

Light environment, gas exchange, and annual growth of saplings of three species of rain forest trees in Costa Rica

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ABSTRACT. Light environment, leaf physiological characteristics, and growth were compared for forest-grown saplings of three species of tropical trees with known life histories. Light environment was assessed both by hemispherical canopy photography and a quantitative visual index of crown illumination. Leaf gas exchange characteristics were measured by infrared gas analysis. The species tested included *Lecythis ampla*, a species tolerant of understorey conditions, *Pithecellobium elegans*, a species found in relatively bright sites, and *Simarouba amara*, a fast-growing, light-demanding species.

Annual height and diameter growth did not significantly differ between the three species, but highest average rates were found for *Simarouba*. Likewise, saplings of the three species were found in similar low light environments although *Simarouba* saplings were found in slightly brighter sites and *Lecythis* saplings were found in the lowest light environments. Despite similar light regimes, the species differed markedly in leaf area and gas exchange. Leaf areas of *Lecythis* saplings were five and ten-fold greater than *Simarouba* and *Pithecellobium* saplings, respectively. Light-saturated leaf photosynthesis and leaf dark respiration rates of *Lecythis* were about half those of *Simarouba*; rates of *Pithecellobium* were intermediate. *Lecythis* had the highest leaf photosynthesis at understorey diffuse light levels. Measures of annual growth were positively correlated with estimates of both direct and diffuse light with the strongest correlations between sapling performance and diffuse light.

KEY WORDS: Costa Rica, hemispherical photograph, direct light, diffuse light, dark respiration, light-saturated photosynthesis, non-pioneer.

INTRODUCTION

Recent studies of the ecophysiology of tropical trees have focused on the ecophysiological characteristics associated with different regeneration patterns (Augspurger 1984, Bazzaz 1984, Bazzaz & Pickett 1980, Fetcher *et al.* 1983,

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1987, Hogan 1988, Langenheim *et al.* 1984, Oberbauer & Strain 1984, Percy 1987, Popma & Bongers 1991). However, in only a few cases has assignment to regeneration pattern been based on quantitative demographic information rather than on experienced observation. Furthermore, comparisons of the ecophysiology of tropical trees have often used seedlings grown in containers in controlled environments (Fetcher *et al.* 1983, 1987, Langenheim *et al.* 1984, Oberbauer & Strain 1984), but it is not clear that such results can be extrapolated to plants growing in the forest (Clark & Clark 1987). In this study we investigate the light environment and *in situ* ecophysiological characteristics of saplings of three species of tropical wet forest trees with known life histories in the context of a long-term study of the growth, survivorship, and ecophysiology of tropical tree species.

The aim of the study was to address the following questions: (1) In what type of light environments are species with different life histories found? (2) How do species with different life histories differ in terms of leaf physiology? (3) How does light environment relate to their growth and leaf physiology?

The species examined included two canopy emergents, *Lecythis ampla* Miers and *Pithecellobium elegans* Ducke, and one canopy species *Simarouba amara* Aubl. *Lecythis* has been classified as a shade-tolerant species (Fetcher *et al.* 1987). Sapling *Lecythis* are associated with low crown illumination index (a quantitative visual score of crown light environment) and mature-phase forest (Clark & Clark 1992). Small saplings have a morphology similar to understory shrubs, with many long-lived leaves located on multiple branches with active growing points. *Pithecellobium elegans* is a nodulated legume most commonly found on upland terraces. *Pithecellobium* are typically found in gap or building-phase forest both as small saplings and as subcanopy trees, but are found in mature phase forest as intermediate-sized saplings (Clark & Clark 1992). In contrast to *Lecythis*, the typical sapling growth form of *Pithecellobium* is a straight vertical pole with one or two active growing points and a few bipinnately-compound leaves. *Simarouba amara* has been classified as a high light demander in Surinam (Schulz 1960) and as one of the faster growing species on Barro Colorado Island, Panama (Lang & Knight 1983). As juveniles, these trees show substantial size-dependent increases in crown illumination index and are associated with gap or building-phase forest (Clark & Clark 1992). *Simarouba* saplings have a similar growth form to that of *Pithecellobium* saplings with a single active growing point and a few pinnately-compound leaves. Saplings of all three of the study species are rare in primary forest.

MATERIALS AND METHODS

Study site

This study was conducted at the La Selva Biological Station operated by the Organization for Tropical Studies in the Atlantic lowlands of Costa Rica (83° 59' W, 10° 26' N). The site is predominantly evergreen forest and has been

classified as tropical wet forest (Hartshorn 1983). Detailed descriptions of the site can be found in Hartshorn (1983).

Growth measurements

Ten saplings of each of the study species were censused by methods described in Clark & Clark (1992); growth measurements were conducted annually during the dry season in March or April of 1989, 1990, and 1991. Saplings were initially found by extensive searches (Clark & Clark 1992). Measurements taken included annual height growth, diameter growth, survivorship, and modified crown illumination index (Dawkins & Field 1978, Clark & Clark 1992). The trees studied were a subset of a larger database of long-term growth of tropical trees and were selected from individuals taller than 25 cm but less than 300 cm tall. Diameters were measured with calipers at a permanently marked location on the stem. Repeated measurements of the same stems indicate that the precision of diameter measurements for these small saplings is better than 0.4 mm. Crown illumination index ranges from one to five, with a value of 5 indicating a completely open canopy overhead with full lateral direct light, 4 indicating full overhead light but lateral light partially or completely blocked, 3 indicating some overhead light, 2.5, 2.0, 1.5 indicating high, medium, or low lateral light, and 1 indicating no direct light either vertically or laterally.

Sapling light environment

In addition to the crown illumination index, the light environment for each sapling was quantified using hemispherical photographs taken in April 1990. Photographs were analysed using CANOPY (Rich 1989), a microcomputer program that uses a hemispherical canopy photograph and the solar track for the site's longitude and latitude to estimate the proportion of annual intercepted direct (direct site factor) and diffuse (diffuse site factor) radiation relative to a completely open site (Anderson 1964). These estimates are based on the interaction between the solar track and the canopy under windless and cloudless conditions, so actual direct and diffuse radiation, particularly in the short term, may differ substantially from that estimated by hemispherical photographs. However, the power of these measurements is that they provide estimates of potential radiation over the long term. Values of both direct site factor and diffuse site factor range from zero to one. To minimize operator bias, all photographs were analysed by the same individual and each photograph was analysed repeatedly until two measurements of direct site factor were within 0.5% of each other.

Sapling leaf area

Total leaf areas of the saplings were estimated nondestructively in March 1990. For *Simarouba*, images of one leaf (7–15 leaflets) per sapling were made with photosensitive paper. The areas of these imprints were measured with an area meter (LI-3100, Li-Cor Inc, Lincoln Nebraska) and a regression between

leaflet area and the product of leaflet width and length determined; the r^2 for the regression was 0.98. All leaflets on a sapling were measured for length and width and whole plant leaf area calculated using the regression mentioned above. For *Pithecellobium*, prints of all leaves were made using photosensitive paper and the areas of the prints were analysed using an image analysis system (Rich *et al.* 1989). For saplings of *Lecythis*, which may have hundreds of leaves, prints of 20 to 45 leaves were made using photosensitive paper, the prints were measured for area, and an average leaf size calculated for each sapling. Total leaf number was counted and multiplied by average leaf area to estimate the total leaf area of a plant. The 1990 leaf area data for one *Lecythis* sapling were lost. Consequently, leaf area estimated the following year (1991) was used in the analyses. Considering the approximate nature of the leaf area estimates, the slow growth of *Lecythis* saplings, and the absence of major changes in that sapling's light environment, leaf area in 1991 was likely a close approximation of 1990 leaf area.

Sapling gas exchange

Light-saturated photosynthesis (A_{\max}), photosynthesis at low light (A_{diffuse}) and dark respiration (R_{dark}) were measured for each sapling in March 1990 using a portable photosynthesis system (Li-6200, Li-Cor Inc., Lincoln, Nebraska) with a 1-litre cuvette mounted on a tripod. Leaf areas used in the leaf chamber were 5.9 cm² for *Simarouba*, 8.1 cm² for *Lecythis*, and an average of 6.7 cm² for *Pithecellobium*. Three of the youngest fully-developed leaves were measured per plant. In some cases, the most recently expanded leaves were clearly several months old. For *Lecythis* saplings, which typically have more than one active growing point, measured leaves were usually from different branches. However, for the other two species for which there is usually only a single active shoot meristem, leaves were by necessity from the same growing points and therefore differed in age. In the case of one *Pithecellobium* sapling, only a single leaf was present.

Irradiance during photosynthesis measurements was provided by a 75 W halogen projector lamp operated from 12 V gel-cells. The sequence of measurements was the following. A low light measurement was made at 15–20 $\mu\text{mol m}^{-2} \text{sec}^{-1}$ to approximate understorey diffuse light conditions. Readings were taken until a constant value was obtained. The chamber was opened between readings to reestablish ambient humidity and temperature conditions within the cuvette. Stable readings were obtained quickly for this light level, usually within 5 min. Light-saturated measurements were taken by irradiating the leaves to at least 600 $\mu\text{mol m}^{-2} \text{sec}^{-1}$. Prior experience with *in situ* tropical saplings under these conditions indicated that light-saturation occurred below 500 $\mu\text{mol m}^{-2} \text{sec}^{-1}$ (S. F. Oberbauer & M. Quesada, unpublished data). Plants were illuminated at least 15 min before readings were begun, and readings were repeated until steady or declining values were obtained, usually within 5 to 10 min. The chamber was opened between readings to maintain temperature and

humidity conditions as close to ambient as possible. Because of the logistical difficulties of measuring night-time respiration of saplings in the forest, we estimated leaf respiratory losses by measuring CO₂ exchange when the chamber was covered with a heavy black cloth. Leaf temperatures within the chamber averaged 29.0°C (range of 26.0–32.0°C) during dark respiration measurements and 29.4°C (range of 26.5–33.2°C) during light-saturated measurements. Destructive sampling of leaves was avoided because the plants are part of a long-term study. Consequently, photosynthesis data are presented on an area basis only. To estimate leaf specific weight for the species at this size class, recently fallen leaves were collected from beneath the saplings in 1991 or 1992, measured for area, dried at 70°C for 48 h, and weighed.

Data analysis

Comparisons of species in terms of growth, light environment, and gas exchange characteristics were made using Kruskal-Wallis nonparametric analysis of variance. In the case of the gas exchange measurements, the mean of the three replicate measurements made for each plant was used for comparisons between species. However, the maximum value measured for a plant was also used in the correlation analyses to minimize the effect of leaf age for *Pithecellobium* and *Simarouba*. Product-moment methods were used for the correlation analyses.

RESULTS

Sapling size and growth characteristics

In March 1990, saplings ranged from 0.25–2.50 m in height and from 0.4–1.7 cm diameter (Table 1). Mean heights and diameters were slightly larger for *Lecythis* though differences were not statistically significant. Despite similar heights and diameters, leaf areas of *Lecythis* differed significantly from the other two species. Leaf areas of *Lecythis* were more than five-fold greater than leaf areas of *Simarouba* and ten-fold greater than those of *Pithecellobium* (Table 1).

Sapling height and diameter growth were compared for the years preceding (1989–90) and following (1990–91) measurement of sapling light environment and gas exchange in March 1990 (Table 1). In both years, some saplings lost substantial height as a result of physical damage from debris falling from the canopy. These losses were greater than growth increases of the other saplings and resulted in negative average height growth for *Pithecellobium* in 1989–90 and for *Lecythis* in 1990–91. When these damaged individuals were excluded, the three species showed similar average height increases of approximately 10 to 15 cm y⁻¹ for saplings of mean heights of 116–146 cm (Table 1). Diameter increments were not significantly different for the three species over the period from 1989 to 1990, though mean diameter increments for *Simarouba* (0.6 mm y⁻¹) were somewhat larger than the other two species (0.3 mm y⁻¹). The same

Table 1. Height, diameter, total leaf area, and annual height and diameter growth increments from 1989 to 1990 and 1990 to 1991 for saplings of three species of Costa Rican wet forest trees (N = 10). Values are means \pm one standard error of the mean. Means within a row followed by a different letter are significantly different at $P \leq 0.05$. Height, diameter, and leaf area are for measurements taken in 1990.

| | <i>Lecythis</i> | <i>Pithecellobium</i> | <i>Simarouba</i> |
|------------------------------|---------------------|-----------------------|------------------|
| Height (cm) | 146 \pm 21a | 123 \pm 20a | 116 \pm 13a |
| Diameter (mm) | 11.2 \pm 1.5a | 10.0 \pm 1.1a | 8.7 \pm 0.6a |
| Leaf area (cm ²) | 5170 \pm 1638a | 499 \pm 106b | 955 \pm 184b |
| Height growth 1989–90 (cm) | 8.4 \pm 4.2a | -4.5 \pm 9.4a* | 9.6 \pm 5.8a** |
| Height growth 1990–91 (cm) | -4.9 \pm 10.7a*** | — | 9.3 \pm 1.8a |
| Diameter growth 1989–90 (mm) | 0.3 \pm 0.2a | 0.2 \pm 0.2a | 0.6 \pm 0.2a |
| Diameter growth 1990–91 (mm) | 0.3 \pm 0.1a | — | 0.3 \pm 0.2a |

*Includes two saplings that lost more than 20 cm from physical damage. When excluded, height growth = 8.5 \pm 2.8.

**Includes one sapling that lost more than 20 cm from physical damage. When excluded, height growth = 14.9 \pm 2.7.

***Includes two saplings that lost more than 20 cm from physical damage. When excluded, height growth = 10.4 \pm 3.9.

basic pattern was found when the data were calculated as relative growth rates (data not shown).

For the period from 1990–1991, diameter increments of *Lecythis* and *Simarouba* were similar at 0.3 mm y⁻¹. Also notable was the death of six of the ten *Pithecellobium* saplings between 1990 and 1991, even though mortality of saplings of this size class is usually fairly low (less than 20%, Clark & Clark 1992). Of the six that died, three decreased in height and the other three decreased in diameter in the year prior to their death. Because of the reduced sample size, *Pithecellobium* was excluded from the analyses for 1990–91.

Sapling light environment

Crown illumination index and hemispherical photographs both indicated that saplings of all three species were growing in relatively low light sites, although saplings of *Simarouba* occupied microsites with the highest average light availability. Mean crown illumination indices for *Pithecellobium* and *Lecythis* were nearly identical (1.9) with *Simarouba* somewhat higher (2.1). An analysis for species differences in crown illumination index was close to significance ($P = 0.06$). Direct site factor, a photographic estimate of the light contributed by sunflecks, averaged less than 0.035 for all three species and was not statistically different (Figure 1). The ranges of direct site factor encompassed by saplings of *Lecythis* and *Simarouba* were similar though *Simarouba* ranged to slightly higher direct site factor than *Pithecellobium* or *Lecythis* (Figure 1). Perhaps a better indicator of a species' light requirements than the maximum direct site factor is the minimum direct site factor at which saplings can be found. An intolerant tree species cannot survive in sites that are too dark, whereas all but extreme-shade species can tolerate the light environment within small to medium-sized gaps, and therefore by chance will be found in them. *Lecythis* ranged to the lowest

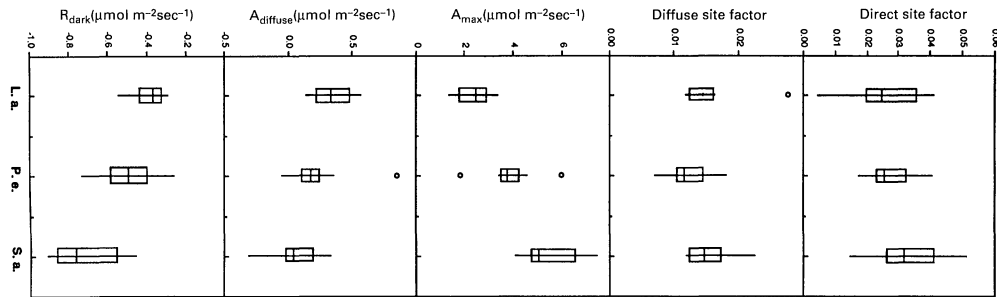


Figure 1. Box and whisker plots of direct site factor, diffuse site factor, light-saturated photosynthesis (A_{max}), photosynthesis at diffuse light ($15\text{--}20 \mu\text{mol m}^{-2} \text{sec}^{-1}$, A_{diffuse}), and dark respiration (R_{dark}) for saplings of three species of tropical wet forest trees growing *in situ*. $N = 10$. Vertical lines within box indicate median, right and left vertical lines of boxes indicate 75th and 25th percentile, and horizontal line indicates range. Circles indicate outliers. L.a. indicates *Lecythis ampla*, P.e. indicates *Pithecellobium elegans*, and S.a. indicates *Simarouba amara*.

direct site factor followed by *Simarouba* and then *Pithecellobium*, a finding that is consistent with the classification of *Lecythis* as the most tolerant of the study species. Diffuse site factor also did not significantly differ between species, though the average was highest for *Lecythis*, followed by *Simarouba* and *Pithecellobium*.

The mortality of six of the *Pithecellobium* saplings provided further insights into the light requirements of that species. The saplings that died during 1990–1991 were those on the low end of the ranges for direct and diffuse site factors for the measured saplings. The four survivors included the saplings with the first, second, third, and fifth highest diffuse site factor and the saplings with three of the four highest direct site factors. The surviving sapling with a low direct site factor had the highest diffuse site factor of the *Pithecellobium* as well as the second largest leaf area. The diffuse site factors of the survivors were significantly greater than direct site factors of those that died (Mann-Whitney U test, $P < 0.01$). The four *Pithecellobium* saplings that survived included the three with the largest leaf areas in 1990. The surviving sapling with a low leaf area had the largest direct site factor of all the *Pithecellobium* saplings.

Sapling gas exchange

Although the ranges of direct and diffuse site factors were similar for saplings of the three species, the leaf gas exchange properties were quite different (Figure 1). Light-saturated photosynthesis rates were highest for *Simarouba* and lowest for *Lecythis*. A_{max} values for *Lecythis* were very low, less than half those of *Simarouba*. Leaf specific weights of *Simarouba* (32.9 g m^{-2}) and *Lecythis* (32.4 g m^{-2}) were similar. As a result, the relative difference in A_{max} between the two species on a leaf weight basis was comparable to that of A_{max} on an area basis. In contrast, the leaf specific weight of *Pithecellobium* (17.4 g m^{-2}) was lower than those of the other two species and as a result, A_{max} on a leaf weight basis was highest for *Pithecellobium*.

Variability of photosynthesis within the individual saplings was similar for all three species; coefficients of variation of A_{\max} averaged 18.7, 21.7, and 21.4 for *Lecythis*, *Pithecellobium*, and *Simarouba*, respectively. The absolute range of A_{\max} for all ten saplings was greatest for *Pithecellobium* and lowest for *Lecythis*. All three species had positive average photosynthetic rates under photon fluxes between 15–20 $\mu\text{mol m}^{-2} \text{sec}^{-1}$, with the highest rates found for *Lecythis* and lowest for *Simarouba*. The pattern of dark respiration was consistent with that of photosynthesis at understorey diffuse light levels; dark respiration rates were highest for *Simarouba* and lowest for *Lecythis* with rates averaging 0.72, 0.50, and 0.39 $\mu\text{mol m}^{-2} \text{sec}^{-1}$ for *Simarouba*, *Pithecellobium*, and *Lecythis* respectively. Significant species differences were found for all three measures of leaf gas exchange ($P \leq 0.01$).

Correlation analysis

Sapling growth characteristics were tested for correlations with sapling light environment and physiological characteristics (Table 2). For those saplings that lost height as a result of physical damage, height growth was treated as zero (Clark & Clark 1992), although eliminating damaged individuals from the analysis did not change the level of significance of any correlation. Crown illumination index was significantly positively correlated with diameter growth of *Simarouba* for both 1989–90 and nearly so for 1990–91, but not with either height or diameter growth of the other two species. Direct site factor was significantly correlated with height growth of *Simarouba* for 1990–1991 and nearly so for diameter growth of *Simarouba* and *Lecythis* for 1990–91. Diffuse site factor was

Table 2. Correlation coefficients (r) between sapling growth and light environment and leaf characteristics for saplings of three species of Costa Rican rain forest trees ($N = 10$). An asterisk indicates correlation is significant at $P \leq 0.05$. Plant A_{\max} is the maximum light-saturated photosynthesis value measured for a sapling.

| | 1989–1990 growth | | 1990–1991 growth | |
|-----------------------|------------------|----------|------------------|----------|
| | Height | Diameter | Height | Diameter |
| <i>Lecythis</i> | | | | |
| Crown illumination | -0.08 | -0.01 | 0.28 | -0.02 |
| Direct site factor | 0.47 | 0.44 | 0.25 | 0.62 |
| Diffuse site factor | 0.69* | 0.11 | 0.68* | 0.69* |
| Leaf area | 0.86* | 0.28 | 0.71* | 0.84* |
| Plant A_{\max} | 0.41 | 0.36 | 0.15 | 0.57 |
| <i>Pithecellobium</i> | | | | |
| Crown illumination | 0.24 | -0.16 | — | — |
| Direct site factor | 0.24 | -0.19 | — | — |
| Diffuse site factor | 0.68* | -0.17 | — | — |
| Leaf area | 0.94* | -0.38 | — | — |
| Plant A_{\max} | 0.41 | -0.16 | — | — |
| <i>Simarouba</i> | | | | |
| Crown illumination | -0.33 | 0.65* | 0.50 | 0.59 |
| Direct site factor | -0.44 | -0.13 | 0.68* | 0.60 |
| Diffuse site factor | -0.32 | 0.39 | 0.74* | 0.72* |
| Leaf area | 0.21 | 0.51 | 0.38 | 0.17 |
| Plant A_{\max} | 0.17 | 0.71* | 0.74* | 0.56 |

Table 3. Correlation coefficients (r) between leaf characteristics and light environment for saplings of three species of Costa Rican rain forest trees. Mean A_{\max} is sapling average light-saturated photosynthetic rate. Plant A_{\max} is maximum light-saturated photosynthetic rate measured for a sapling. Dark respiration is sapling average dark respiration ($N = 10$). An asterisk indicates correlation is significant at $P \leq 0.05$.

| | Mean A_{\max} | Plant A_{\max} | Dark respiration | Leaf area |
|-----------------------|--------------------|---------------------|---------------------|--------------|
| <i>Lecythis</i> | | | | |
| Crown illumination | -0.62 | -0.59 | 0.60 | 0.25 |
| Direct site factor | 0.07 | 0.13 | -0.12 | 0.54 |
| Diffuse site factor | 0.12 | 0.39 | -0.05 | 0.76* |
| <i>Pithecellobium</i> | | | | |
| Crown illumination | 0.13 | 0.22 | -0.12 | 0.28 |
| Direct site factor | 0.30 | 0.17 | 0.37 | 0.12 |
| Diffuse site factor | 0.08 | 0.20 | -0.44 | 0.71* |
| <i>Simarouba</i> | | | | |
| Crown illumination | 0.56 | 0.49 | 0.06 | 0.32 |
| Direct site factor | 0.39 | 0.51 | 0.52 | 0.02 |
| Diffuse site factor | 0.43 | 0.54 | 0.04 | 0.22 |

correlated with height growth of *Lecythis* and *Pithecellobium* for 1989–90 and height and diameter growth of *Lecythis* and *Simarouba* for 1990–1991. The differences between correlations of *Simarouba* for 1989–90 and 1990–1991 were largely due to the loss of 38 cm height caused by physical damage to the sapling with the largest direct site factor and diffuse site factor. Correlations between growth and light environment and leaf physiological characteristics for the three species were not improved by using relative growth rates rather than absolute growth.

Sapling total leaf area was significantly correlated with height growth of *Lecythis* in both years, with diameter growth of *Lecythis* for 1990–91, and with height growth of *Pithecellobium* for 1989–90. Maximum photosynthesis was significantly correlated with sapling diameter growth of *Simarouba* in 1989–1990 and height growth of *Simarouba* the following year. Dark respiration was not significantly correlated with any growth parameters.

Sapling leaf characteristics were tested for correlations with light environment (Table 3). Crown illumination index and direct site factor were not significantly correlated with any of the characteristics examined. However, diffuse site factor was significantly correlated with leaf area of both *Lecythis* and *Pithecellobium*.

DISCUSSION

The results of the present study indicate that small saplings (<3 m height) of three species with different regeneration patterns differ only slightly in light environment and growth rates. These results agree with previous comparisons of small saplings of species with different regeneration patterns (Clark & Clark 1992, Oberbauer *et al.* 1988, 1989). For example, a comparison of sapling light environment of *Lecythis* with that of *Dipteryx panamensis* (Pitt.) Record & Mell, a gap species, revealed that *Dipteryx* was found in only slightly brighter micro-

sites than *Lecythis* (Oberbauer *et al.* 1988). Likewise, *Pithecellobium* was growing in only slightly brighter microsites than *Miconia guianensis* Aubl., a shade species (Oberbauer *et al.* 1989). Thus, although light environment differences among saplings of these species are small in absolute terms, the large species differences in leaf gas exchange found in the present study suggest that slight differences in light environment can be of considerable importance to sapling performance, and, along with differences in carbon allocation, help explain how similar height and diameter growth are possible given the large species differences in leaf area. The shade species, *Lecythis*, had substantially lower dark respiration rates and higher photosynthesis than the other species at understorey diffuse light levels, a finding that is consistent with the presence of *Lecythis* saplings at the lowest direct site factor. In contrast, saplings of *Pithecellobium* and *Simarouba* had considerably higher photosynthesis at high light, suggesting they should have greater carbon gain under the direct light of sunflecks (Hogan 1988), if there are not substantial differences in the photosynthetic induction characteristics (Chazdon & Pearcy 1986a,b, Pearcy 1988) among the species. The photosynthetic induction characteristics of these species growing under forest understorey conditions are unknown.

The results of this study are consistent with predictions of photosynthetic rates and light environments for tree species of different life history strategies (Bazzaz 1984, Bazzaz & Pickett 1980, Riddoch *et al.* 1991). As expected, the shade species, *Lecythis*, had the lowest photosynthetic and respiration rates and was found in the darkest sites. In addition, the coefficient of variation of A_{\max} for *Lecythis* was lower than those of *Simarouba* and *Pithecellobium* saplings, even though the coefficient of variation for direct site factor for *Lecythis* (45.6) was greater than that of *Pithecellobium* (16.9) or *Simarouba* (33.0). This result is consistent with the finding by Fetcher *et al.* (1987) that light acclimation in *Lecythis* is small.

Gas exchange differences are also consistent with sapling architectural differences. Both *Simarouba* and *Pithecellobium*, with their single growing point, pole morphology, increase in height with any increase in leaf area, a pattern that will ultimately lead to improved leaf light environment with minimum biomass allocation (Hogan 1988). Their higher photosynthetic capacity should allow them to take better advantage of higher quantum fluxes than *Lecythis*. In contrast, the shrub-like morphology of *Lecythis*, in which leaf area is added without concomitant increases in height, is consistent with maximizing light capture in a low light environment. Also, the low photosynthetic rates and low light acclimation capacity of *Lecythis* preclude any great advantage to allocation to rapid height growth. Interpretation of gas exchange characteristics in relation to architecture would be further aided by information on carbon allocation in these species. Unfortunately, little is known about carbon allocation in these species, particularly for allocation to below-ground structures.

The differences between species gas exchange were large given the small differences in sapling light environment. This finding emphasizes that for non-

pioneer tree species (Swaine & Whitmore 1988), even those that are fast-growing, seedlings germinating in a relatively bright site have a high likelihood of being overtopped and suppressed by the existing saplings and trees. As a result, small saplings of most tree species, regardless of their life history pattern, will be found in relatively similar low light environments in the first few metres of height in the forest understorey. The *Pithecellobium* in this study represent such a case of saplings being overtopped during gap closure. Most of the *Pithecellobium* saplings were fairly close to each other under a low canopy of building-phase forest that may have been the remnant of a single large gap. The sapling mortality in the darker sites suggests that the minimum light environment in which a *Pithecellobium* sapling can survive was higher than indicated by the minimum direct site factor in 1990. Based on observations of growth and light environment of larger saplings (Clark & Clark 1992), we had expected that *Pithecellobium* would have higher light requirements than *Simarouba*, an idea supported by the minimum direct site factor at which saplings were found and mean A_{\max} on a leaf weight basis, but not by the mean direct site factor. The discrepancy may have occurred because six of the *Pithecellobium* were apparently declining at the time of measurement.

The strongest correlations with growth were found for leaf area, an expected result given that leaf area is the carbon principal by which plants acquire further biomass. In the case of *Pithecellobium*, leaf area, along with diffuse site factor and direct site factor, provided a strong basis for interpretation of the pattern of sapling mortality. Also notable were the differences in strength of correlations with light environment and leaf area between 1989–1990 and 1990–1991. Difference in correlations from year to year can be in part explained by the finding that the growth of small saplings is not strongly correlated from one year to the next (Clark & Clark 1992). Both height and diameter growth of *Lecythis* and *Simarouba* over 1989–1990 were not significantly correlated with growth the following year, probably because small changes in light environment and physical damage have potentially large effects for trees of this size.

The results of the correlation analysis also suggest sapling performance is associated with both direct light (sunflecks) and diffuse light; direct or diffuse site factor was significantly correlated with some measure of growth for all three species. While the amount of sunflecks has a very large effect on the total amount of light received at a site and on leaf carbon gain (Chazdon 1988, Pearcy 1983, Pfitsch & Pearcy 1989a,b), for all three species in the present study, diffuse site factor tended to be more strongly correlated with growth and leaf area than direct site factor. If a single factor consisting of direct site factor weighted by 0.33 and diffuse site factor weighted by 0.66 is tested against growth, correlations were stronger than those of diffuse site factor alone for both *Simarouba* and *Lecythis*. In the case of *Pithecellobium*, the significance level of a comparison of the light environment of the surviving saplings versus that of those that died can be improved over diffuse site factor alone by using a similar weighting. These findings are consistent with the results of Rich *et al.*

(1993), who found that such a weighting of diffuse site factor and direct site factor gave the closest correspondence to long term measures of photosynthetic photon fluxes in forest understorey. The basis for this finding in part lies in the high frequency of cloud cover at La Selva, where a very large proportion of the photosynthetically active radiation is received as diffuse light. For 17 days of sampling in May 1992 during a period with almost no rainfall, diffuse light accounted for 42% of the incoming photon flux density. These results suggest that in cloudy sites such as La Selva, photographic estimates of diffuse light may be a better predictor of sapling performance in the understorey than direct light.

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