ECOPHYSIOLOGY

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A functional analysis of the crown architecture of tropical forest *Psychotria* species: do species vary in light capture efficiency and consequently in carbon gain and growth?

Abstract The crown architectures of 11 *Psychotria* species native to Barro Colorado Island, Panama were reconstructed from field measurements of leaf and branch geometry with the three-dimensional simulation model Y-plant. The objective was to assess the role of species differences in architecture in light capture and carbon gain in their natural understory environment. When species were grouped according to their putative light environment preference, the shade tolerant species were found to have a small but significantly higher efficiency of light capture for both diffuse and direct light as compared to the light demanding species. Within each grouping, however, there were few significant differences in light capture efficiency among species. The lower efficiencies of light demanding species was due to slightly higher self-shading and slightly lower angular efficiencies. Simulations of whole plant assimilation showed that light demanding species had greater daily assimilation in both direct and diffuse light due to the significantly greater light availability in the sites where light demanding species were found, as compared to those where shade tolerant species occurred. Among light demanding species, the above ground relative growth rate measured over a 1-year period by applying allometric equations for mass versus linear dimensions, was positively correlated with diffuse PFD and with mean daily assimilation estimated from Y-plant. For the shade tolerant plants, there was no significant correlation between RGR and mean daily assimilation or with any measure of light availability, probably because they occurred over a much narrower range of light environments. Overall, the results reveal a strong convergence in light capture efficiencies among the *Psychotria* species at lower values than previously observed in understory plants using similar approaches. Constraints imposed by other crown functions such as hydraulics and biomechanical support may place upper limits on light capture efficiency.

Abbreviations E_a: Efficiency of light absorption (dimensionless) · $E_a$dir: Efficiency of direct light absorption (dimensionless) · $E_a$dif: Efficiency of diffuse light absorption (dimensionless) · D_E: Display efficiency (dimensionless) · P_E: Projection efficiency (dimensionless) · *CosI*: Mean cosine of incidence (dimensionless) · *aLAR$_e$*: Effective leaf area ratio ($m^2\,g^{-1}$) · A_{tot}: Daily assimilation (mmol m^{-2} day^{-1}) · A_{dir}: Daily assimilation in direct PFD (mmol m^{-2} day^{-1}) · A_{dif}: Daily assimilation in diffuse PFD (mmol m^{-2} day^{-1})

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Introduction

The capture of light by a plant depends on the amount and spatial distribution of radiation and the architectural arrangement of leaves within the plant's crown. The architectural arrangement determines the leaf orientations relative to the sources of light and the degree of self-shading resulting from leaf overlap in a plane orthogonal to the light source. The role of leaf orientation in light

Table 1 Sub-genus status, leaf longevity, leaf size, crown characteristics and habitat of the *Psychotria* species utilized in this study

Species	Species code	Sub-genus[a]	Median leaf Longevity[b], days	Leaf size[c], cm^2	Branching frequency	Bifurcation	Habitat
Light demanding							
P. brachiata	PBR	H	391	29	infrequent	asymmetric	permanently moist sites, stream banks
P. capitata	PCA	H	1200	53	moderately frequent	asymmetric, often produces two lateral axes along with a more robust vertical axis at a node	dry ridge tops, wind throw areas
P. micrantha	PMI	P	547	164	moderately frequent	asymmetric	large gaps, forest edges, moist to wet forest
P. pubescens	PPU	H	234	55	infrequent	asymmetric	gaps, forest edges, dry to moist forest
Shade tolerant							
P. acuminata	PAC	H	754	36	frequent	symmetric vertical and lateral axis	widespread in shaded dry forest
P. chagrensis	PCH	P	665	5	frequent	highly asymmetric, short orthotropic leaf-bearing shoots on long plagiotropic branches	restricted to shaded moist sites
P. deflexa	PDE	H	930	27	frequent	asymmetric vertical axis symmetric lateral axis	shaded dry slopes, ridges
P. hoffmannseggiana	PHF	H	383	10	frequent	asymmetric vertical axis, symmetric lateral axis	widespread in shaded moist to dry forest
P. horizontalis	PHO	P	791	28	frequent	asymmetric lateral and vertical axes	widespread, from dry to wet forest
P. limonensis	PLI	P	811	153	infrequent	symmetric	most abundant in moist to wet sites
P. marginata	PMA	P	714	37	moderately frequent	asymmetric vertical, asymmetric lateral axes	widespread in shaded moist to dry forest

[a] P: subgenus *Psychotria*; H: subgenus *Heteropsychotria*

[b] S.J. Wright: unpublished results from monthly census of marked leaves on 3–12 individuals of each species over a 5-year period. Median longevities are based only on leaves that were born and died within this period

[c] Mean leaf area of fully expanded leaves (n=35–50)

interception by individual leaves and plant canopies has been well documented (Ehleringer and Forseth 1980; Hebert 1996; Muraoka et al. 1998; Niinemets 1998) but less attention, especially at a quantitative level, has been given to the self shading within canopies. In understory environments where light is strongly limiting, minimizing self-shading should be important for maximizing carbon gain. However, Sterck et al. (2003) found no relationship between simple indices of self shading based on crown dimensions and leaf numbers and growth or survival of saplings of two tree species in the understory. They suggested that other constraints on crown shape overrode the expected relationships. Minimizing self-shading increases the mean light level per unit surface area and therefore increases the mean photosynthetic carbon gain return of the leaves. Except in the unusual case of some forest herbs producing at most a few leaves, or very young seedlings, essentially all plant crowns exhibit substantial self-shading. Minimizing self-shading is costly since it requires investment in stems and petioles to minimize leaf overlap. Studies have emphasized the role of monolayer versus multilayer canopies (Field 1988; Horn 1971), plagiotropic branching versus vertical extension (Kohyama 1991; Kohyama and Hotta 1990), branch bifurcation ratios (Whitney 1976; Steingraeber et al. 1979), shoot phyllotaxy (Niklas 1988; Valladares 1999), branching angles (Honda and Fisher 1978; Hatta et al. 1999), petiole length (Pearcy and Yang 1998; Yamada et al. 2000; Galvez and Pearcy 2004), and leaf shape (Givnish 1978; Niklas 1989; Takenaka 1994) in minimizing self-shading. Studies with simple 3-dimensional models (Niklas 1988; Takenaka 1994) show that apparently inefficient characters can be compensated for by other characters. Thus, quite different character combinations can result in plant crowns with similar efficiencies of light capture. These compensations also mean that the role of any one character can only be studied in the context of the other characters. Most early quantitative studies treated crowns as two dimensional arrays of leaves with light being received only from above, but the development of three-dimensional simulation models (Takenaka 1994; Pearcy and Yang 1996) has allowed for a more realistic evaluation of light capture by plant crowns in complex light environments.

Valladares et al. (2002) examined the relationships between leaf and crown characteristics and light capture efficiency for 24 understory species from a tropical forest on Barro Colorado Island, Panama using the three-dimensional crown architecture model, Y-plant (Pearcy and Yang 1996). The species studied represented a wide range of taxa, life forms and crown architectures and the objective of the study was to determine the functional correlates between light capture efficiency and leaf and crown characteristics. A strong convergence in light capture efficiency was found, indicating that constraints on light capture could be offset by other compensatory adjustments in crown architecture. Although, strong convergence was evident, the remaining variation in light capture efficiency could still be significant since

increasing light capture efficiency in the understory should lead to increased whole plant photosynthesis.

In the study reported here, we examined the variation in crown architecture of 11 shrub species in a single genus, *Psychotria,* occurring on Barro Colorado Island using Y-plant to assess the consequences for light capture efficiency and photosynthetic carbon gain. This genus was chosen because the Barro Colorado Island species exhibit a diversity of architectures as well as distinct habitat preferences in terms of shade tolerant versus light demanding species. *Psychotria* consists of 1,700 mostly shrubby or tree species worldwide with 21 species occurring on Barro Colorado Island (Croat 1978). Although the species on BCI range from 0.25 m tall sub-shrubs to 8–12 m tall understory trees, most are 1–2.5 m tall shrubs. The majority are understory species showing no discernable dependence on tree fall gaps for survival to reproduction, but some are found principally in gaps or along forest edges. We included light demanding gap species and shade-tolerant understory species in the study to determine if there were differences in light capture efficiency among plants specializing on different parts of the light availability gradient. We also used Y-plant simulations from sequential measurements 1 year apart to estimate relative growth rates and compared these relative growth rates to estimates of light capture.

Materials and methods

We selected 11 *Psychotria* species (Table 1) representing the full range of crown architectures, leaf longevities and habitat specialization of the species occurring on Barro Colorado Island for characterization of crown architecture. The species selected exhibited a 5-fold range of leaf longevities, a 30-fold range of leaf sizes and contrasting branching patterns, giving them divergent architectures and appearances (Figs. 1, 2). Hamilton (1985) has previously shown that the branching characteristics are taxonomically diagnostic. The species also contrast in habitat preferences, ranging from those found principally in deeply shaded moist understories to tree fall gap or forest edge-dependent species occurring on seasonally dry ridges and slopes. For each species, detailed geometric measurements required for input for Y-plant were made on 3–10 individuals for a total of 45 individual plants. These plants will be referred to as the Y-plant plants. The criteria for selection of the plants were that they were apparently healthy with minimal herbivore or other apparent mechanical damage such as lost branches. We attempted to include for each species individuals of different sizes so that any size dependence of architectural properties could be examined. For some species, the largest individuals were excluded because they were impractical to measure in terms of height or number of leaves. Thus the largest individuals measured were <2 m tall and had 200–500 leaves whereas the smallest were approximately 0.3 m tall and had 6–10 leaves.

Measurements of crown geometry

Details of the measurement protocols required for the input to Y-plant and the equations of the basic simulation model are given in Pearcy and Yang (1996). Briefly, measurements were based around a "node" as the fundamental unit that could have attached to it a stem segment, a branch segment and/or a leaf supported by a petiole. A node was connected to a "mother node" by a stem or branch segment of a given length, diameter angle, and azimuth originating
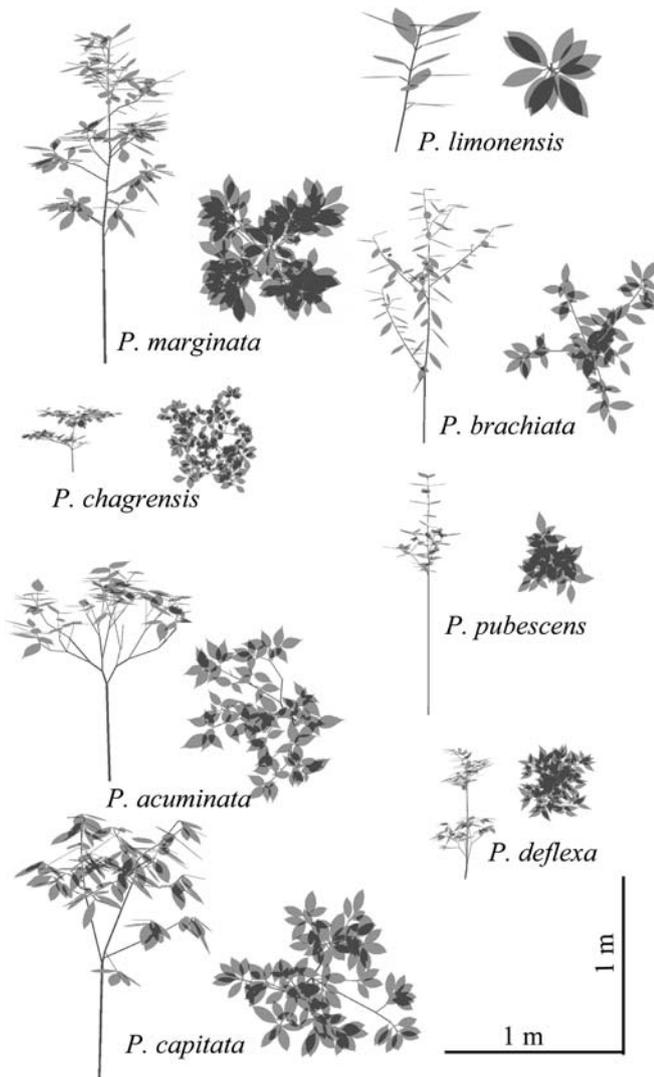
Fig. 1 Images created by Y-plant of representative individuals of eight *Psychotria* species utilized in this study. Shown are an image from the side and from directly above the plant. The dark areas in each image represent self-shading from this viewpoint
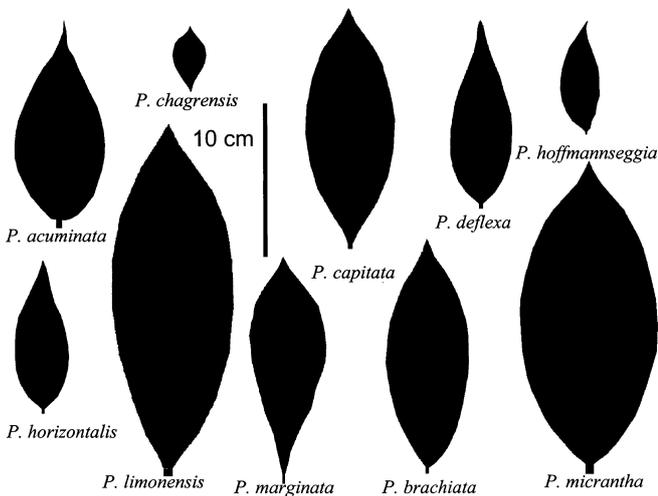

Fig. 2 The sizes and shapes of the leaves of the *Psychotria* species in this study. The leaf tips face up

from the mother node. In this way, the entire structure of the plant could be mapped and then reconstructed in 3-dimensional computer space. The opposite leaves of *Psychotria* were simulated as occurring at two nodes in this chain separated by a 0.1-mm length internode. Angles and azimuths to the nearest degree, and lengths to the nearest 1 mm of each of these parts, as determined with a compass, an angle finder and a ruler, respectively, were used to specify their positions in space. Diameters of the stem, branch segments and the petiole segments were measured with calipers to the nearest 0.1 mm to scale the simulated diameters appropriately. Leaves were simulated from the coordinates of their outlines, which were then scaled to size according to the leaf length. Their position in space was defined by the angle, azimuth and length of the petiole and the angle and azimuth of the leaf surface normal, and the azimuth of the midrib (see Pearcy and Yang 1996). Measurements were made in February to April 1995, and then repeated on the same plants 1 year later in order to characterize the changes in crown structure. Leaves were marked on the adaxial surface with a waterproof marker pen in 1995 so that it was possible in 1996 to determine the new growth and the leaves and branches that were lost. Hemispherical photographs were taken over each plant in 1995 and again in 1996. The plants were periodically revisited during 1995–1996 to remark any leaves on which the labels were fading. This was an infrequent problem but the remarking helped to ensure that individual leaves could be followed. Visual comparisons between adjacent marked and unmarked plants revealed no discernable effect of marking on leaf longevity or subsequent growth.

Leaf gas exchange

Leaf photosynthetic parameters required for input to Y-plant were determined from the photosynthetic response to PFD as measured in the field with a CIRAS−1 portable photosynthesis system (PP-systems, Hitchin, Herts, UK). Light response curves were measured by first increasing the PFD to saturating values and waiting for full induction before decreasing the PFD in steps to darkness and recording after attainment of steady rates the resulting net CO_2 assimilation rate. A least squares fit to the equation:

$$A(I) = R_{d}$$
$$+ \frac{\alpha I + (A_{\max} + R_{d}) - \sqrt{(\alpha I + (A_{\max} + R_{d}))^{2} - 4\theta\alpha I(A_{\max} + R_{d})}}{2\theta}$$
(1)

(Thornley 1976) where R_d is the day respiration rate, I is the PFD, A_{max} is the photosynthetic capacity, α is the quantum yield, and θ is the curvature factor was used to determine the necessary parameter values required for Y-plant. The mean values of A_{max}, θ and α from three light response curves on different plants were used as inputs to Y-plant. Dark respiration rates were determined in a leaf disk O_2 electrode (Hansatech, Norfolk, UK). Day respiration rates were estimated as being 40% of the dark respiration rates to account for the light inhibition of mitochondrial respiration (Atkin et al. 1998). Leaf absorptances and reflectances from 400 to 700 nm were measured with a Li−1800 integrating sphere spectral radiometer (Li-Cor, Lincoln, Neb., USA). Light compensation points (LCP) were determined by linear regression of A versus I over the lower, essentially linear part of the light response curve. Leaf nitrogen (N) contents were determined with a CHN analyzer in the DANR Analytical Laboratory at the University of California, Davis.

Estimation of plant light environments via hemispherical photography

Hemispherical photography (Pearcy 1989; Rich 1990) was used for characterizing the light environment of each plant. Comparisons between direct quantum sensor readings in the understory and estimates of PFD from hemispherical photography have been shown to be highly correlated with direct quantum sensor measurements (1:1 slope) in the understory on Barro Colorado Island and have been shown to be well suited for comparisons among a relatively large number of sites (Engelbrecht and Herz 2001). We took photos directly above each plant with a Nikon FM 35 mm camera equipped with an 8 mm focal length Nikkor fisheye lens. The camera was carefully leveled with a custom-made gimbal mount supported by a tripod and oriented so that the top of the image faced north. LED lamps mounted on the gimbal platform so that they were just visible at the image edge were used to mark the horizon in the image. Tri-X film developed at normal speed in Kodak Microdol developer was used. The red filter internally mounted in the lens was used to increase the contrast between sky and foliage. Photos were taken on either overcast days or early or late in the day to avoid problems with the image of the sun washing out part of the canopy image. The negatives were then digitized into bitmap images using a Nikon LS −1000 35 mm slide scanner.

Processing of the resulting images with the analysis program HemiView 2.1 (Delta-T Instruments, Cambridge, UK) yielded the required inputs for Y-plant. These inputs are gap fractions in each of 160 sky sectors (8 azimuth classes and 20 elevation angle classes), and for a specific day, the time series (1 min interval) of openness along the solar track. The gap fractions for the sky sectors were used to compute the diffuse PFD incident from all directions using a standard overcast sky algorithm (Moon and Spencer 1942). Values of openness along the solar track ranged from 1 when the solar disc was completely within a canopy gap to 0 when the solar disc was completely behind canopy in the image. Intermediate values, which simulated penumbral effects, corresponded to fractional exposure of the solar disc. The values of openness along the solar track were multiplied by the direct solar radiation (clear sky conditions) at the top of the canopy simulated with standard equations for solar azimuth and angle and airmass (Gates 1980) for the time, date and latitude to give the direct solar radiation incident on the Y-plant crown. Time series were determined for Julian days 1, 60, 120 and 180. Since these solar tracks also match a set occurring from July through December, they gave a good coverage of the entire year.

Simulation of whole-plant light capture and daily assimilation

Reconstruction of the 3-dimensional crown architecture in Y-plant was used to simulate light absorption and assimilation. We have shown in a previous study that there is good agreement between the frequency distribution of PFD values incident on the leaf surfaces as measured with leaf-mounted sensors and the simulations from Y-plant (Valladares and Pearcy 1998). Simulations were at 30-min intervals during periods of diffuse light, and more frequently, depending on sunfleck duration, when sunflecks were incident on the crown. For each daily simulation, the simulated absorbed PFDs and assimilation rates were summed over all leaves and integrated over the day to yield whole-plant daily totals of absorbed direct and diffuse PFD and assimilation. Quantity and units for each measure of light capture efficiency and assimilation derived from Y-plant simulations are given above. The efficiency of light absorption, E_a, defined as the PFD absorbed by the crown divided by the PFD incident on a horizontal surface of the same total area (Pearcy and Yang 1996), was calculated at each simulation interval during the day. Since the sky distribution of diffuse PFD did not change over the day, E_a during periods when only diffuse radiation was received (when the direct beam was blocked) was constant. This value was taken as the E_a for diffuse radiation ($E_a dif$). The E_a for direct PFD ($E_a dir$) depended on the solar elevation angle and azimuth and therefore changed over the day. For comparative purposes, we selected the E_a during sunflecks occurring in the middle of the day (1000–1400 hours) as a measure of the $E_a dir$. Since most sunflecks occur during the middle of the day E_a at this time provides a reasonable measure of the efficiency of capture of direct PFD. The E_a's for both direct and diffuse radiation depend on both the display of the leaves and the angular distribution of PFD as determined by the distribution of canopy gaps (and in the case of direct PFD, the solar elevation angle and azimuth at the time). Thus, these measures include the effects of any plastic responses to the local light environment such as leaf reorientation or patterns of branch development. E_a also includes the effects of leaf absorptance for photosynthetically active radiation that potentially can differ between species.

Three other measures related to the display of leaf area were also determined to further assess light capture. The projection efficiency (P_E) is the leaf area of a plant projected in a particular direction divided by the actual leaf area on the plant. For a given direction, the P_E is equal to the average cosine of incidence, ranging from one if the leaf surfaces are all perpendicular to the beam direction to zero if the leaf surfaces are all parallel to the beam direction. P_E is therefore a measure of the effect of leaf angle distribution on potential light capture. The display efficiency (D_E) is the leaf area displayed in a particular direction relative to the actual leaf area on the plant. It is therefore equal to P_E minus the fraction of leaf area that is overlapped by other leaves in the plane perpendicular to the beam. Thus, D_E includes both the effect of leaf angles and the spatial distribution of leaves that influences their self-shading. The fraction of leaf area that is self-shaded is $P_E - D_E$. For comparisons between species, we determined the average P_E, D_E and fraction self shaded for the sky sectors with a zenith angle <45° since most PFD in forest understories and small gaps originates from overhead. In contrast to E_a, the P_E, D_E and fraction self-shaded are measures of light capture efficiency that depend only on the architectural distribution of leaf area in the crown and not on the distribution of canopy gaps per se.

Non destructive estimation of plant mass

The above ground biomass and leaf area of each plant was estimated by harvesting stems and branches of other nearby individuals of the same species. After separation into leaves, petioles and stems the stems were cut into segments and 40–80 segments covering the range of diameters were weighed for development of regression equations of dry mass per millimeter length versus diameter. The resulting equations were then used with the stem diameter and segment length information from the non-destructive measurements obtained for the Y-plant simulations to estimate the stem mass of the Y-plant plants. The same approach was used to estimate the mass of petioles. In Y-plant, leaf areas are predicted from a shape factor that is equal to the proportion of the area of a square with sides equal to the leaf length that is actually filled by the leaf outline. Since within a given *Psychotria* species the shape of the leaves was similar for all leaf sizes, the areas could be predicted from their lengths. We then used the specific leaf area (SLA, cm^2 g^{-1}) determined from the harvested leaves to predict the leaf mass of the Y-plant plants. Areas of the fresh leaves were determined with a Li-Cor 3100 leaf area meter while masses were determined by weighing after oven drying for 24 h at 60°C. For 5 of the 11 species SLA was found to depend on leaf size. For these species, we used the regression of 1/SLA versus leaf area to predict leaf mass of the Y-plant plants. Whole-plant above ground biomass and the proportional allocation to stems leaves and petioles for each of the Y-plant plants were then determined from these masses. Masses were calculated for the Y-plant plants in 1995 and 1996 in order to determine the growth, leaf area production and leaf area loss for each plant over this period.

We determined the efficiency of light capture per unit of above-ground biomass invested ($aLAR_e$) as the PFD absorbed per unit of plant mass (mol g^{-1} unit time^{-1}) divided by the PFD incident on a horizontal surface of equivalent area to the total leaf area (mol m^{-2} unit time^{-1}). In practice this is equivalent to $aLAR$ times E_a where $aLAR$ is the aboveground leaf area ratio of the plant. Since E_a is

dimensionless, $aLAR_e$ has the same units of $m^2 g^{-1}$ as LAR and expresses how the effective LAR is reduced because of inefficiencies of display of the leaf area.

Statistical analysis

One-way analysis of variance (ANOVA) was used to test for differences among species, and by grouping species, differences among habitat preference classes (light demanding versus shade tolerant). Relationships between relative growth rate and measures of light availability and photosynthesis were tested with linear regression. All tests were carried out using StatView 5.0 (SAS Institute, Cary, N.C.).

Results

Leaf physiological characteristics

We found significant differences in photosynthetic capacity (A_{max}) and dark respiration (R_d) that correspond generally to the light demanding versus shade tolerant habitat axis (Table 2). With one exception in each category, light demanding species had higher A_{max} and R_d values than the shade tolerant species. Within the light demanding species, *P. capitata* had both low A_{max} and low R_d values that were not significantly different from those of the shade tolerant species. Conversely, among the shade tolerant species *P. limonensis* had higher A_{max} and higher R_d than the other shade tolerant species. *P. capitata* had the longest leaf lifespan of any of the species measured while *P. limonensis* had the shortest leaf lifespan of the shade tolerant species. However, across all species, leaf lifespan was not a significant predictor of A_{max}. There were no significant differences among species in leaf absorptance as well as no consistent pattern to the differences in SLA among species.

Efficiency of light capture

When species were grouped according to their putative light environment preference (light demanding versus shade tolerant), significant differences were found between the groups in the efficiency of diffuse light capture (Table 3). Shade tolerant species had higher P_E's ($F =4.11$, $P=0.048$), D_E's ($F=5.59$, $P=0.02$) and lower fractions self shaded ($F=4.20$, $P=0.046$) than the light demanding species. Similarly, the efficiency of diffuse light absorption ($E_a dif$; $F=16.7$, $P =0.0002$) and the effective leaf area ratio ($aLAR_e$: $F=7.95$, $P=0.007$) were significantly higher for the shade tolerant group as compared to the light demanding group. We used ANOVA for the separate groups to test whether there were species differences within each group. No significant differences were found for either D_E (for light demanding $F=0.594$, $P=0.63$, for shade tolerant: $F=0.636$, $P=0.70$) or P_E (for light demanding: $F=3.29$, $P=0.072$, for shade tolerant: $F=1.06$, $P=0.41$). For the fraction of leaf area that is self-shaded, no significant differences were found between species in the shade tolerant grouping ($F=0.595$, $P=0.73$), but a significant difference was found between species in the light demanding group ($F=4.55$ $P=0.003$). This was driven largely by a significant difference between *P. micrantha* and *P. pubescens* with the other two species not being significantly different from either *P. micrantha* or *P. pubescens*. *P. pubescens* had a significantly lower $E_a dif$ than the other three species within the light demanding group whereas no significant species differences were evident in the shade tolerant group. Conversely, no significant species differences were found in $aLAR_e$ within the light demanding group, but within the shade tolerant group *P. marginata* had a significantly lower $aLAR_e$ than *P. acuminata* and *P. chagrensis* but did not differ significantly from the other species. The narrow, mostly unbranched crown of *P. pubescens* results in more self-shading in the vertical direction as compared to the other

Table 2 Leaf gas exchange properties, leaf absorptance, specific leaf area of the *Psychotria* species utilized in this study. (Mean ±1 SE, $n=3$, ($n=5$ for SLA) values sharing the same superscript letter are not significantly different at $P=0.05$ level as determined with Tukey-Kramer multiple comparisons test. No significant differences among species at the $P=0.05$ level were found via ANOVA for those columns with no superscripts)

Species	A_{max} (µmol $m^{-2}s^{-1}$)	R_d (µmol $m^{-2}s^{-1}$)	LCP (µmol $m^{-2} s^{-1}$)	Leaf absorptance	SLA ($cm^2 g^{-1}$)	Leaf N (g m^{-2})
Light demanding						
P. brachiata	6.55±1.07 [c*]	−0.33	10	0.901±0.012	280±4 [b]	0.92±0.01
P. capitata	2.62±0.33 [a,c]	−0.26	6	0.907±0.013	217±3 [c]	0.83±0.05
P. micrantha	9.50±0.57 [c]	−0.68	20	0.902± 0.028	165±4 [c]	1.31±0.07
P. pubescens	9.50±1.00 [c]	−0.43	19	0.909± 0.004	457±17 [e]	1.59±0.08
Shade tolerant						
P. acuminata	2.85±0.33 [a]	−0.22	9	0.900±0.001	372±12 [a]	0.77±0.01
P. chagrensis	3.80±0.62 [a]	−0.17	6	0.901±0.010	263±7 [bcd]	0.74±0.01
P. deflexa	3.55±0.51 [a]	−0.28	4	0.914±0.013	242±11 [bcd]	1.08±0.04
P. hoffmannseggiana	3.31±0.30 [a]	−0.24	7	0.889±0.018	369±6 [a]	0.82±0.02
P. horizontalis	3.85±0.45 [a]	−0.29	12	0.886±0.024	359±23 [a]	0.78±0.09
P. limonensis	5.10±0.41 [b]	−0.46	10	0.870±0.031	254±11 [bcd]	0.93±0.03
P. marginata	3.82±0.45 [a]	−0.31	13	0.870±0.028	194±8 [c]	0.95±0.02

Table 3 Measures of light capture efficiency for diffuse irradiance of the *Psychotria* species utilized in this study. The values in the table are the mean ± 1 SE. Within a column, values sharing the same superscript letter are not significanlty different at the *P*=0.05 level. See Table 2 for details

Species	n	D_E	P_E	Fraction self-shaded	$E_a dif$	aLARe (m^2 g^{-1})
Light demanding						
P. brachiata	3	0.537±0.024	0.813±0.031	0.276±0.021c,d	0.575± 0.022d	45.1±6.0
P. capitata	3	0.488±0.033	0.753±0.016	0.264±0.051c,d	0.552±0.032d	35.9±8.0
P. micrantha	4	0.538±0.028	0.713±0.026	0.175±0.032c	0.563± 0.028d	39.1±4.5
P. pubescens	5	0.474±0.076	0.797±0.025	0.323±0.094d	0.437± 0.135c	31.9±6.5
Mean		0.512±0.020 [a]	0.765±0.016 [a]	0.253±0.021 [a]	0.516±0.019 [a]	36.3±3.0 [a]
Shade tolerant						
P. acuminata	9	0.597±0.025	0.801±0.014	0.204±0.021	0.619± 0.018	73.1±10.8 [d]
P. chagrensis	3	0.570±0.034	0.804±0.006	0.234±0.034	0.644±0.028	89.2±8.3 [d]
P. deflexa	4	0.507±0.008	0.779±0.023	0.272±0.028	0.554±0.016	66.5±15.8 [c,d]
P. hoffmannseggiana	3	0.542±0.029	0.826±0.021	0.283±0.017	0.597±0.028	64.2±5.6 [c,d]
P. horizontalis	3	0.572±0.022	0.811±0.005	0.239±0.027	0.588±0.021	50.2±6.2 [c,d]
P. limonensis	3	0.595±0.026	0.804±0.029	0.209±0.015	0.612±0.025	48.0±8.7 [c,d]
P. marginata	9	0.584±0.043	0.781±0.020	0.196±0.034	0.610±0.041	27.4±3.4 [c]
Mean		0.574±0.014 [b]	0.797±0.008 [b]	0.223±0.012 [b]	0.609±0.012 [b]	57.3±4.9 [b]

Fig. 3 Dependence of E_a for diffuse light and $aLAR_e$ on plant mass
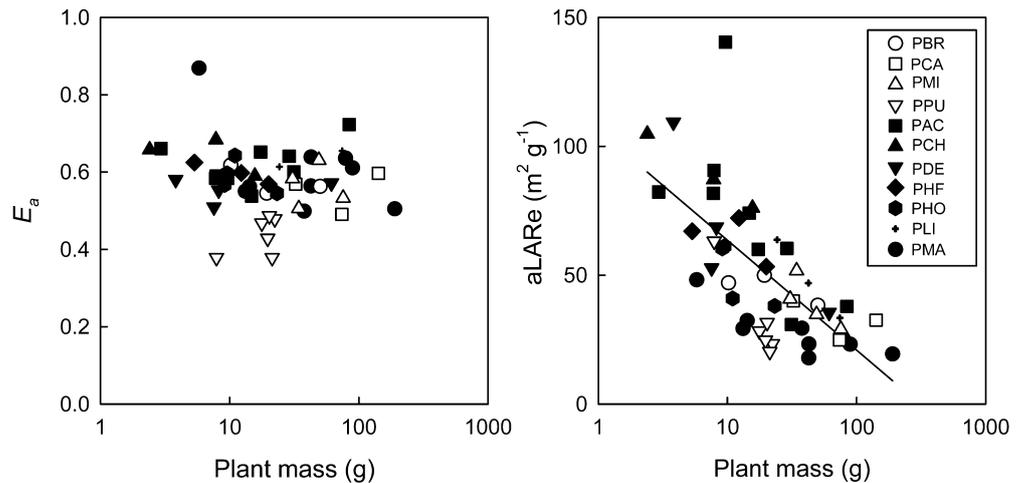
light demanding species. For *P. marginata*, the low SLA as compared to other shade tolerant species is mostly responsible for its lower $aLAR_e$. Overall, the results reveal that within the shade tolerant and light demanding groupings, species behave mostly similarly but that as a group the shade tolerant species have higher efficiencies of light capture than the light demanding species. The higher efficiencies are a result of a slightly higher mean P_E's combined with lesser self-shading in the shade tolerant as compared to the light demanding group.

Since measures of crown performance could be expected to be size dependent, we examined the relationships between the measures of efficiency and plant mass and plant leaf area. No relationship was evident between $E_a dif$ and plant mass (Fig. 3a), or between D_E, P_E or fraction self shaded and plant mass (data not shown). Similarly, no relationship was found between these measures and total plant leaf area. However, $aLAR_e$ exhibited a strong inverse linear relationship (R^2=0.49; *P*

>0.001) with log transformed plant mass (Fig. 3b). Since $E_a dif$ was independent of mass, the decline in $aLAR_e$ was due to a decrease in LAR as the plants increased in mass. This occurred because woody mass accumulated whereas leaves turned over giving a smaller increase in leaf area than in mass of stems and branches. Using plant mass as a covariate did not however reveal any further significant species differences. At a given plant size, light demanding species had on average a lower $aLAR_e$ than the shade tolerant species, but the dependence on plant size was not significantly different between these groupings.

A limitation of the method that Y-plant uses to determine interception of PFD is that it assumes that the direct PFD incident on the crown is a parallel beam, leading to a lack of penumbra created within the crown itself. If a significant fraction of the leaf area were in penumbra rather than in full direct-bean irradiance or umbra, then leaf and whole plant assimilation rates could be significantly underestimated by the method used in Y-

Table 4 Measures of light capture efficiency for direct irradiance of the *Psychotria* species utilized in this study. The values in the table are the mean ±1 SE

Species	n	$E_a dir$	CosI	Percent self-shaded by 1 layer	Percent self-shaded by 2 layers	Percent self-shaded by >2 layers
Light demanding						
P. brachiata	3	0.524±0.027	0.886±0.031	25.1±0.3	8.2± 1.3	3.8±0.6
P. capitata	3	0.548±0.013	0.827±0.016	25.1±0.3	9.0±2.2	6.8±3.5
P. micrantha	4	0.494±0.056	0.776±0.026	24.5±2.3	7.1±2.1	2.5±1.3
P. pubescens	5	0.456±0.075	0.839±0.014	25.5±1.3	11.6±3.1	8.7±3.9
Mean		0.502±0.025 [a]	0.827±0.016 [a]	25.0±0.7 [a]	8.8±1.1 [a]	5.2±1.3
Shade tolerant						
P. acuminata	9	0.653±0.027	0.887±0.010	19.2±1.2	2.9± 0.9	0.9±0.4
P. chagrensis	3	0.495±0.034	0.870±0.030	25.9±0.4	8.5±1.4	5.4±2.4
P. deflexa	4	0.600±0.054	0.866±0.022	22.3±3.2	7.8±2.3	5.7±3.1
P. hoffmannseggiana	3	0.624±0.112	0.873±0.066	20.5±3.8	5.6±2.6	3.7±2.0
P. horizontalis	3	0.530±0.041	0.856±0.018	22.9±0.8	7.6±2.0	5.5±2.8
P. limonensis	3	0.540±0.032	0.817±0.056	22.3±1.4	3.9±0.6	2.0±0.5
P. marginata	9	0.535±0.028	0.868±0.013	23.9±1.5	7.5±1.1	3.1±0.9
Mean		0.572±0.017 [b]	0.867±0.007 [b]	22.1±0.75 [b]	6.0±0.6 [b]	3.2±0.6

Includes shading by stems

[a,b] mean values having different superscript letters are significantly different at the P=0.05 level

plant. We examined whether this is a problem by determining the mean distance along the direct beam between edges of leaves casting shadows and the shadow itself on a lower leaf. This computation was done for the period between 1000 and 1400 hours. Ratios of this distance to the width of the upper leaf ranged from 0.4 to 2.4 (mean =1.1) with no significant differences among species or among habitat preference groups (ANOVA). This result is consistent with a co-variation of leaf size and the distance between shading and shaded leaves. A ratio of 50–70 is required before a lower leaf would be entirely in penumbral shade with no umbra (Horn 1971). Thus the small ratios observed indicate that during midday when most sunflecks occur, the surfaces of leaves would primarily be either in direct PFD or umbra with little of the leaf area in penumbra.

Measures of the efficiencies of direct PFD absorption exhibited the same pattern of differences as those found for diffuse PFD (Table 4). Shade tolerant species had a significantly higher E_a for direct PFD ($E_a dir$) than light demanding species ($F=4.85$, $P=0.03$) but within each habitat grouping there were no significant differences among the respective species. Linear regression of $E_a dir$ against $E_a dif$ revealed an almost 1:1 relationship ($E_a dir=0.008+0.975\times E_a dif$; $R^2=0.90$). Thus, the architectural attributes determining $E_a dir$ are likely the same as those determining $E_a dif$. Clearly there is no tradeoff between use of direct and diffuse PFD among these species. We computed a mean cosine of incidence ($CosI$) of the direct beam on the leaf surfaces between 1000 and 1400 hours as a measure of the angular efficiency of capture of direct PFD. $CosI$ is directly proportional to the reduction in incident PFD as the beam angle with the surface changes, ranging from one for a perpendicular beam to zero for a beam parallel to the surface. $CosI$ is thus analogous with D_E for diffuse light except that it is for a more restrictive set of directions corresponding to the solar track over the time interval. Although the $CosI$ for light demanding versus shade tolerant species was quite similar (0.827 ± 0.058 SD versus 0.867 ± 0.041 SD for light demanding and shade tolerant groupings, respectively) the differences were statistically significant ($F=7.06$, $P=0.011$). Within each habitat grouping, however, no significant species differences were found. Since the incident PFD on the leaf surface is equal to the PFD in the direct beam times the $CosI$, the 4% greater $CosI$ of the shade tolerant as compared to the light demanding species means that the former would intercept 4% more direct PFD per unit surface area than the latter.

Since the direct beam PFD transmitted through a leaf can be significant, simulations with Y-plant were modified to also yield the fractions of leaf area shaded by one, two, three or more layers of leaves and by stems for azimuths and solar elevation angles along the solar track. These served as more detailed measures of the effectiveness of the display of leaf area for capture of direct PFD. Light demanding species had significantly more shading by one ($F=4.73$, $P=0.035$) or two ($F=5.2$, $P=0.026$) layers than did shade tolerant species. However there were no

significant differences for the fraction shaded by three or more layers or by stem. These latter categories were but a small fraction of the total leaf area so the differences between light demanding and shade tolerant species in self-shading were driven by the differences in shading by one or two layers.

Performance in crown light environments

Light demanding species occurred in microsites with a higher daily total PFD as well as a higher daily diffuse PFD than shade tolerant species. Although the mean daily direct PFD received by light demanding species was 50% higher than that received by shade tolerant species, the difference was not significant because of the large variation between plants within each group. Within each habitat grouping, there were no significant differences among species in daily total PFD or daily direct PFD received. However, among the light demanding species, *P. brachiata* received significantly higher daily diffuse PFD than other species whereas among the shade tolerant species there were no significant differences.

The occurrence in higher light environments as well as differences in leaf physiology (Table 2) resulted in light demanding species having a 3-fold greater daily assimilation (A_{tot}) than shade tolerant species ($F=20.8$, $P<0.0001$). This was due to a 2-fold greater A_{dir} ($F=9.9$, $P=0.003$) and a 6-fold greater A_{dif} ($F=13.12$, $P=0.0007$) in light demanding as compared to shade tolerant species. Within the light demanding species, *P. brachiata* had a significantly higher A_{dif} ($F=13.70$, $P=0.001$) than the other species but otherwise there were no significant differences between species. Among the shade tolerant species, *P. chagrensis* had a significantly higher A_{tot} ($F=2.90$, $P=0.022$) but did not differ significantly from the others in A_{dir}. For A_{dif}, *P. acuminata* and *P. chagrensis* had significantly higher values than the other species. This was a result of the occurrence of *P. acuminata* and *P. chagrensis* in microsites with higher diffuse PFD as well as their lower dark respiration rates as compared to the other shade tolerant species.

The above ground biomasses derived from sequential Y-plant measurements over the 1 year interval were used to calculate above-ground relative growth rates which were then examined in relation to measures of light availability and photosynthetic performance in the different microenvironments. Since leaves were shed over the interval, a net RGR that was based only on the apparent change in mass, and a gross RGR that included the shed leaf mass were calculated. Some plants (12 of 45) shed enough leaves that they actually decreased in mass over the year interval, giving slightly negative net RGRs. However, with one exception, gross RGR values were all positive, albeit small for many plants. We found no evidence that leaf shedding or the resulting difference between gross RGR and net RGR was related to any measure of the light environment or plant photosynthesis (r^2 all <0.29; P all >0.05). Thus, we used gross RGR for further analysis

|	Light demanding $n=10$		Shade tolerant $n=34$		All $n=44$	
	R^2	P	r^2	P	r^2	P
Diffuse PFD (mol m^{-2} day^{-1})	**0.803**	**0.0005**	0.022	0.405	**0.477**	**<0.0001**
Direct PFD (mol m^{-2} day^{-1})	0.015	0.737	0.096	0.074	0.106	0.0310
Total PFD (mol m^{-2} day^{-1})	0.132	0.301	0.100	0.069	**0.248**	**0.0006**
A_{dif} (mmol m^{-2} day^{-1})	**0.566**	**0.012**	0.000	0.995	**0.373**	**<0.0001**
A_{dir} (mmol m^{-2} day^{-1})	0.070	0.459	**0.177**	**0.013**	0.210	0.0017
A_{tot} (mmol m^{-2} day^{-1})	**0.775**	**0.0008**	0.031	0.320	**0.476**	**<0.0001**
E_a	0.034	0.610	0.000	0.921	0.009	0.542
$aLAR_e$ (m^{2}g^{-1})	0.016	0.726	0.024	0.385	0.002	0.782
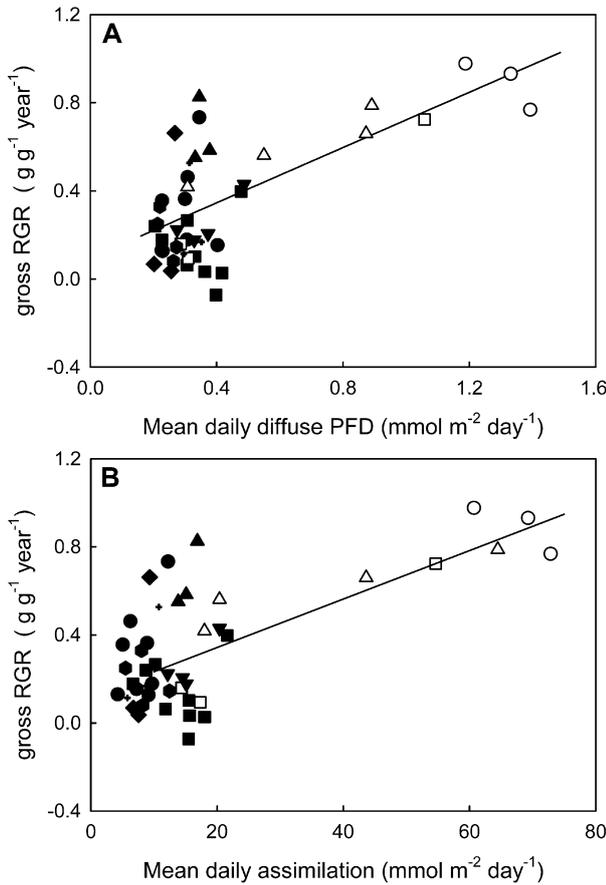
Fig. 4 The dependence of shoot gross RGR on **A** mean daily diffuse PFD and **B** mean daily assimilation. The symbols for the different species are the same as in Fig. 1. The lines are the least squares fit to the data points for the light demanding species

since it should be functionally most closely related to light capture and photosynthetic performance.

Table 5 gives the coefficients of determination for gross RGR and estimates of light capture or photosynthesis derived from Y-plant simulations. When species were stratified according to habitat preference (light demanding versus shade tolerant) significant relationships were found between gross RGR and diffuse PFD, mean daily assimilation in diffuse PFD (A_{dif}) and mean daily assimilation (A_{tot}) for light demanding plants whereas for the plants of

shade tolerant species only the mean daily assimilation in direct PFD (A_{dir}) was significant. When all plants were considered, gross RGR was significantly related to diffuse PFD, total PFD and all measures of photosynthesis. While for the light demanding plants, gross RGRs were significantly correlated with diffuse PFD there was no significant correlation with direct PFD. This may be because diffuse PFD, which is related to the total canopy openness, is a better predictor of the light environment and its effect on photosynthesis than is direct PFD. Fig. 4 shows the relationship between gross RGR and mean daily diffuse PFD, and gross RGR mean daily assimilation for both light demanding and shade tolerant species. The plants of light demanding species that were measured occurred over a much wider range of light environments and consequently a stronger relationship between gross RGR and diffuse PFD was evident. For the shade tolerant species, other environmental variation, disease and herbivory effects as well as uncertainties in the determination of light environments via hemispherical photography probably contributed to the lack of a significant relationship. No significant relationships between RGR and measures of light capture efficiency, E_a and $aLAR_e$ were found.

We explored the relationship between E_adif and A_{dif} by running simulations in which the light environment was either specific for the plant site (i.e. the photograph taken above the plant) or the same (i.e. the same hemispherical photograph) for all plants (Fig. 5). For the former (Fig 5a), A_{dif} is dependent on differences in the diffuse PFD as dictated by the canopy openness at the site, E_adif and on the species-specific physiological attributes of the leaves. The latter (Fig. 5b) removes the effect of the light environment though it results in slight changes in E_adif because of changes in the relationship between leaf display and the geometry of canopy openness. Finally, simulations were run in which the leaf physiological attributes were all set to be equal to those of a *P. marginata* leaf. In this case (Fig. 5c) only the effects of E_adif on diffuse light capture remain. When variation in light environment, species specific leaf physiology, and E_adif are included (Fig. 5a) there is a wide range of variation in A_{dif} and no significant relationship to E_adif. When the variation in light environment is eliminated, there is a smaller but still substantial range in A_{dif}. Examination of the symbols for the
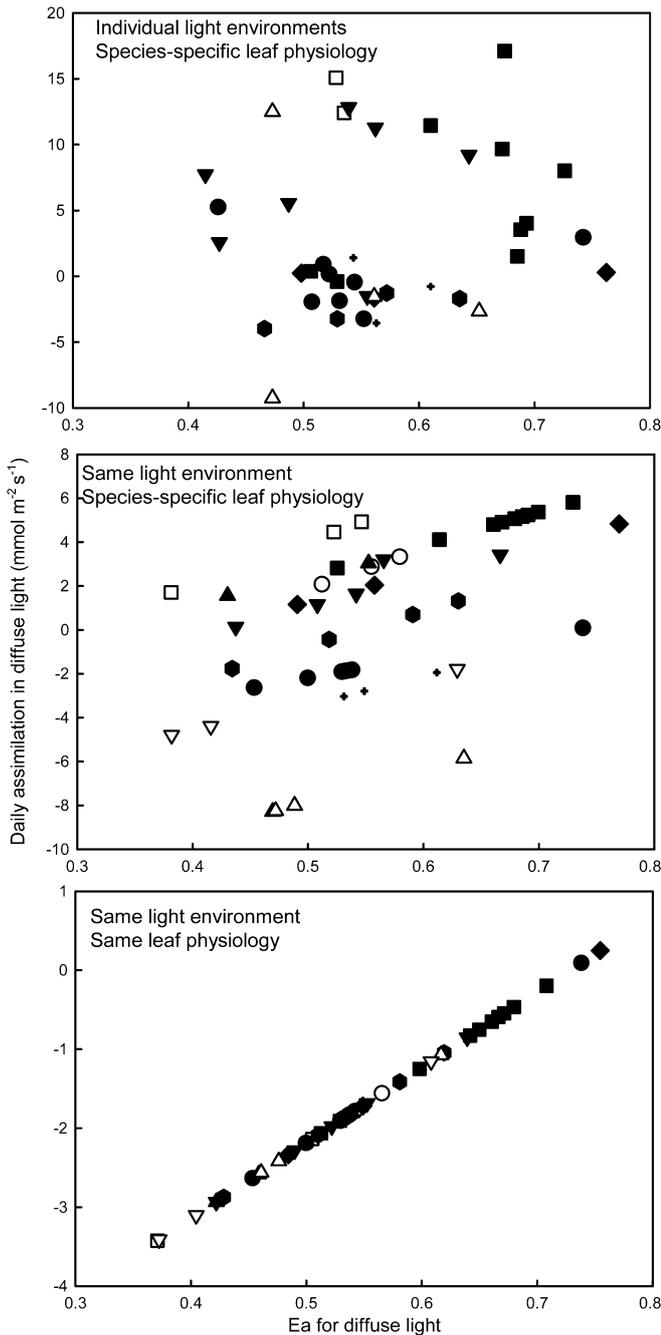
Fig. 5 Dependence of daily assimilation in diffuse light on E_a for diffuse light in simulations where both the light environment and leaf physiology varied as sampled in the field (*top panel*) or where simulations were all run with the same light environment but leaf physiological properties varied according to the measured values for each species (*middle panel*). The *lower panel* shows the result of holding constant both the light environment and leaf physiological properties so that only the effect of variation in E_a between plant crowns is apparent

daily assimilation in diffuse light. When the leaves of all species were assigned the same physiological attributes then the result was a single line with the slope reflecting the effect of $E_a dif$ on A_{dif}. It can be seen that the range of $E_a dif$ found for the *Psychotria* plants has a significant effect on assimilation in diffuse light.

Leaf production and turnover

Since it was possible to examine the light capture and assimilation of individual leaves, and add back leaves that had been shed by a Y-plant plant, we explored the potential contribution of different demographic classes of leaves. The demographic classes were (1) leaves that were present in 1995 and also in 1996 (Fig. 6, crosshatched bars), (2) leaves present 1995 but shed prior to the 1996 measurements (Fig. 6, solid bars) and (3) new leaves produced between the 1995 and 1996 measurements (Fig. 6, open bars). These simulations were run for four species differing in architecture and leaf longevity (see Table 1). In all cases, leaves that survived from 1995 to 1996 exhibited lower daily assimilation in 1996 as compared to 1995. For *P. marginata* and *P. capitata*, the leaves that were shed had a lower daily assimilation than those that remained, and if these leaves had remained, they would have contributed even less to the daily carbon gain.
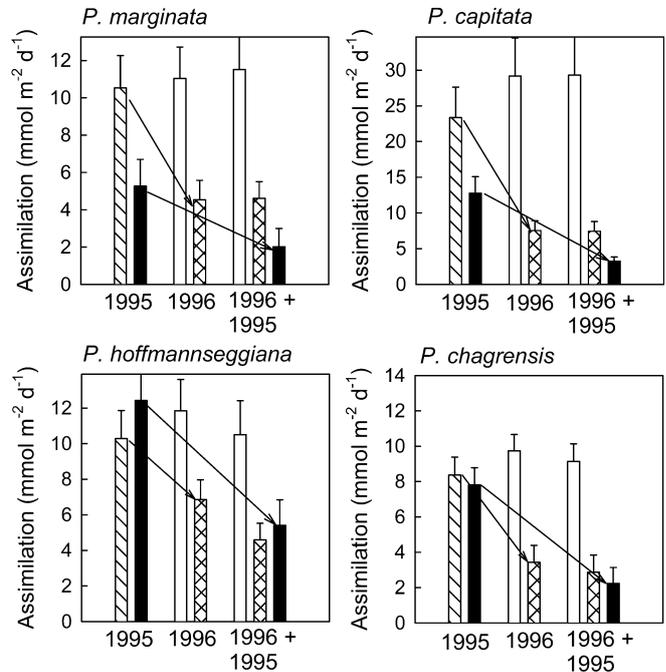

Fig. 6 Daily photosynthetic carbon gain for leaves of different demographic classes within the crowns of four *Psychotria* species. The *arrows* connect the classes, either from year to year or when they were added back. The *solid bars* are the leaves that were present in 1995 but were shed before the 1996 re-measurement. The *hatched bars* are the leaves present in 1995 and through the 1996 re-measurement. The *open bars* are new leaves produced between the 1995 and 1996 measurements and remaining through the 1996 re-measurement. The bars give the means and standard errors for 25 leaves randomly selected from each class on the sampled plants

individual species shows that they line up as parallel lines but at different A_{dif} values. These differences are due to the effect of the species-specific leaf physiological attributes; whereas the slopes of these parallel lines connecting the symbols for a given species represent the effect of $E_a dif$ on

Thus increasing leaf longevity itself would contribute little to the assimilation of these species because the leaves are being displaced into crown microsites with greater self-shading. Conversely, new leaves had generally higher daily assimilation indicating that they were being produced in more favorable crown microsites in terms of light environment. For *P. hoffmannseggiana*, a species with a short leaf lifespan and consequently more leaf turnover between 1995 and 1996, there was no significant difference in the daily assimilation between the leaves that remained versus those that were shed. In this species it would appear that increasing leaf longevity would increase daily assimilation, though not by as much as is contributed by the production on new leaves in more favorable crown microsites. The results for *P. chagrensis* were somewhat intermediate in that there was no significant difference in daily assimilation between the leaves that remained and those that were shed, but if those that were shed were added back they would have made relatively little contribution to daily assimilation.

Effects of leaf shape

Leaves of the *Psychotria* species differ in shape ranging from those with attenuate bases and acuminate tips with most of the leaf area displaced towards the tip (*P. marginata*) to those with attenuate tips and rounded bases and most of the leaf area more basally arranged (Fig. 2). We explored how these different leaf shapes influenced light capture and assimilation by substituting the basic leaf shape of each species for the natural leaf shape while leaving the leaf physiological attributes of the species unchanged. By adjusting the leaf length, it was possible to change only the leaf shape without changing the leaf area. Simulations for six species showed that there
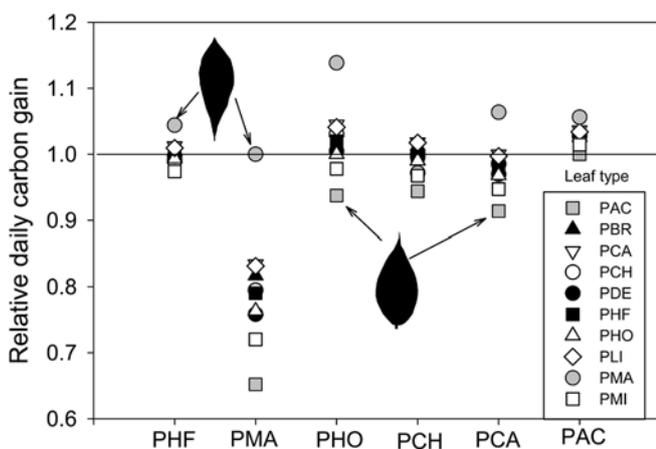

Fig. 7 Effects of leaf shape on the relative daily carbon gain for diffuse light. The leaf shapes shown are for *P. marginata* and *P. acuminata* with the bases facing down. See text for details of the method. The daily carbon gain determined for the plant with its natural leaf shape was set to be one. Substitution of leaf shapes of other species while maintaining the same leaf area then caused the relative daily carbon gain to increase or decrease

was a consistent effect of leaf shape on light capture and hence carbon gain but no evidence that the particular leaf shape of a given species was best matched with the architecture of that species (Fig. 7). Instead, the leaf shape of *P. marginata* always gave the highest relative daily assimilation whereas that of *P. acuminata* always gave the lowest daily assimilation. The order of relative daily carbon gains for different leaf shapes remained unchanged between species. The leaf shape of *P. marginata* gave high relative daily carbon gains as compared to those for other leaf shapes because leaf area was displaced away from the shoot axis, minimizing self-shading. In contrast, area for the *P. acuminata* leaf shape was concentrated towards the leaf base, giving higher self shading.

Discussion

Notwithstanding the substantial variation in leaf size, branching patterns and general appearance of the crowns of the *Psychotria* species, the most remarkable features of the results are the relatively small variations in measures of light capture efficiency among species and, overall, the rather low values of E_a. Valladares et al. (2002) surveyed 24 understorey species covering a wide range of taxa and growth forms occurring in the shade tolerant on BCI and found that there was substantial convergence in E_a and D_E. However, excluding some very low E_a values determined for climbers, E_a ranged from 0.3 to 0.83 with 50% of the species sampled having E_a's >0.72. In contrast, the *Psychotria* species sampled in the present study had E_a values ranging from 0.43 to 0.64 with an overall mean of 0.56. In the Valladares et al. study, path analysis revealed that leaf angle was a major contributor to variation in D_E with steep-leaved herbs and climbers having low E_a's. Following this, investment of biomass into support and specific leaf area also contributed to variation in D_E. For the *Psychotria* species, the P_E values exhibit a small but significant difference between light demanding and shade tolerant species as does *CosI* for direct beam PFD. While the differences are small, in both cases they nevertheless contribute significantly to greater diffuse and direct light capture by shade tolerant as compared to light demanding species. Much of the remainder of the variation in E_a for either direct or diffuse PFD is due to differences in self-shading between light demanding and shade tolerant species caused by the architectural arrangement of leaves in space. Indeed, multiple regression of E_a against P_E and self-shading as independent variables yielded an R^2 of 0.91. For both diffuse and direct PFD, orientation of the leaves for efficient capture of light from zenith angles of 0–45°, corresponding to a cosine of 1–0.707, reduces the efficiency of light capture from lower angles. In tropical forest understories most of the PFD originates from near the zenith because of the shorter path length through the overstory canopy at high as compared to low angles. Similarly, in small gaps, most of the PFD originates from directly overhead. Thus, the tradeoff in efficiencies between high and low angles may be generally of little

consequence. In specific situations such as forest edges or along the edges of larger gaps where sidelight may be more prevalent, then leaf reorientation so that the lamina are facing the predominant source of PFD (Ackerly and Bazzaz 1995; Clearwater and Gould 1995) can enhance light capture efficiency.

When light is predominantly received from above, minimizing self-shading requires a horizontal displacement of the leaf surface to minimize overlap in this plane. The *Psychotria* shrubs studied here have both orthotropic shoots responsible for height growth and plagiotropic branches contributing to lateral spread, with some species differences in the importance of each (Table 1, Fig. 1). Moreover, the mechanisms, or at least the significance of the mechanisms involved in lateral displacement of leaf area in orthotropic and plagiotropic shoots differ and have different consequences for self-shading within shoots. Pearcy and Yang (1998) and Takenaka et al. (2001) have shown that there can be an optimal partitioning between petiole and leaf lamina that maximizes light capture and shoot carbon gain. Since the petioles of *Psychotria* species studied here are short, other mechanisms take precedence. On the plagiotropic shoots, the principal mechanisms for displacement are increases in the ratio of internode length to leaf size, branching patterns, and changes in leaf shape. Increases in internode length are costly because of the extra carbon and other resources required, which then cannot be allocated to production of more leaf area. Changes in leaf shape in the *Psychotria* species also clearly impact self-shading (Fig. 6) but here there may also be tradeoffs. Displacement of the leaf area away from the point of attachment of the petiole increases the moment of force, requiring additional investment in support (Givnish 1986; Niklas 1992; Niinemets and Fleck 2002). Leaves of *P. marginata* have the greatest displacement of lamina area away from the petiole attachment point, which causes the increased E_a. This species also has a low SLA as compared to the other species (Table 2), which is consistent with a greater investment in support. Decreased SLA reduces the leaf area per unit of biomass investment and consequently reduces light capture. In contrast, the leaf shape of *P. acuminata* causes increased self-shading but is biomechanically more efficient.

For orthotropic shoots increasing internode length has been shown to have little effect on E_a or light capture from above (Niklas 1988; Takenaka 1994; Galvez and Pearcy 2003) though it results in enhanced capture of side light. This is especially true for the opposite decussate phyllotaxy of *Psychotria* since every second leaf pair is potentially positioned in the same vertical projection. However Galvez and Pearcy (2003) found that in the orthotropic shoots of *P. limonensis*, bending of the petioles of lower leaves, which occurred as a new leaf pair developed directly above, rotated the lamina into positions where the self shading was minimized, substantially enhancing whole-plant light capture and carbon gain. This type of twisting can be observed in the other *Psychotria* species and indeed in a wide variety of other shade tolerant plants. Petiole twisting and bending as well

as possibly internode twisting occurs in plagiotropic branches of *Psychotria* to reorient the leaves from the basic opposite decussate phyllotaxy into a horizontal plane, thereby increasing light interception. Furthermore, observations indicate that these leaves may exhibit a further lateral reorientation to minimize within shoot self-shading in a manner analogous to that reported for *P. limonensis*.

While internode elongation may not play a significant role in minimizing within-shoot self-shading on orthotropic shoots, it can have important consequences for between-shoot self-shading occurring when the leaves on one branch shade those on another. In *P. marginata*, and probably in most others *Psychotria* species on BCI, a specific pattern of branch initiation occurs in which a new branch develops essentially only at a rotation of 450° (D. Galvez, personal communication). Since in an opposite-decussate phyllotaxy, each node pair is rotated 90° from the previous one, five nodes must consequently be produced before a new branch will develop. If a branch does not develop then, in the absence of injury, five more nodes are produced before another branch is initiated. This causes branch initiation to effectively rotate around the plant and maximizes the distance between branches for a given average internode length. By maximizing the distance between branches, leaves on the upper branch obscure less of the hemisphere allowing greater receipt of diffuse light. Longer internodes would therefore increase the distance between successive branches, enhancing E_a for diffuse PFD.

Comparison of the simulations of the 1995 and 1996 plants shows that the new leaves were placed in more favorable light microenvironments, while leaves present in 1995 were more shaded with a lower carbon gain in 1996 than 1995. Furthermore, if the leaves that were shed between the 1995 and 1996 sampling were added back, these leaves would have been in even more shaded crown microsites and would have contributed little to whole plant carbon gain. Indeed many of the added-back leaves had slightly negative daily carbon gain though on average the carbon gains were just slightly positive in three of the four species. The fourth, *P. hoffmannseggiana*, a species with short-lived, low-cost leaves (Table 1 and Mulkey et al. 1993), would have received some apparent carbon gain benefit if leaves had lived longer. This species has also been shown to have much higher mortality rates than either *P. marginata* or *P. limonensis*, and may be selected to maximize reproductive effort per reproductive bout rather than long-term survival (Mulkey et al. 1993). Thus, it has characteristics expected of a shade adapted "weed" capable of responding to microsites within the shade tolerant with transiently higher light availability. Indeed, two of the three plants sampled exhibited negative net RGR, which would be consistent with a decrease in microsite light availability leading to greater leaf mortality than leaf production.

Leaf turnover moves resources, especially nitrogen, from less favorable to more favorable crown microenvironments (Mooney and Gulmon 1982; Field 1983; Hirose

and Werger 1987). Current theory (Kikuzawa 1991; Ackerly 1999) has focused on two alternative explanations for the pattern of senescence expected with a crown; senescence is age dependent or senescence is position (i.e. light microenvironment) dependent. The low carbon gain contribution of the leaves that were actually lost in crowns is consistent with the latter and shows that retaining those leaves would provide little whole-plant carbon gain benefit whereas recovery of N from the senescing leaves and its redeployment in new leaves could provide benefit in maximizing the efficiency of N use. Carbon costs also need to be considered since most of the carbon is in immobile structure such as cell walls and therefore cannot be recovered. Production of leaves and associated support structures depends on carbon gain, which is extremely limited in the shade. Thus within a crown there must be a balance between leaf gain and loss such that leaves are replaced along a shoot maintaining a standing leaf number, and as new shoots develop, a net gain in leaves.

Y-plant simulations integrate the effects of leaf physiology, allocation and crown architecture to give whole plant assimilation. It could be expected that this integrative estimate of whole plant performance would be more closely related to actual whole plant performance measured in the shade tolerant species as RGR than either leaf physiology or architecture alone. While for the light demanding species, significant correlations were found between gross RGR and diffuse PFD captured, A_{dif} and A_{tot}, the relationships for shade tolerant species were either not significant or only marginally significant. The light demanding species occurred over a much wider range of light environments than did the shade tolerant species. The lack of significant relationships for the shade tolerant species may have been due to inaccuracies in the hemispherical photo technique coupled with the narrow range of light availabilities. In addition other factors, including disease, herbivory and belowground processes not considered nor measured in Y-plant may have added to the variability in gross RGR, obscuring any potential correlations with measure of performance from Y-plant simulations.

Overall, the results of this study reveal small but significant differences when species are grouped into light demanding and shade tolerant habitat preferences, but overall a strong convergence in crown function for light capture among the *Psychotria* species despite considerable variation in individual characteristics such as leaf size, leaf longevity and branching patterns. This convergence occurs around values of E_a for the *Psychotria* species are certainly lower than those determined for a majority of other shade tolerant species surveyed on BCI by Valladares et al. (2002). Thus, it is somewhat paradoxical that on one hand a higher E_a should lead to higher assimilation, yet the *Psychotria* with their lower E_a are the single most abundant genus making up about 5% of the shade tolerant stems on BCI. Clearly, a high E_a is not a prerequisite for success in the shade tolerant environment. Plant crowns perform multiple functions including supply of water, biomechanical support of leaves and reproduc-

tive structures and space capture for competitive advantage, and therefore have multiple constraints on their form and function. Thus while there should be selection pressure to maximize E_a, the values achieved may be constrained by other crown design considerations. The role of these other functions in constraining the design of *Psychotria* crowns will be addressed in another paper (Pearcy and Cordero, unpublished data). Selection pressure for different crown functions could also be expected to differ between understories where efficient investment for light capture may be important and gaps where competitive occupation of space may take priority in crown design parameters. Ackerly (1999) has suggested that in fast-growing gap pioneers, leaf production and height growth may be more appropriate measures of performance than net carbon export from the shoot. Ultimately, multi-objective optimization approaches (Farnsworth and Niklas 1995) may be required to understand the relationships between form and function in plant crowns.

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