Structure and Biomass of Four Lowland Neotropical Forests[1]

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ABSTRACT

We contrasted the structure and biomass of four lowland Neotropical forests (La Selva, Costa Rica; Barro Colorado Island, Panama; Cocha Cashu, Peru; and KM41, Brazil) to determine if commonalities exist within and among forests differing in latitude, rainfall, seasonality, and soil fertility. We examined the effect of soil fertility specifically by measuring the density and basal area of trees, lianas, and palms on two soil types differing in fertility at each site. We used allometric relationships to estimate the contribution of the various life-forms to total aboveground biomass (AGB) and compared two relationships for trees 30 cm diameter or greater. Estimated liana density and AGB were similar among sites, but the density and AGB of trees and palms, estimated using diameter alone, differed significantly. Basal area and AGB of trees 10 cm diameter at breast height (DBH) or greater differed among forests and averaged 30.2 m²/ha and 250 Mg/ha, respectively. Cocha Cashu and KM41 had higher tree basal area and AGB than La Selva or Barro Colorado Island. Across forests, lianas and small trees (1–10 cm DBH) each contributed between 4 and 5 percent of the total AGB and small palms contributed *ca* 1 percent. Many forest inventories ignore lianas, as well as trees and palms less than 10 cm DBH, and therefore underestimate AGB by *ca* 10 percent. Soil type had little influence on the forest structure within sites, except at Cocha Cashu where total AGB was much higher and liana density much lower on the more fertile old floodplain Entisols than the *terra firme* Oxisols. Although total stem density, basal area, and some biomass components differed significantly among forests, they seemed less variable than other quantitative measures (*e.g.,* species richness).

RESUMEN

Contrastamos la estructura y la biomasa de cuatro bosques de bajura Neotropicales (La Selva, Costa Rica; Isla Barro Colorado, Panamá; Cocha Cashu, Perú; y KM41, Brasil) para determinar si existen patrones comunes entre bosques que difieren en la latitud, en la lluvia total, en la estacionalidad, y en la fertilidad de suelo. Examinamos el efecto de la fertilidad de suelo en cada sitio específicamente midiendo el área basal y densidad de árboles, lianas, y palmas en dos tipos de suelo que difieren en fertilidad. Usamos ecuaciones alométricas para estimar la contribución relativa de las varias formas de vida a la biomasa aérea (AGB) y comparamos dos ecuaciones para estimar biomasa con base en árboles ≥ 30 cm diámetro. La densidad y AGB estimada de lianas fueron similares entre sitios, pero la densidad y AGB de árboles y palmas estimada en base solamente a diámetros fueron significativamente distintas. El área basal y la AGB de árboles ≥ 10 cm diámetro a la altura de pecho (DAP) difirieron entre bosques y promediaron 30.2 m²/ha y 250 Mg/ha. En Cocha Cashu y KM41 observamos mayor área basal y AGB para árboles que en La Selva o la Isla Barro Colorado. En general lianas y árboles pequeños (1–10 cm DAP) contribuyeron entre 4–5 porciento del AGB total cada uno y palmas pequeñas contribuyeron alrededor de 1 porciento. Muchos inventarios del bosque ignoran tanto las lianas como los árboles y palmas <10 cm DAP y por lo tanto subestiman AGB en alrededor de un 10 porciento. El tipo del suelo mostró una influencia pequeña en la estructura del bosque dentro de sitios, menos en Cocha Cashu donde AGB total fue mucho más alto y densidad de lianas y palmas fue más bajo en los Entisols de mayor fertilidad que los Ultisols de menor fertilidad. Aunque la densidad de tallos, área basal, y algunos componentes de la biomasa difirieron significativamente entre bosques, estos parecieron menos variables que otras medidas cuantitativas (por ejemplo, riqueza de especies).

Key words: aboveground biomass; Brazil; Costa Rica; large trees; lianas; palms; Panama; Peru.

THE WEALTH OF SPECIES IN TROPICAL FORESTS often overwhelms attempts to find commonalities among them. Are there similarities in lowland tropical forest structure across latitude, rainfall, seasonality, and soil fertility? Leigh (1999), following on earlier research (*e.g.*, Dawkins 1958), took an engineering approach to this problem and proposed that a number of forest structural variables are conserved across lowland tropical forests. Two of his proposed "constants of the forest" are the mean tree basal area, *ca* 30 m²/ha, and the dry matter aboveground biomass (AGB), *ca* 300 Mg/ha (Leigh 1999). Why they might be similar among forests is an open question but may be related to equilibrium distributions of tree heights and diameters imposed by structural constraints on architecture (Leigh 1999, Enquist & Niklas 2001, 2002). In addition to the constants found by Leigh (1999), Gentry (1982) found that total woody stem and liana densities for stems 2.5 cm diameter or greater were similar across seven moist and wet lowland tropical Neotropical forests (x̄ stems per 0.1 ha ± 1 SD; all stems = 330 ± 50; lianas = 59 ± 17), also suggesting that these two variables may be constants, at least within the Neotropics. Such constants help simplify the complexity of tropical forests and allow application of process-based ecosystem models to the regional scale (Enquist & Niklas 2001, Moorcroft *et al.* 2001). Deviations of these constants have also been reported for some forests, however, and it is important to reassess whether this variation is due to methodological differences or to real variation in forest structure.

Other than the series of transects conducted worldwide by A. Gentry (1982, 1988a, 1991), few studies have used a consistent method to compare tropical forest structure and biomass among sites. Plots maintained by the Center for Tropical Forest Science are surveyed using consistent methods (Condit 1998) but exclude lianas, which make important contributions to tropical forest structure and species richness (Schnitzer & Bongers 2002). More constants of the forest may become apparent if consistent methods and frequently ignored life-forms are included (Malhi *et al.* 2002).

Commonalities in AGB across forests would be useful to identify because tropical forests play a major role in the global carbon cycle (Malhi & Grace 2000). As little is known of the biomass in root systems (Jeník 1971) or in soils, AGB often serves as a proxy for total forest biomass. There is considerable debate about whether biomass is increasing in tropical forests and about how the methods used to estimate biomass may affect conclusions (Phillips *et al.* 2002). Many of these debates arise over the application of allometric equations developed for one forest and applied elsewhere (Clark *et al.* 2001a), the measurement of large trees over (rather than above) buttresses (Clark 2002), and the failure to capture biomass held in life-forms other than trees 10 cm diameter or greater (*e.g.*, small trees and lianas; Gerwing & Farias 2000, Clark *et al.* 2001a). Large trees are difficult to measure because special equipment is usually needed to get diameters above buttresses; however, trees 30 cm diameter or greater hold 70–80 percent of the AGB and are thus the most important component of AGB (Chave *et al.* 2001). The need to address these various issues has been noted in global carbon cycle studies (Brown & Lugo 1984, Dixon *et al.* 1994, Phillips *et al.* 1994, Malhi & Grace 2000, Houghton *et al.* 2001, Keller *et al.* 2001). Clark *et al.* (2001b) recommended that on-site allometric equations be developed to accurately estimate AGB in each forest. In part, this recommendation stems from differences in wood specific gravity and diameter–height relationships that vary considerably among species and sites. Obviously, finding commonalities among forests for AGB will depend on how well these issues are addressed.

Variation in environmental factors such as topography, hydrology, and edaphic characteristics (*e.g.*, soil nutrient availability) may also complicate attempts to generalize stand density and AGB over regional or landscape scales (Clark & Clark 2000). The effect of environmental gradients on forest structure remains unclear because different studies have found conflicting results. For example, Laurance *et al.* (1999) found that AGB increases with soil fertility in Central Amazonia, whereas Clark and Clark (2000) found no difference in AGB among dominant soil types at La Selva. In addition, no relationship was found between soil nutrient concentrations and AGB across four lowland forests in Sarawak (Proctor *et al.* 1983). Liana abundance and biomass have been hypothesized to be greater on soils of higher fertility (Proctor *et al.* 1983, Putz & Chai 1987, Gentry 1991), but tests of this hypothesis have yielded mixed results (Balfour & Bond 1993, Laurance *et al.* 2001, Ibarra-Manríquez & Martínez-Ramos 2002).

In this study, we tested the hypothesis of constancy in density, basal area, and AGB by examining the similarities and differences in woody plant structure and AGB among four lowland Neo-

tropical forests. Specifically, we tested if forest structure and biomass are sensitive to soil fertility. To do this, we stratified placement of sampling units over two soil types within each of four well studied Neotropical forests to estimate the abundance and AGB of trees, palms, and lianas across the dominant environmental gradient at each site. In some of the study sites, AGB and stem density have been measured in much larger sampling plots (Laurance et al. 1999, Clark & Clark 2000, Chave et al. 2003). This allowed us to test whether or not our results are consistent with results based on larger sample areas and greater sampling intensity.

METHODS

This study was carried out between September and November 2001 in four Neotropical field stations located in lowland tropical moist to wet rain forest: La Selva Biological Station (LS) in Costa Rica, Barro Colorado Island (BCI) in central Panama, Cocha Cashu Biological Station (CC) within Manu National Park in Peru, and the Kilometer 41 (KM41) field camp of the Biological Dynamics of Forest Fragments Project, north of Manaus, Brazil (Powers 2004). The four sites are arrayed along an axis of increasing relative soil fertility: KM41 < CC ≤ BCI < LS (Powers 2004); they also span a range of latitudes, total annual rainfall, and seasonality of rainfall. Tree species richness differs considerably among the four sites (A. de Oliveira and J. Chave, pers. comm.).

At each site, we established six 10 × 50 m transects located at least 200 m apart in old-growth forest with mean canopy height above 15 m. Transects were placed to avoid obvious canopy gaps, swamps, and steep slopes. These "central transects" were overlaid by "expanded transects" (20 × 70 m) in which only large trees (≥30 cm diam) were measured. Within sites, two soil types were assessed as having relatively higher or lower fertility based on soil order (U.S. taxonomy; Powers 2004), and three transects were located on each soil type. Differences in soil orders reflect variation in state factors affecting soil formation (e.g., parent material, topography, soil age) and processes of formation (e.g., weathering, erosion, and podzolization).

FIELD MEASUREMENTS.—Within each central transect, we counted and measured all trees and palms 1 cm or more and all lianas 0.5 cm diameter at breast height (DBH) or greater that were rooted in the transects. For density tabulations, plants with aboveground connections were defined as an individual plant and apparent genets were counted only once (e.g., clonal palms arising from a common base). Apparent liana genets were measured only once, but the DBH of each palm ramet was measured for basal area and biomass estimation. The diameter of each liana was measured at its thickest point devoid of stem abnormalities if growing horizontally or at 130 cm above the ground if growing only vertically (as in DeWalt et al. 2000). This diameter measurement is also referred to as DBH in this study. Lianas in this study included all climbing woody dicots that were permanently rooted in the ground as well as two genera of woody monocots, Desmoncus (Arecaceae) and Smilax (Smilacaceae), and one gymnosperm genus, Gnetum (Gnetaceae); however, hemi-epiphytes, aroids (Araceae), and bamboos (Poaceae) were not included. Freestanding lianas were counted as trees because it was not always possible to determine whether an unsupported stem was a tree or liana. Calipers were used to measure diameters of lianas and trees less than 4 cm DBH and a cloth diameter tape was used for larger stems without irregularities. Flattened stems were measured twice at right angles, and the geometric average was calculated to determine the average stem diameter.

Within expanded transects, trees 30 cm or greater were mapped, measured, and identified to species when possible. Diameters of these large trees were measured at 130 cm above the ground if the stem was devoid of irregularities or above irregularities such as buttresses otherwise (referred to as DBH even if not measured at breast height). A rapid method was developed to measure tree diameter above buttresses when direct measurement with a cloth diameter tape was impossible (Chave, pers. obs.). This method was calibrated with direct diameter measurements at LS and BCI and generally yielded diameters within 5 percent of the direct measurements, except for a few tree forms (strangling figs and very irregular trees, such as adult Aspidosperma spp.). Species identifications of large trees were made with the help of experienced botanists at each site.

A liana of 0.5 cm DBH is approximately equivalent in biomass to a tree of 1.3 cm (see below under AGB Estimation). Thus, the smallest lianas and trees measured in this study have similar minimum biomasses. The term "all woody stems" will refer to all measured lianas, trees, and palms. The category of trees includes palms unless specified otherwise.

AGB ESTIMATION.—Tree AGB was estimated by regressions, such as the ones suggested by Brown et al. (1989), Brown (1997), Chave et al. (2001), and Chambers et al. (2001). We used the relationship published by Chave et al. (2001) for biomass estimation of trees and palms less than 30 cm DBH. Although AGB estimation methods were developed from destructively harvested trees generally 5 cm DBH or greater, we applied them for trees less than 5 cm. Independent studies have shown that this does not lead to a serious bias in the estimate of AGB stocks in the smallest diameter classes (J. Chave, pers. obs.).

To estimate AGB of trees 30 cm DBH or greater, we compared two methods. Method 1 used the relationship from Chave et al. (2001): $AGB = \exp[-2.0 + 2.42 \ln(D)]$. This equation relates the AGB of a tree, expressed in kilograms of dry matter to its diameter D, expressed in cm. In method 2, we included wood specific gravity (ρ, oven-dry weight of wood per volume of fresh wood) in the allometric equation. We assumed that only the multiplicative factor of the above regression should depend on the wood specific gravity: $AGB = f(\rho) \times \exp[-2.0 + 2.42 \ln(D)]$. The function f is a linear function of the wood specific gravity, and we chose $f(\rho) = \rho/<\rho>$, where $<\rho>$ is the among-species mean wood specific gravity calculated from a data set of 1400 Neotropical tree species (Chave et al. 2003, in press). We found $<\rho> = 0.61$. And ρ is a wood specific gravity value assigned to every tree ≥ 30 cm DBH or greater (Muller-Landau 2004). We used specific gravity values compiled by Muller-Landau (2004) that represented those measured from cores taken with an increment borer from large trees in the expanded transects (162 individuals, only at CC and KM41), average species' values taken from the literature and unpublished sources (151 individuals), or the mean value for trees at the site (21 individuals). Hence, method 2 was expressed as: $AGB = \rho/\langle\rho\rangle\exp[-2.0 + 2.42 \ln(D)]$ (see also Baker et al. in press).

A regression equation was used to estimate the AGB of lianas from basal area. We used data from two destructive harvest experiments carried out in the Neotropics: one for 17 individuals in the Rio Negro Basin of Venezuela (Putz 1983) and one for 19 individuals in Eastern Amazonian forest of Brazil (Gerwing & Farias 2000; J. Gerwing pers. comm.). Pooling these two data sets, we found the following regression: $AGB = \exp[0.298 + 1.027 \ln(BA)]$, $R^2 = 0.87$, for which BA is the stem basal area ($BA = \pi D^2/4$) in cm^2.

ANALYSIS.—Contributions of trees, palms, and lianas to stem densities and biomass were contrasted among the four sites and within each site between soil types using analysis of variance (ANOVA) with the GLM procedure in SAS version 8 (SAS 2000). Significant differences among sites or soil types within sites were evaluated with post hoc Tukey HSD tests ($P < 0.05$).

RESULTS

ACROSS FOUR FORESTS.—In the total 1.2 ha of central transects sampled across the four forests, we measured 5950 palm, tree, and liana individuals. Of this total, 75 percent were trees, 19 percent lianas, and 6 percent palms. A total of 334 large trees (≥ 30 cm DBH) were measured and identified in the 3.36 ha of expanded transects. Overall woody stem, tree, and palm genet densities differed significantly among the four forests, whereas liana density did not (Table 1).

Total stem density tended to be lower on less fertile soils (Table 1). At the two extremes of the soil fertility gradient, La Selva was characterized by a low liana and tree but high palm density (especially the clonal palm Geonoma congesta), whereas KM41 had a high tree but low palm density. Small, and often spiny, understory palms (e.g., Astrocaryum gynacanthum and Bactris spp.) were abundant at KM41, but they tended to be smaller than 1 cm DBH. BCI also had a relatively low palm genet density, although clusters of the clonal palm Oenocarpus mapora often contained more than five stems. For trees and palms, across-site averages ($\bar{x} \pm 1$ SD) per 0.1 ha were $402 \pm 114 \geq 1.0$ cm, $208 \pm 47 \geq 2.5$ cm, or $56 \pm 16 \geq 10$ cm DBH (see also Table 2). For lianas, there were on average 93 ± 52 lianas ≥ 0.5 cm, $72 \pm 46 \geq 1.0$ cm, and $30 \pm 17 \geq 2.5$ cm DBH per 0.1 ha (see also Table 3).

Differences in basal area and estimated AGB among sites tended to follow patterns in density (Tables 1, 4). Cocha Cashu and KM41 had significantly greater tree basal area and AGB than LS or BCI. At KM41, tree AGB was high because of the high density and AGB of trees 1–30 cm DBH. In particular, medium-sized trees (30–50 cm DBH) were relatively more abundant, but larger trees (≥ 50 cm DBH) were less abundant than at other sites (Table 2). Trees 30 cm DBH or greater were most abundant at CC, and thus estimated AGB was large for this size class. Palm basal area and AGB was also greatest at CC compared to the other sites. La Selva had many clusters of understory

TABLE 1. *Mean number of individuals and basal area of trees, palms, lianas, and all woody stems per hectare in four Neotropical forests. Sites are listed in order of increasing relative soil fertility. Values are x̄ ± 1 SD scaled to 1 ha from N = 6 transects per site. Results of one-way ANOVA for each variable are shown at the bottom of the table. NS = Not significant. For each variable, sites followed by the same letter are not significantly different from each other at P < 0.05 (Tukey test).*

Site	Number of individuals/ha				Basal area (m²/ha)			
	Trees	Palms	Lianas	All stems	Trees	Palms	Lianas	All stems
KM41	5093 ± 860 c	97 ± 94 a	960 ± 250 a	6150 ± 962 b	37.6 ± 7.0 b	0.2 ± 0.2 a	0.8 ± 0.4 a	38.6 ± 6.9 bc
Cocha Cashu	3827 ± 988 bc	497 ± 417 b	1053 ± 753 a	5377 ± 1469 b	39.0 ± 9.3 b	5.3 ± 2.9 b	1.0 ± 0.7 a	45.3 ± 7.4 c
BCI	3620 ± 691 b	113 ± 56 a	1177 ± 523 a	4910 ± 1059 ab	25.1 ± 4.6 a	1.7 ± 1.2 a	1.2 ± 0.4 a	27.9 ± 4.4 a
La Selva	2263 ± 595 a	570 ± 133 b	527 ± 248 a	3360 ± 748 a	25.8 ± 6.1 a	2.9 ± 1.2 ab	0.5 ± 0.5 a	29.2 ± 6.5 ab
x̄ ± SD	3701 ± 1267	319 ± 304	929 ± 522	4949 ± 1456	31.8 ± 9.24	2.5 ± 2.5	0.9 ± 0.5	35.3 ± 9.4
% all stems	74.8	6.4	18.8	100.0	90.3	7.2	2.5	100.0
$F_{3, 20}$	12.7	7.32	1.99	6.97	6.91	9.72	1.63	10.1
P	<0.0001	<0.01	NS	<0.01	<0.01	<0.001	NS	<0.001

palms (*e.g., G. congesta*), but because they were relatively small, the basal area and AGB of palms was not significantly higher than at other sites. In contrast, the higher density of palms that grow to large sizes (*e.g., Iriartea deltoidea, Attalea butyracea,* and *Astrocaryum murumuru sl.*) at CC created high total palm basal area at this site. Neither liana basal area nor liana AGB differed significantly among the four forests, despite BCI and CC having roughly twice the mean basal area and AGB as LS.

All woody stem basal area averaged 35 m²/ha. Basal area and AGB of trees and palms 10 cm DBH or more, estimated using method 1, averaged 30.2 m²/ha and 250 Mg/ha, respectively. Basal area and AGB of this size class differed significantly among forests (basal area: $F_{3, 20} = 9.78$, $P < 0.01$; AGB: $F_{3, 20} = 7.78$, $P < 0.01$), primarily because of CC, which had more basal area and AGB than the other three sites.

VARIATION WITHIN EACH FOREST.—Between soil types within each forest, the size class structures of trees and lianas (Tables 2, 3) were generally similar and few structural or biomass characteristics were significantly different (Tables 5, 6). No differences in any of the measured variables were apparent between the La Selva Ultisols and Inceptisols. Liana density and basal area differed between BCI Oxisols and Alfisols, but this difference was driven by a single Alfisol transect with a relatively low canopy height and many lianas. Palm basal area and biomass were significantly higher on more fertile plateau Oxisols than on baixio Spodosols at KM41. The largest difference among the forests on different soil types was at CC, where lianas and palms were four and five times more abundant, respectively, on less fertile and older *terra firme* Ultisols than on more fertile and younger floodplain Entisols. Although the total number of trees did not differ significantly among soil types, large trees were more abundant on Entisols than on Ultisols (Table 2). Thus, tree basal area and large tree biomass were higher on the more fertile soil type.

SOURCE OF BIOMASS VARIATION.—Aboveground biomass was heavily dominated by the contribution of large trees (67% of AGB; Table 4). Although liana and palm AGB estimates were higher on Cocha Cashu Ultisols than Entisols, the biomass of large trees was lower and thus the total AGB was estimated to be lower on that soil type. The contribution of lianas to total AGB (4.7%) was similar to the 4.2 percent accounted for by small trees (1–

TABLE 2.   *Size-class frequency distribution of trees per hectare for each soil type in the four forests. Sites and soil types are listed from left to right in order of increasing relative soil fertility. The number of trees and palms 1–30 cm is extrapolated from the sum of individuals on three central transects on each soil type (0.15 ha), and the number of trees 30 cm or greater is extrapolated from the sum of three expanded transects (0.42 ha).*

| | KM41 | | Cocha Cashu | | BCI | | La Selva | | |
DBH (cm)	Spodosol	Oxisol	Ultisol	Entisol	Oxisol	Alfisol	Ultisol	Inceptisol	$\bar{x}$
1–10	4720	4300	3767	3520	3287	3380	2627	2067	3458
10–20	340	413	567	320	213	240	340	280	339
20–30	147	153	120	127	67	87	93	73	108
30–40	57	98	34	36	43	30	30	14	43
40–50	39	20	20	16	14	14	20	25	21
50–60	11	9	16	18	20	5	14	18	14
60–70	5	14	2	20	7	2	9	14	9
70–80	0	0	0	9	7	2	2	2	3
80–90	0	0	2	5	0	2	0	0	1
90–100	2	0	5	5	0	0	5	0	2
100–110	0	0	0	0	0	2	0	0	0
110–120	0	0	2	2	0	0	2	0	1
120–130	0	0	0	2	0	0	0	0	0
≥130	0	0	0	2	0	0	0	0	0
Total	5320	5008	4535	4083	3658	3763	3142	2493	4000

10 cm DBH). Small palms further added 1.1 percent (data not shown).

These biomass estimates were based only on diameter of trees and palms (method 1) and lianas. Including the species-specific wood gravity for large tree biomass estimation (method 2) tended to increase appreciably the estimated tree AGB on both soil types for KM41 (300 vs. 269 Mg/ha) and to decrease the estimate at BCI (199 vs. 214) and LS (206 vs. 234; Table 7). AGB using method 2 was 7 percent lower than AGB estimated with method 1 at BCI, 12 percent lower at La Selva, and 11 percent higher at KM41. There was no difference at CC. The ranking of sites for large tree or total AGB was consistent across methods of large tree biomass estimation (Table 7). Using method 1, only CC had significantly more total AGB than the other sites (Table 4), but using method 2, KM41 was statistically intermediate between CC and the other two sites for total AGB (data not shown).

DISCUSSION

Our approach of using transects to measure tree, liana, and palm abundance and estimate biomass assumes that our sampled areas are representative of old-growth areas within each of the four forests. Our sampled areas, however, were small for each site (0.3 ha for small stems and 0.84 ha for large trees) and were subjectively located to avoid gaps, slopes, and canopies less than 15 m tall. We prob-

ably were biased in our site selection toward parts of each forest with more total basal area and AGB than found on average within each forest. The strength of our data lies in the standard method used across the four forests, the accurate measurement of large tree diameters, and inclusion of lianas, a frequently ignored yet important component of tropical forest structure and composition. We acknowledge the importance of gaps in forest dynamics and higher turnover on steep slopes, and thus limit our discussion to intact, level understory areas of these forests. Extrapolations to larger spatial scales may bias our estimates of large tree density and AGB upwards while underestimating liana density, which tends to be greater in gaps and disturbed areas. In addition, we assume that we were working within areas in which large-scale, severe natural and anthropogenic disturbances have not occurred for at least several hundred years. Our sites likely were at least 100 years old, and forest structure tends to recover within 70 to 190 years to mature-forest levels, depending on soil fertility (Saldarriaga *et al.* 1988, DeWalt *et al.* 2003).

FOUR FOREST CHARACTERISTICS.—The four forests differed primarily in the density of trees and palms. The most fertile site, LS, had a dense understory herb and palm layer (Harms *et al.* 2004) but fewer trees and lianas than the other sites. BCI had a higher tree and liana density but relatively few understory palms. A high density of medium-sized trees, many acaulescent palms, and few caulescent

TABLE 3. *Size-class frequency distribution of liana individuals per hectare for each soil type in the four forests. Sites and soil types are listed from left to right in order of increasing relative soil fertility. The number of lianas on each soil type is extrapolated from the sum of three central transects (0.15 ha).*

	KM41		Cocha Cashu		BCI		La Selva		
DBH (cm)	Spodosol	Oxisol	Ultisol	Entisol	Oxisol	Alfisol	Ultisol	Inceptisol	$\bar{x}$
0.5–1	287	333	347	153	247	207	127	133	229
1–2	327	280	680	107	393	580	153	200	340
2–3	153	133	340	20	153	233	113	93	155
3–4	87	60	113	47	73	133	53	27	74
4–5	47	40	47	20	20	87	13	7	35
5–6	33	33	60	7	7	40	13	13	26
6–7	33	13	53	13	20	33	13	20	25
7–8	7	13	40	7	13	27	13	7	16
8–9	0	0	7	0	7	13	20	0	6
9–10	0	13	7	7	0	0	7	0	4
10–11	7	0	0	13	0	13	0	0	4
11–12	7	0	0	7	13	20	0	0	6
≥12	27	0	13	7	20	7	7	20	13
Total	1013	920	1707	407	967	1393	533	520	933

palms characterized the nutrient-poor KM41 forest. In this forest, buttresses and very large diameter trees were uncommon. The two areas examined at CC differed enough to be considered distinct forests and are treated as such here. The abundance of large trees in the old floodplain was high, although lower than previously reported (Gentry & Terborgh 1990). Understory vegetation was scarce (Montgomery 2004), and palms and lianas fairly depauperate relative to the *terra firme* uplands of CC. These areas had a high density of small trees, lianas, and understory palms, whereas the density of large trees was low compared to the old floodplain forest.

Greater tree density corresponded with lower soil fertility, but palm density showed no relationship with soil fertility. Total basal area differed more among forests than total AGB, regardless of the method used to estimate AGB for trees 30 cm or greater. Total AGB was greatest at CC and lowest at BCI. No trends were detected in any of the structural variables across sites in relation to climatic variables, such as seasonality or mean annual rainfall. These climatic variables, in addition to soil fertility, may also affect forest structure, biomass, and species richness (Gentry 1988a, Clinebell *et al.* 1995, ter Steege *et al.* 2003)

EFFECT OF SOIL TYPE ON FOREST STRUCTURE AND AGB ESTIMATES.—Our study only found differences in estimated AGB between soil types at CC in Peru. Interestingly, the greatest difference in soil fertility among soil types in each of the four forests occurs at CC (J. Powers and M. Lerdau, pers. comm.).

Higher total AGB occurred on the more fertile Entisols than the less fertile Ultisols at CC. We should caution, however, that these differences may have resulted from other factors such as differences in successional age (Entisols are younger than the Ultisols) or annual tree mortality rates (2.3% on the Ultisols vs. 1.6% for the Entisols; Gentry & Terborgh 1990; J. Terborgh, pers. comm.). The higher mortality rates on the Ultisols may have been caused by a hardpan 70 cm below the soil surface (J. Terborgh, pers. comm.). At La Selva, Clark and Clark (2000) also found no difference in AGB estimates between flat areas on Inceptisols and Ultisols. In contrast, Laurance *et al.* (1999) found that soil fertility accounted for a third or more of the AGB variation in *terra firme* forests on Ferralsols (Oxisols) in the Brazilian Amazon. Aboveground biomass was higher on soils with greater nitrogen, organic matter, and exchangeable bases. From the study by Laurance *et al.* (1999), we expected to find differences in AGB among even slight differences in soil fertility at KM41, but we found no difference between the soil types for AGB.

The hypothesis that liana abundance and AGB would be greater on more fertile soil types within sites was not supported. Our results differ from other studies showing that lianas tend to be more abundant on richer soils (Proctor *et al.* 1983, Putz & Chai 1987, Laurance *et al.* 2001), but are in accord with Balfour and Bond (1993), who found that climber abundance was not limited by soil nutrient availability. The only site in our study where liana abundance differed among soil types was at CC, where contrary to predictions, lianas were

TABLE 4. Mean AGB in mg/ha of trees of different diameter size classes, palms, and lianas in four Neotropical forests. Sites are listed in order of increasing relative soil fertility. Biomass estimates for trees are calculated using method 1. Values are x̄ ± SD scaled to 1 ha from N = 6 transects per site. Results of one-way ANOVA for each variable by site are shown at the bottom of the table. NS = Not significant. For each variable, sites followed by the same letter are not significantly different from each other at P < 0.05 (Tukey test).

	Trees			Palms	Lianas	Total
Site	1–10 cm	10–30 cm	≥30 cm	≥1 cm	≥0.5 cm	
KM41	16.0 ± 4.2 b	75.5 ± 9.5 b	164.7 ± 43.2 a	1.2 ± 1.1 a	11.9 ± 6.2 a	269.2 ± 45.5 a
Cocha Cashu	11.1 ± 2.1 a	53.6 ± 14.0 a	279.2 ± 108.2 b	33.1 ± 18.8 b	15.0 ± 10.6 a	392.1 ± 96.9 b
BCI	11.1 ± 2.4 a	44.7 ± 16.7 a	134.4 ± 56.6 a	7.1 ± 5.2 a	17.2 ± 5.3 a	214.4 ± 46.4 a
La Selva	8.2 ± 1.9 a	36.8 ± 9.9 a	166.4 ± 48.4 ab	14.6 ± 7.7 a	8.0 ± 8.0 a	234.0 ± 60.9 a
x̄ ± SD	11.5 ± 3.9	52.7 ± 19.0	186.2 ± 85.7	14.0 ± 15.7	13.0 ± 8.1	277.4 ± 93.5
% of all stems	4.2	19.0	67.0	5.0	4.7	100.0
$F_{3, 20}$	8.21	10.11	4.99	10.47	1.58	8.7
P	<0.001	<0.001	<0.01	<0.001	NS	<0.001

TABLE 5. Mean number of individuals and basal area of trees, palms, lianas, and all woody stems per hectare on two soil types in four Neotropical forests. Sites and soil orders within sites are listed in order of increasing relative soil fertility. Values are x̄ ± SD scaled to ha from N = 3 transects per site and soil type. Sets of bolded numbers within sites indicate a significant difference between the two soil types (P < 0.05).

		Number of individuals/ha				Basal area (m²/ha)			
Site	Soil type	Trees	Palms	Lianas	All stems	Trees	Palms	Lianas	All stems
KM41	Spodosol	5287 ± 1049	67 ± 42	1013 ± 332	6367 ± 1170	34.6 ± 6.9	**0.1 ± 0.0**	1.1 ± 0.4	35.8 ± 6.9
	Oxisol	4900 ± 797	127 ± 133	907 ± 194	5933 ± 898	40.5 ± 6.9	**0.4 ± 0.1**	0.5 ± 0.2	41.4 ± 6.8
Cocha Cashu	Ultisol	3707 ± 460	**833 ± 283**	**1700 ± 367**	6240 ± 896	**31.5 ± 3.3**	6.4 ± 1.8	1.5 ± 0.7	**39.4 ± 2.1**
	Entisol	3947 ± 1478	**160 ± 122**	**407 ± 172**	4513 ± 1536	**46.5 ± 6.0**	4.2 ± 3.8	0.5 ± 0.1	**51.2 ± 5.1**
BCI	Oxisol	3600 ± 726	93 ± 64	967 ± 383	4660 ± 1052	27.0 ± 4.5	2.4 ± 1.4	**0.9 ± 0.3**	30.2 ± 4.1
	Alfisol	3640 ± 817	133 ± 50	1387 ± 636	5160 ± 1228	23.2 ± 4.7	1.0 ± 0.6	**1.4 ± 0.1**	25.6 ± 4.0
La Selva	Ultisol	2547 ± 371	620 ± 174	533 ± 283	3700 ± 303	28.3 ± 8.4	3.2 ± 0.7	0.6 ± 0.7	32.0 ± 9.0
	Inceptisol	1980 ± 711	520 ± 80	520 ± 271	3020 ± 980	23.2 ± 1.6	2.7 ± 1.7	0.5 ± 0.5	26.5 ± 1.8

TABLE 6. *Mean AGB in Mg/ha of trees, palms, and lianas on two soil types in four Neotropical forests. Sites and soil orders within sites are listed in order of increasing relative soil fertility. Biomass estimates for trees are calculated using method 1. Biomass estimates for lianas are calculated using an equation constructed from the combined data of Putz (1983) and Gerwing and Farias (2000). Values are x̄ ± SD scaled to ha for N = 3 transects per site and soil type. Sets of bolded numbers within sites indicate a significant difference between the two soil types (P < 0.05).*

Site	Soil type	Trees			Palms ≥1 cm	Lianas ≥0.5 cm	Total
		1–10 cm	10–30 cm	≥30 cm			
KM41	Spodosol	17.6 ± 3.5	70.1 ± 5.2	158.5 ± 64.2	**0.2 ± 0.1**	7.6 ± 2.97	262.7 ± 67.9
	Oxisol	14.4 ± 4.9	80.8 ± 10.6	170.8 ± 20.6	**2.1 ± 0.6**	16.2 ± 5.5	275.7 ± 20.8
Cocha Cashu	Ultisol	11.0 ± 1.9	53.4 ± 18.5	**185.8 ± 39.8**	37.9 ± 12.7	22.2 ± 10.9	**310.4 ± 36.4**
	Entisol	11.1 ± 2.7	53.8 ± 12.2	**372.5 ± 39.3**	28.4 ± 25.7	7.8 ± 2.0	**473.9 ± 45.8**
BCI	Oxisol	9.7 ± 1.0	39.4 ± 17.5	160.1 ± 27.1	10.0 ± 6.0	**13.2 ± 4.8**	232.4 ± 38.2
	Alfisol	12.3 ± 2.9	50.0 ± 17.3	108.7 ± 72.8	4.2 ± 2.5	**21.2 ± 1.0**	196.4 ± 54.2
La Selva	Ultisol	8.8 ± 2.0	40.9 ± 13.7	190.6 ± 63.6	15.8 ± 4.1	8.2 ± 10.2	264.4 ± 79.9
	Inceptisol	7.5 ± 1.6	32.8 ± 2.7	142.1 ± 7.1	13.4 ± 11.3	7.8 ± 7.5	203.6 ± 10.5

more abundant on the less fertile *terra firme* Ultisols than on old floodplain Entisols. The four-fold difference in liana abundance between the two soil types may be driven more by differences in tree mortality rates or successional age than by differences in soil fertility. Indeed, liana abundance is higher in gaps than forest understory (Schnitzer & Carson 2001), and it is therefore likely that liana abundance is positively correlated with treefall frequency.

ACCURACY OF OUR RAPID ASSESSMENT COMPARED TO OTHER SURVEYS.—The densities of trees and lianas found in this study correspond well with most other studies conducted in Neotropical old-growth forest (summarized in Leigh 1999). Our estimated average of 435 trees 10 cm DBH or greater per hectare across the four sites (Table 3) was similar to published densities for permanent plots. In addition, our estimated densities of trees 10 cm or greater differed by only 19 percent at LS (515 on Ultisols vs. 418 for plateau; Lieberman *et al.* 1985), 9 percent at BCI (371 on Oxisols vs. 409; Leigh 1999), 13 percent for CC floodplain (563 vs. 650; Gentry 1988b), and 8–12 percent for KM41 plateau Oxisols (708 vs. 618–654; Oliveira & Mori 1999). For lianas (Table 3), our results were consistent with other studies conducted near our sites at BCI (Putz 1984, DeWalt *et al.* 2000) and near KM41 (Laurance *et al.* 2001). Mascaro et al. (2004), however, found 200% and 61% more lianas per ha 1 cm DBH and above and 2.5 cm DBH and above, respectively, than we did at La Selva. This large discrepancy in liana density between our studies, particularly for small size classes, may be due to inclusion of free-standing lianas in their study and omission in ours as well as the small areas sampled in both studies (0.08 ha per plot in Mascaro et al. (2004) and 0.05 ha per plot in this study).

Our densities were markedly different at individual sites and for averages among lowland Neotropical rain forest sites reported by Gentry (Gentry 1982, 1991; Phillips & Miller 2002). Gentry also recorded only rooted trees and lianas along transects; however, he included many monocots and pteridophytes (Phillips & Miller 2002). To compare data sets, we downloaded Gentry's dataset (http://www.mobot.org/MOBOT/Research/gentry/transect.shtml) and adjusted it to mimic our sampling scheme by deleting all monocots (except *Smilax* and *Desmoncus*) and all pteridophytes. In addition, we used only those Gentry transects conducted in sites that were located between 23°N and

TABLE 7. *Mean AGB in Mg/ha of trees 30 cm DBH or greater for each soil type of four Neotropical forests. Sites and soil types are listed in order of increasing relative soil fertility. Biomass estimates for trees are calculated using the allometric equation in Chave et al. (2001; method 1) and using the same equation but multiplying it by the specific gravity for each individual divided by the average specific gravity across sites (method 2). Values are x̄ ± SD scaled to hectare for N = 3 transects per site and soil type.*

Site	Soil type	AGB Method 1	AGB Method 2
KM41	Spodosol	158.5 ± 64.2	190.4 ± 73.6
	Oxisol	170.8 ± 20.6	200.3 ± 23.4
Cocha Cashu	Ultisol	185.8 ± 39.8	176.1 ± 34.9
	Entisol	372.5 ± 39.3	383.5 ± 28.9
BCI	Oxisol	160.1 ± 27.1	127.0 ± 32.3
	Alfisol	108.7 ± 72.8	110.5 ± 75.6
La Selva	Ultisol	190.6 ± 63.6	157.4 ± 51.5
	Inceptisol	142.1 ± 7.1	119.6 ± 9.6
x̄		186.2	183.9

23°S, situated lower than 1000 m elevation, and receive more than 1700 mm annual rainfall. Across the 69 sites that fit this description, his averages of 68 ± 30 lianas and 287 ± 58 trees per 0.1 ha were higher than our average for lianas by 100 percent and for trees by 38 percent. Gentry also recorded considerably more lianas and trees than we did on Cocha Cashu Entisols (Gentry > this study: lianas: 77 > 14; trees: 271 > 146); and La Selva Ultisols (lianas 50 > 21; trees: 259 > 191). In addition, the average percentage of woody stems 2.5 cm or greater composed by lianas in our study (13%) was lower than Gentry's average (19%). We think that Gentry sampled transects greater than 0.1 ha in area given his sampling scheme (the "exploded transect design" of ten 2 × 50m transects). A slight overestimation in the transect width could easily account for the observed 38 percent increase in average tree stem density. Differences in methodology are also a potentially important bias; indeed, for lianas rooted within the plot, Gentry simply recorded its greatest stem diameter if at any point it was 2.5 cm or greater (Phillips & Miller 2002). In addition, he measured all liana stems (ramets). We only measured lianas that were 130 cm or taller and rooted in the transect, and we attempted to measure genets only once. These two differences in methods explain a large part of the observed disparity in density estimates and is a clear warning against comparing liana densities without knowing the methods employed.

BIOMASS ESTIMATION.—Many factors can influence the accuracy of biomass estimation in tropical forests (Clark et al. 2001a). We examined how inclusion of small trees and lianas and use of different allometric equations affect biomass estimates in the four forests. As a significant fraction of the AGB is stored in very large trees (≥70 cm), the choice of allometric equation based on diameters for this size class greatly influences the biomass estimate (Clark & Clark 2000). Incorporating specific gravity of species into biomass estimation in this study (method 2) increased estimated AGB at KM41 and on the more fertile soil type at CC. Estimated large tree and total AGB was lower for LS and BCI when method 2 was used. The differences among sites in the direction of change in AGB with different methods were caused by the higher wood specific gravities of trees in the Amazonian than Central American sites (Muller-Landau 2004). For example, the mean specific gravity of trees at KM41 was 50 percent greater than the mean of trees at LS (Muller-Landau 2004).

Lianas and small trees (1–10 cm and including palms) composed roughly similar amounts (ca 5% each) of the total AGB. Stemless palms, which we did not measure in this study, likely contribute only ca 0.3 percent of total living AGB, as was found in another study near KM41 where stemless palms are common (Nascimento & Laurance 2002). Most forest inventories ignore small trees and palms and all lianas and therefore underestimate living AGB by about 10 percent; however, the choice of allometric equation used to estimate biomass of large trees seems to have a similar effect on total AGB estimates (0–12% difference depending on the site).

Our AGB estimates are within reported ranges for these and other Neotropical forests (Laurance et al. 1999, Clark & Clark 2000, Chave et al. 2003). Thus, our biomass estimates from small sample areas are fairly representative of larger areas and greater sampling effort. Our estimates from

CC may provide the first comparison between the AGB held in old floodplain and upland rain forests of this region. Floodplain forests traditionally have been more thoroughly sampled because they are more accessible (Kvist & Nebel 2001). These fertile forests, however, which have large average AGB per hectare, represent only a small area of Western Amazonia (Tuomisto 1998). This fact should be taken into account when extrapolating biomass estimates at the regional scale.

NEOTROPICAL FOREST CONSTANTS.—We examined four biological stations in the Neotropical moist to wet tropical forests and found them to differ in their structure and biomass. Looking at data from many more forests and including the Paleotropics, Leigh (1999) found that total basal area of trees 10 cm or greater measured at 130 cm above the ground or above buttresses was consistently near 30 m²/ha and AGB was near 300 mg/ha. We found that mean basal area for trees 10 cm DBH or greater across the four forests was very close to Leigh's (1999) findings at 30.2 m²/ha, but it differed significantly among forests. Tree basal area was high in transects on the old floodplain Entisols at CC and on both soil types at KM41. The average for AGB using method 1 for trees and palms 10 cm or greater was 250 Mg/ha, substantially lower than what Leigh (1999) proposed as a constant; however, the value for AGB is subject to adjustment given the multitude of factors that affect its estimation. In addition, AGB for trees and palms 10 cm or greater differed among sites. The four forests, however, shared a common density and biomass of lianas 0.5 cm DBH or greater and these could be considered constants for intact understory areas of old-growth rain forests in the Neotropics.

Overall, our results are contrary to Leigh's (1999) proposal that basal area and biomass are both constant across lowland Neotropical forests.

Should we support the view that common denominators can be found across mesic to wet forests in the Neotropics? We believe that seeking and documenting such patterns is a valuable goal in tropical forest ecology, a field that is traditionally dominated by the search for peculiarities rather than general trends. The complexity of tropical forest ecosystems should not prevent us from searching for simplifying patterns. Obviously, no biological variable is truly constant and variability should be acknowledged. Although stem density, basal area, and some biomass components differed significantly among the forests we studied, it is interesting to observe that they seem less variable than other quantities (e.g., tree species richness). This observed "saturation" could be related to general architectural rules shared by flowering plants (Enquist & Niklas 2001, 2002).

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