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Fire in the Brazilian Amazon:
1. Biomass, nutrient pools, and losses in slashed primary forests

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Abstract Deforestation in the Brazilian Amazon has resulted in the conversion of > 230,000 km^2 of tropical forest, yet little is known on the quantities of biomass consumed or the losses of nutrients from the ecosystem. We quantified the above-ground biomass, nutrient pools and the effects of biomass burning in four slashed primary tropical moist forests in the Brazilian Amazon. Total above-ground biomass (TAGB) ranged from 292 Mg ha^{-1} to 436 Mg ha^{-1}. Coarse wood debris (> 20.5 cm diameter) was the dominant fuel component. However, structure of the four sites were variable. Coarse wood debris comprised from 44% to 69% of the TAGB, while the forest floor (litter and rootmat) comprised from 3.7 to 8.0% of the TAGB. Total biomass consumption ranged from 42% to 57%. Fires resulted in the consumption of > 99% of the litter and rootmat, yet < 50% of the coarse wood debris. Dramatic losses in C, N, and S were quantified. Lesser quantities of P, K, and Ca were lost by combustion processes. Carbon losses from the ecosystem were 58–112 Mg ha^{-1}. Nitrogen losses ranged from 817 to 1605 kg ha^{-1} and S losses ranged from 92 to 122 kg ha^{-1}. This represents losses that are as high as 56%, 68%, and 49% of the total above-ground pools of these nutrients, respectively. Losses of P were as high as 20 kg ha^{-1} or 32% of the above-ground pool. Losses to the atmosphere arising from primary slash fires were variable among sites due to site differences in concentration, fuel biomass, and fuel structure, climatic fluctuations, and anthropogenic influences. Compared to fires in other forest ecosystems, fires in slashed primary tropical evergreen forests result in among the highest total losses of nutrients ever measured. In addition, the proportion of the total nutrient pool lost from slash fires is higher in this ecosystem compared to other ecosystems due to a higher percentage of nutrients stored in above-ground biomass.

Key words Tropical forests · Biomass burning · Carbon cycling · Nutrient cycling · Slash-and-burn

Introduction

Deforestation and biomass burning of tropical forests continues to be among the most devastating of anthropogenic activities with respect to the diminution of biological diversity, site productivity, and influences on global biogeochemical cycles. Estimates of deforestation in the Legal Amazon range from 230,000 (through 1988) to 415,000 km^2 (through 1990) (Fearnside 1992; Skole and Tucker 1993). Direct measurements of the biomass of Amazon forests range from 143 to 666 Mg ha^{-1} (Fearnside et al. 1993). Average total above-ground biomass (TAGB) in Amazonian tall evergreen tropical forests have been variously estimated to range from 227 to 394 Mg ha^{-1} (Brown and Lugo 1992; Fearnside 1992).

While estimates of the extent of deforestation and TAGB have improved, little quantitative information exists on biomass of slashed forests, quantities of biomass consumed by slash fires, mass of nutrient pools subjected to fire or the losses of nutrients during fire. Few estimates of biomass loss by combustion processes have been derived from quantitative sources. Estimates of biomass consumption by fires in primary slashed forests ranged from 28% to 40% (Detwiler and Hall 1988; Crutzen and Andreae 1990; Houghton 1991). Even less data are available on nutrient concentration, mass and losses from TAGB pools during combustion processes. These pools are known to be significant

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nutrient sinks in maintaining the nutrient balance of tropical forests (Jordan and Uhl 1978; Jordan 1982; Medina and Cuevas 1989). Because many soils of the Amazon Basin are highly weathered, the nutrient balance and hence site productivity is largely maintained through atmospheric deposition and efficient cycling of nutrients within tropical forests (Jordan 1982; Vitousek and Sanford 1986; Bruijnzeel 1991). As a result, significant and abrupt losses of nutrients from the ecosystem associated with anthropogenic disturbances can severely limit ecosystem recovery, site productivity and hence limit the potential of the site to sequester C in the future.

To address these issues, we sampled the influences of fire in four slashed primary forests of the Brazilian Amazon. Our objectives were to: (1) quantify the range in total above-ground biomass prior to, and after, slash fires, (2) quantify the range in concentration, distribution, and mass of nutrient pools of the above-ground biomass, (3) quantify the distribution and mass of residual pools, and (4) quantify the range in nutrient losses that occurred during combustion processes.

Materials and methods

Study area

The study areas were located in the Brazilian States of Para and Rondonia. These regions of the Brazilian Amazon have been, and are currently undergoing, rapid rates of deforestation (Skole and Tucker 1993). Principal causations of deforestation include pasture conversion, shifting cultivation, and timber exploitation.

The intact primary forests of the area are classified as Floresta tropical perenifolia de terra firme (upland tropical evergreen forest) by Eiten (1983) or as Floresta ombrofila densa-submontana (sub-montane dense forest) in Para and Floresta ombrofila aberta submontana (sub-montane open forest) in Rondonia by Radam (Brazil, Projeto RADAMBRASIL, 1978).

The first study area sampled, near the town of Nova Jacunda, Para (04°3′S, 49°0′W), was cut and burned during the dry season of 1990. The second site, 50 km south of Maraba, Para, was cut and burned in 1991. The third and fourth sites, near the mining village of Santa Barbara and town of Jamari, Rondonia (~ 9 °12′S, 60 °3′W), respectively, were cut and burned in 1992. Hereafter, these sites will be referred as the Jacunda, Maraba, Santa Barbara, and Jamari sites, respectively.

Climatological data were collected from the nearest stations at Maraba, Para (approximately 75 km south of the Jacunda site and 50 km north of the Maraba site), and at Porto Velho, Rondonia (approximately 100 km northwest of the Santa Barbara and Jamari sites). Mean average precipitation of the two stations is 2088 and 2354 mm, respectively. A pronounced dry season exists from June to September with precipitation normally <100 mm during these months. Mean average temperatures are 26.1 °C and 25.2 °C, minimum temperatures are 22.1 °C and 20.9 °C, maximum temperatures are 31.7 °C and 31.1 °C and mean relative humidity is 82% and 85%, respectively (Departamento Nacional de Metereologia, Brasil 1992).

Our objective was to sample the environment and influences of anthropogenic fires in a manner that would not be biased by our scientific measurements. All decisions of cutting and burning were left to local landowners. Sites had already been felled when our measurements began and there was no a priori knowledge of either biomass, or nutrient pools prior to sampling. All sites sampled were on areas occupied by small farms (< 1,000 ha). This land use is representative of ~ 70% and 47% of the land tenure in Rondonia and Para, respectively (Fearnside 1992). Land use objectives were different for each site. The Jacunda site was to be utilized the first year for crops (rice, manioc and corn) and then to be converted to cattle pasture. The Maraba and Jamari sites were cleared with the objective of conversion to cattle pastures. The Santa Barbara site was cleared for use only as shifting cultivation (rice and manioc). The Jacunda and Santa Barbara sites had not previously been disturbed through timber extraction activities. The Jamari and Maraba sites were bisected by an old logging trail. However, the degree of timber extraction (if any) was undetectable and likely minimal.

All sites were deforested in a similar manner. At the onset of the dry season, the understory was cleared utilizing only hand tools. Following this, large trees were felled utilizing chainsaws. Some trees were left standing in all sites because of their value or because they are illegal to cut (e.g., Brazil nut, *Bertholletia excelsa*). Occasionally, trees were cut by chainsaw, yet did not fall. These residual standing trees were not included in biomass measurements. Towards the end of the dry season, 60–70 days following deforestation, the sites were burned. All sites were burned utilizing circle-fire ignition patterns where the perimeter was ignited causing the fires to burn most intensely towards the center. Typically, sites were ignited when the temperature was warmest and relative humidity lowest (1200 to 1400 hours). Usually, landowners select cloudless days following at least a week without significant precipitation.

Above-ground biomass

Fuels are termed as being as equivalent to the above-ground biomass of the slashed primary forests. Fuels were partitioned on the basis of their influence on fire behavior, value as a nutrient pool, plant morphology, and considerations of sampling approach. Fuel categories include downed wood debris (including vines), attached foliage, litter, rootmat, and residual live plants (seedlings and resprouts).

The prefire mass of wood debris, the amounts consumed by fire, and the postfire residual wood debris were estimated nondestructively utilizing planar intersect models modified specifically for each site (Van Wagner 1968; Brown and Roussopoulous 1974). At each site, 32 planar intersect transects were systematically established to ensure sample dispersion through the slashed areas. All transects were marked with small aluminum stakes prior to burning. This facilitated exact relocation and remeasurement following fire. Diameters of all wood particles intersecting each sample plane were measured. We partitioned the wood debris into standardized size classes based on their diameter. Wood particle diameter is a good predictor of the rate of moisture loss (e.g., a time-lag constant) and hence relationships to combustion and fire behavior (Deeming et al. 1977). These diameter size classes have also been shown to vary inversely with nutrient concentrations and improve calculations of loss or redistribution by fire (Kauffman et al. 1993, 1994). The time-lag constant of a fuel particle is defined as the time required for a fuel particle to lose 63% of the difference between its initial equilibrium moisture content under standard conditions of 27 °C and 20% relative humidity (Pyne 1984). The diameter classes used to partition wood debris were 1-h (0–0.65 cm), 10-h (0.64–2.54 cm), 100-h (2.55–7.5 cm), 1000-h sound and rotten classes (7.6–20.5 cm) and 10000-h sound and rotten classes (>20.5 cm). Lengths of the sampling plane varied among the wood debris size classes: 1 m for wood particles ≤ 0.64 cm diameter, 2 m for wood debris 0.65–2.54 cm diameter; 5 m for wood debris 2.55–7.6 cm diameter; and 11 m for all coarse wood particles ≥ 7.6 cm diameter. The diameter of each coarse wood debris particle intercepting the plane was measured to the nearest half centimeter. For the three wood debris size classes < 7.6 cm diameter, a quadratic mean diameter was utilized for equations through measurement of 100 particles of each size class at each site. Thereafter, for these classes we counted the number of particles that intersected the sampling plane. Bias due to fuel particle tilt and slope was corrected for as outlined in Van Wagner (1968) and Brown and Roussopoulous (1974). Thirty randomly collected samples of each size class were measured for specific gravity (particle density) at each site.

The biomass of attached foliage (i.e., leaves, flowers, and seeds that remained attached to the slashed woody debris) was ascertained through determination of the ratio between its biomass and that of the 0–0.64 cm diameter wood particles. At each site, 50 randomly collected samples of the 1-h time-lag fuels and their associated attached foliage were collected, oven-dried and their mass ratios determined. The mass of attached foliage was then estimated by multiplying the biomass of the 1-h time-lag fuels by this ratio.

The biomass of litter, rootmat (if present), seedlings, and sprouts were destructively sampled through collection of all materials in 25 × 25 cm microplots. A microplot was placed at the 2 m mark of each planar intersect transect (i.e., $n = 32$ plots per site). The mass of litter, rootmat and live plants within each microplot was separated, oven-dried and weighed. Following fire, another microplot established 2 m away from the prefire microplot was collected for determination of the postfire mass of these components.

Ash mass at the Jacunda and Maraba site was measured following methods similar to that of Ewel et al. (1981). Ash depth was measured to the nearest millimeter at 100 random points the day following fire. Ten ash samples of known volume and weight were collected in 10 cm diameter glass petri dishes to determine bulk density. Ash mass was then determined by multiplying depth by mean bulk density. At the Santa Barbara and Jamari sites, ash mass was sampled from within sixteen 50 × 50 cm microplots 1 day after the fire. A portable electric generator and vacuum cleaner was utilized to collect the ash within each microplot. Given the difficulties in accurately measuring ash depth (without disturbance) and in collection of representative bulk densities of ash, we believe the latter method was a more efficient and representative method of ash quantification.

Nutrient pools

Above-ground nutrient pools were partitioned into the same classes as above-ground biomass. Prior to burning, five samples of each fuel component were collected at each site. Each of these samples consisted of a composite mix of 10–20 collections of materials. Ash samples were collected in the same manner following fire. At each site five soil samples at depths of 0–2.5 cm and 2.5–10 cm were also collected. Following fire, soils at the Jacunda, Maraba, and Santa Barbara site were re-sampled approximately 1 m away from the prefire soil sampling areas. At the Maraba site, an additional prefire collection at the 10–30 cm depth was also made. Samples for the calculation of soil bulk density were collected in the same areas as nutrient samples. All samples were air-dried for at least 1 week, placed in plastic bags and transported to the laboratory for nutrient analysis.

All plant and ash samples were analyzed for total N, P, K, C, S, and Ca. Soils at the Santa Barbara and Jamari site were also analyzed for these elements. However, only N was analyzed at the Jacunda site and only C and N were analyzed at the Maraba site. Prior to analysis, plant and ash samples were ground to pass through a 40 mesh screen (0.5 mm) in a Wiley mill. Total N was determined from Kjeldahl digestion (Bremner and Mulvanay 1982). Total Ca, K, and S were determined by atomic absorption (Tabatabai and Bremner 1970). Total P was determined colorimetrically following wet digestion utilizing a Kjeldahl procedure (Watanabe and Olsen 1965). Total C was analyzed by the induction furnace method (Perkin-Elmer 2400 elemental analyzer for the Jacunda and Maraba sites and a Carlo-Erba NA Series 1500 for the Santa Barbara and Jamari sites) (Nelson and Sommers 1982). Organic matter was determined through complete combustion of samples at 500 °C for 8 h in a muffle furnace (Davies 1974).

Fuel moisture content, air temperature, relative humidity, and flame length were recorded at each site prior to, and during, the flaming phase of combustion. Moisture content (dry-weight basis) was calculated through collection of 5–10 samples of the following components: soil surface, litter, dicots, attached foliage, wood 0.65–2.54 cm diameter and wood > 7.6 cm diameter. Samples were weighed in the field with a portable digital balance. They were then oven-dried at 60 °C for 5–7 days to calculate dry weight. Air temperature and relative humidity was measured with a sling psychrometer and wind speed was measured with a portable anemometer.

Differences in prefire biomass and nutrient pools, postfire biomass and residual nutrient pools, ash and nutrients lost from the site were tested between the four different slashed primary forests through analysis of variance in a completely randomized design. If significant, the protected least significant difference multiple range test was utilized to determine statistical significance among the sites sampled ($P \leq 0.10$).

Results

Biomass

Total above-ground biomass of the slashed tropical moist forests ranged from 290 to 435 Mg ha^{-1} (Table 1). Biomass of the Maraba site was ~49% greater than that of the Jacunda or Santa Barbara site even though they are classified as the same forest type. Structure of the forest sites were highly variable as well. For example, wood debris > 20.5 cm diameter was the dominant fuel component at all sites (133–303 Mg ha^{-1}). However, this component comprised 69% of the TAGB at Maraba compared to 44% at Jamari. A well developed rootmat was present at the Santa Barbara site (12.7 Mg ha^{-1}). In contrast, rootmats were not present in the two sites sampled in Para. The forest floor (litter layer and rootmat combined) comprised 8% of the TAGB at the Santa Barbara site, but ≤ 4% at the other sites. Fine fuels (i.e., the forest floor, attached foliage, sprouts and seedlings, and wood debris ≤ 2.54 cm diameter) ranged from 38 to 52 Mg ha^{-1}. This component comprised 9.5% of the TAGB at the Maraba site, and 17.9% of the TAGB at the Santa Barbara site. While significant differences in TAGB did not exist when comparing the combined Para forests to the combined Rondonia forests, general structural differences were apparent; the Rondonia forests had a greater proportion of TAGB in fine fuels while the Para forests had a higher proportion in wood debris > 20.5 cm diameter (Table 1).

All fires were conducted at the end of the dry season (September) when the majority of burning occurs in these regions (Table 2). All fires were first ignited at midday when temperatures were warmest (32–40 °C) and relative humidity was lowest (37–55%). Moisture contents of the measured dead fine fuels (i.e., those likely to be responsible for the sustained propagation of fire) were well below the threshold of combustion (Uhl and Kauffman 1990). Moisture content of attached foliage ranged from 6% to 10% and moisture content of litter ranged from 2% to 10%. In contrast,

Table 1 Total above-ground fuel biomass (Mg ha^{-1}) prior to and following biomass burning in slashed primary tropical moist forests of Para and Rondonia, Brazil. Numbers are mean ± 1 SE. Different *superscripted capital letters* denote a significant difference in biomass among the four forest sites prior to fire. Different *superscripted lower case letters* indicate a significant difference in biomass among the four sites after fire (– components not present in the ecosystems, *nd* components not separated during sampling)

	Jacunda, Para 1990		Maraba, Para 1991		Santa Barbara, Rondonia 1992		Jamari, Rondonia 1992	
	Prefire	Postfire	Prefire	Postfire	Prefire	Postfire	Prefire	Postfire
Litter	11.8 ± 1.6^{a}	0.0 ± 0.0^{A}	16.2 ± 1.4^{B}	0.1 ± 0.1^{a}	11.0 ± 1.5^{A}	0.2 ± 0.1^{a}	11.8 ± 1.2^{A}	0.1 ± 0.1^{a}
Rootmat	–	–	–	–	12.7 ± 1.3^{A}	3.3 ± 1.2^{a}	3.0 ± 0.7^{B}	0.0 ± 0.0^{b}
Total forest floor	11.8 ± 1.6^{A}	0.0 ± 0.0^{a}	16.2 ± 1.4^{B}	0.1 ± 0.1^{a}	23.4 ± 2.1^{C}	3.4 ± 1.2^{b}	14.8 ± 1.3^{AB}	0.1 ± 0.1^{a}
Dicots	1.1 ± 0.4^{A}	0.0 ± 0.0^{a}	0.4 ± 0.2^{AB}	0.0 ± 0.0^{a}	0.8 ± 0.4^{A}	0.1 ± 0.1^{a}	0.8 ± 0.5^{A}	0.0 ± 0.0^{a}
Attached foliage	2.8 ± 0.3^{A}	0.3 ± 0.2^{a}	4.9 ± 0.8^{B}	0.0 ± 0.0^{a}	6.4 ± 0.8^{B}	0.1 ± 0.1^{a}	9.0 ± 1.0^{C}	0.1 ± 0.1^{a}
Wood debris (cm diameter)								
< 0.64	3.5 ± 0.4^{A}	0.3 ± 0.2^{a}	3.0 ± 0.5^{A}	0.1 ± 0.0^{a}	5.4 ± 0.7^{B}	0.1 ± 0.1^{a}	7.6 ± 0.8^{C}	0.1 ± 0.0^{a}
0.65–2.54	18.8 ± 2.0^{A}	3.6 ± 0.5^{b}	17.2 ± 3.1^{A}	1.9 ± 0.5^{a}	15.7 ± 2.0^{A}	1.2 ± 2.0^{a}	20.1 ± 0.4^{A}	1.0 ± 0.3^{a}
2.55–7.6	31.6 ± 3.1^{A}	12.9 ± 1.8^{a}	33.0 ± 5.2^{A}	11.3 ± 1.3^{a}	35.9 ± 3.9^{A}	11.2 ± 1.7^{ab}	54.6 ± 6.9^{B}	7.5 ± 1.4^{b}
7.6–20.5 sound	nd	nd	53.0 ± 6.2^{A}	39.6 ± 7.3^{a}	65.5 ± 7.4^{A}	45.5 ± 5.1^{a}	93.4 ± 9.6^{B}	45.3 ± 5.8^{a}
rotten	nd	nd	3.6 ± 1.3^{A}	0.0 ± 0.0^{a}	4.5 ± 1.4^{A}	0.9 ± 0.6^{a}	3.8 ± 1.0^{A}	0.9 ± 0.6^{a}
total	67.8 ± 6.4^{A}	49.4 ± 4.3^{a}	56.6 ± 6.2^{A}	39.6 ± 7.3^{a}	70.0 ± 7.4^{A}	46.0 ± 5.1^{a}	97.2 ± 9.6^{B}	46.2 ± 5.6^{a}
> 20.5 sound	nd	nd	283.7 ± 63.7^{A}	154.1 ± 52.0^{a}	124.5 ± 18.3^{B}	102.9 ± 18.0^{a}	144.7 ± 27.8^{B}	91.5 ± 22.0^{a}
rotten	nd	nd	19.5 ± 10.1^{A}	0.0 ± 0.0^{a}	8.1 ± 4.8^{A}	0.0 ± 0.0^{a}	13.2 ± 4.4^{A}	9.1 ± 4.1^{b}
total	155.0 ± 34.5^{A}	73.5 ± 17.1^{a}	303.3 ± 64.5^{B}	154.1 ± 520.0^{a}	132.7 ± 17.8^{A}	102.9 ± 18.0^{a}	157.8 ± 27.5^{B}	100.6 ± 22.4^{a}
Total wood	176.8 ± 36.2^{A}	139.6 ± 24.3^{a}	413.1 ± 71.0^{B}	207.0 ± 53.7^{a}	259.9 ± 20.2^{A}	161.3 ± 18.5^{a}	337.4 ± 36.3^{AB}	155.4 ± 24.1^{a}
Total biomass	292.4 ± 35.8^{A}	139.9 ± 24.3^{a}	434.6 ± 72.2^{B}	207.1 ± 53.7^{a}	290.2 ± 20.4^{A}	165.1 ± 19.2^{a}	361.2 ± 36.8^{AB}	155.4 ± 24.1^{a}
Ash		8.8 ± 6.6^{a}		10.9 ± 1.0^{b}		9.4 ± 1.4^{ab}		7.2 ± 1.3^{a}

the moisture content of litter in an adjacent intact primary forest at the Santa Barbara site was 36%. Coarse wood debris moisture content ranged from 28% to 73%. Total above-ground mass of water in these ecosystems at the time of burning ranged from 73 Mg ha^{-1} at Santa Barbara to 292 Mg ha^{-1} for Maraba. This is equivalent to 25% and 45% of the dry mass of these sites, respectively (Tables 1, 2). Fire behavior was highly variable at all sites with a mean flame length of 8–15 m (Table 2). At all sites, the fire completely covered the areas.

Fires consumed 42–57% of the TAGB of the slashed primary forest sites. Residual (postfire) TAGB ranged from 140 to 207 Mg ha^{-1} (Table 1). Ash biomass ranged from 7.2 to 10.9 Mg ha^{-1}. The fine fuel fractions (i.e., those likely consumed during the process of flaming combustion) were consumed at levels of 78 to 100%. In contrast, consumption of coarse wood debris (i.e., that component likely to be consumed after the passage of the flame front by flaming and smoldering combustion processes) was 16% at the Santa Barbara site. Consumption of this component was 44%, 46%, and 34% at the Jacunda, Maraba, and Jamari sites, respectively. Given that the water content of fuels and the ratio of water to dry mass was lowest at the Santa Barbara site (Table 2), we would have expected levels of consumption to be highest at this site. However, a significant precipitation event occurred the night following the Santa Barbara fire extinguishing all residual combustion. In contrast, at the other sites where there was no rainfall the week following fires, smoldering combustion of the coarse wood debris continued for > 7 days.

The rotten coarse wood debris represents a portion of the dead and downed wood and/or snags originating from the standing forest. Biomass of this component ranged from 8 to 20 Mg ha^{-1} and was consumed in greater quantities than sound wood of the same diameter class (43–100%). The levels of biomass consumption on land clearing was judged to be satisfactory by each of the landowners.

Nutrient pools

Nutrient concentrations were typically highest in the non-wood components (litter, rootmat, dicots, foliage) of the ecosystem which were also the most susceptible to complete consumption by fire (Table 3). Concentration of N ranged from 19 to 23 mg g^{-1} and concentration of P ranged from 0.50 to 0.95 mg g^{-1} in these components. In contrast, concentration of N and P in sound coarse wood fuels was ~ 4 and 0.15 mg g^{-1}, respectively. Among the sound wood components, nutrient concentrations were inversely related to stem diameter. Rotten wood debris was higher in concentration of N, S, and Ca than sound wood debris. With the exception of the rootmat, C did not show any

Table 2 General weather conditions, moisture content of selected fuel particles at the time of burning and the flame length of the flame front during fires in slashed tropical moist forests of Para and Rondonia, Brazil (*nd* no data collected)

	Jacunda, Para	Maraba, Para	Santa Barbara, Rondonia	Jamari, Rondonia
Date of burn	9 September 1990	4 September 1991	5 September 1992	23 September 1992
Temperature (°C)	40	32	32	32
Relative humidity	41	37	46–55	53
Wind speed (km/h)	0–10	5–8	0–8	0–13
Moisture content (%)				
Soil surface	7 ± 1	16 ± 2	28 ± 2	35 ± 4
Litter	9 ± 1	2 ± 1	7 ± 1[a]	10 ± 0.2
Dicots	nd	185 ± 30	144 ± 36	194 ± 40
Attached foliage	8 ± 0.5	6 ± 1	nd	10 ± 2
Wood 0.65–2.54 cm diameter	20 ± 3	nd	14 ± 6	13 ± 1
Wood >7.6 cm diameter	40 ± 8	48 ± 5	28 ± 3	38 ± 14
Water mass (Mg ha^{-1})	109	194	73	125
Water : dry mass ratio	0.37	0.45	0.25	0.35
Flame length (M)	nd	15 ± 3	9 ± 2	8 ± 2

[a] Moisture content of litter in an adjacent intact forest was 36 ± 2% at this time

Table 3 Mean nutrient concentrations of above-ground fuel biomass of slashed primary forests. Numbers are means ± standard errors of all samples combined from all sites in Para and Rondonia, Brazil

Component	Carbon (%)	Nitrogen (mg g^{-1})	Sulphur (mg g^{-1})	Phosphorus (mg g^{-1})	Potassium (mg g^{-1})	Calcium (mg g^{-1})
Dicots	49.19 ± 0.36	18.69 ± 1.54	1.88 ± 0.11	0.95 ± 0.27	9.39 ± 1.60	3.50 ± 0.81
Litter	49.90 ± 0.87	18.91 ± 1.09	2.26 ± 0.27	0.65 ± 0.04	3.59 ± 0.43	5.94 ± 0.71
Rootmat	34.21 ± 1.88	18.97 ± 1.26	1.74 ± 0.06	0.50 ± 0.07	1.28 ± 0.09	1.08 ± 0.16
Attached foliage	51.10 ± 0.32	23.32 ± 1.89	2.61 ± 0.18	0.92 ± 0.07	6.41 ± 0.61	4.21 ± 0.71
Wood debris (cm diameter)						
0–0.64	49.96 ± 0.27	10.54 ± 1.54	1.60 ± 0.01	0.46 ± 0.05	3.89 ± 0.65	4.54 ± 0.67
0.65–2.54	50.17 ± 0.45	7.73 ± 0.51	0.90 ± 0.13	0.27 ± 0.03	2.54 ± 0.30	3.96 ± 0.41
2.55–7.6	49.65 ± 0.34	5.23 ± 0.47	0.71 ± 0.07	0.16 ± 0.03	1.63 ± 0.23	2.26 ± 0.63
> 7.6 sound	50.14 ± 0.24	4.17 ± 0.28	0.69 ± 0.07	0.15 ± 0.01	1.60 ± 0.30	2.06 ± 0.63
> 7.6 rotten	49.95 ± 0.57	7.85 ± 0.67	0.96 ± 0.16	0.15 ± 0.01	1.36 ± 0.05	3.78 ± 0.81

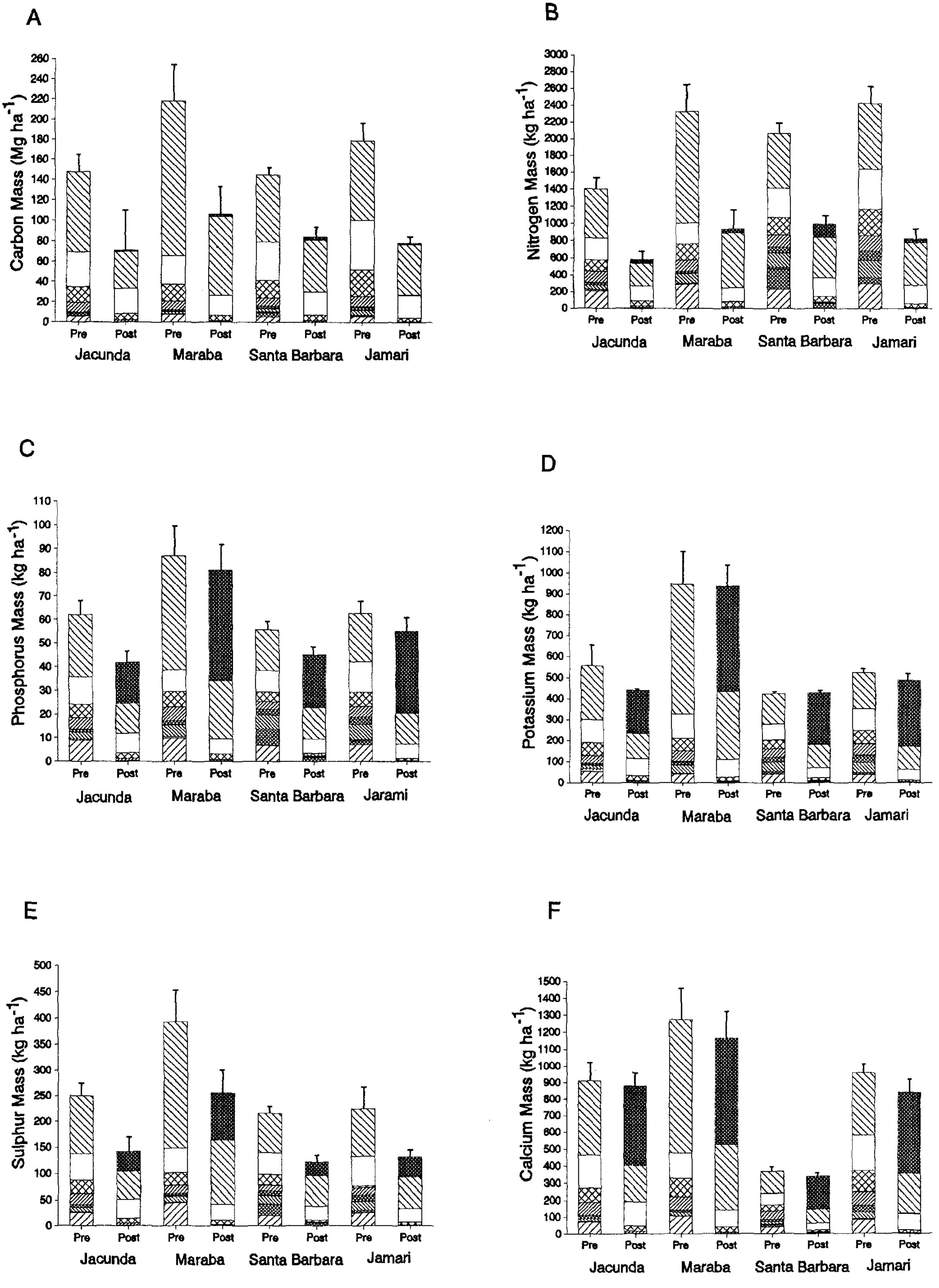
Table 4 Nutrient and organic matter concentration of ash following fires in slashed primary tropical moist forests of Para and Rondonia, Brazil. Numbers are mean ±1 SE (*nd* no data)

Component	Jacunda, Para	Maraba, Para	Santa Barbara, Rondonia	Jamari, Rondonia
Nitrogen (mg g^{-1})	5.44 ± 0.82	5.44 ± 0.73	16.69 ± 0.29	5.55 ± 1.17
Carbon (%)	18.75 ± 1.04	20.91 ± 6.01	33.20 ± 4.33	20.27 ± 3.65
Sulphur (mg g^{-1})	42.4 ± 0.46	9.86 ± 1.24	2.76 ± 0.20	5.04 ± 0.39
Phosphorus (mg g^{-1})	20.3 ± 0.33	4.97 ± 0.52	2.56 ± 0.15	5.34 ± 0.45
Potassium (mg g^{-1})	23.89 ± 3.85	53.40 ± 12.12	28.52 ± 10.44	54.07 ± 8.27
Calcium (mg g^{-1})	54.07 ± 9.33	67.50 ± 10.47	22.06 ± 3.36	76.54 ± 8.51
Organic matter (%)	nd	nd	45.34 ± 5.56	24.87 ± 4.06

difference in concentration among the various fuel components. C ranged from 49.2% to 50.2% of the biomass among the fuel components except in the rootmat, which had a mean concentration of 34.2%.

Nutrient mass (Fig. 1A–1F) was calculated through multiplication of biomass by the nutrient concentration of samples that were collected on that site. While only the means of all sites combined are reported in Table 3, there were significant differences in nutrient concentrations among sites. In all fuel components, concentration of S was lower at the Santa Barbara site. Concentration of N was consistently lower at the Jacunda site compared to the others. In general, the N concentration in fuels was higher at the Rondonia sites than the Para sites. For example, N concentration of fine wood debris (< 0.64 cm diameter) was 8.0 mg g^{-1} at the Jacunda site but >13 mg g^{-1} at the Rondonia sites. Calcium concentrations were consistently lower at the Santa Barbara site than others. For example, concentration in coarse wood debris was 0.83 mg g^{-1} at Santa Barbara and > 2.5 mg g^{-1} at the others.

The variability of the nutrient concentrations in ash was much greater among sites than the concentrations in unburned biomass (Table 4). For example, ash concentration of P ranged from 2.6 mg g^{-1} at Santa Barbara to 20.3 mg g^{-1} at Jacunda. Nitrogen and C concentration of ash was highest at the Santa Barbara site than all others. Similarly, those nutrient


A
Carbon Mass (Mg ha^{-1})
0
20
40
60
80
100
120
140
160
180
200
220
240
260
Pre
Post
Pre
Post
Pre
Post
Pre
Post
Jacunda
Maraba
Santa Barbara
Jamari
B
Nitrogen Mass (kg ha^{-1})
0
200
400
600
800
1000
1200
1400
1600
1800
2000
2200
2400
2600
2800
3000
Pre
Post
Pre
Post
Pre
Post
Pre
Post
Jacunda
Maraba
Santa Barbara
Jamari
C
Phosphorus Mass (kg ha^{-1})
0
10
20
30
40
50
60
70
80
90
100
110
Pre
Post
Pre
Post
Pre
Post
Pre
Post
Jacunda
Maraba
Santa Barbara
Jarami
D
Potassium Mass (kg ha^{-1})
0
100
200
300
400
500
600
700
800
900
1000
1100
1200
Pre
Post
Pre
Post
Pre
Post
Pre
Post
Jacunda
Maraba
Santa Barbara
Jamari
E
Sulphur Mass (kg ha^{-1})
0
50
100
150
200
250
300
350
400
450
500
Pre
Post
Pre
Post
Pre
Post
Pre
Post
Jacunda
Maraba
Santa Barbara
Jamari
F
Calcium Mass (kg ha^{-1})
0
100
200
300
400
500
600
700
800
900
1000
1100
1200
1300
1400
1500
Pre
Post
Pre
Post
Pre
Post
Pre
Post
Jacunda
Maraba
Santa Barbara
Jamari

components with higher temperatures of volatilization (S, P, Ca, and K) were typically low at the Santa Barbara site. This is likely related to the precipitation event the night of the Santa Barbara fire which halted combustion and perhaps leached some of the water soluble cations out of the ash. The effects of rainfall on the completeness of combustion may be reflected in the organic matter concentration of ash at the Rondonia sites. Organic matter comprised 45% of the ash at Santa Barbara but only 25% of the ash concentration at Jamari.

Typically, the concentrations of nutrients with low temperatures of volatilization (N and C) were lower in ash than in fuels. Conversely, concentrations of nutrients with higher temperatures (e.g., S, P. K, and Ca) were higher in ash than in fuels (Tables 3, 4). For example, mean concentration of C was 18–33% in ash but ~ 50% in fuels. Mean concentration of N in ash was approximately similar to that of coarse wood debris at the Jacunda, Maraba, and Jamari sites. Mean concentration of K was ~ 9.4 mg g^{-1} in dicots and 1.6 mg g^{-1} in coarse wood, but 24–54 mg g^{-1} in ash.

Among the four slashed primary forests, there were dramatic differences in the total prefire mass of nutrient pools as well as the partitioning of nutrients within pools (Fig. 1A–1F; Table 5). The total prefire pool of C, S, K, and Ca was significantly greater at the Maraba site than the others. Total above-ground pools of N ranged from 1,401 kg ha^{-1} at Jacunda to 2,427 kg ha^{-1} at Jamari. The C pools ranged from 58 Mg ha^{-1} at Santa Barbara to 112 Mg ha^{-1} at Maraba. Above-ground pools of S ranged from 216 to 392 kg ha^{-1}; above-ground pools of P ranged from 56 to 87 kg ha^{-1}; above-ground pools of K ranged from 432 to 949 kg ha^{-1}; and pools of Ca ranged from 368 to 1,274 kg ha^{-1}.

The variability of above-ground nutrient mass among forest sites did not necessarily parallel the differences in total above-ground biomass. This is particularly evident among the N and Ca pools. For example, the above-ground N pool at Jamari was greater than that of the Maraba site even though its TAGB was 73 Mg ha^{-1} less. While TAGB of the Jacunda site and Santa Barbara sites were similar, the N pool of the latter exceeded the former by 600 kg ha^{-1}. Conversely, the Ca pool in the Jacunda site was ~ 2.5-fold greater than the Santa Barbara site (910 versus 368 kg ha^{-1}; Table 5; Fig. 1F).

The proportion of the nutrient pool contained within the fine fuel fractions exceeded their proportional biomass of the ecosystem. At the Jacunda and Jamari sites, the litter layer comprised 4% of the total biomass, but it contained 15% of the N pool. At the Santa Barbara site, fine fuels accounted for 18% of the TAGB but 42%, 36% and 41% of the N, S, and P above-ground pools, respectively.

Fig. 1A–F Nutrient pools of primary tropical moist forest slash before and after fires in Para and Rondonia, Brazil. The vertical lines represent one SE of the total nutrient pools. Litter is signified by ▨, rootmat by ■, dicots by ▩, attached foliage by ■, wood debris 0–0.64 cm diameter by ■, 0.65–2.54 cm diameter by ▨, 2.55–7.6 cm diameter by ■, 7.6–20.5 cm diameter by □, >20.5 cm diameter by ▧, and ash by ■

In general, a greater proportion of nutrients were stored in coarse wood debris at the Para sites than the Rondonia sites. For example, coarse wood comprised approximately 36%, and fine fuels comprised approximately 29–36% of the above-ground S pool at Rondonia sites. In contrast, coarse wood comprised 45–62% and fine fuels comprised 20–25% of the S pools at Para sites. Coarse wood comprised < 38% of the total Ca above-ground pool at the Rondonia sites and 48–63% at the Para sites (Fig. 1F).

Site losses of N were quite dramatic; 817–1,605 kg ha^{-1} were lost during combustion. Losses of C were 58–112 Mg ha^{-1} (Table 5). These represent losses of 51–62% of the above-ground N pool and 40–56% of the above-ground C pool. Atmospheric losses of S ranged from 92 to 137 kg ha^{-1} or 35–49% of the above-ground pool. P losses from the ecosystem were quite variable; 7–32% of the aboveground pool were lost during fire (6–20 kg ha^{-1}). Smaller losses of Ca and K were recorded; less than 20% of the above-ground pool of these nutrients were lost by fire. In terms of mass, inputs of water vapor into the atmosphere was second only to C. Atmospheric inputs of water from fuels during combustion processes were estimated to be 54, 95, 28, and 126 Mg ha^{-1} for the Jacunda, Maraba, Santa Barbara and Jamari sites, respectively.

Following fire, there were only two significant above-ground pools of nutrients – ash and residual wood debris (Fig. 1A–1F; Table 5). However, this varied among nutrients. Ash comprised < 16% of the postfire above-ground N pool but comprised > 54% of the postfire pool of Ca and K. Ash comprised only 0.8–2.2% of the residual postfire C pool. This is important because this fraction may contain recalcitrant forms of C (charcoal or char) which are resistant to decomposition.

Soil nutrients

Nitrogen and C concentrations of soils 0–2.5 cm in depth were higher at the Rondonia than the Para sites (Table 6). This followed the same general pattern of higher N concentrations in vegetation of the Rondonia sites. N and C concentrations of soils from the 0–2.5 cm layer at the Jamari site were twice that of the Maraba site. There was also great variability among the two Rondonia sites. Concentration of S and Ca was significantly higher at the Jamari site than the Santa Barbara site. Again, the relationship between plant and soil nutrient concentration was apparent at these sites (Tables 3, 6). Soils from the 0–2.5 cm layer were consistently higher in nutrient concentration than the

Table 5 Dynamics of selected above-ground nutrient pools before and after burning slashed primary tropical moist forest, Para and Rondonia, Brazil. Numbers are mean ± 1 SE. Different *superscript* letters denote a significant difference among the four slashed primary forest sites. (*TAGB* total above-ground biomass)

	Jacunda, Para	Maraba, Para	Santa Barbara, Rondonia	Jamari, Rondonia
		Nitrogen (kg ha^{-1})		
Total pool-prefire	1401.4 ± 130.4^{a}	2327.3 ± 329.1^{b}	2063.8 ± 118.7^{ab}	2426.9 ± 195.8^{b}
% of TAGB	0.50	0.53	0.71	0.67
Residual fuels-postfire	537.2 ± 91.9^{a}	888.5 ± 223.8^{a}	842.6 ± 103.5^{a}	782.3 ± 116.9^{a}
Released from biomass	864.2 ± 79.6^{a}	1438.7 ± 244.9^{ab}	1221.1 ± 119.6^{a}	1644.5 ± 150.8^{b}
Ash	46.83 ± 3.4^{a}	51.5 ± 5.5^{a}	157.0 ± 23.6^{b}	40.06 ± 7.19^{a}
Residual + ash	584.8 ± 91.9^{a}	940.1 ± 224.7^{a}	999.63 ± 101.42^{a}	822.37 ± 116.4^{a}
Site loss	816.6 ± 79.6^{a}	1387.2 ± 245.5^{ab}	1064.2 ± 116.5^{a}	1604.5 ± 150.3^{b}
		Carbon (Mg ha^{-1})		
Total pool-prefire	147.6 ± 18.1^{ab}	218.2 ± 36.3^{a}	142.1 ± 10.1^{b}	178.9 ± 18.2^{ab}
% of TAGB	50.5	49.7	48.9	49.6
Residual fuels-postfire	69.9 ± 12.4^{a}	104.0 ± 27.0^{a}	81.32 ± 9.4^{a}	77.2 ± 12.0^{a}
Released from biomass	77.7 ± 12.4^{ab}	114.2 ± 26.04^{a}	60.8 ± 8.5^{b}	101.8 ± 12.6^{a}
Ash	1.6 ± 0.2^{ab}	2.28 ± 0.22^{b}	3.1 ± 0.3^{c}	1.5 ± 0.2^{a}
Residual + ash	71.5 ± 39.2^{a}	106.3 ± 27.0^{a}	84.4 ± 9.4^{a}	78.6 ± 12.0^{a}
Site loss	76.0 ± 9.7^{ab}	111.9 ± 26.1^{a}	57.6 ± 8.3^{b}	100.3 ± 12.6^{ab}
		Sulphur (kg ha^{-1})		
Total pool-prefire	250.7 ± 25.8^{a}	392.1 ± 59.9^{b}	215.6 ± 13.1^{a}	251.8 ± 22.1^{a}
% of TAGB	0.085	0.091	0.070	0.070
Residual fuels-postfire	104.3 ± 18.1^{ab}	162.2 ± 42.0^{a}	98.1 ± 11.9^{a}	90.4 ± 13.8^{a}
Released from biomass	146.5 ± 14.8^{ab}	229.9 ± 43.9^{a}	117.5 ± 12.2^{b}	161.3 ± 6.0^{b}
Ash	37.4 ± 2.6^{a}	93.4 ± 9.9^{b}	25.9 ± 2.7^{a}	39.0 ± 4.9^{a}
Residual + ash	141.6 ± 18.1^{a}	155.6 ± 44.8^{b}	124.0 ± 14.1^{a}	129.5 ± 14.1^{a}
Site loss	109.1 ± 14.8	136.5 ± 45.8	91.6 ± 11.7	122.3 ± 16.4
		Phosphorus (kg ha^{-1})		
Total pool-prefire	62.2 ± 6.0^{ab}	87.1 ± 12.4^{b}	56.0 ± 3.3^{a}	62.8 ± 5.2^{ab}
% of TAGB	0.02	0.02	0.02	0.02
Residual fuels-postfire	24.5 ± 4.2^{a}	34.1 ± 8.6^{a}	22.8 ± 2.8^{a}	20.4 ± 3.2^{a}
Released from biomass	37.7 ± 3.6^{ab}	53.0 ± 9.1^{a}	33.1 ± 3.1^{b}	42.3 ± 3.9^{ab}
Ash	17.9 ± 1.3^{a}	47.1 ± 5.0^{c}	22.2 ± 2.2^{a}	34.7 ± 4.0^{b}
Residual + Ash	42.4 ± 4.2^{a}	81.2 ± 10.7^{b}	45.1 ± 3.5^{a}	55.2 ± 5.8^{a}
Site loss	19.8 ± 3.6^{a}	5.9 ± 10.7^{a}	10.9 ± 3.5^{a}	7.6 ± 6.0^{a}
		Potassium (kg ha^{-1})		
Total pool-prefire	555.8 ± 59.0^{a}	948.9 ± 155.5^{b}	431.9 ± 26.9^{b}	523.6 ± 44.7^{a}
% of TAGB	0.19	0.22	0.15	0.15
Residual fuels-postfire	234.2 ± 40.9^{ab}	434.5 ± 112.8^{a}	181.2 ± 21.4^{b}	172.2 ± 26.1^{b}
Released from biomass	321.5 ± 33.9^{ab}	514.3 ± 111.5^{c}	250.7 ± 25.4^{a}	351.3 ± 34.0^{abc}
Ash	210.5 ± 14.7^{a}	506.0 ± 53.7^{b}	247.6 ± 24.0^{a}	315.8 ± 32.0^{a}
Residual + ash	444.8 ± 40.8^{a}	940.5 ± 132.8^{b}	428.8 ± 32.3^{a}	488.0 ± 39.8^{a}
Site loss	111.0 ± 33.9^{a}	8.3 ± 127.3^{a}	3.09 ± 29.7^{a}	35.5 ± 48.2^{a}
		Calcium (kg ha^{-1})		
Total pool-prefire	909.8 ± 101.4^{a}	1274.2 ± 195.1^{b}	367.5 ± 23.3^{c}	926.8 ± 81.8^{a}
% of TAGB	0.31	0.29	0.13	0.26
Residual fuels-postfire	403.0 ± 69.7^{a}	526.5 ± 133.6^{a}	145.7 ± 17.0^{b}	342.5 ± 51.5^{a}
Released from biomass	506.8 ± 57.1^{ab}	747.8 ± 145.8^{a}	221.9 ± 24.4^{b}	584.3 ± 60.6^{b}
Ash	476.5 ± 33.3^{a}	639.6 ± 67.9^{b}	191.5 ± 18.6^{a}	485.5 ± 56.0^{a}
Residual + ash	879.49 ± 69.7^{ab}	1166.1 ± 159.7^{b}	337.2 ± 24.4^{c}	828.0 ± 89.3^{a}
Site loss	30.3 ± 57.1^{a}	108.1 ± 166.3^{a}	30.3 ± 25.6^{a}	98.8 ± 87.5^{a}

2.5–10 cm layer. For example, at the Jamari site, the concentration of Ca and K in the 0–2.5 cm soil layer was ~ four-fold and seven-fold greater than in the 2.5–10 cm soil layer.

Preburn surface soil mass (0–10 cm) of nitrogen ranged from 1,167 kg ha^{-1} at Jacunda to 2,420 kg ha^{-1} at Maraba. Soil C pools of soils to a depth of 10 cm ranged from 28 to 30 Mg ha-1 (Table 7). These soil N pools were approximately equivalent to above-ground N pools while soil C mass was substantially lower than the above-ground pool (Tables 5, 7). Soil C accounted for 11–17% of the soil and above-ground pools combined. At the Santa Barbara and Jamari sites, prefire soil nutrient pools (0–10 cm) were, respectively, 204 and 318 kg ha^{-1} for S; 120 and 108 kg ha^{-1} for P; 104 and 163 kg ha^{-1} for K, and 77 and 174 kg ha^{-1} for Ca. The surface soil pool of S was approximately equivalent to that of above-ground pools. Soil P comprised >63% of the combined above-ground and below-ground pool. In contrast, soil pools of K and

Table 6 Surface soil nutrient concentration (mg g^{-1}) in slashed primary forests of Para and Rondonia, Brazil. Numbers are mean ± 1 SE

Soil depth (cm)	Jacunda, Para Prefire	 Postfire	Maraba, Para Prefire	 Postfire	Santa Barbara, Rondonia Prefire	 Postfire	Jamari, Rondonia Prefire
			Nitrogen (mg g^{-1})				
0–2.5	1.37 ± 0.12	1.08 ± 0.08	2.34 ± 0.24	2.48 ± 0.26	3.96 ± 0.33	4.10 ± 0.37	4.79 ± 0.39
2.5–10	0.93 ± 0.08	0.86 ± 0.64	1.87 ± 0.15	1.87 ± 0.16	2.52 ± 1.57	1.92 ± 0.12	2.52 ± 0.17
10–30			1.05 ± 0.03				
			Carbon (mg g^{-1})				
0–2.5			30.11 ± 5.47	27.37 ± 2.58	54.86 ± 5.93	52.51 ± 6.24	62.65 ± 73.46
2.5–10			24.34	20.78 ± 1.41	31.93 ± 22.87	23.01 ± 1.87	29.08 ± 2.24
			Sulphur (mg g^{-1})				
0–2.5					0.35 ± 0.02	0.36 ± 0.02	0.49 ± 0.04
2.5–10					0.23 ± 0.04	0.20 ± 0.01	0.37 ± 0.02
			Phosphorus (mg g^{-1})				
0–2.5					0.16 ± 0.01	0.27 ± 0.06	0.22 ± 0.02
2.5–10					0.15 ± 0.00	0.17 ± 0.01	0.11 ± 0.01
			Potassium (mg g^{-1})				
0–2.5					0.17 ± 0.01	0.30 ± 0.05	0.50 ± 0.05
2.5–10					0.12 ± 0.02	0.08 ± 0.00	0.11 ± 0.01
			Calcium (mg g^{-1})				
0–2.5					0.21 ± 0.02	0.25 ± 0.05	0.65 ± 0.08
2.5–10					0.06 ± 0.02	0.13 ± 0.00	0.08 ± 0.01

Table 7 Soil nutrient mass (kg ha^{-1}) in slashed primary forests of Para and Rondonia, Brazil. Numbers are mean and standard error

Soil depth (cm)	Jacunda, Para Prefire	 Postfire	Maraba, Para Prefire	 Postfire	Santa Barbara, Rondonia Prefire	 Postfire	Jamari, Rondonia Prefire
			Nitrogen (kg ha^{-1})				
0–2.5	368 ± 13	290 ± 11	628 ± 23	665 ± 24	776 ± 26	803 ± 27	938 ± 31
2.5–10	799 ± 22	733 ± 21	1603 ± 45	1603 ± 45	1479 ± 49	1129 ± 37	1482 ± 89
10–30	2049 ± 106	1921 ± 100	2683 ± 139				
			Carbon (kg ha^{-1})				
0–2.5			6.95 ± 0.98	6.21 ± 0.57	10.8 ± 0.4	10.3 ± 0.3	12.3 ± 0.4
2.5–10			20.63 ± 1.91	14.16 ± 0.96	18.8 ± 0.6	13.5 ± 0.5	17.1 ± 0.1
10–30			28.75 ± 0.71				
			Sulphur (kg ha^{-1})				
0–2.5					69.5 ± 2.3	72.0 ± 2.3	97.0 ± 3.2
2.5–10					134.8 ± 4.4	123.1 ± 4.1	221.4 ± 7.3
			Phosphorus (kg ha^{-1})				
0–2.5					31.4 ± 1.0	52.9 ± 1.8	43.1 ± 1.4
2.5–10					88.2 ± 2.9	100.0 ± 3.3	64.7 ± 2.1
			Potassium (kg ha^{-1})				
0–2.5					33.3 ± 1.1	58.8 ± 2.0	98.0 ± 3.2
2.5–10					70.6 ± 2.3	47.0 ± 1.6	64.7 ± 2.1
			Calcium (kg ha^{-1})				
0–2.5					41.6 ± 1.4	49.0 ± 1.7	127.4 ± 4.2
2.5–10					35.3 ± 1.2	76.4 ± 2.5	47.0 ± 1.6

Ca comprised < 25% of the total combined pool of soils and above-ground mass.

There were no significant trends or dramatic changes in total soil N and C following fire in any of the sampled areas (Table 7). At the Santa Barbara site, increases in concentrations of P, K, and Ca were measured. However, because of the precipitation event between the fire and our postfire sampling, it is difficult to interpret fire effects from the potential movement of cations from ash to soil surface horizons. Nutrient concentrations of cations in ash at Santa Barbara were consistently at the low end of our samples. Whether this is the result of leaching losses, lower levels of biomass combustion (also due to the rain) or a combination of the two is unknown.

Combining the soil and above-ground nutrient pools provide an insight into ecosystem effects of these slash fires. Nitrogen losses by fire were 25–33% of this com-

Table 8 Nutrient losses through biomass burning of selected tropical and temperate ecosystems. Losses are reported in Mg ha^{-1} for C and kg ha^{-1} for all other nutrients (*nd* data not collected)

Site	C	N	P	S	K	Ca	Source
Cerrado (savanna-woodland and gradient), Brazil	2.6–3.3	22–26	0.8–1.6	3.0–4.2	5.8–7.9	4.7–10.8	Kauffman et al. 1994
Tropical dry forest slash, Brazil	25–32	428–530	1–21	nd	nd	nd	Kauffman et al. 1993
Temperate coniferous forest slash, Canada	nd	10–982	2–77	nd	0–76	4–211	Feller 1989
Cattle pastures, Brazil	11–21	205–261	1–11	16–25	11–33	0–16	Kauffman et al. 1995
Tropical second-growth slash, Costa Rica	16	490	0	0	0	0	Ewel et al. 1981
Tropical second-growth forests, Brazil	22–47	206–587	2–20	27–44	20–95	10–124	Kauffman et al. 1995
Tropical primary forest, Para	76, 112	816, 1387	6, 20	109, 137	8, 111	30, 108	This study
Tropical primary forest, Rondonia	58, 100	1064, 1605	8, 11	92, 122	3, 36	30, 99	This study

bined soil and above-ground pool. Losses of C were equivalent to 34–48% of this total pool. Losses of S were ~ 22% and losses of P, K, and Ca were < 10% of the combined pools (Tables 5, 7). While ecosystem losses of P, K, and Ca appear to be small, it is important to note that the majority of the postfire above-ground pool of these nutrients was in the ash (Table 5); a form highly susceptible to erosion or leaching losses.

Discussion

Above-ground biomass

Total above-ground biomass of sites in this study ranged from 290 to 435 Mg ha^{-1} and appears to be representative of many tropical moist forests currently being felled in Para and Rondonia. For example, direct measurements of the TAGB of Para forests have been reported to range from 108 to 607 Mg ha^{-1} (Uhl et al. 1988; Fearnside et al. 1993). In Rondonia, other studies have reported TAGB to range from 328 to 403 Mg ha^{-1} (Martenelli et al. 1988; Fearnside et al. 1993). In contrast, our estimates tend to be somewhat higher than indirect modeled estimates based upon forest inventories; Brown and Lugo (1992) estimated TAGB of Para and Rondonia forests to be 263 and 252 Mg ha^{-1}, respectively. These lower estimates would be expected since their models did not include trees < 10 cm dbh (diameter at breast height, i.e., at 1.3 m), palms, dead coarse wood debris, or the forest floor. In our study, the combined biomass of the forest floor, dicots, and rotten coarse wood debris (a portion of the dead wood legacy from the intact forest) ranged from 33 to 45 Mg ha^{-1} or 9–13% of the TAGB. Our rotten coarse wood debris component (13–23 Mg ha^{-1}) is likely to be an underestimate of the dead coarse wood debris that originated from the intact primary forest because some dead wood in forests would not be rotten. Other studies have reported coarse wood debris in intact "Terra Firme" Amazonian forests to range from 8 to 42 Mg ha^{-1} of which 39–69% was considered sound (Kauffman et al. 1988; Uhl et al. 1988; Uhl and Kauffman 1990). The rotten coarse wood debris was the only large wood fraction that was consumed in high quantities. For example, at the Santa Barbara and Maraba sites, > 90% of the rotten coarse wood debris was consumed while < 46% of the sound coarse wood debris was consumed. Clearly, these fractions are of importance both in terms of C pools and in their contribution to atmospheric inputs following fire.

The mean of TAGB consumed by fire (i.e., the combustion factor or combustion efficiency) of the four slashed primary forest sites was 51 ± 3% (Table 1). The mean C loss from the four sites was 50 ± 3% (Table 5; Fig. 1A). These values are much higher than those utilized in many studies of net changes of C between terrestrial ecosystems and the atmosphere. For example, Fearnside (1992) and Crutzen and Andreae (1990) utilized a combustion factor of ~28% to calculate C inputs from slashed primary tropical forest fires. Fearnside (1992) estimated that 28.4% of the preburn C would be released by fire with 69% being released through decay. Houghton (1991) assumed that 39% of biomass from cleared and harvest sites was burned and 61% released through decay. These estimates of biomass combustion and C release are likely low for regions such as Rondonia and Para where substantial areas are being subjected to deforestation and biomass burning. Conversely, atmospheric inputs of C via decomposition processes are likely greatly overestimated by these studies. In addition, our estimates of biomass release from fire does not include the additional losses arising from the common practice of "encoivaramento" where, following the initial fire, residual quantities of those wood materials that can be moved by hand are piled and then reburned.

Decomposition losses would also likely be retarded following fire because those readily decomposible components of the ecosystem (i.e., fine particles with lower C : N ratios) are consumed in high quantities during burning. The mean C : N ratio of the TAGB prior to fire was 85.4 as compared to 110.5 for the postfire residual biomass (Table 5). The C : N ratio of the fuels that were consumed by fire was significantly lower, 70.2.

Compared to other tropical ecosystems, the combustion efficiency of tropical moist forests is low. In Brazilian tropical dry forests, Kauffman et al. (1993) measured combustion factors of 78–88%. The combustion factor of Brazilian savannas and woodlands (cerrado) was 72–100% (Kauffman et al. 1994). However, the forest and fuel biomass of Brazilian tropical dry forest and savannas are substantially lower than that of tropical moist forests. In Brazil, mean biomass of tropical dry forests was 74 Mg ha^{-1}. The TAGB of Brazilian cerrados ranged from 7 to 48 Mg ha^{-1} (Cummings et al. 1993) and fuel loads ranged from 7 to 10 Mg ha^{-1} (Kauffman et al. 1994).

Nutrient pools

The nutrient concentrations of TAGB in slashed primary tropical moist forest was low. The percentage of TAGB comprised of nutrients was 0.5–0.7% for N, 0.07–0.09% for S, 0.02% for P, 0.13–0.31% for Ca, and 0.15–0.22% for K (Table 5). These concentrations are similar for biomass susceptible to combustion in cerrado ecosystems (Kauffman et al. 1994). However, they are lower than those reported for Brazilian tropical dry forests where N accounted for approximately 0.73– 0.78% and P accounted for 0.05% of the TAGB (Kauffman et al. 1993). Gross TAGB nutrient concentrations for these tropical moist forests are also at the low end of the range, or, in the case of K and S, below the global range reported by Bowen (1979), Crutzen and Andreae (1990), and Deevey (1970).

Because of a relatively high TAGB, nutrient pools susceptible to combustion were dramatically higher in tropical moist forests than either a tropical dry forest or cerrado. For example, above-ground N pools are 1,401–2,427 kg ha^{-1}, 539–579 kg ha^{-1}, and 23–55 kg ha^{-1} for Brazilian tropical moist forest, tropical dry forest, and cerrado, respectively (Table 5; Kauffman et al. 1993, 1994).

While nutrient pools susceptible to fire in tropical moist forests are high relative to other tropical ecosystems, they may be equivalent or lower than slashed temperate coniferous forests. For example, the TAGB of primary *Pseudotsuga-Tsuga* forests of northwestern North America ranged from 783 to 1765 Mg ha^{-1} (Grier and Logan 1977; Agee and Huff 1987). However, vast quantities of wood are often removed by timber harvest in temperate coniferous ecosystems. Therefore, slash biomass is often lower or equivalent in the temperate coniferous ecosystems (e.g., 71–356 Mg ha^{-1}: Little and Ohmann 1988) compared to slashed tropical moist forests.

A paucity of information exists concerning the nutrient losses by slash fires. Losses of C, N, S, and Ca reported in this study are the highest that we could find reported in the literature (Table 8; Kauffman et al. 1992). These represent significant losses with respect to atmospheric/terrestrial interactions as well as significant negative influences on long-term site productivity. While losses during combustion of K, Ca, and P were relatively low compared to those nutrients with a low temperature of volatilization, large quantities of the postfire above-ground pool of these nutrients remained in the form of ash (Table 5). This portion of the residual above-ground nutrient pool is highly susceptible to site losses. For example, Kauffman et al. (1993) reported that 57% of the ash in a burned tropical dry forest was lost 17 days after burning via wind erosion.

The nutrient losses from fires in slashed primary forests are not only among the greatest in terms of mass inputs into the atmosphere, but also in terms of total depletions of the ecosystem pool. We base this on comparisons of losses by fire in relation to the TAGB and soil surface pools combined. For example, we found that N losses by slash fires in tropical moist forests accounted for 25–33% of the TAGB/soil pool. Proportional losses of the same pool by slash fires in tropical dry forest were 20– 24% (Kauffman et al. 1993). There are tremendous differences when comparing ecosystem losses by anthropogenic fires in slashed forest ecosystems compared to fires of natural fuels in the savanna-woodland complex of the cerrado. Nitrogen losses in the Cerrado, where frequent fires are a dominant ecological process was 2.2–4.7% of the above-ground fuel/soil pool (Kauffman et al. 1994).

While nutrient losses by biomass burning in slashed primary forests are among the highest reported in the literature, these represent only a fraction of losses when considering cumulative long-term influences of current land use practices. In addition to erosional losses, the dominant land use practices in Amazonia will likely result in the continued depletion or export of nutrients from perturbed sites through purposeful and accidental pasture fires or the reclearing of second-growth forests (Table 8). Until feasible alternatives to the current forms of land use are developed and implemented,there can be little hope of decreasing or even preventing an increase in deforestation, biomass burning, and the subsequent impoverishment of this ecosystem and its inhabitants.

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