

Variation in Crown Light Utilization Characteristics among Tropical Canopy Trees

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• **Background and Aims** Light extinction through crowns of canopy trees determines light availability at lower levels within forests. The goal of this paper is the exploration of foliage distribution and light extinction in crowns of five canopy tree species in relation to their shoot architecture, leaf traits (mean leaf angle, life span, photosynthetic characteristics) and successional status (from pioneers to persistent).

• **Methods** Light extinction was examined at three hierarchical levels of foliage organization, the whole crown, the outermost canopy and the individual shoots, in a tropical moist forest with direct canopy access with a tower crane. Photon flux density and cumulative leaf area index (LAI) were measured at intervals of 0.25–1 m along multiple vertical transects through three to five mature tree crowns of each species to estimate light extinction coefficients (K).

• **Results** *Cecropia longipes*, a pioneer species with the shortest leaf life span, had crown LAI <0.5. Among the remaining four species, crown LAI ranged from 2 to 8, and species with orthotropic terminal shoots exhibited lower light extinction coefficients (0.35) than those with plagiotropic shoots (0.53–0.80). Within each type, later successional species exhibited greater maximum LAI and total light extinction. A dense layer of leaves at the outermost crown of a late successional species resulted in an average light extinction of 61 % within 0.5 m from the surface. In late successional species, leaf position within individual shoots does not predict the light availability at the individual leaf surface, which may explain their slow decline of photosynthetic capacity with leaf age and weak differentiation of sun and shade leaves.

• **Conclusion** Later-successional tree crowns, especially those with orthotropic branches, exhibit lower light extinction coefficients, but greater total LAI and total light extinction, which contribute to their efficient use of light and competitive dominance. © 2004 Annals of Botany Company

Key words: *Anacardium excelsum*, *Antirrhoea trichantha*, architecture, *Castilla elastica*, *Cecropia longipes*, crown LAI, forest canopy, leaf angle, light extinction coefficient, *Luehea seemannii*, photosynthesis, tropical trees.

INTRODUCTION

Light available to individual leaves decreases according to the Beer's law of light extinction within a plant canopy (Monsi and Saeki, 1953). Since no leaf should exist below the light compensation point, the leaf area index (LAI), the total leaf area per square meter of ground, is ultimately constrained by the pattern of light extinction in the canopy. Typical LAI is in the range of 5–7 in temperate broad-leaved forests, and 6–8 in lowland tropical forests (Leigh, 1999). Although herbaceous communities may have LAI as high as in forests, light utilization by forest plants differs from those in herbaceous communities in many aspects. Vertical distribution of leaves takes place over a much greater distance in forests than in herbaceous communities, and this allows forest plants to exploit available light with a wide range of morphologies (e.g. trees, treelets, shrubs, vines, epiphytes, etc.). The great height of canopy trees in particular poses biomechanical challenges to optimize foliage distribution and to supply adequate amounts of water (Borchert and Tomlinson, 1984; Niklas, 1994). Consequently, leaf and light distributions in the forest canopy are expected to be spatially and temporally complex, especially in tropical forests where taxonomic and morphological diversities are high (Corner, 1964; Hallé

et al., 1978; Leigh, 1990). Due to this complexity and the difficulty of reaching the canopy, analysis of light extinction through forest tree crowns as a function of cumulative LAI poses a much greater challenge than similar analyses for herbaceous communities. Monsi and Saeki (1953) predicted that plants in full sun should have inclined leaves to achieve lower light extinction coefficients and high LAI to maximize canopy photosynthesis (see Hirose, 2005). Greater inclination of not only leaves, but also terminal shoots, should result in more uniform distribution and efficient use of light in canopy tree crowns. In this paper is reported how light utilization characteristics of crowns of tall mature trees in a tropical forest vary among species in relation to differences in their architecture and leaf arrangement patterns.

Although irradiance generally decreases as one descends from the canopy of a tropical forest (Yoda, 1974; Yoda *et al.*, 1983), there is a great variation from point to point (Koike and Syahbuddin, 1993; Baldocchi and Collineau, 1994; Parker and Brown, 2000; Montgomery and Chazdon, 2001). Koike and Syahbuddin (1993) concluded from their study of a West Sumatran forest that there is no continuous stratified upper canopy layer, but that the upper canopy consists of individual crowns that protrude upwards. Theories predict that architecture of tree crowns and patterns of leaf arrangement should affect the light extinction

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characteristics of the canopy (Anderson, 1966; Horn, 1971; Kuuluvainen and Pukkala, 1989). Because solar tracks run near the zenith throughout the year at tropical latitudes, light exploitation characteristics of individual tree crowns should exert a greater influence on the light environment below them in tropical than in temperate forests (Horn, 1971; Terborgh, 1985). Although significant effects of overall tree architecture (e.g. the ratio of projected crown area to height) on understorey light environments have been demonstrated (e.g. Canham *et al.*, 1994; Kabakoff and Chazdon, 1996; Montgomery and Chazdon, 2001), effects of species differences in shoot architecture and leaf arrangements on light extinction characteristics within individual tree crowns have rarely been examined.

Leaf distribution within a crown can be viewed as an outcome of evolution for optimal spatial distribution of carbon and nutrients to photosynthetic and support tissues (Mooney *et al.*, 1981; Field, 1983; Hirose and Werger, 1987a; Sands, 1995). Architecture and leaf phenology interact to create a gradient of leaf age and self-shading within a tree crown (Kikuzawa, 1995; Kikuzawa *et al.*, 1996). For example, many pioneer trees exhibit orthotropic (vertically oriented) shoots that successively produce leaves in spiral or decussate phyllotaxy (Ashton, 1978; Shukla and Ramakrishnan, 1986). Consequently, such plants exhibit a clear gradient of self-shading with leaf position, as well as accompanying gradients of leaf nitrogen and photosynthetic capacity as predicted by theories of optimal nitrogen allocation (Field, 1983; Hirose and Werger, 1987a; Traw and Ackerly, 1995; Hikosaka, 1996; Kitajima *et al.*, 2002). Other species, including many understorey and later successional trees have plagiotropic (horizontally inclined) shoots that produce leaves in distinctive seasonal or annual flushes (Kohyama, 1991; Kikuzawa *et al.*, 1996). In species with plagiotropic shoots, light incident on the individual leaf surface is affected more by among-branch shading than by within-branch shading. However, the orthotropic-plagiotropic dichotomy is an oversimplification as a correlate of successional status. Ackerly (1996) concludes that no single architectural model is 'typical or optimal' for pioneer species. For example, some tropical pioneer trees produce a combination of vertical and horizontal shoots, with plagiotropic lateral branches that are successively produced along orthotropic leader shoots or from the main trunk. In such cases, self-shading gradients are expected to occur at two levels of organization: shading of lower horizontal branches by younger horizontal branches that are successively produced above them, as well as gradients within each horizontal branch from younger leaves produced at more distal positions to old leaves located near central leader shoots that are heavily shaded by higher branches. Whereas many studies have addressed the effects of crown architecture on light utilization for understorey saplings and treelets (Kohyama, 1987; Kohyama and Hotta, 1990; King *et al.*, 1997; Valladares *et al.*, 2002), little information is available about the link between shoot architecture and light absorption characteristics of dominant canopy trees.

For crowns of dominant canopy trees, it may be useful to examine the link between architecture and light-utilization

patterns at three hierarchical levels: crown as a whole, canopy crust and individual shoots. The canopy crust is defined as the dense layer of leaves borne on terminal shoots at the outermost position of an individual crown (e.g. within 1–2 m from the external surface of the crown). Light extinction can be as much as 94 % over short distances within the canopy crust (Johnson and Atwood, 1970). Many canopy trees have protruding crowns (Koike and Syahbuddin, 1993), and light availability at the surface of the canopy crust should also differ depending on the position relative to the apex of the crown. Orthotropic shoot orientation and steeper leaf angle should result in lower light extinction coefficients but greater total LAI and total light extinction through the crown than plagiotropic shoots. Also predicted is that leaves at lower shaded branches should be more horizontally oriented than leaves on well-exposed branches at the crown surface.

Here are presented the results of a study that explored the species differences in vertical distribution of light and foliage in the tree crowns of a tropical seasonal forest, using a tower crane for access to the canopy. Five common canopy tree species that differ in their successional status, architecture and typical leaf angles were chosen. Also documented is light utilization at the surface and inside the canopy crust of an emergent crown of a dominant, late successional species. Whether the light environment at the surface of a leaf is predictable by its position within a terminal shoot in the upper canopy was examined in three species with contrasting shoot architecture. It was found that tree crowns as a whole exhibited predictable patterns of light extinction in relation to leaf and shoot angles, but that leaf position within a shoot was not correlated with light incident on individual leaves. Also, the photosynthetic traits of leaves at sunny and shaded locations of trees were documented to explore possible relationships of leaf photosynthetic traits with architecture and crown light utilization patterns.

MATERIALS AND METHODS

Study site, canopy access and species

The study was conducted in a seasonal tropical forest the Parque Natural Metropolitano near Panama City, Republic of Panama. It is a 75–150-year-old stand that consists of pioneers as well as early successional tree species that persist in later successional stands, with tree heights ranging up to 38 m (Table 1). Annual rainfall averages 1740 mm, the majority of which occurs during the rainy season of mid-May through to mid-December. Light availability is 48 % greater in February and March than in the cloudy wet season (Kitajima *et al.*, 1997b). The upper canopy of this forest was approached from above with a 42-m-tall construction crane maintained by the Smithsonian Tropical Research Institute. A metal cage (gondola) suspended from the 51-m-long arm of the crane could carry up to three researchers to any height within the radius of the crane's horizontal arm.

At least three individuals for each of five common tree species growing within the reach of the crane were sampled (Table 1). For each tree, crown radius was determined as the mean distance from the trunk to the projected edge in eight

TABLE 1. Relevant characteristics of five tree species studied for vertical leaf and light distribution

Species	Successional status	Branch orientation	N	Height (m)	Crown depth (m)	Crown radius (m)	Leaf contacts	Leaf angle (°)	Leaf absorptance
<i>Anacardium excelsum</i>	Early-late	Orthotropic	4 (71)	22.6–28.9	7.0 (4.6)	8.61 (2.92)	5.0 ^{ab}	50.6 ^a	0.89 ^{bc}
<i>Luehea seemannii</i>	Early-late	Plagiotropic	4 (41)	18.4–26.2	6.3 (4.3)	3.96 (1.75)	3.9 ^b	31.5 ^b	0.91 ^a
<i>Antirrhoea trichantha</i>	Early	Orthotropic	3 (33)	12.0–18.4	4.8 (2.3)	2.64 (1.04)	5.9 ^a	22.8 ^c	0.87 ^d
<i>Castilla elastica</i>	Early	Plagiotropic	5 (45)	13.8–19.1	1.8 (1.1)	3.40 (1.65)	1.8 ^c	33.6 ^b	0.88 ^{cd}
<i>Cecropia longipes</i>	Pioneer	Orthotropic	4 (56)	16.3–23.3	1.1 (0.7)	3.24 (2.36)	0.3 ^d	27.7 ^{bc}	0.90 ^{ab}

N is the number of trees sampled followed by the total number of vertical transects in parentheses. Height is the range of height among study trees. All others are means followed by standard deviation in parentheses or letters indicating significant difference between species (Tukey–HSD, $P < 0.05$).

Leaf contacts, the total number of leaf contact per vertical transects; leaf angle, the angle from the horizontal plane; leaf absorptance, PFD absorptance for individual leaf lamina.

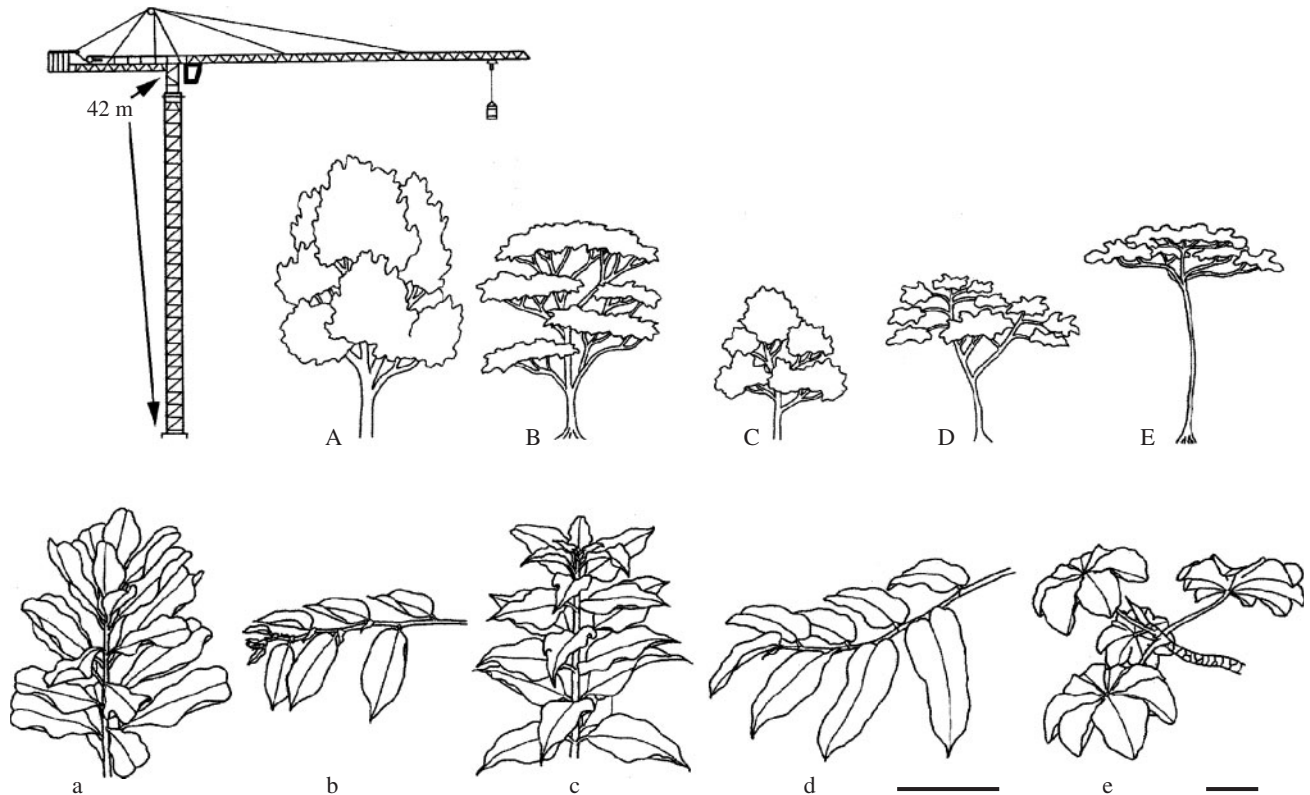


FIG. 1. Line drawings of typical mature trees (A–E) and terminal shoots (a–e) of the study species in the reversed order of successional status: *Anacardium excelsum* (late successional species with the greatest leaf longevity among the study species (A and a); *Luehea seemannii* (B and b); *Antirrhoea trichantha* (C and c); *Castilla elastica* (D and d); *Cecropia longipes* (shortest-lived pioneer; E and e). The whole trees are drawn to the scale of the tower crane (42 m tall) to show their relative sizes and crown shapes. Scales for branch drawings are shown as bars at the bottom (0.2 m, shared for a–d, separate for e).

compass directions, while crown depth was measured as the distance between the crown apex and the lowest foliated branch. These species contrast in overall architecture and successional status (Fig. 1). *Anacardium excelsum* (Anacardiaceae) and *Luehea seemannii* (Tiliaceae) have maximum height approx. 30 m; they are common in early successional stands, but persist in late successional and mature forests. *Antirrhoea trichantha* (Rubiaceae) and *Castilla elastica* (Moraceae) have maximum height <20 m; they are restricted to early successional stands <100 years old. *Cecropia longipes* (Moraceae) is a pioneer typical of early successional stands, but is also found as a rare element

in late successional stands as a gap specialist. Species nomenclature is based on D'Arcy (1987) and successional status is taken from Croat (1978) and personal observations. Hereafter the species are referred to by their genera, as species within the same genus usually exhibit similar branch architecture.

Leaf production and survival were recorded monthly for marked leaves on three exposed branches per individual for all species, and also on three shaded lower branches per tree for the two late successional species, *Anacardium* and *Luehea*, for 1–3 years (duration varied among species). From these measurements, seasonal changes in standing

leaf crop were estimated. Details of phenology, leaf longevities and photosynthetic characteristics of these species are reported in previous publications from the same site (Mulkey *et al.*, 1995; Kitajima *et al.*, 1997a, b, 2002).

The five study species represent three contrasting architecture models according to the classification schemes of Hallé *et al.* (1978) and Leigh (1990). *Anacardium* and *Antirrhoea* have relay branches developing orthotropically that are bunched around monopodial trunks (Scarrone's model; Fig. 1A and C). *Cecropia* also has relay branches attached to a monopodial main trunk; however, branching is sparse and each branch grows relatively horizontally before tipping upward (Fig. 1E). Leaves of *Anacardium* and *Antirrhoea* are arranged in dense spirals around branches, which creates strong self-shading within each shoot (Fig. 1a and c), while leaves of *Cecropia* are arranged sparsely around branch tips and have long petioles which minimize overlap and self-shading (Fig. 1e). *Luehea* exhibits sympodial trunk development, in which relay branches sprout upwards but curve evenly to end as horizontal terminal shoots that usually develop second-order horizontal branches (Troll's model; Fig. 1B). Leaves of this species are distichously arrayed on horizontal branches, and often hang down by 10–40° from the horizontal plane (Fig. 1b). *Castilla* also has plagiotropic branches that are arranged continuously along monopodial trunks and bear distichous leaves (Cook's model; Fig. 1D and d); these branches do not develop second-order branches and are shed as units. However, branches of *Castilla* are often in layers or whorls, in which case the architecture follows Massart's model.

Vertical light gradients through whole crowns

Photon flux density (PFD) was sampled along vertical transects spaced every 1 m over the surface of each tree crown in January–March, 1993 (see Table 1 for sample size). Sampling was between 1000 and 1430 h local time on predominantly clear days. Based on standing leaf crop estimated from monthly leaf censuses, the study species exhibited the maximum standing leaf number between August and November, but still had 60–90 % of the maxima at the time of measurements (beginning of dry season). With the gondola positioned above each crown and from its sunny side, a quantum sensor (LI-190SA, Li-Cor, Lincoln, NE, USA) mounted on a self-levelling (gimbaled) platform (10 cm × 15 cm) along each vertical transect, was lowered to set depths below the crown surface. These depths were each 0.25 m for the first 2 m from the crown surface, and then at 1-m intervals until there was no more foliage of the study tree present directly below. The exception was *Luehea*, for which the first 3 m of the crown was sampled at 0.25, 0.75, 1.25 and 3 m from the crown surface. Instantaneous PFD was recorded with a data logger (LI-1000, LI-COR) connected with a long cable to the sensor at these depths. The data logger also simultaneously recorded instantaneous PFD read by a reference (unshaded) sensor placed in direct beam irradiance 1 m from the sunny side of the gondola. From these measurements, % PFD transmission (%T) was calculated for each measurement point along

the vertical transects. All tree crowns were at the uppermost layer of the canopy, and well exposed to direct sunlight during the measurements. The gondola and the cables hanging the PFD platform never shaded the sensor during the measurements, and their effects on diffuse radiation should be negligible.

The cumulative leaf area to each depth into the crown was estimated from the number of leaves intersecting the vertical transect. A metal rod, 1 m in length and 6 mm in diameter, was attached beneath the PFD sensor platform. As the platform and rod descended, observers in the gondola and on the ground recorded the number of leaves contacted by the rod during each vertical interval, with the aid of binoculars. The cumulative LAI was then estimated by dividing the cumulative leaf number by the cosine of the median leaf angle for each species (Table 1). Leaf angle was measured for a total of 60–155 leaves of each species with a similar sample size from upper and lower crown positions. Leaf angle was measured with a protractor attached to a level as the tilt of the leaf blade (approximated as a flat plate) from the horizontal plane (0–90°, read as positive values whether leaves are tipped up or hanging down from the petiole). With the exception of *Luehea*, in most species, there was no significant difference in leaf angle between upper and lower crown. Thus, the median leaf angle was applied for the entire crown for the cosine correction for estimating LAI from leaf contact number. For *Luehea*, leaves on shade branches were more horizontal (20°) than those on upper canopy branches (35°) ($P = 0.0002$ with Wilcoxon Rank test). However, since the majority of leaves were found in the upper canopy branches, the median angle for the upper canopy branches was used for *Luehea*.

Canopy crust measurements

For a single 34-m *Anacardium* tree, two transects were laid with a metre tape along the crown surface from the crown summit in two directions to the edge of the crown: south-east (125° from north, 8 m long horizontally, 34–19 m above the ground) and north-west (300° from north, 13 m long horizontally, 34–15 m above the ground). The transect orientation was chosen to sample east- and west-facing sides of the crown, while minimizing the effect of the crane's tower and gondola position on the measurements. At every 1 m along each transect, the height from the ground was determined to describe the vertical profile of the transects, and light and foliage distribution at the crown surface and 0.5 m into the canopy crust were optically measured with a LAI-2000 canopy analyser (Li-Cor) and a quantum sensor mounted 8 cm behind the LAI-2000's optical sensor. All measurements were taken under overcast conditions in the mid-wet season (August 1994) when *Anacardium* trees exhibited their maximum standing leaf number. Simultaneous measurements were taken every 15 s with another unit of the canopy analyser placed at the top of the canopy crane's central tower. The LAI-2000's wand was mounted on a 2-m-long beam to place the sensor horizontally at 1.5 m away from the gondola's edge. The quarter of the optical sensor in the direction of the operator was masked to remove

the effect of the operator and gondola, and the same sky sector was masked in the reference sensor. LAI was estimated with LI-COR C2000 Software (Welles and Norman, 1991). This optically estimated LAI reflects not only the leaves directly above the point of measurements but also other foliage and objects within the 148° view of the sensor. Furthermore, because of non-random distribution of shoots and leaves, optically estimated LAI should be considered as a correlate rather than as a measure of true LAI. From the PFD recorded by the quantum sensors mounted on the canopy analysers, % PFD transmission (%T) was calculated as the ratio of PFD at measurement locations to open sky PFD measured above canopy.

Leaf position effects within shoots

How light availability at the surface of individual leaves was affected by their positions (measured by the number of leaves distal to the focal leaf within the same terminal shoot) was examined for three species with contrasting architecture and successional status (*Anacardium*, *Luehea* and *Cecropia*; Table 1). Two or three terminal shoots were selected in well-lit positions (sun branches) and an equal number from lower shaded positions (shade branches) of each species, and selected leaves at five randomly selected positions within each shoot for measurements. For *Cecropia*, only sun branches existed. A single GaAsP photodiode (G1118, Hamamatsu, Japan) calibrated against a LI-190SA quantum sensor was attached to the adaxial surface near the centre of each sampled leaf. Total daily PFD was calculated from 10-min averages for PFD sampled every 5 s recorded with LI-1000 data loggers. Care was taken to maintain the natural angle and orientation of measured leaves during the measurements. For typical leaf and solar angles, cosine-error correction for these sensors would have little effect on estimated total daily PFD (Pearcy *et al.*, 1990). Each leaf was measured continuously for 3–5 full days, and % total daily PFD was calculated for each leaf for each day as a percentage of total daily PFD at the horizontal plane above the forest canopy. From this, mean % total daily PFD was calculated for each leaf over the measurement duration that encompassed variable weather conditions. These measurements for *Anacardium* and *Luehea* were taken in January–February 1995, when these two evergreen species had 60–90 % of the maximum standing leaf number, while measurements for *Cecropia* were taken in June–July 1996 when *Cecropia* canopy had 80–90 % of its maximum leaf number.

Leaf photosynthesis

Photosynthetic rate at light saturation (A_{\max}) and stomatal conductance to water vapour (g_s) were measured *in situ* for mature, non-senescent leaves of known age (1–3 months old) in branches at well-lit and shaded locations within crowns of study trees (except in *Cecropia* which had leaves only in well-exposed locations). For shade branches of *Anacardium* and *Luehea*, % total daily PFD was quantified for a subsample of the leaves as described in the previous section. Shade branches of *Antirrhoea* and *Castilla* were

chosen from those below the middle of the crown that were shaded by larger branch systems above. Based on ambient PFD during the gas exchange measurements, these shade leaves received 3–6 % of above canopy PFD around midday under clear-to-lightly overcast conditions (above canopy PFD >700 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Field-portable infrared gas analysers for CO₂ and water were used that provided supplemental light at 1100–1300 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ and supplied CO₂ at 38 Pa to the leaf chamber (CIRAS-1; PP Systems, Hertfordshire, UK for measurements in June–August, 1994 for *Anacardium*, *Luehea* and *Antirrhoea*, and in April 1995 for *Anacardium*; LI-6400, Li-Cor, for measurements in June–July, 1996 for *Antirrhoea*, *Castilla* and *Cecropia*). Leaf disks (10 cm²) were sampled from the leaves measured for gas exchange and other leaves of similar age, to determine leaf absorptance of PFD with a LI-1800 spectroradiometer with an external integrating sphere (Li-Cor), and leaf mass per area (LMA) after drying at 60°C.

Data analysis

Within a species, light and leaf distributions along vertical transects were similar among individuals, and the data pooled for each species was analysed. From these two measurements, we calculated the light extinction coefficients for each species (K) as the Model II regression slope for the natural logarithm of mean %T vs. mean cumulative LAI, following Monsi and Saeki (1953). Model II regression was used because random error was associated with both axes. K was also calculated from the relationship between %T and optically estimated LAI for each canopy crust transect on an *Anacardium* tree, using only the measurements at 0.5 m below the canopy surface. All analyses were performed with JMP software (Version 3.1, SAS Institute, USA).

RESULTS

Foliage and light distribution through the tree crown

The study species differed in canopy depth and mean number of leaf contacts per vertical transect (Table 1). Many of the vertical transects through the periphery of the crowns were very short. There was also a large within-species variance in cumulative leaf contact number at a given depth, with greater variance within the first few metres [coefficient of variance (CV) >100 %] than at greater depth (50–90 % depending on species). Percentage PFD transmission also varied, with CV ranging from 60–150 % below 1 m depth without clear inter- or intraspecific trends. The later successional species with greater maximum height (*Anacardium* and *Luehea*) had larger crown radius and crown depth. The mean number of leaf contacts per transect was a function of crown depth, branch architecture and crown allometry (Table 1). The mean number of leaf contacts per transect was similarly high for *Anacardium* and *Antirrhoea* with densely arranged leaves on orthotropic branches. Between these two, there were slightly more leaf contacts per transect in *Antirrhoea* with less tilted leaves and a more compact crown (low ratio of crown radius to crown depth) than in *Anacardium*, despite lower crown

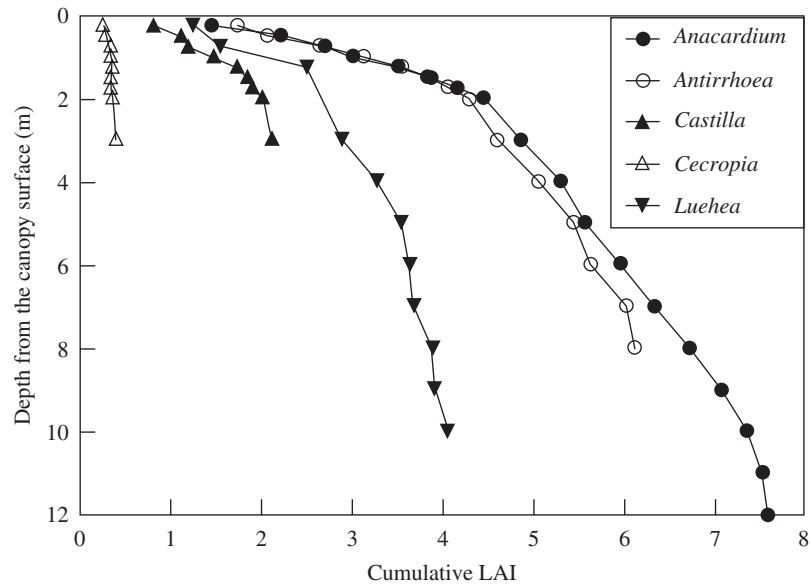


FIG. 2. Mean cumulative leaf area index (horizontal axis) as a function of depth from the crown surface (vertical axis) for five canopy trees. Leaf contacts were counted for every 0.25–1 m down to the lowest leaf along each vertical transect through each crown. The cumulative LAI was estimated by dividing cumulative leaf contact with cosine of the median leaf angle of each species.

depth in the former. The mean number of leaf contacts per transect was intermediate to low for plagiotropic species (*Luehea* and *Castilla*), and lowest for *Cecropia*, which presents leaves in a manner to avoid overlap at the tip of terminal branches (Fig. 1). Absorptance of individual leaves did not differ significantly between well-lit sun branches and shade branches, except for *Anacardium* (0.87 for shade leaves vs. 0.90 for sun leaves, $P = 0.02$). Thus, species medians for pooled data were compared among species (Table 1). Leaf angle and absorptance differed significantly among species but lacked any apparent relationship with branch orientation, overall architecture or successional status. *Anacardium* had more steeply angled leaves than all other species.

The five species differed greatly in the average leaf area accumulation rates with depth, as well as the maximum crown LAI (Fig. 2). Branch orientation appeared to be more important as a determinant of the patterns of LAI increase with crown depth than successional status. Two species with orthotropic branches, *Anacardium* and *Antirrhoea*, accumulated LAI very rapidly within the top 2 m from the crown surface (Fig. 2). They continuously accumulated LAI at slower rates at deeper crown depths to achieve high total crown LAI, that was greater for *Anacardium* with a greater crown depth than for *Antirrhoea*. Two species with plagiotropic branches, *Luehea* and *Castilla*, accumulated LAI rapidly within the first 1 m of the outermost crown surface, and then more slowly to result in much lower total LAI. Their LAI accumulation was slower with a lower maximum than that of *Anacardium* and *Antirrhoea*. *Cecropia*, a pioneer species with non-overlapping leaves at branch tips (Fig. 1E and J) had low crown LAI (maximum <0.5).

Light transmitted through tree crowns decreased as an exponential function of cumulative LAI in all species but

Cecropia as predicted by the Beer's law of light extinction (Fig. 3). Unlike the other four species, *Cecropia* did not show any predictable light extinction, as LAI did not accumulate through the crowns of this species (open triangles clustered at the upper left corner in Fig. 3). The remaining four species differed in light extinction coefficients in relation to their terminal shoot inclination (Fig. 3). *Anacardium* and *Antirrhoea* with orthotropic branches showed similarly low extinction coefficients ($K = 0.347$ and 0.345 , respectively) even though individual leaves are more inclined in *Anacardium* than in *Antirrhoea* (Table 2). *Anacardium* had higher %T for a given value of cumulative LAI (Fig. 3) because *Anacardium* trees were taller and received, on average, greater light at the crown surface than *Antirrhoea*. However, the minimal PFD was lower for *Anacardium* due to its greater total crown LAI and canopy depth than *Antirrhoea*. Two species with plagiotropic terminal shoots had significantly greater extinction coefficients than those with orthotropic terminal shoots. *Luehea* with curving relay branches that end with plagiotropic terminal shoots had an extinction coefficient of 0.526, whereas *Castilla* whose horizontal branches cluster around a monopodial trunk had an even higher coefficient of 0.795. Thus, *Luehea* with more inclined branches on average had a slower rate of light extinction than *Castilla*, even though their median leaf angles were similar (Table 1). However, it was darker under later successional *Luehea* than under *Castilla* as a result of the greater total LAI of the former (Fig. 3).

Light extinction in the canopy crust of *Anacardium*

The crown surface of an emergent *Anacardium* tree showed asymmetric topography in both horizontal and vertical directions (Fig. 4A and B). The crown spread was much more extensive to north-west than to south-east;

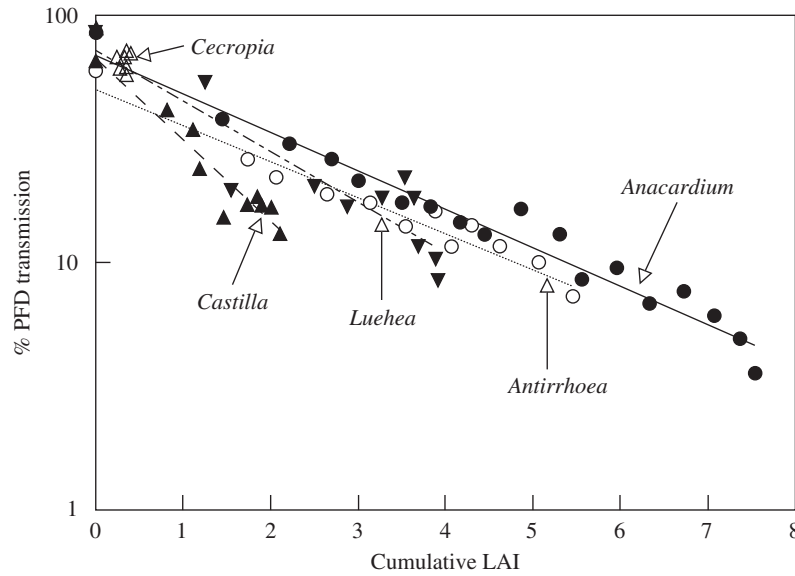


FIG. 3. Light extinction as a function of cumulative leaf area index (LAI) through crowns of five neotropical tree species (see Table 1 for full names). Mean % PFD transmission (vertical axis) at a given depth from the canopy surface is plotted against mean LAI (horizontal axis) above that depth.

TABLE 2. Means (s.d.) for gas exchange characteristics and leaf mass per area (LMA) for leaves grown in exposed (sun) and shaded (shade) regions of the crowns of five canopy tree species

Species	Branch light	N	Median leaf life span (d)	N	A_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	g_s ($\text{mol m}^{-2} \text{s}^{-1}$)	N	LMA (g m^{-2})
<i>Anacardium excelsum</i>	Sun	5873	250	82	7.3 (2.8)**	0.213 (0.098)*	20	111.9 (23.4)***
	Shade	1739	186	28	5.3 (3.6)	0.164 (0.128)	20	90.7 (13.0)
<i>Luehea seemannii</i>	Sun	5736	158***	16	10.5 (3.1)*	0.505 (0.283)**	25	138.1 (28.8)***
	Shade	1448	189	10	8.0 (2.5)	0.217 (0.069)	19	78.6 (13.1)
<i>Antirrhoea trichantha</i>	Sun	2764	155	26	10.8 (3.0)***	0.412 (0.182)***	6	65.3 (8.8)***
	Shade	—	—	12	5.5 (2.8)	0.264 (0.192)	6	32.7 (2.9)
<i>Castilla elastica</i>	Sun	515	180	13	13.7 (2.2)***	0.276 (0.083)***	13	87.2 (6.5)***
	Shade	—	—	16	4.5 (1.5)	0.139 (0.084)	16	32.7 (8.7)
<i>Cecropia longipes</i>	Sun	699	84	10	25.5 (3.6)	0.800 (0.345)	15	88.7 (13.2)

Samples size (N) for g_s is the same as that for A_{max} . Note that there were no shade leaves for *Cecropia*.

The median leaf life span (data for shade branches available only for the first two species) is indicated.

Asterisks indicate significant difference between sun and shade branches (* $P < 0.05$; ** $P < 0.005$; *** $P < 0.0005$).

along the north-west transect, crown surface sloped more gently, and foliated branches were found as far as 19 m below the crown apex, and 13 m away in the horizontal direction. Optically estimated LAI at the surface of and 0.5 m inside the canopy crust increased with descent from the apex along each transect (Fig. 4C and D). The optically estimated LAI reflects leaf area distribution within the 148° view angle above the point of measurement. Consequently, optically estimated LAI at the crown surface was greater than zero at lower heights (Fig. 4C and D, open circles) because of neighbour trees as well as high portions of the same tree crown. The optical LAI at 0.5 m inside the canopy crust reflected these neighbour effects plus those of the foliage immediately over the measurement positions (Fig. 4C and D, lines through closed circles). The LAI difference between the surface and inside of the canopy

crust, which could be considered as an estimate of the LAI of the 0.5 m deep crown crust itself, was generally <3.0 at a given measurement position but somewhat greater at lower heights. The maximum values of optical LAI was similar between the two transects, even though the north-west transect extended to a lower height from the ground. The ratio of PFD inside to that at the surface of the crown crust was 0.04–1.00 with a mean of 0.39 (i.e. a 0.5-m-deep layer of crown crust caused 61 % reduction of PFD). The PFD extinction as a function of optical LAI was steeper inside than at the surface of the canopy crust in the south-east transect, but it was similar in the north-west transect (Fig. 4E and F). Light extinction coefficients estimated as regression slopes for 0.5 m inside the crown crust were 0.621 and 0.760 for north-west and south-east transects, respectively (Fig. 4E and F, closed symbols). These values

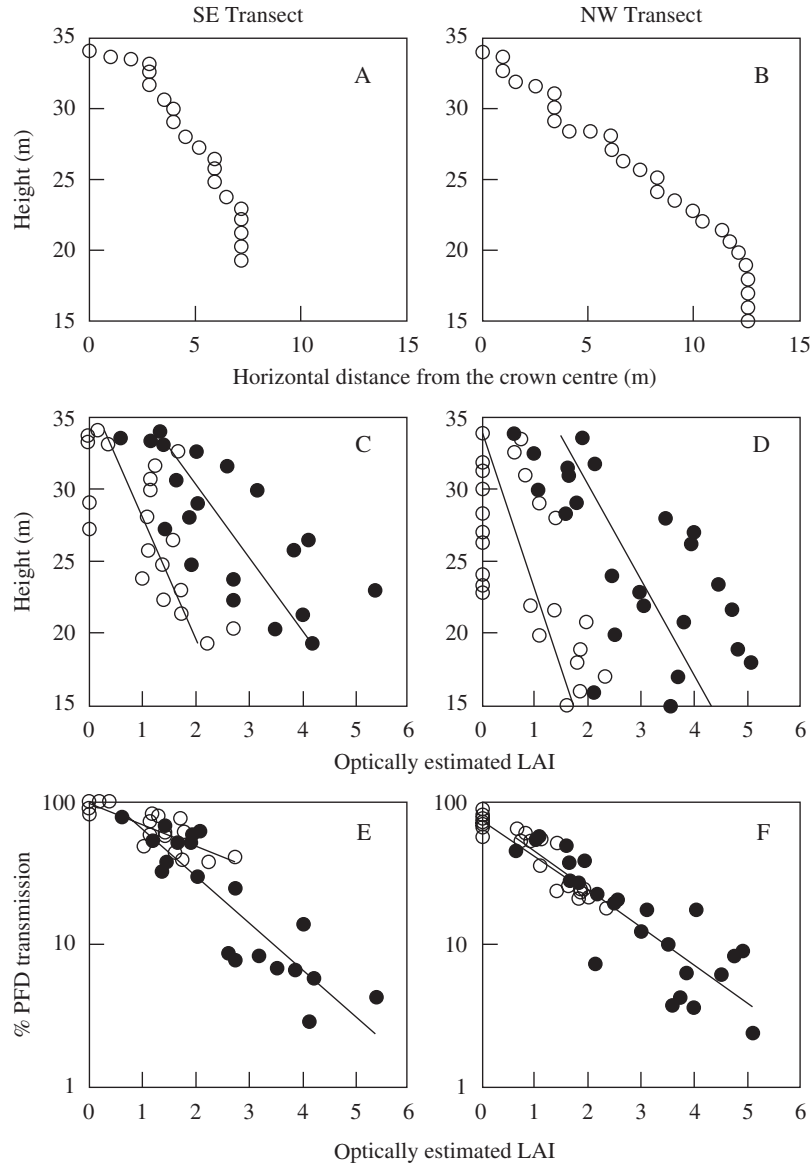


FIG. 4. Foliage and light distribution at the surface (open circles) and 0.5 m inside (closed circles) of the crown crust of an emergent *Anacardium excelsum* tree. (A, B) Canopy surface topography along two transects laid from the apex of the crown to south-east (125°) and north-west (300°); height from the ground and horizontal distance from the apex was measured at every 1-m interval along the transects. (C, D) LAI estimated optically with a canopy analyser (LAI-2000, Li-Cor) as a function of the height from the ground. (E, F) Percentage PFD transmission as a function of optically estimated LAI within the canopy crust.

based on optical LAI were higher than the extinction coefficient estimated from vertical transects for the whole crown for the same species (0.347; Fig. 3).

Leaf position effects within branches

Relative total daily PFD at the individual leaf surface, expressed as the percentage of the above-canopy daily PFD, showed a significant negative correlation with leaf position for shade branches of *Anacardium* (Fig. 5A; $r^2 = 0.59$, $P = 0.0014$) and sun branches of *Cecropia* (Fig. 5C; $r^2 = 0.59$, $P = 0.0008$). Although older leaves at more proximal positions (i.e. farther away from the

tip) should experience greater degrees of self-shading, the light environment at the surface of a leaf was independent of its position within sun branches of *Anacardium* (Fig. 5A) and both types of branches of *Luehea* (Fig. 5B). Examination of data for individual shoots did not reveal better relationships. In all cases, leaves at similar positions experienced widely different relative daily PFD, probably due to variation in leaf orientation. Even leaves at the most distal positions near the tips of well-exposed sun branches usually experienced PFD much less than 100 % PFD at the horizontal plane, probably due to leaf angles, leaf orientation and effects of neighbouring branches. Not surprisingly, leaves on the shade branches received less light than those on the sun branches (closed vs. open circles, Fig. 5A and B).

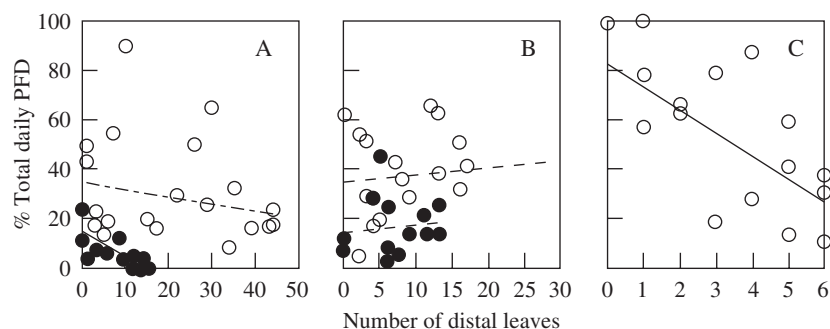


FIG. 5. The relationship of % total daily PFD at individual leaf surface ($100 \times$ total daily PFD per unit leaf area divided by above-canopy PFD on the horizontal plane, vertical axis) to leaf position within the terminal shoots (indicated by the number of distal leaves relative to the focal leaf, horizontal axis) for three canopy tree species with contrasting branch architecture. (A) *Anacardium* with steeply angled leaves around orthotropic shoots, (B) *Luehea* with variously angled leaves along plagiotropic shoots, and (C) *Cecropia* with minimally overlapping leaves at the tips of orthotropic shoots. Open circles, upper canopy branches; closed circles, shade branches in the lower part of the crown. No shade branch existed for *Cecropia*. Solid and broken lines indicate significant ($P < 0.05$) and non-significant regressions, respectively, for sun and shade branches.

No leaves existed below 10 % of full sun for *Cecropia*, which lacked shade branches.

Leaf traits in sun vs. shade branches

Leaves on sun branches had higher photosynthetic rates (A_{\max}) and stomatal conductance (g_s) under saturating light than those on shade branches (Table 2). These differences were accompanied by differences in leaf mass per area (LMA), but little difference in photosynthetic rates per unit mass (A_{\max}/LMA). Two later successional species, *Anacardium* and *Luehea*, showed smaller differences between sun and shade branches than did two early successional species, *Antirrhoea* and *Castilla*. Leaf life-span data for shade branches were available only for *Anacardium* and *Luehea*. Leaves on sun branches had shorter life span than those on shaded branches in *Luehea*, but there was no significant difference in *Anacardium* (Table 2).

DISCUSSION

The inclination of individual leaves determines the light extinction coefficient in herbaceous canopies (Monsi and Saeki, 1953; Saeki, 1960). In contrast, the inclination of terminal shoots, rather than individual leaves, appears to be more important for light extinction through tree canopies. Light measured on a horizontal plane declined more slowly along the vertical transects through crowns of the species with orthotropic shoots (*Anacardium* and *Antirrhoea*) than those with plagiotropic shoots (*Luehea* and *Castilla*). The milder gradient of PFD in crowns consisting of orthotropic shoots was accompanied by a greater total LAI and darker environment underneath. Within each group, later successional species exhibited a greater total LAI and light extinction than did early successional species (*Anacardium* > *Antirrhoea*; *Luehea* > *Castilla*). Further, light availability at the individual leaf surface was not a simple function of leaf position within the terminal shoot in canopy trees. Rather, light availability at individual leaves varied widely at similar positions within the terminal shoot due to variation in leaf orientation and angle. The causes and

implications of these findings are discussed in relation to species differences in architecture and leaf arrangement.

Light extinction through the whole crown

The light extinction characteristics of tree crowns differed among species in relation to several traits, including successional status, tree and branch architecture, and leaf angles. Estimated light extinction coefficients (0.37–0.80) generally corresponded to those for steeply inclined leaves in herbaceous communities (<1.0). Measurements were taken mostly under clear sky conditions, which should result in a greater light extinction coefficient for a given leaf angle than under overcast conditions (Saeki, 1963). Under overcast conditions, extinction coefficients should be even lower. Both LAI and light intensity showed large variation at a given depth among trees within each species; but on average, they exhibited patterns that could be linked to species-specific architecture. However, the light incident on individual leaves was unrelated to the position of leaves within shoots in the upper crown for both orthotropic *Anacardium* and plagiotropic *Luehea* (Fig. 5). Thus, simulations of tree architecture and light utilization, which treat foliated branches as a unit, are appropriate for most tree species (e.g. Takenaka, 1994). Crowns of later successional species exhibited greater canopy depth and total crown LAI. This explains the pattern found by Brown and Parker (1994) at the community level for a temperate broad-leaved forest; early successional stands have higher extinction coefficients and lower total LAI than late successional stands. The greater total LAI and total light extinction exhibited by individual crowns of later successional species may be an adaptive strategy to extract light resources and cast shade upon their subdominant neighbours (Horn, 1971; Canham *et al.*, 1994). Although canopy species composition can significantly affect light transmittance at the stand level in the absence of gaps (Messier and Bellefleur, 1988; Canham *et al.*, 1994; Kabakoff and Chazdon, 1996), the understorey light environment is affected also by subcanopy trees and understorey plants (Nicotra *et al.*, 1999; Denslow and Guzman, 2000; Montgomery and Chazdon, 2001).

At our site, canopy openness and total daily PFD at 1.8 m above the ground directly below crowns of *Anacardium*, *Luehea* and *Castilla* did not differ significantly among species despite strong interspecific differences in total crown LAI and percentage transmittance, except in the late dry season when *Castilla* crowns were completely deciduous (K. Kitajima, S. S. Mulkey and S. J. Wright, unpubl. res.).

Canopy crust topography and light utilization

The arrangement of the photosynthetic surface in curved or tilted layers results in more uniform light distribution among leaves and enhances the photosynthetic productivity of the canopy as a whole, such that stand-level productivity per unit ground area continuously increases with increasing PFD (Boysen Jensen, 1932; Monsi and Saeki, 1953). The rough surface topography of forest tree crowns achieves this on a large spatial scale. The height of the forest canopy surface at the present study site was very heterogeneous, partly because this stand included both tall species that persist into late successional stands (e.g. *Anacardium* and *Luehea*) and shorter species that are restricted to early successional stands (e.g. *Antirrhoea* and *Castilla*). Community-level measurements of canopy topography at this study site (G. Parker, pers. comm.) also support this view (also see Parker and Brown, 2000). Thus, the heterogeneity of canopy structure at the present study site (a 75–100-year-old successional stand) resembles mature stands more than the successional stands (15–20 years old) in Costa Rica studied by Montgomery and Chazdon (2001).

Both height and orientation are important aspects of crown surface topography. Tree crown development is often asymmetric because crowns tend to grow away from near neighbours and into adjacent tree-fall gaps (Jones and Harper, 1987; Young and Hubbell, 1991; Young and Perkocha, 1994; Umeki, 1995; Olsen, 2001). In contrast, variation in crown topography relative to the diurnal course of the sun has not been well studied. Zotz *et al.* (1995) found that east-facing leaves that received direct sunlight during the early morning achieved greater photosynthetic production and higher photosynthetic water use efficiency than west-facing leaves for a canopy tree, *Ficus insipida*, at the present study site. The more moderate sloping of crown surface to west than to east (Fig. 4A) thus increased interception of more valuable morning light for the crown as a whole than would a completely symmetrical crown. The effects of orientation on crown topology and leaf physiology may be worth examining in the future. Overall, light extinction at 0.5 m below the crown surface appeared to follow Beer's law of light extinction, but this analysis is somewhat circular because LAI was optically estimated. The heterogeneous distribution of foliage was likely to cause an underestimation of LAI by optical method (Welles and Norman, 1991), and consequently a greater estimated light extinction coefficient for the crown crust (Fig. 4) than for the whole crown of the same species (Fig. 3). Nevertheless, the optical method may be useful in assessing the effects of neighbours at different positions in the upper canopy.

Lack of light gradients within terminal shoots

Unlike pioneer trees with orthotropic terminal shoots (Fig. 5C; also Ackerly, 1999; Kitajima *et al.*, 2002), two mature canopy tree species exhibited no relationship between leaf position and leaf light environment within sun branches (Fig. 5A and B). *Luehea* with plagiotropic branches showed a complete lack of relationship both for sun branches and shade branches, because self-shading was caused by upper branches rather than by distal leaves within a horizontal branch. *Anacardium* with orthotropic branches showed a non-significant trend in sun branches and a significant gradient in shade branches. This species displays steeply inclined leaves in dense spirals (Fig. 1a), which probably resulted in unpredictable shading patterns within terminal sun branches. But, in shade branches that received most light as diffused radiation, there was a more predictable self-shading gradient even though shade branches are inclined more horizontally. Light availability at individual leaf surfaces may be predicted only through analysis with a three-dimensional architecture program that takes into account the precise orientation and angle of leaves, as well as shading by neighbouring leaves and branches (Percy and Yang, 1996).

Whether light availability predictably declines with leaf position within shoots should affect the rate at which leaf nitrogen content and photosynthetic capacity change with leaf age. Grassland plants and pioneer trees develop leaves successively at regular intervals, and leaf nitrogen content and photosynthetic capacity decline linearly with leaf age and position within shoots. The relatively short leaf life spans of such species are predicted to equal the leaf age at which the daily net photosynthetic rate declines to zero by an optimality model in which the lifetime carbon gain for each leaf is maximized (Saeki, 1960; Mooney *et al.*, 1981; Hikosaka *et al.*, 1994; Hikosaka, 1996; Ackerly, 1999; Kitajima *et al.*, 2002). In contrast, later successional trees extend shoots and produce new leaves in pulses, resulting in non-steady development of self-shading with leaf ageing, especially in species with plagiotropic terminal shoots (Kikuzawa *et al.*, 1996). This decoupling of leaf age and leaf position, in combination with the lack of predictable self-shading in relation to a leaf position (Fig. 5A and B), provide an explanation for slower declines of photosynthetic rates with leaf age in late successional species with long leaf life spans, such as *Anacardium* and *Luehea* (Kitajima *et al.*, 1997a). Indeed, for these species, the observed leaf life span is predicted only by an alternative optimality model in which daily carbon gain rate averaged across leaf lifetime is maximized (Kikuzawa, 1991; Kitajima 1997a; Kikuzawa and Ackerly, 1999; Hikosaka, 2005). It is concluded that late successional trees exhibit patterns of leaf display that result in more equal sharing of available light among leaves within shoots, which leads to lower overall light extinction coefficients at the crown level and slower declines of leaf nitrogen content and photosynthetic rate in relation to leaf age.

Sun vs. shade branches

Unlike most herbaceous plants and pioneer trees that produce leaves only near their upper part, trees produce

leaves in both well-lit and shaded positions of the crown. This allows tree crowns to exploit light more completely (Terashima *et al.*, 2005). Three of our study species exhibited the classical phenotypic differentiation of sun vs. shade leaves (Table 2); higher leaf mass, photosynthetic capacity and stomatal conductance per unit leaf area for leaves on sun branches than those on shaded branches. In addition, the shorter leaf life span of *Luehea* for sun branches than shade branches was also expected because greater productivity and growth in the upper canopy layer should result in shorter mean leaf longevity and greater leaf turn-over rates (Koike, 1986; Osada *et al.*, 2001).

Anacardium exhibited only weak differentiation to sun vs. shade phenotypes and showed no difference in leaf life span between sun and shade branches (Table 2). Phenotypic plasticity of leaf photosynthetic traits is often weaker for late successional species (Strauss-Debenedetti and Bazzaz, 1991; Valladares *et al.*, 2000). Lack of sun-shade acclimation of leaves is uncommon, but it is found among various life forms of tropical forest plants (Mulkey, 1986; Hogan, 1988; Mulkey *et al.*, 1991; Kitajima, 1994). The steeply inclined leaves of *Anacardium*, which are presented in dense whorls, resulted in more uniform sharing of light among leaves and smaller differences in leaf phenotype between upper and lower branches within the crown. During the period of active leaf production (February–March), *Anacardium* leaves on sun branches become shaded by newer leaves that are successively produced above them even before they mature physiologically. Only half of the *Anacardium* leaves on sun branches received >20 % total daily PFD (Fig. 5A). Lack of strongly sun-acclimated leaves in this species is part of a strategy to distribute light more uniformly within its crown through strongly inclined leaves surrounding orthotropic branches.

Diversity of leaf display strategies in time and space

Only a small fraction of the diversity of leaf presentation strategies observed among tropical trees is reported here. For understorey plants, Valladares *et al.* (2002) concluded that various architecture and leaf display patterns result in surprisingly similar light use efficiency estimated by a three dimensional simulation. In contrast, the present analysis of canopy trees suggests a large variation in light use efficiency among species. Functional diversity in light utilization characteristics by tree crowns should be examined not only in space, but also in time (Mulkey *et al.*, 1996; Wright, 1996). Water becomes increasingly limiting during the dry season, whereas the heavy cloud cover during the wet season limits light availability and canopy productivity (Wright and Van Schaik, 1994; Graham *et al.*, 2003). In most species in the present study site, canopy leaf area builds up over the course of 5–8 months during the wet season, except for *Anacardium* which produces leaves during the dry season (S. J. Wright, unpubl. res.). In four of the study species, leaves produced during the early wet season have lower LMA and photosynthetic capacity than those produced immediately before the dry season (Kitajima *et al.*, 1997b). In a much shorter time scale, *Luehea* leaves increase their angles by >30°, on average, in response to

water and light stress later in the day (K. Kitajima, S. S. Mulkey and S. J. Wright, unpubl. res.). Canopy trees acclimate to daily and seasonal heterogeneity in resource availability by adjusting when to display what types of leaves at what angles and degrees of self-shading.

Optimization of carbon gain with respect to availability of light and water is achieved through a diversity of leaf displays in time and space. Greater inclination of leaves and shoots are often, but not always associated with more uniform sharing of light within a crown, which in turn enables greater total LAI and more complete light exploitation. Crowns of later successional trees often, but not necessarily cast deeper shade underneath. Combinations of certain traits, such as orientation of terminal shoots and leaves, leaf longevity and leaf phenology, provide useful guidelines to understand functionally convergent patterns of leaf display among forest trees.

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