

## LEAF OPTICAL PROPERTIES ALONG A VERTICAL GRADIENT IN A TROPICAL RAIN FOREST CANOPY IN COSTA RICA<sup>1</sup>

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Leaf optical properties (400–1,100 nm) were compared for four species of rain forest trees with crowns in understory, mid-canopy, and canopy positions to test whether optical properties change with light environment. The species tested represent a spectrum of regeneration patterns ranging from shade tolerant to light demanding. Overall, leaf optical properties of the four species were similar. Differences in absorptance were small, but statistically significant among the species and positions along the canopy gradient. Species absorptance differences corresponded somewhat to shade tolerance; two of the shade species showed higher absorptance in lower light environments, while the sun species showed the reverse pattern. Specific leaf mass (leaf weight per unit area) and chlorophyll content per unit leaf weight also changed along the canopy gradient. Specific leaf mass was positively correlated and chlorophyll per unit leaf weight was negatively correlated with increasing light environment. Consequently, the efficiency of absorption, as represented by the absorptance per unit leaf weight, increased as light level decreased, largely due to changes in specific leaf mass. In contrast, efficiency of absorption per unit leaf chlorophyll was relatively constant with light environment for the two species measured for chlorophyll.

Rain forest canopy trees typically encounter a wide range of microenvironments during their lifetimes. In the understory, leaves of seedlings and saplings experience low light levels, but high relative humidity and moderate temperatures. In contrast, leaves in the canopy are exposed to high light levels, but also high temperatures, wind speeds, and vapor pressure deficits (Chiariello, 1984; Fetcher, Oberbauer, and Strain, 1985; Kira and Yoda, 1989). Of these factors, light presents the largest environmental gradient and is thought to be an important, and in some cases the most important, determinant of establishment, growth, and survival (Fetcher, Oberbauer, and Chazdon, 1994). In general only  $\approx 1\%$  of the photosynthetically active radiation (PAR) reaches the forest floor (Chazdon and Fetcher, 1984; Chazdon, 1988), and that which does has an altered spectrum due to the selective filtering of the forest canopy (Endler, 1993). Red light levels are more strongly reduced than far-red levels, resulting in a red : far-red ratio that may be 10% of that in the open (Lee, 1987; Endler, 1993; Turnbull and Yates, 1993). In contrast, light in the upper canopy is often well above the light saturation level of photosynthesis for canopy species (Fetcher et al., 1987).

As light is a limiting resource, trees might be expected to maximize light interception in the most efficient way,

that is, at the lowest costs in terms of support, construction, and transpiration (Horn, 1971; Givnish, 1984). How do canopy trees cope with this strong vertical gradient in light availability while regulating temperatures and transpirational losses? Trees adjust their morphological and physiological properties at different hierarchical levels, e.g., at the whole tree level and at the leaf level. For instance, trees with well-exposed crowns in the canopy have a different allometry (lower height/diameter ratio; Hallé, Oldeman, and Tomlinson, 1978), crown architecture, and leaf arrangement (Horn, 1971) compared to trees in the understory. Likewise, at the leaf level, exposed leaves in the canopy are thicker, more vertically inclined, and have a higher specific leaf mass, lower chlorophyll content per unit weight, and a higher chlorophyll *a/b* ratio compared to understory leaves (Oberbauer and Strain, 1986; Givnish, 1987; Pearcy, 1987; Bongers and Popma, 1988; Fetcher, Oberbauer, and Chazdon, 1994). Most of these leaf characteristics should affect leaf light capture, but few studies have directly examined light absorptance in response to the canopy gradient.

In this paper we focus on leaf-level changes across the canopy gradient. Here we test the hypothesis that light absorptance changes along the vertical gradient in the forest from understory to canopy and examine whether understory leaves capture light in a more efficient way than canopy leaves.

Given the light incident on a leaf, the absorptance by the leaf determines the amount of light that actually becomes available for photosynthesis. Generally, mature green leaves absorb 80–90% of the incident PAR (Gates et al., 1965; Ehleringer, 1981; Lee and Graham, 1986). As light in the understory is very low, understory leaves should absorb more PAR than canopy leaves, which have to balance light absorption with requirements for tem-

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perature regulation (Givnish, 1984). Similarly, understory leaves might be expected to absorb more light in the 700–750 nm range than canopy leaves, as PAR is scarce in the understory, and far-red light is relatively more available. Although quantum efficiencies are low in this spectral region, these wavelengths may contribute significantly to overall carbon gain (Lee and Graham, 1986). Finally, as carbon gain is low in the forest understory, understory leaves are expected to use their resources more efficiently than canopy leaves, and capture more light per unit dry matter or per mole of chlorophyll invested (Osborne and Raven, 1986).

## MATERIALS AND METHODS

This research was carried out at the La Selva Biological Station, a research facility of the Organization for Tropical Studies, situated in the Atlantic lowlands of Costa Rica (83°59'W, 10°26'N). The elevation ranges from 30 to 100 m and the annual precipitation is  $\approx$  3,900 mm, with a short dry period from January to April (Sanford et al., 1994). The forest has been classified as a tropical wet forest (Hartshorn, 1983).

The species examined included two emergent tree species, *Lecythis ampla* Miers (Lecythidaceae) and *Dipteryx panamensis* (Pittier) Record & Mell. (Papilionaceae), and two canopy species, *Minuartia guianensis* Aubl. (Olaaceae) and *Simarouba amara* Aubl. (Simaroubaceae). All species are part of a long-term study on the demography and ecophysiology of rain forest trees (Clark and Clark, 1987). They can be distinguished into two groups with distinct life history patterns (Clark and Clark, 1992). *Minuartia* and *Lecythis* are shade-tolerant species of which saplings can be found under low light conditions in mature-phase forest (sensu Whitmore, 1975). *Dipteryx* and *Simarouba* on the other hand, are shade tolerant and high-light-demanding species, respectively, that start their life cycle in the understory, but as juvenile tree size increases, they are increasingly found in more sunlit conditions in gap- and building-phase forest.

Measurements of leaf characteristics were conducted in June and July of 1991. Leaves used in measurements were collected from trees with crowns in either of three height levels in the forest canopy: the understory ( $\approx$  2 m), the mid-canopy ( $\approx$  10 m), and canopy ( $>$  20 m). The understory and mid-canopy trees were situated under closed canopy, whereas the canopy trees were exposed to direct light at least during some part of the day. By using a pruner or a rifle, healthy, fully expanded green leaves were collected just below the top of the tree in the case of understory and mid-canopy trees, and from exposed sunlit branches in the case of canopy trees. The youngest fully mature leaves were collected from trees in the understory, but because leaf production rates are low and leaf lifespans are long in the understory, in some cases these leaves may have been older than leaves from the mid-canopy and canopy. For the species with compound leaves (*Dipteryx* and *Simarouba*), the largest leaflets were taken. In total, 300 leaves were sampled: four species, three height levels in the canopy, five trees per height level, and five leaves per tree.

All individual trees from which leaves were taken, except for five understory saplings of *Dipteryx*, were part of

the long-term study on tree growth and censused by methods described in Clark and Clark (1992).

Collected leaves were stored under humid conditions and analyzed for their spectral properties within 24 hr. For *Dipteryx*, *Minuartia*, and *Lecythis*, the petioles were excised before measuring leaf area and not included in the analysis. Leaf area was measured with an area meter (LI-3100, LI-COR Inc., Lincoln, NE). Of the five leaves sampled per tree, one representative leaf was analyzed for its optical properties by means of a spectroradiometer (LI-1800, LI-COR Inc.) with an external integrating sphere. Only leaves without epiphylls were used in these measurements and leaves were carefully cleaned with damp tissue prior to measurement. Reflectance and transmittance were determined at 2-nm intervals at a wavelength range of 400–1,100 nm. Absorptance was calculated according to the formula:

$$\text{Absorptance} = 1 - \text{reflectance} - \text{transmittance}. \quad (1)$$

Total absorptance was calculated separately for the wavelength ranges 400–1,100 nm, 700–750 nm (far red), and 400–700 nm (PAR). Absorptance values presented here are absorptances from leaves exposed to an artificial light source. To determine the actual absorptances by leaves in the field, the measured absorptances should be multiplied by the spectral distribution of the mean in situ light environment. However, the spectral distribution of light in the forest is spatially and temporally highly variable, due to occurrence of sunflecks, the reflectance of light by clouds, the leaf area of the surrounding vegetation, and the absorptance characteristics of the vegetation (Ender, 1993). For comparisons, we measured leaves under equivalent full light conditions as presented by an artificial light source with a radiation spectrum reasonably similar to that of sunlight.

For two of the species, *Dipteryx* and *Lecythis*, chlorophyll content was measured for the same leaves used for absorptance measurements, i.e., one leaf per tree sampled. Chlorophyll was extracted and measured following methods of Porra, Thompson, and Kriedemann (1989). Afterwards leaves were oven dried for 48 hr at 70 C and weighed separately. Mean specific leaf mass per tree was calculated on the basis of five leaves per tree.

Because leaf light environment cannot necessarily be inferred from height in the canopy, we also compared leaf spectral characteristics to visual indexes of leaf light environment. These measurements include crown illumination index (based on Dawkins and Field, 1978) and number of crowns above the tree. Tree growth has been shown to be strongly correlated with both of these measures (Clark and Clark, 1992). Crown illumination index ranges from 1 to 5, with a value of 1 indicating no direct light, 1.5, 2, 2.5 indicating low, medium or high lateral light, 3 indicating some overhead light, 4 indicating full overhead light but lateral light partially or completely blocked, and a value of 5 indicating an open canopy overhead with full lateral direct light. For these comparisons, light index measurements taken in 1990, the year prior to measurement of leaf optical properties, were used so that light environment present at the time the leaves were developed was most closely approximated.

Statistical analysis was carried out with the SPSS package (SPSS, 1990). A two-way ANOVA and a Tukey test

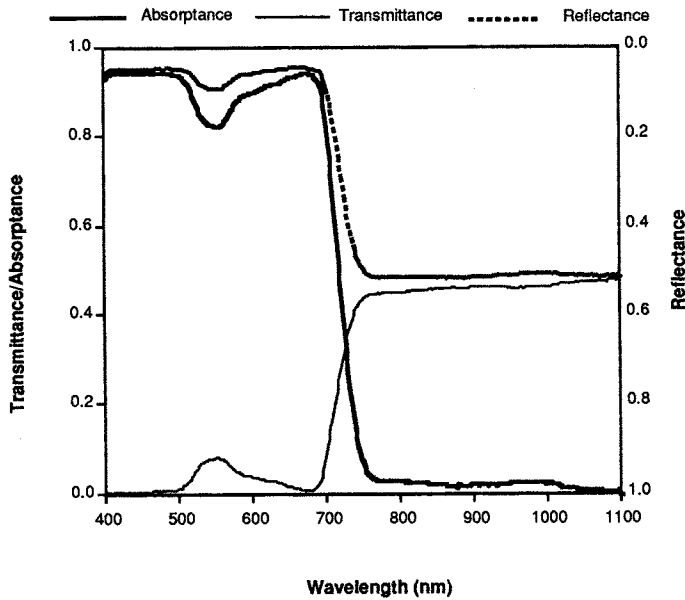


Fig. 1. Reflectance (dotted line), transmittance (dashed line), and absorbance (solid line) spectra for a representative leaf of *Dipteryx panamensis*.

were used for discriminating between species-, height-, and interaction effects. Data were logtransformed if they did not meet the assumption of normality or if variances had to be stabilized. Absorbance values were arcsine transformed prior to analysis to meet the assumption that data were symmetrically distributed and not truncated. Results were regarded significant if *P* values were <0.05.

RESULTS

**Spectral properties**—Leaves of the four tree species showed essentially the same basic patterns in their spectral properties. Leaves were characterized by low reflectance and transmittance in the PAR range (e.g., Fig. 1), whereas both were high for the wavelength range from 700 to 1,100 nm. The resultant was a strong absorbance in the PAR range, with only a small dip around 550 nm. Absorbance declined sharply above 700 nm, and was very low for higher wavelengths.

Absorbances of leaves were very similar for the four species. Mean PAR absorbance ranged from 89.6 to 92.5%, and matching coefficients of variation were also very low, ranging from 0.8% to 1.4% (Table 1). Despite the small range in absorbances, a significant difference across species was found (*P* < 0.001).

There was also a significant effect of canopy position on leaf absorbance (*P* < 0.001); for two species, absorbance was slightly higher for mid-canopy leaves than for canopy leaves (cf. Fig. 2). This result was mostly due to an increased absorbance around 550 nm (Fig. 2). Although there was a height effect on the absorbance of leaves in the 700–750 nm range, it was rather equivocal for the different species (Table 1).

Mean transmittance differed significantly with position in the forest canopy (*P* < 0.001), but reflectance did not (Table 1). For *Lecythis*, transmittance in the PAR range was higher for leaves in the canopy than for understory

TABLE 1. Mean spectral properties of understory, mid-canopy, and canopy leaves of *Dipteryx panamensis* (Dp), *Simarouba amara* (Sa), *Minquartia guianensis* (Mg), and *Lecythis amplia* (La). Arithmetic means (*N* = 5), standard deviations (SD), and coefficients of variation (cv) are given as well as the results of two-way ANOVA. Values in the same column followed by the same letter are not significantly different at the 5% level.

|             | Absorbance 400–700 nm (%) |       |       |        | Absorbance 700–750 nm (%) |        |        |       | Reflectance 400–700 nm (%) |      |      |      | Transmittance 400–700 nm (%) |      |      |  |
|-------------|---------------------------|-------|-------|--------|---------------------------|--------|--------|-------|----------------------------|------|------|------|------------------------------|------|------|--|
|             | Dp                        | Sa    | Mg    | La     | All                       | Dp     | Sa     | Mg    | La                         | All  | Dp   | Sa   | Mg                           | La   | All  |  |
| Understory  | 89.3ab                    | 91.7a | 91.9a | 90.1ab | 90.7                      | 33.7a  | 37.3a  | 38.0a | 37.0a                      | 36.5 | 6.5a | 6.3a | 6.3a                         | 6.3a | 4.3a |  |
| Mid-canopy  | 91.1b                     | 92.8a | 92.9a | 90.5b  | 91.8                      | 40.5b  | 41.6ab | 41.0a | 37.9a                      | 40.3 | 6.5a | 6.1a | 6.1a                         | 6.2a | 2.5b |  |
| Canopy      | 89.0a                     | 93.1a | 91.9a | 88.2a  | 90.4                      | 36.6ab | 46.1b  | 41.0a | 31.6a                      | 38.4 | 6.6a | 5.2a | 6.3a                         | 6.8a | 6.3  |  |
| Mean        | 89.9                      | 92.5  | 92.2  | 89.6   | 91.0                      | 36.9   | 41.3   | 39.9  | 35.5                       | 38.4 | 6.5  | 5.9  | 5.9                          | 6.5  | 6.2  |  |
| SD          | 1.25                      | 0.76  | 1.1   | 1.4    | 1.8                       | 4.1    | 4.5    | 3.7   | 3.7                        | 4.5  | 0.4  | 1.5  | 0.5                          | 0.9  | 1.1  |  |
| cv (%)      | 1                         | 1     | 1     | 1      | 2                         | 11     | 11     | 9     | 10                         | 12   | 6    | 26   | 9                            | 8    | 30   |  |
| Height      |                           |       | ***   |        |                           |        |        | **    |                            |      |      |      |                              |      | 14   |  |
| Species     |                           |       | ***   |        |                           |        |        | ***   |                            |      |      |      |                              |      | ns   |  |
| Interaction |                           |       | **    |        |                           |        |        | **    |                            |      |      |      |                              |      | ***  |  |

\* *P* < 0.05; \*\* *P* < 0.01, \*\*\* *P* < 0.001, ns *P* > 0.05.

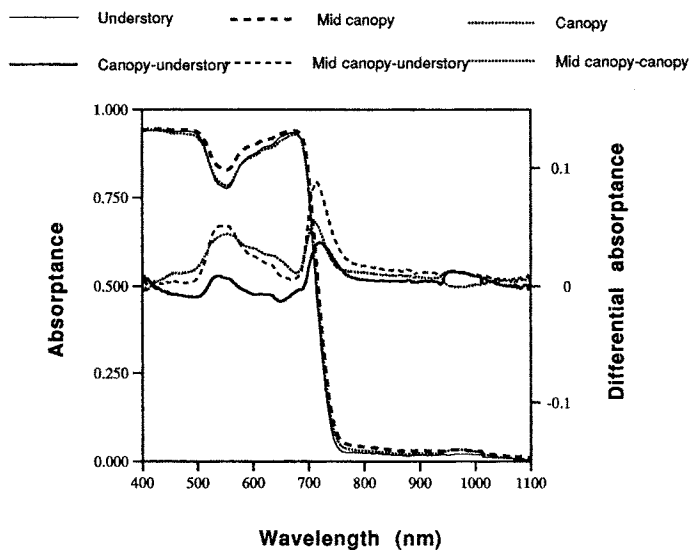


Fig. 2. Mean absorbance ( $N = 5$ ) for *Dipteryx panamensis* leaves from three different height positions in the forest canopy; the understory (solid line), the mid-canopy (dashed line), and the canopy (dotted line). The right y-axis indicates the mean difference spectrum among leaves with different canopy position.

leaves. For *Simarouba*, which has very heavy leaves in the canopy, the reverse was found.

**Canopy trends in SLM and chlorophyll**—The specific leaf mass increased strongly with height in the forest canopy for all species ( $P < 0.001$ ). *Simarouba* and *Dipteryx* showed the largest increase with canopy height (Table 2) as indicated by their larger coefficients of variation than those of the more shade-tolerant species, *Minquartia* and *Lecythis* (61% and 41% vs. 24% and 27%, respectively).

The two species analyzed for chlorophyll content, *Dipteryx* and *Lecythis*, did not differ significantly in the chlorophyll per unit leaf area or leaf dry weight (Table 3). However, chlorophyll characteristics responded moderately to a position gradient in the canopy; chlorophyll *a/b* ratios increased with height in the canopy ( $P < 0.05$ ), whereas chlorophyll content per unit weight decreased ( $P < 0.001$ ). Total chlorophyll content per unit area was not significantly different for leaves along the canopy gradient (Table 3).

**Correlations with light environment**—Within a species, SLM correlated well with estimates of the light environment. For all species except *Minquartia*, SLM was positively correlated with crown illumination index ( $P < 0.05$ ), and negatively correlated with the number of crowns above the tree ( $P < 0.05$ ; Table 4). In the case of *Minquartia*, the range of crown illumination environments was smaller than those of the other species, so significant correlations were less likely to be found. Also, estimates of the light environment were unavailable for the five smallest *Dipteryx* saplings in the understory, which probably experienced the lowest light conditions. Had they been included, correlations for *Dipteryx* individuals with light environment likely would have been even stronger.

Correlations with light environment were weaker for PAR absorbance than for SLM. Only *Dipteryx* leaves

TABLE 2. Mean specific leaf mass (SLM) of understory, mid-canopy, and canopy leaves of four rain forest tree species. Symbols as in Table 1.

|             | Specific leaf mass (g/m <sup>2</sup> ) |           |           |           |      |
|-------------|--|-----------|-----------|-----------|------|
|             | <i>Dp</i>                              | <i>Sa</i> | <i>Mg</i> | <i>La</i> | All  |
| Understory  | 30.0a                                  | 36.9a     | 52.1a     | 36.6a     | 38.8 |
| Mid-canopy  | 48.6b                                  | 55.4b     | 64.9a     | 36.9a     | 51.4 |
| Canopy      | 68.6c                                  | 135.2c    | 73.8a     | 56.0b     | 83.4 |
| All         | 49.1                                   | 75.8      | 63.6      | 43.2      | 57.9 |
| SD          | 19.0                                   | 45.9      | 15.3      | 11.7      | 29.0 |
| cv (%)      | 41                                     | 61        | 24        | 27        | 50   |
| Height      |  |           | ***       |           |      |
| Species     |  |           | ***       |           |      |
| Interaction |  |           | ***       |           |      |

showed a significant negative correlation between absorbance and crown illumination index, that is, leaves in closed-canopy environments absorbed more PAR than leaves from sunny environments (Table 4). *Lecythis* leaves showed a similar tendency, but the correlation was only close to significance ( $r_s = -0.50$ ,  $P = 0.056$ ). Correlations were stronger between absorbance and number of crowns above (Table 4, Fig. 3). Absorbance of *Dipteryx* and *Lecythis* were positively correlated with number of crowns above, whereas *Simarouba* showed the opposite trend.

**Efficiency of absorbance**—Efficiency of light capture by leaves can be expressed as PAR absorbance per unit biomass or per unit chlorophyll invested. All species showed similar responses in terms of efficiencies of PAR absorbance per unit dry weight; efficiencies were 20–100% higher for understory leaves than for canopy leaves ( $P < 0.001$ , Fig. 4). Efficiencies of absorbance tended also to be species-specific ( $P < 0.001$ ). This result was largely due to interspecific variation in SLM; species with the lowest SLM also had the highest efficiency.

When efficiency was expressed as light capture per unit chlorophyll, however, another picture emerged. In that case, absorbance efficiencies were similar for leaves with different heights in the canopy ( $P > 0.05$ ; Table 5).

## DISCUSSION

**Spectral properties**—Mean PAR absorbances of the four tropical tree species were as high as 91%, which

TABLE 3. Mean chlorophyll content per unit leaf weight and leaf area, and chlorophyll *a* to chlorophyll *b* ratios of understory, mid-canopy, and canopy leaves of two rain forest tree species. Symbols as in Table 1.

|             | Chlorophyll (mg/g) |           | Chlorophyll (mg/m <sup>2</sup> ) |           | Chlorophyll <i>a/b</i> |           |
|-------------|--------------------|-----------|----------------------------------|-----------|------------------------|-----------|
|             | <i>Dp</i>          | <i>La</i> | <i>Dp</i>                        | <i>La</i> | <i>Dp</i>              | <i>La</i> |
| Understory  | 15.5a              | 16.1a     | 458a                             | 580a      | 2.37a                  | 2.13a     |
| Mid-canopy  | 12.4ab             | 14.4ab    | 604a                             | 527a      | 2.40a                  | 2.24a     |
| Canopy      | 9.2b               | 8.2b      | 595a                             | 446a      | 2.70a                  | 2.26a     |
| All         | 12.3               | 12.9      | 552                              | 517       | 2.49                   | 2.21      |
| SD          | 3.4                | 4.3       | 121                              | 92        | 0.21                   | 0.20      |
| cv (%)      | 28                 | 33        | 22                               | 18        | 8                      | 9         |
| Height      | ***                |           | ns                               |           | *                      |           |
| Species     | ns                 |           | ns                               |           | ***                    |           |
| Interaction | ns                 |           | *                                |           | ns                     |           |

TABLE 4. Spearman's rank correlation coefficients between leaf characteristics and light environment for individuals of four rain forest tree species. Parameters included in the analysis are specific leaf mass (SLM), light absorptance of leaves in the 400–700 nm range (ABS), crown illumination index (CII), and the number of crowns above an individual (CA). The number of replicates is given in parentheses.

|           | <i>Dipteryx</i> | <i>Simarouba</i> | <i>Minquartia</i> | <i>Lecythis</i> |
|-----------|-----------------|------------------|-------------------|-----------------|
| ABS × CII | -0.86** (10)    | ns (13)          | ns (14)           | ns (15)         |
| ABS × CA  | 0.86** (10)     | -0.60* (13)      | ns (14)           | 0.69** (15)     |
| SLM × CII | 0.67* (10)      | 0.85*** (14)     | ns (14)           | 0.81*** (15)    |
| SLM × CA  | -0.71* (10)     | -0.88*** (14)    | ns (14)           | -0.79*** (15)   |

closely resembles absorptance values reported for a range of other rain forest species (Lee and Graham, 1986). Generally, PAR absorptances for green leaves average ≈85%, but they may be strongly reduced due to modifications of the leaf surface, such as waxes, hairs, and salt bladders that increase reflectance (Ehleringer and Werk, 1984; Vogelmann, 1993). Leaf absorptances of plant communities tend to increase with humidity of the habitat (Ehleringer and Werk, 1984), which is consistent with the high absorptance values found for the species studied here.

Furthermore, little intraspecific variation was found in the absorptance of leaves of the study species with canopy position despite large differences in leaf mass and presumably leaf thickness (Fetcher, Oberbauer, and Chazdon, 1994). For two of the species, PAR absorptances were slightly higher for mid-canopy leaves than for canopy leaves, but overall, differences in absorptance were small, and corresponding coefficients of variation were low. The same was found for absorptance in the 700–750 nm region. Apparently it is advantageous for a leaf to maximize potential light absorptance, whether in the understory or canopy. Similarly, Lee and Graham (1986) did not find differences in mean PAR absorptances of light-demanding

species compared with shade-tolerant species from rain forest.

Both transmittance and reflectance also differed little for leaves of different canopy positions. It has been suggested that in sunny microenvironments such as the forest canopy, increased reflectance is beneficial for the leaf, as it reduces the heat load and thus transpirational and photosynthetic costs (when leaf temperatures exceed the thermal optimum for photosynthesis; Givnish, 1984). This argument does not hold, however, if transmittance decreases at the same time, resulting in an absorptance that is similar for understory and canopy leaves, as was found in the present study. Hollinger (1989) also found that reflectance by the adaxial leaf surface for montane *Nothofagus* stayed relatively the same with height in the canopy. Interestingly, the reflectance of the pubescent abaxial leaf surface increased with height in the canopy, which he suggested might increase the photosynthetic photon flux density in the lower canopy by backscattering.

**Canopy trends in SLM and chlorophyll**—SLM increased with height in the canopy for all four species, a finding consistent with results of prior studies (Jurik, 1986;

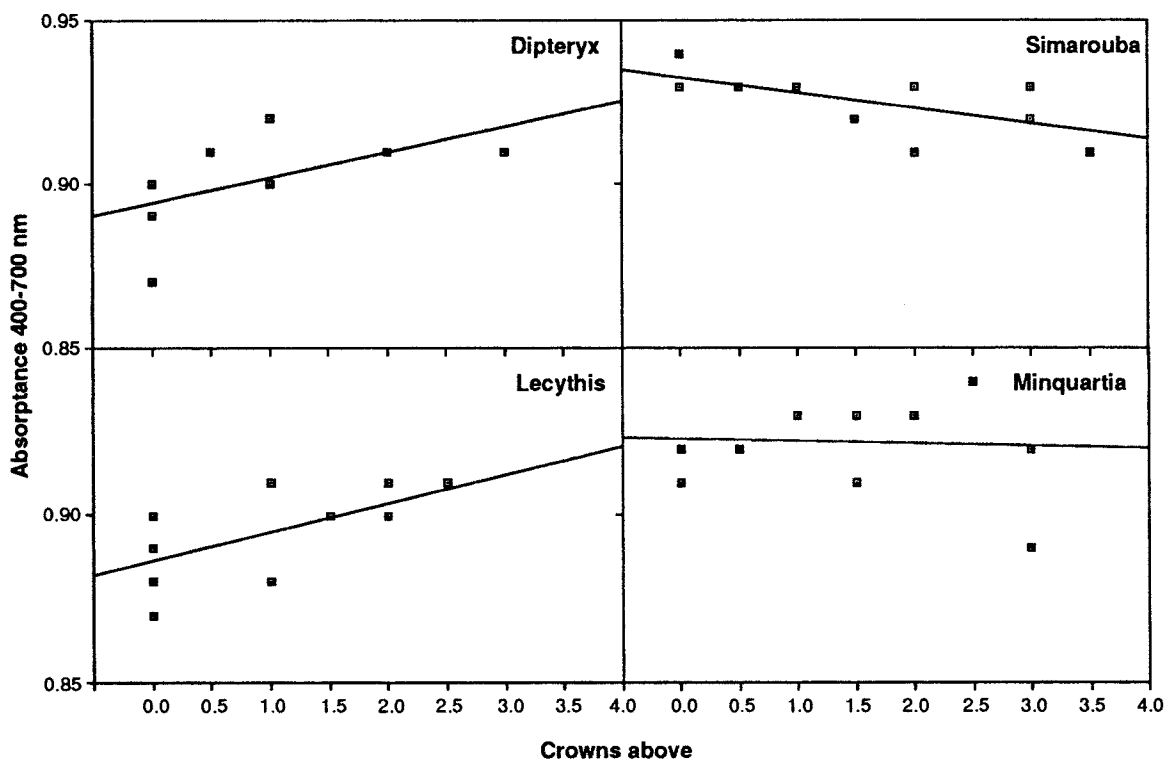


Fig. 3. Relationship between PAR absorptance and number of crowns above the tree for *Dipteryx*, *Simarouba*, *Minquartia*, and *Lecythis* leaves.

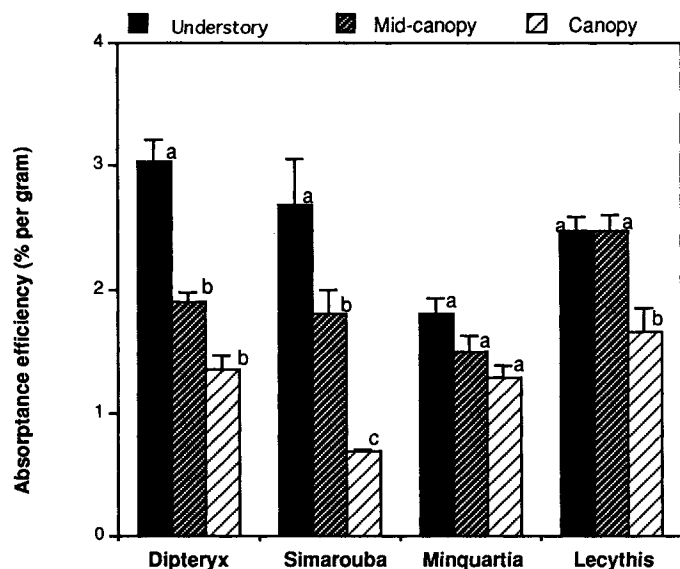


Fig. 4. Absorbance efficiencies (% PAR absorbed per unit biomass) for *Dipteryx*, *Simarouba*, *Miquartia*, and *Lecythis* leaves from three different positions in the canopy. Error bars indicate standard errors of the mean. Within each species, means that share the same letter are not significantly different at the 5% level. Data were arcsine transformed prior to statistical analysis.

Oberbauer and Strain, 1986; Hollinger, 1989; Ellsworth and Reich, 1993; Fetcher, Oberbauer, and Chazdon, 1994). Increases in SLM were particularly strong for the light-demanding species. A higher SLM often is associated with: (1) thicker leaves, (2) greater mesophyll development, and (3) higher nitrogen content per unit leaf area (Chabot, Jurik, and Chabot, 1979; Mooney, 1985; Hollinger, 1989; Bongers and Popma, 1990). Greater leaf thickness might be a xeromorphic response to an environment with a low relative humidity and a high evaporative demand. Greater mesophyll development, hence more photosynthetic apparatus and the nitrogen associated with it, should lead to a greater per unit area photosynthetic rate in a light-saturated environment (Jurik, 1986; Ellsworth and Reich, 1993). For understory environments on the other hand, leaves with a low SLM are advantageous, as they have a higher productivity per unit biomass invested (Bongers and Popma, 1988).

Compared to SLM, the chlorophyll content per unit biomass showed an opposite trend in that it was higher for shaded understory leaves than for exposed canopy leaves. Opposite patterns in SLM and chlorophyll content per unit biomass lead ultimately to a chlorophyll content per unit area that is similar for understory and canopy leaves.

Chlorophyll *a/b* ratios tended to be lowest for leaves from the forest understory. Interestingly, as in SLM, the more light demanding species of the two species measured for chlorophyll, *Dipteryx*, showed the greatest changes in chlorophyll *a/b* ratios. Furthermore, chlorophyll *a/b* ratios of understory leaves of *Dipteryx* were similar to those of canopy leaves of the shade species, *Lecythis*. These results are consistent with the idea that chlorophyll *a/b* ratio changes are a response to the far-red-enriched spectral distribution of light in the shade (Björkman, 1981).

TABLE 5. Mean absorbance efficiencies per unit chlorophyll of understory, mid-canopy, and canopy leaves of two rain forest tree species. Symbols as in Table 1.

|             | Absorbance 400–700/chl (%/mg) |                  |
|-------------|-------------------------------|------------------|
|             | <i>Dipteryx</i>               | <i>Simarouba</i> |
| Understory  | 0.196a                        | 0.161a           |
| Mid-canopy  | 0.156a                        | 0.173a           |
| Canopy      | 0.156a                        | 0.200a           |
| All         | 0.169                         | 0.178            |
| SD          | 0.034                         | 0.030            |
| cv (%)      | 20                            | 17               |
| Height      |                               | ns               |
| Species     |                               | ns               |
| Interaction |                               | *                |

**Relations with light environment**—Comparing leaf parameters for trees with different height positions in the canopy does not allow us to determine if the measured parameters responded to changes in tree ontogeny or to an increase in light availability, because trees typically encounter more sunlit conditions as they get older. However, correlation of leaf parameters with estimates of the light environment at least show that indeed, changes in leaf parameters co-occur with changes in the light environment. Overall, correlations between leaf parameters and light environment were stronger when light environment was assessed by numbers of crowns above the tree, instead of crown illumination index, possibly because canopy illumination index and the number of crowns above a tree weigh direct and diffuse light differently. More crowns above a tree represent a higher cumulative leaf area index, whereas a higher canopy illumination index represents a greater amount of open sky. These weightings may be important because increased leaf thickness and palisade layering are thought to increase the path length of direct light, but not diffuse light, through the leaf (Vogelmann, 1993).

Overall, although absorbance varied only slightly in response to light environment, the results for some of the species indicate that leaves under low light conditions do indeed absorb more light than leaves under sunlit conditions, giving some support for Givnish's (1984) hypothesis that shade-adapted understory trees absorb more PAR than canopy trees.

**Efficiency of absorbance**—Despite similar absorbances for canopy and understory leaves, the latter are far more efficient in their light capture per unit biomass. Such a high efficiency may give an advantage in an understory environment, where carbon fixation rates are low and where there is a premium on efficient use of biomass. Similarly, Lee and Graham (1986) found shade-tolerant species to be more efficient than sun species. How is it that understory leaves capture a similar amount of light as canopy leaves, with a smaller investment in biomass?

Lee and Graham (1986) concluded that inherent species differences in anatomical features were the basis for the differences in absorbance efficiency. Shade-tolerant species have a thin palisade layer with more equal dimensions of the cells, creating a narrow, continuous and dense layer of chloroplasts, that maximizes light capture efficiency (Lee et al., 1990). In contrast, the more columnar cells of

sun species allow light to pass through the central vacuoles and reach chloroplasts in lower cell layers (Lee et al., 1990; Vogelmann, 1993). Hence, the number of chloroplasts exposed to saturating light levels, and therefore photosynthetic capacity, is increased, but at the expense of a reduced efficiency of light capture.

In addition to anatomical differences, another plausible explanation is the higher chlorophyll content per unit biomass of understory leaves relative to canopy leaves. Higher chlorophyll per unit biomass, in combination with a lower SLM, results in similar chlorophyll contents per unit area, hence similar light-harvesting capabilities, for leaves from different canopy positions.

### LITERATURE CITED

- BJÖRCKMAN, O. 1981. Responses to different quantum flux densities. In O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler [eds.], *Physiological plant ecology. I. Encyclopedia of plant physiology*, 57–107. Springer-Verlag, Heidelberg.
- BONGERS, F., AND J. POPMA. 1988. Is exposure-related variation in leaf characteristics of tropical rain forest species adaptive? In M. J. A. Werger, P. J. M. van der Aart, H. J. Daring, and J. T. A. Verhoeven [eds.], *Plant form and vegetation structure*, 191–200. SPB Academic Press, The Hague.
- , AND ———. 1990. Leaf characteristics of the tropical rain forest flora of Los Tuxtlas, Mexico. *Botanical Gazette* 151: 354–365.
- CHABOT, B. F., T. W. JURIK, AND J. F. CHABOT. 1979. Influence of instantaneous and integrated light flux density on leaf anatomy and photosynthesis. *American Journal of Botany* 66: 940–945.
- CHAZDON, R. L. 1988. Sunflecks and their importance to forest understory plants. *Advances in Ecological Research* 18: 1–63.
- , AND N. FETCHER. 1984. Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. *Journal of Ecology* 72: 553–564.
- CHIARIELLO, N. 1984. Leaf energy balance in the wet lowland tropics. In E. Medina, H. A. Mooney, and C. Vazquez Yanes [eds.], *Physiological ecology of plants in the wet tropics. Tasks for Vegetation Science* 12, 55–89. Junk, The Hague.
- CLARK, D. A., AND D. B. CLARK. 1987. Análisis de la regeneración de árboles del dosel en bosque muy húmedo tropical: aspectos teóricos y prácticos. *Revista Biología Tropical* 35(Suppl.): 41–54.
- , AND ———. 1992. Life history diversity of canopy and emergent trees in a Neotropical rain forest. *Ecological Monographs* 62: 315–344.
- DAWKINS, H. C., AND D. R. B. FIELD. 1978. A long-term surveillance system for British woodland vegetation. Department of Forestry, Oxford University, Oxford.
- EHLERINGER, J. R. 1981. Leaf absorptances of Mohave and Sonoran desert plants. *Oecologia* 49: 366–370.
- , AND K. S. WERK. 1984. Modifications of solar-radiation absorption patterns and implications for carbon gain at the leaf level. In T. J. Givnish [ed.], *On the economy of plant form and function*, 57–82. Cambridge University Press, Cambridge.
- ELLSWORTH, D. S., AND P. B. REICH. 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia* 96: 169–178.
- ENDLER, J. A. 1993. The color of light in forests and its implications. *Ecological Monographs* 63: 1–27.
- FETCHER, N., S. F. OBERBAUER, AND R. L. CHAZDON. 1994. Physiological ecology of plants. In L. McDade, K. S. Bawa, H. Hespeneide, and G. S. Hartshorn [eds.], *La Selva: ecology and natural history of a neotropical rain forest*, 128–141. University of Chicago Press, Chicago, IL.
- , G. ROJAS, AND B. R. STRAIN. 1987. Efectos del régimen de luz sobre la fotosíntesis y el crecimiento en plántulas de árboles de un bosque lluvioso tropical de Costa Rica. *Revista Biología Tropical* 35(Suppl.): 97–110.
- , ———, AND B. R. STRAIN. 1985. Vegetation effects on microclimate in lowland tropical forest in Costa Rica. *International Journal of Biometeorology* 29: 145–155.
- GATES, D. M., H. J. KEEGAN, J. C. SCHLETER, AND V. R. WEIDNER. 1965. Spectral properties of plants. *Applied Optics* 4: 11–20.
- GIVNISH, T. J. 1984. Leaf and canopy adaptations in tropical forests. In E. Medina, H. A. Mooney, and C. Vazquez Yanes [eds.], *Physiological ecology of plants in the wet tropics. Tasks for Vegetation Science* 12, 51–84. Junk, The Hague.
- . 1987. Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. *New Phytologist* 106: 131–160.
- HALLÉ, F., R. A. A. OLDEMAN, AND P. B. TOMLINSON. 1978. *Tropical trees and forests*. Springer-Verlag, Berlin.
- HARTSHORN, G. S. 1983. Plants. In D. H. Janzen [ed.], *Costa Rican natural history*, 118–157. University of Chicago Press, Chicago, IL.
- HOLLINGER, D. Y. 1989. Canopy organization and foliage photosynthetic capacity in a broad-leaved evergreen montane forest. *Functional Ecology* 3: 53–62.
- HORN, H. S. 1971. *The adaptive geometry of tree form*. Princeton University Press, Princeton, NJ.
- JURIK, T. W. 1986. Temporal and spatial patterns of specific leaf weight in successional northern hardwood tree species. *American Journal of Botany* 73: 1083–1092.
- KIRA, T., AND K. YODA. 1989. Vertical stratification in microclimate. In H. Lieth and M. J. A. Werger [eds.], *Tropical rain forest ecosystems: biogeographical and ecological studies*, 57–72. Elsevier, Amsterdam.
- LEE, D. W. 1987. The spectral distribution of radiation in two neotropical forests. *Biotropica* 19: 161–166.
- , R. A. BONE, S. L. TARSIS, AND D. STORCH. 1990. Correlates of leaf optical properties in tropical forest sun and extreme shade plants. *American Journal of Botany* 77: 370–380.
- , AND R. GRAHAM. 1986. Leaf optical properties of rainforest sun and extreme shade plants. *American Journal of Botany* 73: 1100–1108.
- MOONEY, H. A. 1985. Photosynthesis. In M. J. Crawley [ed.], *Plant Ecology*, 345–374. Blackwell Scientific, Oxford.
- OBERBAUER, S. F., AND B. R. STRAIN. 1986. Effects of canopy position and irradiance on the leaf physiology and morphology of *Pentaclethra maculosa* (Mimosaceae). *American Journal of Botany* 73: 409–416.
- OSBORNE, B. A., AND J. A. RAVEN. 1986. Light absorption by plants and its implications for photosynthesis. *Biological Reviews* 61: 1–61.
- PEARCY, R. W. 1987. Photosynthetic gas exchange responses of Australian tropical forest trees in canopy, gap and understory microenvironments. *Functional Ecology* 1: 169–178.
- PORRA, R. J., W. A. THOMPSON, AND P. E. KRIEDEMANN. 1989. Determinations of accurate extinction coefficients and simultaneous equations for assaying chlorophylls a and b extracted with four different solvents: verification of the concentration of chlorophyll standards by atomic absorption spectroscopy. *Biochimica Biophysica Acta* 975: 384–394.
- SANFORD, R. L., P. PAABY, J. C. LUVALL, AND E. PHILLIPS. 1994. Climate, geomorphology, and aquatic systems. In L. McDade, K. S. Bawa, H. Hespeneide, and G. S. Hartshorn [eds.], *La Selva: ecology and natural history of a neotropical rain forest*, 19–33. University of Chicago Press, Chicago, IL.
- SPSS. 1990. *SPSS/PC+ V4.0 Base manual*. SPSS INC, Chicago, IL.
- TURNBULL, M., AND D. J. YATES. 1993. Seasonal variation in the red/far-red ratio and photon flux density in an Australian sub-tropical rainforest. *Agricultural and Forest Meteorology* 64: 111–127.
- VOGELMANN, T. C. 1993. Plant tissue optics. *Annual Review of Plant Physiology and Molecular Biology* 44: 231–252.
- WHITMORE, T. C. 1975. *Tropical rain forests of the far east*. Clarendon Press, Oxford.