

LETTER

First direct landscape-scale measurement of tropical rain forest Leaf Area Index, a key driver of global primary productivity

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Abstract

Leaf Area Index (leaf area per unit ground area, LAI) is a key driver of forest productivity but has never previously been measured directly at the landscape scale in tropical rain forest (TRF). We used a modular tower and stratified random sampling to harvest all foliage from forest floor to canopy top in 55 vertical transects (4.6 m²) across 500 ha of old growth in Costa Rica. Landscape LAI was 6.00 ± 0.32 SEM. Trees, palms and lianas accounted for 89% of the total, and trees and lianas were 95% of the upper canopy. All vertical transects were organized into quantitatively defined strata, partially resolving the long-standing controversy over canopy stratification in TRF. Total LAI was strongly correlated with forest height up to 21 m, while the number of canopy strata increased with forest height across the full height range. These data are a benchmark for understanding the structure and functional composition of TRF canopies at landscape scales, and also provide insights for improving ecosystem models and remote sensing validation.

Keywords

Canopy stratification, landscape ecology, Leaf Area Index, MODIS, tropical rain forest.

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INTRODUCTION

Tropical rain forests (TRFs) contain *c.* 13% of the global carbon stores of all terrestrial ecosystems (Malhi *et al.* 2002). They account for *c.* 30% of terrestrial photosynthesis (Field *et al.* 1998) and strongly regulate regional and global climate (Betts *et al.* 2007). These globally important roles are based on a simple structural unit: the leaf. The number and photosynthetic capacity of the leaves of any forest control primary productivity and carbon exchange. Not surprisingly, most ecosystem process models require an estimate of leaf area and its vertical distribution, as well as the response of

these leaves to environmental drivers such as light and water (Borchers *et al.* 1995; Ryan *et al.* 1996). Because leaf area regulates productivity for all ecosystems (Asner *et al.* 2003), there has been extensive research into methods for estimating LAI from remotely sensed data (Morsdorf *et al.* 2006; Pisek & Chen 2007).

Leaf Area Index (LAI) is defined as the amount of leaf area per unit ground area (Asner *et al.* 2003). As such it can only be directly assessed by harvesting all the leaves over a given ground area (Gower *et al.* 1999) or in deciduous forests by collecting total leaf-fall (Leuschner *et al.* 2006). Assessing LAI is particularly challenging in TRFs, which are

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typically tall, structurally complex and evergreen ecosystems. Previous direct measurements of TRF LAI have been limited to very small areas (e.g. Ogawa *et al.* 1965; Putz 1983; McWilliam *et al.* 1993; Richards 1996), so it has not been possible to assess the within-landscape variation in LAI and its relation to environmental drivers such as soil fertility, topography and disturbance history.

Leaf Area Index can be assessed indirectly in several ways. One class of indirect estimates involves measurement of transmitted or reflected light and calculations using a series of assumptions and models. Examples include estimates from satellites like MODIS and SPOT (Myneni *et al.* 1997; Pisek & Chen 2007), airborne lasers (Morsdorf *et al.* 2006), or from ground-based light sensors such as the LI-COR LAI-2000 Plant Canopy Analyzer (Aragão *et al.* 2005) or hemispherical photography (LeBlanc *et al.* 2005). These methods provide a radiation index more accurately described as Estimated Leaf (or Plant) Area Index. Indirect estimates of LAI can also be obtained via allometric equations based on harvest data and applying these at the stand scale (Gower *et al.* 1999). Indirect methods require validation with directly measured data, and calibration coefficients are frequently necessary to adjust indirect estimates to field data (Gower *et al.* 1999). Without data on directly measured LAI it has been impossible to assess the accuracy of existing indirect estimates of TRF LAI.

From the point of view of understanding photosynthesis and plant water use, knowing total LAI is only a first step. Another issue is the distribution of this leaf area among physiologically distinct plant types. This is especially challenging in TRFs, where plant diversity can easily exceed 2000 species (Hartshorn & Hammel 1994). Because plant functional groups differ widely in physiological performance (Geron *et al.* 2002; Cavaleri *et al.* 2006; Santiago & Wright 2007), realistic carbon uptake models require a landscape-scale understanding of the functional-group composition of LAI. It is also possible that the relative abundances of different plant functional groups are already changing due to global climate change (Phillips *et al.* 2002). In spite of the inherent scientific interest in understanding the three-dimensional distribution of plant functional groups, to date there has been no landscape-scale assessment of plant functional groups LAI in any TRF.

Another challenge that has intrigued biologists for more than a century is the three-dimensional distribution of TRF LAI. Early observers suggested that TRF canopies are organized into distinct strata, while later researchers questioned this view (Richards 1996). The existence and distribution of such strata in TRF has profound consequences for energy absorption and photosynthesis (Wu *et al.* 2000) as well as for the abundance and distribution of plants and animals. Progress on the issue has been stymied by a

lack of replicated sampling of the three-dimensional distribution of LAI at the landscape scale, as well by the confusing multiplicity of definitions for canopy strata (Parker & Brown 2000).

Here, we report the first use of a novel approach to directly measure the three-dimensional physical and biological structure of the foliage over an old-growth TRF landscape, and to assess how this structure relates to environmental variation. This research is part of a larger project (Clark & Clark 2000; Loescher *et al.* 2003; Cavaleri *et al.* 2006) to combine these data with measured physiological responses to parameterize process models of TRF forest carbon cycling, and to assess these models using field measurements of forest performance across this landscape.

We applied two new approaches to address the multiple challenges for obtaining an unbiased sample of the three-dimensional distribution of LAI for each plant functional group at the landscape scale. First, we developed a rigorous statistical design to ensure unbiased sampling across the landscape. This design explicitly incorporated major landscape gradients and addressed the issues of lack of replication and limited spatial extent affecting previous direct measurements of TRF LAI. Our second innovation was to incorporate a movable 46-m tall modular tower (Fig. 1) that was repeatedly built, disassembled, moved and rebuilt in locations determined by the statistical design. The tower enabled us to directly harvest all leaves in vertical transects from the forest floor to the top of the highest canopy. This approach eliminated the calibration and validation problems associated with indirect LAI estimates and enabled a quantitative evaluation of the biological composition and three-dimensional distribution of forest LAI.

The combination of the sampling design and movable tower permitted us to directly measure the horizontal and vertical distribution of LAI across an old-growth TRF landscape, to assess how LAI varied across major environmental gradients, and to measure the vertical distribution of LAI among plant functional groups. We discuss our findings in terms of their relation to landscape forest dynamics and canopy organization as well as to global issues in understanding and measuring ecosystem processes in TRFs. Finally, we show how this approach can be used to calibrate and validate currently widely used indirect estimates of landscape-scale LAI.

METHODS

The study was carried out in a 515 ha section of upland old-growth tropical wet forest at the La Selva Biological Station in the Atlantic lowlands of Costa Rica. Annual rainfall is *c.* 4000 mm and mean temperature *c.* 26 °C (Sanford *et al.* 1994). A modular walk-up tower (Fig. 1) was used to harvest



Figure 1 Construction of a practice tower in an open field. Tower is at level 10 (18.6 m tall) of 24 possible levels (sections). Field crew is preparing to lift another section using a small davit visible to the left of the top installed section of the tower.

all leaves and branches in 55 vertical transects from forest floor to the highest leaf. The transect footprint was 2.42 m² (1.30 × 1.86 m) for the first four transects (June–August 2003). We then obtained a side platform (Fig. S1) to expand the area sampled to 4.56 m² (2.45 × 1.86 m) for the next 51 transects (August 2003–March 2005). Because data from the two configurations did not differ significantly in LAI or forest height (data not presented), we analysed all transects together.

Locations for 45 vertical transect sites (Fig. 2) were selected using a stratified random design based on (1) GIS coverages (<http://www.ots.duke.edu/en/laselva/gis.shtml>) of predicted total soil phosphorus at 0–10 cm depth (kriged from 1200 soil P measurements, Clark *et al.*, unpubl. data), and (2) degree of slope predicted from a Digital Terrain Model. At La Selva phosphorus appears to be a major limiting nutrient (Lovelock *et al.* 2004; Espeleta & Clark 2007), and forest structure varies with slope (Clark & Clark 2000). The 45 random sites included few low-canopy sites, as would be expected from the rarity of such sites at the landscape scale (e.g. 1.5% of forest heights are ≤2 m; Clark

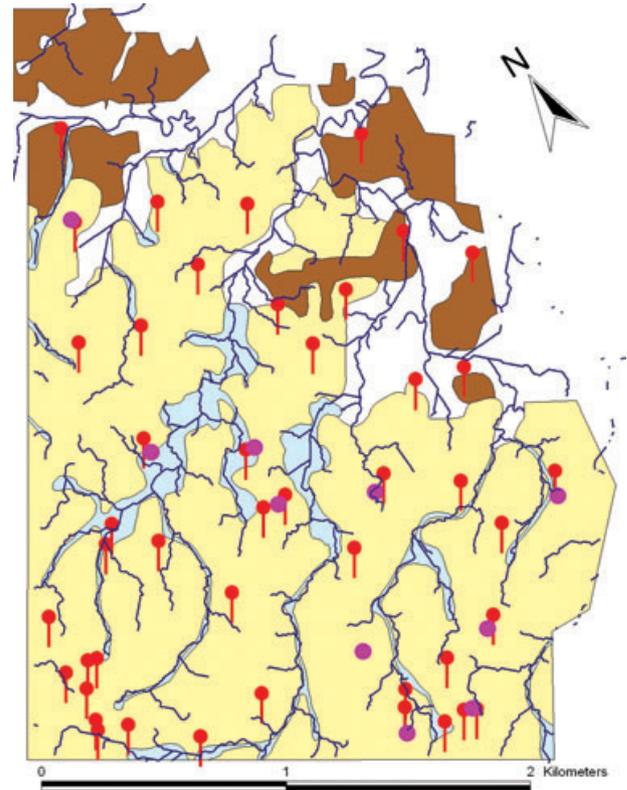


Figure 2 Locations of the 45 randomly sampled towers (red push-pins) and 10 low-canopy-height sites (pink circles) over 515 ha of upland (non-flooded) old-growth tropical rain forest at the La Selva Biological Station, Costa Rica. Principal soil types are old alluvial terrace inceptisols (brown), stream valley colluvial soils (blue) and residual ultisols (yellow) (Clark *et al.* 1998). Intercalated white areas are frequently flooded or waterlogged soils (swamp and recent alluvium) and were not sampled.

et al. 1996 and Fig. S2). We designed a separate random protocol for unbiased selection of an additional 10 sample sites with canopy top heights ≤16 m. Further detail on site selection is given in Appendix S1.

For analyses of landscape-scale patterns we use data from the 45 stratified random sites. For analyses involving relations with forest height (height of the highest leaf in each vertical transect) we use the combined data set (45 random sites + 10 low-canopy sites).

At each site all leaves within each 1.86-m-tall tower section were harvested, with sections harvested sequentially from the ground through the highest section with plant material. At harvest we separated leaves into nine functional groups (Table 1). Leaves were bagged by tower section and functional group and taken to the laboratory where one-sided leaf area was measured with a LI-COR-3100 leaf area meter. Finely compound leaves were divided into small pieces to avoid overlapping and leaf area

Table 1 Mean Leaf Area Index (LAI, $\text{m}^2 \text{m}^{-2}$) for all plant functional groups based on 45 stratified random samples (see Methods)

Functional group	Mean		Basal area ($\text{m}^2 \text{ha}^{-1}$)	% Basal area
	LAI	%LAI		
Trees except <i>Pentaclethra</i>	2.46	40.9	15.2	52.7%
<i>Pentaclethra</i>	0.83	13.9	10.2	35.3%
Palms	1.33	22.1	2.9	10.1
Lianas	0.73	12.1	0.5	1.9
Herbaceous climbers	0.24	3.9	–	–
Herbs	0.15	2.6	–	–
Ferns	0.11	1.9	–	–
Non-woody epiphytes	0.10	1.7	–	–
Woody epiphytes	0.05	0.8	–	–
Total	6.00	100.0%	28.8	100.0%
All trees	3.29	54.8	25.4	88.0%
Palms	1.33	22.1	2.9	10.1
Lianas	0.73	12.1	0.5	1.9
All others	0.66	10.9	–	–
Total	6.00	100.0%	28.8	100.0%

The dominant tree *Pentaclethra macroloba* was treated as a separate functional group during sampling; the species is combined in the 'All Trees' category for the summary comparisons. Basal area data are for stems ≥ 5 cm diameter occurring within 10 m of the towers (see Methods); data are re-scaled to $\text{m}^2 \text{ha}^{-1}$.

underestimation. For species such as *Pentaclethra macroloba* (Willd.) Kuntze that tend to close their leaflets when harvested, leaves were kept attached to the branches and put in water to stimulate leaf reopening the next day. Leaves that did not reopen were measured as is and the folded area multiplied by 2. The raw data for LAI for all 55 towers, divided by tower section height and plant functional group, are given in Appendix S2.

We assessed stem number and basal area of all woody stems ≥ 5 cm diameter in 10-m radius circular plots centred on tower footprints ($n = 54$; data were inadvertently not taken for one tower). Using a diameter tape, we measured stem diameter (mm) at 1.3 m height or above basal irregularities such as buttresses. Using a half-core auger, we collected 8–10 soil samples to 10 cm depth within 1–2 m of each tower footprint and then bulked them for a single soil sample per tower. Soil nutrients were analysed at the Institute of Soil Science and Forest Nutrition, University of Goettingen, Germany using standard methods (König & Fortmann 1996a,b).

We measured light gradients in each vertical transect by taking a hemispherical photograph at the centre of the floor of each tower section before the vegetation was harvested from the section. We used a Nikon Coolpix 4500 camera with a Nikon fisheye converter (FC-E8 0.21 \times) and the program Gap Light Analyzer (Version 2), Forest Ecology

Lab, Simon Fraser University, Burnaby, B.C., Canada, to calculate canopy openness.

We visually assessed areas of high leaf-area density (canopy strata) in each vertical profile by arranging all vertical 55 profile graphs side by side and looking for decision rules that quantified our visual impressions of stratification. We determined that two simple criteria were sufficient to divide the data into two classes that differed in mean LAI and leaf density by more than an order of magnitude (see Results). 'Strata' were defined as profile segments within which the LAI of each included tower section was ≥ 0.200 , or if the stratum was a single tower section, with a sectional LAI ≥ 0.300 . We term the very low leaf-density spaces between strata 'free air space'. While the quantitative limits to these classes are somewhat arbitrary, this classification lead to highly interpretable relations with forest structure (see Results). This approach is a quantitative extension of the Connell *et al.* (1997) presence-absence model and is similar to using a threshold in LiDAR remotely sensed data to define open and closed sub-canopy space (Lefsky *et al.* 2002). Our definition also corresponds to Definition 7 of canopy strata by Parker & Brown (2000), 'Stratification = Clumped Leaf Area with Height'.

MODIS satellite indirect estimates of LAI are used by researchers worldwide. As an example of using directly measured LAI to validate indirectly measured estimates, we assessed the MODIS estimates of LAI at our study site by analysing all available MODIS data for the period of tower construction (20 June 2003–16 March 2005) for the 4 1-km² pixels covering our study area (tiles 25,26,32,33). The product analysed was the MODIS ASCII Subsets Leaf Area Index 8-Day Composite [Collection 4] (ftp://daac.ornl.gov/data/modis_ascii_subsets/C4_MOD15A2/data/MOD15A2.fn_crlselv.txt). We used only data for which the quality control variable MODLAND was 00 (Excellent) or 01 (OK but not the best).

RESULTS

Landscape patterns of LAI

The landscape mean LAI was 6.00 ($n = 45$, range 1.20–12.94, SEM ± 0.32). In spite of the effects of scattered emergent trees (Fig. S2), high plant diversity, and tree mortality rates of 2–3% year⁻¹ (Lieberman *et al.* 1990), the coefficient of variation in LAI among sites was only 36%. Trees were the most important functional group (LAI 3.29), followed by palms (1.33) and lianas (0.73, Table 1). Although groups like epiphytes, ferns and herbs contribute important fractions of plant biodiversity (Hartshorn & Hammel 1994), in total they accounted for only 11% of total LAI (Table 1).

The ratio of plant functional group LAI to the corresponding basal area in the forest inventory plots was 1.34 LAI m⁻² of stem for lianas, 0.46 for palms and 0.13 for trees. Lianas, which are structural parasites, use approximately an order of magnitude less stem basal area per unit of leaf area than do trees. Palms, which are unbranched and have very large leaves, are intermediate between these two life forms in leaf area display efficiency.

At the spatial scale of the vertical transect footprints (4.6 m²), sites with very low LAI were rare. None of the random-sampled sites (*n* = 45) had an LAI of <1.

The densest concentration of LAI was at 0–4 m above the ground (Fig. 3a, Table S1). Among-site variation in LAI at a given height was lowest near the ground (0–4 m), intermediate from 5 to 24 m, and highest in the upper

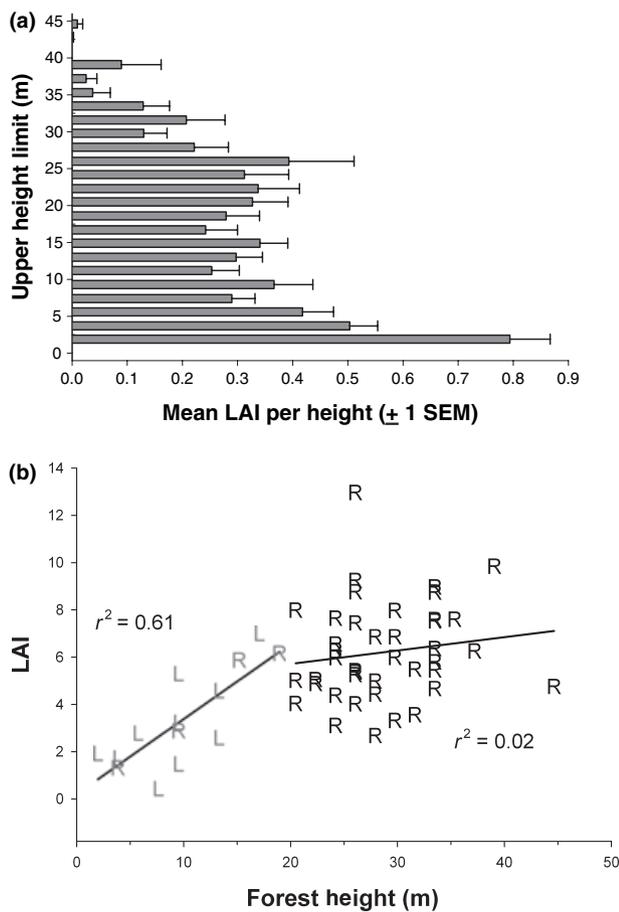


Figure 3 (a) Mean LAI ± 1 SEM per height interval sampled for 45 randomly sampled vertical profiles in old-growth tropical rain forest, La Selva, Costa Rica. (b) LAI increases linearly with forest height up to *c.* 21 m and is not related to canopy height above 21 m. The 45 sites labelled ‘R’ were selected with a stratified random design based on three levels of total predicted soil P and three levels of slope class (five sites in each of nine classes); the 10 ‘L’ sites were selected to have low canopy heights.

canopy. At the landscape scale the cumulative LAI increase from the ground was approximately linear to *c.* 26 m (Fig. 4a). A cumulative LAI of 1 was reached by *c.* 4 m height, so that on average understory plants were shaded by 5 units of LAI vertically overhead. The topmost (highest above the ground) unit of LAI, that most accessible to many aircraft- or satellite-borne remote sensing instruments, was distributed between 25 and 45 m (Fig. 4a).

Functional group composition varied greatly with height above the ground (Fig. 4b, Table S2). Palms and minor functional groups like herbs (Table 1) dominated LAI below 2 m, and palms were also important up to the lower canopy. Although lianas contributed only 12% of total LAI

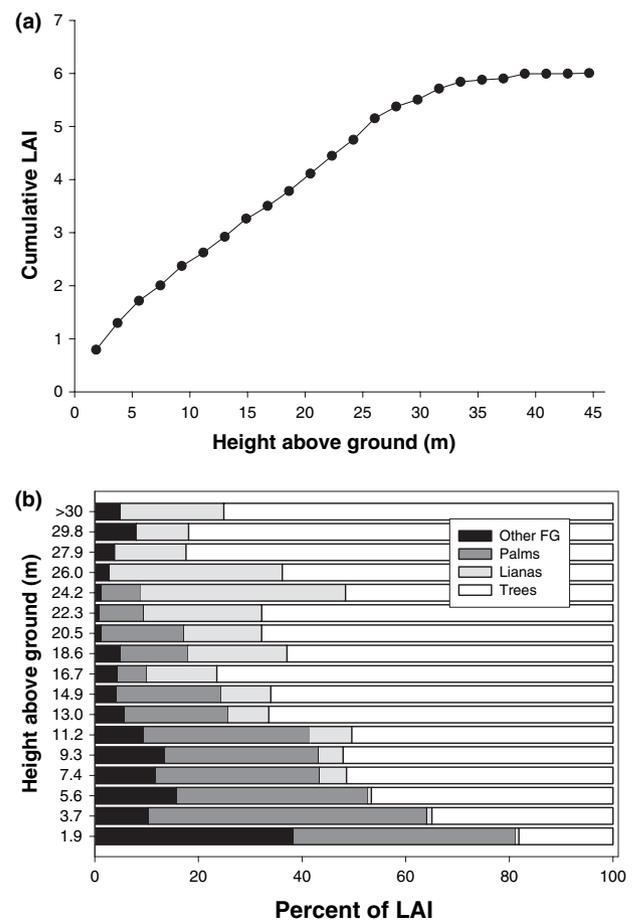


Figure 4 (a) Cumulative LAI (black circles) as a function of height above the ground, based on mean values for 45 randomly sampled vertical profiles in old-growth tropical rain forest at the La Selva Biological Station, Costa Rica. (b) LAI composition by plant functional group as a function of height for the same 45 random samples. ‘Trees’ includes the dominant species *Pentaclethra macroloba*; ‘Other FG’ – herbs, ferns, epiphytes, herbaceous vines. Heights above 30 m are grouped because the cumulative total LAI above this height was <0.5 (a).

(Table 1), they were highly biased towards the high-energy upper canopy and accounted for 22% of the topmost LAI. Trees dominated LAI at heights above 6 m. *Pentaclethra* contributed 28% of the tree LAI above 26 m, consistent with its contributing 32% of tree basal area for all trees ≥ 10 cm diameter in this forest (Clark & Clark 2000). The topmost LAI was composed almost entirely (95%) of the leaves of trees and lianas.

Factors determining local LAI

Forest structure

In the combined data set (45 random sites + 10 low-canopy sites) LAI increased with local vegetation height ($r^2 = 0.34$, $P_{1\text{-tail}} < 0.0005$, $df = 54$). However the relation was entirely due to the low canopy sites (Fig. 3b). For sites < 21 m tall LAI increased linearly with forest height ($r^2 = 0.61$, $n = 17$); sites taller than 21 m showed no correlation ($r^2 = 0.02$, $n = 38$). Thus the build-up of LAI at a given site is initially strongly driven by upward regeneration in canopy gaps, while factors other than canopy height are responsible for the fivefold variation in LAI in the taller-canopy sites (LAI range 2.66–12.94, $n = 38$).

Site LAI was correlated with tree basal area around each tower. The highest correlation was with the sum of weighted basal area within 10 m of the tower, weighting each tree's basal area by the factor $[1/(\text{distance to tower})^2]$. The resulting equation was: $\text{LAI} = 3.73 + 2.67(\Sigma(\text{BA}/\text{Distance}^2)) - 3.56(\Sigma(\text{BA}/\text{Distance}^2) - 0.94)^2$ ($P < 0.003$, $r^2 = 0.21$, $n = 54$). The highest site LAI was thus found at intermediate local basal area, with lower LAI at both the lowest- and highest-basal area sites.

Edaphic effects, local basal area and seasonality

Because forest height so strongly determined total LAI at sites < 21 m tall, we restricted our analyses of other

possible determinants of local LAI to sites > 21 m tall. Over the threefold gradient in soil P and N among the tower sites we found no relation between site LAI and levels of any soil nutrient (0–10 cm depth; % N, C or total P, concentrations of K, Ca, or Mg, all $r^2 < 0.01$, data not shown). Although forest height decreased somewhat with increasing slope angle ($r^2 = 0.12$, $P_{1\text{-tail}} < 0.025$, $df = 37$), site LAI was not related to slope angle ($r^2 < 0.01$, $df = 37$).

At tall sites (> 21 m) LAI did not differ between sites sampled in the dry season (January–May) or in the wet season ($P > 0.51$, $n = 10$, 28) for the 2003–2005 sample period.

Canopy stratification

At the landscape-scale this forest, like many old-growth sites, is a complicated mosaic of patches of different disturbance histories and therefore different local canopy heights (Fig. S2). Under these conditions a uniform canopy stratification across the landscape would not be expected. At the local (individual tower) scale, however, the vertical distribution of LAI was distinctly stratified in alternating layers of high leaf density (canopy strata) and of free air space (Fig. 5). This canopy stratification was ubiquitous. All 45 random-point sites had at least one stratum and all had a ground stratum (Fig. 5). Of the 10 low-canopy sites, nine were stratified and all of these had at least a ground stratum (data not shown).

The total LAI within a stratum averaged 2.00 ± 0.14 SEM ($n = 141$) compared with an average LAI of 0.18 ± 0.02 SEM in the free air spaces ($n = 87$). Foliage density (LAI per volume) averaged 0.39 and $0.03 \text{ m}^2 \text{ m}^{-3}$ in strata and free air spaces, respectively. Median depth for both canopy strata and free air spaces was 2 tower sections (3.72 m vertically). In contrast to site total LAI, the number

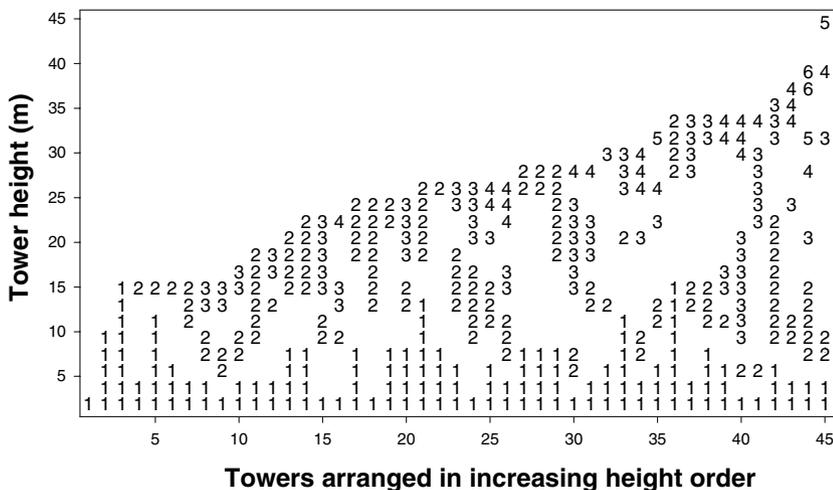


Figure 5 Canopy strata (layers of high foliage density; see Methods) for 45 vertical transects from the ground to the canopy top in old-growth lowland tropical rain forest at the La Selva Biological Station, Costa Rica. Here vertical transects are arranged on the x-axis in increasing height order (their locations on the ground are widely separated; Fig. 2). Canopy strata are numbered consecutively from lowest to highest above the ground (ground stratum = 1); blank areas indicate subcanopy free air space.

of canopy strata increased linearly with forest height, even considering only the sites taller than 21 m ($r^2 = 0.62$, $P < 0.001$ for all 55 sites, $r^2 = 0.39$, $P < 0.001$ for the 38 sites >21 m tall).

The structure of alternating canopy strata and free air space strongly influenced light absorption by foliage and branches. The mean rate of decline in light from the top of the canopy to the ground, calculated as the per cent decrease in hemispherical photograph openness per vertical meter descended, was $-1.77 \pm 0.28\%$ SEM per m descended within canopy strata ($n = 103$) compared with only $-0.41 \pm 0.21\%$ SEM per m descended in free air spaces ($n = 82$). Within both canopy strata and free air spaces this rate of decrease increased with height above the ground (closer to the canopy top). This relation (per m rate of decline in light vs. height above the ground) was positive and highly significant ($P < 0.001$) for both strata and free spaces, although the r^2 and the regression slope were considerably larger for strata (respective $r^2 = 0.36$, 0.14 ; respective $b = 0.20$, 0.08). In contrast the rate of decline in light was not related to segment depth for either strata or free air spaces.

There were a surprising number of reversed vertical light gradients. In pairwise comparisons of light levels at the top and bottom of canopy strata or free spaces, light increased towards the ground for 11.7% of strata (12/103) and for 39.0% (32/82) of the free air spaces.

Validation of MODIS satellite remotely sensed indirect estimates

There was no significant difference in estimated LAI over this period among the 4 1-km² MODIS pixels covering our study area (Wilcoxon KW: $P > 0.66$, $n = 24$ dates with good data in all 4 pixels). In each pixel the median estimated LAI was 6.1, and the 95% confidence intervals of MODIS LAI estimates for each 1 km² pixel included the landscape mean (6.0) measured in this study.

DISCUSSION

This first direct assessment of LAI at the landscape scale in a TRF revealed an unexpected degree of predictability for this complex ecosystem. In spite of the heterogeneity imposed by the gap regeneration cycle, by the large number of plant species and by the presence of occasional emergent trees (Fig. S2), we found useful simplifying patterns and relationships underlying the structure of this forest.

Forest height

Forest height emerged as a key variable for understanding the quantity and vertical distribution of patch-level LAI and

light absorption. LAI accumulated linearly up to *c.* 21 m height in a predictable fashion. Canopy strata averaging *c.* 4 m depth were added in a predictable linear relationship with height up to the highest forest heights measured. Light levels decreased moderately rapidly within canopy strata but decreased much less rapidly or frequently increased with descent through free air spaces. These relationships could be widely tested in other tropical forests using remote sensing, as forest height and to some extent canopy stratification are directly measurable with LiDAR (Lefsky *et al.* 2002).

For taller sites in this forest, however, the fourfold variation in LAI (LAI 3–13; $n = 38$, Fig. 3b) was not related to forest height (Fig. 3b), soil nutrients (Williams *et al.* 2002) or season of sampling (Myneni *et al.* 2007). Our working hypothesis is that total leaf area in taller sites is strongly affected by the amount of lateral light, which in turn is related to the disturbance histories of the immediately adjacent forest vegetation. Influences from the adjacent forest on within-profile light levels include vertical growth of plants in canopy gaps, tree mortality, branch pruning, and branch damage from small-scale disturbance. This interpretation is supported by the large number of inverted (increasing from top to bottom) light gradients in free air spaces. These reverse gradients, fully a third of the total, can only be caused by lateral lighting. For low-canopy sites, in contrast, much of the lateral view angle is blocked, restricting the impact of changes in adjacent forest structure.

Ubiquitous canopy stratification

The universal occurrence of foliar clumps (strata) in our randomly selected sites and in 90% of the low-canopy height sites shows that, in this old-growth tropical forest and at the spatial scale we sampled (tower footprints of 4.6 m²), canopies were organized vertically in highly predictable patterns. Forest height alone explained 49% of the variance in the number of foliage strata at the randomly selected sites.

The ubiquity of canopy strata found in this study in one sense resolves the long discussion in tropical ecology over the existence or generality of such strata in TRF (Richards 1996; Baker & Wilson 2000). At the tower-footprint scale we found that foliage was clearly stratified into alternating layers differing by more than an order of magnitude in leaf density. However the horizontal extent of the sampled strata is not resolvable with our data, as the random sample points were widely spaced across the landscape. Now the most productive question about TRF canopy stratification may not be 'Are TRF canopies stratified?', but rather, 'What is the horizontal extent of the average area of equal stratification?' Given the relation shown here between the number of strata and forest height, the upper-bound answer

to this question is likely to be the average horizontal extent of areas of similar forest height, which is measurable with LiDAR remote sensing.

Functional group simplification

In this study we dealt with the challenge posed by tropical forests' high species diversity by classifying plant species into functional groups. Our results show that in terms of forest carbon uptake, further simplification is possible. Three plant functional groups – trees, palms and lianas – accounted for 89% of total forest leaf area. In the high-energy and high-photosynthesis environment where the topmost unit of LAI occurs (heights >24 m, Fig. 4a) functional group concentration was even higher, with trees and lianas accounting for 95% of LAI. It thus seems likely that realistic carbon uptake models can be built with only three plant functional groups, and perhaps with only two.

Lianas have previously been hypothesized to be linked to increased forest dynamics in this biome (Phillips *et al.* 2002). At La Selva we found lianas contributed 22% of the topmost LAI at the landscape scale. A related study based on the same vertical transects (Cavaleri *et al.* 2006) found that lianas account for a quarter of this forest's aboveground woody respiration. Intensified research into lianas' physiological and demographic performance would thus be of particular interest.

Remote sensing implications

The upper canopy (the topmost LAI) is almost entirely composed of leaves from two plant groups: the subset of trees that reach canopy level, and lianas. Most of TRF plant species diversity is therefore not directly observable in the visible wavelengths even with very high spatial resolution passive remote sensing. For estimates of biodiversity based on passive remote sensing, surrogates for total plant species diversity will likely have to be sought in some additional aspect of forest structure. Our results suggest that research on TRF canopies could profitably focus on the spectral and structural characteristics of the most frequent canopy trees (Clark *et al.* 2005) and lianas. Here again lianas are of particular interest, particularly if they have different spectral signatures than canopy trees (Castro-Esau *et al.* 2004).

The close correspondence of the MODIS satellite LAI estimates with our directly measured value for old-growth forest at La Selva suggests that the MODIS algorithm works well over this type of forest. Because this is the first time LAI has been directly measured at the landscape scale, similar studies on other tropical forest landscapes will be necessary to determine how generally applicable the MODIS LAI estimates are across the wide variation in

forest structure, floristics, and phenology found in this biome.

LAI and functional groups – the landscape view

This study demonstrated that it is possible to obtain unbiased assessments of key ecosystem properties of old-growth TRF through direct harvest-based measurements stratified and replicated at the landscape scale. Our data provide the first such landscape-scale estimate of total LAI for this biome, as well as a quantitative assessment of its vertical distribution, its relation to the within-landscape edaphic gradients, and the relative contributions of plant functional groups. In addition to the inherent interest in this data set, it demonstrates the feasibility of parameterizing vegetation process models for this biome with estimators based on directly sampled field data. Obtaining these data was moderately expensive as well as logistically intensive. It is therefore of practical as well as scientific interest to know if models parameterized with such data perform better than current formulations, and, if so, to quantify the degree of improvement. Such work is currently underway at our site.

With the data from this study we can evaluate the effort required to replicate this work in a TRF of similar structure. Based on La Selva's mean LAI and degree of structural variation, only 15 towers would be necessary to estimate landscape LAI with a 95% probability of sampling within $\pm 20\%$ of the true mean (Zar 1996). Our estimate based on 45 towers was considerably better, with an SEM equal to only 5% of the mean. Similar studies can be planned based on the accuracy required for a given project.

This research used GIS databases available at an intensive research site to incorporate major within-landscape environmental gradients into the sampling design. Although equivalent environmental information will not be available at many TRF sites, Landsat coverages and Shuttle Terrain Radar terrain maps are broadly available. These would be completely sufficient to construct an unbiased stratified random sampling design. With such a design, issues of insufficient sampling and biased site selection can be eliminated and statistically robust estimators applicable to entire landscapes can be obtained.

A disproportionate percentage of TRF ecosystem science has been conducted at a few intensive research sites. Further, much of this research has been limited to small and/or unreplicated plots. Understanding the responses of TRF to global climate change and to other anthropogenic impacts requires analyses at much larger spatial scales. Bridging the gap from plot studies to global scales is a major challenge in TRF ecology. Studies such as this one, that expand the spatial scale of direct field measurements from plots to entire landscapes, offer one route towards this goal.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Figure S1 Field sampling procedure.

Figure S2 LiDAR imagery of canopy height distribution.

Table S1 Detailed statistics of total LAI distribution by height above ground.

Table S2 Breakdown of total LAI by plant functional group and height above ground.

Appendix S1 Extended methods description.

Appendix S2 Raw data for LAI for all towers, stratified by tower section and plant functional groups.

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