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Landscape-scale variation in forest structure and biomass in a tropical rain forest

D.B. Clark^{*,1}, D.A. Clark

University of Missouri-St. Louis, St. Louis, Missouri, USA, and La Selva Biological Station, Costa Rica, USA

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Abstract

A better understanding of the reasons for variation in tropical rain forest (TRF) structure is important for quantifying global above-ground biomass (AGBM). We used three data sets to estimate stem number, basal area, and AGBM over a 600-ha old-growth TRF landscape (La Selva, N.E. Costa Rica). We analyzed the effects of soil type, slope angle, topographic position, and different sample designs and measurement techniques on these estimates. All three data sets were for woody stems ≥ 10 cm in diameter. Estimated AGBM was determined from stand-level measurements using Brown's (Brown, 1997) allometric equation for Tropical Wet Forest trees. One data set was from three subjectively-sited 4-ha plots (the 'OTS plots'), another was based on 1170 0.01 ha plots spaced on a regular grid (the 'Vegetation map plots'), and the third was from 18 0.5 ha plots (the 'Carbono plots') sited to provide unbiased samples of three edaphic conditions: flat inceptisol old alluvial terraces; flat ultisol hill-tops; and steep ultisol slopes. Basal area, estimated AGBM and the contributions of major life forms were similar among studies, in spite of the differences in sampling design and measurement techniques. Although the Carbono plots on flat inceptisols had significantly larger and fewer trees than those on ultisols, AGBM did not vary over the relatively small edaphic gradient in upland areas at La Selva. On residual soils, the largest trees were on the flattest topographic positions. Slope angle per se was not correlated with basal area or AGBM within the residual soils. Errors introduced by palm and liana life forms, as well as hollow trees, did not significantly affect AGBM estimates. In contrast, the methods used to measure buttressed trees had a large impact. Plot sizes of 0.35–0.5 ha were sufficient to achieve coefficients of variation of $<12\%$ for basal area with only six replicates in a given edaphic type. AGBM estimates ranged from 161 to 186 Mg/ha. These low values appear to be mainly due to the Tropical Wet Forest allometry equation used. This in turn may be indicative of a real and substantially lower ratio of biomass/basal area in Tropical Wet Forest than in Tropical Moist, as previously noted by Brown (1996).

Our results indicate that for upland TRF landscapes with levels of environmental variation similar to La Selva, AGBM will be relatively insensitive to soil type and topography. However, because topography and soil type had much stronger effects on stem size, stand density, and spatial heterogeneity of stems, stand dynamics may be more sensitive than AGBM to this range of conditions. We recommend that future studies of landscape-scale forest structure employ stratified sampling designs across major environmental gradients. Unbiased sampling with replication, combined with consistent and well-documented measurement techniques, will lead to a greatly improved understanding of the magnitude of and reasons for variation in forest structure and AGBM within TRF landscapes. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Tropical rain forest; Landscape ecology; Forest mensuration; Carbon stocks; Edaphic effects; Soils; Topographic effects; Mesoscale landscapes

* Corresponding author. Tel.: +1-506-766-6565/146; fax: +1-506-766-6535.

E-mail address: dbclark@sloth.ots.ac.cr (D.B. Clark).

¹ Interlink 341, P.O. Box 025635, Miami, Florida, 33102-5635.

1. Introduction

Low-latitude forests are estimated to contain ca. 60% of the total above-ground carbon in world forest vegetation (Dixon et al., 1994). Nevertheless, for a variety of reasons there is still considerable uncertainty about carbon stocks in tropical forests at landscape scales (Brown, 1997). A better understanding of tropical biomass distribution at this scale is therefore of great theoretical and practical interest (Schimel, 1995). Because above-ground carbon stocks are primarily determined by the size-frequency distribution of trees, one avenue for improving estimates of carbon stocks is to improve our understanding of factors causing within-landscape variation in forest structure. By ‘forest structure’ we mean the size-frequency distribution of stems, the percentage contribution of major life forms such as trees and palms, and the spatial organization of structurally distinct patches such as treefall gaps. Large-scale mapping of forest structure must rely on remote sensing techniques, including existing satellites such as Landsat (c.f. Hall et al., 1995) and newer techniques such as satellite lidar mapping (Dubayah et al., 1997). Ultimately, however, these remote-sensed data have to be ground-truthed at the scale of tropical landscapes.

Tropical rain forest (TRF) structure and biomass is known to vary with soil type (Pires and Prance, 1985; Tuomisto et al., 1995), soil nutrients (Laurance et al., 1999), climate (Holdridge, 1979; Gentry, 1982), disturbance regime (Lugo and Scatena, 1996), successional status (Saldarriaga et al., 1988), topographic position (Austin et al., 1996), and human impacts (Brown et al., 1994; Laurance et al., 1997; Gaston et al., 1998). However, the degree to which the structure of old-growth TRF varies across mesoscale (1–100 km²) landscapes, and how this variation relates to environmental variables, are poorly known. One reason for this is that few TRF forest studies have been explicitly designed for extrapolation to landscape scales (Korning and Balslev, 1994; Brown et al., 1994; Grace et al., 1995; Laurance et al., 1999 are exceptions). Most ecological data in this biome have been taken on single plots, frequently ≤ 1 ha. For example, when Phillips et al. (1994) examined forest dynamics in 25 tropical forest plots, the median plot size was 1 ha. Even the largest ‘ecological’ plots are commonly ≤ 50 ha. Such plots are typically unrepli-

cated with respect to edaphic factors, and they may be sited in areas unrepresentative of the larger landscape (Brown and Lugo, 1992). Without replication, even large plots are poorly suited for statistical analyses of forest structure at landscape scales.

In this paper, we evaluate the influence of edaphic factors on forest structure over a 600-ha landscape of old-growth tropical rain forest. This spatial scale, which is one to two orders of magnitude larger than the scale of most plot-based tropical forest ecological studies, is sufficient to encompass a diversity of soil types, topographic positions, and multiple watersheds at our study site. Our study was made possible by some exceptional on-site resources. One was a site-wide 50 × 100 m grid system, surveyed to decimeter accuracy (Clark, 1998). The grid greatly facilitates large-scale regular sampling as well as unbiased blocked sampling. From a previous study (Clark et al., 1998), topographic data as well as soil type were available for each of the 1170 grid points within our study area. A topographic map generated by cartographic interpolation of several thousand transit-surveyed points was also available (OTS unpublished data). To our knowledge, this intensity of georeferenced data resources is currently unique for a mesoscale landscape in old-growth Tropical Wet Forest.

In addition, we had access to three different forest inventory data sets from the study site. These data were gathered for differing purposes and with somewhat different techniques. We were therefore interested to see the degree to which independent data from the same site concurred in describing forest structure and its relation to edaphic factors.

In this paper, we present two classes of findings. The first describes how forest structure on this particular mesoscale landscape varies in relation to edaphic factors. Secondly, we examine the impact of different sampling methods on these results. We conclude by analyzing our findings in the context of global TRF biomass estimates, and by recommending improvements for future studies of carbon stocks in this biome.

2. Methods

The study was carried out in old-growth forest at the La Selva Biological Station in the Atlantic lowlands

of Costa Rica, Central America. The area is a mosaic of several distinct edaphic zones (Sollins et al., 1994), including alluvial terraces formed by contemporaneous or prehistoric flooding, areas of residual soils (mainly ultisols) formed by in-place weathering of lava flows, swamps and infertile colluvial soils of small stream valleys (Fig. 1). A description of these soils is given by Clark et al. (1998). The forest is classified as Tropical Wet Forest in the Holdridge system (Hartshorn and Peralta, 1988). Rainfall averages ca. 4000 mm annually, with an average temperature of 26° (Sanford et al., 1994).

We analyzed three different sets of forest inventory data, each one based on total inventory for woody stems ≥ 10 cm diameter above buttresses. One set comes from 1170 circular 0.01 ha plots centered on the grid posts of a previously-established 50 × 100 m grid that covers the La Selva reserve (Clark, 1998). All grid points in a 573 ha area of old growth were sampled (Fig. 1). At each plot, diameter of each stem was measured using a fabric diameter tape (± 1 mm resolution) at breast height or above buttresses or major stem irregularities. Two 3-m interconnectable ladder sections were used to reach above buttresses. In

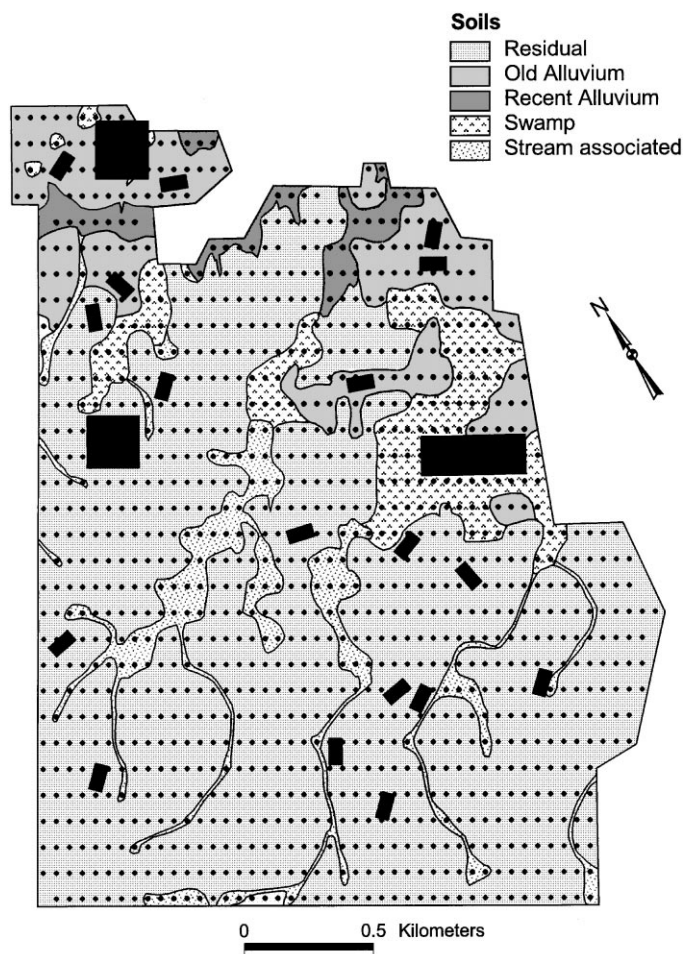


Fig. 1. Soil map and plot locations of the study area at the La Selva Biological Station, Costa Rica. Dots represent posts in the station's grid (used as plot centers for the 1170 0.01 ha Vegetation map plots). The three larger plots are the OTS plots, while the smaller rectangles represent the 18 0.5 ha Carbono plots, stratified by soil type and topography (see Section 2).

some cases, the boles were still not cylindrical at ca. 7 m above the ground. In these cases, the stem diameter was either measured at the highest reachable point, or the diameter was estimated with one person on the ladder holding a linear-scale tape against the trunk and a ground observer estimating the cylindrical bole diameter. Topographic position of each plot was classified as flat terrain (terrace or ridgetop); upper slope; mid-slope; base of slope/riparian. Slope angle in the direction of greatest slope was measured using a clinometer and sighting between two 1.5 m tall staffs placed 1 m above and below the grid post. Because these data were from a project designed to study landscape-scale vegetation patterns, we call these the ‘Vegetation map plots’. Plot soil type was taken from the data by Clark et al. (1998).

A second data set, made available to this study by M. Lieberman and D. Lieberman, comes from three long-term forest inventory plots at La Selva (Fig. 1). The plots measure 4, 4, and 4.4 ha (hereafter, ‘3 4-ha plots’). The plots were subjectively sited to cover a range of soil types (Lieberman and Lieberman, 1994). Descriptions of the plots and census techniques are given by Lieberman et al. (1985) and Lieberman and Lieberman (1994). Here, we use data from measurements made in 1988–1989. We used the above-buttress measurements exclusively except in one analysis comparing measurements at breast height with above buttress measurements. We refer to these data as the ‘OTS plots’ data.

The third data set comes from 18 0.5 ha plots (each 50 × 100 m) that are part of a landscape-scale study on carbon storage and flux in old-growth TRF (the Carbono Project). Plot locations were established using the La Selva GIS topographic coverage and Clark et al.’s (Clark et al., 1998) soil coverage. Six plots were allocated each of three edaphic conditions: relatively fertile flat inceptisols (old alluvial terraces); relatively infertile ultisol areas on ridgetops; and ultisol steep slopes (Fig. 1). Soil units were blocked to produce approximately equal sample intensity within each unit. The exact locations of the plots were determined in the laboratory from the GIS map. Plots were then sited in the field at those exact coordinates, surveyed to decimeters from the nearest grid post; the only exceptions were plots that would not fit in the field where they were mapped due to the small-scale inaccuracies of the topographic coverage. In these

cases, the plots were either rotated until they fit within the desired edaphic position (if possible), or the site was discarded and a new one selected by the same criteria. Plots were surveyed using a transit and slope-corrected distances. Forest structure was explicitly ignored during plot establishment, to ensure that these plots were unbiased by any consideration of forest structure. In each of the 18 plots, diameter above buttresses was measured as in the Vegetation map plots, except that up to 4 3-m sections of ladder were used to measure boles above buttresses or basal deformities. We refer to these data as the Carbono plots data.

All diameters, including those of palms and lianas, were transformed into estimated above-ground biomass (AGBM) using the Tropical Wet Forest allometric equation of Brown (1997):

$$\text{Biomass (kg)} = 21.297 - 6.953\text{DBH} + 0.740(\text{DBH}^2)$$

where DBH is diameter in cm at breast height or above buttresses.

3. Results

3.1. Landscape-scale estimates of forest basal area and biomass

Even though the three studies employed very different designs, estimates of landscape-scale basal area and estimated AGBM differed by only 10 and 16%, respectively, among the studies (Table 1). The AGBM of trees <70 cm diameter was particularly constant, varying only 7% among studies. Larger differences were seen in the contributions of trees ≥70 cm diameter; estimates of density of these trees and of their contribution to the total AGBM varied by a factor of 2 among studies.

The contribution of the dominant tree species *Pentaclethra macroloba* (Willd.) Kuntze (Mimosaceae) and the relative frequencies of trees, palms, and lianas were similar among studies (Table 2). Trees accounted for ≥90% of the basal area and biomass, and *Pentaclethra* by itself was 36–38% of the total estimated AGBM. Palms accounted for 25–26% of the stems, but due to their smaller average size were only 5–7% of the estimated AGBM.

Table 1
Forest structure as evaluated by three different studies^a

Data set	Plot size (ha)	Number of plots	Mean <i>N</i> stems/ha	Mean basal area/ha (m ²)	Mean AGBM ^b (dry mass) (Mg/ha)	AGBM ^b in trees <70 cm diameter	AGBM ^b in trees >70 cm diameter (%)	<i>N</i> trees ≥70 cm diameter/ha
OTS plots	4, 4, 4.4	3	462 ± 47	25.8 ± 0.7	182.9 ± 8.4	139.2	23.8	8.6
Carbono plots	0.5	18	504 ± 22	23.6 ± 0.5	160.5 ± 4.2	137.9	14.1	4.7
Vegetation map plots	0.01	1170	448 ± 6	26.0 ± 0.8	186.1 ± 6.6	130.7	29.7	10.1

^a All studies were based on total inventory of woody stems ≥10 cm diameter above buttresses (details in Section 2).

^b Estimated aboveground biomass, calculated from the diameter of individual trees using the Tropical Wet Forest allometric equation by Brown (1997). Data are standardized to a per hectare basis. Mean data are means ± SEM.

3.2. Factors affecting variation in forest structure: soil type

Since the Vegetation map plots and the Carbono plots were replicated with respect to soil type, the data from these studies can be used to examine variation in forest structure among soil types (Table 3). The Vegetation map data show that all aspects of forest structure examined varied significantly among soil types. Plots on recent Alluvial soil were the most distinctive in

having fewer and small trees, with a resulting low basal area and estimated AGBM. Between the two largest soil classes, Residual and Old Alluvial, the number of stems was lower and the average tree diameter was larger on the more nutrient-rich old alluvial soil. However, the product of these numbers, basal area, as well as estimated AGBM, did not differ between soil types.

The Vegetation map plots sampled much topographic variation within each soil type. Because the

Table 2

The absolute and proportional abundance of the dominant tree species (*Pentaclethra maculosa*, Mimosaceae), and of trees, palms and lianas in the three data sets (described in Section 2)

	OTS plots		Carbono plots		Vegetation map plots	
	<i>N</i> /ha	Stems (%)	<i>N</i> /ha	Stems (%)	<i>N</i> /ha	Stems (%)
(A) Absolute and proportional abundance						
<i>Pentaclethra</i>	60.2	13.1	58.4	11.6	59.4	13.3
All trees	329.6	71.6	367.1	72.8	326.3	72.9
All palms	120.3	26.1	128.7	25.5	112.1	25.0
All lianas	10.6	2.3	8.8	1.7	9.1	2.0
All stems	460.6		504.6		447.5	
Total <i>N</i> , stems	5711		4541		5236	
(B) The contribution of these groups to basal area (BA)						
	BA (m ² /ha)	Total (%)	BA (m ² /ha)	Total (%)	BA (m ² /ha)	Total (%)
<i>Pentaclethra</i>	8.8	34.0	7.6	32.3	9.1	34.9
All trees	23.4	90.7	21.1	89.6	23.8	91.3
All palms	2.2	8.6	2.3	9.7	2.1	7.9
All lianas	0.1	0.6	0.1	0.6	0.2	0.6
(C) The contribution of these groups to estimated above-ground biomass (AGBM, Mg dry mass/ha)						
	AGBM (Mg/ha)	Total AGBM (%)	AGBM (Mg/ha)	Total AGBM (%)	AGBM (Mg/ha)	Total AGBM (%)
<i>Pentaclethra</i>	67.7	37.1	58.0	36.1	70.9	38.1
All trees	171.1	93.7	148.7	92.7	175.1	94.1
All palms	10.9	6.0	11.1	6.9	10.1	5.4
All lianas	0.7	0.4	0.6	0.4	0.8	0.4
Total	182.9		160.5		186.1	

Table 3

Variation in forest structure in relation to soil type in old-growth Tropical Wet Forest at the La Selva Biological Station, Costa Rica

Soil type	Number stems/ha	Basal area (m ² /ha)	AGBM ^a (Mg/ha)	<i>N</i> plots	Mean diameter (cm)	<i>N</i> individuals
(A) Vegetation map plots						
Residual	477.6	26.0	183.5	798	21.6	3811
Old alluvial	425.0	27.0	195.2	140	23.1	595
Stream valley	383.0	30.1	226.3	94	24.6	360
Swamp	349.1	24.3	179.4	106	23.5	370
Recent alluvial	312.5	16.4	114.2	32	21.5	100
Kruskal–Wallis <i>p</i>	<0.0001	<0.0006	<0.0002		<0.03	
(B) Carbono plots						
Ultisol — flat	510.3	22.2	149.1	6	20.0	1531
Ultisol — steep slopes	592.7	24.9	165.5	6	19.8	1778
Old alluvial	410.3	23.5	166.8	6	22.3	1231
Kruskal–Wallis <i>p</i>	<0.0002	NS	NS		<0.03	

^a Above-ground biomass (Mg dry mass/ha), estimated using Brown's (Brown, 1997) Tropical Wet Forest equation.

Carbono plots were stratified by topographic position within one soil type (flat ultisol versus steeply sloping ultisol), it was possible to test for a pure soil-type effect, independent of topography (Table 4). Results were similar to those from the Vegetation map data. Flat Old Alluvial plots had significantly fewer but larger trees than flat ultisol plots, while the basal area and plot biomass did not differ among the two soil classes.

3.3. Factors affecting variation in forest structure: topographic position

Residual soils, mainly ultisols, covered the majority of the study area and also had the steepest topography. We used two sets of data to examine the effect of topographic position on forest structure while controlling for soil type. Among the Carbono ultisol plots, stem number per plot and plot basal area were sig-

nificantly higher on slopes than on flat plots (Tables 3 and 4). A finer scale of resolution was possible using all the Vegetation map plots that occurred on Residual soils (Table 5). The largest trees occurred on the flattest topographic positions, i.e. alluvial terraces, ridgetops, bases of slopes and riparian zones by small streams. Stem density was lower at the lower slope positions (Table 5).

3.4. Factors affecting variation in forest structure: slope angle

We examined the relation of forest structure to slope angle, controlling for soil type, by analyzing only the Vegetation map data from residual soil plots (*N* = 798 plots and 3811 stems). In these plots, the median slope angle was 14°, and the top quartile ranged from 21 to 44°. Neither the number of stems, plot basal area nor estimated AGBM were significantly related to slope

Table 4

Results of comparisons between Carbono plots on flat old alluvial (FA) sites, flat ultisol sites (FU), and steeply sloping ultisol sites (SU)^a

	Stem number per plot	Median tree size	Plot basal area	Plot biomass
Flat alluvium × flat ultisol	FU > FA**	FA > FU**	NS ^b	NS
Flat ultisol × slope ultisol	SU > FU*	NS	SU > FU*	NS

^a The comparisons between flat alluvium and flat ultisol test for an effect of soil type. The comparisons between flat ultisol and steeply sloping ultisol sites test for an effect of slope within one soil type. Data are shown in Table 3. Probabilities are from two-tailed Mann–Whitney *U* tests.

^b Not significant.

* *p* < 0.05; ** *p* < 0.01.

Table 5

Variance in forest structure in relation to topographic position within the Vegetation map plots on Residual soil (see Fig. 1)

Topographic position	Mean N/ha^a	N plots	Mean individual diameter (cm) ^a	N individuals
Terrace/ridgetop	495.7 a	23	22.1 a,b	114
Upper slope	515.1 a,b	205	20.5 a	1056
Mid-slope	470.6 b	472	21.4 a	2221
Base slope/riparian	428.6 b	98	24.8 b	420
Kruskal–Wallis p	<0.008	798	<0.0001	

^a Plots with the same letter are not statistically different in a non-parametric *a posteriori* test, $p > 0.05$.

angle (Spearman's r , $p > 0.05$, $N = 798$). For individual trees ($N = 3811$), neither diameter, basal area, nor estimated AGBM were related to slope angle. For each of these six analyses the Spearman's correlation coefficient was less than ± 0.02 . Because of the small size of these plots (0.01 ha), there was enormous variance in the structural variables (see below). This undoubtedly made detection of pattern difficult.

Forest on steep ultisol slopes was considerably more variable in basal area at small spatial scales than areas on old alluvial terraces or ultisol ridgetops (Fig. 2). This effect was evidently due solely to factors related to slope. The old alluvial terraces and ultisol ridgetops had very similar relations of basal area

variation to plot area (Fig. 2), in spite of their differing soil nutrient conditions and stem densities (Table 3).

3.5. Factors affecting variation in forest structure: patch size

Gaps caused by tree falls and the sites of subsequent regrowth create patches of characteristic structure on all old-growth TRF landscapes. The size distribution and frequency of treefall gaps is one factor causing the high variance in basal area estimates at small plot sizes, as shown in Fig. 2. The average area of gaps (vertical projection) at La Selva has been reported to be on the order of 0.01–0.02 ha, with only 4% of the

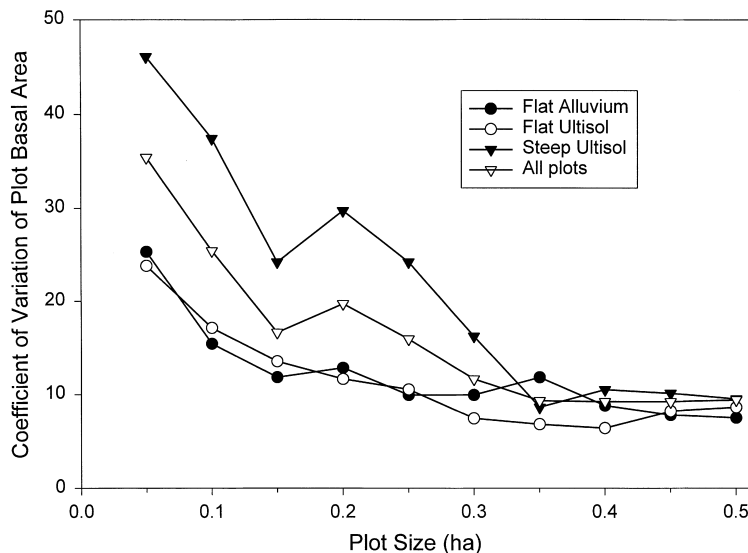


Fig. 2. Coefficient of variation of plot basal area in relation to plot size for the 18 Carbono plots. The analyses are completely nested, so that for example all the data used for the 0.05 ha analyses are included in every analysis for larger plot sizes. $N = 6$ plots for each topographic-soil category, and $N = 18$ for all plots combined.

gaps exceeding 500 m² (Sanford et al., 1986). Inter-sample variance in basal area estimates begins to stabilize for plots sizes above 0.25 ha (Fig. 2). This stabilization thus occurred when plot size was ≈ 20 times greater than the estimated median gap size, or 5 times larger than the estimated size of the largest gaps at La Selva.

3.6. Plant life form effects on AGBM estimates

For AGBM estimates we used the same allometric equation for trees, palms, and lianas. Putz (1983) developed an allometric equation specifically for lianas. When applied to the Carbono plots data, the Putz equation yielded substantially larger estimates of individual liana biomass (mean of 124 kg vs. 69 kg for the Brown equation). The Putz equation is undoubtedly more accurate, since it was developed from direct measurements of lianas. However, at a landscape scale rooted lianas were not abundant (9/ha), so the increase in total AGBM by applying the Putz equation would be negligible (0.5 Mg/ha).

Compared to trees, canopy and subcanopy palms change relatively little in diameter while greatly increasing in height and biomass. In addition, the relation of height to diameter varies substantially among species (Rich, 1986). We know of no general equation for palm biomass based solely on trunk diameter. Brown (1997) suggests developing biomass equations from local harvest of palms for forests where palms are numerous. The only palm biomass data from La Selva are given in wet weight (Rich, 1986). The range of wet weights for La Selva palm species that attain ≥ 10 cm diameter was 33–446 kg in Rich's data, whereas the range of predicted dry weight values (using Brown's, 1997 equation) for the Carbono plots data was 26–396 kg. We suspect that the tree-based allometric equation used here somewhat overestimates palm biomass. The overall effect on biomass estimates however may be relatively minor. If we overestimated palm biomass by a factor of 2, this would only alter the Carbono plots biomass estimates by 5% (Table 2C).

3.7. Effects of hollow trees on AGBM estimates

The allometric equations for estimating biomass from diameter are almost certainly biased due to a

preference of harvesters for non-hollowed out trees. An upper limit on this bias can be calculated from the total amount of hollowed out volume in downed logs. This is likely to be an upper limit, because downed logs have decayed further while on the ground and presumably are more likely to be hollow than standing trees. We mapped and measured all pieces of dead wood ≥ 30 cm diameter in the Carbono plots (D.B. Clark and D.A. Clark, unpublished data). The hollowed-out space was 1.7% of the total log volume. This suggests the effects of hollowed-out trees on the total AGBM estimate is minor, at least at La Selva.

3.8. Measurement technique effects of AGBM estimates

Estimates of AGBM differed by 16% among the three data sets analyzed here (Table 1). Differences in measurement techniques account for some of these differences. To determine the order of magnitude of the effects caused by including or excluding buttresses, we analyzed the OTS plots data using both around-buttress measurements and above-buttress data. The average increase in basal area for individual trees measured around buttresses compared to above buttresses was 32% for basal area and 43% for biomass. Although all three data sets analyzed here were ostensibly measured 'above buttresses', the degree to which this was done varied among data sets. We remeasured 12 trees ≥ 70 cm above-buttresses that had been measured during the Vegetation map project 2–3 years before remeasurement. At the remeasurement we used up to four sections (12 m) of climbing ladder and applied the measurement protocols employed in the Carbono plots. In the Carbono project, we require maximum precision for annual diameter growth, and great care is taken in selecting the most regular bole measurement site available up to 12 m above the ground (4 sections of climbing ladder). When remeasured using the Carbono Project protocols, these 12 trees measured an average of 16 cm in diameter less than when they were measured in the Vegetation map project, in spite of the several years' accumulated growth between the two measurements. Differences due to different measurement protocols clearly account for some of the differences among data sets in the numbers of large trees, basal area, and biomass (Table 1).

4. Discussion

4.1. Landscape-scale variance in forest structure

We found clear effects of both soil type and topographic position on forest structure across this TRF landscape. The forest on the most fertile soil, the Recent Alluvium, was by far the most distinct in having significantly lower stem number, basal area, and AGBM. We believe this is not due to the high nutrient status of the soil, but rather reflects the occurrence of treeless areas due to localized frequent flooding. For example, 22% of the 0.01 ha Vegetation map plots on Recent Alluvium ($N = 32$) had ≤ 1 tree, compared to only 7% of the plots on other soil types ($N = 1138$).

The Carbono plots were especially designed to separate the effects of soil type and topographic position. The data (Tables 3 and 4) show that both soil type and topography affected stem number. Steep slopes on ultisols averaged 44% more stems per hectare than flat inceptisol plots. Two other studies at La Selva have also reported higher stem densities on slopes. For woody stems ≥ 10 cm diameter in the three OTS plots, Lieberman et al. (1985) found 26% more stems/ha on the plot with highest topographic relief compared to the flattest plot. Similarly, Denslow (1995) found 18% higher sapling density on slopes compared to flat sites.

At La Selva plot basal area and estimated AGBM biomass varied only 12% among the Carbono Plot treatments. This contrasts strongly with Laurance et al.'s (Laurance et al., 1999) results from central Amazonian Tropical Moist Forest. They found that biomass varied by a factor of two over upland sites in a 1000 km² area, and that biomass was positively correlated with soil nutrients and organic carbon. A possible explanation for the different results may be that the landscape sampled in Amazonia has a greater range of variation in soil chemistry than La Selva.

To generalize the findings from La Selva, it is useful to consider a broad environmental characterization of the old-growth upland (non-swamp, not frequently flooded) forest. This landscape consists of zonal acid and high-clay soils, a modal pH between 4 and 5 and varying $\lesssim 1.5$ pH units among soil units (Sollins et al., 1994), with a topography of moderate to steep slopes

usually ≤ 50 m in length. Over an upland landscape with this degree of variance, we expect that soil type and topographic relief will be minor factors in determining forest AGBM. For forest dynamics, however, the variance is likely to be much more significant. The differences in stem number, median tree size and the higher spatial variance in basal area suggest that forest dynamics on steep slopes may be quite different than on flat areas. This could lead to significant differences in carbon fluxes among edaphic patch types, even though their above-ground carbon stocks are similar.

4.2. La Selva compared to other tropical rain forests

The La Selva values for basal area and particularly for AGBM (Table 1) are low compared to those reported from other TRFs. Phillips et al. (1994) summarized basal area data for 24 TRFs worldwide; 22 of these had basal areas greater than the maximum estimate found for La Selva. For AGBM, Brown et al. (1991) used a figure of 225 Mg/ha for tropical Asia (including disturbed forests), while the data by Gaston et al. (1998) suggest a total of 302 Mg for tropical moist forest in Africa (calculated from their number for total biomass and an estimated root/shoot ratio of 0.18). Brown (1997) summarizes AGBM estimates based on forest inventories from a variety of tropical forest types. For 12 inventories in neotropical moist and wet forest, the median AGBM for high-density closed forest on upland sites was 241 Mg/ha, and only one value is below 204 Mg/ha. Data from plot-based ecological studies in neotropical TRF give estimates that are similar or higher, with means ranging from ca. 221 to 399 Mg/ha (Golley et al., 1969; Saldarriaga et al., 1988; Jordan, 1989; Brown and Lugo, 1992; Fearnside et al., 1993; Lieberman and Lieberman, 1994; Brown et al., 1995; Alves et al., 1997; Delaney et al., 1997; Salomão et al., 1998; Laurance et al., 1999).

Several factors might account for the generally lower basal area and biomass figures we obtained for La Selva compared to other studies. The first is that most studies have been done in Tropical Moist Forests, whereas La Selva is Tropical Wet. Brown (1996) reports above-ground biomass estimates in relation to basal area. Her estimates for tropical America suggest that for a given basal area, Tropical Moist Forests are considerably more massive than

Tropical Wet. For example, for forests with basal areas of 25 m²/ha, the difference is on the order of 100 Mg/ha (estimated from her figure 11.1). Data from 65 1-ha plots in central Amazonian Tropical Moist Forest support this idea. Laurance et al. (1999) report a mean AGBM of 318 Mg/ha for stems ≥ 10 cm diameter. These biomass data were calculated using an allometric equation based on entirely different data than those used to develop the Tropical Moist Forest equation of Brown (1997). Nevertheless, the relation of biomass to basal area is very close to that independently predicted by the forest inventory data by Brown, 1996 (Fig. 11.1). We obtained basal area data for 32 of the Laurance et al. (1999) plots. While the Amazonian plots had significantly higher basal areas than the Carbono plots (Mann–Whitney U , $p < 0.0001$, $n = 32.18$), the mean difference was only 19%. In contrast, the mean biomass difference was almost 100% (318 vs. 160 Mg/ha). This suggests that much or most of the difference between La Selva is due to the difference in allometric equations between Tropical Wet and Moist forests. The effect of different allometric equations is shown graphically in Fig. 3. The difference in predicted tree biomass between life zones increases with bole diameter, and for trees above 100 cm diameter the differences range from ca. 10 000 to 50 000 kg. If the Laurance et al. (1999)

allometric equation is applied to the Carbono plots data, AGBM estimates increase from 160 to 286 Mg/ha, which is well within the range of Tropical Moist Forest estimates. The Tropical Wet Forest equation we use here (from Brown, 1997) is based on 169 trees. Our results suggest that for better estimation of Tropical Wet Forest biomass, increased biomass sampling, particularly of larger trees (cf. Brown, 1996), should be given high priority.

Even within a life zone, the allometric equations used to derive AGBM are a potential source of error. For example, because the biomass equation in Lieberman and Lieberman (1994) gives negative biomass for trees <140 mm diameter, the biomass figure they report from La Selva is questionable. There are at least two additional possible sources of error. One is that generalized allometric equations for a given life zone may not correctly describe the allometry of tree species at a particular study site. Without harvesting local trees, it is not possible to evaluate the extent of such errors. Equations that misrepresent local trees could either increase or decrease the whole forest biomass estimate, depending on local conditions. In the specific case of the Brown (1997) equations and the La Selva data set, however, this issue is minimized. More than half of the trees in the Tropical Wet Forest equation were harvested within 20 k of La Selva

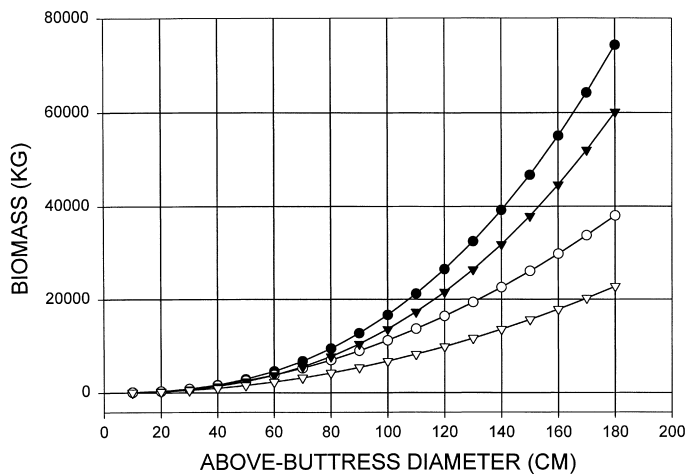


Fig. 3. Estimated above-ground biomass for trees as a function of above-buttress bole diameter, using four different allometric equations. The upper curve is generated by the equation used by Laurance et al., 1999, which was developed from trees harvested in Tropical Moist Forest in the Central Amazon. The middle two curves are the two Tropical Moist Forest equations from Brown, 1997, and the lower curve is the Tropical Wet Forest equation of Brown, 1997. Tropical Moist Forest trees are predicted by all three equations to be more massive at a given diameter than trees of Tropical Wet Forest.

(S. Brown personal communication). Nevertheless, the potential for site-specific departures from a generalized relationship is shown by the range of DBH/height relationships found by Lieberman et al. (1996) in plots separated by ≤ 500 m elevation.

A more subtle issue is the physical condition of the trees that were harvested to develop the allometric equations. If these trees are perfect specimens of each size class, they will lead to equations that overestimate the average biomass of trees of that size, due to their failure to represent senescent, diseased, and damaged individuals. In the case of the trees harvested near La Selva by the Brown (1997) biomass equation, the forester in charge stated that he chose trees ‘of good form and without defects’ (Edgar Ortiz personal communication). We suspect that when the great logistic effort of a whole-tree harvest is planned, particularly for large trees, less than perfect individuals are usually avoided. This bias will inflate whole-forest estimates of biomass, because not all trees are perfect. The magnitude of this bias is currently unknown.

One way to avoid the problems associated with allometric scaling is intensive harvesting of small plots (Golley et al., 1969; Klinge and Rodrigues, 1973; Fearnside et al., 1993). While valuable and necessary to quantify the biomass contributions of different life-forms in a given TRF, because of cost such harvests will necessarily be few and spatially restricted. For example, the total area sampled in the three studies cited above is only 0.51 ha. Unless the plots are carefully located and replicated to permit generalization to large landscapes, caution should be used when extrapolating harvest data from small plots to larger spatial scales.

Another important factor affecting estimates of forest structure and biomass is the method by which plots or transects were sited. Within any forested landscape, even controlling for soil and slope, patches vary in tree density. For example, for the 18 0.5 ha Carbono plots, stratified by soil and topography and randomly sited with respect to forest structure, basal area of the densest plot was 41% greater than in the smallest plot. A striking example of plot location effect is evident in the data of Holdridge et al. (1971). Using a 0.8 ha plot at La Selva, they reported an above-buttress basal area of 51.4 m²/ha, almost double the estimate from our study. Holdridge et al. clearly selected a site that was not representative of the

Table 6

The number of plots of different sizes necessary to estimate landscape-scale basal area using plots of different sizes^a

Number necessary to estimate basal area within:		
Plot size	±10%	±20%
0.01 ha	1662	418
0.5 ha	17	6
4.0 ha	6	4

^a The number of plots was calculated using the formula of (Zar, 1996, p. 108) using the mean and variance from the three data sets: 1170 0.01 ha Vegetation map plots, 18 0.5 ha Carbono plots, and 3 4-ha OTS plots.

larger landscape. This problem has been noted previously by Brown and Lugo (1992).

An additional problem is replication. Because many ‘ecological’ studies are based on unreplicated plots, there are no error bounds on the resulting estimates. The data from our study can be used to evaluate the degree of replication necessary for plots of different sizes in order to measure landscape scale basal area and AGBM to a given accuracy (Table 6). In terms of total plot area and the number of plots to be sited in an unbiased fashion, these data suggest that a plot size of 0.5 ha would be the most efficient way to sample basal area and AGBM across this landscape (see also Fig. 2). Brown et al. (1995) found a similar result for plot size in R ondonia, Brazil. Plots of ca. 0.35–0.5 ha appear to be large enough to incorporate the patch size distribution of old-growth TRF, and are small enough to permit significant replication. We emphasize that this conclusion applies only to stand structural variables and biomass. For demographic or floristic studies, larger or smaller plot sizes may be more appropriate (cf. Condit et al., 1995; Clark et al., 1999).

Another issue that affects the assessment of TRF biomass is methodological: where were the trees measured in relation to buttresses and basal trunk irregularities? In most modern ecological studies in TRF, trees are measured above these features (Manokaran and LaFrankie, 1990; Clark and Clark, 1992; Condit et al., 1995), but in some older studies diameters were measured at breast height. Buttresses and basal area irregularities are common in TRF. For example, 22% of the stems in the Carbono plots were measured above breast height. Buttressing increases with increasing tree size. In the Carbono plots, only 1 of 42 trees ≥ 70 cm diameter was measured at breast

height; the others required two to four 3-m sections of ladder to reach an approximately cylindrical point of measurement. In the OTS plots, below buttress-basal area and estimated AGBM were 35 and 43% higher, respectively, than above-buttress plot estimates. Clearly the above- or below-buttress distinction is critical for evaluating basal area and AGBM in TRFs. Less important, but still noticeable, is the exact criterion of 'above buttress'. This will particularly be the case for very large trees, where a large percentage of the individuals are buttressed (see above). Although few in number, these individuals have a substantial impact on the AGBM estimates, because estimated biomass generally scales non-linearly with stem diameter (cf. Fig. 3). In our study, the considerably lower diameters we obtained upon remeasurement of the large trees in the Vegetation plots using the Carbone plots protocols show the importance of clearly defined and documented field methods for choosing above-buttress points of measurement.

4.3. Conclusions and recommendations

In spite of numerous plot-based studies and forest inventories, there are surprisingly few data on basal area and biomass that can be used to assess variation in these factors and their relation to edaphic conditions across mesoscale (1–100 km²) TRF landscapes. In this study, we showed that an efficient approach at our study site was to use 0.35–0.50 ha plots replicated across the major soil and topographic gradients of the landscape. For future studies, we recommend that a preliminary reconnaissance be made to identify the major habitat gradients of the target landscape. These will frequently be geohydrologic (swamp versus upland), nutrient-based (white sands versus other soils), and topographic (sloping versus flat). With even a rough idea of the distribution of such habitat patches within a landscape, areas can be blocked by patch type, and sample intensity weighed by the relative importance of the patch type. Within the blocked habitat types, exact plot locations should be selected by a non-biased method. Global Positioning Systems offer a relatively inexpensive and efficient way to locate previously-determined plot positions in the field.

Although estimating forest structure requires only relatively straight-forward techniques, a great deal

remains to be done to understand the mesoscale organization of neotropical forests. Statistically robust sampling designs that span major environmental gradients, using consistent and well-documented measurement techniques, will permit a new level of estimation accuracy for landscape-scale variation in forest structure and biomass. Recognizing and documenting this variation is a first step towards understanding the internal structure and functioning of TRF landscapes.

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