CONVERGENCE IN LIGHT CAPTURE EFFICIENCIES AMONG TROPICAL FOREST UNDERSTORY PLANTS WITH CONTRASTING CROWN ARCHITECTURES: A CASE OF MORPHOLOGICAL COMPENSATION[1]

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Leaf and crown characteristics were examined for 24 tree and herbaceous species of contrasting architectures from the understory of a lowland rainforest. Light-capture efficiency was estimated for the crowns of the different species with a three-dimensional geometric modeling program. Causal relationships among traits affecting light absorption at two hierarchical levels (leaf and whole crown) were quantified using path analysis. Light-capture and foliage display efficiency were found to be very similar among the 24 species studied, with most converging on a narrow range of light absorption efficiencies (ratio of absorbed vs. available light of 0.60–0.75). Exceptionally low values were found for the climber vines and, to a lesser extent, for the Bromeliad *Aechmea magdalenae*. Differences in photosynthetic photon flux density (PFD) absorbed per unit leaf area by individual plants were mostly determined by site to site variation in PFD and not by the differences in crown architecture among individuals or species. Leaf angle, and to a lesser extent also supporting biomass, specific leaf area, and internode length, had a significant effect on foliage display efficiency. Potential constraints on light capture such as the phyllotactic pattern were generally offset by other compensatory adjustments of crown structure such as internode length, arching stems, and plagiotropy. The variety of shoot morphologies capable of efficiently capturing light in tropical forest understories is greater than initially thought, extending over species with very different phyllotactic patterns, crown architectures, leaf sizes, and morphologies.

Key words: crown architecture; display efficiency of the foliage; leaf absorptance; light harvesting; phyllotaxis; shade tolerance; tropical rainforest; understory light environment.

Light is one of the most important determinants of plant establishment, growth, and survival in tropical rainforests (Osunkoya et al., 1992; Nicotra, Chazdon, and Iriarte, 1999). In general, less than 2% of the photosynthetically active radiation above the canopy reaches a tropical rainforest floor. This consists of very low background diffuse radiation that is randomly punctuated by generally short duration sunflecks (Pearcy, 1983; Chazdon and Fetcher, 1984; Canham et al., 1990). Under these strongly limiting light conditions, plants might be expected to maximize light capture in the most efficient way, i.e., at the lowest costs in terms of construction and maintenance (Givnish, 1988). Tropical plants have been shown to adjust their morphology and physiology to available light at different hierarchical levels including: leaf gas exchange properties (photosynthesis, respiration), leaf optical properties (absorptance, transmittance), specific leaf area (area to mass ratio of leaves), crown allometry (e.g., height to diameter ratio, supporting to non supporting tissues mass ratio, leaf area ratio), and crown architecture (branching pattern, foliage arrangement) (Hallé, Oldeman, and Tomlinson, 1978;

Kohyama and Hotta, 1990; King, 1991; Kitajima, 1996; Valladares, 1999; Poorter et al., 2000; Valladares et al., 2000).

A striking feature of tropical rainforest understory vegetation is the large variation in leaf morphology and crown architecture (Bongers and Popma, 1990; Leigh, 1998; Turner et al., 2000). We were interested in knowing if these contrasting habits and morphologies render functionally equivalent architectures in terms of light-capture efficiency or, alternatively, if differences among understory species in efficiency exist. Branching pattern and leaf arrangement have a direct impact on leaf-display efficiency and consequently on light capture and photosynthesis (Valladares, 1999; Valladares and Pearcy, 1999). For plants in shaded habitats, minimum leaf overlap in the horizontal plane, which minimizes self-shading for light from above, is an expected characteristic given that it increases the mean light capture per unit leaf area (Pearcy and Yang, 1998; Pearcy and Valladares, 1999). For this reason, the geometry of leaf arrangement on stems (phyllotaxis) in low light is typically considered in terms of selection pressures favoring light interception (Sekimura, 1995; Adler, Barabe, and Jean, 1997). However, the extent to which phyllotaxis influences light capture remains poorly known because other morphological characteristics interact with and can compensate for suboptimal phyllotaxies (Niklas, 1988). Additionally, other crown functions such as water transport and biomechanical support may constrain selection pressures for maximizing light capture (Pearcy and Valladares, 1999). Interactions between different constraints on crown configuration could explain the large range of architectures apparent in tropical rainforest understories.

We have examined leaf and crown characteristics for 24 tree and herbaceous species of contrasting crown architectures co-occurring in a neotropical, lowland rainforest understory. The central objective of this study was to see if there were discernible patterns among taxa or growth form for light capture characteristics of the crown. Foliage display efficiency and light capture were estimated with a three-dimensional geometric modeling program (Y-plant; Pearcy and Yang, 1996), which has been successfully used for this purpose in a number of previous studies (e.g., Pearcy and Yang, 1998; Pearcy and Valladares, 1999; Valladares and Pearcy, 1999). Causal relationships among traits that determine light absorption at two hierarchical levels (leaf and whole crown) were structured and quantified using path analysis (Mitchell, 1993; Scheiner, Mitchell, and Callahan, 2000), which allowed for partitioning into direct and indirect or correlated effects of the traits on light absorption.

MATERIALS AND METHODS

Study site and plant material—The study was carried out in Panama at the Smithsonian Tropical Research Institute, Barro Colorado Island (BCI) field station (9°9′ N, 79°51′ W). Barro Colorado Island has a tropical monsoon climate, with a wet season typically lasting from April through December (Croat, 1978; Leigh, 1998). The mean annual precipitation is 2600 mm and mean monthly air temperature ranges from 21° to 32°C (annual mean = 27°C). Most of BCI supports a highly diverse, semi-evergreen moist tropical forest. More than 120 tree species (>2.5 cm in diameter at breast height) per hectare and more than 1370 species of vascular plants have been recorded on this 15.6 km² island (Leigh, 1998). The principal vegetation of the deeply shaded forest floor consists of shrubs, tree, and liana seedlings, herbaceous vines, and herbaceous ground plants.

In this study, 13 monocotyledoneous and 11 dicotyledoneous species of different families, habits, growth forms, and leaf attributes were selected for comparison of light-capture efficiencies and capacities (Table 1). All plants studied were selected from shaded understory sites. Three to ten individuals of each species were harvested and separated into stems, branches, petioles, and leaves to determine stem and petiole densities (in grams per cubic centimetre), and specific leaf areas (SLA, in square centimetres per gram). Leaf area was determined immediately after collection with an LI-3000 area meter (LI-COR Instruments, Lincoln, Nebraska, USA). Stems, branches, and petioles were cut into segments with a uniform diameter along their length and the volume of these segments was determined from their diameter and length. Following this, the plant parts were placed in individual paper bags and dried in an oven at 65°C for a minimum of 72 h (10 d in the case of thick, woody material) until a constant mass was achieved.

Characterization of the light environment—The light environments of the plants were characterized using hemispherical photography. Photographs were taken at the crown top of each plant using a leveled Nikon 8 mm fish-eye lens (180° field of view) on a Nikon 8008 camera body (Nikon, Tokyo, Japan). We used high contrast black and white film (ASA 400, Tri-X; Eastman Kodak, Rochester, New York, USA) with the lens' internal red filter to enhance contrast between gap (sky) and foliage. Photographs were taken at the speed and f-stop indicated by the camera exposure meter and ±1 stop. The image yielding the best detail of foliage and canopy openings was selected and analyzed for canopy openness using a video digitizer and the program CANOPY (Rich, 1989). The direct site factor (DSF), indirect site factor (ISF), and the global site factor (GSF) were computed by CANOPY. These factors are estimates of the fraction of direct, daily, and total radiation, respectively, expected to reach the site of the photograph compared to the radiation above the canopy (Anderson, 1964). Weighting factor for diffuse light was 0.1 of total light. Daily photosynthetic photon flux density (PFD, in moles per square metre per day) available at each site was calculated from Y-plant simulations as discussed below for a completely clear day (1 January, 50.6 mol·m⁻²·d⁻¹ reaching the overstory).

Leaf optical properties—Five to 20 leaves of each species studied were collected in the field and brought immediately to the laboratory for determination of their optical properties. Selected leaves were mature but not senescent, and macroscopic epiphylls were carefully removed before measuring the optical properties. Absorptance, reflectance, and transmittance of PFD by leaf disks were measured with an LI-1800 spectroradiometer (LI-COR Instruments).

Crown three-dimensional reconstruction and estimation of light-capture efficiency—Measurements of the crown geometric properties required for running Y-plant were made on three individuals of each species. For each plant, the angles and azimuths of the stem, of any branch, and of the petiole and surface of any leaf originating from a node were recorded with a compass-protractor. In addition, the azimuth of the midrib, the lengths of internodes, petioles and leaves, and the diameters of the petioles and internodes were recorded. Nodes were numbered proceeding from the base to the top of the plant and along each branch. Values used for the different variables were not mean values for the plant but the specific values at each node for each organ or section of the organ. By recording the mothernode (the node from which a subsequent node arises) for each node, the proper topology of the crown could be reconstructed by Y-plant. Leaf shape was established from x, y coordinates of the leaf margins, and up to 20 leaf shapes were considered for each species. Leaf size was then scaled from the measured leaf length. In order to reconstruct curved leaves such as those of Bromeliaceae (the current version of Y-plant can only handle flat leaves), leaves were divided into segments of varying elevation angle and attached one after another. In the case of climber plants (i.e., *Monstera* sp.), the stem of the host tree was also measured and included in Y-plant as if it were part of the plant in order to mimic the shade cast by the trunk on the target plant. The realistic graphic display of the reconstructed crowns (see Fig. 1) allowed for error checking by comparison with the appearance of the real plant in the field.

Following reconstruction of the three-dimensional plant image, Y-plant was then used to determine the absorption of diffuse PFD from 160 sky sectors covering the entire hemisphere and direct PFD from specific angles and azimuths corresponding to the solar track of a given day (1 January). Standard equations were used to simulate the radiation above the canopy on a completely clear day (Pearcy, 1989). The PFD incident at the plant from a given sky sector was simulated from the sky PFD and the fraction of open sky visible (not blocked by the overstory canopy) in that sector. The simulated absorption of PFD by the plant was then determined with a simple ray tracing technique (Pearcy and Yang, 1996). Summation over all sectors gave the total diffuse PFD absorbed. A similar approach was used for direct PFD except in this case direct PFD was assumed to be absorbed only when the solar disk as calculated from standard equations was within a gap along the solar track. The outputs of Y-plant used in this study were the absorbed PFD (in moles per square metre per day) resulting from the combination of the crown display, the optical properties of the leaf, and the light environment at the plant, and measures of the efficiency of the crown for light capture. These efficiency measures were the projection efficiency (foliage area projected towards a given sky direction divided by the total foliage area [E_p]), the display efficiency (the fraction of foliage that is not self-shaded and is projected towards a given sky region [E_d]), and the efficiency of light absorption (mean PFD per unit leaf area absorbed by the plant divided by PFD incident on a horizontal surface right above the plant [E_a]). In addition, we used the allometric equations to calculate the aboveground leaf area ratio (aLAR, in square metres per kilogram) and the fraction of aboveground biomass invested in support tissue (stems, branches, and petioles, S). Then, from Y-plant simulations, we calculated the aboveground effective leaf area ratio (PFD absorbed per unit plant mass divided by PFD incident per unit surface area [aLAR$_e$, in square metres per kilogram). This is equivalent to aLAR multiplied by E_a and expresses how effectively the leaf area is deployed by a plant for light capture. Note that as defined here aLAR and aLAR$_e$ do not take into account belowground biomass.

The mass of the sampled plants was calculated applying the measured stem and petiole densities from other harvested plants to the volumes of each segment calculated from the Y-plant measurements. Leaf mass was calculated from the leaf area as scaled from the measured leaf lengths in Y-plant. After

TABLE 1.   Scientific name, family, growth form, leaf morphology and phyllotaxy, and relative size of the individuals sampled of the 24 species studied. M = monocotyledonous, D = dicotyledonous.

Species	Family	Growth form	Leaves	Individuals studied
Aechmea magdalenae (Andre) Andre ex Baker	Bromeliaceae (M)	Acaulescent herb (rosette)	Spirally arranged, linear	Small-medium
Alseis blackiana Hemsl.	Rubiaceae (D)	Tree	Clustered at apex of branches	Sapling (unbranched)
Calathea inocephala (O. Kuntze) Kenn. & Nic.	Marantaceae (M)	Acaulescent, erect herb	Elliptic	Medium
Calophyllum longifolium Willd.	Guttiferae (D)	Tree	Decusate, oblong	Sapling (unbranched)
Coccoloba manzanillensis Beurl.	Polygonaceae (D)	Tree	Alternate, obovate	Sapling (unbranched)
Costus pulverulentus Presl	Zingiberaceae (M)	Erect herb, spiral stem	Spirally arranged, elliptic	Medium
Cyclanthus bipartitus Poit.	Cyclanthaceae (M)	Acaulescent, erect herb	Long, bisected	Small-medium
Dichorisandra hexandra (Aubl.) Standl. in Standl. & Cald.	Commelinaceae (M)	Erect, shrub-like herb	Alternate, distichous, whorl	Medium
Dieffenbachia longispatha Engler & Krause	Araceae (M)	Caulescent, erect herb	Alternate, oblong	Medium
Faramea occidentalis (L.) A. Rich.	Rubiaceae (D)	Small tree	Opposite, elliptic	Sapling
Geonoma interrupta (R. & P.) Mart.	Palmae (M)	Small, unbranched tree	Entire, irregularly pinnate	Small
Gustavia superba (H.B.K.) Berg.	Lecythidaceae (D)	Tree	Clustered at apex of branches	Sapling (unbranched)
Heliconia vaginalis Benth.	Musaceae (M)	Caulescent, erect herb	Distichous, oblong	Medium
Hybanthus prunifolius (Schult.) Schulze	Violaceae (D)	Shrub	Alternate, elliptic	Small-medium
Monstera dilacerata C. Koch	Araceae (M)	Climbing herb	Alternate, lanceolate	Juveniles
Monstera dubia (H.B.K.) Engler & Krause	Araceae (M)	Climbing herb	Alternate, appressed to bark	Juveniles
Ossaea quinquenervia (P. Mill.) Cogn. in A. DC.	Melastomataceae (D)	Shrub	Opposite, ovate	Small-medium
Paullinia bracteosa Radlk.	Sapindaceae (D)	Liana	Pinnate, winged rachis	Small
Pharus latifolius L.	Gramineae (M)	Erect, perennial herb	Alternate, oblong	Medium
Piper cordulatum C. DC.	Piperaceae (D)	Shrub	Alternate, lanceolate	Small-medium
Piper reticulatum L.	Piperaceae (D)	Shrub	Alternate, ovate	Small-medium
Renealmia cernua (Sw.) Macbr.	Zingiberaceae (M)	Erect herb, arced stem	Distichous, elliptic	Medium
Thevetia ahouai (L.) A. DC.	Apocynaceae (D)	Small tree	Alternate, oblanceolate	Sapling (unbranched)
Xanthosoma helleborifolium (Jacq.) Schott	Araceae (M)	Erect, annual herb	Deeply dissected	Medium

summation over all plant parts, the total plant biomass, the percentage of plant mass invested in support (*S*), and aLAR were calculated.

Statistics—One-way analysis of variance (ANOVA, Tukey test; SPSS, 1996) was used to test for differences among species in their light environment, crown architecture, and light-capture efficiency. In all cases, the data met the assumptions of normality and homoscedasticity. Significant differences among species are only considered when the power of the test was equal or larger than 0.85 for $\alpha = 0.01$.

Following the procedures of path analysis as described by Mitchell (1993), we analyzed the dependence of display efficiency and daily absorbed PFD by the 72 plants studied on supporting biomass, leaf angle, relative internode length (IL/LL; internode length to leaf length ratio), specific leaf area (SLA), leaf absorptance, and global site factor. Path analysis is a more general form of multiple regression that allows consideration of complicated causal schemes and that can be used when independent variables are not truly independent or are correlated. Our path diagram was kept uncomplicated by

using only simple factors known to affect foliage display and light capture (Russell, Marshall, and Jarvis, 1989; Pearcy and Valladares, 1999; Valladares, 1999). In path analysis, the thickness of the arrow in the diagram is proportional to the path value and represents the relative strength of a given relationship. Path values are derived from standardized partial regression coefficients so path values can be quantitatively compared. While other paths may also be feasible, our intent was not to explore the relative goodness-of-fit of different models but to quantitatively compare the relative influence on light capture of the different morphological and geometric features of the crowns. In addition to direct effects, we used path analysis to calculate the strengths of the indirect influences of a given factor on another as described by Mitchell (1993) and Scheiner, Mitchell, and Callahan (2000).

RESULTS

All of the sampled plants were located in very dark understory sites with global site factors ranging from 0.4 to 6.7%

Aechmea magdalenea   *Alseis blackiana*   *Calathea inocephala*   *Calophyllum longifolium*   *Coccoloba manzanillensis*

Costus pulverulentus   *Cyclanthus bipartitus*   *Dichorisandra hexandra*   *Dieffembachia longispatha*

Faramea occidentalis   *Geonoma interrupta*   *Gustavia superba*   *Heliconia vaginalis*   *Monstera dilacerata*   *Monstera dubia*

Hybanthus prunifolium   *Ossea quinquenervia*   *Paullinia bracteosa*   *Pharus latifolius*   *Piper cordulatum*

Piper reticulatum   *Renealmia cernua*   *Thevetia ahouai*   *Xanthosoma helleborifolium*
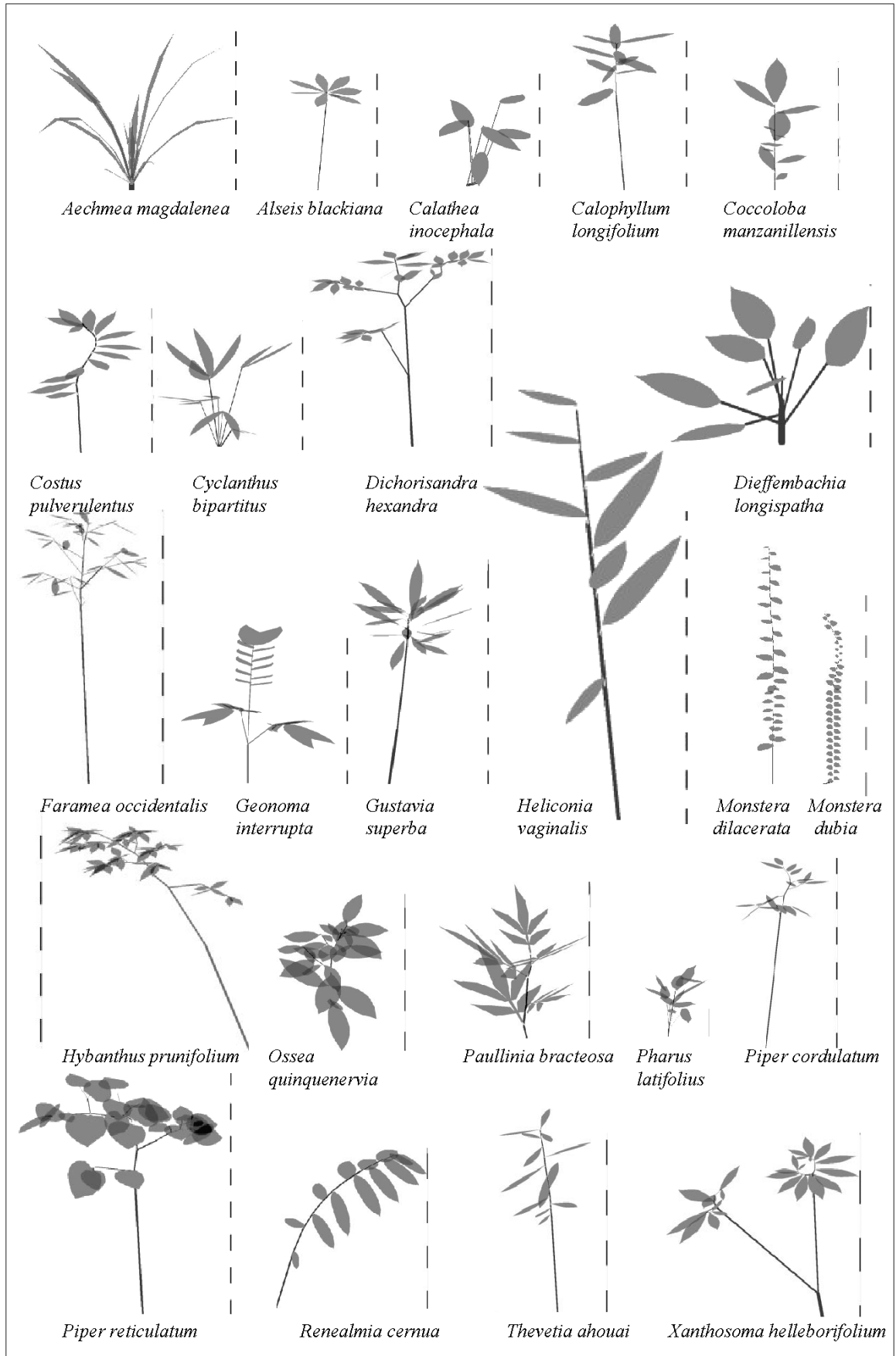
TABLE 2. Light environment of the plants studied estimated by hemispherical canopy photography. Values are the mean and the standard deviation (SD) for indirect site factor (ISF), direct site factor (DSF), global site factor (GSF), and daily photosynthetic photon flux density (PFD, calculated for a clear day of 50.6 mol·m^{-2}·d^{-1} reaching the canopy). There were no significant differences among the means for each species for either of the four variables (ANOVA, $P = 0.63$, $P = 0.53$, $P = 0.54$, $P = 0.79$, respectively).

Variable	Mean	SD
ISF (%)	2.3	2.0
DSF (%)	2.8	2.9
GSF (%)	2.8	2.7
PFD (mol·m^{-2}·d^{-1})	1.4	1.3

and daily PFD from 0.2 to 3.9 mol·m^{-2}·d^{-1} on a clear day (Table 2). Although this range indicates a substantial microsite to microsite variation in available PFD in the understory, there was no evidence that the species studied were differentially distributed with respect to this light variation (Table 2).

Species exhibited significant differences in growth form and in crown and leaf size and shape (Fig. 1, Table 1). Crowns varied in leaf number from as few as 4 large leaves per plant (*Calathea inocephala*) to about 80 much smaller leaves per plant in the largest individuals studied of the shrub species *Faramea occidentalis* and *Hybanthus prunifolius* (Table 3). Mean leaf sizes ranged from <4 cm² (*Monstera dubia*) to >600 cm² (*Dieffenbachia longispatha*) and SLA ranged from 61 cm²/g (*Aechmea magdalenea*) to 550 cm²/g (*Xanthosoma helleborifolium*). Leaf optical properties differed significantly among the species, with absorptances ranging from 0.82 for the very thin leaves of *M. dubia* to 0.91 for the thick leaves of *A. magdalenea* (Table 3).

Species also exhibited contrasting heights: from only 25 cm in *Pharus latifolius* to more than 2 m in the largest *Heliconia vaginalis* individuals (Table 4). The fraction of aboveground biomass invested in supporting structures (stems, branches, and petioles) varied widely, with some species investing <20% (*Ossea quinquenervia*, *A. magdalenea*), and others investing >80% (*Hybanthus prunifolium*, *Alseis blackiana*, *Thevetia ahouai*) of their biomass in these structures (Fig. 2). Petiole and stem densities were significantly higher in dicotyledonous than in monocotyledonous species, but for all the other morphological and allometric variables examined differences within these two main groups of plants were larger than between them, and the same was true for other natural grouping of species (e.g., growth form, phyllotactic pattern).

Despite the significant differences for all morphological variables studied (Tables 3 and 4), the species were remarkably similar in foliage display and light-capture efficiencies (Fig. 3, Table 4). This convergence in display efficiency led to no significant species differences in the absorbed PFD per day at each particular site (Table 4). Only the three climber species (*Monstera dilacerata* and *Monstera dubia*, both monocot vines, and *Paullinia bracteata*, a dicot liana) exhibited an E_a

lower than 0.5, while most species tended to converge towards E_a values of 0.7 (Fig. 3). With the exception of *M. dubia*, which has the leaves appressed to the bark of the supporting tree, all species projected their foliage towards the brightest regions of the sky, i.e., towards sky sectors within the sunpaths delineating the annual variation and at zenith angles of 45–90° (Fig. 4).

The path analysis revealed that the foliage display efficiency was significantly affected by leaf angle and SLA. It was also affected, but to a lesser extent, by IL/LL and S (Fig. 5). The IL/LL and SLA had both direct and indirect effects on E_d. Direct effects resulted from the greater spatial separation required to avoid mutual shading among leaves of high SLA, which must be arranged at long internodes and/or at the end of long petioles. Indirect effects of SLA and IL/LL also resulted since both factors affected supporting biomass, which in turn, affected E_d. Total effects of SLA on display efficiency equaled 0.45 (0.30 direct plus 0.15 indirect). Total effects of IL/LL equaled 0.32 (0.2 direct plus 0.12 indirect). Except for leaf angle, all effects on E_d were positive. The SLA had a significant, negative effect on leaf absorptance. Differences in leaf display (E_d) and leaf absorptance among the 72 plants studied did not significantly effect daily absorbed PFD. Light availability at each site (estimated by the global site factor) was the only factor having a significant, positive influence on daily absorbed PFD (Fig. 5).

DISCUSSION

The most immediate and obvious evidence for high diversity in tropical forests is the dramatic variation in appearance among different plant taxa and growth forms (Medina, 1999). In the deeply shaded forest understory on BCI, graminoid and broad-leaf herbs, vines, lianas, shrubs, palms, mature subcanopy trees, and immature canopy tree saplings can all be found in close proximity (Croat, 1978). Particularly striking is the broad variety of plant sizes and architectures found within the herbaceous monocots, which, by contrast, contribute relatively little to the understory flora in temperate forests. However, in spite of the contrasting crown architecture and leaf habit, the efficiency of foliage display and light absorption was found to be very similar among the 24 species studied. The exceptions were the climber species and, to a lesser extent, the Bromeliad rosette *Aechmea magdalenae*, which had lower efficiencies because of their steeper leaf angles. In fact, differences in PFD absorbed by individual plants were mostly determined by the PFD available at each particular site and only to a small extent by differences in crown architecture between individuals or species (Table 4, Fig. 5). In a study of six rainforest tree species Poorter and Werger (1999) reached a parallel conclusion on the relative importance of environmental vs. specific differences: differences in crown architecture between plants growing in different environments (sun-shade) were more significant than those between species within the same environment. One of the species studied here, *Alseis blackiana*, was

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Fig. 1. Lateral view of a three-dimensional crown reconstruction of one individual of each of the 24 understory species studied. Darker areas of the foliage represent leaf overlapping. Plants are only approximately at the same scale; real sizes can be estimated using the corresponding scale (each segment = 10 cm) given for each individual plant. While the portions studied of the liana (*Paullinia bracteosa*) were free-standing, the individuals of the two climbing species (*Monstera* sp.) were closely attached to the bark of the host tree. The stem of the tree is not shown here for clarity but its shade was taken into account in the calculations of light absorption by the climber.

TABLE 3. Leaf attributes of the 24 species studied: number of leaves (or folioles or functionally independent units in dissected leaves) per plant, leaf size, specific leaf area, absorptance, and transmittance. Mean and standard deviation (SD) for three plants per species are given. There were significant differences among species for the five variables examined (ANOVA, $P < 0.0001$). Letter code indicates significantly different groups of species (Tukey test, $P < 0.01$).

Species	Number of leaves per plant		Leaf size (cm^2)		Specific leaf area (cm^2/g^1)		Absorptance (%)		Transmittance (%)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Aechmea magdalenae	10.7[a,b]	3.2	177.6[b]	92.5	61.5[a]	2.3	91.2[a]	0.8	4.7[d]	0.9
Alseis blackiana	10.0[a,b]	2.0	148.3[b]	73.4	457.0[b]	16.8	84.4[d,e]	0.9	8.7[b]	0.8
Calathea inocephala	4.0[b]	1.7	347.4[a,b]	43.7	150.4[c]	0.4	87.8[b,c]	0.9	6.6	0.9
Calophyllum longifolium	13.7[a,b]	3.8	185.8[b]	37.6	109.8[h]	1.0	87.8[b,c]	0.8	6.3[c]	0.9
Coccoloba manzanillensis	9.3[a,b]	2.1	346.8[a,b]	186.9	132.4[g]	2.3	85.1[d,e]	0.8	7.9[b,c]	0.9
Costus pulverulentus	15.7[a,b]	2.5	198.3[b]	71.5	288.6[d]	1.3	85.0[d,e]	0.8	7.9[b,c]	0.9
Cyclanthus bipartitus	6.7[b]	0.6	172.9[b]	82.0	238.5[f]	48.9	87.0[c,d]	0.9	6.5[b,c]	0.8
Dichorisandra hexandra	32.0[a,b]	12.8	31.3[c]	5.5	411.0[k]	6.6	87.8[b,c]	0.9	5.8[c]	0.8
Dieffenbachia longispatha	9.7[a,b]	3.8	613.6[a]	149.5	146.1[c]	9.3	86.7[c,d]	0.8	6.7[b,c]	0.8
Faramea occidentalis	52.0[a]	20.3	21.7[c]	4.0	206.6[i]	3.1	86.5[c,d]	0.9	6.6[b,c]	1.0
Geonoma interrupta	17.7[a,b]	9.7	131.4[b]	42.5	258.1[e]	2.0	85.7[c,d]	0.9	7.2[b,c]	0.9
Gustavia superba	13.7[a,b]	5.7	92.2[b,c]	61.8	198.7[i,j]	1.5	88.9[b]	0.9	4.9[d]	0.8
Heliconia vaginalis	9.0[a,b]	1.0	570.6[a,b]	156.6	188.4[j]	26.4	85.7[c,d]	0.9	7.7[b,c]	0.9
Hybanthus prunifolia	40.7[a,b]	34.0	20.8[c]	6.5	431.7[l]	4.3	86.6[c,d]	0.8	7.5[b,c]	0.8
Monstera dilacerata	27.3[a,b]	12.4	23.3[c]	17.1	204.8[i]	3.5	89.4[b]	0.8	4.7[d]	0.9
Monstera dubia	32.7[a,b]	13.4	4.0[d]	0.5	284.3[d]	13.6	82.2[e]	0.8	11.4[a]	0.9
Ossea quinquenervia	33.0[a,b]	25.5	77.0[b,c]	42.5	275.2[m]	0.8	88.4[b,c]	1.0	6.2[c]	0.9
Paullinia bracteata	5.3[b]	1.5	150.5[b]	52.5	209.9[i]	14.3	84.6[d,e]	0.9	7.2[b,c]	0.8
Pharus latifolia	12.0[a,b]	2.0	31.5[c]	5.7	207.9[i]	3.5	86.5[c,d]	0.8	6.1[c]	0.9
Piper cordulatum	23.3[a,b]	4.0	34.8[c]	9.3	172.5[j]	4.1	87.0[c,d]	0.9	6.2[c]	0.9
Piper reticulatum	16.0[a,b]	8.9	360.2[a,b]	96.4	258.8[e]	18.8	87.0[c,d]	0.8	6.8[b,c]	0.9
Renealmia cernua	14.3[a,b]	2.3	178.0[b]	68.2	203.7[i]	1.5	89.2[b]	0.9	4.6[d]	0.8
Thevetia ahouai	13.3[a,b]	0.6	59.5[b,c]	22.3	331.4[n]	57.3	87.3[c,d]	0.9	6.4[b,c]	0.9
Xanthosoma helleborifolium	28.0[a,b]	6.9	28.0[c]	9.6	549.1[o]	4.4	83.3[d,e]	0.9	8.7[b]	0.9

described as a pioneer tree of a remarkable shade tolerance (Dalling et al., 2001). Shade tolerance of the seedlings of this tree was suspected to be achieved at least in part by an efficient light interception. However, our comparative results indicate that E_a of *A. blackiana* was not significantly larger than that of other 16 co-occurring, morphologically contrasting species (Fig. 3) and its E_d only differed from that of the climber species (Table 4).

Among the variables studied, leaf angle had the largest effect on foliage display efficiency (Fig. 5) while S, SLA, and IL/LL, which are related to allocation to leaf area, leaf spacing and support, had smaller but still significant effects. Our results indicate that plant foliage in the understory is, in general, preferentially oriented towards the brightest regions of the sky (i.e., sky sectors within the annual range of sunpaths and at 45–90° zenith angle, Fig. 4). As most light originates near the zenith in tropical forest understories this conforms to the common observation that understory plants typically have horizontally displayed leaves. The canopy gap fraction is typically greatest near the zenith because at lower elevation angles the pathlength through the canopy is greater. A trade-off to orienting most of the foliage towards a particular region of the sky is that there is a decreased efficiency of light absorption because of increased self-shading and reduced cosines of incidence for other regions of the sky. In sites with strong side-light such as gap edges, Ackerly and Bazzaz (1995) and Clearwater and Gould (1995) have demonstrated a pronounced reorientation of leaves so that the lamina are facing the brightest regions.

Efficient light capture generally requires substantial biomass allocation to support leaves in a manner that minimizes self-shading and maintains efficient angular display relative to the prevailing light direction. However, thin leaves and increased allocation to leaf vs. supporting tissues are characteristic features of shade-tolerant species (King, 1991). There must also be a continuous redeployment of resources during growth to minimize self-shading, which can become prohibitively expensive in light-limited habitats (King, 1991; Poorter and Werger, 1999). Also, constraining the dynamic function of crown expansion is the trade-off between the height growth required to take advantage of the strong vertical gradient of light availability even at the lowest levels in the understory and the lateral crown extension that is helpful in minimizing self-shading (Kohyama and Hotta, 1990). In addition, other crown functions, such as hydraulics, reproduction, and minimizing damage due to falling debris in the understory, all impact the evolution of crown form. These constraints and trade-offs may account for the values of E_a exhibiting an apparent ceiling of about 0.75 (Fig. 3). As argued by Kohyama (1987), the architectural and allometric diversity found in forest understory plants can be related to trade-offs between these different traits and functions. This is consistent with the emergence in adaptive walk models of a greater number of potential optimal crown forms as more functions are considered (Niklas, 1994).

Although there is a strong convergence in light-capture efficiency, the remaining small differences in E_a can have important consequences for light capture and carbon gain (Pearcy and Yang, 1998). Comparison of *Hybanthus prunifolium* and *Ossea quinquenervia* nicely illustrates important architectural trade-offs. The aLAR of *O. quinquenervia* was more than threefold higher than that of *H. prunifolium* (Table 4). However, *O. quinquenervia* invested relatively little in support and consequently exhibited considerable self-shading and an E_a of 0.55, which was at the lower end of the range observed. In contrast, *H. prunifolium* invested far more in support to achieve a low level of self-shading and consequently exhibited

TABLE 4. Crown allometry, architecture, and light capture for the 24 species studied: petiole and stem density, crown height, relative internode length (IL/LL, internode length to leaf length ratio), aboveground leaf area ratio (aLAR), leaf display efficiency (E_d) for sky sectors within the sunpath and 45–90° of zenith angle, and absorbed photosynthetic photon flux density (PFD) on a clear day. Each value is the mean or the standard deviation (SD) of three individuals of each species. There were significant differences (ANOVA, $P < 0.001$) among species for all variables except for the absorbed PFD ($P = 0.515$). Letter code indicates significantly different groups of species (Tukey test, $P < 0.01$). NA = not applicable.

Species	Petiole density (g/cm³)		Stem density (g/cm³)		Crown height (cm)		Crown mass (g)		Leaf angle (degrees)		Leaves per crown height (no./m)		IL/LL (%)		aLAR (m²/kg)		E_d		Absorbed PFD (mol·m⁻²·d⁻¹)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Aechmea magdalenae	NA	NA	NA	NA	75.4^{cd}	34.0	33.2^{ab}	21.9	47.7^{b}	9.3	15.5^{d}	7.1	1.2^{d}	0.3	6.1^{c}	0.0	0.49^{bc}	0.09	0.78	1.26
Alseis blackiana	0.29^{c}	0.02	0.44^{cd}	NA	117.1^{b}	41.8	16.1^{c}	6.7	15.7^{c}	1.5	9.1^{d}	2.4	45.0^{a}	14.3	8.9^{bc}	2.1	0.80^{bc}	0.06	0.41	0.59
Calathea inocephala	0.13^{e}	0.01	NA	NA	66.2^{d}	12.3	15.5^{c}	8.5	31.3^{c}	13.3	6.4^{e}	3.7	45.0^{a}	20.8	9.4^{bc}	1.7	0.76^{a}	0.11	1.63	2.24
Calophyllum longifolium	0.24^{cd}	0.00	0.60^{b}	0.00	116.6^{b}	30.7	48.4^{ab}	25.9	16.3^{c}	6.4	11.8^{d}	1.4	26.9^{bc}	3.2	5.5^{a}	0.5	0.63^{ab}	0.08	0.61	0.73
Coccoloba manzanillensis	0.36^{c}	0.00	0.42^{d}	0.00	155.3^{ab}	78.1	100.5^{ab}	74.4	18.7^{c}	6.1	8.1^{d}	6.7	49.4^{a}	27.8	4.7^{c}	3.6	0.67^{ab}	0.08	0.13	0.14
Costus pulverulentus	0.29^{c}	0.02	0.16^{h}	0.02	85.1^{bc}	34.6	27.7^{ab}	13.7	9.7^{d}	0.6	21.0^{d}	11.0	18.6^{b}	7.9	11.6^{bc}	1.4	0.82^{a}	0.05	2.01	0.34
Cyclanthus bipartitus	0.11^{e}	0.02	0.25^{f}	0.02	48.2^{d}	18.5	8.4^{d}	4.7	18.0^{c}	2.6	15.4^{d}	6.1	25.3^{bc}	8.1	14.4^{b}	0.9	0.80^{a}	0.02	1.38	1.24
Dichorisandra hexandra	0.12^{e}	0.00	0.30^{f}	0.00	77.6^{c}	26.5	9.9^{d}	6.9	19.3^{c}	5.0	40.6^{c}	3.1	17.7^{c}	1.3	14.1^{b}	7.8	0.83^{a}	0.03	1.02	0.50
Dieffenbachia longispatha	0.06^{f}	0.00	0.11^{i}	0.00	100.3^{b}	11.0	138.6^{a}	60.5	26.3^{c}	8.5	9.5^{d}	2.6	18.5^{c}	4.5	4.4^{c}	1.0	0.73^{ab}	0.04	0.29	0.25
Faramea occidentalis	0.42^{c}	0.01	0.43^{d}	0.01	101.5^{b}	41.0	21.3^{c}	11.5	18.0^{c}	6.2	53.5^{c}	13.6	16.4^{c}	4.9	5.8^{c}	1.2	0.73^{ab}	0.04	0.58	0.88
Geonoma interrupta	0.12^{e}	0.01	0.23^{g}	0.01	63.6^{d}	34.6	18.0^{c}	13.5	16.0^{c}	9.6	28.3^{c}	7.1	12.3^{c}	3.1	14.3^{b}	2.5	0.76^{a}	0.04	0.91	0.15
Gustavia superba	0.32^{c}	0.00	0.46^{c}	0.00	75.8^{c}	49.1	33.8^{ab}	45.7	19.7^{c}	3.8	20.4^{d}	8.1	17.3^{c}	5.6	6.7^{c}	2.8	0.72^{ab}	0.10	2.59	3.23
Heliconia vaginalis	0.11^{e}	0.00	0.05^{j}	0.00	175.5^{a}	37.2	48.0^{ab}	13.2	19.7^{c}	3.1	5.4^{e}	1.9	38.4^{ab}	11.8	10.7^{bc}	1.3	0.66^{ab}	0.04	0.69	0.43
Hybanthus prunifolia	0.74^{a}	0.02	0.36^{e}	0.02	78.9^{c}	16.9	14.9^{c}	11.5	18.3^{c}	4.0	47.4^{c}	31.9	17.4^{c}	9.9	6.3^{c}	3.6	0.79^{a}	0.04	0.16	0.14
Monstera dilacerata	0.10^{e}	0.02	0.16^{h}	0.02	104.4	53.7	4.7^{d}	3.7	9.3^{d}	4.2	26.8^{c}	7.0	38.9^{a}	9.0	13.3^{b}	3.4	0.33^{c}	0.12	0.14	0.10
Monstera dubia	0.10^{e}	0.00	0.29^{f}	0.00	51.3^{d}	20.6	1.0^{e}	0.5	88.0^{a}	1.0	67.3^{a}	21.5	40.4^{a}	15.5	14.4^{b}	4.5	0.11^{d}	0.03	0.07	0.07
Ossea quinquenervia	0.36^{c}	0.02	0.38^{e}	0.02	54.8^{d}	23.9	9.3^{d}	5.7	29.3^{c}	9.2	54.1^{bc}	21.2	11.4^{c}	4.6	22.8^{a}	1.4	0.54^{ab}	0.13	1.58	1.36
Paullinia bracteata	0.51^{b}	0.02	0.69^{a}	0.02	78.5^{c}	14.8	29.1^{ab}	20.1	21.7^{c}	9.6	7.0^{e}	2.4	13.1^{c}	3.9	15.5^{b}	5.1	0.78^{a}	0.10	0.55	0.70
Pharus latifolia	0.10^{e}	0.02	0.22^{g}	0.02	25.1^{e}	5.5	2.3^{e}	0.1	19.7^{c}	0.6	50.6^{e}	19.5	15.6^{c}	6.0	16.3^{b}	0.8	0.72^{ab}	0.09	1.31	0.09
Piper cordulatum	0.18^{cd}	0.02	0.36^{e}	0.02	90.2^{b}	7.7	10.6^{d}	4.4	24.7^{c}	9.7	25.9^{d}	4.4	24.6^{bc}	4.1	8.3^{bc}	4.0	0.68^{ab}	0.09	0.68	1.01
Piper reticulatum	0.31^{c}	0.01	0.40^{d}	0.01	156.8^{ab}	29.3	100.3^{ab}	53.1	30.3^{c}	8.1	10.5^{d}	6.4	53.3^{a}	24.2	6.6^{c}	3.5	0.60^{ab}	0.02	0.70	0.89
Renealmia cernua	0.11^{e}	0.00	0.28^{f}	0.00	120.7^{b}	50.7	37.3^{ab}	24.7	26.7^{c}	6.1	13.3^{d}	5.2	35.9^{ab}	17.8	7.8^{bc}	2.4	0.68^{ab}	0.09	1.36	2.12
Thevetia ahouai	0.11^{e}	0.00	0.33^{e}	0.00	98.9^{b}	36.6	17.1^{c}	16.1	16.3^{c}	6.7	14.7^{d}	4.8	41.5^{a}	16.4	6.5^{c}	3.1	0.76^{a}	0.06	0.19	0.16
Xanthosoma helleboriifolium	0.13^{e}	0.00	0.13^{h}	0.00	58.2^{d}	5.3	5.7^{d}	0.7	15.7^{c}	6.4	48.2^{c}	10.9	11.9^{c}	2.6	13.1^{b}	1.3	0.83^{a}	0.02	1.53	1.66

a = 80.6 b = 68.8 c = 57.0 d = 48.3 e = 43.8 f = 32.8
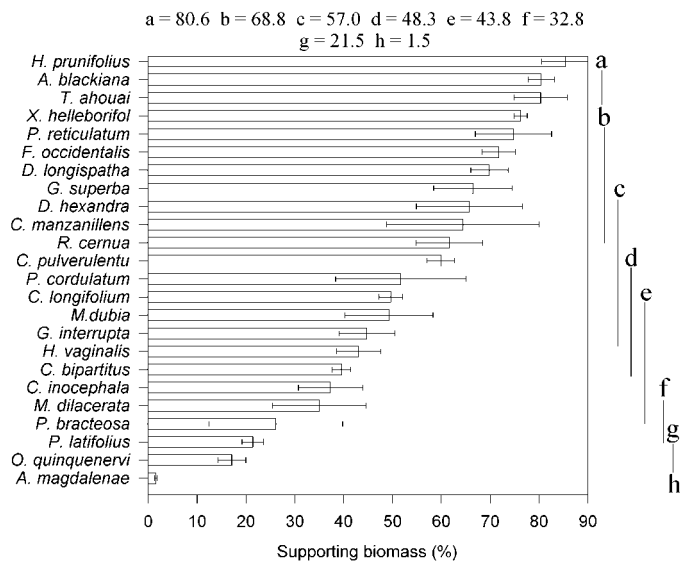g = 21.5 h = 1.5

Fig. 2. Percentage of aboveground biomass invested in support (stem, branches, petioles) for the 24 understory species studied. Bars represent the mean $\pm$ SD for three individuals. Letter code indicates significantly different groups of species (Tukey test, $P < 0.01$). The mean for each group is given at the top of the graph.

a higher E_a of 0.74. Because of its low self-shading, *H. prunifolium* absorbed approximately 30% more of the available PFD per unit leaf area than *O. quinquenervia*. But despite its much lower E_a, *O. quinquenervia* was able to maintain a higher aboveground aLAR$_e$ than *H. prunifolium* (data not shown, 12.5 vs. 5.0 m^2/kg, respectively) because of its small investment in support tissues. These differences translate into potentially higher daily carbon gain for *O. quinquenervia* as compared to *H. prunifolium* (data not shown, 2.0 vs. 0.7 mol CO$_2\cdot$m$^{-2}\cdot$d^{-1}, respectively; simulated in Y-plant using mean shade-plant photosynthetic properties from BCI, see Vallada-

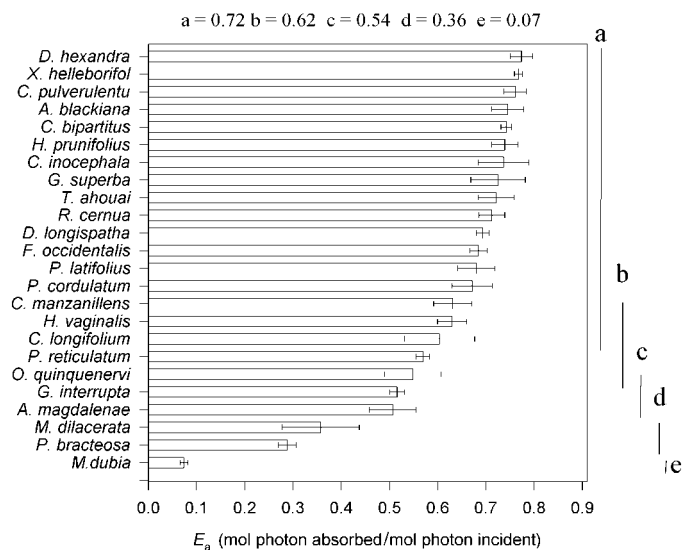a = 0.72 b = 0.62 c = 0.54 d = 0.36 e = 0.07

Fig. 3. Fraction of the photosynthetic photon flux density available at each site that was absorbed by the 24 understory species studied. Bars represent the mean $\pm$ SD for three individuals. Letter code indicates significantly different groups of species (Tukey test, $P < 0.01$). The mean for each group is given at the top of the graph.
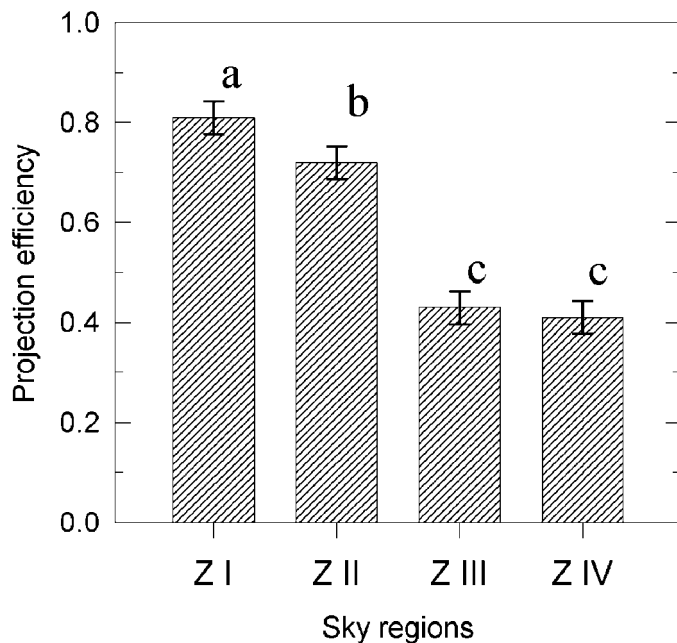

Fig. 4. Mean fraction of the total leaf area of the plant that is oriented towards four different regions of the sky (projection efficiency): zone I = sky sectors within the sunpath and of 45–90° zenith angle, zone II = sectors not within the sunpath and of 45–90° zenith angle, zone III = sectors within the sunpath and of 0–45° zenith angle, and zone IV = sectors not within the sunpath and of 0–45° zenith angle. Bars are the mean $\pm$ SD of 72 plants (three individuals of each of the 24 species studied). Letters indicate significantly different mean values (Tukey test, $P < 0.01$).
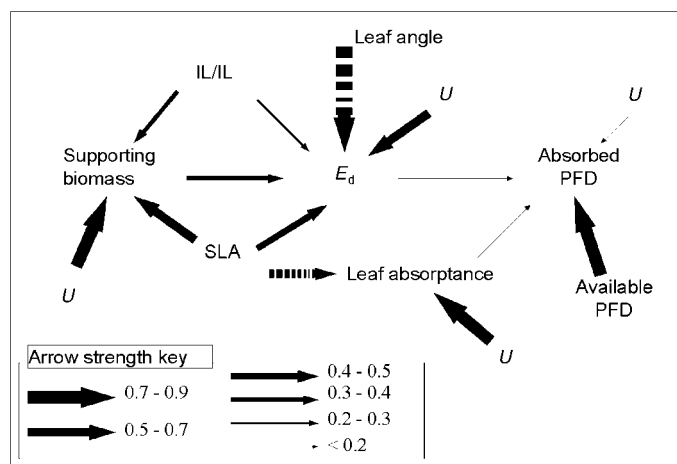

Fig. 5. Path diagram for describing the dependence of display efficiency (E_d, fraction of total leaf area effectively displayed towards the brightest sky sectors, i.e., sectors within the sunpath and from 45° to 90° zenith angle) and daily absorbed photosynthetic photon flux density (PFD) by the 72 plants studied on supporting biomass, leaf angle, relative internode length (IL/LL, internode length to leaf length ratio), specific leaf area (SLA), leaf absorptance, and global site factor (relative canopy openness of the overstory). Arrows indicate dependence (paths) and the strength of the dependence is indicated by their thickness according to the key provided. Discontinuous line denotes negative effects. All paths $\geq$ 0.2 are significant ($P < 0.01$). The residual terms are represented by U.

res, Allen, and Pearcy, 1997; Valladares et al., 2000). The arching stem of *H. prunifolium* may however give it an offsetting competitive advantage over *O. quinquenervia* since it is generally taller. Moreover, greater root costs to support water supply to the greater leaf area may offset some of the carbon gain advantage of *O. quinquenervia*.

Interestingly, the three climber species had the three lowest E_a values (Fig. 3). The E_a is significantly influenced by self-shading, and, in the case of the climbers, shading by the host tree. Climbing species are constrained in their growth direction and leaf display by the host orientation. This results in reduced whole-plant light capture in the understory on a leaf area basis. However, climbers typically invest relatively little in support per unit crown leaf area. Consequently, aLAR$_e$ values for two of these climbing species (*Monstera dilacerata* and *Paullinia bracteosa*), although low, were not ranked at the bottom as they had been for E_a (data not shown). In the case of the third climbing species (*Monstera dubia*), leaves were vertically oriented and tightly appressed to the tree in the juvenile stage. This further reduced the efficiency of light absorption on a leaf area basis, which translated in a very low aLAR$_e$.

It is also interesting to note that among the 21 nonclimber species, *Aechmea magdalenae* had, on average, the lowest canopy light absorption efficiency (Fig. 3). It has been shown that on BCI this Bromeliad species has a significantly higher photosynthetic capacity and allocates significantly more biomass to photosynthetic tissues than comparable co-occurring understory plants (Skillman, Garcia, and Winter, 1999). Paradoxically, despite having a high potential for plant carbon gain based upon both leaf physiology and biomass allocation, Skillman, Garcia, and Winter (1999) found that *Aechmea magdalenae* has a lower aboveground relative growth rate than comparable co-occurring understory plants on BCI. Our findings that the vertically oriented leaves of this Bromeliad rosette result in E_a values significantly lower than most of the other understory species in this survey seems to resolve this paradox. Indeed, the high photosynthetic capacity and the high biomass allocation to leaf tissue observed in *Aechmea magdalenae* may be viewed as means of compensating for the characteristic vertical leaf orientation that is suboptimal for light capture in the shade.

In most plants, leaf primordia at the apex originate as far as possible from each other (Hofmeister's rule; Jean, 1984; Kirchoff and Rutishauser, 1990), which in plants with a helical phyllotaxy yields a divergence angle between consecutive leaves that is close to the "golden angle" of 137.5°. For an erect shoot, such an angle minimizes leaf overlap in the vertical projection (Bell, 1993; Valladares, 1999), leading to its interpretation as a mechanism for increasing leaf display efficiency (Adler, Barabe, and Jean, 1997). Some unusual patterns, such as the monostichous phyllotaxis of *Costus* (see Fig. 2) with low divergence angles (20–30°), are by themselves difficult to interpret even after many years of study (Kirchoff and Rutishauser, 1990; and references therein) because significant leaf overlap occurs. However, when coupled with a helical twining of the stem, such as is observed in *Costus pulverulentus* (yielding a spiromonostichous phyllotaxis; Bell, 1993), the leaves are displaced laterally, significantly increasing E_a. The Y-plant simulations, with either a helical stem or a straight vertical stem, demonstrated that the latter gave 20% lower values of E_a, demonstrating the importance of coupling the monostichous phyllotaxy with a helical stem in this instance.

Distichy, characteristically orthodistichy, which is the typical phyllotaxy of monocotyledons (Wilder, 1992; and references therein), causes there to be two vertical rows of leaves and therefore the potential for much mutual shading in understory environments. For the monocot species studied here, compensation for the potentially inefficient leaf display was achieved by either an arced stem (*Renealmia cernua*; Fig. 1), by plagiotropic shoots (*Dichorisandra hexandra*), long petioles (*Heliconia vaginalis*), or by sparse canopies (*Cyclanthus bipartitus*). Studies of simulated, simple shoot architectures have demonstrated that other architectural characters can compensate for potentially inefficient phyllotaxes (Niklas, 1988; Sekimura, 1995). Our study demonstrates that compensation for potentially inefficient phyllotaxes also can be observed among real plants in a tropical forest understory.

Leaves are the ultimate sink for light, and their optical properties can significantly affect whole plant light capture. Shade plants usually have higher chlorophyll contents per unit leaf mass basis but also thinner leaves with high specific leaf areas as compared to sun plants (e.g., Bongers and Popma, 1990). As observed in previous studies (see Poorter et al. [2000]; and references therein), SLA had a negative effect on leaf absorptance. However, leaf absorptance did not significantly affect the total PFD absorbed by the whole plant due to the narrow range of leaf absorptances exhibited by the different species studied here (82–92%). Consequently, available PFD at each site was the only variable leading to significant differences in light harvesting among the plants studied.

Terrestrial plants are developmentally versatile because as sedentary light capturers they must accommodate the diurnal, seasonal, and long-term changes in light environments (Niklas, 1988). Tropical plants exhibit a remarkable phenotypic plasticity, and a large effort has gone into the investigation of their response to light gradients (Kitajima, 1996; Agyeman, Swaine, and Thompson, 1999; Valladares, 2000; Valladares et al., 2000). Most of these studies address leaf-level physiology (e.g., Evans, von Caemmerer, and Adams, 1988; Valladares, Allen, and Pearcy, 1997; see also Lambers, Chapin, and Pons, 1998) but resource allocation to maintaining an efficient leaf display that minimizes leaf overlap is at least as critical if less studied. Our results emphasize the compensatory role of different leaf and crown characters in determining the efficiency of light capture and indicate that the variety of shoot morphologies capable of capturing similar fluxes of solar radiation is larger than initially thought, extending over species with very different phyllotactic patterns and contrasting crown architectures and leaf sizes.

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