

RESEARCH ARTICLES

Evaluation of methods to estimate foliage density in the understory of a tropical evergreen forest

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Foliage density and leaf area index are important vegetation structure variables. They can be measured by several methods but few have been tested in tropical forests which have high structural heterogeneity. In this study, foliage density estimates by two indirect methods, the point quadrat and photographic methods, were compared with those obtained by direct leaf counts in the understory of a wet evergreen forest in southern India. The point quadrat method has a tendency to overestimate, whereas the photographic method consistently and significantly underestimates foliage density. There was stratification within the understory, with areas close to the ground having higher foliage densities.

Keywords: Forest structure, foliage density, leaf area index, point quadrat, Western Ghats.

VEGETATION is an essential element of all major ecosystems, performing many functions, including fuelling the system by trapping solar energy. Precise estimates of vegetation structure variables are critical to understanding trophic relationships and ecosystem processes such as matter and energy fluxes, transpiration and photosynthesis^{1,2}. Exact knowledge of vegetation structure and distribution is also vital to assessing habitat use and selection by animals.

There is an extensive body of research into estimating variables that describe vegetation structure. Commonly used variables for quantifying vegetation structure include leaf area index (LAI) and foliage (or leaf area) density. LAI and foliage density estimates have received particular attention because of their widespread application in ecosystem ecology, where knowledge of these is crucial in estimating primary productivity and carbon fluxes.

A number of studies on the estimation of LAI, foliage density and leaf inclination have been carried out in agricultural fields, open grasslands or young stands with small or stunted plants³⁻⁵. Others have been carried out in mature stands and forests^{2,6,7}. However, in spite of the

well-known fact that tropical forests are more heterogeneous than their temperate counterparts, that they house most of the earth's terrestrial biodiversity⁸ and account for a large proportion of terrestrial carbon stores and photosynthesis⁹, most work on vegetation structure sampling has been carried out in the temperate regions. Recently, a few studies have been carried out in tropical deciduous and semideciduous forests¹⁰⁻¹³. Similar studies on tropical evergreen forests are scarce^{14,15}. Tropical evergreen forests are multilayered and complex in their architectural characteristics. Their heterogeneity raises the question whether the methods developed in temperate and deciduous systems can be directly applied to tropical evergreen forests.

Several methods, both direct and indirect, have been developed and used for more than four decades to describe and evaluate vegetation structure¹⁶. Direct methods include techniques such as the stratified clip method¹⁷, dispersed individual plant method¹⁶, correlating LAI with tree height or tree diameter and leaf litter collection¹⁸. Indirect methods include the line intercept method¹⁹, point quadrats²⁰, densiometer technique²¹ and the checker-board method⁶. Other indirect methods use gap fraction theory, for example, hemispherical photography²² and/or measure light transmission using direct (DEMON) or diffused light transmission sensors (Li-Cor LAI-2000).

All methods have their inaccuracies and limitations. Direct methods such as the harvest technique are often destructive and require considerable effort in sampling. Methods such as litter fall collection depend on a single season of leaf fall, which limits their application to certain vegetation types. Indirect methods are time and effort efficient, and many instruments and techniques have been developed for the same. Optical instruments such as the Plant Canopy Analyser (PCA), LAI-2000 and canopy beam transmittance measuring devices (DEMON) are used to measure LAI and light regimes. These methods have their own drawbacks. The biggest restriction is that one needs to get reference measurements of light readings above the forest canopy, which is quite difficult¹² unless there is a tower or a canopy walkway at the study site. In the absence of these structures, one has to rely on readings taken in an open area. Dufrene and Breda⁷ remark

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that it is difficult to get such readings without any edge effect. Besides, these instruments operate only under specific light and weather conditions, imposing spatial and temporal restrictions on their use²³. Welles and Cohen²⁴ have remarked that measurements with these instruments can be especially problematic in rain forests. In forests, LAI estimation using these instruments has been reported to be difficult due to vertical and horizontal heterogeneity²⁵. Financial constraints, apart from other technical and practical considerations, limit the use of these instruments by developing nations, which contain most of the tropical forests. The sampling pin or point quadrat method^{20,26} and checkered-board method⁶ on the other hand, have shown particular promise for estimating LAI and foliage density and offer the potential for analysis of foliage distribution across different vertical strata²⁷. The methods are easy to carry out in different vegetation types and are rather inexpensive.

In spite of the advantages offered by the point quadrat and checkered-board methods, no study so far, to the best of our knowledge, has compared these two methods with each other or verified the accuracy of their estimates of foliage density by comparing them with actual leaf surface area in tropical forests. In this study, we tested the accuracy of these two indirect methods (point quadrat and photographic method) in estimating foliage density of the understorey of a tropical wet evergreen forest by comparing the estimates of foliage density obtained by these with that obtained from a direct method (total count).

Methods

Study site

The study was conducted in a tropical wet evergreen forest in Kudremukh National Park (lat. 13°01'–13°29'N, long. 75°01'–75°25'E), which is situated on the windward slopes of the Western Ghats in Karnataka. The average annual rainfall is 4000 mm and the elevation ranges from 50 to 1892 m asl. The trees include evergreen species such as *Artocarpus hirsutus*, *Hopea parviflora*, *Knema attenuata* and *Poeciloneuron indicum* (nomenclature follows Saldanha^{28,29}). The vegetation in the National Park consists primarily of evergreen and semi-evergreen forests. Higher altitudes have grasslands and shola patches. The forest structure in the study area consisted of leaf litter-covered ground devoid of grasses, a herb layer constituted by seedlings and herbs (≤ 1 m), understorey (1–8 m) and canopy (12–30 m). The study was carried out in the post-monsoon dry season between November 2005 and January 2006.

Three test quadrats ($5 \times 5 \times 5$ m) that had good vegetation structure representative of the forest were selected such that any two quadrats were at least a 100 m apart. The criteria for selection included (i) presence of a herb layer, (ii) well-defined understorey and (iii) absence of

large canopy gaps. Each quadrat was then subdivided into $25 \times 1 \times 1 \times 5$ m subquadrats (5 m being the height) using rope grids.

Terminology

LAI is defined as the total one-sided leaf area per unit ground area (m^2/m^2). Foliage angle is the inclination of the foliage to the ground. Foliage density is the total leaf surface area per unit volume of space (m^2/m^3).

Total count method of foliage density estimation

The total number of leaves of each plant species (N_i) within the quadrat was counted *in situ*. This was done by flagging each plant and counting all leaves branch by branch. For plants with more than 100 leaves, each branch was tagged after all leaves of the branch were counted to avoid repetition. The species identity and the total number of leaves of each individual plant were noted. For each plant species recorded in a quadrat, five leaves from each of the three height classes 0–1, 1–3 and 3–5 m were collected randomly from plants outside the quadrat. The leaves were pressed and pasted on a sheet of paper according to species and height class and photographs were taken using a Sony DSCH1 digital camera. Using the software ImageJ (version 1.32j, Wayne Rasband, National Institutes of Health, USA), the average one-sided leaf surface area (averaged over 15 leaves) for each plant species was calculated. Then the total surface area contributed by leaves of each species in a quadrat was calculated by multiplying the species-specific total leaf numbers with the average leaf surface area of each species. Finally, the total surface area occupied by leaves in a quadrat was calculated by adding up the total leaf surface area of all plant species. This was carried out in each of the three quadrats.

The foliage density by the total count method was calculated as:

$$\text{Foliage density (area/unit volume)} = \sum_{i=1-n} \frac{N_i * \text{ASA}_i}{\text{Volume of quadrat}}$$

where i is the plant species i , n the total number of plant species in a quadrat, N the total number of leaves and ASA_i the average leaf surface area of the i th species.

LAI was calculated by multiplying the foliage density with the height of the quadrat.

Indirect methods of foliage density estimation

Point quadrat method: The point quadrat or sampling pin method is carried out by passing a pin of known

dimension through the vegetation at an inclination³⁰. All contacts of the pin with the vegetation are then scored. A formula developed by Warren Wilson³⁰ can then be used to convert these data to an estimate of foliage density. If the height of contact is also recorded, it is possible to estimate the foliage density–height profile. The pin used for the purpose of this study was a 5 m long pole with a diameter of 3 cm. In each of the 25 1 × 1 × 5 m subquadrats of a test quadrat the pin was planted vertically (90° to ground). All contacts of leaves with the pin, the height of contact and species identity of the leaves were noted. This was done five times in each subquadrat. The pin was placed in the four corners and centre of the subquadrat. A total of 125 pins (5 in each subquadrat) were inserted. All contacts of leaves with all pins inserted were summed and this was divided by the number of insertions to give the mean number of contacts. This value divided by the length of the pin (5 m) gave the mean number of contacts/unit insertion/unit length of pin, also known as ‘contact frequency’ or F_{β} , β being the angle of insertion of the pin with respect to the horizontal³⁰. Foliage density ‘ F ’ can then be calculated using the equation developed by Warren Wilson³⁰.

$$F_{\beta}/F = \cos \alpha \sin \beta, \quad \text{or} \quad F = F_{\beta}/\cos \alpha \sin \beta,$$

where F_{β} is the contact frequency, α the foliage angle, β the inclination of pin.

The foliage angle of the leaves was not measured and was assumed to be 0°. This assumption is based on empirical observation of leaf angles in the study area where most leaves were parallel to the ground. Warren Wilson³¹ suggested that for a given pin diameter, errors occur in calculating contact frequency due to the dimensions of the foliage. He developed a theoretical treatment for such errors which is as follows:

$$CF = (L * B)/(L + D) (B + D),$$

where CF is the correction factor, L the length of leaf, B the breadth of leaf and D the diameter of pin.

In the case of sampling carried out in temperate forests or in mono-dominant patches it is possible to multiply F_{β} with a CF to get the corrected value of F_{β} . Tropical forests, owing to high species diversity are, however, extremely heterogeneous and such a general treatment is not advisable. Hence, for the purpose of this study species-specific length and breadth were measured using ImageJ for all collected leaves. A species-specific correction factor was then calculated using the formula described here. Once we had the correction factor values, the number of contacts of the pin for the total number of pin insertions was corrected as shown here:

$$\begin{aligned} \text{Total number of pin insertions in a quadrat} &= 5 * 25 \\ \text{(number of subquadrats in a quadrat)} &= 125 \end{aligned}$$

Species X total number of contacts for 125 pin insertions = 3

Correction factor for Species X = 0.5

Corrected number of contacts = 3 * 0.5 = 1.5

Species Y number of contacts = 5

Correction factor for Species Y = 0.6

Corrected number of contacts = 5 * 0.6 = 3.

This was repeated for all species of that quadrat to give the corrected number of contacts per species for 125 pin insertions. The data were then pooled across species to get at the total number of contacts for 125 pin insertions. Then, as described by Warren Wilson³¹, the corrected contact frequency was calculated which was further used to calculate foliage density according to the formula described here.

The analysis was repeated at the subquadrat (1 × 1 × 5 m) level to obtain 25 estimates of foliage density to examine the variation within a quadrat. Subquadrat data were used to compute mean values of foliage density, as well as the standard deviation and confidence intervals for each quadrat. Detailed observation of contacts of foliage with the pin, including species identity and height of contact, made it possible to calculate not only the corrected mean foliage density of each quadrat but also the height class-wise foliage density profile for each quadrat.

Photographic method: This method has been adapted from the checkered-board method described by MacArthur and MacArthur⁶. It involves raising a checkered board on a pole and moving it away horizontally from an observer (at the same height) until half of the board’s surface is obscured by foliage. The distance between the observer and the board is then noted. This is done at a sequence of heights above the ground. The data is then converted into estimates of foliage density and LAI using the following equations.

$$k = \log_e 2/D \quad \text{and} \quad n = \log_e 2,$$

where k is the foliage density, D the horizontal distance between observer and board and n the leaf area index.

There are difficulties in putting MacArthur’s method into practice. Firstly, in absence of any artificial structure in the forest, it is a formidable task for an observer to rise up to the same height as that of the board. Again, visually estimating 50% coverage of the board by foliage and recording that distance will probably be inconsistent and prone to error due to observer variability and this will worsen with uneven foliage distribution. To minimize these difficulties and inconsistencies, the method was suitably modified to improve the expediency and accuracy of the technique.

The test quadrats were divided into four height classes (0–1, 1–2, 2–3.5 and 3.5–5 m). In each subquadrat, a

white board (1 × 1 m) was placed at 2, 3.5 and 5 m (parallel to the ground) for the height classes 1–2, 2–3.5 and 3.5–5 m respectively. A picture of the foliage was taken from below the board for each height class using a Nikon FM10 camera. For the height class 0–1 m, the ground covered by white paper formed the background and the picture of the foliage on the ground was taken from above. The pictures were then digitized and the total area of the background (board/ground covered with paper) obscured by foliage was measured using ImageJ software. Foliage density in each height class of each subquadrat was calculated using the method described by MacArthur and MacArthur⁶.

$$k = \ln(1/X)/D,$$

where *k* is the foliage density, *X* the proportion of background unobscured and *D* the height class interval.

In each test quadrat, foliage density values of all subquadrats of each height class were pooled appropriately and average foliage density of the quadrat was calculated. As with the point quadrat method, the above analysis was repeated at the subquadrat (1 × 1 × 5 m) level to get 25 estimates of foliage density to examine variation within the quadrat. Subquadrat data were used to compute mean values of foliage density, as well as the standard deviation and confidence intervals for each quadrat.

Results

Plant species composition and leaf surface area

A total of 66 plant species was recorded from the three quadrats (see Appendix 1). Of these, quadrat 1 (Q1) recorded the lowest number of species (23), whereas quadrat 2 (Q2) and quadrat 3 (Q3) had approximately equal numbers (44 and 43 respectively). The number of individuals of each plant species varied from 1 to 32 in Q1, 1 to 22 in Q2 (with the exception of *Poeciloneuron indicum* that had 134 individuals) and 1 to 43 in Q3 (Figure 1). Species rank abundance plots revealed marked dominance in all three quadrats (Figure 1). In Q1, the three most abundant species were *Psychotria thwaitesi* and *Psychotria flavida* (species number 53 and 52; Figure 1 a), which are understory shrubs, and *Syzygium gardneri*, a tree species (species number 58; Figure 1 a). The second quadrat was dominated by saplings of *P. indicum* (species number 49; Figure 1 b), an evergreen tree species. The dominant species in Q3 were also *P. indicum*, *Psychotria flavida*, an unidentified species of the genus *Pteris* and *Psychotria thwaitesi* (species number 49, 52, 54 and 53 respectively; Figure 1 c).

The dominance profile was reflected in the relative contribution of number of leaves as well as total leaf area: a small proportion of species (4/23 in Q1, 5/44 in Q2 and 2/43 in Q3) contributed more than 50% of leaves

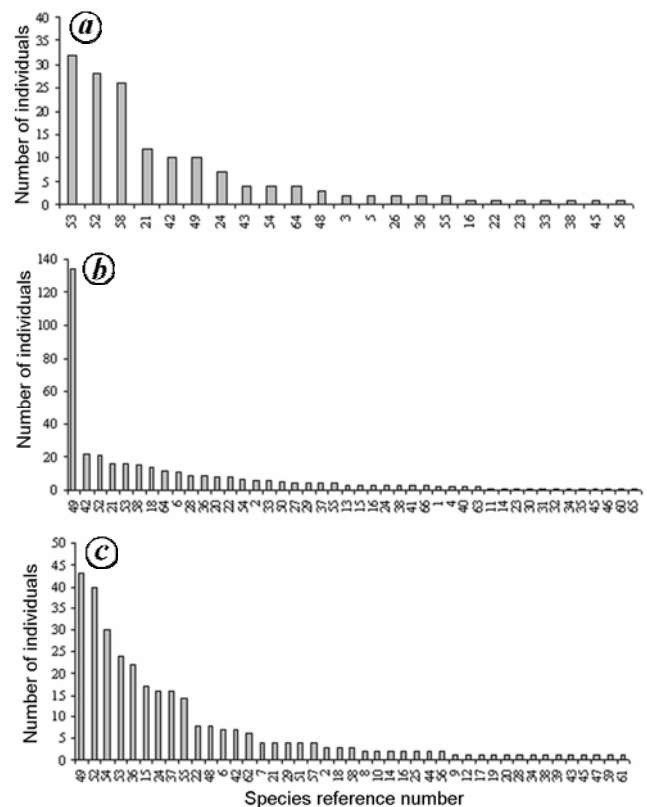


Figure 1. Species rank abundance plots for the three quadrats. a, Quadrat 1; b, quadrat 2; c, quadrat 3. Refer to Appendix 1 for species names.

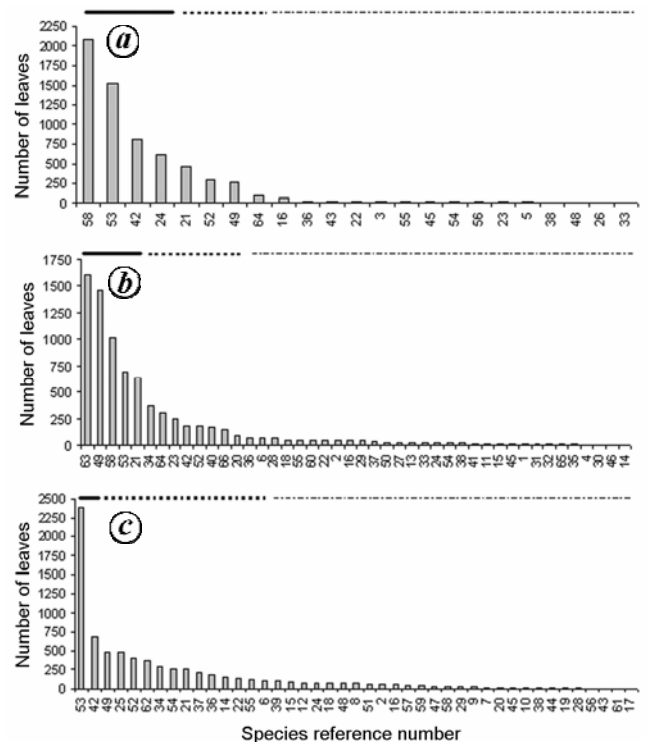


Figure 2. Rank abundance plots for number of leaves contributed by all species in each quadrat. Number of leaves >500: solid line; 100–500: dashed line; <100: dashed line with dots. a, b, c as in Figure 1.

and leaf area to the total (Figure 2). The frequency distribution of leaf surface areas in each quadrat (Figure 3) revealed three modes in the size classes of 10–20 (30–40 in Q3), 50–60 and 70–80 cm².

Comparison of three methods to estimate foliage density

The results from the total count method were considered as the reference values for the indirect foliage density estimates (Figure 4). The photographic method consistently underestimated foliage density in all three quadrats. This underestimation was by 18% in Q1 and 22% in Q3. In Q2, however, the underestimation was by as much as 45%. For two out of three quadrats, the total count estimate lay above the 95% confidence interval of the estimate using the photographic method (Figure 4), suggesting that the underestimation was not only due to sampling error. The point quadrat method, on the other hand, overestimated foliage density by about 19% in Q1, 18% in Q2 and 21% in Q3. In two out of three cases, however, the total count estimate lay well within the 95% confidence interval of the point quadrat estimate. In spite

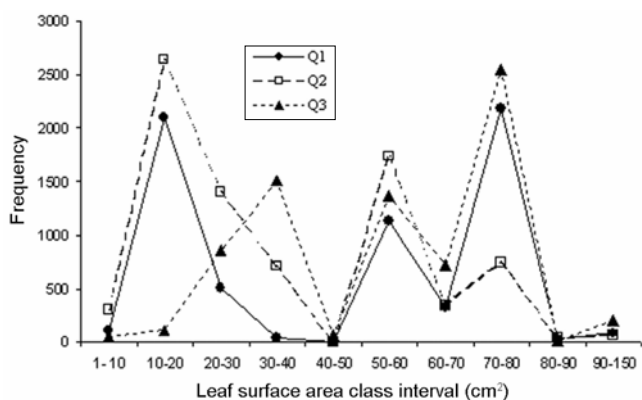


Figure 3. Frequency histograms of leaf surface areas in the three quadrats.

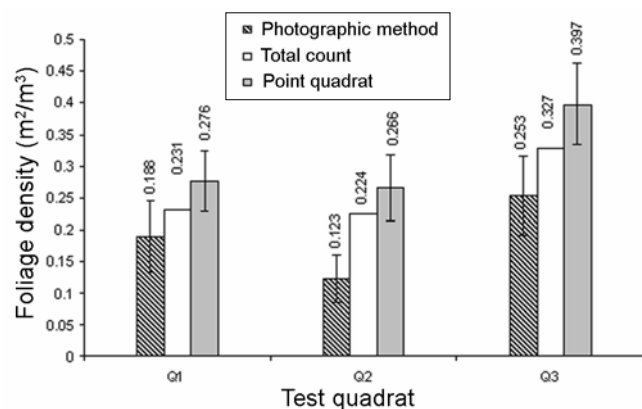


Figure 4. Foliage density estimates using direct and indirect methods for the three quadrats. Error bars represent 95% confidence intervals.

of the discrepancies among the three techniques, Q3 showed the maximum foliage density and Q2 the minimum by all three methods (Figure 4).

LAI for the understorey as calculated from the total count method was 1.155, 1.12 and 1.265 in Q1, Q2 and Q3 respectively.

Foliage density–height profile

Foliage density varied with height in all three quadrats (Figure 5). In Q1 and Q3, foliage density was high in the lower three layers of 0–1, 1–2 and 2–3 m. In Q2, however, the foliage density distribution was skewed with the 0–1 m layer recording three times higher foliage density than any other layer. The upper height classes (3–4 and 4–5 m) had relatively lesser foliage density than the lower ones in all three quadrats.

Discussion

Foliage density estimates with direct and indirect methods

There are a number of previous studies that have compared direct and indirect estimates of foliage density and

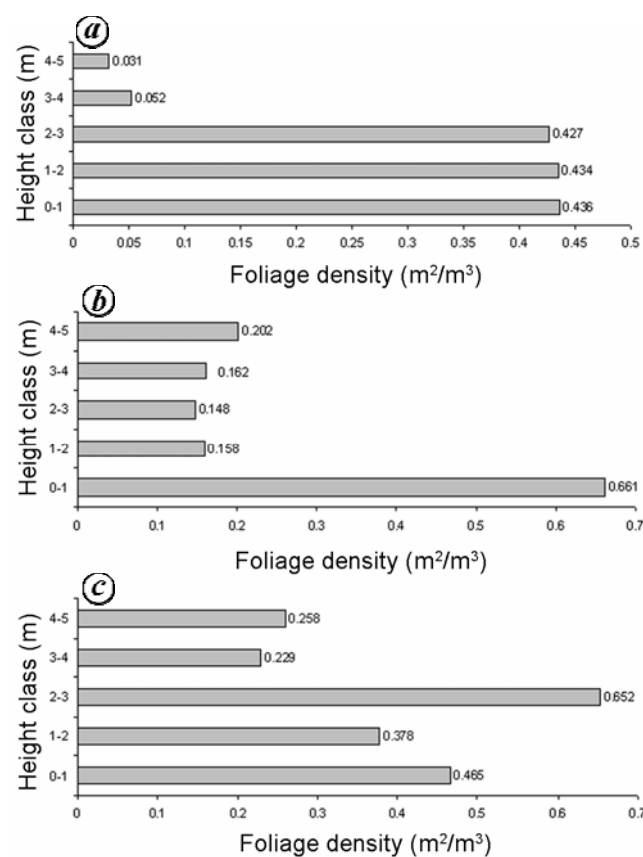


Figure 5. Foliage density–height profiles in the three quadrats obtained using the point quadrat method. a, b, c as in Figure 1.

Appendix 1. Plant species with mean leaf surface area

Species reference number	Scientific name	Family	Mean leaf surface area (cm ²)	Correction factor
1	<i>Actinodaphne malabarica</i>	Lauraceae	50.33	0.53
2	<i>Aglaiia lawii</i>	Meliaceae	25.35	0.39
3	<i>Apama siliquosa</i>	Aristolochiaceae	51.89	0.49
4	<i>Arenga wightii</i>	Arecaceae	78.98	0.47
5	<i>Artocarpus hirsutus</i>	Moraceae	27.45	0.59
6	<i>Beilschmiedia bourdillonii</i>	Lauraceae	63.29	0.55
7	<i>Calamus thwaitesii</i>	Arecaceae	27.62	0.30
8	<i>Calophyllum polyanthum</i>	Clusiaceae	17.47	0.35
9	<i>Canthium rheedii</i>	Rubiaceae	20.44	0.37
10	<i>Canthium</i> sp.	Rubiaceae	42.90	0.48
11	<i>Carex</i> sp.	Cyperaceae	14.49	0.16
12	<i>Casearia wynadensis</i>	Flacourtiaceae	20.99	0.35
13	<i>Chassalia curviflora</i>	Rubiaceae	80.27	0.57
14	<i>Cinnamomum malabratrum</i>	Lauraceae	106.15	0.56
15	<i>Combretum albidum</i>	Combretaceae	62.61	0.52
16	<i>Cryptocarya bourdillonii</i>	Lauraceae	144.41	0.63
17	<i>Cyclea</i> sp.	Menispermaceae	33.64	0.46
18	<i>Derris scandens</i>	Fabaceae	21.66	0.36
19	<i>Connarus</i> sp.	Fabaceae	50.20	0.50
20	<i>Desmos lawii</i>	Annonaceae	26.76	0.37
21	<i>Dichopetalum gelonioides</i>	Dichapetalaceae	24.04	0.39
22	<i>Dimocarpus longan</i>	Sapindaceae	67.34	0.47
23	<i>Diospyros oocarpa</i>	Ebenaceae	29.11	0.38
24	<i>Diospyros sylvatica</i>	Ebenaceae	70.86	0.54
25	<i>Dysoxylum</i> sp.	Meliaceae	30.15	0.41
26	<i>Elaeocarpus tuberculatus</i>	Elaeocarpaceae	127.31	0.63
27	<i>Euonymus indicus</i>	Celastraceae	20.37	0.42
28	<i>Garcinia gummi-gutta</i>	Clusiaceae	33.89	0.44
29	<i>Garcinia morella</i>	Clusiaceae	26.36	0.43
30	<i>Gnetum scandens</i>	Gnetaceae	57.02	0.51
31	<i>Gomphandra coriacea</i>	Icacinaceae	36.27	0.46
32	<i>Grewia</i> sp.	Tiliaceae	31.61	0.45
33	<i>Holigarna ferruginea</i>	Anacardiaceae	68.75	0.53
34	<i>Ixora nigricans</i>	Rubiaceae	30.30	0.45
35	<i>Jasminum flexile</i>	Oleaceae	20.04	0.31
36	<i>Knema attenuata</i>	Myristicaceae	56.17	0.56
37	<i>Kunstleria keralensis</i>	Fabaceae	31.84	0.43
38	<i>Litsea ghatica</i>	Lauraceae	26.55	0.39
39	<i>Memecylon randerianum</i>	Melastomataceae	32.85	0.48
40	<i>Micromelum pubescens</i>	Rutaceae	27.87	0.62
41	<i>Myristica beddomei</i>	Myristicaceae	134.10	0.43
42	<i>Nothopegia racemosa</i>	Anacardiaceae	50.64	0.48
43	<i>Ochna lanceolata</i>	Ochnaceae	73.78	0.52
44	<i>Palaquium ellipticum</i>	Sapotaceae	53.99	0.52
45	<i>Pavetta hispidula</i>	Rubiaceae	81.05	0.53
46	<i>Peliosanthes teta</i>	Haemodoraceae	73.01	0.52
47	<i>Pingara dixonii</i>	Arecaceae	99.32	0.54
48	<i>Piper attenuatum</i>	Piperaceae	79.46	0.44
49	<i>Poeciloneuron indicum</i>	Clusiaceae	56.23	0.53
50	<i>Polyalthia fragrans</i>	Annonaceae	74.34	0.55
51	<i>Pothos scandens</i>	Araceae	8.27	0.26
52	<i>Psychotria flavida</i>	Rubiaceae	65.76	0.52
53	<i>Psychotria thwaitesii</i>	Rubiaceae	70.67	0.56
54	<i>Pteris</i> sp.	Pteridaceae	39.79	0.22
55	<i>Salacia fruticosa</i>	Hippocratiaceae	38.98	0.43
56	<i>Smilax zeylanica</i>	Liliaceae	28.40	0.34
57	<i>Spatholobus purpureus</i>	Fabaceae	48.97	0.59
58	<i>Syzygium gardneri</i>	Myrtaceae	12.63	0.32
59	<i>Syzygium laetum</i>	Myrtaceae	30.47	0.47
60	<i>Syzygium memecylifolia</i>	Myrtaceae	20.14	0.40
61	<i>Tetrastigma muricatum</i>	Vitaceae	15.97	0.34
62	<i>Thunbergia mysorensis</i>	Acanthaceae	29.62	0.41
63	<i>Meiogyne pannosa</i>	Annonaceae	14.91	0.36
64	<i>Ventilago madraspatana</i>	Rhamnaceae	6.48	0.33
65	<i>Vepris bilocularis</i>	Rutaceae	18.04	0.33
66	<i>Walsura trifolia</i>	Meliaceae	31.18	0.44

LAI, mostly in temperate deciduous forests. The accuracy of the photographic methods of MacArthur and MacArthur⁶ and MacArthur and Horn³² has been evaluated in temperate deciduous forests^{1,10,33}. Similar to our results for a tropical evergreen forest, Aber¹ found that the photographic method consistently underestimated LAI by 20–45% in broad-leaved temperate deciduous forests. In addition, he could not find a significant regression between direct estimates from litter fall and the estimates using the photographic method. Conner and O'Halloran³³ also found that the photographic method underestimated foliage density by up to 50%; the estimates obtained by direct and indirect methods were, however, highly correlated and they stated that the method was thus accurate for relative estimates. Our results corroborate these and show underestimation by 18–45% using the photographic method. One caveat to be kept in mind is that our direct method is also an estimate; we used species-specific average leaf areas together with total leaf counts to estimate total leaf area in the quadrat. Ideally, one should measure the surface area of every leaf in the quadrat and use the sum as a reference; this typically involves harvesting of all leaves, which was not possible within a National Park.

The reasons for underestimation by the photographic method may include leaf size and shape heterogeneity³³, heterogeneity in foliage angles and a non-random or clumped distribution of foliage¹. Comparisons of estimates of LAI using other indirect methods based on direct beam or diffuse light penetration with direct estimates based on litter fall in temperate, deciduous forests also reveal underestimation of LAI by the indirect methods^{7,34} by 20–45%. Interestingly, these indirect methods are also based on the assumption of a Poisson distribution of leaves and on gap fraction theory. Non-random and clumpy distribution of foliage has been evoked as the explanation for this underestimation³⁴.

LAI in tropical forests

There are few studies on tropical forests that have examined foliage density or LAI in a quantitative manner through vertical strata. Since our study focused on the understorey, we can compare our estimates of LAI only with those that have examined foliage height profiles. Our values of LAI for the understorey (up to a height of 5 m) range from 1.12 to 1.265 based on the total count method. These values correspond with those obtained for the lowest stratum in an Amazonian rainforest (0.8–1) by direct harvesting methods¹⁴. They are also similar to those obtained in a recent study in a lowland rain forest in Costa Rica¹⁵, which estimated mean LAI in the lowest height class at about 0.8 (sampled 45 times using footprints of 4.56 m²). Interestingly, our values for a palaeotropical wet evergreen forest are somewhat higher than

the neotropical rainforests. Both these studies also corroborate our finding that there is a marked drop in foliage density above 2–3 m in the understorey. LAI values for a wet semi-deciduous rainforest in Panama¹¹ are, however much lower (from about 0.1–0.5 on average below 5 m), suggesting a much sparser understorey in this type of forest. More data from different forest types and geographical regions are required to establish whether there are common themes of vertical stratification and forest architecture that characterize particular vegetation types across geographical regions.

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