The Spectral Distribution of Radiation in Two Neotropical Rainforests

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ABSTRACT

The spectral quality of radiation in the understory of two neotropical rainforests, Barro Colorado Island in Panama and La Selva in Costa Rica, is profoundly affected by the density of the canopy. Understory light conditions in both forests bear similar spectral characteristics. In both the greatest changes in spectral quality occur at low flux densities, as in the transition from extreme shade to small light flecks. Change in spectral quality, as assessed by the red : far-red (R:FR) ratio, the ratio of radiant energy 400–700: 300–1100 nm, and the ratio of quantum flux density 400–700:300–1100 nm, is strongly correlated with a drop in percentage of solar radiation as measurable by a quantum radiometer. Thus, by knowing the percentage of photosynthetic photon flux density (PPFD) in relation to full sunlight, it is possible to estimate the spectral quality in the forest at a particular time and microsite.

Knowledge of light climates of tropical rainforests is a necessary background for understanding the physiological ecology of plants growing in them (Mooney *et al.* 1980). The slow progress in the analysis of light climates of these forests is due to their inaccessibility, to a previous lack of instrumentation suitable for field measurements, and to the heterogeneity of light conditions within forests (Anderson 1970, Idso & de Wit 1970, Reifsnyder *et al.* 1970, Hutchison *et al.* 1980). Recent studies on radiation levels in forests have concentrated on the radiation available for photosynthesis (400–700 nm). Chazdon and Fetcher (1984a) have described photosynthetic light environments at a rainforest site in Costa Rica, and Pearcy (1983) has studied the light climate in a Hawaiian forest. In these forest understories, brief sun flecks may contribute well over 50 percent of daily photosynthetic flux density. The importance of the spectral alteration of solar radiation passing through foliage to the development and ecology of plants is coming to be more widely appreciated (Smith 1982). Leaves typically transmit and reflect little radiation in the visible wavelengths (400–700 nm), and do the opposite for wavelengths beyond 750 nm (Fig. 1). Absorptance of radiation by leaves and plant canopies is a function of these two properties (absorptance = 1 − reflectance − transmittance). Therefore, greater canopy density or thickness should spectrally alter the incident solar radiation to a greater extent. A growing body of literature documenting the effects of altered R:FR ratios on plant development (Child *et al.* 1981, Smith 1982) suggests that such changes in the spectral quality of radiation may partly control development in understory plants. Developmental features that may be especially important are those of germination (Vásquez-Yánes 1980, Frankland 1981), stem extension (Morgan & Smith 1980), leaf morphology (Hébant & Lee 1984), and juvenility (Madison 1977).

Although the spectral distribution of radiation may have profound effects on patterns of plant growth and development (Smith 1982), little is known about the spectral quality of light in humid tropical forests (Holmes 1981, Chazdon & Fetcher 1984b). Earlier documentations of temperate forest light climates were given by Coombe (1957) and Federer and Tanner (1966), but these studies suffered from the limitation of using low-resolution, band-pass filters and a silicon sensor. More recently Tasker and Smith (1977b) have characterized precisely the spectral distribution of radiation in temperate woodlands; however, it may be altered in humid tropical forests by their lack of seasonality and the density and height of tree canopies. Björkman and Ludlow (1972) described the spectral distribution of radiation at a rainforest site in Queensland, and Stoutjestijk (1972) reported differences in spectral transmission of radiation at a site in Sumatra, both with limitations of the earlier-mentioned studies. Sasaki and Mori (1981) reported some measurements of spectral distribution of radiation in forests of the Malayan Peninsula.

The purpose of this study was to measure the spectral distribution of radiation at two neotropical rainforest sites, La Selva in Costa Rica and Barro Colorado Island in Panama. Such documentation is relevant to studies on the growth and development of understory plants. An additional purpose was to demonstrate a relationship between solar radiation available for photosynthesis (photosynthetic photon flux density 400–700 nm, or PPFD) as measured by a radiometer and spectral quality. The absorptance of radiation by forest canopy can be described by an equation analogous to the Lambert-Beer Law (Monsi & Saeki 1953). This relationship suggests that the effect on spectral measurements in relationship to a reference of full sunlight above the canopy should be correlated in a manner that allows the estimation of light quality from measurements

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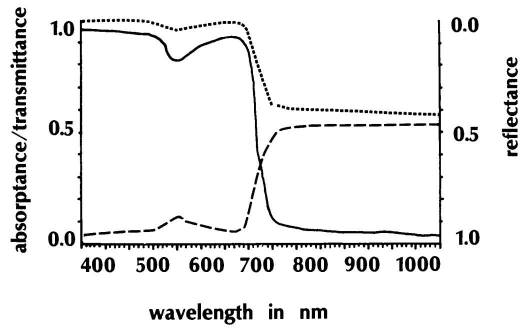

FIGURE 1. Optical properties of the mean of five leaves of *Bursera simaruba* L. (Lee, in press). Dashed line represents diffuse transmittance; dotted line represents diffuse reflectance; and solid line represents absorptance. The leaves of this species absorb 90.7% of PPFD, and absorb only 12.6% of quanta 700–1100 nm.

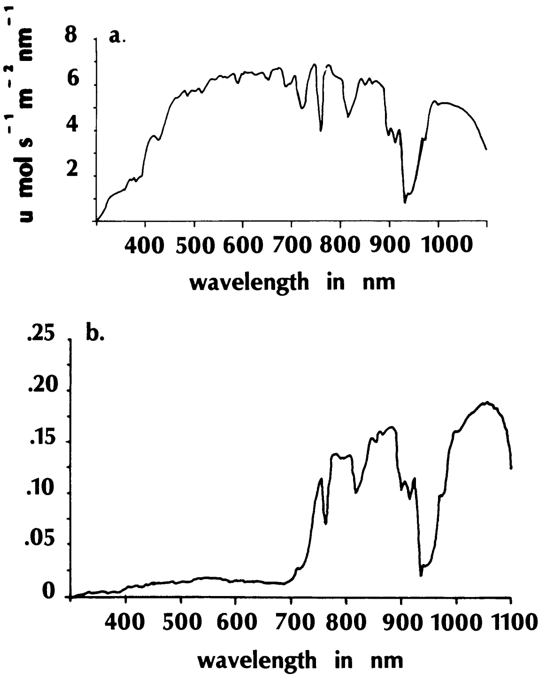

FIGURE 2. Spectral distribution of radiation at two representative rainforest sites. a. Full sun in a clearing at La Selva: PPFD = 1737 μmol/sec/m²; total energy 300–1100 nm = 690 W/m²; and R:FR = 1.28. b. Deep shade in the site at La Selva: PPFD = 5.46 μmol/sec/m² (0.3% of full sunlight); total energy 300–1100 nm = 9.10 W/m² (1.7% of full sunlight); and R:FR = 0.31.

of shade vs full sunlight with an inexpensive quantum radiometer.

METHODS

Measurements of the spectral distribution of radiation were performed with a Li-1800 spectroradiometer (Li-Cor Instruments, Lincoln, Nebraska 68504, U.S.A.). This instrument measures a spectral range of 300–1100 nm (about 75% of the radiant energy of solar radiation), with a half-peak band width of 6 nm. All scans were performed at 2-nm intervals and took approximately 60 sec to complete. The instrument's microcomputer performed the following calculations used in this study: (1) PPFD, or photosynthetic photon flux density, 400–700 nm in μmol/sec/m²; (2) total quantum flux density between 300 and 1100 nm; (3) radiant energy as W/m²; (4) radiant energy at 400–700 nm; and (5) the red to far-red ratio (or R:FR (as defined by Smith [1982] as the quantum ratio between 658–662 and 728–732 nm). All values are given as means plus or minus standard deviations.

Measurements were made at two forest sites. Finca La Selva (10°26′N), at an altitude of 37–100 m in the Atlantic lowlands of Costa Rica, was visited in April 1983 and April 1984. This is mature forest with a discontinuous canopy some 35 m above the ground; annual rainfall is approximately 4000 m, with appreciable amounts every month (Frankie *et al.* 1974). La Selva is a research station of the Organization for Tropical Studies, and radiation was measured at the same level sites used for studies of the diurnal distribution of PPFD (Chazdon & Fetcher 1984a).

Barro Colorado Island (BCI, at 9°9′N) on Gatun Lake, Panama, was visited in June 1983. Radiation was measured in the study site of the Environmental Science Program, a long-term microclimate investigation conducted by the Smithsonian Institution. The forest has not been disturbed for approximately a century (Leigh *et al.* 1983); the site occupies a shallow gully and has a discontinuous canopy some 35 m high.

The results reported here involve measurements taken within the forest under conditions of full sunlight and compared with measurements taken within 30 min in a clearing adjacent to the forest. In none of the measurements was the sun obscured by large branches or trunks of trees. An attempt was made to measure radiation in a variety of sites, including deep shade, light flecks, and gaps. Measurements to compare the spectral quality of sunny and cloudy skies were made in Dade County, Florida, in August 1983.

Unless otherwise stated all measurements were taken within 90 min of the solar zenith with the cosine-corrected sensor oriented horizontally. To determine the relationship of percentage of full solar PPFD to the other parameters, type II regression analyses were performed; regression lines were compared using Bartlett's 3-group method (Sokal & Rohlf 1981). The slopes and origins of lines of the BCI and La Selva data were statistically compared (Kleinbaum & Kupper 1978).

TABLE 1. *Summary of measurements in various light conditions at the BCI and La Selva sites.*

	PPFD*	% PPFD of full sunlight	W/m^2	W/m^2 400–700: 300–1100 nm	R:FR
Full sunlight					
La Selva	$N = 8$				
Mean	1141	100.0	467.1	0.52	1.22
SD	589.8		231.6	0.02	0.07
Range	422.2–1911		1866–774.1	.49–.56	1.14–1.37
BCI	$N = 9$				
	1418	100.0	553.8	0.56	1.33
	292.5		113.2	0.01	0.03
	990–1851		384.1–727.4	.52–.57	1.27–1.40
Gaps					
La Selva	$N = 16$				
	368.0	28.86	175.1	0.40	0.90
	480.9	27.22	218.0	0.06	0.17
	44.41–1603	4.15–90.00	29.46–770.0	.30–.53	.59–1.25
BCI	$N = 6$				
	994.8	67.59	418.0	0.52	1.15
	50.6	21.10	192.3	0.03	0.11
	347.0–1730	37.36–96.11	158.6–702.0	.48–.54	.97–1.17
Flecks					
La Selva	$N = 11$				
	161.9	10.67	69.97	0.36	0.87
	149.9	8.71	61.18	0.10	0.23
	24.24–468.8	1.70–29.73	15.62–171.2	.22–.50	.37–1.17
BCI	$N = 13$				
	111.4	9.30	66.69	0.38	0.95
	95.04	8.10	43.92	0.09	0.23
	17.04–307.2	1.29–13.32	16.75–142.5	.22–.50	.58–1.30
Shade					
La Selva	$N = 20$				
	11.41	1.17	13.27	0.17	0.40
	9.53	0.91	7.11	0.07	0.14
	1.54–36.22	.09–3.76	5.10–30.12	.06–.32	.17–.70
BCI	$N = 35$				
	18.69	1.49	21.29	0.17	0.35
	14.32	1.23	8.96	0.08	0.16
	4.21–44.70	.17–3.64	7.06–42.97	.06–.32	.13–.67

* The numbers of decimal places reflect the accuracy of measurements at the appropriate levels of radiation.

RESULTS AND DISCUSSION

The spectral distribution of radiation on the forest floor is quite different from that in full sunlight. Two typical examples illustrate these differences. The first is of full sunlight versus shade at La Selva (Fig. 2). In full sunlight the total irradiance 300–1100 nm is 690 W/m^2, which represents approximately 75 percent of total radiant energy (Fig. 2A). The range of 400–700 nm contains a significant portion of this amount, 56 percent of total radiant energy and 47 percent of total quantum flux density. The quantum ratio of R:FR is 1.28, which is typical of sunlight. In contrast, a typical understory shade environment at La Selva (Fig. 2B) has low total irradiance (9.10 W/m^2) and less PPFD. The percentage of that above the canopy is 1.7 for radiant energy 300–1100 nm, but only 0.3 of PPFD. This difference in percentage demonstrates the relatively greater availability of radiation above 700 nm in the shade, whether measured as quanta or as energy. The spectral alteration of radiation in the forest shade is shown clearly by the much smaller R:FR of 0.31.

A second example is a series of measurements of 4 light environments at BCI, each measurement plotted relative to that of full sunlight (Fig. 3). A summary of measurements in 3 qualitatively different understory light environments (diffuse shade, sun fleck, and gap) and full sunlight is given for both forests in Table 1. Only flecks of a diameter of less than 0.5 m were measured. Gaps were measured with the sun partly obscured by the surrounding canopy, since measurements with the sun fully

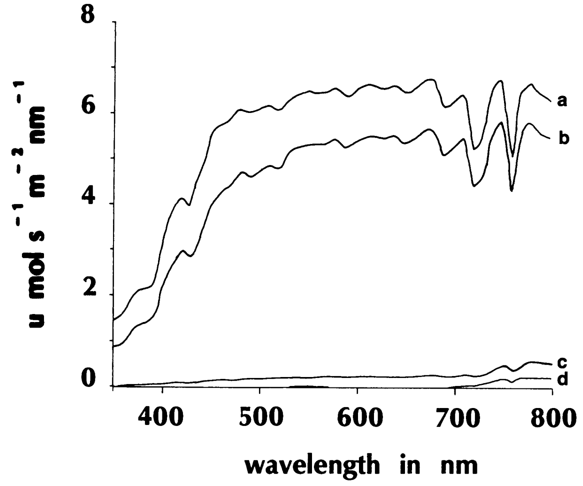

FIGURE 3. Spectral distribution of different levels of radiation at BCI, measured within 60 min of each other. a. Full sun: 1850 μmol/sec/m² of PPFD; 727 W/m² of radiant energy 300–1100 nm; R:FR = 1.27. b. A gap approximately 12 m across with sun partly exposed to the sensor: 1439 μmol/sec/m² PPFD; 576 W/m²; R:FR = 1.20. c. Small light fleck 0.5 m across: 65.72 μmol/sec/m² PPFD; 65.73 W/m²; R:FR = 0.87. d. Deep shade: 4.74 μmol/sec/m² PPFD; 10.73 W/m²; R:FR = 0.19.

exposed were identical to full sunlight in a large clearing. These data are biased by an aim to measure as many light levels as possible and by the subjective determination of what constitutes a fleck versus more open shade or a small gap. Thus, values for shade reported here may be higher than those more systematically measured. For instance, much lower light levels were measured at locations of *Trichomanes elegans* Rich, an extremely shade-adapted, filmy fern growing in a gully in the central part of the La Selva reserve. For 30 measurements adjacent to 8 plants, the mean percentage of full sunlight PPFD was 0.28 ± 0.16 percent, and the mean R:FR was 0.18 ± 0.07 percent. Light flecks were rare at this location, and most of the plants were growing directly under other understory plants. Measurements with the sensor oriented vertically 1 m above the ground and facing north and south at La Selva gave even lower percentages of full sunlight (0.15 ± 0.07%, *N* = 22) and greater spectral alteration (R:FR = 0.10 ± 0.02).

The spectral distributions of solar radiation were slightly different between the two sites. This result is possibly explained by the atmospheric conditions at the times of the measurements. In 1983 the sky at La Selva was extremely hazy from dust and smoke accumulated at the end of the dry season, so the values for PPFD (Table 1) are much lower than would be expected. The sky at BCI (measured at the beginning of the wet season) was clearer. Measurements of dry and very clear skies at La Selva a year later yielded higher PPFD values (2166 ± 245 μmol/sec/m², *N* = 10) and lower R:FR (1.20 ± 0.04). Thus the R:FR ratio and ratios of radiant energy (400–700:300–1100 nm) may be slightly affected by atmospheric conditions. Tasker and Smith (1977a) also observed small differences of spectral quality with different sky conditions.

Values for light flecks and gaps are intermediate between those of full sun and diffuse shade, for both flux density and spectral quality (Table 1). This change in spectral distribution with increase in percentage of full sunlight is documented in Figure 3.

Statistical analysis of data from both sites demonstrates that spectral distribution of radiation is predictably related to the percentage of full sunlight. This relationship is seen

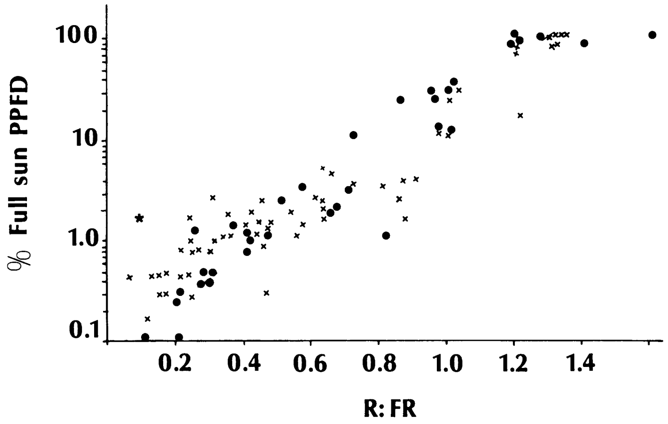

FIGURE 4. Regression analysis of log percentage of full sun PPFD and R:FR of measurements at BCI (X) and La Selva (O). For BCI, Y = −2.760 + 2.000X (r = .967); for La Selva, Y = −3.126 + 2.521X (r = .953). * = mean of 5 measurements within a canopy of *Eichhornia crassipes* Solms (Lee 1985a).

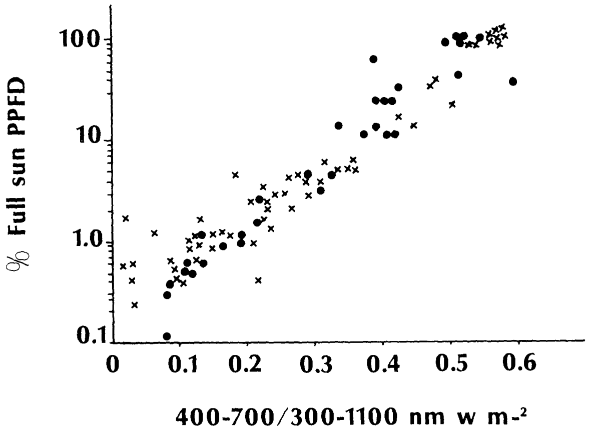

FIGURE 5. Regression analysis of log percentage of full sun PPFD compared to the ratio of W/m^2 400–700:300–1100 nm, symbols as in Figure 4. For BCI, $Y = -2.719 + 5.814X$ ($r = .804$); for La Selva, $Y = -2.897 + 6.638X$ ($r = .962$).

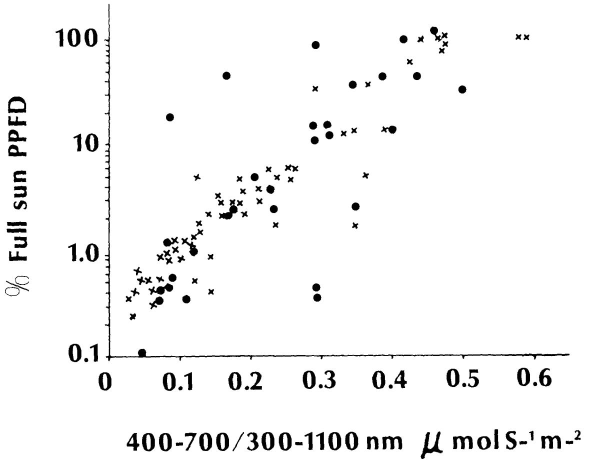

FIGURE 6. Regression analysis of log percentage of full sun PPFD compared to the ratio of quantum flux density in μmol/sec/m^2 400–700:300–1100 nm, symbols as in Figure 5. For BCI, $Y = -2.796 + 4.480X$ ($r = .815$); for La Selva, $Y = -3.239 + 5.964X$ ($r = .917$).

in plots of the percentages of full sunlight PPFD to R:FR (Fig. 4), of radiant energy 400–700 nm to that of 300–1100 nm (Fig. 5), and to quantum flux density 300–1100 nm (Fig. 6). Each plot is of 38 measurements from La Selva and 60 measurements from BCI, restricted to full sunlight conditions of more than 1500 μmol/sec/m^2. The regression lines of the two sites for each of these plots are not significantly different at a level of $P = 0.05$. Much of the scatter in the plots (especially in Fig. 6) may be due to slight changes in atmospheric haze during the time of the spectral scans. There is also a strong correlation between R:FR and PPFD at shade readings below 500 μmol/sec/m^2, with regression equations of log PPFD versus R:FR of $Y = -0.043 + 0.427X$ (coefficient of correlation = 0.938) for La Selva and $Y = -0.365 + 0.629X$ ($r = .904$) for BCI.

These results document the changes in spectral quality that accompany increases in quantum flux density within the forest. There is a large difference in spectral quality between dense shade and even a rather small fleck. These results suggest that changes in a light environment from dense shade to only slightly lighter conditions could function as an environmental signal in the control of plant development.

The results also suggest that radiation measurements within a forest compared with those in full sunlight, using a standard quantum radiometer, can be used to estimate the spectral distribution of radiation. For the conditions of this study (measurements performed when the sun was unobstructed and near the solar zenith), the accuracy of the estimate should be within R:FR = 0.2. Similar relationships should exist for cloudy skies, but the slightly different spectral properties of cloudy skies (Tasker & Smith 1977a) and the rapid changes in quantum flux densities as cloud cover changes would make such estimates more difficult. Cloud cover may increase R:FR (1.39 ± 0.03, $N = 12$, compared with R:FR = 1.27 ± 0.04, $N = 24$, for full sun in Dade County). A significant portion of light reaching the forest floor, even in dense shade, is due to the penumbral effects of solar radiation passing through small holes in the canopy (Bone *et al.* 1985). Such radiation is unaltered by the filtering of the canopy (as diffuse radiation is), and its relative contribution might be expected to change the relationship between percentage of full sunlight and spectral quality. For instance, a single leaf of *Bursera simaruba* (Fig. 1) would alter the R:FR of full sunlight (Fig. 2A) from 1.28 to 0.12 immediately beneath the leaf. Measurements beneath water hyacinth plants had lower R:FR ratios than would be predicted by the regression analysis (Fig. 4; Lee 1985). The contribution of penumbral light to forest shade is predictable and is only important when the sun is near the solar zenith and more likely to pass through small holes in the canopy (Bone *et al.* 1985). However, light measurements taken at BCI early and late in the day are well within the range of values plotted in Figures 4–6. Finally, the relationship of percentages of full sun PPFD to R:FR of understory environments in a subtropical hardwood hammock in South Florida (with a canopy some 10 m high; Lee 1985a) was not statistically different than those of the tropical forests described in this article.

These results document the profound changes in the spectral quality of radiation that may occur within tropical rainforests. Such changes are likely to affect mechanisms of growth and development of the plants living in these environments, and thus may be an important ecological factor aside from the direct effect of light quantity.

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