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ECOSYSTEMS

Heterogeneity of Soils and Vegetation in an Eastern Amazonian Rain Forest: Implications for Scaling Up Biomass and Production

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Abstract

Transferring fine-scale ecological knowledge into an understanding of earth system processes presents a considerable challenge to ecologists. Our objective here was to identify and quantify heterogeneity of, and relationships among, vegetation and soil properties in terra firme rain forest ecosystems in eastern Amazonia and assess implications for generating regional predictions of carbon (C) exchange. Some of these properties showed considerable variation among sites; soil textures varied from 11% to 92% clay. But we did not find any significant correlations between soil characteristics (percentage clay, nitrogen [N], C, organic matter) and vegetation characteristics (leaf area index [LAI], foliar N concentration, basal area, biomass, stem density). We found some evidence for increased drought stress on the sandier sites: There was a significant correlation between soil texture and wood $\delta^{13}C$ (but not with foliar $\delta^{13}C$); volumetric soil moisture was lower at sandier sites; and some canopy foliage had large, negative dawn water potentials (ψ_{ld}), indicating limited water availability in the rooting zone. However, at every site at least one foliage sample indicated full or nearly full rehydration, suggesting significant interspecific variability in drought vulnerability. There were significant differences in foliar $\delta^{15}N$ among sites, but not in foliar % N, suggesting differences in N cycling but not in plant access to N. We used an ecophysiological model to examine the sensitivity of gross primary production (GPP) to observed inter- and intrasite variation in key driving variables—LAI, foliar N, and ψ_{ld}. The greatest sensitivity was to foliar N; standard errors on foliar N data translated into uncertainty in GPP predictions up to ±10% on sunny days and ±5% on cloudy days. Local variability in LAI had a minor influence on uncertainty, especially on sunny days. The largest observed reductions in ψ_{ld} reduced GPP by 4%–6%. If uncertainty in foliar N estimates is propagated into the model, then GPP estimates are not significantly different among sites. Our results suggest that water restrictions in the sandier sites are not enough to reduce production significantly and that texture is not the key control on plant access to N.

Key words: carbon and nitrogen isotopes; leaf area index (LAI); gross primary production (GPP); Large-Scale Biosphere–Atmosphere experiment; soil texture; Amazonia.

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Introduction

Uncertainties about the role of the Amazon basin in regional and global biogeochemistry, and the basin's interactions with global climate, have motivated an international, Brazil-led study, the Large-Scale Biosphere–Atmosphere experiment in Amazonia (LBA). A significant proportion of global vegetation carbon (C) stocks are located in the Amazon basin, and recent research has quantified the high productivity of rain forest ecosystems (Malhi and others 1999). However, attempts to generate accurate regional estimates of C or nutrient stocks and fluxes are hampered by limited data. Continuous C exchange measurements are only available for a few sites, and although the number of sites is steadily increasing, coverage is very patchy. Remote-sensing data offers the possibility of frequent, spatially extensive data, but generating meaningful relationships with ecological parameters, such as biomass, requires an investment in intensive field work and the development of new technology to cope with saturation responses (Waring and Running 1998). Although atmospheric sampling from aircraft or flask networks offers the possibility of constraining regional flux estimates, connecting detailed field measurements to these broader, integrated data sets requires a detailed understanding of heterogeneity of ecological structure and activity across a range of scales.

Generating bottom–up estimates of regional C budgets thus requires information on the heterogeneity and diversity of ecosystem types and structure on many scales (Williams and others 2001). A particular concern is that the parameters used at one scale account for intrinsic variability at finer scales. For example, current models of global and regional C exchange typically use spatial resolutions varying from 8×8 km to $1° \times 1°$ (Potter and others 1998). However, critical drivers such as leaf area index (LAI) or soil texture are likely to vary over finer scales than these.

Understanding the nature of this variability is clearly important for characterizing the uncertainty connected with the model predictions (Williams and Rastetter 1999). Our objective was to identify and quantify the heterogeneity of, and relationships among, vegetation and soil properties in terra firme rain forest ecosystems in eastern Amazonia and assess the implications for generating regional predictions of C exchange.

The Amazon basin is geologically old with diverse patterns of soil texture—there is considerable heterogeneity of soil types in tropical lowlands. Soil heterogeneity is potentially important, because texture affects the ability of soils to retain water, nutrient ions, and carbon (Silver and others 2000). Sandy soils are associated with higher fine-root biomass and slower litter turnover rates than loam or clay soils (Cuevas and Medina 1988). Some studies have identified correlations between soil and vegetation properties (Laurance and others 1999), but it is unclear to what extent these are general. If relationships between soil and vegetation do exist, they would assist the construction of C budgets by providing extra constraints on estimates. These relationships would also provide insight into underlying function.

We devised a methodology to investigate three linked hypotheses concerning expected patterns in ecosystem structure and function, patterns that could ultimately assist the process of scaling up. We proposed that:

1. Soil texture is a key control on soil moisture content and thus leaf water status. Expected observation: Leaf water potential measurements and biomass C isotope data will indicate greater soil moisture stress on sandier soils.
2. Soil texture is a key control on total soil nutrient content and thus on ecosystem nutrient cycling. Expected observation: Vegetation nutrient stocks will be lower on sandy soils than on loam and clay soils.
3. Available soil water and soil nutrient stocks are critical controls on C cycling. Expected observation: Increased soil moisture stress and lower soil nutrient stocks on sandy soils will result in reduced primary production and less standing biomass than on clay and loam soils.

An associated science question was to investigate how variation in the key biotic controls on gross primary production (GPP) observed within and among sites is propagated into predictions of GPP. Is there significant variability in GPP among sites? And how does variability in the biotic constraints on production at fine scales translate into uncertainty in regional predictions?

Methods

Study Area

The study region is located within the Tapajós National Forest (TNF), 50 km south of Santarém, Pará, Brazil, lying between latitudes 2°45′S and 4°S and longitudes 54°50′W and 55°20′W. The TNF is bordered on its western edge by the Tapajós River (29 m a.s.l.), a major tributary of the Amazon. The steep escarpment along the river (50 m a.s.l.) pre-

vents flooding of the TNF during high-flow events. Above the escarpment, the TNF is characterized in the north by old erosional remnant plateaus, with further escarpments corresponding to changes in soil texture. There is a very limited drainage network, and the underlying geology is comprised of slanted alternating beds of sand and clay deposited as a lacustrine–fluvial sequence. The southern TNF is drained by a small river flowing east, and the terrain is more dissected and variable. Most of the TNF is at altitudes of 150–200 m a.s.l., and water table depths typically vary from 60 to 140 m (E. Moran and R. Cosme personal communications).

Selection of Survey Sites

We surveyed 13 sites within the TNF during November 1999. The sites were grouped in four subregions of the TNF. Sites 1–4 were located in the north, close to the km 67 forest camp (Figure 1). Sites 1, 3, and 4 were located at the top and site 2 at the bottom of an approximately 50-m escarpment that runs roughly parallel to the river. Sites 3 and 4 were located off the access road connecting the km 67 camp to BR 163, the mostly unpaved national route than runs along the eastern flank of the TNF. At the top of the escarpment, depth to water table exceeded 110 m. Since the escarpment was approximately 50 m high, we estimate that water table depth at site 2 still exceeded 50 m.

Sites 5–8 were located near the km 117 forest camp, in the central and eastern portion of the TNF. A roughly 50-m escarpment separated sites 5 and 6 (top) from sites 7 and 8 (bottom). Sites 9 and 10 were located in the southeastern corner of the TNF, near the small town of Ruropolis, at an altitude of 200 m. Site 9 was within a few hundred meters of a tributary of the Tapajós River that runs along the southern border of the TNF. Site 10 was located in more hilly terrain further to the northeast. We accessed sites 11–13 from the eastern shore of the Tapajós River; all were located on bluffs that rose steeply from the shore, and all sites were at an altitude of approximately 50 m. Much of the shore showed signs of human disturbance, except for the area we selected where the bluffs had restricted access.

At each site, we marked out a transect 250 m long and 10 m wide. Transects were oriented away from the entry direction and perpendicular to any access trail and/or nearby river, and thus away from likely sources of disturbance. Each transect was divided into five equally sized subplots with a length of 50 m.

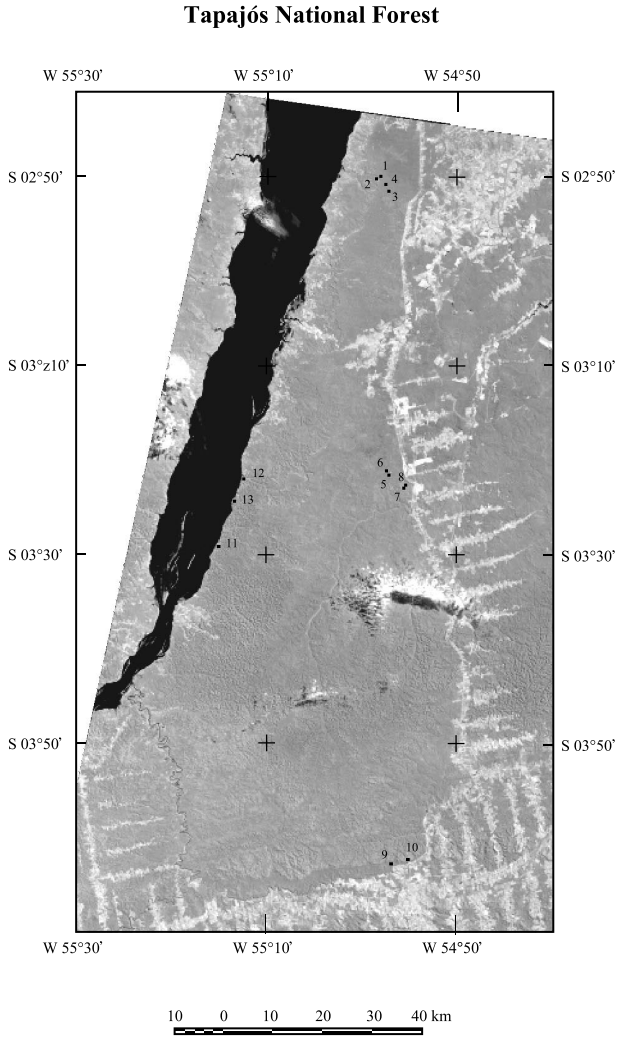

Figure 1. The location of the 13 study sites within the Tapajós National Forest in Para state, Brazil. Locations are marked on a Thematic Mapper/Landsat image, path 227, row 062, 10 secs dislocated south, from 2 August, 1999, 30-m resolution. A color composition of bands 5(R), 4(G), 3(B) has been converted to gray scales. Note the Tapajós River in black along the western edge of the forest and the BR 163 road marking the eastern boundary. Clouds obscure some parts of the image.

Soil Surveys

Within each transect, we dug two soil pits approximately 0.6 m deep and prepared a smooth vertical face. We then collected paired soil cores from the face at three depths—0.1 m, 0.3 m, and 0.5 m—using a precision-lathed stainless steel corer. From a nearby area, we brushed away litter and collected paired cores of surface soil by vertical insertion. We combined paired cores and recorded wet mass. Samples were then dried at 60°C for 2 days and shipped to the soils laboratory of Raimundo Cosme

at EMBRAPA, Belem, PA, Brazil. There samples were analyzed for dry mass, texture, percentage C, percentage organic matter, and percentage nitrogen (N). From volumes of corers, we determined the bulk density for each soil layer.

Vegetation Surveys

To determine woody biomass within each transect, we recorded the diameter at 1.35 m (DBH) of all stems larger than 0.1 m DBH. Buttressed trees were measured just above the buttress. We estimated biomass (B) using an allometric relationships described in Laurance and others (1999) that is a function of DBH, with a 12% increment applied to account for the presence of trees smaller than 0.1 m DBH:

$$B = 600\ (\exp\{3.323 + (2.456(\ln(d/100)))\})$$

A local *mateiro* (woodsman) identified the common name associated with each stem. We used a pair of LAI-2000 plant canopy analyzers (LI-COR Inc., Lincoln, NE, USA) to estimate leaf area index (LAI). Along each transect, survey points were located at 10-m intervals (26 in all). To minimize the confounding effects of direct sun on the instruments, we collected readings at dusk or dawn. In addition, the analyzers were oriented so that the observer's back was to the sun at all times. To determine a differential reading for LAI estimation, the paired instruments were used contemporaneously, one located on level ground in a clearing near the study site (usually the forest camp or the river shore), the other deployed along the transect.

We sampled foliage from the upper canopy with a shotgun. At each site we collected six or seven samples from different canopy species, tending to select the larger and more accessible trees. We collected at least five leaves for each sample, avoiding yellow and brownish leaves. All leaf outlines were traced onto paper. In the laboratory, we cut out the tracings and determined leaf area using a LI 3100 area meter (LI-COR Inc.) and recorded the mass of the associated dried leaves. We then estimated leaf mass per area for each sample.

We collected wood samples with a coring hammer from at least a dozen larger stems in the first 50-m section of the 250-m transect at each site. At each soil pit, we also collected leaflitter grab samples and fine roots from the surface soil layers. Fine-root samples were washed gently later on the day of sampling. All vegetation samples were dried at 60°C for 48 h and then shipped to the laboratory of Reynaldo Victoria at the Centro de Energia Nuclear na Agricultura (CENA), Piricicaba, SP, Brazil. Samples were then weighed, ground, and analyzed for percentage C, percentage N, and stable isotope ratios of C and N.

At each site, close to dawn (between 6 AM and 7 AM), we collected three to seven foliage samples from the upper canopy using a shotgun. We then determined dawn leaf water potential (ψ_{Id}) for individual leaves using a scholander pressure bomb (model 600; PMS Instrument Co., Corvallis, OR, USA). We estimated by eye the height from which the foliage was collected (height estimates ranged from 10 to 37 m) and applied a gravitational correction (0.01 MPa m^{-1}) to give an estimate of water potential in the rooting zone. We judged the instrumental precision at $\pm$0.1 MPa. Estimating height by eye is relatively imprecise, but an imprecision of $\pm$5 m in height propagates into an error of $\pm$0.05 MPa in water potential estimates. Given that effects of height-based uncertainty and/or bias are thus likely similar to or smaller than instrumental error, more precise techniques for height estimate are not justified.

Modeling GPP

We investigated differences in GPP among sites using a process-based model of the soil–plant–atmosphere continuum (SPA) (Williams and others 1996). The model incorporates detailed radiative transfer calculations, leaf-level energy balance, and colimitation of photosynthesis by biochemical metabolism (Farquhar 1989) and diffusive constraints. A mechanistic description of liquid and vapor phase water fluxes in the plant canopy controls stomatal opening. The model was run on an hourly time step and divided the canopy into 10 vertical layers. To drive the model, we used hourly meteorological data collected during 1999 at Belterra, a few km north of the TNF (D. Fitzjarrald, personal communication). We simulated photosynthesis for a typical sunny day (radiation = 18 MJ m^{-2} d^{-1}; temperature = 30.7°C (max) and 21.7°C (min); maximum vapor pressure deficit = 1.6 kPa) and a cloudy day (radiation = 5.4 MJ m^{-2} d^{-1}; temperature = 27.8°C (max) and 21.7°C (min); maximum vapor pressure deficit = 0.7 kPa). We did not generate full annual predictions because our goal was a sensitivity analysis to characterize differences among sites given similar meteorology.

We used a calibration of the SPA model previously corroborated for rain forest in central Amazonia (Williams and others 1998). For each of the TNF study sites, we varied the parameterization according to measured differences in LAI. To estimate photosynthetic parameters (V_{cmax} and J_{max}), we used detailed leaf physiological measurements

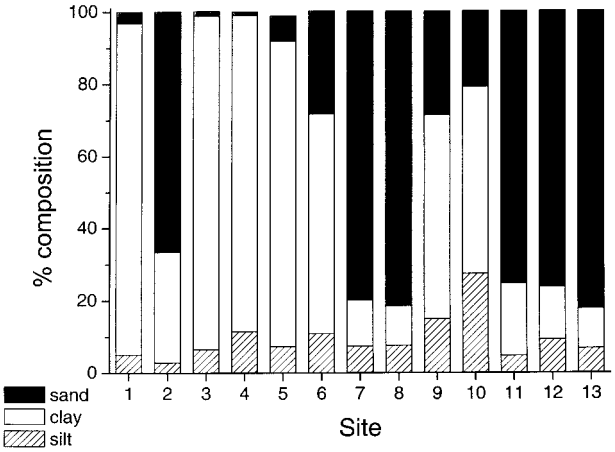

Figure 2. Soil texture for the 13 study sites.

undertaken at a rain forest site in central Amazonia by Carswell and others (2000) to develop linear regressions between foliar N and the photosynthetic rate parameters, V_{cmax} and J_{max}. Based on specific foliar N data, we used these regression equations to predict V_{cmax} and J_{max} in upper canopy leaves at each of the 13 sites. We assumed that foliar N and the rate parameters decreased linearly down through the remaining nine canopy layers, so that the lowest layer had 50% of the N content of the upper layer (Meir and others 2001).

Results

Soils

There was a very broad variation in soil textures among the sites (Figure 2), ranging from 1% sand and 92% clay (site 3) to 82% sand and 11% clay (site 13). There was a clear connection between topography and soil texture. In two clusters of sites (1–4 and 5–8), the sites at the bottom of the escarpment cutting through each cluster were predominantly sandy (for example, site 2), while the high sites were mostly clay (for example, sites 1, 3, and 4). Soil bulk density varied between 0.8 and 1.3 g cm^{-3}. Soil percentage N showed a larger relative variation, from 0.06% to 0.22%; soil percentage C varied from 0.6% to 2.4% (Figure 3). We found that these soil properties were often closely correlated with texture (Table 1). Bulk density was greater in sandier soils, whereas water content, percentage N, percentage C, and percentage organic matter (OM) were generally greater in clay soils. Soil C:N ratios (Figure 3) were not correlated with other soil properties (Table 1). Water content (mass fraction) showed very large variation among sites,

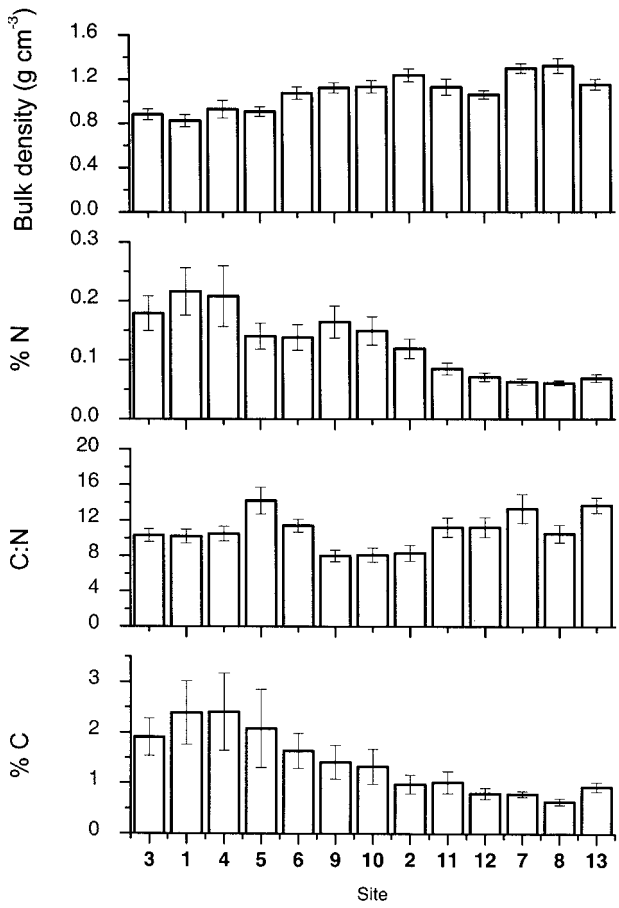

Figure 3. Mean bulk density, percentage nitrogen content, C:N ratio, and percentage carbon content for pooled soil samples with sites arranged along a texture gradient (high clay to the left). Standard errors are indicated.

from 0.06 to 0.34, and was positively correlated with clay content.

Analysis of variance (ANOVA) among all samples indicated significant differences ($P < 0.01$) in bulk density, percentage C, percentage OM, and percentage N with depth; however, texture and water content did not show significant differences down soil profiles. Upper soils tended to have greater organic matter, greater C and N content, and lower bulk density. ANOVA confirmed that there were significant differences among sites ($P < 0.01$) in all soil variables except C:N ratio.

Stems and Aboveground Woody Biomass

We surveyed 1380 stems across the 13 study sites and identified 505 different common names (species/genus) among them. The most common stems were *Protium spp.* ($n = 91$), *Pouteria spp.* ($n = 74$), *Amphirrhox surinamensis* ($n = 50$), and *Inga spp.* ($n = 38$). There were links between distribution of some

Table 1. Pearson Product-Moment Correlations among Soil Properties of the 13 Sites

	Soil water (%)	Clay (%)	Sand (%)	Soil C (%)	Soil Organic Matter (%)	Soil N (%)	Soil C:N Ratio	Soil Bulk Density (g cm^{-3})
Soil Water (%)	1.00	**.92**	**−.91**	**.89**	**.89**	**.76**	.09	**−.82**
Clay (%)	**.92**	1.00	**−.98**	**.96**	**.96**	**.94**	−.15	**−.86**
Sand (%)	**−.91**	**−.98**	1.00	**−.94**	**−.94**	**−.94**	.22	**.82**
Soil C (%)	**.89**	**.96**	**−.94**	1.00	1.00	**.92**	−.04	**−.89**
OM (%)	**.89**	**.96**	**−.94**	1.00	1.00	**.92**	−.04	**−.89**
Soil N (%)	**.76**	**.94**	**−.94**	**.92**	**.92**	1.00	−.41	−.78
Soil C:N	.09	−.15	.22	−.04	−.04	−.41	1.00	−.07
Soil Bulk Density	**−.82**	**−.86**	**.82**	**−.89**	**−.89**	**−.78**	−.07	1.00

Marked correlations (in bold type) are significant at $P < 0.05$. $n = 13$ (casewise deletion of missing data).

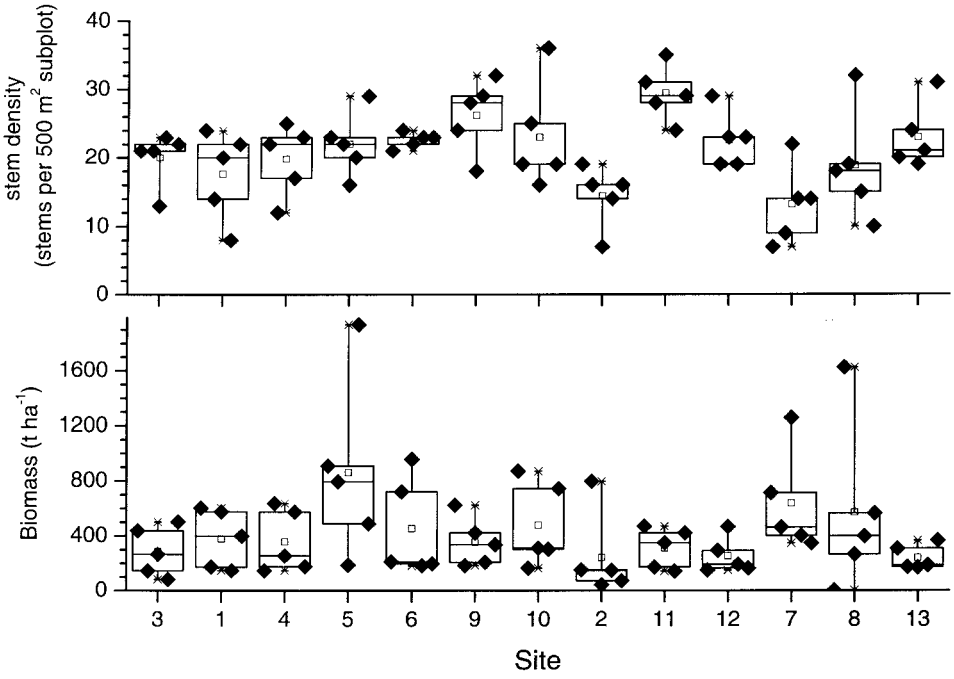

Figure 4. Stem density (*top*) and biomass (*bottom*) for each site, with sites ranked along a gradient of soil texture (high clay to the left). Biomass was determined by the allometric equations from Laurance and others (1999). The box plots indicate the raw data (◆), mean (□), maximum and minimum values (×). The box outlines the 25th and 75th percentiles; the whiskers are determined by the 5th and 95th percentiles.

species and local soil textures. For instance, *Amphirrhox surinamensis* was found at six sites, but all had soil clay contents above 50%. Of the 28 *Swartzia panacoco* surveyed, 27 were located at sites with soil clay contents above 31%.

Across all sites, the basal area of all stems larger than 0.1 m DBH ranged from 15.0 to 42.2 m^2 ha^{-1}; the overall mean was 24.4 m^2 ha^{-1}. The range among subplots was greater, from 0.3 to 73.1 m^2 ha^{-1}. The median DBH for all sites varied between 0.13 and 0.22 m. The number of tree species in each site (more than 0.1 m DBH) varied from 38 to 73; the median was 49. Tree stem density (more than 0.1 m DBH) varied from 66 to 147 stems per 0.25-ha site, with a median of 110 stems (Figure 4). The number of stems in the smallest size class (0.1–0.2 m) as a percentage of the total varied from 45% to 74%; the stem size distribution is consistently skewed toward smaller stems. Estimates of stem biomass ranged from 241 to 864 t ha^{-1}; the mean among all sites was 419 t ha^{-1}. The patchiness of stem biomass distributions was such that subplot biomass was generally not normally distributed (Figure 4); therefore, we avoided statistical tests of significant differences in biomass among sites.

We did not find any significant correlations between soil characteristics (percentage sand, percentage clay, percentage N, percentage C, percent-

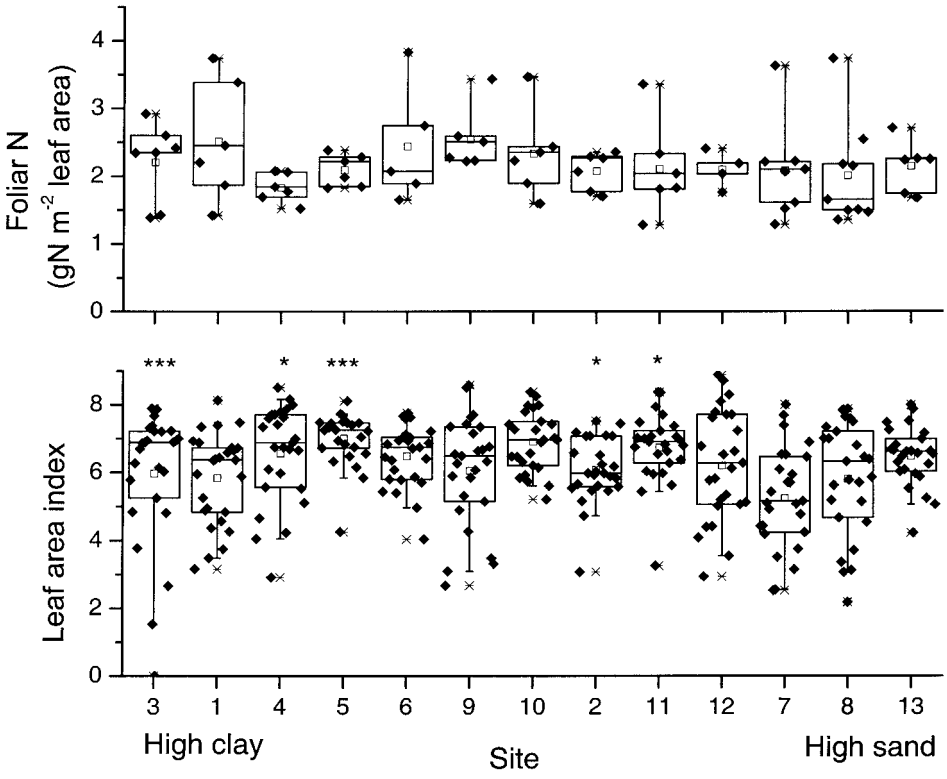

Figure 5. Nitrogen per leaf area (*top*) and leaf area index (*bottom*) for each site, sorted along a soil texture gradient (high clay on the left). Data are displayed both as raw points (diamonds) and as a box chart (see Figure 4 for description of box charts). For LAI data, the results of a Shapiro-Wilks's *W* test for deviations from normality are displayed (*$P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

age OM) and stems characteristics (basal area, biomass, stem density, number of species), except for a negative correlation between sand content and number of species.

Tissue Chemistry

The mean N concentration of all samples varied between 1.3% and 4.2%. The mean values of foliar N at each site ($6 \leq n \leq 10$) varied between 1.9% and 2.9%. Analysis of variance of foliar percentage N and C:N failed to identify any significant difference among site mean values. The mean N concentrations of wood, root, and litter were 0.5%, 2.1%, and 1.9%, respectively. Among all sites, wood percentage N was significantly ($P < 0.001$) less than that of the other tissues, and foliar percentage N was significantly ($P < 0.001$) greater than litter percentage N. The mean C:N ratio for all wood samples (97.0) was significantly greater ($P < 0.001$) than that for leaves (23.1), roots (22.7), and litter (23.5); there was no significant difference between the ratios for the latter three tissues.

Canopy Characteristics

The mean LAI (one-sided) for each site varied from 5.2 to 7.0, with a mean among sites of 6.2. However, there was considerable variation in measured LAI within each site at the 26 survey points (Figure 5). In five sites, the LAI distribution was significantly negatively skewed (Shapiro-Wilks's W test for normality, $P < 0.05$), and even log and square-root transforms of these data did not provide normal distributions. Mean leaf mass per area (LMA) for upper canopy foliage was 99 g DW m^{-2}; means among sites varied between 73 and 129 g m^{-2}. The mean N content of all foliage was 2.2 g N m^{-2} leaf area, with mean site values ranging from 1.8 to 2.5 g N m^{-2} (Figure 5). Individual foliage N content was positively correlated with LMA ($P = 0.002$) (Table 2). We did not find any correlations across sites between mean canopy characteristics (LAI, LMA, foliar N) and soil characteristics (sand and clay content, water content, bulk density, percentage C, percentage N, percentage OM). Analysis of variance suggested no significant differences ($P < 0.05$) between mean LMA or mean foliar N among sites.

Isotopes

Mean $\delta^{13}C$ values across all sites varied from –29.2‰ (roots) to –30.3‰ (litter); values for foliage (–29.7‰) and wood (–29.6‰) were intermediate. Litter values were significantly different from other tissues ($P < 0.001$; except foliage, $P = 0.017$). Values for foliage were significantly different from those of roots ($P = 0.03$). There were no clear

Table 2. Pearson Product-Moment Correlations among Foliage Properties Collected at the 13 Sites

	$\delta^{13}C$	$\delta^{15}N$	%N	C:N	LMA	NLA
$\delta^{13}C$	1.00	0.07	0.00	−0.04	0.09	0.16
$\delta^{15}N$	0.07	1.00	**0.26**	**−0.29**	−0.11	0.08
%N	0.00	**0.26**	1.00	**−0.94**	**−0.53**	**0.26**
C:N	−0.04	**−0.29**	**−0.94**	1.00	**0.58**	−0.19
LMA	0.09	−0.11	**−0.53**	**0.58**	1.00	**0.64**
NLA	0.16	0.08	**0.26**	−0.19	**0.64**	1.00

Marked correlations (in bold type) are significant at $P < 0.05$. $n = 81$ (casewise deletion of missing data). Properties include C and N isotope discrimination, N concentration, C:N ratio, leaf mass per unit area (LMA), and nitrogen content per leaf area (NLA).

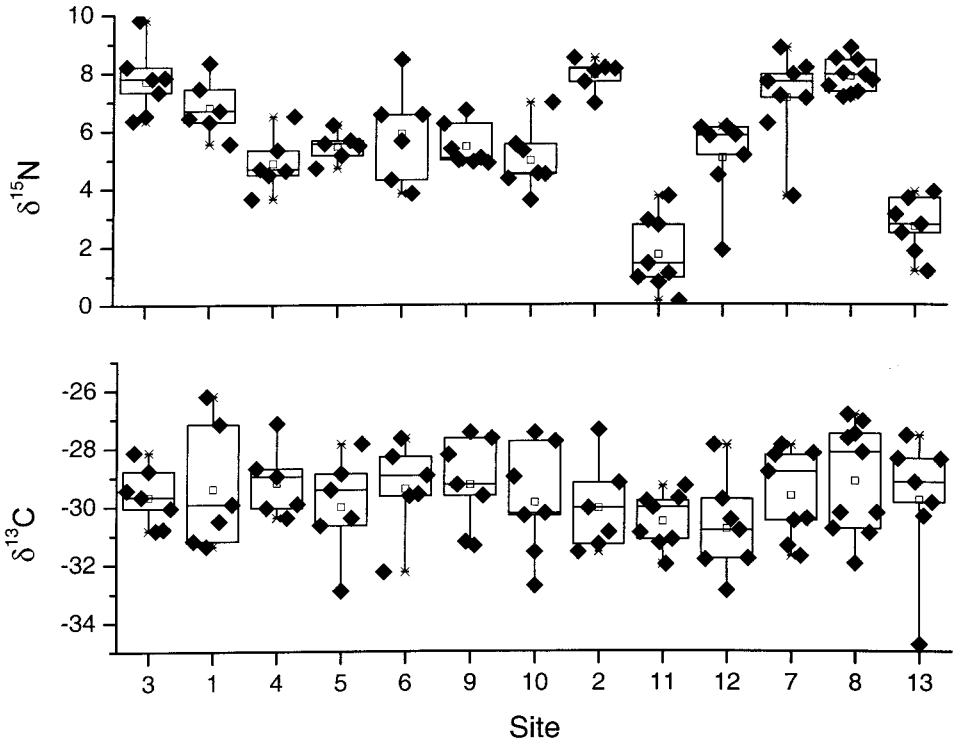

Figure 6. Nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotope discrimination in full sunlit leaves at sites ranked along a gradient of soil texture (high clay to the left). Data are displayed both as raw points for all samples (diamonds) and as a statistical box chart (see Figure 4 for description of box charts).

trends among tissues in $\delta^{13}C$ values across sites ($P > 0.05$ for all Pearson product-moment correlation tests) (Figure. 6). We examined whether there were any correlations among site soil and canopy characteristics and tissue isotope ratios. The only significant correlations ($P < 0.05$) were (a) between wood $\delta^{13}C$ and soil texture (a positive correlation with sand content) and (b) between litter $\delta^{13}C$ and mean basal area.

At the site level, mean $\delta^{15}N$ values across all sites varied from 3.6‰ in roots to 5.8‰ in litter, with foliage (5.7‰) and wood (4.2‰) intermediate. The values for roots were significantly different ($P < 0.05$) from those for litter and foliage. The trends of litter, foliage, and root $\delta^{15}N$ values were strongly correlated ($P < 0.05$) across sites; values for wood showed no correlations with other tissue types. There were no significant correlations between $\delta^{15}N$ values and soil characteristics, such as texture.

Examination of individual foliage samples indicated that there was no correlation between foliar N content (on a mass or areal basis) and discrimination of ^{13}C (Table 2). However, there was a correlation between N discrimination and foliar N status (Table 2). Analysis of variance of isotopic fractionation in foliage ($n = 92$), grouped by site ($n = 13$), indicated a significant difference ($F = 22$, $P < 0.001$) in mean $\delta^{15}N$ among sites (Figure 6) but not for $\delta^{13}C$. Analysis of variance in foliage, grouped by species ($n = 64$), indicated significant ($P < 0.001$) intraspecific variation both in $\delta^{15}N$ and $\delta^{13}C$. An examination of all foliage samples revealed no cor-

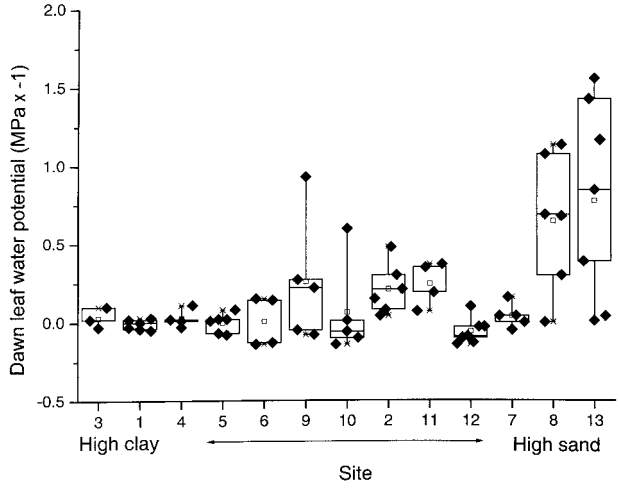

Figure 7. Dawn water potential for canopy foliage along a gradient of soil texture. Potentials have been corrected for gravitational effects, and the data are displayed both as raw points (diamonds) and as a box chart (see Figure 4 for description of box charts).

relation between $\delta^{13}C$ and $\delta^{15}N$ in individual leaves (Table 2).

Dawn Water Potential

On sites with high clay content (for example, sites 1, 3, 4, and 5), gravitationally corrected leaf water potential (ψ_{ld*}) for most leaves was close to zero (Figure 7), indicating full rehydration of foliage overnight. However, in the sandier sites, there were several samples with large, negative ψ_{ld*}; however, at every site, at least one foliage sample indicated full or nearly full rehydration. The sandiest sites (sites 8 and 13) had the driest soils (0.07 and 0.06 mass fraction, respectively), with mean ψ_{ld*} of −0.65 and −0.78 MPa, respectively; in both cases, two or three foliage samples had a ψ_{ld*} of less than −1 MPa. There was no significant correlation between C isotope discrimination and dawn water potential from individual leaf samples.

Gross Primary Production

The mean predicted GPP for a typical sunny day was 11.9 g C m^{-2} d^{-1} and varied among sites from 10.9 to 13.0 g C m^{-2} d^{-1}. For cloudy conditions, mean GPP was 6.1 g C m^{-2} d^{-1}, varying from 5.7 to 6.3 g C m^{-2} d^{-1}. There were no correlations between these GPP estimates and observed stand biomass. A response surface generated by SPA showed that GPP was more sensitive to variation in observed values of foliar N rather than to values of LAI (Figure 8) (particularly on sunny days) or to values

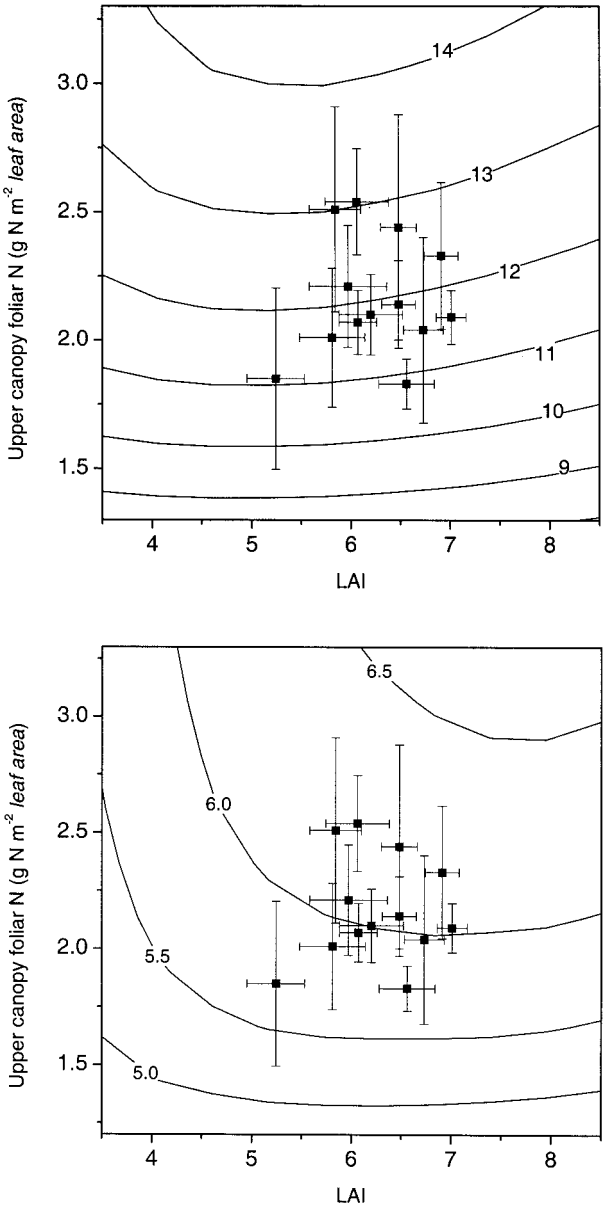

Figure 8. Analysis of the sensitivity of gross primary production (*isolines*) to variation in LAI and upper canopy foliar N. Contour lines connect points of equal GPP (units g C m^{-2} d^{-1}). Also plotted are the mean values for each study site, with standard error bars (these should be interpreted with caution since LAI data were nonnormally distributed at some sites). *Upper plot*: sunny conditions; *lower plot*: cloudy conditions.

of leaf–soil water potential difference (Figure 9). Intrasite variation in foliar N translated into an uncertainty in GPP predictions up to ±10% on sunny days and ±5% on cloudy days. Local variability in LAI had a much smaller influence on uncertainty (less than 1%) (Figure 8). The mean observed reductions in dawn water potential at the

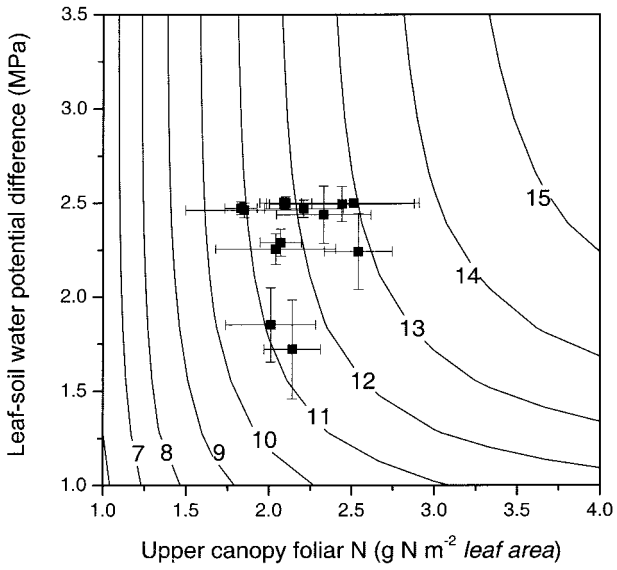

Figure 9. Analysis of the sensitivity of gross primary production (*isolines*) to variation in canopy foliar N and leaf–soil water potential difference. Contour lines connect points of equal GPP (units g C m^{-2} d^{-1}). Also plotted are the mean values for each study site, with standard error bars.

two most stressed sites reduced daily GPP by 4%–6% (Figure 9). GPP was more sensitive to observed uncertainty in local foliar N at these sites.

Discussion

Comparison with Other Amazonian Studies

The results of our survey were in general agreement with those from other studies in the Amazon basin. Using similar allometric equations, biomass estimates from TNF were not significantly different ($P < 0.05$) from a broad survey in an area of rain forest north of Manaus (Laurance and others 1999). There was also a close correspondence between LAI estimates in the two areas (McWilliam and others 1993) and in the range of soil percentage N (Laurance and others 1999). Foliar percentage N contents in TNF were slightly higher than the average value for tropical trees (1.9%) reported by Martinelli and others (1999). However, data from across the TNF did not support the findings of Silver and others (2000) in the northern TNF that C:N ratios of roots were much higher in sands than in clays.

Interpreting $\delta^{15}N$ Data

Foliar $\delta^{15}N$ data from TNF confirmed the trend for tropical vegetation to be enriched in ^{15}N (Guehl and others 1998; Martinelli and others 1999). The TNF showed greater enrichment than the rain forests of French Guyana, where no values greater than 4.2‰ were found (Guehl and others 1998), but TNF data were similar to the average value for tropical foliage (4.2 ± 2.1‰) reported by Martinelli and others (1999). Hogberg (1997) has suggested that high $\delta^{15}N$ values signify that an ecosystem is losing large amounts of N and is thus enriched in the heavier isotope, which is less likely to be denitrified. In the northern TNF, Silver and others (2000) found that clay soils had significantly higher $\delta^{15}N$ than sandy soils; confirming Hogberg's hypothesis, they correlated higher $\delta^{15}N$ to measurements of greater denitrification enzyme activity and greater rates of nitrification. However, if soil and vegetation $\delta^{15}N$ are closely linked, our survey of vegetation $\delta^{15}N$ was not consistent with these conclusions. Although the two sites with the lowest foliar $\delta^{15}N$ values were relatively sandy, there were also sites with sandy soils and foliar $\delta^{15}N$ values as high as those found on clay sites (Figure 6).

Martinelli and others (1999) reported that, for two terra firme rain forests, the site with the higher elemental concentration of N in leaves also showed a significantly higher average $\delta^{15}N$ value. They claimed that these data supported the contention that tropical forests are N rich and have open N cycles. We did find a correlation between N concentrations and the $\delta^{15}N$ values of individual leaves. However, at the site level, we only found significant differences among mean N discrimination data and not among mean foliar N concentrations.

Another possible factor controlling foliar $\delta^{15}N$ is the presence of N-fixing plants, because $\delta^{15}N$ of biologically fixed N ranges between –2‰ and 0‰. Site visits indicated greater human activity along the shore of the Tapajós River than along the road, and data confirmed greater stem density in the river shore sites (11–13) (Figure 4). Significantly lower $\delta^{15}N$ in sites 11 and 13 may be related to recent disturbance, forest regrowth, and the presence of N-fixing species. As partial confirmation, *Diplotropis purpurea*, a species that has been observed with bacterial nodules (Guehl and others 1998), was present at site 13.

Testing the First Hypothesis: Links between Soil and Vegetation Water Status

Our first hypothesis was that soil texture would be linked to soil moisture content and leaf water status. We found clear relationships between texture and gravimetric soil moisture. Clay soils tended to be moister, and water potential measurements indicated significant drought stress in the foliage of some samples from sandier sites. However, at sites

where some of the foliage had water potentials indicative of stress, the foliage of other species was unstressed (that is, it had water potentials close to zero). This dichotomy suggests either a very patchy distribution of soil moisture within each site, which we consider unlikely, or that some species access soil water more effectively than others, perhaps through deeper rooting (Nepstad and others 1994). As far as we know, these are the first data from tropical rain forests recording dawn leaf water potentials indicative of hydraulic stress (Gash and others 1996). The evidence that rooting depth and drought vulnerability vary significantly among species within a stand is significant, potentially complicating efforts to predict the response of forests to changes in patterns of precipitation (Williams and others 1998; Cox and others 2000; Crossley and others 2000).

Testing the Second Hypothesis: Links between Soil and Vegetation N Status

We hypothesized that soil texture was a key control on total soil nutrient content and that it was also connected to rates of ecosystem nutrient cycling. We did find clear links between texture and soil percentage N and soil organic matter (SOM) content. We also found clear differences in tissue $\delta^{15}N$ among sites, which suggests that there were significant differences in N cycling, but these were not obviously related to soil texture; there was significant variability ($P < 0.01$) between foliar $\delta^{15}N$ from sites with similarly sandy soils (sites 8 and 13), or similarly clayey soils (sites 3 and 4). As suggested above, disturbance history and the presence of N-fixers are likely to be important factors in controlling isotope discrimination.

In a modeling exercise with CENTURY for Tapajós forests, Silver and others (2000) suggested that texture controls the availability of N; because less N is stabilized on sands, less N is available for mineralization, and productivity equilibrates at a lower value. However, we were unable to confirm the hypothesis that vegetation N stocks were lower on sandy soils than on loam and clay soils, and there were no clear correlations between soil properties and vegetation chemistry. Silver and others (2000) showed that low cation exchange capacity (CEC) was common in soils of the northern TNF, probably as a result of high litter inputs and turnover. They suggested that the lack of pattern in CEC along a texture gradient suggests that factors other than soil texture may exert a strong influence on soil properties—and thus on vegetation.

Testing the Third Hypothesis: Patterns of Primary Production and Aboveground Biomass

Our final hypothesis held that soil-available water and soil nutrient stocks are critical controls on C cycling, and that reduced available soil moisture and lower soil nutrient stocks on sandy soils result in reduced primary production and less standing biomass than on clay and loam soils. However, we found little support for this hypothesis. Although wood $\delta^{13}C$ was correlated with soil texture, we cannot determine if there were significant differences among sites because the wood samples from each site were lumped together before analysis. Foliar $\delta^{13}C$ data from the same foliage used in the water potential measurements did not confirm the patterns of stress indicated in the water potential data. There were no significant differences in foliar $\delta^{13}C$ across sites; assuming similar illumination and given the lack of significant foliar N differences among sites, these data suggest that C assimilation did not differ significantly among sites.

The modeling sensitivity studies also suggested that GPP did not differ among sites. Although there were significant differences in dawn water potential among sites, the greatest observed degree of water stress would have only a small impact on daily GPP, approximately a 5% reduction. Given the lengthy wet season in the TNF, this reduction would be effective for just a portion of the year. Conversely, predicted GPP was highly sensitive to N, but foliar N data were not significantly different among sites. In the model, the uncertainty in foliar N estimates overwhelms the impact of water potential differences; GPP estimates were correlated with mean foliar N measurements, not with water potential data. The uncertainty in foliar N data propagates into GPP predictions; therefore, we cannot conclude that there are significant differences in GPP among sites.

The lack of significant differences in GPP predictions may be one reason we did not find any significant relationships between soil properties and aboveground biomass. However, soil–biomass relationships could also be obscured by sampling limitations; a few large stems in a sample can have a major influence on biomass totals. Surveying over broader spatial scales (larger than 1 ha rather than the 0.25-ha standard used in this study) may serve to diminish this variability. We also lack data on rates of respiration and mortality, important influences on stand biomass. Moreover, lack of data on phosphorus (P) content in a potentially P-limited

system (Vitousek 1984) prevented exploration of other possible soil controls on vegetation.

Our surveys suggest that, in the TNF, GPP did not vary significantly among the primary forests we surveyed. Soil moisture constraints on GPP are likely limited by the deep soils across the TNF, which provide enough exploitable rooting volume to buffer trees against the relatively brief dry season. In areas where deep rooting is prevented by a hard pan, soil texture is likely to be a more critical control on soil moisture stress. And, in areas where the water table nears the soil surface, shallow rooting may have important implications for C allocation and biomass accumulation. The lack of P data prevents a full understanding of nutrient constraints on plant processes across the texture gradients, but foliar N data suggest that texture is not a useful indicator of N availability to plants; more detailed studies on N cycling are required to resolve controls on plant access to N.

GPP predictions were more sensitive to observed variations in foliar N than to factors connected to water relations. The sensitivity analyses suggest that accurate assessments of canopy chemistry (for example, N content, V_{cmax}, J_{max}) will most improve the accuracy of regional predictions of GPP in the TNF. These assessments can best be achieved through a combination of intensive field collections and improvements in remote sensing of canopy chemistry. We found the largest variability in canopy properties is at scales of approximately 10 m, the size of a tree crown, rather than at the scale of 0.25 ha, the size of our transects, so high-resolution data is critical. Because LAI data were not always normally distributed, using mean LAI values for characterizing the forest may introduce bias. However, this will only be a factor in areas with low LAI values, because sensitivity of GPP to LAI values above 4 is small. Although isotopic studies and measurements of dawn water potential are suggestive of some water limitation on photosynthesis on sandier sites, there is no evidence that they have resulted in significant differences in GPP across soil texture classes in the areas of the TNF we studied. More detailed process-based studies on C–water relations are required to test this result further. Unraveling the controls on nutrient cycling and plant nutrient uptake as related to soil properties is another important area of research.

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