Seasonal and Spatial Variation in the Light Environment in a Tropical Dipterocarp Forest and Gaps

James W. Raich
The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts 02543, U.S.A.

ABSTRACT
Incoming photosynthetically active radiation was continuously monitored for almost one year in closed-canopy dipterocarp forest and in two forest gaps. Mean weekly photosynthetic photon flux densities (PPFD) in the forest and in the small and large gap sites averaged 1.9, 8.3, and 37 percent respectively of the PPFD in the open. There was no apparent seasonality of PPFD in the open, but there was pronounced seasonal variation of PPFD in the forest and gap sites. Therefore, seedlings within forest gaps may be exposed to very different light regimes over the course of the year. Mean daily PPFD was highly correlated with canopy coverage in both short-term and long-term experiments. A short-term study indicated that light penetrating through canopy openings can increase the PPFD near ground level at least 20 m inside the forest from the nearest gap. Forest gaps are not discreet areas, they are environmental continua in both space and time.

Mature, evergreen, lowland tropical rain forests cast a dense shade: only 0.4–3.8 percent of the incident photosynthetically active radiation (PAR) reaches the understory (Chazdon & Fether 1984b). Thus, seedling growth in the understory is suppressed. Forest gaps allow more light to reach the understory, and this phenomenon is important to tropical forest regeneration (e.g., Hartshorn 1978). Nevertheless, little information is available concerning the effects of gaps on photosynthetic light regimes in tropical forests. Presented here are the results of a one-year study of the light regimes in closed-canopy lowland dipterocarp forest, and in two adjacent forest gaps.

STUDY AREA AND METHODS
All work was conducted in the Pantai Acheh Forest Reserve on the north end of Penang Island, Malaysia (5°28’N, 100°12’E). Mean rainfall is about 2.8 m, and temperatures average about 28°C. The forest is classified as coastal hill dipterocarp forest sensu Wyatt-Smith et al. (1963). It is evergreen, with only a few species shedding their leaves during the 1–3 month dry season (January–March). The canopy is uneven; emergents range from 30 to 57 m in height (Gong & Ong 1984). Additional details of forest structure, floristics, and climate are provided by Ong and Gong (1979), Gong and Ong (1984), Raich (1987), and Raich and Christensen (1989).

Photosynthetically active radiation was monitored in three sites on a north-facing slope of 22°, at an elevation of about 180 m. Two sites, a large and a small gap, were separated by about 5 m of undisturbed vegetation. The third site, in closed-canopy forest, was 50 m uphill from the gap sites. The large gap was overgrown with bermia (Engeiorea triste Griff., Arecaceae) and the rhizomatous fern Dichroanthera sp. (Gleicheniaceae). The former was repeatedly cut back to ground level, and the latter was removed by hand to create a new gap within the old canopy opening. There was little understory vegetation in the small gap. The canopy openings over the large and small gaps covered approximately 100 m² and 15 m² respectively.

Photosynthetically active radiation was measured with line quantum sensors (Li-Cor, Inc., Model LI-191SB) attached to PAR integrators (LI-Cor, Inc., Model LI-510B) which were read weekly. The data provide a spatially and temporally integrated measure of the total incident PAR, including both direct and diffuse radiation, over a one meter by one centimeter area. One sensor was placed beneath the center of the canopy opening in each of the two gap sites; a third was placed in a randomly located closed-canopy forest site, 50 m uphill from the gaps. All three sensors were placed at a height of 25 cm above the soil with their long axes oriented east-west. A fourth sensor was placed on the rooftop of the laboratory building in the Muka Head Biological Station, which is near the seacoast at the base of the hill upon which the other sensors were placed. This latter sensor was used to monitor unobstructed PAR. All sensors were calibrated just prior to the measurements by direct comparison, in the open, with a factory-calibrated sensor that was not used for measurements.

Horizontal variation in PAR within the gaps and adjacent forest was monitored on 28 February 1986, an essentially cloud-free day. On this date a transect was established that extended from the east side of the large gap, through the large and small gaps, and 30 m into the forest to the west of the small gap. Instantaneous spot
measurements of the photosynthetic photon flux density (PPFD) were made at 11 points along the transect 12 times between 0830 to 1700 local time (solar noon was ca 1300). Measurements were made with a Li-Cor, Inc. Quantum Sensor (Model LI-192SB) attached to a Quantum/Radiometer/Photometer (Model LI-185B). The slope of the transect was 1°. Canopy coverage over each point was estimated with a spherical densiometer patterned after that of Lemmon (1957).

RESULTS

The mean PPFD from March 1985 through January 1986 was 31.3 mol·m⁻²·d⁻¹ in the open, with no apparent seasonal variation (Fig. 1). However, there was a dramatic seasonal fluctuation in the amount of PAR that reached the understories of the closed-canopy forest and gap sites (Fig. 1). During July the light regimes in the three sites differed little, whereas in November the sites had very different light environments. Over the course of the investigation the mean PPFD in the forest, small gap, and large gap averaged 1.9, 8.3, and 37 percent respectively of the mean PPFD in the open. Canopy coverage of the three sites averaged 99, 89, and 68 percent respectively, as determined from at least four measurements in each site. Mean PPFD in the four locations in which long-term measurements were made was linearly correlated with canopy coverage:

$$PPFD = -23 \times C + 30 \quad (r^2 = 0.95, P < 0.02)$$

where PPFD = mol·m⁻²·d⁻¹, and C = the arcsine transformation of canopy coverage expressed as a proportion (range = 0–1), in radians. This transformation is recommended by Sokal and Rohlf (1981, p. 427).

The spatial variation of PPFD within individual gaps is large, as demonstrated by spot measurements collected along the 50 m transect on 28 February 1986 (Fig. 2). Mean daytime PPFD at each of the eleven measurement points along this transect, as calculated from the instantaneous readings, was linearly correlated with canopy coverage:

$$PPFD = -336 \times C + 505 \quad (r^2 = 0.81, P < 0.0001)$$

where PPFD = μmol·m⁻²·s⁻¹ and C is as defined above. Although the western edge of the small gap was at 20 m along the transect, light penetrating through the canopy openings clearly increased the understory PPFD at the 40 m point, 20 m from the nearest gap edge.

DISCUSSION

It is widely recognized that treefall gaps are complex, variable environments. However, seasonal and spatial variations of environmental factors within tropical forest gaps remain poorly quantified. The results of this study clearly indicate that more light reached the understory in the sampled gaps than in closed-canopy forest, but the mag-
nitude of the difference varied seasonally. Incident PAR was similar in the forest and gap sites during July; differences among sites peaked during November. The seasonal patterns observed are not readily explained by the topography of the hillside study site, nor by any other measured variable. They nevertheless occurred.

The improved light environment that follows gap formation is unquestionably of importance in promoting the growth and regeneration of seedlings within gaps. The data indicate that even seedlings located up to 20 m from a gap edge may benefit (Fig. 2). However, the amount of PAR received by a particular seedling will depend upon the specific location of that seedling and, at the text site, the time of year. During some months a seedling may be exposed to extended periods of direct radiation; during other months diffuse radiation (sky light) may predomi-
nate. The ability to maximize net photosynthesis over a wide range of light conditions may therefore be of great benefit to the many species that depend upon light gaps for their successful growth to maturity.

Seasonal variation in the light environment has not been considered an important component of tropical forest gap environments. The sun’s position at its zenith fluctuates 46°54' north-to-south over the course of a year (18° north and 29° south at this site). As a result, the ground beneath a canopy opening that is illuminated by direct radiation changes as the sun moves, both seasonally and diurnally. A theoretical discussion of this phenomenon is provided by Lee (1978, p. 181–185). Chazdon and Fetcher (1984a) found no seasonal differences in light availability in understory or gap environments in Costa Rica, despite that unobstructed PPFD varied over the year. Seasonality in the light environment may have been more pronounced in my study site because of the steep topography, or because of differences in cloudiness or the density of understory vegetation.

The close correlation between PPFD and canopy coverage suggests that canopy density measurements can be valuable. We cannot predict PPFD in forests throughout the world from a regression equation derived from measurements in one forest. However, the data indicate that meaningful comparisons of light environments in different locations within a forest can be obtained by measuring canopy coverage alone. Although the specific relationship between PPFD and canopy coverage may vary on slopes of different orientations and among locations, the consistently close correlation between canopy coverage and PPFD indicates that the former has a real value in estimating the latter. Canopy coverage is easily measured; accurate measurements of PPFD over long time periods are difficult and expensive.

My results also emphasize the importance of considering treefall gaps as continua, and not as discreet entities. As the sun moves overhead, so does the “light shadow” that it generates. Gaps receive more light than do forest understory locations (Fig. 1), but so do points up to 20 m from a gap (Fig. 2). This observation may be explained by the leaf distribution in the forest. Yoda (1974) found that ca 70 percent of the incident light was intercepted by the uppermost canopy of a lowland dipterocarp forest in Malaysia. When this canopy is removed, i.e., when a gap is formed, much more radiation can be expected to penetrate the understory layers. Because the sun’s overhead position changes, the total area influenced by a canopy opening is much larger than the canopy opening itself, and varies both seasonally and diurnally.

ACKNOWLEDGMENTS

Particular thanks go to the staff of the Muka Head Biological Station for assisting with the measurements. I thank the Malaysian government for allowing me to work in Malaysia. Laboratory space and equipment were provided by the School of Biological Sciences, Universiti Sains Malaysia, Penang. Light sensors were provided by J. J. Ewel. Gong Wooi Khoon and K. R. Knaap provided valuable assistance. R. L. Chazdon and N. Fetcher provided useful suggestions on an earlier draft of the manuscript. Financial support was provided by a Fulbright Grant to the author. The Ecosystems Center of the Marine Biological Laboratory, Woods Hole, Massachusetts, provided funds for drafting.

LITERATURE CITED


Garden Club of America Scholarships in Tropical Botany

The Garden Club of America is offering two $5,000 awards to assist with field work in the area of tropical botany. Awards will be made on a competitive basis to graduate students conducting field work in the tropics as part of their doctoral dissertation research. The awards will be made on a one-time basis, and applications are due by December 31, 1989. Recipients will be announced by March 15, 1990. There is no application form, however, students must include the following: 1) a curriculum vitae, including graduate and undergraduate transcripts; 2) evidence of foreign language capability; 3) a two-page outline of the proposed research; 4) a letter stating his or her plans for the future, a long term commitment to conservation of tropical forests and an intent to work in the area will add merit to the application; and 5) a letter of recommendation from the advisor, which should include an evaluation of the student’s progress to date. U.S. citizenship is not a requirement, however, students must be enrolled in a U.S. university to be eligible for this scholarship. Please mail applications to: Jane MacKnight World Wildlife Fund/Garden Club of America Scholarships in Tropical Botany World Wildlife Fund, 1250 Twenty-fourth Street, NW, Washington, D.C. 20037.