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Comparative analysis of photosynthetic light environments within the crowns of juvenile rain forest trees

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Summary

Irradiances within the crowns of saplings of two tropical tree species were simultaneously compared in primary rain forest in Costa Rica. The species examined, *Minquartia guianensis* Aubl., a relatively slow-growing, canopy species, and *Pithecellobium pedicellare* (DC) Benth., a less-tolerant, emergent species, have different crown and leaf display patterns. Crown light environments were assessed by placing arrays of quantum sensors among leaves and recording at 5-s intervals for seven days with microloggers.

Median total daily quantum flux densities for saplings of both species were less than 2% of full sun and did not differ significantly. More than 90% of the measurements within the crowns of these saplings were less than 25 µmol m^{-2} s^{-1}. Spatial variability of photon flux densities within sapling crowns was similar for the two species despite differences in leaf display patterns. In saplings of both species, photon flux densities varied significantly over the relatively short distances within crowns and from day to day. Height growth of both species was significantly correlated with total daily photon flux densities and with percentage of full sun. However, only the tolerant species, *Minquartia*, showed a significant correlation between diameter growth and crown light environment.

Introduction

Studies of the regeneration of tropical trees have primarily focused on seedlings because of their abundance and the dynamic nature of sapling populations (see for example, Augspurger 1984, Becker and Wong 1985, Clark and Clark 1985, Clark and Clark 1987*a*). While much can be learned from seedling studies, the probability that a seedling under study will survive to contribute to the adult cohort is very small, particularly for rare, long-lived, and fast-growing species (Clark 85, Clark 1986). Unlike seedlings, saplings of many tropical species are relatively rare and, as a result, there is very little information on the biology and microsite distribution of trees in the intermediate stages of growth between seedling and adult, and almost no data on their light environment (Oberbauer et al. 1988).

In this study we report on the light environments occupied by saplings of two species of rain forest trees differing in tolerance *sensu* Spurr and Barnes (1980), where tolerance is the relative capacity of a forest plant to survive and thrive in the understory. The species compared were *Minquartia guianensis* Aubl., a tolerant, canopy species, and *Pithecellobium pedicellare* (DC.) Benth., a less-tolerant, emergent species. Saplings of *Minquartia* are relatively common, slow-growing, and have high survival rates (Clark and Clark, unpublished data). Crowns of *Minquartia* saplings are multi-branched with many leaves. *Pithecellobium* saplings are rare, potentially fast-growing, and have lower survival rates than *Minquartia* saplings (Clark and Clark, unpublished). Crowns of *Pithecellobium* have a few large, bipinnately compound leaves arranged on a single vertical axis. Both *Minquartia* and *Pithecellobium* are included in a long-term study of the growth, demography, and ecophysiology of rain forest trees (Clark and Clark 1987*b*).

The objective of this study was to quantify the crown light environments of saplings of rain forest trees with different regeneration and leaf display patterns to determine if saplings of tolerant species were growing in more shaded sites than those of less tolerant species and if long-term growth could be related to light environment. In a similar study, Oberbauer et al. (1988) compared the light environments of saplings of a slow-growing, tolerant, emergent species with an emergent species classified as gap-dependent. The height growth of both species was significantly correlated with daily total photosynthetic photon flux densities.

Materials and methods

Study site

Measurements were made at the La Selva Biological Station of the Organization for Tropical Studies. La Selva is located in the Atlantic lowlands of Costa Rica (83°59′ W, 10°26′ N) in tropical wet forest (Hartshorn 1983). Detailed descriptions of the site can be found in Hartshorn (1983) and Lieberman et al. (1985). Rainfall at the site averages approximately 4 m annually (Organization for Tropical Studies, unpublished data). On average, January through April receive less rain than do the remaining months. Measurements were made from November 16, 1986 to March 13, 1987.

Light environment within sapling canopies

Photosynthetic photon flux densities (PPFD) were measured within the crowns of saplings with microloggers (CR-21X, Campbell Scientific, Inc., Logan, UT, USA) with gallium arsenide phosphide (GaAsP) photodiodes (Hamamatsu G1118, Hamamatsu Corporation, Middlesex, NJ, USA). The spectral response of the G1118 photodiode is nearly identical to that of the NEC PH201A (L. Giles, unpublished data) used by Gutschick et al. (1985) and Chazdon and Field (1987). Sensors were calibrated every two weeks with a quantum sensor (Li-190, Li-Cor Inc., Lincoln, NE, USA) under a metal-halide, multivapor lamp. The regressions of photodiode output against quantum sensor readings were always linear with $r^2 \geq 0.99$.

Sensors were scanned at 5-s intervals and the data recorded as means, maxima, minima, and histograms at half-hour intervals between 0430 and 1830 h solar time. Data in histograms were stored in 25 μmol m^{-2} s^{-1} increments between 0 and 1000

μmol m^{-2} s^{-1}. A more detailed description of the measurement procedures can be found in Oberbauer et al. (1988). A quantum sensor (Li-190) placed in a large clearing was monitored at the same time as the sensors placed on saplings to provide a reference value for the daily weather variations. Henceforth, measurements made in the large clearing will be referred to as full sun.

The species were compared by simultaneously measuring one sapling of each species over a seven-day period. Ten saplings of each species in the 1.5- to 3.5-m height class were chosen from natural populations growing in undisturbed forest. We selected saplings to represent the entire range of annual height increments for each species in this size class; sample individuals were therefore selected on the basis of performance, not on the basis of the microhabitats they occupied. For both species, the height and diameter growth of saplings measured for light environment did not differ significantly from that of the remaining individuals in the population of the same size class. This result suggests that the saplings measured for light environment were representative of the population as a whole in terms of growth and microsite. The sites in which saplings were found ranged from locations covered by three or more canopy layers of other trees to a recently formed gap. Saplings within the 1- to 3.5-m height class were paired on the basis of their intraspecific annual height growth for 1985–1986; for example, the *Minquartia* sapling with the largest height growth increment was paired with the *Pithecellobium* sapling with the largest height growth. Because light environment measurements were made from November 1986 to March 1987, we used 1986–1987 growth data to compare growth with crown light environment rather than the 1985–1986 data that were the basis for the pairing of saplings. Interestingly, the Spearman's rank correlation between height growth in 1985–86 and that in 1986–87 was not significant for *Minquartia* ($r_S = 0.53$) and was significant only at the 5% level for *Pithecellobium* ($r_S = 0.63$), suggesting that we were unsuccessful in matching pairs of saplings in accordance with their long-term growth.

Fifteen or 16 sensors were placed within the crowns of each sapling. Sensors were distributed within the crowns by eye to provide the most even coverage of the sapling leaf area, that is, so that the density of sensors within the leaf area was approximately the same throughout the sapling crown. Sensor angles and azimuths were positioned to match that of the nearest leaf. In the case of the simple leaves of *Minquartia*, sensors were positioned on the edge of leaves rather than through them (Gutschick et al. 1985) to avoid leaf damage, whereas for the compound leaves of *Pithecellobium*, sensors were placed among leaflets.

Sapling crown characteristics

Leaf areas and distribution of leaf area in the crown of each sapling were estimated and recorded. Leaf areas of *Minquartia* were determined by measuring the area of leaf tracings. Estimation of the areas of the bipinnately compound leaves of *Pithecellobium* was more complex. The outlines of the leaves were imprinted on photosensitive paper. The images were photographed and the areal coverage of these images was then analyzed with a video image-processing system (Rich 1988).

Statistical analysis

The base data set consisted of the half-hour means of the irradiance measurements taken every 5 s for each of 15 or 16 sensors per saplings and their frequency distribution. Frequency distributions for each sensor were averaged for each day and week to produce mean frequency distributions. Daily irradiance totals for each sensor were computed by averaging the half-hour means. Sapling daily and weekly totals were calculated by averaging sensor daily totals. Coefficients of variation were calculated for two levels of variability; coefficients of variation in PPFD among saplings were calculated using the sapling daily totals ($n = 70$), and coefficients of spatial variation within the crowns of saplings were calculated using the sensor daily totals ($n = 15$ or 16). Because the data tended to be nonnormally distributed with heterogeneous variances, statistical analyses were done using nonparametric tests (Conover 1980). Comparisons between species were made with the Wilcoxon signed rank test. Friedman's method was used for two-way comparisons.

Results

Comparison between species

Growth Although the species did not differ significantly in height and diameter, *Minquartia* saplings had a leaf area ten times that of *Pithecellobium* saplings (Table 1). The average annual height and diameter growth increments of *Minquartia* saplings were five and three times those of *Pithecellobium* saplings, respectively, but the differences were not significant. Much of the diameter growth observed in the *Minquartia* saplings was attributed to the growth of a single sapling located within a gap.

Table 1. Morphological and growth characteristics for *in situ* saplings of *Minquartia guianensis* and *Pithecellobium pedicellare* compared for crown light environments. ($n = 10$ except for diameter growth of *Pithecellobium* where $n = 9$). Parenthesis enclose the range of values. P values are for results of Wilcoxon signed rank test.

	Minquartia	*Pithecellobium*	P
Mean height 1987 (cm)	200 (114 – 314)	172 (117 – 315)	0.13
Mean diameter 1987 (mm)	11.8 (7.2 – 18.1)	8.7 (5.4 – 17.7)	0.07
Diameter growth 1986 – 87 (mm)	1.6 (−0.2 – 3.9)	0.5 (−0.1 – 1.4)	0.07
Height growth 1986 – 87 (cm)	26.6 (5.4 – 63.7)	5.1 (−23.3 – 26.1)	0.13
Leaf area (m^2)	1.01 (0.25 – 3.56)	0.09 (0.01 – 0.48)	0.0001

Light environment Total irradiance in full sun averaged 27.9 mole m^{-2} d^{-1} (range 6.9 to 46.1 mole m^{-2} d^{-1}, $n = 65$ days). Clouds strongly influenced the daily radiation regime as illustrated by the large difference between the mean and maximum total daily irradiances in full sun.

The median total daily sapling irradiance was similar and not significantly different for the two species as tested by Wilcoxon signed rank test (0.37 mole m^{-2} d^{-1} for *Minquartia versus* 0.44 mole m^{-2} d^{-1} for *Pithecellobium*, Figure 1). The data were highly skewed; as a result, when means were compared, *Minquartia*, the tolerant species, had a higher total daily PPFD than *Pithecellobium*, the less tolerant species. This difference was primarily a result of the *Minquartia* sapling growing in a gap. When this sapling was excluded from the data set, the mean was nearly identical to that of *Pithecellobium*. The median total daily PPFD for both species amounted to less than 2% of the simultaneously measured full sun value and did not differ significantly (Table 2). Some individual saplings of both species occupied sites that received 0.5% or less of full sun. In contrast, the *Minquartia* sapling in the gap averaged more than 10% of full sun. With or without the sapling in the gap, intersapling variation was greater for *Minquartia* than for *Pithecellobium* as measured by coefficient of variation for sapling daily totals (Table 2).

For both species, the mean frequency distributions indicate that the PPFD was less than 25 µmol m^{-2} s^{-1} for more than 90% of the measurements (Figure 2). *Minquartia* received a larger fraction of PPFD above 25 µmol m^{-2} s^{-1} than did *Pithecellobium*, largely due to the sapling in the gap. The mean frequency distribution of the two species differed significantly ($P < 0.05$ as tested by the Kolmogorov-Smirnov statistic).

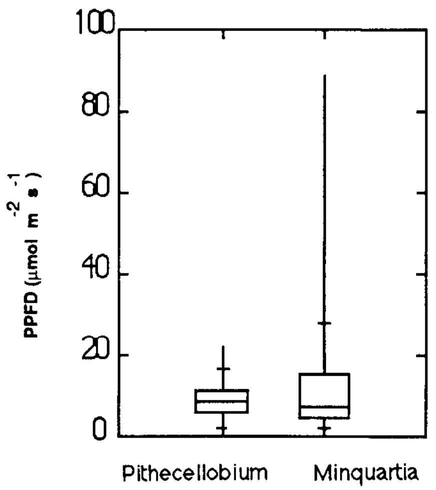

Figure 1. Variation in daily photosynthetic photon flux densities for saplings of *Minquartia guianensis* and *Pithecellobium pedicellare*. Data are based on mean daily crown PPFD of 10 saplings measured for 7 days ($n = 70$ sapling-days per species). Internal horizontal bars represent median values for each species. Boxes enclose 25th and 75th percentiles, external horizontal bars indicate 5th and 95th percentiles, and vertical bars extend to the range.

Table 2. Daily irradiance totals as percentage of full sun for saplings of *Minquartia guianensis* and *Pithecellobium pedicellare*. Medians and means are based on seven days observation of ten individuals per species.

	Daily % of full sun				
Species	Median	Mean	CV	Range	*n*
Minquartia	1.70	2.61	111.3	0.3–13.8	65
Minquartia[1]	1.60	1.68	55.2	0.3 – 4.3	58
Pithecellobium	1.50	1.71	49.3	0.5 – 4.0	65

[1] *Minquartia* values with sapling growing in gap excluded.

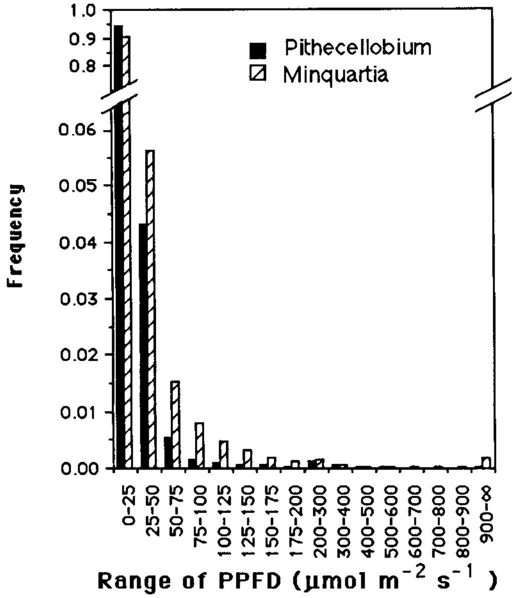

Figure 2. Frequency distributions of PPFD within the crowns of saplings of *Minquartia guianensis* and *Pithecellobium pedicellare*. *n* = 10 saplings for each species.

If PPFD values greater than 50 µmol m^{-2} s^{-1} are assumed to be sunflecks (Chazdon 1986), then *Minquartia* saplings on average received 33.2 min of sunflecks per day with a range of 1.1 min to 241 min. When the *Minquartia* sapling growing in the gap was excluded, mean minutes in sunflecks for that species was lowered to 10.2 min. In comparison, *Pithecellobium* saplings received an average of 10.7 min of sunflecks with a range of 0.5 min for the shadiest location and 18.4 min for the brightest location.

The species also differed significantly ($P < 0.0001$, $n = 1047$, Kruskal-Wallis test) in time of day when the maximum half-hour of irradiance occurred. *Pithecellobium* received less of its maximum insolation in the afternoon than did *Minquartia* (Figure 3).

Within crown variation in PPFD

Despite differences in crown structure between the two species, spatial variability of irradiance within crowns was similar for both. Mean coefficients of variation of sensor daily totals, which represent the variability across the 15 or 16 sensors within a crown, averaged more than 120 for both species (Figure 4) and were not significantly different as tested by Wilcoxon signed rank test. The mean coefficient of variation for *Minquartia* (122) was slightly lower than that of *Pithecellobium* (135). Spatial variability within the crown was significantly correlated to the sapling percentage of full sun for *Minquartia* ($r_S = 0.83$) but not *Pithecellobium* ($r_S = -0.09$, Figure 4).

To test for spatial and temporal variation within the sapling crowns, Friedman nonparametric two-way analysis of variance (Conover 1980) of PPFD for each sapling was done using days and sensors as categorical variables. For all saplings of both species, significant effects ($P < 0.0005$) were found for both days and sensors (position within the crown).

For both species, the half hour with the greatest mean PPFD for each day occurred most often between 1200 and 1300 h solar time. For *Minquartia*, maxima decreased symmetrically toward earlier and later in the day (Figure 3), whereas *Pithecellobium* showed the previously mentioned reduction of afternoon maxima. Both species

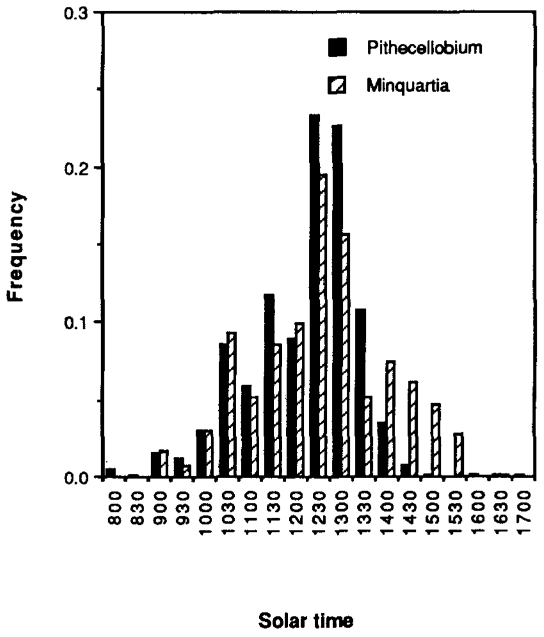

Figure 3. Distribution of times of occurrence for the daily maximum half hour of irradiance within the crowns of *Minquartia guianensis* and *Pithecellobium pedicellare*. $n = 1047$ sensor days.

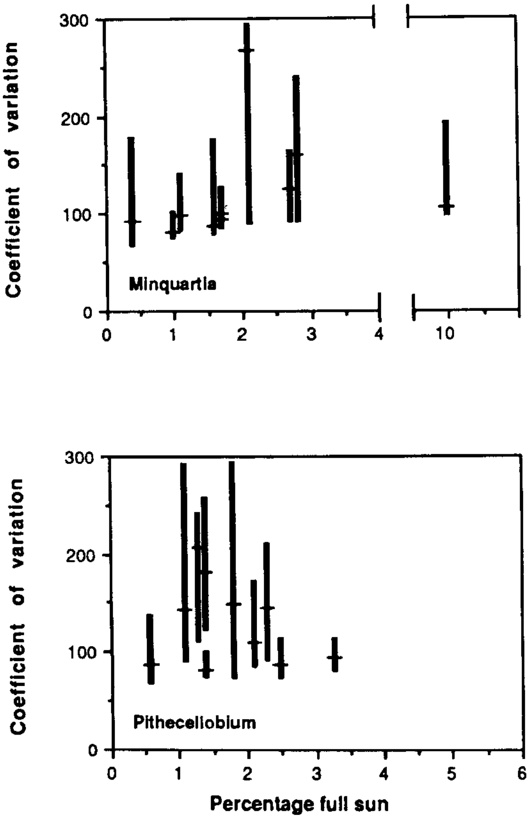

Figure 4. Daily intracrown spatial variation in PPFD for saplings of *Minquartia guianensis* and *Pithecellobium pedicellare*. Horizontal bars indicate median coefficients of variations (CV) for PPFD within a sapling crown and vertical bars span the range of CV (n = 7). Saplings are arranged in order of increasing daily percentage of full sun.

showed an early morning peak between 1000 and 1030 h solar time suggesting that lateral light through the canopy in the morning may make an important contribution to total PPFD.

Friedman nonparameteric two-way analysis of variance (Conover 1980) of the time of maximum half hour of irradiance was done using sensor (position within the sapling crown) and day (of the seven-day measurement period) as categorical variables. For all 20 saplings, there was a significant effect of day indicating that the maximum irradiance did not occur at the same time every day. For five of the *Minquartia* saplings and four of the *Pithecellobium* saplings, a statistically significant sensor effect was found indicating that different positions within the same crown received their maximum irradiances at different times of day.

Crown light environment and growth characteristics

Annual diameter and height growth of the saplings from 1986 to 1987 were tested for correlations with crown light environment characteristics. Mean total daily PPFD and percentage of full sun were significantly correlated with height growth of both species (Table 3). For *Pithecellobium*, the correlation between diameter growth and both measures of crown light environment were very weak and not statistically significant. In contrast, the correlations between the measures of crown light environment and diameter were highly significant for *Minquartia* (Table 3). Diameter growth was also significantly correlated with sapling leaf area for *Minquartia* but not *Pithecellobium*. Strong correlations were found for *Minquartia* between both measures of growth and an index of intercepted irradiance, (leaf area × total daily PPFD).

Discussion

The light environments occupied by 1- to 3.5-m tall saplings of the tolerant emergent species, *Minquartia guianensis*, and the much less tolerant emergent species, *Pithecellobium pedicellare*, were surprisingly similar. Based on detailed analysis of crown lighting for saplings across the observed range of performance of each species in primary forest (from the fastest- to the slowest-growing individuals), there was no significant difference in sapling light environments for these two tree species of different tolerance characteristics. This finding confirms the work of Clark and Clark (1987*b*), who found very similar canopy position indices (an estimate of light environment) for saplings of these species. In the present study, we found that median irradiance environments for both species were less than 2% of full sun, levels of irradiance considered characteristic of the understory (Björkman and Ludlow 1972, Pearcy 1983, Chazdon and Fetcher 1984, Chazdon 1986). Some saplings of both species were found in sites with 0.5% or less of full sun.

The finding that the greatest sapling total daily PPFD and the greatest range of light environments were found for the tolerant species, *Minquartia*, seems inconsistent with the perceived regeneration types for these species. However, the results were strongly influenced by the presence of a single sapling in a gap. Because gap

Table 3. Spearman's rank correlations (r_S) between 1986–1987 growth characteristics and crown light environment for *Minquartia guianensis* (*Mg*) and *Pithecellobium pedicellare* (*Pp*). $n = 10$ for all comparisons except for diameter growth of *Pithecellobium* ($n = 9$).

	Height growth		Diameter growth	
	Mg	*Pp*	*Mg*	*Pp*
Total daily PPFD	0.60*[1]	0.56*	0.87**	0.21
Mean % full sun	0.65*	0.66*	0.87**	−0.10
Leaf area	0.50	−0.10	0.67*	0.23
Leaf area × Total PPFD	0.70*	0.12	0.93**	0.22

[1] * = $P \le 0.05$, ** = $P \le 0.01$.

formation over a sapling is a chance event, the maximum or range of light environments and growth in the case of *Minquartia* is misleadingly high.

Overall, the results suggest that saplings of the two species do not occupy fundamentally different light environments, although the difference in timing of maximum irradiance between the two species is intriguing and merits further investigation. Not only were total daily PPFD values similar for the two species, when the *Minquartia* sapling in the gap was excluded, the mean time in sunflecks was nearly identical for the two species. These results correspond quite closely to those found in a study of saplings of a tolerant and relatively intolerant emergent species (Oberbauer et al. 1988). In that study, the more-tolerant species also had slightly higher mean, but lower median PPFD levels, and both species were growing in less than 2% of full sun. In both that and the current study, the correlation between PPFD and diameter growth of the more-tolerant species was greater than that of the less-tolerant species, and leaf areas of the more-tolerant species were much greater than those of the less-tolerant species. Variability of PPFD within the crowns of the species examined by Oberbauer et al. (1988) was very high and similar to that found in the present study; coefficients of variation for intracrown irradiance of all four species ranged from 122 to 141, despite differences in crown architecture. This lack of differences between species may be explained by the results of Chazdon et al. (1988), which suggest that much of the variability in irradiance within the crowns of understory plants is a result of understory environmental conditions rather than crown architecture.

The results of the present study and that of Oberbauer et al. (1988) have shown that tropical wet forest tree species with differing tolerance characteristics can occupy extremely similar light environments as saplings. The data demonstrate that all four species can survive as saplings in sites of low irradiance, and that they all show growth responses to small differences in PPFD in such sites. Nevertheless, consistent interspecific differences in several characteristics suggest that the more tolerant species, *Minquartia* (this study) and *Lecythis* (Oberbauer et al. 1988), have more positive carbon balances than the less-tolerant species *Pithecellobium* (this study) and *Dipteryx* (Oberbauer et al. 1988). In both studies the more-tolerant species had greater leaf area, greater branching, and relatively greater diameter than the intolerant species. In the present study, of the saplings found at light levels below 0.5% of full sun, only those of the tolerant species, *Minquartia*, exhibited positive growth.

These studies have examined the light environments of one size class of saplings, based on one week of measurement per sapling. When compared in this way, the four species are impressively similar. When the long-term success of saplings is known, however, there may well be significant interspecific differences in the light environments of those individuals which recruit to the next size class. Evaluating this possibility will require both detailed short-term measurement of crown light environments and on-going demographic study of saplings over their potential range of forest microsites.

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