentrations for soils under gaps, while in the same forest Vitousek & Denslow (1986) found no differences in nitrate concentrations between gaps and undisturbed forest. A study in Guyana to 120 cm depth showed that nitrate levels peaked 0.5–1.5 years after gap formation (Brouwer, 2001), indicating that our nitrate sampling period was within the range of peak nitrate levels. Disturbance intensity, in addition to time, plays a

role in soil N stocks following logging, as soil N decreased in surface soils (<10 cm depth) with increasing disturbance intensity (McNabb *et al.*, 1997). No increase was found in nitrate in soil leachate water to 120 cm depth in small gaps (e.g. <200 m²); increased nitrate percolation was found only in gaps >400 m² (Brouwer, 2001). Furthermore, commercial timber tree species are clumped rather than dispersed (Feldpausch *et al.*, 2006), so that selective harvesting would result in locally spatially aggregated N fluxes resulting from forest disturbance and bole export from patches of merchantable trees.

Nitrate losses through leaching are generally considered small in primary tropical forests, where nitrate may be retained in these infertile soils through a number of mechanisms. Trees in the seasonally dry regions of the Amazon Basin are known to extend roots to well beyond 8 m depth (Nepstad *et al.*, 1994), although their roots do not draw all nutrients equally from all depths (Poszwa *et al.*, 2002). Anion exchange capacity of soils, formed by the protonation of hydroxyl groups on the edges of silicate clays and surfaces of metal oxide clays, may play a role in reducing nitrate leaching into the subsoils (Cahn *et al.*, 1992; Melgar *et al.*, 1992; Lehmann *et al.*, 2004). Measuring nitrate to 2 m depth under primary forest in central Amazonia, Schroth *et al.* (1999) reported higher nitrate at 150–200 cm depth than at 30–100 cm depth indicating some nitrate retention at depth. Soil macrofauna could be a source of subsurface soil nitrate, since in secondary forests in eastern Amazonia leaf-cutting ants were shown to increase soil nitrate at depths of up to 3 m (Verchot *et al.*, 2003).

Amazon basin-wide N turnover

Annual selective logging rates from 1999 to 2002 ranged from 12 075 to 19 823 km² for the Amazonian states of Pará, Mato Grosso, Rondônia, Roraima, and Acre, where ~90% of logging occurs in Amazonia (Asner *et al.*, 2005). Based on our conservative estimate of 2.6 trees selectively logged per hectare (published rates range from 1.1 to 4.5), conservative N turnover estimates (based on Method 2, allometry) caused by tree damage from logging activities (81.9 kg ha⁻¹) and the range of annual selective logging rates, Amazon Basin-wide estimates of N turnover following selective logging are 0.10 ± 0.07 to 0.16 ± 0.11 Tg N (± SD; error propagated from wood flux, leaf turnover, and N estimates) for 1999 to 2002 rates. This value increases to 0.14 ± 0.07 to 0.23 ± 0.12 Tg N yr⁻¹, respectively, when including boles exported from the site as timber. These values should be considered a first attempt to estimate basin-wide turnover and may vary greatly for the following reason: the estimates are based on lower than

average logging rates in our study (see Feldpausch *et al.*, 2005 for CL vs. RIL rates); selective logging rates vary considerable and there is expected high uncertainty for the Asner *et al.* (2005) estimates based on remotely sensed data; regional-scale N turnover is likely much higher since conventional logging, with higher logging rates and greater forest disturbance, is practiced over a much larger area than RIL in Amazonia.

Our results do not indicate soil impoverishment through N leaching; however, losses from mineralization and denitrification of selective logging-generated necromass could result in depletion of N reserves and reduce logging sustainability. N pathways following mineralization will vary considerably and depend on site-to-site factors such as rainfall and the speed that roots recolonize disturbed areas. Broad estimates of excess N₂O loss (7.9 kg N₂O ha⁻¹ yr⁻¹) following selective logging on similar soils to this study were approximately 30% of background emission levels (Keller *et al.*, 2005). Considering that precipitation and temperature patterns may be shifting across Amazonia (Malhi *et al.*, 2008), these pathways are likely to change.

We present some of the first comprehensive above-ground N turnover estimates and deep nitrate measurements following disturbance under logging. These data help to assess the effects of logging over large areas of the Amazon Basin and determine the sustainability of RIL on the nutrient-limited soils and seasonally high rainfall areas. These results are important, since there is no consensus as to the sustainability of selective logging (Pinard & Putz, 1996; Fredericksen *et al.*, 2003; Keller *et al.*, 2004b). Our 8 m deep N profiles for gaps resulting from logging support the findings for surface soils from other studies (Brouwer, 2001; Olander *et al.*, 2005), that although logging modifies aboveground N pools, N addition to the soil from leaves and wood by logging damage is small relative to the total soil N pool and large nitrate pool found in undisturbed primary forest. Despite the small N addition from vegetation in gaps, we found increased nitrate concentrations at 60–100 cm depth in logging gaps relative to intact forest. However, 1 year after logging there was no significant difference in subsoil (>100 cm) nitrate pools between logging gaps and intact forest. The similarity between nitrate concentrations and total nitrate storage for the 8 m profile between gaps and intact forest suggest that N losses from logging through leaching will be small in comparison with other possible permanent export pathways, such as denitrification and removal of harvested boles.

Acknowledgements

We thank Rohden Indústria Lígnea Ltda. for providing access to the forest, C. A. M. Passos, S. Jirka, B. S. de Andrade, and E. A. de

Souza and I. O. V. L. Costa for assistance with field measurements and logistical support, O. L. dos Santos Weber, E. Selva, L. A. Chig and J. P. N. Filho for assistance with nitrate and texture analysis, and E. C. M. Fernandes for development of the research program. F. E. Putz and an anonymous reviewer provided valuable input on the manuscript. The Brazilian Ministry of Science and Technology (MCT) provided leadership of the Large-Scale Biosphere Atmosphere Experiment in Amazonia (LBA). This research was sponsored by the NASA LBA-Eco program (ND-11).

References

- Asner GP, Keller M, Pereira R, Zweede JC, Silva JNM (2004) Canopy damage and recovery after selective logging in Amazonia: field and satellite studies. *Ecological Applications*, **14**, 5280–5298.
- Asner GP, Knapp DE, Broadbent EN, Oliveira PJC, Keller M, Silva JN (2005) Selective logging in the Brazilian Amazon. *Science*, **310**, 480–482.
- Brouwer L (2001) Leaching in logging gaps: effect of gap size and gap age on nutrient loss. In: *Forest Filled with Gaps: Effects of Gap Size on Water and Nutrient Cycling in Tropical Rain Forest: a Study in Guyana* (ed. Van Dam O), pp. 161–177. PrintPartners Ipskamp B.V., Amsterdam.
- Brown S (1997) *Estimating biomass and biomass change of tropical forests: a primer*. FAO Forestry Paper, 134 pp.
- Buschbacher R, Uhl C, Serrão EAS (1988) Abandoned pastures in eastern Amazonia. II. Nutrient stocks in the soil and vegetation. *Journal of Ecology*, **76**, 682–699.
- Cahn MD, Bouldin DR, Cravo MS (1992) Nitrate sorption in the profile of an acid soil. *Plant and Soil*, **143**, 179–183.
- Chambers JQ, Dos Santos J, Ribeiro RJ, Higuchi N (2001) Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest. *Forest Ecology and Management*, **152**, 73–84.
- Chambers JQ, Higuchi N, Schimel JP, Ferreira LV, Melack JM (2000) Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. *Oecologia*, **122**, 380–388.
- Chambers JQ, Tribuzy ES, Toledo LC *et al.* (2004) Respiration from a tropical forest ecosystem: partitioning of sources and low carbon use efficiency. *Ecological Applications*, **14**, 572–588.
- Davidson EA, Artaxo P (2004) Globally significant changes in biological processes of the Amazon Basin: results of the large-scale biosphere-atmosphere experiment. *Global Change Biology*, **10**, 519–529.
- Denslow JS, Ellison AM, Sanford RE (1998) Treefall gap size effects on above and below ground processes in a tropical wet forest. *Journal of Ecology*, **86**, 597–609.
- FAO-UNESCO (1987) *Soils of the World New York, USA*. Elsevier Science Publishing Co. Inc., NY, USA.
- Feldpausch TR, Jirka S, Passos CAM, Jasper F, Riha SJ (2005) When big trees fall: damage and carbon export by reduced impact logging in southern Amazonia. *Forest Ecology and Management*, **219**, 199–215.
- Feldpausch TR, McDonald AJ, Passos CAM, Lehmann J, Riha SJ (2006) Biomass, harvestable area, and forest structure estimated from commercial timber inventories and remotely sensed imagery in southern Amazonia. *Forest Ecology and Management*, **233**, 121–132.
- Fernandes ECM, Biot Y, Castilla C *et al.* (1997) The impact of selective logging and forest conversion for subsistence agriculture and pastures on terrestrial nutrient dynamics in the Amazon. *Ciencia e Cultura Journal of the Brazilian Association for the Advancement of Science*, **49**, 34–47.
- Frazer GW, Canham CD, Lertzman KP (1999) *Gap Light Analyzer (GLA): Imaging Software to Extract Canopy Structure and Gap Light Transmission Indices from True-Colour Fisheye Photographs, Users Manual and Program Documentation (Version 2.0)*. Simon Fraser University and Institute of Ecosystem Studies, Burnaby, British Columbia and Millbrook, NY.
- Fredericksen TS, Putz FE, Pattie P, Pariona W, Pena-Claros M (2003) Sustainable forestry in Bolivia: beyond planned logging. *Journal of Forestry*, **101**, 37–40.
- Gerwing JJ (2002) Degradation of forests through logging and fire in the eastern Brazilian Amazon. *Forest Ecology and Management*, **157**, 131–141.
- Henderson J (1990) *Damage-Controlled Logging in Managed Rain Forest in Suriname*. Agricultural University of Wageningen, Wageningen, Netherlands.
- Hodnett MGJ, Filho ADOM, Oyama MD (1996) Deep soil water uptake by forest and pasture in central Amazonia: predictions from long-term daily rainfall data using a simple water balance model. In: *Amazonian Deforestation and Climate* (eds Gash JHC, Nobre CA, Roberts JM, Victoria RL), pp. 57–77. John Wiley and Sons, New York.
- Ivo WM, Ferreira S, Biot Y, Ross S (1996) Nutrients in soil solution following selective logging of a humid tropical 'terra firme' forest north of Manaus, Brazil. *Environmental Geochemistry and Health*, **18**, 69–75.
- Johns JS, Barreto P, Uhl C (1996) Logging damage during planned and unplanned logging operations in the eastern Amazon. *Forest Ecology and Management*, **89**, 59–77.
- Jonkers WBJ (1987) *Vegetation Structure, Logging Damage and Silviculture in a Tropical Rain Forest in Suriname*. Agricultural University, Wageningen, the Netherlands.
- Kammesheidt L, Kohler P, Huth A (2001) Sustainable timber harvesting in Venezuela: a modelling approach. *Journal of Applied Ecology*, **38**, 756–770.
- Keller M, Alencar A, Asner GP *et al.* (2004a) Ecological research in the large scale biosphere atmosphere experiment in Amazônia (LBA): early results. *Ecological Applications*, **14**, S3–S16.
- Keller M, Asner GP, Silva N, Palace M (2004b) Sustainability of selective logging of upland forests in the Brazilian Amazon: carbon budgets and remote sensing as tools for evaluation of logging effects. In: *Working Forests in the Neotropics: Conservation Through Sustainable Management?* (ed. Zarin D), pp. 41–63. Columbia University Press.
- Keller M, Palace M, Asner GP, Pereira R, Silva JNM (2004c) Coarse woody debris in undisturbed and logged forests in the eastern Brazilian Amazon. *Global Change Biology*, **10**, 784–795.
- Keller M, Varner R, Dias JD, Silva H, Crill P, Oliveira RCD Jr., Asner GP (2005) Soil-atmosphere exchange of nitrous oxide, nitric oxide, methane, and carbon dioxide in logged and undisturbed forest in the Tapajós National Forest, Brazil. *Earth Interactions*, **9**, 1–28. Available at <http://earthinteractions.org/>.
- Lehmann J, Lillienfein J, Rebel K, Lima SD, Wilcke W (2004) Subsoil retention of organic and inorganic nitrogen in a Brazilian savanna Oxisol. *Soil Use and Management*, **20**, 163–172.
- Malhi Y, Roberts JT, Betts RA, Killeen TJ, Li WH, Nobre CA (2008) Climate change, deforestation, and the fate of the Amazon. *Science*, **319**, 169–172.
- Markewitz D, Davidson E, Moutinho P, Nepstad D (2004) Nutrient loss and redistribution after forest clearing on a highly weathered soil in Amazonia. *Ecological Applications*, **14**, S177–S199.
- Martinelli LA, Almeida S, Brown IF *et al.* (2000) Variation in nutrient distribution and potential nutrient losses by selective logging in a humid tropical forest of Rondonia, Brazil. *Biotropica*, **32**, 597–613.
- McNabb KL, Miller MS, Lockaby BG, Stokes BJ, Clawson RG, Stanturf JA, Silva JNM (1997) Selection harvests in Amazonian rainforests: long-term impacts on soil properties. *Forest Ecology and Management*, **93**, 153–160.
- Melgar RJ, Smyth TJ, Sanchez PA, Cravo MS (1992) Fertilizer nitrogen movement in a central Amazon oxisol and entisol cropped to corn. *Fertilizer Research*, **31**, 241–252.
- Minitab (2000) *Minitab Version 13.1 User Guide*. Minitab Inc. Available at <http://www.minitab.com>.

- Nepstad DC, Carvalho CRD, Davidson EA *et al.* (1994) The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature*, **372**, 666–669.
- Nepstad DC, Verissimo A, Alencar A *et al.* (1999) Large-scale impoverishment of Amazonian forests by logging and fire. *Nature*, **398**, 505–508.
- Norman JM, Campbell GS (1989) Canopy structure. In: *Plant Physiological Ecology: Field Methods and Instrumentation* (eds Pearcy JE, Mooney HA, Rundel PW), pp. 301–325. Chapman & Hall, London.
- Olander LP, Bustamante MM, Asner GP, Telles E, Prado Z, Camargo PB (2005) Surface soil changes following selective logging in an eastern Amazon forest. *Earth Interactions*, **9**, 1–19.
- Pereira R, Zweede J, Asner GP, Keller M (2002) Forest canopy damage and recovery in reduced-impact and conventional selective logging in eastern Para, Brazil. *Forest Ecology and Management*, **168**, 77–89.
- Pinard MA, Putz FE (1996) Retaining forest biomass by reducing logging damage. *Biotropica*, **28**, 278–295.
- Poszwa A, Dambrine E, Ferry B, Pollier B, Loubet M (2002) Do deep tree roots provide nutrients to the tropical rainforest? *Biogeochemistry*, **60**, 97–118.
- Reich PB, Ellsworth DS, Uhl C (1995) Leaf carbon and nutrient assimilation and conservation in species of differing successional status in an oligotrophic Amazonian forest. *Functional Ecology*, **9**, 65–76.
- Rice AH, Pyle EH, Saleska SR (2004) Carbon balance and vegetation dynamics in an old-growth Amazonian forest. *Ecological Applications*, **14**, S55–S71.
- Roberts DA, Keller M, Soares JV (2003) Studies of land-cover, land-use, and biophysical properties of vegetation in the large scale biosphere atmosphere experiment in Amazônia. *Remote Sensing of Environment*, **87**, 377–388.
- Runkle JR (1982) Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology*, **63**, 1533–1546.
- Runkle JR (1992) *Guidelines and sample protocol for sampling forest gaps*. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-283.
- Schroth G, Silva LFD, Seixas R, Teixeira WG, Macêdo JLV, Zech W (1999) Subsoil accumulation of mineral nitrogen under polyculture and monoculture plantations, fallow and primary forest in a ferrallitic Amazonian upland soil. *Agriculture, Ecosystems and Environment*, **75**, 109–120.
- Silva FCD (1999) *Manual de análises químicas de solos, plantas e fertilizantes*. Embrapa Comunicação para Transferência de Tecnologia, Brasília, DF.
- Sluiter R, Smit N (2001) Gap size effects on microclimate and soil moisture. In: *Forest Filled with Gaps: Effects of Gap Size on Water and Nutrient Cycling in Tropical Rain Forest: a Study in Guyana* (ed. Van Dam O), pp. 49–66. PrintPartners Ipskamp B.V., Amsterdam.
- Soil Survey Staff (1999) *Soil Taxonomy: a Basic System of Soil Classification for Making and Interpreting Soil Surveys*. US Department of Agriculture Soil Conservation Service, Washington, DC.
- Thompson J, Proctor J, Viana V, Milliken W, Ratter JA, Scott DA (1992) Ecological studies on a lowland evergreen rain forest on Maraca Island, Roraima, Brazil. I. physical environment, forest structure and leaf chemistry. *The Journal of Ecology*, **80**, 689–703.
- Trime (2000) *TRIME Service Manual: TRIME Moisture Measuring System for Soil Science*. MESA Systems Co, Medfield, MA, USA.
- Verchot LV, Moutinho PR, Davidson EA (2003) Leaf-cutting ant (*Atta Sexdens*) and nutrient cycling: deep soil inorganic nitrogen stocks, mineralization, and nitrification in Eastern Amazonia. *Soil Biology and Biochemistry*, **35**, 1219–1222.
- Vitousek PM, Denslow JS (1986) Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rain-forest. *Journal of Ecology*, **74**, 1167–1178.
- Webb EL (1997) Canopy removal and residual stand damage during controlled selective logging in lowland swamp forest of northeast Costa Rica. *Forest Ecology and Management*, **95**, 117–129.