Relationship between soils and Amazon forest biomass: a landscape-scale study

William F. Laurance[a,*], Philip M. Fearnside[b], Susan G. Laurance[a], Patricia Delamonica[a], Thomas E. Lovejoy[c], Judy M. Rankin-de Merona[a], Jeffrey Q. Chambers[d], Claude Gascon[a]

[a]Biological Dynamics of Forest Fragments Project, National Institute for Research in the Amazon (INPA), C.P. 478, Manaus, AM 69011-970, Brazil
[b]Department of Ecology, National Institute for Research in the Amazon (INPA), C.P. 478, Manaus, AM 69011-970, Brazil
[c]Counselor to the Secretary for Biodiversity and Conservation, Smithsonian Institution, Washington D.C. 20036, USA
[d]Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106, USA

Abstract

Above-ground dry biomass of living trees including palms was estimated in 65 1 ha plots spanning a 1000 km^2 landscape in central Amazonia. The study area was located on heavily weathered, nutrient-poor soils that are widespread in the Amazon region. Biomass values were derived by measuring the diameter-at-breast-height (DBH) of all $\geq$10 cm trees in each plot, then using an allometric equation and correction factor for small trees to estimate total tree biomass. Detailed information on soil texture, organic carbon, available water capacity, pH, macro- and micro-nutrients, and trace elements was collected from soil surface samples (0–20 cm) in each plot, while slope was measured with a clinometer. Biomass estimates varied more than two-fold, from 231 to 492 metric tons ha^{-1}, with a mean of 356 ± 47 tons ha^{-1}. Simple correlations with stringent ($p < 0.006$) Bonferroni corrections suggested that biomass was positively associated with total N, total exchangeable bases, K^+, Mg^{2+}, clay, and organic C in soils, and negatively associated with Zn^+, aluminum saturation, and sand. An ordination analysis revealed one major and several minor soil gradients in the study area, with the main gradient discriminating sites with varying proportions of clay (with clayey soils having higher concentrations of total N, organic C, most cations, and lower aluminum saturation and less sand). A multiple regression analysis revealed that the major clay-nutrient gradient was the only significant predictor, with the model explaining 32.3% of the total variation in biomass. Results of the analysis suggest that soil-fertility parameters can account for a third or more of the variation in above-ground biomass in Amazonian terra-firme forests. We suggest that, because the conversion of forest to pasture tends to reduce the nitrogen, clay, organic carbon, and nutrient contents of soils, forests that regenerate on formerly cleared lands may have lower biomass than the original forest, especially in areas with low soil fertility. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Amazon basin; Biomass; Carbon cycle; Ferralsols; Global warming; Pasture conversion; Soils; Terra-firme forests; Tropical rainforests

*Corresponding author. Fax: +55-92-642-2050; e-mail: wfl@inpa.gov.br

1. Introduction

The rapid clearing and burning of tropical forests is an important source of greenhouse gases such as carbon dioxide, methane, and nitrous oxide, which are the main causes of global warming (Houghton, 1991; Fearnside, 1995). Nowhere is deforestation occurring faster than in the Amazon (Dale and Pearson, 1997; Whitmore, 1997). In Brazilian Amazonia, for example, forest clearing has accelerated in recent years, from about 1.4 million ha year^{-1} in the early 1990s to over 2.0 million ha year^{-1} since 1995 (INPE, 1996, 1998; Laurance, 1998).

Data on biomass and carbon storage in Amazonian forests are limited (e.g. Uhl et al., 1988; Brown et al., 1992a, 1995), and have been the subject of considerable controversy (e.g. Brown and Lugo, 1984, 1992; Fearnside, 1985, 1986, 1992). Recent estimates of Amazon biomass have varied by more than a factor of two, largely from the use of differing methodologies and study areas (Brown et al., 1995). Clearly, there is a need for additional studies of Amazon forest biomass, and of factors that cause natural variability in biomass.

Here we report on a large-scale study of biomass and soils in Amazonian terra-firme rainforest. Rainforest occupies most of the Amazon Basin and its biomass greatly exceeds that of any other forest type in South America (Brown, 1987). Very few studies have assessed effects of soils on tropical forest biomass, although investigators have often searched for relationships between soil or drainage features and plant species composition (e.g. Hoberg, 1986; Hubbell and Foster, 1986; Baillie et al., 1987; Brown, 1987; Ter Steege et al., 1993; Clark et al., 1995; Ruokolainen et al., 1997; Sollins, 1998; Tanner et al., 1998). In tropical forests that receive relatively infrequent disturbances, soil fertility is generally negatively correlated with species richness (Huston, 1980), excepting sites of extremely low fertility (such as white sand soils). The majority of rainforests in the Brazilian Amazon occur on heavily weathered, nutrient-poor soils (Brown, 1987), and, compared to rainforests on richer substrates, tend to have lower nutrient budgets and a higher proportion of nutrients contained in the living material of the ecosystem (Klinge, 1976; Herrera and Jordan, 1981).

In this study we describe variation in above-ground tree biomass in 65 1 ha plots spanning an extensive

(ca. 1000 km^2) central Amazonian landscape. Detailed data on soil chemistry and texture are used to assess the influence of soil factors on biomass in each plot. Based on our findings, we consider some ways in which soil degradation associated with pasture conversion could limit the accumulation of biomass in regenerating forests.

2. Methods

2.1. Study area

The study site spans an area of ca. 20 × 50 km in central Amazona, about 80 km N of Manaus, Brazil (2°30′S, 60°W). Today, this area is a partially fragmented landscape (Lovejoy et al., 1986; Laurance et al., 1997, 1998), but all biomass estimates reported here were recorded before or during initial forest clearing, from January 1981 to January 1987. Rainforests in the study area are evergreen and terra-firme (not seasonally flooded), and range from ca. 50–100 m elevation. The climate is tropically hot. Rainfall ranges from 1900–2500 mm annually with a dry season from June to October (Rankin-de Merona et al., 1992).

The dominant soils in the study area would be classified as xanthic ferralsols in the FAO/UNESCO system (and as Allic Haplorthozes [Oxisols] in the U.S. soil taxonomy, and as yellow latosols in the Brazilian system [see Beinroth, 1975]). Ferralsols are widespread in the Amazon Basin, heavily weathered, and usually have a low base saturation. They are often well aggregated, porous, and friable, with variable clay contents. Clay particles in ferralsols can form very durable aggregations, giving the soil poor water-holding characteristics, even with high clay contents (Richter and Babbar, 1991). Xanthic ferralsols in the Manaus area are derived from tertiary deposits and are typically acidic and very poor in nutrients such as P, Ca, and K (Chauvel et al., 1987).

2.2. Biomass

Estimates of above-ground dry biomass (AGBM) of live trees (including palms) were recorded in 65 square, 1 ha plots. AGBM was estimated by carefully measuring (to the nearest 1 mm) the diameters of all

trees ≥ 10 cm diameter-at-breast-height (DBH = 1.3 m above the ground). Buttressed trees were measured just above the buttresses. DBH measurements were converted to biomass estimates with an allometric model derived from 319 trees from local rainforests (Santos, 1996), as follows:

$$AGBM = (\exp(3.323 + (2.546 \times (\ln(DBH/100))))) \times 600 \tag{1}$$

The 319 trees used to derive Eq. (1) ranged from 5–120 cm DBH and were destructively sampled to determine AGBM. The trees were randomly selected at a site ca. 20 km SW of our study area, in very similar lowland terra-firme forest (Santos, 1996). AGBM estimates for each plot were adjusted upward by 12% to account for trees of <10 cm DBH (Jordan and Uhl, 1978). Lianas, the only other abundant woody plants in the study area, account for only a small fraction (<2%) of total AGBM in these forests (Laurance et al., 1997).

2.3. Soil predictors

A total of 25 soil parameters were recorded from soil-surface samples (0–20 cm) collected within each plot, while slope was measured with a clinometer. The field and laboratory methods used for soil analyses are detailed in Fearnside and Leal-Filho (in press), and briefly summarized here.

Each 1 ha plot was divided into 25 quadrats of 20×20 m each. Within each plot, 9–13 quadrats were selected for sampling, using an alternating pattern to provide good coverage of the plot. Within each quadrat, 15 surface samples were collected at haphazard locations using a soil auger, then bulked and subsampled. Composite samples for each quadrat were oven-dried, cleaned by removing stones and charcoal fragments, then passed through 20 and 2 mm sieves. In all the cases, values for soil parameters were derived separately for each quadrat, then combined to yield a mean value for each 1 ha plot.

Textural analyses were conducted to separate samples into clay (particles <0.002 mm diameter), silt (0.002–0.05 mm), fine sand (0.05–0.2 mm), and coarse sand (0.2–2 mm) fractions, using the pipette method. Available water capacity (equivalent to 'maximum plant-available water'), a measure of the

amount of water the soil can hold in a form extractable by plant roots, was estimated as the difference between the field capacity (moisture content retained in soil under a suction of 0.33 atmospheres) and the wilting point (moisture content retained at 15 atmospheres), using a pressure membrane apparatus. As is standard practice, samples were dried, sieved, and re-wetted before determining available water capacity, making the results only an index of water available to plants in the field.

A pH meter was used to measure soil pH. Total N was determined by Kjeldahl digestion (Parkinson and Allen, 1975) and total organic C by dry combustion. Total P was determined by digestion in HNO_3^+, $HClO_4$, and HF (Lim and Jackson, 1982), and reaction with ammonium molybdinate. PO_4^{3-} was measured in an autoanalyzer using the molybdenum blue method (Jorgenson, 1977). K^+ was determined by atomic emission spectroscopy at the Brazilian Center for Nuclear Energy and Agriculture (CENA), Piracicaba, São Paulo, while Ca^{2+}, Mg^{2+}, Na^+, S, Cu, Fe, Mn^{2+}, Zn^+, Al^{3+}, and H^+ in soil were measured by atomic absorption spectrophotometry at CENA after digestion in $HClO_4$, HNO_3, and H_2SO_4 (Jorgenson, 1977). Organic (Walkley–Black) carbon to total nitrogen (C/N) ratios were calculated to provide an index of N availability; if C/N > 15, there is very little N available for plant growth.

Cation measures were derived without Na^+, which is generally a minor constituent of exchangeable bases and was recorded at only a limited number of study sites. These measures included cation exchange capacity (CEC), which is the sum of K^+, Ca^{2+}, Mg^{2+}, Al^{3+}, and H^+; total exchangeable bases (TEB), the sum of K^+, Ca^{2+}, Mg^{2+}, and Na^+; and aluminum saturation, which is $((Al^{3+} + H^+)/CEC) \times 100$. Samples were digested in $HClO_4$, HNO_3, and H_2SO_4, and extracts for cation determination were buffered to pH 7.0, the standard practice in Brazil (SCNLS-EMBRAPA, 1979).

2.4. Data analysis

We used two strategies to search for associations between soil variables and biomass. First, simple correlations were used to test the effect of each variable on biomass. This involved a large number of tests, so a Bonferroni-corrected alpha value ($p = 0.006$) was

employed to reduce the likelihood of spurious corre-
lations. Bonferroni corrections were generated using
an experiment-wise error rate of 0.15 to limit the
probability of Type II statistical errors (cf. Chandler,
1995).

Second, we used an ordination analysis to describe
major gradients in the soil data, using a subset of 19
variables that were recorded at ≥ 38 plots, then tested
the effects of these gradients on biomass using a
multiple regression analysis. This approach ensures
that multiple regressions do not suffer from colinearity
effects because the ordination axes are statistically
independent, and minimizes the chance of spurious
associations because only a few axes are tested. Best-
subsets regression was used to select the predictors
(Sokal and Rohlf, 1995). Performance of the final
regression model was assessed by comparing the
standardized residuals to the fitted values and to each
significant predictor (cf. Crawley, 1993).

We used Principal Components Analysis (PCA) as
the ordination method, with analyses run on the PC-
ORD package (McCune and Mefford, 1995). All
variables were weighted equally prior to analysis,
using the standardization by maximum method
(Noy-Meir et al., 1975). A comparison of PCA with
results from other ordination techniques (Detrended
correspondence analysis, nonmetric multidimensional
scaling) revealed that the PCA axes were concordant
with those from the other methods, suffered from no
'arch effects' (cf. Gauch, 1982), and were slightly
better predictors of AGBM in multiple regression
models.

3. Results

3.1. Variation in biomass

In the 65 plots, AGBM was approximately normally
distributed (Fig. 1). AGBM varied more than two-
fold, from 230.7 to 491.6 metric tons ha^{-1}, although
most (83%) plots ranged from 300–425 tons ha^{-1}. The
overall mean was 355.8 ± 47.0 tons ha^{-1} ($\bar{X} \pm$ SD).

3.2. Simple correlations

Even with the stringent Bonferroni corrections, nine
of the 26 variables were significantly correlated with
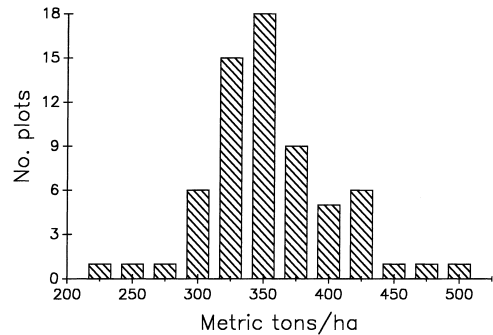AGBM (Table 1). Biomass was positively associated

Fig. 1. Frequency distribution of above-ground dry biomass of live
trees in 65 1 ha plots in central Amazonia.

with total N, total exchangeable bases, K$^+$, Mg^{2+},
clay, and organic C, and negatively associated with
Zn+, aluminum saturation, and fine sand.

Slope clearly had a negative effect on biomass, but
the correlation was marginally non-significant using
the Bonferroni correction ($r = -0.407$, $p = 0.012$),
probably because slope data were recorded at only 37
plots. Slope also had important effects on many soil
variables, with flatter areas having significantly higher
concentrations of clay, silt, organic C, total N, total
exchangeable bases, K$^+$, Mg^{2+}, Fe, and Mn^{2+}, and
steeper areas having more sand and higher aluminum
saturation (Table 2).

3.3. Ordination of soil variables

The ordination analysis revealed three main soil
gradients in the study area (Table 3). Subsequent axes
explained <6% of the total variation in the dataset, and
are not considered further. Axis 1, which captured over
half (53%) of the total variation in the dataset,
described a gradient between plots with high clay
content (high total N, organic C, exchangeable bases,
K$^+$, Mg^{2+}, Ca^{2+}, Al^{3+}, H$^+$, and CEC), and those with
high sand (high aluminum saturation). Axis 2, which
explained 19% of the variation, mainly described a
continuum in soil pH, with more-acidic sites having
less total P and higher Al^{3+} and Ca^{2+}. Axis 3, which
explained 8% of the variation, described a gradient
between sites with higher available water capacity,
and those with more phosphate.

Using best subsets and multiple regression analysis,
only PCA axis 1 was a significant predictor of AGBM
(Fig. 2). The slope of Axis 1 was positive, indicating

Table 1
Pearson correlations between above-ground tree biomass and soil and slope variables in central Amazonia

Variable	No. of plots	R	$\bar{X}$	SD
Soil texture				
Clay (%)	65	0.363[a]	55.0	13.6
Silt (%)	65	0.078	21.4	4.7
Fine sand (%)	65	−0.339[a]	5.3	3.8
Coarse sand (%)	65	−0.306	18.3	13.0
Soil water capacity				
Available water capacity	54	0.255	7.45	1.87
Topography				
Slope (°)	37	−0.407	10.50	8.92
Carbon				
Organic C (%)	65	0.343[a]	1.59	0.26
C/N ratio	38	−0.178	9.80	1.55
Acidity				
pH in water	38	0.320	4.16	0.25
Primary nutrients				
Total N (%)	38	0.619[a]	0.16	0.03
Total P (ppm)	38	0.327	118.9	45.6
PO_4^{3-} (m.e./100 g dry soil)	38	0.199	0.030	0.005
K^+ (m.e./100 g dry soil)	38	0.526[a]	0.06	0.01
Secondary nutrients				
Ca^{2+} (m.e./100 g dry soil)	38	0.349	0.06	0.03
Mg^{2+} (m.e./100 g dry soil)	38	0.491[a]	0.08	0.03
Na^+ (m.e./100 g dry soil)	18	0.103	0.05	0.02
S (ppm)	18	0.178	13.0	1.4
Micronutrients				
Cu (ppm)	24	0.377	0.33	0.12
Fe (ppm)	24	0.323	136.7	30.6
Mn^{2+} (ppm)	24	0.480	1.80	0.49
Zn^+ (ppm)	24	−0.601[a]	1.48	0.78
Other ions				
Al^{3+} (m.e./100 g dry soil)	38	0.143	1.63	0.29
H^+ (m.e./100 g dry soil)	38	0.346	0.70	0.12
Cation measures				
Cation exchange capacity	38	0.275	2.52	0.38
Aluminum saturation	38	−0.562[a]	92.43	1.67
Total exchangeable bases	38	0.529[a]	0.19	0.57

Also shown are the mean and standard deviation for each variable.
[a]Significant correlations, using a Bonferroni-corrected alpha value ($p = 0.006$).

higher biomass on more-clayey substrates. The regression was highly significant ($F_{1,36} = 17.18$, $P = 0.0002$), explaining 32.3% of the total variation in AGBM.

To further assess the effects of soil variables on AGBM, we used partial correlations to remove the effects of PCA Axis 1, then examined residual correlations between AGBM and the original soil variables (Table 4). When a Bonferroni correction was used, no variables were significantly correlated with AGBM, although four (pH, total N, Al^{3+}, CEC) were significant or nearly so at the $p < 0.05$ level. Notably, neither

Table 2
Influence of slope on soil variables in central Amazonia

Variable	No. of plots	R
Clay	37	−0.615[a]
Silt	37	−0.453[a]
Fine sand	37	0.652[a]
Coarse sand	37	0.600[a]
Available water capacity	34	−0.308
Organic C	37	−0.537[a]
C/N ratio	34	0.062
pH in water	34	−0.247
Total N	34	−0.605[a]
Total P	34	−0.332
PO_4^{3-}	34	0.061
K^+	34	−0.487[a]
Ca^{2+}	34	−0.267
Mg^{2+}	34	−0.585[a]
Na^+	16	−0.594
S	11	−0.141
Cu	20	−0.511
Fe	20	−0.652[a]
Mn^{2+}	20	−0.708[a]
Zn^+	20	0.580
Al^{3+}	34	−0.186
H^+	34	−0.370
Cation exchange capacity	34	−0.293
Aluminum saturation	34	0.526[a]
Total exchangeable bases	34	−0.519[a]

[a]Significant correlations, using a Bonferroni-corrected alpha value ($p = 0.006$).

Table 3
Pearson correlations between 19 soil variables and three ordination axes produced by principal components analysis

Variable	Axis 1	Axis 2	Axis 3
Clay	0.976[a]	−0.023	0.027
Silt	0.696[a]	−0.390	0.390
Fine sand	−0.963[a]	0.012	−0.099
Coarse sand	−0.963[a]	0.123	−0.100
Available water capacity	0.456	−0.441	0.497[a]
Organic C	0.788[a]	0.182	−0.335
C/N ratio	−0.337	0.444	−0.365
pH in water	0.066	−0.893[a]	−0.345
N total	0.958[a]	−0.106	−0.073
P total	0.365	−0.824[a]	0.011
PO_4^{3-}	0.063	−0.185	−0.554[a]
K^+	0.759[a]	−0.466	−0.258
Ca^{2+}	0.646[a]	0.637[a]	0.028
Mg^{2+}	0.887[a]	0.136	−0.292
Al^{3+}	0.619[a]	0.665[a]	0.236
H^+	0.738[a]	−0.253	0.209
Aluminum saturation	−0.777[a]	−0.121	0.400
Cation exchange capacity	0.801[a]	0.453	0.216
Total exchangeable bases	0.913[a]	0.269	−0.194
Variation explained (%)	53.1	18.7	8.4

[a]Significant correlations, using a Bonferroni-corrected alpha value ($p = 0.002$).

phosphate nor total P had significant effects on AGBM.

3.4. Effects of nitrogen

As the conversion of forest to pasture can lead to substantial losses of clay, organic C, and N, P, and K stocks in soil, we explicitly assessed the influence of these five factors on AGBM, excluding all other soil variables. Using multiple regression analysis, total N was selected as a highly significant predictor ($F_{1,36} = 22.41$, $p < 0.0001$), accounting for 38.4% of the variation in AGBM (Fig. 3). No other variables were included in the final model, even when a number of additional, key variables were included as potential predictors (available water capacity, C/N ratio, pH, PO_4^{3-}, aluminum saturation, total exchangeable bases).

4. Discussion

4.1. Soil variation

The dominant soils in our study area, ferralsols, are estimated to encompass about 40% of the Amazon Basin (Richter and Babbar, 1991). Although heavily weathered and infertile, these soils often support dense evergreen rainforests that have evolved an array of efficient nutrient-conservation mechanisms in order to cope with the paucity of soil nutrients (Herrera et al., 1978; Stark and Jordan, 1978; Herrera and Jordan, 1981).

On a landscape scale, the dynamics of soils and forests in the central Amazon are markedly influenced by local topography (Table 2). Flat areas have high clay contents (typically 45–75%), which are associated with relatively high (although still very modest) concentrations of important nutrients such as nitrogen and exchangeable bases (K^+, Ca^{2+}, Mg^{2+}, Na^+). On sloping terrain, however, a 'podzolization' process occurs over time because lateral water movement

Fig. 2. Relationship betweeen PCA Axis 1 and above-ground biomass of live trees in central Amazonia.
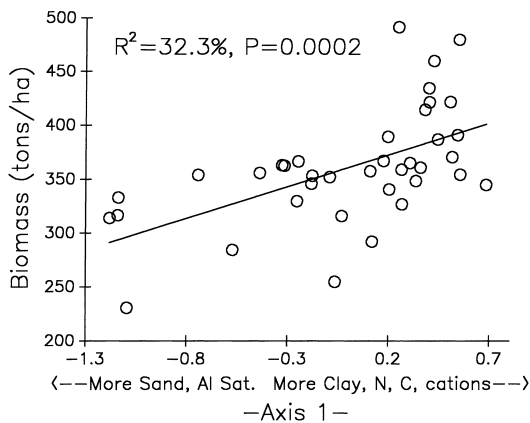

Fig. 3. Relationship between total soil nitrogen and above-ground biomass of live trees in central Amazonia.

Table 4
Associations of soil variables with above-ground tree biomass, after removing effects of PCA Axis 1 with partial correlation analyses ($n = 38$ plots)

Variable	Rresid	p
Clay	−0.115	0.492
Silt	0.018	0.914
Fine sand	0.046	0.784
Coarse sand	0.076	0.650
Available water capacity	0.072	0.668
Organic C	0.131	0.433
C/N ratio	0.018	0.914
pH in water	0.343	0.038
N total	0.318	0.055
P total	0.157	0.347
PO_4^{3-}	0.198	0.233
K^+	0.176	0.291
Ca^{2+}	0.029	0.863
Mg^{2+}	−0.036	0.830
Al^{3+}	−0.324	0.050
H^+	−0.133	0.426
Aluminum saturation	−0.233	0.159
Cation exchange capacity	−0.367	0.025
Total exchangeable bases	0.030	0.858

No variables were significant when a Bonferroni-corrected alpha values ($p = 0.008$) was used.

results in the gradual destruction of clay-rich upper soil horizons. This ultimately leads to the creation of dendritic valley systems with increasing sand on lower slopes and valley bottoms (Chauvel et al., 1987; Bravard and Righi, 1989). At the extreme end of the clay-san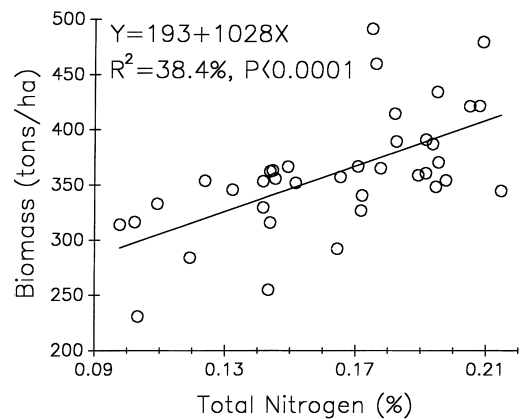d gradient, white sands predominate and may result in the development of heath-like vegetation (termed campina and campinarana), composed of only scrubby trees and shrubs (Guillaumet, 1987; Duivenvoorden, 1996).

The ordination analysis revealed one major and two minor soil gradients in our study area (Table 3). The most important gradient is the clay-sand continuum, with sand increasing on slopes and in gullies. Clayey soils have higher concentrations of nitrogen and most cations, including aluminum ions. Clays have more binding sites for cations, largely because clay content is positively correlated with organic matter, which is an important determinant of cation exchange capacity in soils with clays of low activity, like the Amazonian ferralsols (Lenthe, 1991). In allic (high aluminum) clays that are common in Amazonia, a strong positive correlation also exists between clay content and aluminum (Fearnside and Leal-Filho, in press).

The second gradient is related to soil pH, with more-acidic sites having less total phosphorus and higher aluminum and calcium ion concentrations. Soil pH is known to strongly influence aluminum, calcium, and magnesium ions in tropical soils (Sanchez, 1976; Fearnside, 1984). However, while the relationship between pH and Al^{3+} is in the expected direction, the relationship with Ca^{2+} is the reverse of expected. This, and the fact that Ca^{2+} is also correlated with Axis 1 (Table 3), suggests that Ca^{2+} levels are being influenced by several factors. It is noteworthy that the acidity gradient was largely independent of the major clay-sand continuum.

The third axis was mainly a gradient between soil phosphate and available water capacity. Phosphate, the form of phosphorus available to plants, was not significantly correlated with total phosphorus in the study area ($r = 0.18$, $df = 36$, $p > 0.25$), indicating that additional factors influence phosphate availability. Acidity is probably one key factor; phosphate declines when soil pH falls below 5.5 (Young, 1976), and soils in our study area are highly acidic, with pH ranging from 3.4 to 4.5. Phosphate is also positively associated with organic carbon and iron and aluminum oxides in Amazonian ferralsols, which in turn increase in clayey soils (Bennema, 1977; Proctor, 1995).

4.2. Biomass in relation to soils

Studies that attempt to correlate vegetation with soil features have limitations. Since many soil parameters are inter-correlated, confounding factors may obscure effects of some variables. A failure to find significant correlations can also occur because samples encompass only part of the range of variation in a soil parameter, or because threshold effects create nonlinearities between variables (Sollins, 1998). Thus, following correlative studies, field experiments are needed to firmly establish cause and effect relationships between vegetation and soil parameters (e.g., Tanner et al., 1998).

Despite such limitations, our results clearly suggest that above-ground biomass of Amazonian terra-firme forests, at least those on nutrient-poor ferralsols, are influenced by soil characteristics. This result initially appears at variance with other studies (cf. Proctor, 1995). Based on their review of rainforest mineral nutrition, for example, Vitousek and Sanford (1986) conclude that ''an association between soil fertility and above-ground biomass is ... unlikely in any but the most extreme cases'', while Anderson and Spencer (1991) suggest that ''there appears to be little evidence that the stature and productivity of mature forests are related to the inherent fertility of parent soil''. It may be, however, that the heavily leached soils typical of much of the Amazon represent just the kind of 'extreme case' mentioned by Vitousek and Sanford (1986), where soil nutrients do in fact limit above-ground biomass.

Both the simple correlations (Table 1) and regression models (Fig. 3) suggested that total nitrogen was the single most important soil variable. This result runs counter to several recent studies. In a recent review of soil factors that influence species composition in lowland tropical rainforests, for example, Sollins (1998) suggested the key factors are, in order of decreasing importance, phosphorus availability, aluminum toxicity, drainage, water-holding capacity, and availability of potassium, calcium, and magnesium. Nitrogen availability apparently constrains productivity at tropical montane sites (Vitousek and Sanford, 1986; Tanner et al., 1998), but is thought rarely to limit growth in lowland rainforests (Sollins, 1998). Nitrogen was, however, assumed to limit plant growth in a logging and nutrient-dynamics model developed for a lowland site near our study area (Biot et al., 1997).

It seems possible that nitrogen emerged as a key predictor simply because phosphate, generally regarded as the most critical limiting factor in lowland rainforest soils, varied little across our study area (Table 1). Phosphate levels were uniformly low and ranged from only 0.022 to 0.041 milli-equivalents per 100 g of soil, less than a two-fold difference. Newbery and Proctor (1984) suggest that differences in soil chemistry need to be considerably larger, on the order of 3–5-fold, in order to cause detectable shifts in rainforest floristic composition. It is also possible that the phosphate pool in our study area is seasonally dynamic, and that a single field measurement fails to provide a reliable estimate of long-term phosphate availability.

Aside from the seemingly weak effect of phosphate, our results are intuitively appealing: above-ground biomass increases on clayey soils with greater nitrogen, organic matter, and exchangeable bases, and declines in sandy soils with higher aluminum saturation (Fig. 2). Aluminum ions are toxic to plants in high concentrations, and in acidic soils usually form complexes with phosphate, exacerbating the problem of phosphate limitation (Sanchez, 1976). The strong correlation between biomass and zinc ($r = -0.601$, $p = 0.002$; Table 1) could be an artifact of a small sample size for that variable ($n = 24$ plots), or may reflect intercorrelations with other soil parameters (e.g. zinc was strongly correlated with nitrogen, clay, and total exchangeable bases, $r^2 > 70\%$).

Above-ground biomass in our study area varied more than two-fold, and more than a third of this

variation could be explained by measured soil variables (Fig. 3). Soils could affect tree biomass in at least two ways. First, soils may influence species composition. Large, emergent species which contain a high fraction of forest biomass (Clark and Clark, 1995), for example, could be associated with the most fertile soils. Second, trees could simply grow bigger on the most fertile substrates, regardless of species composition. Soil and drainage factors appear to have a marked influence on floristic composition in Amazonian terra-firme forests (Lescure and Boulet, 1985; Rankin-de Merona et al., 1992; Ruokolainen et al., 1997; Sabatier et al., 1997), suggesting that the first of these mechanisms could be relatively important.

4.3. Management implications

Our findings have several implications. First, the mean value obtained for above-ground biomass of live trees in our extensive study area (356 ± 47 tons ha^{-1}) is up to 120% higher than comparable estimates from other parts of the Amazon (Klinge and Rodrigues, 1973; Uhl and Jordan, 1984; Uhl et al., 1988; Brown and Lugo, 1990, 1992; Brown et al., 1992a, b, 1995; Salomão et al., 1998), and clearly supports Fearnside's (1997) estimate of high biomass values for central Amazonian forests. This is a particular concern because deforestation and logging activities are now rapidly expanding in the central Amazon (Laurance, 1998), and could become a major new source of greenhouse gas emissions.

Second, our results highlight the fact that heavily weathered Amazonian soils are of low fertility, acidic, have poor water-holding characteristics, and contain high concentrations of toxic aluminum ions (Table 1). These factors are likely to be strongly limiting to agricultural development (Fearnside and Leal-Filho, in press), and under such conditions the maintenance of intact forest for natural ecosystem services (e.g. carbon storage, watershed and biodiversity maintenance) is likely to be a far wiser use of land from a long-term perspective.

Finally, the fact that forest biomass appears markedly influenced by soil nitrogen, organic carbon, clay, and cation concentrations is important (Figs. 2 and 3). In the Amazon, extensive areas of forest are regenerating on abandoned cattle pastures (Fearnside, 1996). The burning of slash to clear pastures leads to heavy losses of nitrogen, carbon, and phosphorus from the prefire nutrient-pools (Kauffman et al., 1995), while rapid leaching removes phosphorus and potassium (Moran, 1990), accelerating pasture depletion. Clay also declines in pastures, both from surface erosion and from the downward transport of clay particles by water percolation (Lal, 1977; Feller et al., 1991). Finally, organic carbon in upper soil layers is reduced because repeated burning reduces litter inputs into the soil, because higher soil temperatures (from direct insolation) increase soil respiration rates (Fearnside and Barbosa, 1998), and because the loss of clay means there are fewer iron and aluminum oxides to form stable complexes with organic radicals (Feller et al., 1991).

These patterns suggest that soil degradation may limit the capacity of regenerating forests to accumulate biomass, or at least slow the rate of accumulation. This is especially likely to occur where soils are heavily weathered and infertile. For example, Saldarriaga et al. (1986) concluded that abandoned farms in the Upper Rio Negro Basin required 140–200 years for complete biomass recovery, a much greater period than was needed in more fertile areas in Central America (Snedaker, 1970; Lugo et al., 1974). Thus, on the infertile soils that typify much of Amazonia, pasture conversion is likely have long-lasting effects on forest carbon pools, even where forests are allowed to regenerate.

Acknowledgements

References

Anderson, J.M., Spencer, T., 1991. Carbon, Nutrient and Water Balances of Tropical Rain Forest Ecosystems Subject to

Disturbance: Management Implications and Research Proposals. MAB Digest 7, UNESCO, Paris.

Baillie, I.C., Ashton, P.S., Court, M.N., Anderson, A.R., Fitzpatrick, E.A., Tinsley, J., 1987. Site characteristics and the distribution of tree species in mixed dipterocarp forest on Tertiary sediments in central Sarawak, Malaysia. J. Tropical Ecol. 3, 201–220.

Beinroth, F.H., 1975. Relationships between U.S. soil taxonomy, the Brazilian system, and FAO/UNESCO units. In: Bornemisza, E., Alvarado, A. (Eds.), Soil Management in Tropical America, North Carolina State University, Raleigh, NC, pp. 97–108.

Bennema, J., 1977. Soils. In: Alvim, de T.P., Kozlowski, T.T. (Eds.), Ecophysiology of Tropical Crops. Academic Press, New York, pp. 29–55.

Biot, Y., Brilhante, J., Veloso, J., Ferraz, J., Leal-Filho, N., Higuchi, N., Ferreira, S., Dejardins, T., 1997. INFORM - O modelo florestal do INPA, In: Higuchi, N., Ferraz, J., Antony, L., Luizao, F., Biot, Y., Hunter, I., Proctor, J., Ross, S. (Eds.), Bionte: Biomassa e Nutrientes Florestais: Relatório Final. National Institute for Research in the Amazon (INPA), Manaus, Brazil, pp. 271–318.

Bravard, S., Righi, D., 1989. Geochemical differences in an oxisol-spodosol toposequence of Amazonia Brazil. Geoderma 44, 29–42.

Brown, S., Lugo, A.E., Iverson, L.R., 1992a. Processes and lands for sequestering carbon in the tropical forest landscape Water, Air, and Soil Pollution 64, 139–155.

Brown, I.F., Nepstad, D.C., Pires, O., Luz, L.M., Alechandre, A.S., 1992b. Carbon storage and land-use in extractive reserves, Acre, Brazil. Environmental Conservation 19, 307–315.

Brown, I.F., Martinelli, L.A., Thomas, W.W., Moreira, M.Z., Ferreira, C.A., Victoria, R.A., 1995. Uncertainty in the biomass of Amazonian forests: An example from Rondonia, Brazil. For. Ecol. Manage. 75, 175–189.

Brown, K.S., 1987. Soils and vegetation. In: Whitmore, T.C., Prance, G.T. (Eds.), Biogeography and Quaternary History in Tropical America. Oxford Monographs in Biogeography 3, Oxford, UK, pp. 19–45.

Brown, S., Lugo, A.E., 1984. Biomass of tropical forests: A new estimate based on forest volumes. Science 223, 1290–1293.

Brown, S., Lugo, A.E., 1990. Biomass estimates for Brazil's Amazonian moist forests. In: Forest '90: Annals of the First International Symposium on Environmental Studies on Tropical Rain Forests, Manaus, Brazil, pp. 46–52.

Brown, S., Lugo, A.E., 1992. Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. Interciencia 17, 8–18.

Chandler, C.R., 1995. Practical considerations in the use of simultaneous inference for multiple tests. Anim. Behaviour 49, 524–527.

Chauvel, A., Lucas, Y., Boulet, R., 1987. On the genesis of the soil mantle of the region of Manaus, Central Amazonia, Brazil. Experientia 43, 234–240.

Clark, D.B., Clark, D.A., 1995. Abundance, growth and mortality of very large trees in neotropical lowland rain forest. For. Ecol. Manage. 80, 235–244.

Clark, D.A., Clark, D.B., Rosa, S.M., Marco, V.C.C., 1995. Edaphic and human effects on landscape-scale distributions of tropical rain forest plants. Ecology 76, 2581–2594.

Crawley, M.J., 1993. GLIM for Ecologists. Blackwell, London, UK, p. 379.

Dale, V.H., Pearson, S.M., 1997. Quantifying habitat fragmentation due to land use change in Amazonia. In: Laurance, W.F., Bierregaard, R.O. (Eds.), Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. University of Chicago Press, Chicago, pp. 400–410.

Duivenvoorden, J.F., 1996. Patterns of tree species richness in rain forests of the Middle Caqueta area, Columbia, NW Amazonia. Biotropica 28, 142–158.

Fearnside, P.M., 1984. Initial soil quality conditions on the Trans-Amazon Highway of Brazil and their simulation in models for estimating human carrying capacity. Tropical Ecol. 25, 1–21.

Fearnside, P.M., 1985. Brazil's Amazon forest and the global carbon problem. Interciencia 10, 179–186.

Fearnside, P.M., 1986. Brazil's Amazon forest and the global carbon problem: Reply to Lugo and Brown. Interciencia 11, 58–64.

Fearnside, P.M., 1992. Forest biomass in Brazilian Amazonia: Comments on the estimate by Brown and Lugo. Interciencia 17, 19–27.

Fearnside, P.M., 1995. Hydroelectric dams in the Brazilian Amazon as sources of greenhouse gases. Environ. Conservation 22, 7–19.

Fearnside, P.M., 1996. Amazonian deforestation and global warming: Carbon stocks in vegetation replacing Brazil's Amazon forest. For. Ecol. Manage. 80, 21–34.

Fearnside's, P.M., 1997. Greenhouse gases from deforestation in Brazilian Amazonia: Net committed emissions. Climatic Change 35, 321–360.

Fearnside, P.M., Barbosa, R.I., 1998. Soil carbon changes from conversion of forest to pasture in Brazilian Amazonia. For. Ecol. Manage. 108, 147–166.

Fearnside, P.M., Leal-Filho, N., in press. Soil and development in Amazonia: lessons from the Biological Dynamics of Forest Fragments Project. In: Bierregaard, R.O., Gascon, C., Lovejoy, T.E., Mesquita, R. (Eds.), Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest. Yale University Press, New Haven, Connecticut.

Feller, C., Fritsch, E., Poss, R., Valentin, C., 1991. Effet de la texture sur le stockage et al dynamique des matieres organiques dans qualques sols ferugineux et feralitiques. Cahiers ORSTOM, Serie Pedologie 26, 25–36.

Gauch, H.G., 1982. Multivariate Analysis in Community Ecology. Cambridge University Press, Cambridge, UK, pp. 298.

Guillaumet, J.-L., 1987. Some structural and floristic aspects of the forest. Experientia 43, 241–251.

Herrera, R., Jordan, C.F., 1981. Nitrogen cycle in a tropical Amazonian rain forest: The caatinga of low mineral nutrient status. Ecology Bulletin (Stockholm) 33, 493–505.

Herrera, R., Merida, T., Stark, N., Jordan, C.F., 1978. Direct phosphorus transfer from leaf litter to roots. Naturwissenschaften 65, 208–209.

Hoberg, P., 1986. Soil nutrient availability, root symbioses and tree species composition in tropical Africa: A review. J. Tropical Ecol. 2, 359–372.

Houghton, R.A., 1991. Tropical deforestation and atmospheric carbon dioxide. Climatic Change 19, 99–118.

Hubbell, S.P., Foster, R.B., 1986. Commonness and rarity in a neotropical forest: Implications for tropical tree conservation. In: Soule. M.E. (Ed.), Conservation Biology: The Science of Scarcity and Diversity. Sinauer, Sunderland, Massachusetts, pp. 205–231.

Huston, M., 1980. Soil nutrients and tree species richness in Costa Rican forests. J. Biogeography 7, 147–157.

INPE, 1996. Deforestation estimates in the Brazilian Amazon, 1992–1994. Instituto Nacional de Pesquisas Espaciais, São José dos Campos, Brazil.

INPE, 1998. Deforestation estimates in the Brazilian Amazon, 1995–1997. Instituto Nacional de Pesquisas Espaciais, São José dos Campos, Brazil.

Jordan, C., Uhl, C., 1978. Biomass of a tierra firme forest of the Amazon Basin. Oecologia Plantarum 13, 387–400.

Jorgenson, S.S., 1977. Guia Analítico: Metodologia Utilizada para Análises Químicas de Rotina. Centro de Energia Nuclear na Agricultura (CENA), Piracicaba, Sao Paulo, Brazil, p. 24.

Kauffman, J.B., Cummings, D.L., Ward, D.E., Babbitt, R., 1995. Fire in the Brazilian Amazon: Biomass, nutrient pools, and losses from slashed primary forests. Oecologia 104, 397–408.

Klinge, H., 1976. Root mass estimation in lowland tropical rainforests of Central Amazonia, Brazil. III. Nutrients in fine roots from giant humus podzols. Tropical Ecol. 16, 28–38.

Klinge, H., Rodrigues, W.A., 1973. Biomass estimation in central Amazonian rain forest. Acta Cientifica Venezolana 24, 225–237.

Lal, R., 1977. Analysis of factors affecting rainfall erosivity and soil erodibility. In: Greenland, D.J., Lal, R. (Eds.), Soil Conservation and Management in the Humid Tropics. Wiley, New York, pp. 49–56.

Laurance, W.F., 1998. A crisis in the making: Responses of Amazonian forests to land use and climate change. Trends in Ecol. Evol. 13, 411–415.

Laurance, W.F., Ferreira, L.V., Rankin-de Merona, J.M., Laurance, S.G., 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology 69, 2032–2040.

Laurance, W.F., Laurance, S.G., Ferreira, L.V., Rankin-de Merona, J.M., Gascon, C., Lovejoy, T.E., 1997. Biomass collapse in Amazonian forest fragments. Science 278, 1117–1118.

Lenthe, H.R., 1991. Methods for monitoring organic matter in soil. In: Studies on the Utilization and Conservation of Soil in the Eastern Amazon Region. Deutsche Gesellschaft fur Technische Zusammenarbeit, Eschborn, Germany, pp. 119–129.

Lescure, J.P., Boulet, R., 1985. Relationships between soil and vegetation in a tropical rain forest in French Guiana. Biotropica 17, 155–164.

Lim, C.H., Jackson, M.L., 1982. Dissolution for total elemental analysis. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), Methods of Soil Analysis, Part 2: Chemical and Microbiological Properties. Am. Soc. Agron. and Soil Sci. Soc. Am., Madison, WI, pp. 1–12.

Lovejoy, T.E., Bierregaard, R.O., Rylands, A.B., Malcolm, J.R., Quintela, C.E., Harper, L.H., Brown, K.S., Powell, A.H., Powell, G. V.N., Schubart, H.O.R., Hays, M.B., 1986. Edge and other effects of isolation on Amazon forest fragments. In: Soule, M.E. (Ed.), Conservation Biology: The Science of Scarcity and Diversity. Sinauer, Sunderland, MA, pp. 257–285.

Lugo, A.E., Brinson, M., Ceranevivas, M., Gist, C., Inger, R., Jordan, C., Lieth, H., Milstead, W., Murphy, P., Smythe, N., Snedaker, S., 1974. Tropical ecosystem structure and function. In: Farnworth, E.G., Golley, F.B. (Eds.), Fragile Ecosystems. Springer, New York, pp. 67–111.

McCune, B., Mefford, M.J., 1995. PC-ORD: Multivariate Analysis of Ecological Data, Version 2.0. MjM Software, Glenenden Beach, Oregon, USA, p. 126.

Moran, E.F., 1990. A Ecologia Humana das Populações da Amazonia. Editoria Vozes, Petrópolis, Brazil, p. 367.

Newbery, D.M., Proctor, J., 1984. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. J. Ecol. 72, 475–493.

Noy-Meir, I., Walker, D., Williams, W.T., 1975. Data transformations in ecological ordination. II. On the meaning of data standardization. J. Ecol. 63, 779–800.

Parkinson, J.A., Allen, S.E., 1975. A wet oxidation procedure suitable for the determination of nitrogen and mineral nutrients in biological material. Commun. Soil Sci. Plant Analysis 6, 1–11.

Proctor, J., 1995. Rainforests and their soils. In: Primack, R.B., Lovejoy, T.E. (Eds.), Ecology, Conservation, and Management of Southeast Asian Rainforests. Yale University Press, New Haven, CT, pp. 87–104.

Rankin-de Merona, J.M., Prance, J.M., Hutchings, R.W., Silva, M.F., Rodrigues, W.A., Uehling, M.A., 1992. Preliminary results of a large-scale inventory of upland rain forest in the central Amazon. Acta Amazonica 22, 493–534.

Richter, D.D., Babbar, L.I., 1991. Soil diversity in the tropics. Adv. Ecological Res. 21, 315–389.

Ruokolainen, K., Linna, A., Tuomisto, H., 1997. Use of Melastomaceae and pteridophytes for revealing phytogeographical patterns in Amazonian rain forests. J. Tropical Ecol. 13, 243–256.

Sabatier, D., Grimaldi, M., Prevost, M.-F., Guillaumet, J.L., Godron, M., Dosso, M., Curmi, P., 1997. The influence of soil cover organization on the floristic and structural heterogeneity of a Guianan rain forest. Plant Ecol. 131, 81–108.

Saldarriaga, J.G., West, D.C., Tharp, M.L., 1986. Forest Succession in the Upper Rio Negro of Colombia and Venezuela. Environmental Sciences Division Publication 2694, Oak Ridge National Laboratory, Oak Ridge, Tennessee.

Salomão, R.P., Nepstad, D.C., Vieira, I.C., 1998. Biomassa e estoque de carbono de florestas tropicais primarias e secundarias. In: Gascon, C., Moutinho, P. (Eds.), Floresta Amazônica: Dinamica, Regeneração e Manejo. National Institute for Research in the Amazon (INPA), Manaus, Brazil, pp. 99–119.

Sanchez, P.A., 1976. Properties and Management of Soil in the Tropics. Wiley, New York, p. 618.

Santos, J., 1996. Análise de modelos de regressao para estimar a fitomassa de floresta tropical umida de terra-firme da

Amazonia Central. Ph.D. thesis, Universidade Federal de Vicosa, Minas Gerais, Brazil.

SCNLS-EMBRAPA., 1979. Manual de Métodos de Análise de Solo. Servio Nacional de Levantamento e Conservação de Solos-Empresa Brasileira de Pesquisa Agropecuária (SNCLS-EMBRAPA), Rio de Janeiro, Brazil.

Sokal, R.F., Rohlf, F.H.J., 1995. Biometry, 3rd ed. W. H. Freeman, San Francisco, p. 887.

Sollins, P., 1998. Factors influencing species composition in tropical lowland rain forest: Does soil matter? Ecology 79, 23–30.

Snedaker, S.C., 1970. Ecological studies on tropical moist forest succession in eastern lowland Guatemala. Ph.D. thesis, University of Florida, Gainesville, FL, p. 131.

Stark, N.M., Jordan, C.F., 1978. Nutrient retention by the root mat of an Amazonian rain forest. Ecology 59, 434–437.

Tanner, E.V., Vitousek, P.M., Cuevas, E., 1998. Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. Ecology 79, 10–22.

Ter Steege, H., Jetten, V.G., Polak, A.M., Werger, M.J.A., 1993. Tropical rain forest types and soil factors in a watershed area in Guyana. J. Vegetation Sci. 4, 705–716.

Uhl, C., Buschbacher, R., Serrao, E.A.S., 1988. Abandoned pastures in eastern Amazonia. I. Patterns of plant succession. J. Ecology 76, 633–681.

Uhl, C., Jordan, C.F., 1984. Vegetation and nutrient dynamics during 5 years of succession following forest cutting and burning in the Rio Negro Region of Amazonia. Ecology 65, 1976–1990.

Vitousek, P.M., Sanford, R.L., 1986. Nutrient cycling in moist tropical forest. Ann. Rev. Ecol. Systematics 17, 137–167.

Whitmore, T.C., 1997. Tropical forest disturbance, disappearance, and species loss. In: Laurance, W.F., Bierregaard, R.O. (Eds.), Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. University of Chicago Press, Chicago, pp. 3–12.

Young, A., 1976. Tropical Soils and Soil Surveys. Cambridge University Press, Cambridge, UK, p. 468.