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THE COLOR OF LIGHT IN FORESTS AND ITS IMPLICATIONS¹

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Abstract. Forests exhibit much variation in light environments, and this can affect communication among animals, communication between animals and plants, photosynthesis, and plant morphogenesis. Light environments are caused by, and can be predicted from, the geometry of the light paths, the weather conditions, and the time of day. The structure of forests leads to four major light habitats when the sun is not blocked by clouds: forest shade, woodland shade, small gaps, and large gaps. These are characterized by yellow-green, blue-gray, reddish, and “white” ambient light spectra, respectively. When the sun is blocked by clouds, the spectra of these four habitats converge on that of large gaps and open areas, so the single light environment during cloudy weather will be called open/cloudy. An additional light environment (early/late) is associated with low sun angles (near dawn or dusk); it is purplish. Each light environment is well defined and was found in forests of Trinidad, Panama, Costa Rica, Australia, California, and Florida. Scattered literature references suggest similar patterns elsewhere in North America, Europe, and Java. Perceived colors of animals, flowers, and fruits depend upon the interaction between ambient light color and the reflectance color of the animal or plant parts. As a result, an animal or plant may have a different appearance in each environment, i.e., a color pattern may be relatively cryptic in some light environments while relatively conspicuous in others. This has strong implications for the joint evolution of visual signals and vision, as well as microhabitat choice. Plant growth and form may also be affected by variation in the color of forest light.

Key words: color patterns; crypsis; forests; habitat choice; light environment; plant growth and form; predation; sexual selection; visual signals.

INTRODUCTION

Forests present a complex, changing, and heterogeneous light environment. In them animals and plants signal visually to their mates, pollinators, and dispersers, and try to avoid sending the wrong signals to their predators, parasitoids, nectar/pollen robbers, and herbivores. Visual signals are a product of signaler's reflectance spectrum and ambient light (Endler 1990) and so are strongly dependent upon the environment. If the ambient light spectrum changes, a color pattern may change from inconspicuous to conspicuous or vice versa. As light varies in time and place, so too does the efficiency of communication, so fitness can depend strongly upon lighting conditions (Endler 1986, 1988, 1990, 1991).

Variation in the spectral composition of the near-ultraviolet (350–400 nm) and “visible” spectrum (400–700 nm) affects the visibility of animals, flowers, and fruits to vertebrates and invertebrates (Lythgoe 1979, Endler 1986, 1990, 1991, 1992). I will refer to the spectral composition of light between 350 and 700 nm as *color*, to distinguish it from the red/far-red ratio (ζ ; Smith 1981a) and other measures of light “quality”

used by plant physiologists. I will predict ambient light spectra from forest geometry, characterize the color of forest light environments, and will present some of its implications to animals and plants.

CONCEPTUAL BACKGROUND AND PREDICTIONS

Light sources, radiance, and irradiance

The appearance of a color pattern element or patch depends both upon its reflectance spectrum and the ambient light arriving at the patch (Endler 1990). The distribution of ambient light intensity (Q) with wavelength (λ) is called the irradiance spectrum $Q(\lambda)$. The irradiance spectrum is the sum of radiances from all light sources (Fig. 1). Radiance comes from objects that produce light and from objects that reflect or transmit light. Radiant sources include the sun, blue sky, and cloudy sky showing through holes in the canopy, illuminated leaves, shaded leaves, trunks, branches, other vegetation, leaf litter, and soil. Plant physiologists traditionally divide ambient light into two radiance components, direct and diffuse (for example, Anderson 1964a, b, c, Chazdon and Field 1987); direct light is light coming directly from the sun while diffuse light is light arriving directly from all other sources. The dichotomy between direct and diffuse light sources is

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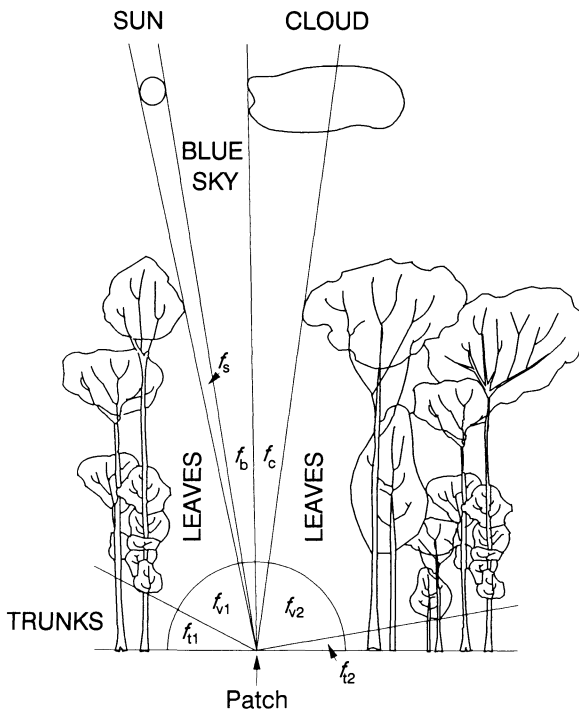


FIG. 1. Generalized cross section of the hemisphere that consists of all light sources contributing light to a color pattern element facing upward. Light sources include trunks and branches, leaves, the sun, blue sky, and clouds. The solid angles each light source subtends are: trunks f_{t1} , f_{t2} ; leaves (vegetation) f_{v1} , f_{v2} ; the sun f_s ; blue sky f_b ; clouds f_c . The total solid angle for trunks and branches would be $f_t = f_{t1} + f_{t2}$, and for leaves $f_v = f_{v1} + f_{v2}$. Light habitats vary in the relative sizes of these solid angles.

insufficient for studies of color because diffuse light components, such as blue sky, clouds, leaves, and bark, differ strongly in spectral composition. Because radiant spectra differ in shape, changes in the proportions of various light sources can cause changes in the color of ambient light. In order to describe how irradiance spectra should change with forest geometry, I will first present the radiance spectra of some common light sources and then use them to predict qualitatively the irradiance spectra they generate in conjunction with vegetation geometry.

Fig. 2 shows characteristic radiance spectra of the major classes of light sources illuminating color patterns in forests. These spectra were recorded by means of a LI-COR (Lincoln, Nebraska) LI-1800-06 telescope, LI-1800-06A 3° field of view attachment, and LI-1800-10 quartz fiber optic cable, connected to a LI-1800 portable spectroradiometer. The system was calibrated with the LI-1800-02 optical radiance calibrator and 1800-02RA radiance calibration accessory. The 3° acceptance angle setting was used to measure all natural light sources except that of the sun. Because the sun is so bright and its diameter subtends only $\approx 0.5^\circ$ to the ground, the smallest aperture setting (0.8°) and filters were used for the sun. To measure the sun's radiance

spectrum, the telescope was aimed and aligned with the sun while a Celestion Solar Filter covered the objective lens, the solar filter was replaced by a spectrally calibrated 3 log unit neutral density filter, measurements were made, and scan was corrected by the filter transmission spectrum. Data were taken in a riparian forest at the Santa Barbara Botanic Garden, and the sun was measured at the campus of the University of California, Santa Barbara.

The radiant sources vary in brightness (total radiance) by several orders of magnitude (Fig. 2). They also vary in color (spectral shape; for examples of spectral shape and named colors see Endler 1990). The spectrum of the sun is richer in long wavelengths (redder) than the white of clouds; the blue sky is richer in shorter wavelengths, leaves are rich in middle wavelengths, and bark is richer in middle to long wavelengths (brown). There is nothing surprising about these spectra. The radiance spectrum of the sun is similar to Rozenberg's (1966) and Kondratyev's (1969) spectra. The radiance spectrum of blue sky is similar to those of Rozenberg (1966), Kondratyev (1969), and McFarland and Munz (1975a, 1976, Munz and McFarland 1973). These authors recorded in detail the spectral changes in the sky radiance spectra with solar azimuth; both total intensity and chroma (color saturation) vary with relative and absolute azimuth, as well as with atmospheric conditions. I could not find published radiance spectra of clouds, but these results are expected from the optical properties of clouds discussed by Feigelson (1984), and Coulson's (1975) brightness data. The leaf radiance spectra are just what one would expect from the optical properties of leaves (Gates et al. 1965, Scott et al. 1968, Federer 1970, Wooley 1971, Stoutjesdijk 1972a, Gausman and Allen 1973, Lee 1986, 1987, Lee and Graham 1986). These data are presented only for the purposes of explaining the qualitative relationship between forest geometry and ambient light color; a more detailed survey will be presented elsewhere.

The radiance spectra can be used to derive the relationship between forest geometry and light environments. Radiance can be defined as the light reaching a patch from a particular light source subtending a particular solid angle on the patch, corrected to a unit angle (1 steradian, sr). The irradiance spectrum $Q(\lambda)$ is a function of the radiant spectra $q_i(\lambda)$ of all light sources i that illuminate the patch. If the patch is flat, then the light is effectively being collected from a hemisphere, a solid angle of 180° or 2π steradians. If the patch is convex, then $>2\pi$ sr will be collected, while if the patch is concave, then $<2\pi$ sr will be collected (see Appendix). Radiance units relevant to vision and photosynthesis are micromoles per square metre per steradian per nanometre while irradiance units are micromoles per square metre per second per nanometre (Lythgoe 1979, Endler 1990). The contribution of a given light source to ambient light is a function of its

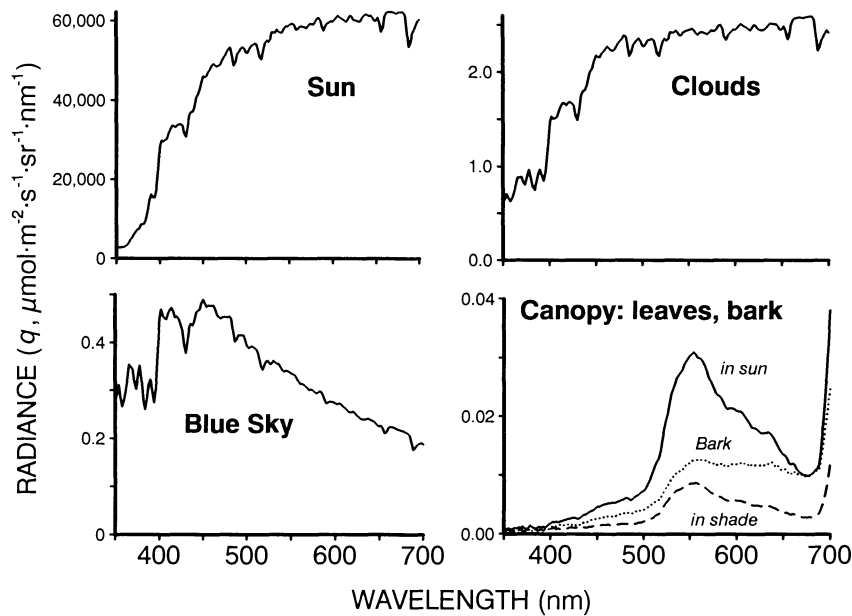


FIG. 2. Radiance spectra $q(\lambda)$ of various components of ambient light in forests. The total radiance $q_T = \int q(\lambda)d\lambda$ (in the wavelength range 400–700 nm) for these light sources are sun: 1.648×10^7 ; clouds: 689.7, blue sky: 101.1, leaves in sun: 23.52, leaves in shade: 1.250, bark in light shade 2.440 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}\cdot\text{sr}^{-1}$. Clouds and canopy varied by 45%.

radiant spectrum (e.g., Fig. 2) and the solid angle it subtends on the patch (e.g., Fig. 1). Therefore, the ambient light spectrum $Q(\lambda)$ is equal to the sum of the light sources' radiant spectra, weighted by the solid angles they subtend, or

$$Q(\lambda) = \sum f_i q_i(\lambda), \quad (1)$$

where f_i is the solid angle subtended by light source i and $q_i(\lambda)$ is its radiance spectrum. If the product of solid angle and radiance of a particular light source is large relative to other sources, then the irradiance spectrum will be most strongly influenced by that light source. For light sources of roughly equal radiance, those subtending large angles will contribute more to the color of ambient light than those subtending small angles. However, some small sources, such as the sun or a bright cloud showing through a canopy hole, can have very high radiance, and some large sources, such as shaded leaves, can have very low radiances (Fig. 2); it is the product $f_i q_i(\lambda)$ that determines the relative contribution of a given light source to the ambient light spectrum.

Most color pattern elements are flat surfaces rather than points. As a consequence, the intensity at which a patch is illuminated by a light source declines with the cosine of the angle of the source from that normal (perpendicular) to the patch (Kirk 1983); a source perpendicular to the patch (0°) will contribute more to the irradiance than a source of the same $f_i q_i(\lambda)$ illuminating the patch at a greater angle. Therefore, for a color pattern element or patch, the irradiance spectrum is ap-

proximately

$$Q(\lambda) = \sum f_i q_i(\lambda) \cos(\phi_i), \quad (2)$$

where ϕ_i is the angle of the center of light source i from that normal to the patch. Eq. 2 will be less accurate for large sources (large f_i) because the lower (larger ϕ) side of such a source will be less effective than the upper side (smaller ϕ) of the source in illuminating the patch. Corrections can be made by subdividing each source into smaller sources. Subdivision should also be done for any source that varies spectrally over its solid angle f_i .

The effect of the cosine correction is to increase the relative contribution of light sources perpendicular (small ϕ) to the color pattern surface and to reduce the relative contribution of light sources that strike the surface at large angles (ϕ). For surfaces facing upwards (as in Fig. 1) this means that the relative contribution of canopy holes will be greater and vegetation less, but for the sides of animals, this means that vegetation will contribute relatively more and skylight relatively less, because most gaps will be over a given location and fewer will be at the sides (Anderson 1964a, b, c). On the other hand, at or near forest edges or on the tops of steep ridges, where canopy holes may be evenly distributed in all directions, the cosine correction will have little or no effect on the *relative* contributions of canopy holes and vegetation. Because the effect of the cosine correction can both increase or decrease the relative contribution of canopy holes, it will be ignored in most of this paper. However, it should be accounted

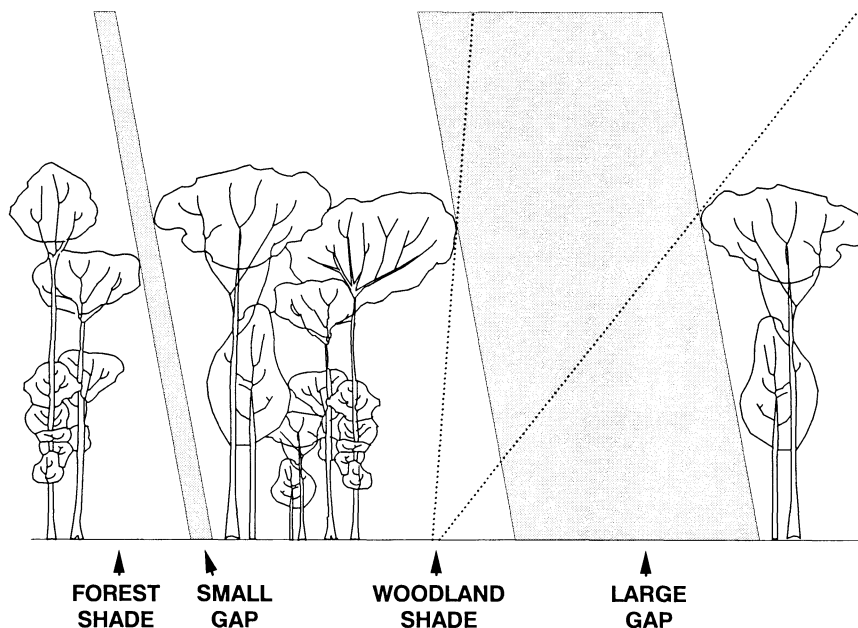


FIG. 3. The major light habitat classes in forests when the sun is not blocked by a cloud. Forest Shade: Canopy closed, or with very small or few gaps; all or virtually all incident light is either reflected from or transmitted through the vegetation. Small Gap: Direct sunlight from a gap in the canopy, essentially no light from the open sky and less than $\approx 10\%$ of the incident light is reflected or transmitted through the vegetation. Woodland Shade: Canopy open; a significant fraction of the incident light comes from the sky, but none comes directly from the sun. Large Gap: Direct sunlight and open sky account for most of the ambient light. Dotted lines: light from the open sky. Stippled trapezoids: direct sunlight.

for in detailed studies in which color pattern orientations are known, or where absolute intensities are required.

Forest geometry and light habitats

Eq. 2 indicates that the solid angle subtended by each light source (f_i) has a very strong effect on the color of the ambient light. Forest geometry determines the f_i of all sources on a given patch (Fig. 1), and the spectral properties of the major forest light sources (Fig. 2) are much less variable than forest geometry (J. A. Endler, *unpublished data*). Therefore, defining light habitats by the geometry of the major light sources should explain and even predict much of the variation in the color of forest light.

Although forests have complex geometry, it is possible to divide them into four habitats with characteristic ratios of f_i for sun, sky, and vegetation (Fig. 3): forest shade, woodland shade, small gaps, and large gaps. These habitats differ in the relative angles subtended by vegetation, skylight, and direct sun; forest shade and small gaps receive little if any skylight, whereas woodland shade and large gaps receive much skylight. Although these light habitats grade into each other (as do woodlands and forests), it is always possible to find large areas with most or all of these light habitats. The names used to describe the light habitats are meant to emphasize the geometrical structure of the forest rather than vegetation type. Forest shade and

woodland shade have been named after the vegetation types in which they are most common, but are not restricted to them. Forests are groups of trees in which most of the crowns overlap, forming a nearly continuous canopy with small holes or gaps. Woodlands are groups of trees in which most of the crowns are separated leaving large as well as small gaps in the canopy. Gaps are patches of direct sunlight, at any level of the forest, that range in size from a few centimetres to many tens of metres, caused by holes in the canopy. There is a wide variety of definitions of "gaps" in the literature; they have been variously called "sun flecks" and "light gaps." The definition used in this paper is different from Brokaw's (1982) definition in that any size sunfleck is included, and from Hubbell and Foster's (1986) definition in that it is not restricted to sunflecks on the ground. Once again, the light habitat definitions are meant to emphasize geometry rather than vegetation type (Fig. 3).

In order to calculate the expected irradiance spectrum from the radiance spectra in each of the light habitats, we need the angles subtended by each radiant source subtended on the patch. For brevity, let f_s , f_b , f_c , and f_v be the total solid angles subtended by the sun, blue sky, clouds, and vegetation, respectively (Fig. 1). For purposes of discussion we will ignore bark, branches, leaf litter, and soil, but they can be included in any calculations. The Appendix gives details of the derivation of all ambient light (irradiance) spectra from

any combination of radiant spectra. The relative values of f_s , f_b , f_c , and f_v are determined by the size of canopy holes, and these holes do not have to be contiguous (Eq. 2; f_s is zero in shade). We can define the *gap fraction*, G , as the fraction of the sky showing through the canopy: $G = (f_s + f_b + f_c)/(2\pi)$. This is similar to the intent of Lieberman et al.'s (1989) canopy closure but measures sky rather than canopy.

Small gaps (Fig. 3) are sunlit locations in the forest (at any height) in which a canopy hole subtends a solid angle similar to that of the sun ($f_s = 0.5259^\circ$ solid angle or 6.6168×10^{-5} sr; Robinson 1966). Therefore, little or no light comes from the open sky ($f_b + f_c$ small or zero), and essentially all of the light comes directly from the sun and vegetation ($f_v \approx 2\pi$ sr). Because the sun is many orders of magnitude brighter than the vegetation (Fig. 2), the solar spectrum should dominate the irradiance spectrum. This is easier to see by considering how the total radiances of each source [$q_{Ti} = \int q_i(\lambda)d\lambda$ over 400–700 nm for source i] combine to make the total irradiance [$Q_T = \sum f_i q_{Ti} \cos(\phi_i)$, as in Eq. 2]. Let the total radiances be similar to those of Fig. 2 (sun $q_T = 1.68 \times 10^7 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, leaves in sun $q_T = 25.0$, leaves in shade $q_T = 1.0$). Ignoring the cosine correction (Eq. 1), the sun contributes $1090.5/(1090.5 + 157.1)$ or 87% of the photons if all leaves contributing light are sunlit and 99% of the photons if all leaves are shaded (most small gaps will be illuminated by both shaded and unshaded leaves). For color patterns facing upwards (as in Fig. 1), the actual fraction of photons contributed by the sun will be even greater than this because most sunlit canopy holes will be at smaller ϕ (overhead), and most vegetation is at larger ϕ (Eq. 2). For color pattern elements facing sideways (or other directions), and for locations on ridgetops, near rivers or forest edges, the cosine correction may decrease or increase the relative contribution of the sun. The main point is that the solar radiance spectrum will dominate the irradiance spectrum in small gaps, and the light will be relatively yellowish-red.

In large gaps (Fig. 3), a significant fraction of light comes from the open sky ($f_b + f_c$ large), as well as the sun ($f_s = 0.5259^\circ$) and vegetation (f_v large). Because the sun, blue sky, and clouds are all much brighter than vegetation (Fig. 2), they will dominate the irradiance spectrum. For very large gaps, as in open areas, the mixture of the yellowish-red of the sun and the blue of the sky yields nearly white irradiance. But as the gap fraction (G) declines, the contribution of blue sky declines, and longer wavelengths dominate irradiance. Thus, large gaps grade into small gaps as the gap fraction declines. We can take a solid angle of 2° (4 times the diameter of the sun or ≈ 0.001 sr) as an approximate threshold between the two light habitats. Eqs. A.6a, b describe the irradiance spectrum of variously sized gaps under various weather conditions.

To illustrate the transition between large and small gaps, consider total radiance and irradiance. Let the

total radiances be similar to Fig. 2 (blue sky $q_T = 100 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, sun and leaves as before). First, consider a cloudless sky showing through the canopy hole ($f_c = 0$). As the gap fraction (G) declines from 0.90 to 0.001 (f_b 1.8 π to 0.002 π sr) the contribution of the sun varies from 65.2 to 87.4%, blue sky contributes 33.8 to 0.05%, while the vegetation (sunlit leaves) contributes 0.94 to 12.6% of the photons in the irradiance spectrum. The same calculations for shaded leaves, which are more characteristic of taller forests and smaller gaps, yields: sun 65.8–99.4%, blue sky 34.1–0.06%, and shaded leaves 0.04–0.57%. Real gaps will fall somewhere between these two sets of calculations, depending upon what fraction of the illuminating vegetation is also in direct sunlight. For color patterns facing upwards, the cosine correction reduces the contribution of vegetation, and for color patterns oriented horizontally the vegetation contribution is greater. In summary, if canopy holes transmit blue sky, then the ambient light will vary from white in large gaps to yellowish-red in small gaps.

Now consider an overcast day with the sun in the same position as in the previous calculations. Let the total radiances be as before, and in addition, use a total radiance typical for darker clouds, $Q_T = 300 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (J. A. Endler, *unpublished data*) with solar transmission of $C = 0.10$ (see Eq. A.6b). As the gap fraction (G) declines from 0.90 to 0.001, the contributions are: sun through thin clouds ($C = 0.10$) 6.04–93.1%, clouds: 93.9–1.59%, vegetation 0.03–5.36%. As gap size decreases, the contribution of the sun and vegetation increases, but the clouds almost always contribute most of the photons except for the very smallest gaps. As a result, the light in gaps of any size is nearly always white if clouds cover most or all of the canopy holes.

In forest shade (Fig. 3), essentially all of the light has been transmitted through or reflected from leaves ($f_v \approx 2\pi$ sr). There is no direct sunlight ($f_s = 0$), and little or no light comes from the open sky ($f_b + f_c$ small or zero). As a result, the greenish leaf radiance spectrum should dominate the irradiance spectrum.

In woodland shade (Fig. 3), much of the light comes from leaves (f_v large), but, in addition, a significant amount of light also comes from the sky through canopy holes ($f_b + f_c$ large, dotted lines in Fig. 3). As in forest shade, no light comes from the sun ($f_s = 0$). Because the sky has a higher radiance than vegetation (Fig. 2), the bluish sky radiance should dominate the irradiance spectrum in woodland shade.

What happens to shade as the gap fraction decreases? Consider a period in which no clouds are visible through the canopy holes ($f_c = 0$). Because the total radiance of blue sky is ≈ 10 times greater than that of vegetation (Fig. 2), the bluish radiance spectrum of blue sky should dominate the irradiance spectrum, except when f_b (and G) is small. As f_b declines, the geometry changes from that of woodland shade to that of forest shade. There-

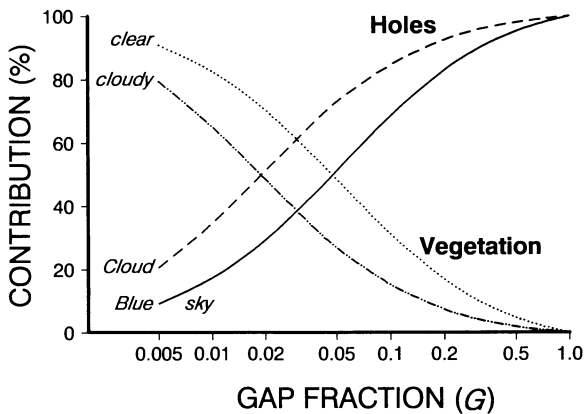


FIG. 4. Contribution of common light sources to calculated ambient light as a function of the fraction of the canopy open to the sky (G). These calculations use radiance spectra of Fig. 2 and Eqs. A.7a, b. On a cloudless day, the vegetation (clear, \cdots) contributes as much as a gap (Blue sky, —) when gaps are about 5% of the canopy. Below 5%, vegetation contributes most light, leading to *forest shade* (Fig. 5). Above 5% the blue sky contributes more and more to the ambient light, and by 30% the conditions yield *woodland shade* (Fig. 5). On a cloudy day, the contribution of vegetation (Cloudy, \cdots) is reduced; vegetation and gap (Cloud, —) contributions are equal at $\approx 2\%$. Consequently, for all but forests with gap fractions less than $\approx 1\%$, the ambient light spectrum resembles open areas during cloudy weather (Fig. 5).

fore, we expect the irradiance spectrum to change from something similar to blue sky radiance to something similar to leaf radiance as the gap fraction decreases. This is shown in Figs. 4 and 5A. Fig. 4 was constructed using the same parameters as in the example gap calculations, except that $f_s = 0$ (no sun). Fig. 5A was constructed using Eq. A.7a and the blue sky and average leaf spectra of Fig. 2. One could define a critical G at which the radiance spectrum of vegetation starts to become significant as an arbitrary distinction between forest shade and woodland shade habitats. In this example, this occurs when $\approx 5\%$ of the sky is visible through the canopy (Figs. 4 and 5). However, the actual critical value will depend upon the total radiance of each light source; for example, if more leaves were sunlit (Fig. 2), the critical G would be higher.

If the sky showing through canopy holes is blocked by clouds (replace f_b with f_c in the previous example), then the irradiance spectrum will be dominated by the white radiance spectrum of clouds rather than the blue of the clear sky. This is shown in Figs. 4 and 5B, which were derived from Eq. A.7b and the data of Fig. 2. Again, vegetation will not have a significant effect on the irradiance spectrum unless the gap fraction (G) is very small. The critical value for cloudy weather (or at least clouds blocking all canopy gaps) will be even smaller than for blue sky ($\approx 2\%$, Fig. 4) because cloud radiance may be 7 times brighter than blue sky (Fig. 2 and J. A. Endler, *unpublished data*). As a result, on average, cloudy weather will shift both the greenish

forest light spectrum or bluish woodland shade spectrum to whitish light. This predicts a convergence of all light habitats on that of large gaps during cloudy weather.

METHODS

Study sites and conditions

In order to test these predictions, and to explore natural light environments, ambient light spectra were measured in forests of Trinidad, Panama, Costa Rica, Australia, Florida, and California (Table 1). The forests range from tropical to temperate, lowland to montane, dry to wet, and closed (forest) to open canopy (woodland). Measurements were taken in shade, gaps of various sizes, and in a few treeless areas for comparison. The primary purpose of the measurements was to test the qualitative predicted spectra for each light habitat rather than to predict the exact total intensities or to estimate the relative abundances of the habitats. Tests of quantitative predictions would require detailed radiance distribution measurements, "fisheye" photographs (for solid angles of each source), and irradiance measures taken simultaneously at each sampling point.

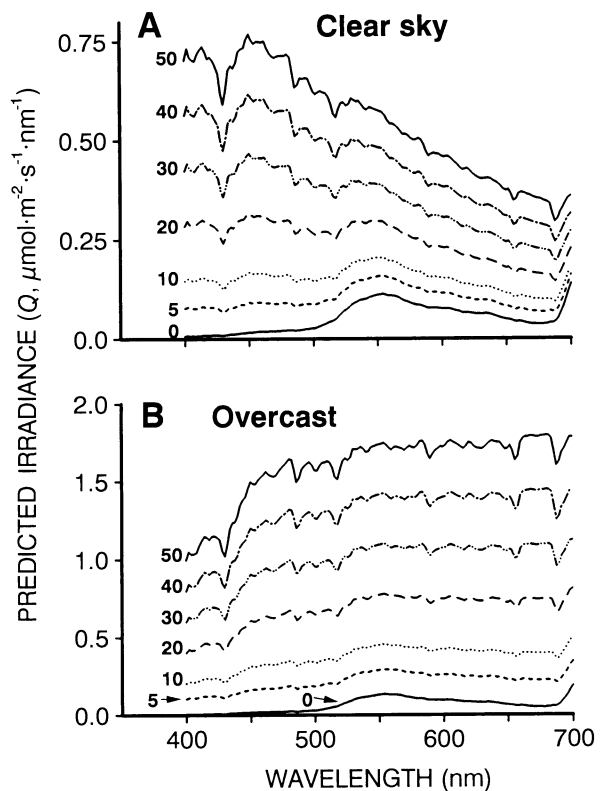


FIG. 5. Calculated effect of the fraction of the canopy open to the sky (G) on ambient light spectrum for clear (A) and overcast (B) conditions, using data in Fig. 2. Numbers to the left of each curve are 100 G . As G increases, forest shade spectra come to resemble woodland shade if the sun is not obstructed by cloud, and to resemble large gaps or open areas if it is overcast.

TABLE 1. Study areas.

Name	Forest type	Location, date	Literature
Trinidad	Submontane tropical rain forest. Closed canopy, few gaps.	Northern Range Mountains, Trinidad,* June 1988	Beebe 1952, Endler 1978
BCI	Lowland tropical rain forest. Closed canopy, many gaps.	Barro Colorado Island,† Panama, March 1989	Croat 1978, Lee 1987
Monteverde	Tropical cloud forest. Closed canopy, many small gaps.	Campbell's Woods, Monteverde, Costa Rica, June–July 1989	Lawton and Dryer 1980, Hartshorn in Janzen 1983
Lamington	Subtropical rain forest. Closed canopy, few gaps.	Lamington National Park and Brisbane Forest Park, Queensland,‡ Australia, July–August 1988	Björkman and Ludlow 1972, McDonald and Whiteman 1979, Williams et al. 1984, Young 1985
Brisbane	Dry forests of <i>Eucalyptus</i> , <i>Casuarina</i> and, or, <i>Callitris</i> . Open canopy.	Lamington National Park, Brisbane Forest Park, and forests in the Conondales, Queensland, July–August 1988	McDonald and Whiteman 1979, Young 1985
Heron Island	<i>Pisonia grandis</i> forest. Closed canopy, many gaps.	Heron Island, Queensland, June 1988	Gillham 1963
Florida	Mixed deciduous and pine forests. Range of closed to open canopy forests.	San Felasco Hammock State Preserve and Devil's Mill Hopper State Park, October 1989	
Santa Barbara	Riparian forest (<i>Platanus</i> , <i>Quercus</i> , <i>Umbellaria</i>). Closed canopy, few gaps.	Santa Barbara Botanical Garden, California, December 1988, June 1990	Smith 1976
Figueroa	Coniferous forest (<i>Pinus</i> , <i>Pseudotsuga</i>) and some <i>Quercus chrysolepis</i> forest. Open and closed canopy.	Figueroa Mountain, Santa Barbara County, California, December 1988	Smith 1976

* Site of my long-term studies of color patterns in guppies, reviewed in Endler (1983).

† Ambient light also studied by Lee (1987).

‡ Ambient light also studied by Björkman and Ludlow (1972).

In order to ensure that each sample would yield a spectrum characteristic of only one light habitat, most measurements were taken at sites that could be assigned unambiguously to one of the four habitats of Fig. 3. Forest shade measurements were taken at least 4 m away from the edges of any small gaps, and, except sometimes at Brisbane (Australia) and Figueroa (California, Table 1), out of sight of large gaps or forest margins. Woodland shade measurements were taken whenever a significant fraction of the sky was visible through the canopy (more than $\approx 25\%$). In addition, at each study site, an effort was made to find the least disturbed, oldest, and most spatially homogeneous canopy architecture.

Following earlier observations (Endler 1978), ambient light spectra were measured under three weather and time conditions (a) sun not blocked by clouds, (b) sun blocked by clouds, and (c) low sun angles (early and late in the day). An effort was made to equalize the number of measurements taken during cloudy and clear conditions, and also in shade and adjacent sun patches (gaps), by taking pairs, and if possible triplets, of readings in these conditions within 10 min. Triplets

were most commonly possible on days with scattered cumulus clouds, as is typical of tropical weather.

Measurement of ambient light spectra

Measurements of ambient light (irradiance) were made with a LI-COR (Lincoln, Nebraska) model LI-1800 portable spectroradiometer, using its standard cosine receptor head (see Gates 1980, Kirk 1983, and Endler 1990 for a review of the general principles and methods of spectral measurement). For the data reported in this paper, the cosine receptor was always oriented upwards, so will underestimate the contribution of vegetation to irradiance of surfaces facing sideways. The spectroradiometer recorded intensity as photon flux density (micromoles per square metre per second per nanometre) at 2-nm intervals; these are the appropriate units for both vision and plant physiology (Endler 1990). The spectroradiometer was calibrated both before and after each field trip by means of a LI-COR model LI-1800-02 optical radiation calibrator.

The LI-1800 spectroradiometer was used at all sites except Monteverde, Costa Rica (Table 1). At Monteverde, measurements of ambient light were made with

a more sensitive spectroradiometer, consisting of an Oriel (Oriel Corporation, Stratford, Connecticut) model 77250 monochromator with variable slits and 1200 lines per inch holographic grating, model 7070 photomultiplier detector, and model 778200 motor drive (wavelength advance). The entry slit of the monochromator was fitted with a LI-COR LI-1800 cosine receptor. The motor drive was controlled through the parallel port of a Toshiba T1000 "laptop" computer that also received, via its serial port and a Remote Measurement Systems ADC-1 analog-to-digital convertor, the output of the photomultiplier (light intensity at the set wavelength). The T1000 program controls the spectroradiometer, collects the data from each scan, converts the photomultiplier output to photon flux units at each wavelength sampled, and stores the scans on diskettes for later analysis. (The PASCAL program and other details are available upon request.) The system was powered by a small automobile battery and inverter. The Oriel system was calibrated with the same light source as the LI-COR system.

Much visual signalling involves the "visible" part of the energy spectrum, between 400 and 700 nm wavelengths (Lythgoe 1979). The range of light used by plants in photosynthesis (PAR) is also 400–700 nm (Kirk 1983). Insects, some fish, reptiles, birds, and possibly even some mammals, can also see into the ultraviolet (300–400 nm; Goldsmith and Bernard 1974, Alberts 1989, Goldsmith 1990; G. H. Jacobs, *personal communication*), and ultraviolet vision is being discovered in more and more vertebrates (Goldsmith 1990). Most measurements of ambient light were made in the "visible" spectrum from 400 to 700 nm, and many were made from 300 to 700 nm. A few scans also ranged to 800 nm.

Most recordings were made on the forest floor or <20 cm above the surface of small tropical forest streams. Some recordings were made in Monteverde, Costa Rica, up to 1 m above the forest floor in order to avoid a dense low shrub layer. A series of recordings were made in direct sunlight and the shade of vegetation at 1.8-m intervals on a 43.9-m tower at Barro Colorado Island (BCI), Panama. Because most recordings were made close to the ground, and the sensor has a 180° solid acceptance angle, scans were not made until the operator was either >5 m away or otherwise below or out of the field of view of the sensor, in order to avoid clothing color artifacts.

Calculations on spectra: shape, hue, chroma, intensity

The physical color of light is defined by the shape of its spectrum $Q(\lambda)$, i.e., the distribution of intensity (photon flux density) with wavelength. The shape of a spectrum, in conjunction with the visual system, will determine how color is perceived by an animal. *Hue* depends upon the wavelengths over which the transi-

tion between high and low light intensity occurs, as well as the sign of its slope. For example, red light has a spectrum with high intensity long wavelengths and low intensity short wavelengths, with the transition around 650 nm. If the transition is around 600 nm the light appears orange, and if about 550 nm, it appears yellow. Blue light is high in short and low in long wavelengths, with a transition around 450 nm, but if the transition is around 500 nm, it will appear green (examples and discussion in Endler 1990). No matter how a visual system works, spectra with differing transition λ will be perceived differently, so the transition λ can be used as a measure of hue. *Chroma*, "saturation," or "purity" depends upon the magnitude of the difference between high and low intensity parts of the spectrum and also upon the maximum slope of $Q(\lambda)$. For example, white light has a flat spectrum, hence zero chroma. A pink light shows relatively little difference between light on either side of 650 nm (low chroma), whereas a red light would show a much greater transition at the same wavelength (high chroma). Chroma is important in color perception because both vertebrate and invertebrate visual systems detect contrast by comparing stimuli from output channels sensitive to different groups of wavelengths (examples and discussion in Endler 1990, 1991). Chroma can be measured independently of visual system by calculating the standardized difference between portions of the spectrum (Endler 1990). Different species may not perceive the same color in the same way, but colors with stronger chroma measured in this way should usually result in stronger perceived chroma. The *intensity*, "value," or "brightness" of a color depends upon the color's total intensity. The intensity of light Q_T is simply the sum, over a given wavelength range, of the photon flux densities at each wavelength [$Q_T = \int Q(\lambda)d\lambda$]. For any visual system, larger Q_T will be perceived as brighter. For more detailed discussion, examples, and methods for calculating hue, chroma, and intensity, see Endler (1990, 1991).

In order to compare the shape (color) of different spectra independent of light intensity, spectra were standardized before calculating standard deviations at each wavelength. First, Q_T (total intensity or brightness) was calculated. At each wavelength λ , the raw spectrum $Q(\lambda)$ was divided by its total intensity Q_T , yielding a standardized spectrum with a total intensity of 1.0. This was multiplied by 10.0 to yield a standardized spectrum $Q_s(\lambda)$ with a Q_T of 10.0 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, similar to that observed for forest shade. The characteristic spectrum of a given light environment was obtained by calculating the mean and standard deviation of $Q_s(\lambda)$ of many samples of that light habitat at each wavelength λ . The standard deviation around the means gives an estimate of the variation in color (spectral shape) among spectra, independent of brightness (Q_T), and the means at each wavelength give the average color for that habitat. $Q_s(\lambda)$ was also

used to calculate chroma, using the methods of Endler (1990).

RESULTS

Forest geometry, weather, and time of day

The results support the predictions; different geometrical relationships between sun, sky, clouds, and vegetation yields consistently different and characteristic ambient light spectra. These spectra depend strongly upon forest geometry, weather, and the time of day, and are largely independent of forest species composition. There was remarkable similarity among the spectra of equivalent light environments among the different forest localities (Table 1), and each locality appeared to contain all light habitats unless the canopy was thin. It is useful to make the distinction between light habitats, which are determined by vegetation geometry (Fig. 3), and light environments, which refer to the ambient light spectra; light habitat names will be given in roman type, and light environment names will be given in *italics*. The light environments are described in detail below.

Open areas and large gaps in sunny conditions

The light in open areas and *large gaps* is whitish (Fig. 6). The spectrum of direct sunlight in open areas away from vegetation (Fig. 6, *no canopy*) has essentially the same shape wherever it is measured (as indicated by the small standard deviations at each wavelength). It is roughly flat, but declines below ≈ 470 nm. The spectrum in large gaps is very similar to that of non-forest conditions; there is only a slight attenuation of shorter wavelengths relative to open areas (Fig. 6). Large gaps are typical of treefalls, or places where a large limb has fallen from a tree, making a large hole in the canopy.

Small gaps, sunny conditions

The spectrum in *small gaps* is variable in color and different from that of large gaps (Fig. 6). *Small gaps* are on average more reddish than large gaps in that they are relatively richer in longer wavelengths. Small gaps frequently occur where small branches have fallen, leaving small holes in the canopy, and in almost completely regenerated treefalls. They are especially common in forests with a very high canopy, a high branch fall rate, slow growth rate, or windy conditions, as in BCI and Monteverde (Table 1).

The gradient between large gaps, small gaps, and forest shade

The transition in color between *large gaps* and *small gaps* occurs when direct sunlight comes from a canopy hole that subtends a solid angle of $\approx 2^\circ$. In a forest with a 30-m canopy, typical of those in most of the study sites, a 2° gap results in a 1 m diameter sun patch on the forest floor. As gaps decrease in size, shorter wave-

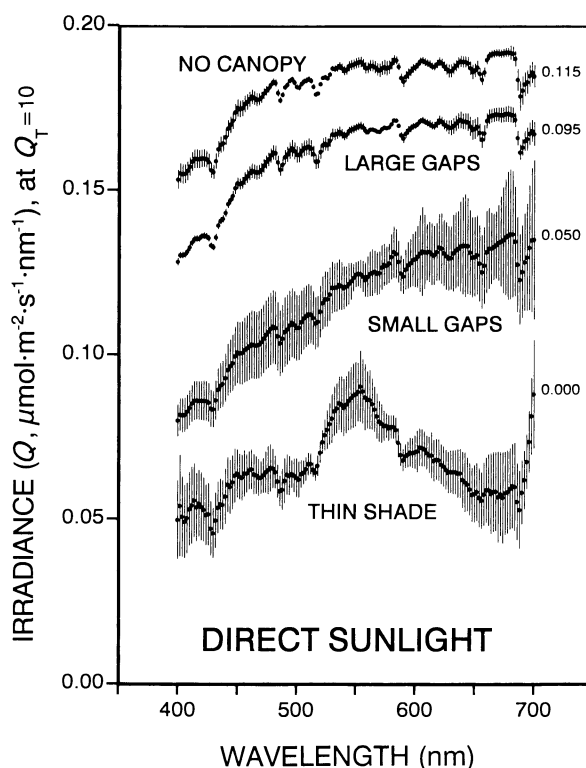


FIG. 6. Spectra from various light habitats with direct solar radiation. Large dots are mean quantum (photon) intensity at each wavelength (2-nm spacing). Vertical lines through the dots enclose the mean ± 1 SD. Before averaging, all spectra were converted to give a total intensity (Q_T) of $10 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. In order to avoid confusing overlap among spectra, means were displaced vertically by adding an amount (offset) shown to the right of each spectrum. The vertical placement of each spectrum implies nothing about total intensity (Q_T); the latter are given in Table 2. No Canopy ($N = 9$): spectra from areas with no forest or other obstructions; all other spectra are from forests. Large Gaps ($N = 6$): sun flecks from canopy holes subtending more than $\approx 2^\circ$. Small Gaps ($N = 31$): sun flecks from canopy holes subtending less than $\approx 2^\circ$. Thin Shade ($N = 12$): small gaps subtending less than $\approx 0.4^\circ$ and mostly obscured by a single layer of leaves.

lengths are progressively relatively less intense, yielding relatively more chroma; this is shown by the range of chroma for each light environment: *small gaps* (chroma 0.091–0.462), *large gaps* (0.087–0.110), and *open areas* (0.093–0.099); perfectly white light would have a chroma of 0.0. As the size of gaps increases through $\approx 2^\circ$, short wavelengths increase, chroma decreases, and the spectra resemble more and more that of *large gaps*.

As gap size falls below $\approx 0.4^\circ$ (≈ 20 cm diameter on the floor of a forest with a 30-m canopy) more and more sun flecks have leaves partially obscuring the sun; penumbral effects become more and more important (Anderson and Miller 1974, Smith et al. 1989). The solar disc subtends $\approx 0.5^\circ$. As the size decreases further it is not clear whether one should call the local area of

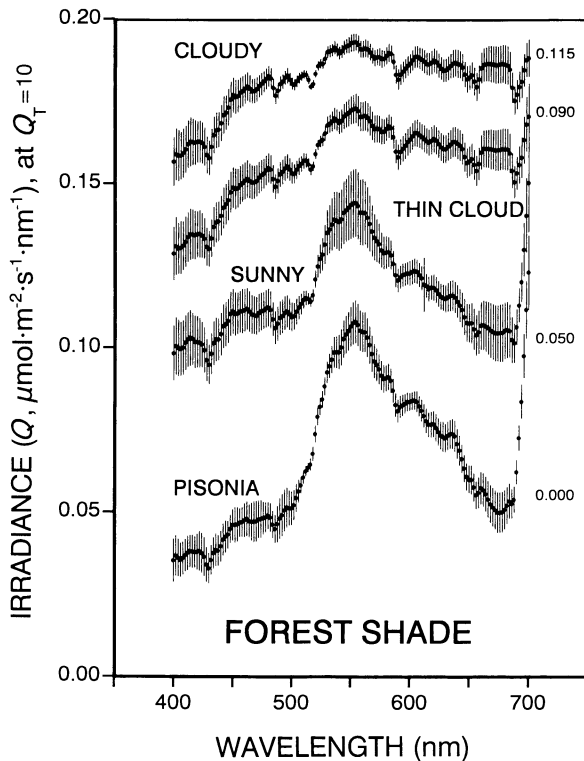


FIG. 7. Forest shade spectra under varying weather conditions. Symbols and offsets as in Fig. 6. Cloudy ($N = 45$): sun blocked by clouds, shadows absent or barely discernible. Thin cloud ($N = 48$): sun blocked by thin clouds or haze, shadows weak or with fuzzy boundaries. Sunny ($N = 74$): sun not blocked by cloud or haze, shadows with distinct edges. *Pisonia* ($N = 10$): shade, sunny conditions in the *Pisonia* forest on Heron Island, Australia. Note the resemblance between spectra during cloudy conditions and direct sunlight spectra (no canopy and large gaps, Fig. 6).

increased sunlight a small gap or an area of thin shade. For the purposes of this paper, thin shade consists of very small gaps ($<0.4^\circ$) in which at least 50% of the canopy hole is blocked by leaves, and much of the light in the sun fleck is from light transmitted through only a single leaf layer. In this case the spectrum is very different from that of unobstructed gaps (Fig. 6). It shows a strong reduction at long and short wavelengths and a large peak between 520 and 620 nm (greenish). This is essentially the same spectrum as is found in *forest shade* (Fig. 7), but data from thin shade were not included in Fig. 7. Penumbra shadows of leaves affect both intensity and color of ambient light.

In summary, *small gaps* are long-wavelength-shifted relative to *large gaps*, so tend to be yellowish to reddish instead of the whitish *large gaps*. The smallest gaps grade into *forest shade*, which is greenish.

Forest shade, sunny conditions

The spectrum of *forest shade* shows little variation among localities, except for Heron Island, Australia (Fig. 7). All sites were similar in showing a broad peak

at ≈ 550 nm, and a rapid increase above ≈ 680 nm; the light is yellow-green to the human eye. *Forest shade* varies mainly in chroma among localities (Table 2). The *Pisonia grandis* forest on Heron Island produces a yellow-green shade with more chroma than the other forests (Fig. 7, Table 2). This is quite apparent to the human eye, and is even more obvious in photographs (for example, Williams 1979: 10). The other forests were relatively similar in chroma when the sun was not obscured by clouds (Table 2). Although no direct measures were taken, it appears that forests with thinner leaves (especially *P. grandis*) yield forest light with greater chroma. In summary, *forest shade* is greenish to yellow-green.

Woodland shade, sunny conditions

Woodland shade spectra are bluish or bluish-gray (Fig. 8). If there are no clouds in the sky then the light is relatively richer in short wavelengths. If there are clouds and the sun is unobstructed, then the short-wavelength enrichment declines with the fraction of blue sky covered by clouds; with many clouds the spectrum is whitish, as in *large gaps*. *Woodland shade* is also grayish if there are no clouds but the sky is not

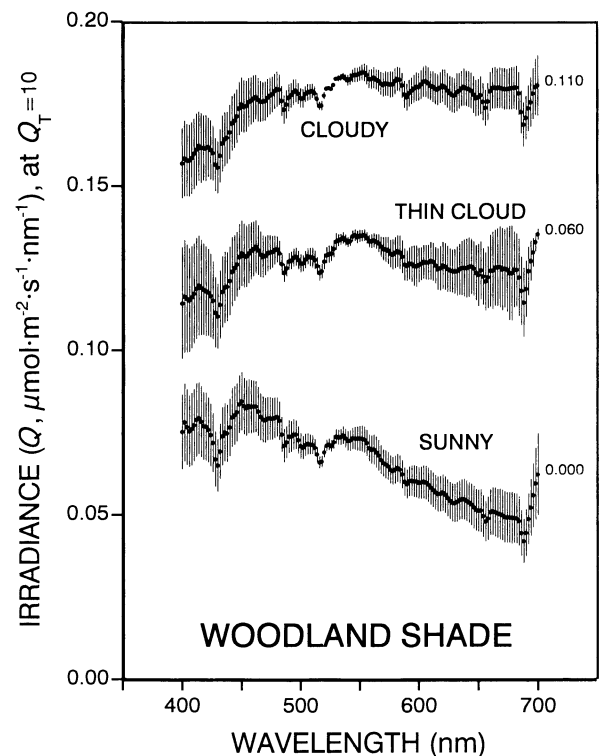


FIG. 8. Woodland shade under varying weather conditions. Symbols and offsets as in Fig. 6. Cloudy ($N = 2$): sun blocked by clouds. Thin cloud ($N = 6$): sun partially blocked by sun or haze. Sunny ($N = 33$): sun not blocked by clouds or haze. Note how when it becomes cloudy, the spectral shape converges on that of direct sunlight, as in forest shade (Figs. 6 and 7).

TABLE 2. Total light intensities (400–700 nm) and *forest shade* chroma between 0900 and 1500 in the various light environments and study areas (means \pm 1 SD). Study areas are arranged in order of increasing chroma.*

Study area	Total light intensities ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)					Chroma \ddagger (<i>Forest shade, sunny</i>)
	<i>Forest shade, sunny</i>	<i>Forest shade, cloudy</i>	<i>Woodland shade, sunny</i>	<i>Small gaps, sunny</i>	<i>Large gaps, sunny</i>	
Figueroa§	1.102 \pm 0.094 12.649 <i>n</i> = 8	No data \dagger	1.475 \pm 0.278 29.85 <i>n</i> = 17	No data \dagger	No data \dagger	0.0538 \pm 0.0233
Lamington and Brisbane	0.875 \pm 0.256 7.504 <i>n</i> = 18	1.039 \pm 0.340 10.95 <i>n</i> = 15	1.477 \pm 0.423 29.98 <i>n</i> = 11	2.445 \pm 0.212 278.85 <i>n</i> = 2	No data \dagger	0.0834 \pm 0.0139
Florida	1.127 \pm 0.198 13.40 <i>n</i> = 17	No data \dagger	1.645 \pm 0.351 44.16 <i>n</i> = 11	1.838 \pm 0.388 68.87 <i>n</i> = 3	3.144 \pm 0.000 1393.2 <i>n</i> = 1	0.0899 \pm 0.0190
Monteverde	1.072 \pm 0.194 11.81 <i>n</i> = 21	1.211 \pm 0.220 16.25 <i>n</i> = 28	No data \dagger	2.316 \pm 0.154 206.9 <i>n</i> = 2	No data \dagger	0.0937 \pm 0.0515
Trinidad	1.234 \pm 0.095 17.12 <i>n</i> = 2	1.530 \pm 0.200 33.87 <i>n</i> = 9	No data \dagger	2.513 \pm 0.222 326.1 <i>n</i> = 3	No data \dagger	0.0941 \pm 0.0224
BCI	0.786 \pm 0.187 6.111 <i>n</i> = 37	0.923 \pm 0.138 8.377 <i>n</i> = 7	No data \dagger	2.280 \pm 0.666 190.6 <i>n</i> = 17	3.078 \pm 0.147 1195.8 <i>n</i> = 6	0.1150 \pm 0.0350
Santa Barbara	1.250 \pm 0.024 17.78 <i>n</i> = 2	1.336 \pm 0.321 21.70 <i>n</i> = 3	1.668 \pm 0.141 46.51 <i>n</i> = 7	2.618 \pm 0.000 415.0 <i>n</i> = 1	2.985 \pm 0.160 966.8 <i>n</i> = 6	0.1401 \pm 0.0012
Heron Island	1.321 \pm 0.192 20.93 <i>n</i> = 120	1.477 \pm 0.158 30.02 <i>n</i> = 5	1.946 \pm 0.012 88.23 <i>n</i> = 2	2.736 \pm 0.242 544.2 <i>n</i> = 4	3.024 \pm 0.099 1056.5 <i>n</i> = 3	0.1853 \pm 0.0279

* The first row for each locality is the mean \pm 1 SD of $\log_{10}(\text{intensity})$ (columns 2–6) or chroma (last column). The second row is the mean $\log(\text{intensity})$ transformed back into the original photon units, and the third row is sample size. For comparison, full sunlight with no canopy with and without clouds averaged (all localities) 1164 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ ($\log_{10} = 3.066 \pm 0.217$; *n* = 7) between 0900 and 1500, and averaged 1728 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ at midday with no clouds.

\dagger No measurements between 0900 and 1500.

\ddagger Chroma calculated using Eq. 16 of Endler (1990) for each *forest shade* spectrum, sunny conditions. White or grey has a chroma of zero; spectra with a greater change of intensity with wavelength (greener in this case) have larger chroma.

§ *Forest shade* on Figueroa Mountain measured under continuous *Quercus chrysolepis* canopy (a "live oak").

blue as a result of fog, haze, smoke from forest fires, or air pollution. *Woodland shade* is particularly common in forests with a high treefall rate or human disturbance, and in drier forests with trees with thin crowns (a large gap fraction, *G*, distributed over large numbers of small holes) such as *Eucalyptus*, *Callitris*, *Casuarina*, and *Pinus* (Brisbane, Figueroa; Table 1).

The gradient between forest shade and woodland shade

Fig. 9 shows a gradient in Queensland between relatively dry rain forest through moist *Eucalyptus* woodland to dry *Eucalyptus* woodland, during cloudless days. The dry rainforest has a nearly closed canopy whereas the dry woodland has the typical *Eucalyptus* woodland structure, with each crown casting relatively little shade. The moist *Eucalyptus* forest is intermediate in structure and spectrum. Ambient light changes from that of *woodland shade* to *forest shade* spectra as the canopy becomes more closed and continuous.

The tower on BCI, Panama, is at the edge of a large gap, but the gap does not extend to ground level at the base of the tower. Spectra from direct sunlight at var-

ious levels were indistinguishable from large gaps. Shade spectra were obtained at 27.4 m and lower (Fig. 10; there was no vegetation shade above 27.4 m). As one descends from the shade of canopy emergents, through the shade at the edge of the gap, to the shade of a closed canopy, the spectra change from that of *woodland shade* to *forest shade*. As in the Queensland transect, the transition from greenish *forest shade* to bluish *woodland shade* corresponds to increases in the fraction of the sky that is unobstructed by vegetation.

Effects of clouds

Clouds make little or no difference to the shape of the spectrum of open areas, indeed the no-canopy data in Fig. 6 include both sunny and cloudy conditions. There is also no significant effect of clouds on the light of large gaps. Clouds, however, do have a significant effect on the other three light habitats of Fig. 3.

The spectrum of light in small gaps shifts to that of large gaps if the sun is blocked by clouds (not shown in Fig. 6); in fact, it is difficult or impossible to identify a point illuminated by small gap geometry (Fig. 3) during cloudy weather unless the sun is alternatively

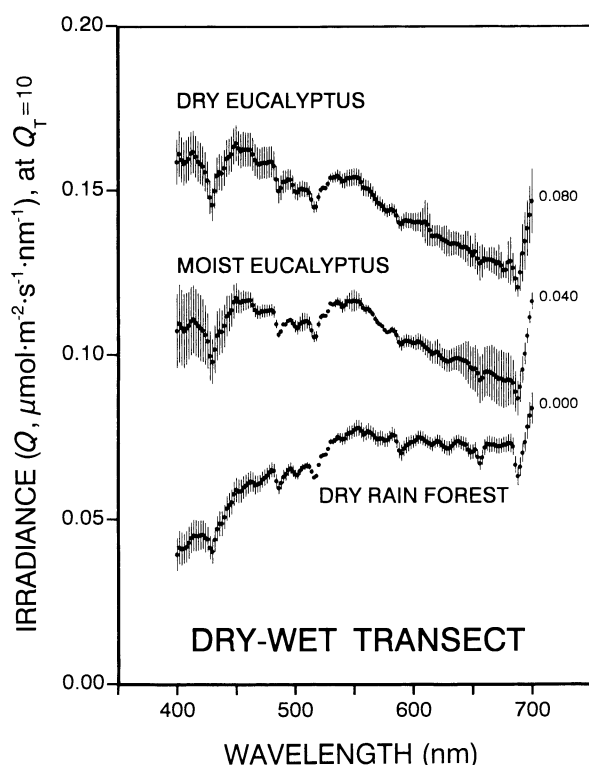


FIG. 9. Transect from dry rain forest ($N = 3$), through moist *Eucalyptus* woodland ($N = 3$) to dry *Eucalyptus* woodland ($N = 28$), in Queensland, Australia. Symbols and offsets as in Fig. 6.

blocked and unblocked by clouds, or one knows the altitude and azimuth of the sun. The chroma of small gaps during cloudy weather ranges from 0.074 to 0.112, compared to 0.091 to 0.462 during sunny weather, indicating the whitening (reduced chroma) under cloudy conditions.

When the sun is obscured by thin or thick clouds, the spectrum of forest shade shifts dramatically (Fig. 7). If the clouds are dense enough so that there are no visible shadows or sun flecks, then the spectrum is nearly flat. Except at Heron Island and BCI sites, the resulting spectra were indistinguishable in shape (color) from the spectrum of large gaps (Fig. 6); the small peak in the cloudy spectrum of Fig. 7 is mainly due to the BCI data. Intermediate degrees of cloud obstruction yield intermediate spectra (Fig. 7, thin cloud). If the clouds are thin enough so that shadows and sun flecks are indistinct, or with fuzzy boundaries, then the amount of flattening of the yellow-green peak is roughly proportional to the density of the cloud obscuring the sun (C, Appendix).

The spectrum of woodland shade habitats is very sensitive to clouds (Fig. 8), as one would expect from the large contribution of skylight to the ambient light spectrum. If the sun is not obstructed by clouds, but clouds obscure some of the sky, then the blue-gray effect is reduced. The blueness is further reduced if

either (a) the sun is unobstructed but most or all of the sky is covered by clouds, or (b) thin clouds obscure the sun (Fig. 8, thin cloud). The color of woodland shade habitats is equivalent to *large gaps* whenever the sun is unobstructed but the rest of the sky is cloudy (white) or if the sun is entirely blocked by clouds (Fig. 8, cloudy). Note that in woodland shade habitats, unlike forest shade habitats, the convergence requires a cloudy sky, but the sun does not have to be blocked by the clouds. In woodlands with thin canopy (a large gap fraction G distributed over large numbers of small holes), however, the shade spectrum will converge on large gap conditions more fully if the sun is both blocked by clouds and the sky is cloudy. Woodland shade light becomes whitish under cloudy conditions.

In summary, under cloudy conditions, small gaps, forest shade, and woodland shade habitats converge in spectral shape (color) on large gaps and open areas, yielding a whitish (low chroma) light environment (Figs. 7 and 8). For this reason, and for brevity, this light environment will be called *open/cloudy*. All shade spectra sampled along any vertical or horizontal tran-

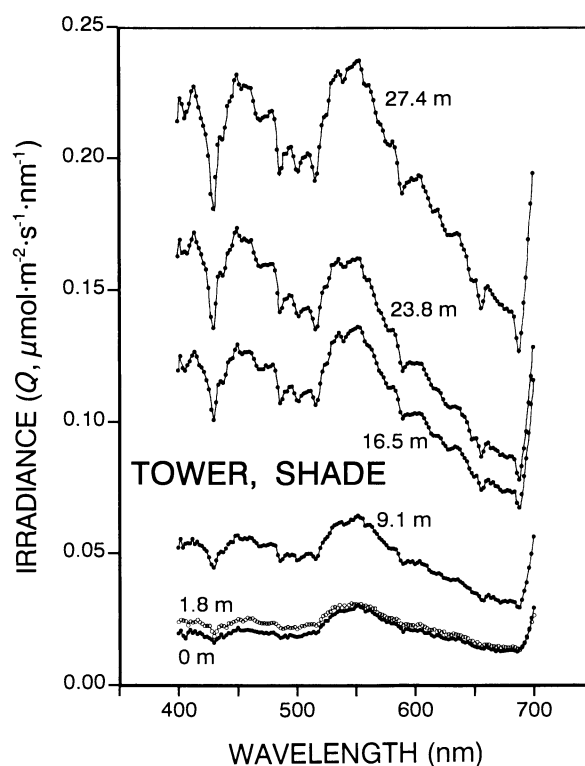


FIG. 10. A transect of the spectral composition of shade from the canopy to the ground on a tower at BCI, Panama. These spectra are absolute (not standardized to a total irradiance of 10). The scans in direct sun (not shown) were indistinguishable from direct sunlight and large gaps (as in Fig. 6). Note the progressive change from spectra resembling *woodland shade*, towards spectra resembling *forest shade*, with decreasing height, as the increasing canopy above the sensor excludes more and more of the blue skylight.

sect will probably have this shape in cloudy weather, and indeed the same shape everywhere in the forest under overcast conditions.

Low sun angles: early/late

The color of ambient light changes considerably at dawn and dusk (Fig. 11). No significant differences were found between dawn and dusk spectra when compared at roughly the same total light intensity or sun angle (standard errors at each wavelength completely overlap). In both morning and evening transitions between daylight, dusk, and twilight, there are either two or three spectral stages, depending upon the weather. For simplicity, the changes will be described in terms of the evening transition. If there are clouds anywhere in the sky then the three stages (Fig. 11) are as follows. Stage 1: as the sun drops below $\approx 10^\circ$ from the horizon, the spectrum first becomes purplish-white, or slightly deficient in middle wavelengths (≈ 570 – 630 nm). Stage 2: light from the setting sun illuminates overhead clouds with a yellow-to-red light, which is then reflected onto the forest floor (this happens outside forests as well). If there are no clouds, then this stage is absent. Stage 3: after the sun sinks below the horizon the loss of

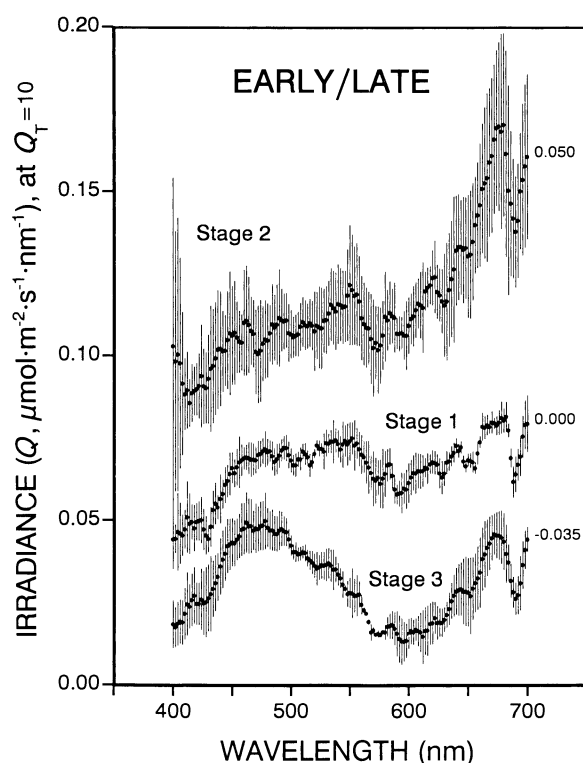


FIG. 11. Early/late sequence measured at equivalent times at dawn and dusk. Stage sequence numbered as if for dusk. Symbols and offsets as in Fig. 6. Stage 1 ($N = 10$): sun setting. Stage 2 ($N = 7$): sun falling below horizon, yellowish and reddish light reflected from cloud cover into forest. This stage is absent if there are no clouds. Stage 3 ($N = 9$): twilight, purplish light declining in intensity to past the limit of color vision.

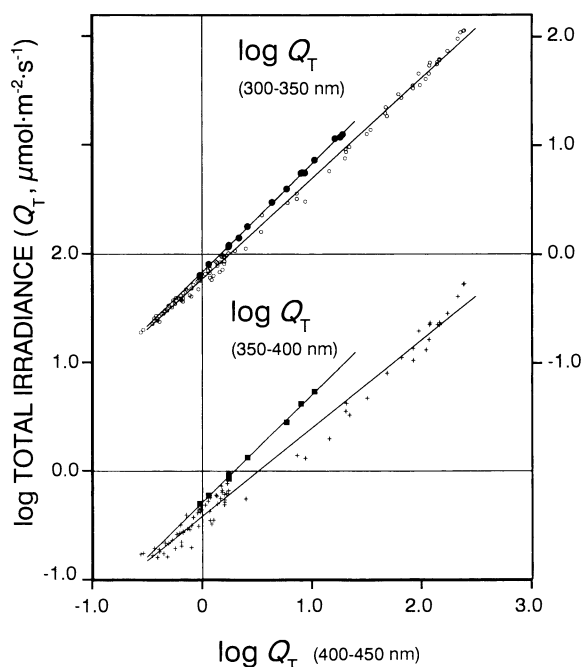


FIG. 12. Predicting the ultraviolet (UV) part of the spectrum from the blue end of the visible spectrum (400–450 nm). Q is the total light intensity (quantum flux) in the given spectral range. Large symbols (●, ■): woodland shade. Small symbols (○, +): forest shade. Regression lines: woodland shade, near UV (350–400 nm, upper graph), $Y = 0.994X - 0.173$ ($N = 15$); forest shade, near UV, $Y = 0.923X - 0.237$ ($N = 100$); woodland shade, far UV (300–350 nm), $Y = 0.991X - 0.293$ ($N = 8$); forest shade, far UV, $Y = 0.82X - 0.419$ ($N = 78$). The slopes of woodland and forest regressions are significantly different from each other ($P < .01$ for near UV and $P < .05$ for far UV).

middle wavelengths (570–630 nm) becomes pronounced; the light becomes purplish and gradually darkens until color vision is no longer possible.

Ultraviolet spectrum

Because the widespread nature of ultraviolet (UV) sensitivity of animals only became apparent during the course of this study (e.g., Goldsmith, 1990), not all scans included the 300–400 nm region. If we define UV color as the shape of the spectrum in this region, then there is very little color difference among the habitats, so little that the total irradiance between 400 and 450 nm is a very good predictor of the ultraviolet irradiance (Fig. 12). The only appreciable difference found was that *woodland shade* (large symbols, Fig. 12) contained proportionally more ultraviolet than *forest shade*.

Red/far red ratio ζ , or light "quality"

Plant physiologists have found that a measure of light "quality," ζ , is important in controlling plant growth and development. The measure is $\zeta = Q_r/Q_{fr}$, where Q_r is the total irradiance between 655 and 666 nm (orange red) and Q_{fr} is the total irradiance between

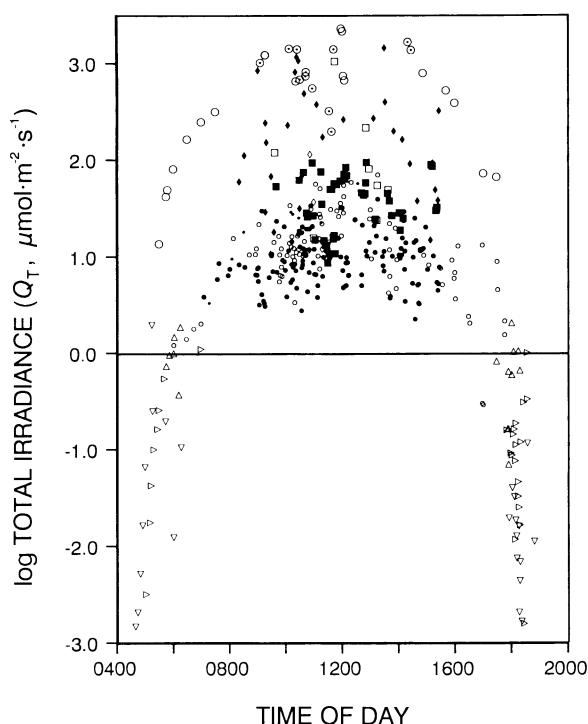


FIG. 13. Light intensity (log units) variation with time of day. Light habitat symbols: ● forest shade, sunny. ○ forest shade, cloudy. ■ woodland shade, sunny. □ woodland shade, cloudy. ◆ small gaps, sunny. ◇ small gaps, cloudy. ○ open areas. ⊙ large gaps, △ early/late, stage 1 (see Fig. 11). ▷ early/late, stage 2. ▽ early/late, stage 3. Note how light intensities in forest shade and woodland shade may sometimes be brighter during cloudy weather.

725 and 735 nm (near infrared) (Smith 1981a). In 94 of the scans, data went up to 735 nm, so it was possible to calculate ζ . The results were as follows (means \pm 1 SD, with sample sizes): *forest shade*, sunny $\zeta = 0.1545 \pm 0.0561$ (45), cloudy 0.6241 ± 0.1435 (10); *woodland shade*, sunny 0.5133 ± 0.01721 (11); *small gaps*, sunny 1.1575 ± 0.3772 (18); *large gaps* 1.4393 ± 0.1193 (10). No data were collected for woodland shade, small gaps, and large gaps during cloudy weather. Note how ζ in forest shade increases by a factor of 4 when clouds block the sun. In addition, *woodland shade* ζ is much larger than *forest shade* when it is sunny, and nearly the same as *forest shade* when it is cloudy. As one might expect, ζ is much larger in *small gaps*, and still larger in *large gaps*.

Light intensity

Data on total light intensity or total irradiance (Q_T) was obtained by integrating the irradiance spectra between 400 and 700 nm (this yields PAR, or photosynthetically active radiation; Kirk 1983). The time course of light intensity is shown in Fig. 13, and the data between 0900 and 1500 at the main habitats are summarized in Table 2. The light intensity of gaps declines with gap size, and gaps are brighter than shade habitats.

Woodland shade is brighter than *forest shade*. Note that the light intensity in forest shade habitats does not necessarily decrease, and may even increase, when the sun becomes obscured by a cloud (Table 2, Fig. 13).

DISCUSSION

The color of forest light depends upon forest geometry, weather, and time of day, and seems to be nearly independent of forest species composition. Once again it is useful to make the distinction between light habitats (determined by geometry, Fig. 3), and light environments (the irradiance spectra within a light habitat). The four habitats differ in the relative proportions (solid angles) of light arriving from the sun, blue sky, clouds, and vegetation (Figs. 1 and 3), each light source having a different color (spectral shape, Fig. 2). The relative strengths and sizes of the light sources, and their varying spectra, determine the ambient light spectrum (Appendix). The four light habitats (Fig. 3), in combination with variation in weather and sun angle, result in five major light environments (summarized in Fig. 14): (1) *forest shade*, greenish or yellow-green; rich in middle wavelengths (and also above 680 nm); (2) *woodland shade*, bluish or bluish-gray; rich in short wavelengths and UV; (3) *small gaps*, reddish; richer in longer wavelengths; (4) *open/cloudy* (includes large gaps in any weather, and forest shade, woodland shade and small gaps during cloudy weather), essentially "white" light; and (5) *early/late*, purplish; deficient in middle wavelengths. All of these light environments were present in all study sites except for those with thin canopies (Table 2).

Because canopy holes are found in all sizes, the four light habitats of Fig. 3 grade into each other; as Lieberman et al. (1989) said, microsites vary in canopy closure. Consequently we expect to find a gradient among the five light environments. We have already seen evidence for this in the wet-dry forest and vertical transects (Figs. 9 and 10), but this is most easily seen by plotting the data in color space (Fig. 15).

The color space of Fig. 15 was devised to compare spectra using a color classification independent of human vision, but retaining general properties of vertebrate and invertebrate visual systems (Endler 1990). Principal components analysis or other multivariate techniques can be used (indeed they yield similar results), but they suffer from the fact that different axes result from each data set. The color space in Fig. 15 has the same axes for any spectrum 400–700 nm, so results are comparable among studies. This classification is similar to the Munsell color system in that any spectrum is represented by a single point in color space, hue is measured as the clockwise angle from the vertical axis to the point, chroma is measured as the distance from the origin to the point, and brightness is measured as the total radiance (or reflectance) of the spectrum and is perpendicular to the hue–chroma plane shown in Fig. 15. Examples of Munsell hues and ap-

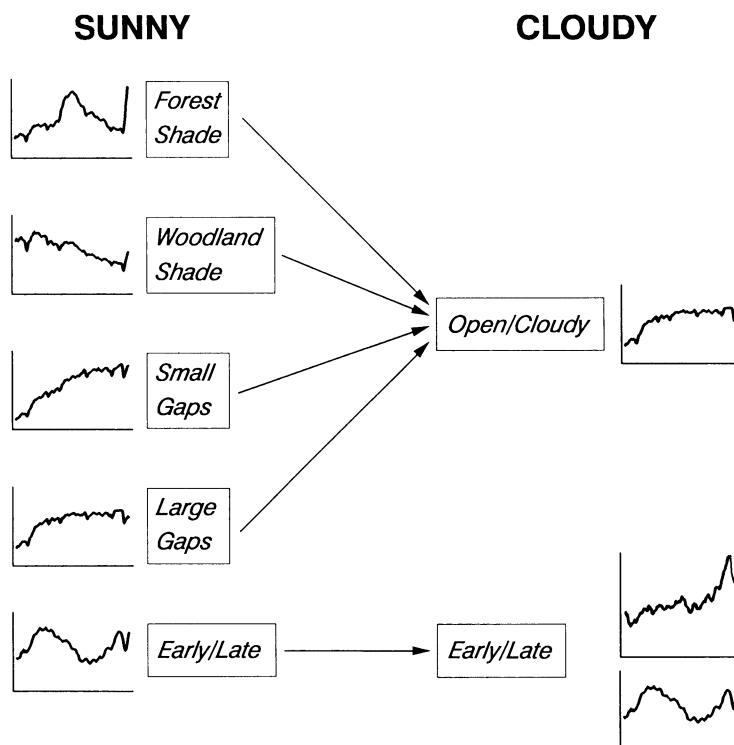


FIG. 14. Summary of the light environments and their changes under cloudy weather. The graphs are irradiance as a function of wavelength between 400 and 700 nm, and repeat the mean curves in Figs. 6–11.

proximate angles in this color space are R (0°), Y (70°), GY (120°), G (170°), R (220°), and P (320°) (see Endler 1990: Fig. 12). Munsell hues at equal chromas plot as ovals rather than circles in this color space because humans are more sensitive to middle wavelengths. For details see Endler (1990).

Fig. 15 shows that, although the light environments found in each light habitat grade into each other, they occupy different regions of color space. Thus, the distinction among the light environments are as useful as the distinction between forests, woodlands, and savannas; they describe entities with characteristic and predictable properties, but do not necessarily imply that they have sharp boundaries.

The radiant spectra of Fig. 2 are also plotted in Fig. 15. Note how the hues of woodland shade samples are very similar to that of blue sky, though the chroma (distance from origin) varies, presumably from variation in the relative contributions of low chroma sources. A similar pattern is found with forest shade and leaves, though here hue varies much more, except in the *Pisonia* forest. The open/cloudy samples cluster near the radiant spectra of clouds and sun. Interestingly, the chroma of many of the small gaps is much higher than that of the sun, indicating that vegetation has a significant effect. A mixture of radiant spectra would appear in this color space as a point between the source radiances, with a distance determined by the relative contribution of each source (Eq. 2). Because the ex-

planations for these color properties are based upon general rather than specific physical and biological phenomena it is reasonable to predict that these light environments will be present in most other forests. This is supported by the literature.

Other studies and additional observations

A survey of the published findings of researchers at other sites, often using different methods and equipment, supports the generality of the light environments described here. The literature suggests that all five light environments have been noticed at one time or another, though not in the same study. Except for a few exemplary studies (e.g., Federer and Tanner 1966, Björkman and Ludlow 1972), published studies rarely present more than one spectrum under the same conditions, and do not present data on the variation among spectra within the same light environments. Nevertheless, when measured in the same units, they are remarkably consistent with Figs. 6–13 (see Table 3).

Open/cloudy.—Published spectra from open areas and large gaps show very little variation, and are very similar to those of this study. The only exception is Smith's (1981b, Smith and Morgan 1981) observation of an enrichment of shorter wavelengths in open areas during cloudy weather. The presence and extent of clouds should have little effect on ambient light color because the radiant spectrum of clouds is similar to the irradiance spectrum on a clear day. One possible

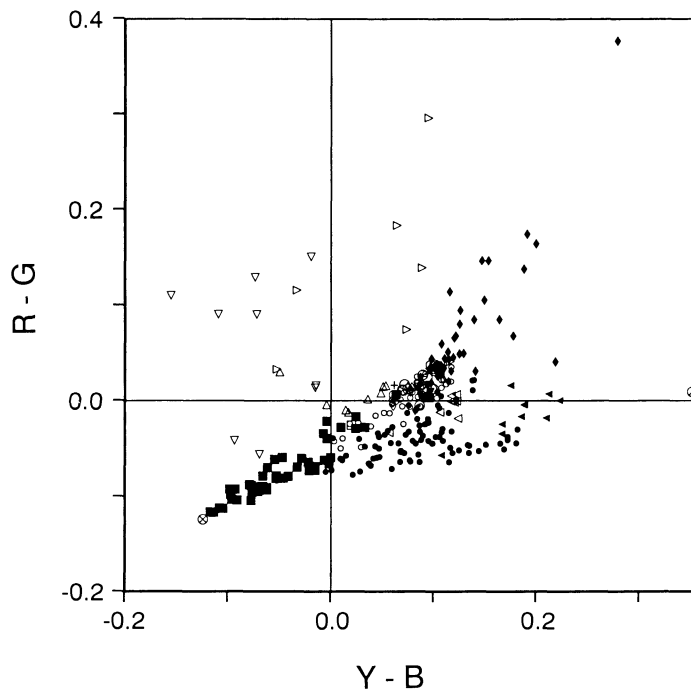


FIG. 15. Plot of the data in the color space of Endler (1990). Each point is a single spectrum. The axes are derived from differences between nonadjacent quarters of the spectrum; Y-B axis positive for more yellow and less blue; R-G axis positive for more red and less green. As in the Munsell color system, hue changes clockwise in a circle centered upon the origin with red at 0° , and chroma (saturation) is proportional to the distance of a point from the origin. Light habitat symbols: \bullet forest shade, sunny. \circ forest shade, cloudy. \blacktriangleleft *Pisonia* forest shade, sunny. \triangleleft *Pisonia* forest shade, cloudy. \blacksquare woodland shade, sunny. \square woodland shade, cloudy. \blacklozenge small gaps, sunny. \lozenge small gaps, cloudy. \circ open areas. \odot large gaps. \triangle early/late, stage 1 (see Fig. 11). \triangleright early/late, stage 2. ∇ early/late, stage 3. The spectra during cloudy weather and open areas cluster so strongly that it is difficult to distinguish them, hence their light environment is called *open/cloudy*. Note how the high chroma *Pisonia* habitats are shifted to the right (more yellow-green). For comparison, the radiance spectra of the light sources in Fig. 2 are also plotted: \otimes blue sky. \odot leaves. $+$ cloud. \times sun.

explanation for Smith's blue shift would be a single dense cloud blocking the sun (Eq. A.4b, cloud transmission C very small), with most of the sky blue (f_b close to 2π). It is also possible that his cloudy weather measurements were made shortly after a rainstorm, and his sunny measurements were made many days or weeks after the last rain, or even during dusty or hazy conditions. A blue shift can be caused by an increase in the Rayleigh/Mie scattering ratio after a rain. Scattering by tiny particles (Rayleigh scattering) is predominant after a rain when particle size is small, and produces the blue of a clear sky with no haze. Scattering by larger particles (Mie scattering) produces a whitish sky, and is much more important in dry weather, when larger particles have not been removed by rains (Robinson 1966, Kondratyev 1969, McCullough and Porter 1971, Coulson 1975, Feigelson 1984). In any case, the differences between cloudy and clear weather that Smith observed were much smaller than the differences among the various light environments in this study.

Small gaps.—Johnson and Atwood (1970) discussed a red shift in spectra of gaps smaller than 1 m, but they do not present data except for one scan of a 1-m gap. Smith and Morgan (1981) noted that deeper gaps (can-

opy holes that go deeper into the vegetation) in crops tended to be more red-shifted than gaps ending closer to the canopy surface. This is expected from the smaller gap fraction (G) subtended by deeper gaps of the same diameter. They did not say what happens in gaps of various depths when the sun was obscured by cloud; presumably they would have observed that the ambient light in deeper gaps (smaller f_c) would have been slightly greener (Eq. A.6b). This could not be tested in the present study because the heights of the forests were too similar among study areas.

Forest shade is similar among published studies of tropical, subtropical, and temperate angiosperm forests (Table 3), and are all similar to this study. Shirley (1929) may have been the first to point out that this light is primarily determined by the reflectance and transmission spectra of leaves and the rest of the vegetation. The light is greenish because light transmitted through and reflected by leaves is richer in middle wavelengths (520–620 nm) than incident light (Gates et al. 1965, Scott et al. 1968, Federer 1970, Wooley 1971, Stoutjesdijk 1972a, Gausman and Allen 1973, Gates 1980, Lee 1986, 1987, Lee and Graham 1986). The data on radiance spectra of leaves measured in

TABLE 3. Other studies of light environments.

Light environments and properties	Comments	References*
<i>Open areas, sunny and cloudy</i> Whitish, sunny = cloudy	Exception: richer in blue when cloudy 26, 27	8, 9, 10, 13, 16, 17, 18, 26, 27
<i>Large gaps, sunny and cloudy</i> Same as <i>Open areas</i>	Assumed by 3	11
<i>Small gaps</i> Yellowish to reddish (richer in long τ)	Red shift at 1-m gap diameter 11. Deeper gaps more red shifted in crops 27.	6, 7, 9, 11, 27, 28
<i>Forest shade, sunny</i> Greenish (550 nm peak)	Northeastern U.S., Canada, Germany, Australia, Panama, Costa Rica, Java	1, 2, 3, 14, 15, 17, 24, 25, 26, 29, 30
<i>Forest shade, cloudy</i> Whitish	Northeastern U.S., Java. Spectral flattening 29. Less "wavelength selective" 9. In crops 20.	3, 5, 9, 20, 29
<i>Woodland shade, sunny</i> Bluish (richer in short τ)	Holarctic, coniferous forests. Hedgerow shade 26.	2, 3, 4, 24, 26, 30
<i>Woodland shade, cloudy</i> Whitish	Northeastern U.S.	3, 5
<i>Early/late</i> Purplish	Most detail in 17	12, 16, 17, 18, 19, 20, 21, 22, 23, 25, 27

* References: 1, Björkman and Ludlow 1972; 2, Coombe 1957; 3, Federer and Tanner 1966; 4, Freyman 1968; 5, Hailman 1979; 6, Holmes 1981; 7, Holmes and McCartney 1976; 8, Holmes and Smith 1977a; 9, Holmes and Smith 1977b; 10, Holmes and Smith 1977c; 11, Johnson and Atwood 1970; 12, Johnson et al. 1967; 13, Kirk 1983; 14, Lee 1987; 15, Lee and Graham 1986; 16, McFarland and Munz 1975a; 17, McFarland and Munz 1976; 18, Munz and McFarland 1973; 19, Roach and Gordon 1973; 20, Robertson 1966; 21, Rozenberg 1966; 22, Salisbury 1981; 23, Scott et al. 1968; 24, Seybold 1936; 25, Smith 1981a; 26, Smith 1981b; 27, Smith and Morgan 1981; 28, Stoutjesdijk 1972a; 29, Stoutjesdijk 1972b; 30, Vézina and Boulter 1966.

this study confirm this (Fig. 2). Leaf radiant spectra have more chroma (are more peaked) than *forest shade* (Figs. 2 and 7); leaves have a chroma of ≤ 0.39 whereas the chroma of *forest shade* is ≤ 0.18 (Tables 2 and 4). Clearly, the greater the proportion of ambient light originating from leaves (f_l), the more similar the ambient light [$Q(\lambda)$] will be to the high chroma leaf radiance [$q(\lambda)$] and the more dissimilar to the relatively less saturated light reflected from the rest of the vegetation [$q_k(\lambda)$, Eq. A.5] and other sources. This may explain some of the fourfold range of chroma among the study sites (Table 2), but there are two more contributing factors, leaf thickness and skylight coming through gaps in the canopy.

Thinner leaves may lead to greater chroma of *forest shade* for two reasons. First, if leaves are thin, then proportionally more of the ambient light will come from light transmitted through rather than reflected from leaves. This is supported by the radiance data: light transmitted through the thinner sycamore leaves was $\approx 50 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \cdot \text{sr}^{-1}$ compared to $\approx 10 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \cdot \text{sr}^{-1}$ for the thick and nearly opaque California bay leaves. Because the chroma of transmitted light is greater than reflected light (data in Lee 1986, 1987, Lee and Graham 1986) a greater fraction of the light sources will have higher chroma in forests with thinner leaves. Second, if leaves are thin, then more light penetrates through the canopy, and more light may be both transmitted and then reflected by leaves. There is some evidence for this effect in the

present study. The study sites in Table 2 have been arranged in order of increasing chroma; this ranking roughly corresponds with decreasing leaf thickness. The sclerophyll *Quercus chrysolepis* of Figueroa and the subtropical rain forests of Queensland (Lamington), have very thick leaves and the least saturated spectra. The California riparian forest contained many trees with thin leaves (mostly *Platanus*) and had the most saturated of *forest shade* spectra aside from Heron Island (Table 2). The *Pisonia* forest on Heron Island has an extremely saturated spectrum (Fig. 3, Table 2), and is different from the others in two ways; its leaves are very much thinner, and the bark and branches are very pale. The pale bark and branches, which have a nearly flat reflectance spectrum, modify the reflected light very

TABLE 4. Fraction of ambient light absorbed by leaves in the five light environments and white light for comparison.

	<i>Ilex cornuta</i> *	<i>Triolena hirsuta</i> †	<i>Bursera simaruba</i> ‡
Chroma‡	0.388	0.220	0.185
White light	0.852	0.832	0.905
<i>Open/cloudy</i>	0.843	0.826	0.902
<i>Small gaps</i>	0.873	0.822	0.899
<i>Forest shade</i>	0.831	0.818	0.896
<i>Woodland shade</i>	0.854	0.834	0.906
<i>Early/late</i>	0.861	0.836	0.906

* Absorbance spectrum from Gates et al. (1965).

† Absorbance spectra from Lee (1986).

‡ Flatter spectra (less change of absorbance with wavelength) have smaller chroma.

little from that transmitted through the leaves, so the ambient light in a *Pisonia* forest is close to that expected if nearly all light is affected only by leaves. The other forests have much thicker leaves than *Pisonia*, so the proportion of transmitted light is lower. In addition, other forests have much darker bark, so the proportion of high chroma reflected light is also lower than in *Pisonia* forest light (Fig. 15).

Although cloudy weather changes the spectrum from greenish to whitish, this is usually not explicitly discussed in the literature. Very few of Hailman's (1979) *forest shade* spectra show a peak at middle wavelengths but he stated (p. 302) that most measurements were made in cloudy or rainy weather.

Woodland shade.—Seybold (1936) appears to have been the first to observe that *woodland shade* can be bluish or blue-gray. He coined the terms "blue shade" (*woodland shade*) and "green shade" (*forest shade*). Although his work has been cited several times (Coombe 1957, Anderson 1964a, Vézina and Boulter 1966), the phenomenon is not well studied, and has been confused with the "transmission" or "absorption" properties of forests (e.g., Coombe 1957). Many but not all North American coniferous forests have a woodland structure with a characteristic blue-gray spectrum (Table 3). Hailman's (1979) coniferous forest data do not show the blue-gray spectrum of other studies, but cloudy weather was present during the recordings (Hailman 1979: 302).

There appear to be no published spectra from transects between forest and woodland, and little has been done with spectral properties of light at various heights in the canopies of forests. Johnson and Atwood (1970) found a reduction in short wavelengths and an increase in long wavelengths ("red-shift") with depth over four levels in an 18-m vertical transect in a Puerto Rican rainforest. Hailman (1979) acquired spectra at 15 m on another tower on BCI in Panama, but this data do not show the blue-gray form; however, he did not specify weather conditions, or whether the samples were taken in shade or direct sunlight.

Early/late spectra are fairly well documented (Table 3), although only McFarland and Munz (1975a, b, 1976, Munz and McFarland 1973) have considered the visual consequences. They (and others) observed the slight reduction in middle wavelengths of stage 1 (Fig. 11; their Fig. 10.8 "presunset"), and the stronger reduction later (stage 3, Fig. 11). McFarland and Munz (1976) did not mention the reddish spectra of stage 2 (Fig. 11), but may have worked only in clear weather. They were able to measure the ambient light spectrum well into the night, and found that the spectrum becomes relatively flat again at lowest light levels. My spectroradiometers were not sensitive enough to detect this stage in forests (which would be stage 4). McFarland and Munz (1976) also presented ambient light spectra for moonlight, which is enriched in long wavelength light relative to full sunlight.

The reduction of middle wavelengths, particularly in stages 1 and 3 of *early/late*, is caused by atmospheric ozone, which is particularly absorbent around 604 nm (Rozenberg 1966, McFarland and Munz 1976). This absorbance only becomes conspicuous at dusk and dawn, when sunlight passes a long distance through the atmosphere, and thus encounters enough ozone to cause an appreciable middle wavelength attenuation. The situation is a little different during cloudy weather. Light from the setting sun must pass a much greater distance through the atmosphere than "normal" daylight as a result of the low sun angle. The atmosphere differentially scatters short wavelengths (this is why a cloudless daytime sky is blue, Coulson 1975), so the photons that have travelled long distances at dusk are more likely to be of longer wavelengths. This illuminates overhead clouds with a yellow-to-red light, which is then reflected onto the forest floor. If there are no clouds, then the long wavelength light escapes into space and this stage is absent. Depending upon the latitude, time of year, and weather, stages 2 and 3 can be as short as a minute or as long as a quarter of an hour. The strongly purplish stage is of shorter duration in the tropics, but there is also more ozone at tropical than temperate latitudes (Caldwell 1981), so the net effect may be that the *early/late* environment varies little with latitude. More data is needed to understand the ambient light in forests at low sun angles. One can only speculate about the conservation implications of the current reduction in the atmospheric ozone layer.

Total irradiance (Q_T).—No attempt was made to survey the very large literature on variation in light intensity within forests. Nevertheless, papers found during the search for spectra gave total intensities (Q_T) that were in general very similar to that of Table 2 and Fig. 13 (e.g., Björkman and Ludlow 1972 in Queensland, Pearcy 1983 in Hawaii, Chazdon and Fetcher 1984a, b in Costa Rica). Lawton's (1990) data for Monteverde cloud forest showed much lower intensities than the other studies, perhaps he was working under very heavy overcast conditions. Some workers give data in terms of light intensity as a fraction of full sunlight (open areas), and this is in general similar to the present study in *forest shade* and *woodland shade* (Table 2). However, these intensities are much lower than found by Reifsnnyder et al. (1970) in deciduous and coniferous forests in Connecticut.

As in this study, Björkman and Ludlow's (1972) data suggest that the light intensity in forest shade does not necessarily decrease, and may even increase, when the sun becomes obscured by a cloud (Table 2, Fig. 13). Anderson (1964c) gave a number of references indicating that the increase in light intensity in forests during cloudy weather is reasonably well known. On the other hand, Lawton (1990) did not find an increase in Q_T during cloudy weather. The contradictory results may have arisen because Q_T depends upon the relative radiances of clouds, blue sky, and vegetation during

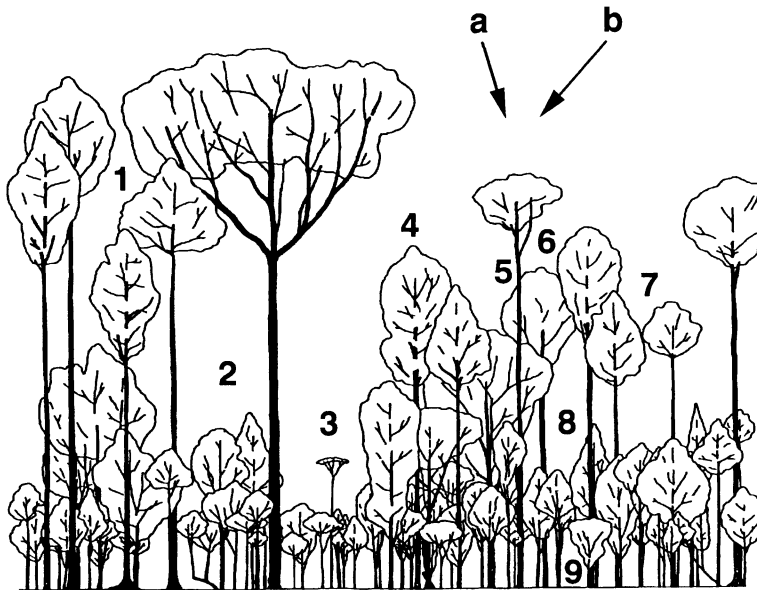


FIG. 16. A transect through a tropical rain forest showing the effects of geometry and time of day on the distribution of light habitats. The horizontal distance is ≈ 150 m and the trees are drawn to scale (after Richards 1939). The arrows marked a and b indicate two different sun angles, and the numbers refer to sites in the forest. Location 1 will be a small gap for sun angle a but woodland shade or forest shade for other angles. Other combinations of locations and sun angles: 2a, forest shade. 2b, large gap. 3a, forest shade. 3b, brighter forest shade than 3a. 4a, woodland shade. 4b, large gap. 5a, bright forest shade. 5b, forest shade. 6a, woodland shade. 6b, large gap. 7a, large gap. 7b, woodland shade. 8a, b, 9a, b, forest shade. These rules are based upon geometry, so would apply on a much smaller scale to the light environments within a single shrub, branch, or smaller plant.

sunny and cloudy periods (Eqs. A.7a, b), and Lawton's (1990) conditions may have included clouds with much lower radiance than the other studies. Heavy overcast conditions should both homogenize the spectrum and reduce light intensity, even if light overcast or broken clouds can result in increased light intensity on the forest floor.

The strong reduction in variation in light intensity (Q_T) throughout the forest floor during cloudy weather was noted by Evans (1966) and Anderson (1964c). The grater radiance of clouds compared to blue sky explains this as well as the convergence of light environments during cloudy weather (Fig. 14). When there are no clouds, a given surface can only receive high intensity light from a canopy hole in the direct line-of-sight of the sun; other holes send only blue skylight at a Q_T less than that of the vegetation (Fig. 2). A surface in the shade will receive only $\approx 10 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (Table 2). When the sun is blocked by clouds, the clouds act as a diffuser, so high intensity cloud radiance (Fig. 2) will reach the surface of a color pattern from all canopy holes. The fact that there are more holes sending high intensity light to the surface may make up for the 15–75% loss in intensity (Coulson 1975) of the hole or holes formerly passing sunlight to the surface of interest. A surface that was not in a sun fleck when the sun passed behind a cloud would then receive more of a normal solar spectrum from the canopy holes, and perhaps much more total light intensity (Fig. 13). The

effects of diffuse light were also discussed by Federer and Tanner (1966).

Generality: variation with height in forests and other vegetation

Because geometry is so important in determining how the light from each light source mixes to produce the irradiance spectrum (Fig. 3), variation in ambient light should be predictable anywhere in a forest, not just on the ground as implied by Figs. 1 and 3. The vertical transect (Fig. 10) confirms this, at least in one site. Consequently it should be possible to say, purely on the basis of forest geometry, sun angle, and weather, where each light environment is found at various positions in and below the canopy of a forest, and a schematic diagram is given in Fig. 16. For example, a shaded animal, fruit, or flower found at any height will experience *woodland shade* whenever a significant fraction of blue sky shows through the canopy holes, and few or no clouds show through the remaining holes. This also suggests that there should be, in general, a gradient from *forest shade* to *woodland shade*, and from *small gaps* to *large gaps*, going vertically in a forest, but note that this does not predict that this transition should necessarily be regular. If the outer canopy is broken and the top canopy varies in height with horizontal distance, then the transition between the light environments will occur at different heights. For example, at position 3 in Fig. 16 the transition will occur

close to the ground, whereas at position 8 it will occur far from the ground. This means that studies of vertical distributions of animals such as birds and butterflies, and plants such as epiphytes, must not only take into account the height at which the individual is spotted, but also the geometry of the vegetation at that height. Two individuals at the same height, but a few metres apart, may experience radically different light environments even though they are both in shade. Because these relationships depend upon geometry, they should be independent of scale. They should therefore apply to the light environments within shrubs and other plants, but on a much smaller scale. The critical parameters are the solid angles of each light source and their radiant spectra (Eq. 2), no matter what the scale.

*Consequences for visual signals by
animals and plants*

The heterogeneity of color within forests has important implications for visual signals of animals and plants, because the light spectrum reaching a viewer's eye $p(\lambda)$ from a color pattern element or patch is a function of the ambient light spectrum $Q(\lambda)$ striking the patch, the patch's reflectance spectrum $R(\lambda)$, and the transmission spectrum of the medium $T(\lambda)$; $p(\lambda) = Q(\lambda)R(\lambda)T(\lambda)$ (see Endler 1990 for detailed discussion). Except in foggy or very dusty weather, we can ignore $T(\lambda)$ of the air, and, except for a few species such as lizards, $R(\lambda)$ is constant during the course of a day. But $Q(\lambda)$ varies with microhabitat, weather, and time (Figs. 3, 14–16), so the color of a patch [shape of $p(\lambda)$] can vary, depending upon when and where it is viewed. Vision and perception of any given $p(\lambda)$ varies among species, but variation in $p(\lambda)$ with light environments is likely to affect the conspicuousness of color patterns regardless of the visual and perceptual abilities of the viewers (Endler 1990, 1991). Ambient light will also affect the conspicuousness of a color pattern against the visual background because both animal (or plant) and background color patterns may change in different ways with different $Q(\lambda)$. Four rules describe the interaction $Q(\lambda)$ and $R(\lambda)$, and these can be utilized to make some general predictions about the kinds of colors [$R(\lambda)$] that should be used under specific conditions and purposes.

Rule 1.—In ambient light of a given color [shape of $Q(\lambda)$], the total brightness of a color pattern element [$p_T = \int p(\lambda)d\lambda$] is proportional to the similarity in shape between reflectance $R(\lambda)$ and ambient light $Q(\lambda)$, when total reflectance [$R_T = \int R(\lambda)d\lambda$] is held constant. For example, in red light [$Q(\lambda)$ rich in long λ], a red patch [$R(\lambda)$ larger at long λ] will be brighter than a patch of any other color because it reflects most strongly in parts of the ambient light spectrum that are most intense. At the other extreme, a saturated (high chroma) blue patch in saturated red light will reflect no light because the blue patch only reflects wavelengths not found in the saturated red light. A red patch will also be brighter

than a white patch in red light if both the red and white spots have equal total reflectance (equal R_T). If we do not hold R_T constant, and instead let both red and white patches have $R(\lambda)$ with equal maxima, then both will be equally bright in red light, and the red patch duller in other $Q(\lambda)$. An equivalent argument can be made for other colors.

Rule 2.—The brightness contrast of a color pattern will be greatest if it consists of patches that vary strongly in the degree to which their reflectance spectra resemble the ambient light spectrum. Color contrast may also be greatest under these conditions. More formally, the contrast of a color pattern will be proportional to the variance of the resemblance between $Q(\lambda)$ and $R_i(\lambda)$ for each patch i , weighted by each patch's relative surface area. The contrast between the visual background and an animal (flower or fruit) will depend both upon the within-pattern contrast and the contrast between the animal (or plant) and background color patterns; both are dependent upon the ambient light spectrum.

Rule 3.—The contrast among patches will change with ambient light, because the change in shape of $Q(\lambda)$ affects its resemblance to the fixed reflectance spectra of the color pattern and background patches. This will affect contrast within and between animals (or flowers, fruits) and their backgrounds.

Rule 4.—The contrast of a color pattern in different light environments will be affected by the chroma of the component patches. The degree of chroma of a patch determines the degree to which its appearance [$p(\lambda)$] is affected by the color of ambient light. A saturated (high chroma) patch has a $R(\lambda)$ that changes rapidly over a small λ interval, and therefore will induce a similar shape in $p(\lambda)$, maintaining its color with varying $Q(\lambda)$. An unsaturated patch has a smoother $R(\lambda)$ and therefore $p(\lambda)$ will vary more freely with $Q(\lambda)$. The extreme case is a gray patch [$R(\lambda) = \text{constant}$], which results in a $p(\lambda)$ that replicates the shape of $Q(\lambda)$. As the color of ambient light [$Q(\lambda)$] varies, unsaturated patches [low chroma $R(\lambda)$] vary more in color [$p(\lambda)$ shape] and brightness (p_T) than saturated patches. As a result, low chroma color patterns will vary strongly with $Q(\lambda)$ in both color and brightness contrast, while high chroma color patterns will vary only slightly. Visual backgrounds mostly consist of low-chroma patches. Therefore low-chroma animals (or plants) will contrast less than high-chroma ones, but may vary more with $Q(\lambda)$. Color patterns consisting of mixtures of high- and low-chroma colors may vary greatly in both within-pattern contrast and contrast with the background when exposed to different light environments.

These rules yield some predictions about the kinds of color patterns we would expect to find in forest animals, flowers, and fruits:

General spectral properties.—Cryptic color patterns should have patches with reflectance spectra similar to that of the background during maximum predation risk (Endler 1978). They should also have low chroma (un-

saturated) spectra because backgrounds are usually unsaturated, and because unsaturated patches change in color with ambient light. Changes in appearance with ambient light may make unsaturated color patterns harder to recognize and track than saturated patterns. Color patterns used in signalling (intraspecific, pollination, or aposematic) should have patches different from that of the background and with high mean and variance in resemblance to ambient light spectra at the time and place of signalling. They also should have patches with saturated spectra for constant appearance and easy recognition in any light environment. If only parts of an overall color pattern are used in signaling, then only these should be saturated. Color patterns that serve in both crypsis and intraspecific communication should be a mixture of saturated and unsaturated patches and intermediate variance of resemblance between $R(\lambda)$ and $Q(\lambda)$; this can result in high contrast in some light environments and low contrast in others.

Conspicuousness varies with environment.—Some patches will be very conspicuous in some light environments but not in others. Therefore, a color pattern may not be cryptic or conspicuous in all light environments and its conspicuousness can change over the course of a day within a given microhabitat (example in Endler 1991).

Habitat specificity.—Certain color combinations will be best for crypsis or for signalling in single light habitats. As a result, characteristic suites of colors should be used by animals or plants signalling in the same light environments. Signal colors in *forest shade* should be yellow or yellow-green to maximize brightness (total reflectance). However, these colors will probably be cryptic or poorly visible against a green or yellow-green background. Consequently, red or orange would be a better color signal. In order to increase contrast, a small amount of blue or blue-green should also be present in the pattern. Signal colors in *woodland shade* should be blue or blue-green (and perhaps ultraviolet) to maximize brightness, with a small amount of red or orange for increased contrast. Because *woodland shade* light is found in the canopies of forests, there should be vertical stratification of the colors used in signals, with blues and blue-greens used more often at greater heights (in shade), and reds and oranges used closer to (and on) the forest floor. Species that seek the direct sunlight of *small gaps* should use red, orange, or yellow to maximize brightness, with some blue or purple for increased contrast. There is no prediction possible for *open/cloudy* because its ambient light is white. However, the reduction in intensity below 450 nm (Fig. 6) might result in a slight disadvantage to blue and possibly green in large gaps. Species signalling in *early/late* conditions should use blues, reds, or purple for maximum brightness, and with a small amount of yellow, yellow-green, or green for maximum contrast. These predictions should be most effective for species that send signals in only one, or mostly one, light en-

vironment and also primarily signal during sunny weather, when light environments are distinct. The predictions break down if species spend > 50% of their time signaling during cloudy weather, when the ambient light is whitish in all habitats, or if the signals are sent equally often in different light environments with conflicting best signal colors (Endler 1991, 1992).

The predictions also apply to fruits and flowers, but may be less successful because plants cannot actively seek out specific light environments as sun angle changes during the day. Nevertheless, shrub, herb, and epiphyte species that specialize in particular light environments such as primary forests (*forest shade*), canopy shade (epiphytes in *woodland shade*), or shady places in woodlands (*woodland shade*), may follow the predictions. For example, on average, red fruits should be more common in forests and blue fruits more common in woodland, forest edges, and forest canopies, as well as forests with thin canopies (large G , as in many coniferous and *Eucalyptus* forests). Flowers with ultraviolet "honey guides" may be more common in woodlands and canopy shade than on the forest floor.

The proportions of the light environments of all forests change with season. Radical changes are found in temperate and tropical deciduous forests, and more subtle changes are found in moist tropical or other evergreen forests. Winter or dry season leaf loss opens up the canopy and reduces the incidence of *forest shade* and *small gaps*. This suggests that species that flower or fruit during the wet or summer seasons should on average have a greater incidence of red, orange, and yellow fruits and flowers. Forest species that flower or fruit during the dry season, or the beginning or end of winter, should show on average a greater frequency of blue, blue-green, and ultraviolet-reflecting flowers. These predictions should only hold true for species growing in shade, and those flowering and fruiting during seasons with little cloud cover; cloud cover results in homogeneous whitish light, yielding no predictions about best signal colors. These seasonal arguments also apply to animals.

Animals can choose the places from which they forage, defend their territories, and attract and court mates. Because color patterns can change in conspicuousness with ambient light, and various activities are not necessarily conducted in the same light environments, color patterns can evolve appropriate combinations of color pattern elements so that the same color pattern may be more conspicuous during intraspecific communication than during predation risk, as in guppies (Endler 1991). Given that there are five different light environments available to a signaling animal (Fig. 14), there is much potential for variation in signals among sympatric forest species, especially species that choose to signal only under specific conditions or seasons. For example, consider Fig. 16. Birds, butterflies, and lizards are known to specialize in different combinations of the microhabitats from which they display, and some

birds and butterflies signal only when the sun is not obstructed by clouds. If each species signals only in one of the sites in Fig. 16, and only at particular sun angles, different combinations of colors will yield the clearest signals. This will lead to a vertical stratification of color patterns in species that signal under sunny conditions, but not in those species that signal at any time, or predominantly under cloudy conditions. Note that the same location can experience several different light environments, so, during the course of the day, different positions will have to be used by a specialist on a single light environment. In addition, for forests without a smooth canopy (BCI compared to Trinidad in this study), the vertical stratification will either disappear, or be more difficult to detect, because the gap fractions will change so rapidly with horizontal distance. It is critically important to know the precise visual conditions during visual signalling in order to test these predictions and to make sense out of color patterns.

In summary, because forests are heterogeneous in ambient light color, the same color pattern will appear differently in different light environments; some combinations of color patterns will be best in each light environment. The same color pattern can be conspicuous to mates but relatively inconspicuous to predators. Species that signal only at certain times and places should evolve characteristic and predictable combinations of colors. Careful studies of signalling behavior of animals need to be made in order to test these ideas. Data are needed on the light environments in which displays are made; these include vegetation geometry (Fig. 1), the sun angle, and whether or not there are clouds (Fig. 16). Théry's (1990) study of seven sympatric manakin species is a good example of the kind of data that are required. He found that three lekking species displayed only at particular light intensities and times of day. Some species were very specific for the amount of open sky, or gap fraction. From the present results (Fig. 16), and Théry's (1990) descriptions and diagrams, it is likely that some species display only in large gaps, some only in forest shade, and others only in woodland shade. Different woodland shade species perhaps display in woodland shade of differing chroma (his Figs. 2 and 3). It would be interesting to know how cloudy weather affects their behavior. The predictions about animal and plant color patterns are general and qualitative, but their accuracy will depend upon the relative importance of other factors affecting color pattern evolution, such as thermoregulation, pigment production costs, or foraging energetics. These predictions also have strong implications for the evolution of signalling behavior and microhabitat choice (Endler 1992).

Some consequences for plant growth

The spectral composition of ambient light has profound effects on plant growth and morphogenesis. Light at shorter wavelengths (blue, ultraviolet) induces or

inhibits production of pigments and chloroplast development. Short wavelengths also affect development or inhibition of germination, primordia, growth form (elongation and expansion) and physiological processes such as stomatal opening (Senger 1980, 1987, Fukushima 1981, Thomas 1981, Zeiger et al. 1981, Cosgrove 1983, Durand 1987). These phenomena, collectively called "the blue light syndrome," are also found in microorganisms and fungi (Senger 1980). Longer wavelengths also affect growth and morphogenesis. The relative intensity of red and near-infrared light (red/far red ratio, ζ) affects seed germination, hypocotyl elongation, tillering rate, growth and elongation of stems, expansion rate of leaves, and photosynthetic rates (Smith 1981a, Derigibus et al. 1985, Fenner 1985, Ballaré et al. 1988). Forest habitats vary strongly in ζ , suggesting heterogeneity in growth and form as well as the cues used to develop them. In addition, plants characteristic of low- and high-light environments differ in their responses to changes in ζ ; this may allow them to grow out of adverse light environments and stay in good ones (Grime and Jarvis 1976, Young 1976, Holmes and Smith 1977c, Barber et al. 1981, Morgan 1981), as well as affecting the induction and breaking of seed dormancy (Fenner 1985).

Light "quality" (ζ) and blue light vary with light environments, so it is possible that morphogenetic processes may differ among species living in different light environments. For example, because *woodland shade* is richer in blue and ultraviolet light than *forest shade* (Fig. 12), the critical light intensities for the blue light response may be quite different between species living in deep forest understories compared to subcanopy and woodland species, and such differences may not be explained simply on the basis of light intensity and height in the canopy. The variation in ζ and intensity among light environments may also provide plants with additional cues for generating the appropriate growth forms or growing into the best light environments. The light environments ranked by increasing ζ are *forest shade*, *woodland shade*, *small gaps*, and *large gaps*, so a particular growth and development response to a particular range of ζ may allow specific responses to specific microhabitats. These results are similar (though on a different scale) to those of Ballaré et al. (1988), who found that ζ decreases with increasing density of *Datura ferox*.

Quantum radiometers are used to estimate photosynthetically active radiation (PAR), or the total quantum flux density (Q_T) between 400 and 700 nm. But, because this is total intensity, ambient light with radically different spectra [$Q(\lambda)$] can yield the same Q_T value. Leaves do not absorb light evenly at all wavelengths; relatively less is absorbed at intermediate (550 \pm 20 nm) and longer (>680 nm) wavelengths (Gates et al. 1965, Wooley 1971, Lee 1986). The absorbance spectrum of leaves is almost the complement of leaf radiance (Fig. 2). Because the wavelengths least ab-

sorbed by leaves are also the wavelengths of greatest intensity in *forest shade*, the amount of useful ambient light absorbed by a leaf in *forest shade* is likely to be less than in that of other light environments. This can be seen most easily by multiplying the absorbance spectrum of a leaf by the mean ambient light spectrum of each light environment. The results for a shrub and two tropical tree species are very similar; the fraction of ambient light absorbed by leaves is smallest in *forest shade* and greatest in *woodland shade* and *early/late* (Table 4). In fact *forest shade* may result in less absorbance by plants than a dark cloudy day (*open/cloudy*) with the same Q_T . A similar effect may occur at low sun angles. Although the total PAR in *early/late* may be too low for positive net photosynthesis, the shift towards purplish light as light intensity declines may mean that the photosynthetically active part of the day is longer than expected purely on the basis of PAR measured by a radiometer. The difference in fraction absorbed between *forest shade* and *woodland shade* ranges from 1.0 to 2.3%, depending upon the chroma of the absorbance spectrum (Table 4). Although this is not a large difference, it could be very important if the total intensity is at or near the steepest part of the light intensity–photosynthesis relationship. One consequence might be more growth in shade-tolerant species in *woodland shade* than in *forest shade*, when corrected for total PAR. *Small gaps* illustrate another interesting relationship between intensity and color. As gap size decreases through very small solid angles ($<0.5^\circ$), the spectrum rapidly shifts towards that of *forest shade*, so the fraction absorbed by leaves declines more rapidly than the total intensity decreases with gap size. Thus, penumbral (Smith et al. 1989) and light intensity (Chazdon and Fetcher 1984a, b, Pearcy 1988) effects on photosynthetic rates may be greater than expected purely on the basis of light intensity. There may be other subtle effects.

Cloudy weather may actually result in increased photosynthesis in plants living in forests with small gap fractions because: (1) the spectrum contains relatively more photons at photosynthetically useful wavelengths (Table 4), (2) there is less spatial (and temporal) heterogeneity in light intensity, and (3) light intensity may actually be greater than *forest shade* (Table 2, Fig. 13). This suggests that there might be more growth in understory plants, seedlings, and saplings during cloudy weather, and that growth may be proportional to the number of cloudy days during the growing season in forest shade habitats. It also suggests that understory plants, seedlings, and saplings may grow more rapidly in cloud forests than in forests with fewer cloudy days. This might explain the dense growth of epiphytes in cloud forests compared to other forests. However, greater productivity from increased light may be offset by relatively lower mean temperatures in cloud forests.

A factor that may eliminate the possible relationship between growth and cloud cover is the presence of sun

flecks. Within a forest, sunflecks (*small gaps*) may contribute a significant fraction of the daily PAR to plants living in forest shade (Chazdon and Fetcher 1984a, b, Pearcy 1988), so plants living in the daily tracts of sunflecks may receive enough light from the sunflecks so that cloudy days make little difference to them. However, in places where the canopy is dense enough so that only a small fraction of microsites experience sunflecks at some time during the day, cloudy weather may make a significant difference. In these places, the heterogeneity in light intensity is greatly reduced during cloudy weather, and for thin clouds, or clouds with very high radiance, Q_T may actually increase (Fig. 13, Table 2). Gaps may be less important in places where there is frequent cloud cover, at least for thin clouds.

The alignment of gaps may be important to shade-intolerant species; plants growing in long narrow gaps aligned north-south may experience less daily PAR than those growing in narrow gaps aligned east-west. Nevertheless, these differences will only be important during sunny weather; in cloudy conditions, bright cloud light comes from all directions, eliminating shade from the edges of gaps. Because all edges of the gap will be illuminated roughly equally in cloudy weather, the importance of gap alignment to plant growth may be proportional to the fraction of sunny days during the growing season.

CONCLUSIONS

The combination of geometrical structure of forests, presence or absence of clouds, and varying sun angle leads to five major light environments: *forest shade*, *woodland shade*, *small gaps*, *open/cloudy*, and *early/late*. These are characterized by yellow-green, blue-gray, reddish, "white," and purplish light spectra, respectively. Each of these light environments is well defined and independent of tree species composition, latitude, or continent. Because the light habitats depend upon geometry and weather, they should also be found in other vegetation and at a smaller scale within shrubs, branches, or small plants. Because perceived colors of animals, flowers, and fruits depend upon the interaction between ambient light color and the reflectance of the animal or plant parts, any given color pattern will have a different appearance in each light environment. A color pattern will be more conspicuous or more cryptic, depending upon when and where it is viewed. Certain colors should be more frequent as visual signals in species characteristic of few or single light environments. If species cannot evolve different color patterns then they can change their visibility by changing their phenology or behavior, allowing displays in different light environments. Because plants use different parts of the 400–700 nm spectrum differently, and the relative proportions of these spectral segments vary with light environment, patterns of plant growth may be different than expected from the simple considerations of total intensity, even controlling for

light "quality" ζ . The color and intensity homogenization caused by cloudy weather may affect generalizations about plant growth based upon sunny weather; heavy epiphyte growth in cloud forests may be made possible by the homogeneous higher and whitish light intensity associated with continuous overcast. The color of forest light is very important in the ecology and evolution of animals and plants.

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APPENDIX

CALCULATIONS OF IRRADIANCE SPECTRA FROM RADIANCE SPECTRA

Basics

A flat color pattern element will receive light collected from all directions, or a total solid angle of 180° or 2π steradians (Endler 1990). The light comes from various sources, such as the solar disk (if not in shade), blue sky, clouds, leaves, branches, and other objects. Plant physiologists traditionally divide the sources into direct and diffuse, direct being light from the sun and diffuse light originating from all other sources. However, the diffuse light sources can have radically different spectra (Fig. 2), so need to be treated separately in order to predict and explain ambient light spectra.

The size of a light source, or more specifically, the angle it subtends on the color pattern element, will affect how much that light source influences the total ambient light spectrum $Q(\lambda)$. For example, a large gap contributes more light than a small one if the sky is uniform and the sun is not in either gap. Lawton's (1990) extensive data on gaps in cloud and montane forest at Monteverde (Costa Rica) show this very nicely. Let f_i be the solid angle subtended by light source i . The 2π steradians making up the ambient light spectrum is simply the sum of the solid angles of each light source, $\Sigma f_i = 2\pi$. Convex or concave surfaces can be accommodated by substituting the actual solid acceptance angle for 2π in the calculations.

The solid angle of a light source is easy to calculate. We

will use a canopy gap as an example, but the principles apply to any light source. Consider a roughly circular hole in the canopy at height h above the color pattern or surface of interest, and having a diameter g (measured perpendicular to an axis from the gap center to the measured gap surface). A point on the surface collects light from a total area of $2\pi h^2$ (half the surface area of a sphere of radius h centered on the point). The same point collects light from the canopy hole with a surface area of $\pi g^2/4$. Therefore, the solid angle subtended by the canopy hole on the point is

$$f_g = 2\pi(\pi g^2/4)/(2\pi h^2) = (\pi/4)(g/h)^2 \quad (\text{A.1})$$

steradians. A similar calculation can be made for a hole of any shape, merely substituting its area A in Eq. A.1: $f_g = A/h^2$. The solid angles of gaps can be calculated directly from "fisheye" calibrated photographs of the canopy (Anderson 1964a, Chazdon and Field 1987); f_g will be $2\pi F_g$, where F_g is the fraction of the hemispherical photograph that is gap. Because it is the ratio g/h that is important rather than absolute size, the solid angle subtended by a large gap in a very tall canopy can be the same as that of a smaller gap in a short canopy. By subtraction, the geometric solid angle for the vegetation is $f_v = 2\pi - \Sigma f_g$, where the summation is done over all gaps. In precise calculations, f_i should be divided up into

sunlit leaves, shaded leaves, bark, mosses, lichen, dead wood, etc., and this should be done either by using Eq. A.1 for each source, or by calibrated "fisheye" photographs.

The relative contribution of a given light source is proportional to its intensity as well as the angle it subtends. Because it is the total number of photons to which photoreceptors respond rather than their source, the ambient light or irradiance spectrum $Q(\lambda)$ is simply the sum of the radiance spectra of all light sources, added at each wavelength, and weighted by the solid angles they subtend on the surface where the ambient light is being measured:

$$Q(\lambda) = \sum f_i q_i(\lambda), \quad (\text{A.2})$$

where f_i is the solid angle subtended by light source i and $q_i(\lambda)$ is its radiance spectrum.

Ambient light above the forest

First consider what happens above the forest. As the earth's distance from the sun varies, the angle subtended by the sun varies from 0.5431° on 1 January to 0.5086° on 1 July. As a result, the total radiance will also vary; above the atmosphere, relative to the solar constant, it varies from 1.0335 on 1 January to 0.9666 on 1 July (Robinson 1966). For the purposes of this paper, we will use the midpoint 0.5259° , or 6.6168×10^{-5} steradians, as the angle subtended by the solar disk; call this f_s .

If we assume an unobstructed horizon and no haze effects (sky solid angle = 2π), then the solid angle subtended by the blue sky is $f_b = 2\pi - f_s$. Let the radiance spectrum of blue sky be $q_b(\lambda)$. Eq. A.2 can be used at each wavelength to calculate the ambient light spectrum above or outside a forest:

$$Q(\lambda) = f_s q_s(\lambda) + (2\pi - f_s) q_b(\lambda). \quad (\text{A.3})$$

Detailed methods for any season, sun angle (except near dawn or dusk), latitude, or altitude are given in McCullough and Porter (1971). In this paper, I will ignore these effects as a first approximation.

The radiance of clouds can also be incorporated into the calculations:

$$Q(\lambda) = f_s q_s(\lambda) + f_b q_b(\lambda) + f_c q_c(\lambda) \quad (\text{sun not obstructed by clouds}), \quad (\text{A.4a})$$

$$Q(\lambda) = C f_s q_s(\lambda) + f_b q_b(\lambda) + f_c q_c(\lambda) \quad (\text{sun obstructed by clouds}), \quad (\text{A.4b})$$

where f_b is the sum of the solid angles subtended by all patches of blue sky, f_c is the sum of the solid angles subtended by all patches of cloud, $f_s + f_b + f_c = 2\pi$, $q_c(\lambda)$ is the average radiance of the clouds, and C is the fraction of photons transmitted by the cloud blocking the sun. This is an approximation, and ignores solar aureole effects in the clouds. The radiance spectra of a given mass of clouds varies at least by a factor of 2 with position in the sky because more light is reflected to the ground by vertical than by horizontal cloud surfaces, and different parts of clouds vary greatly in C . Different kinds of clouds exhibit different brightnesses, for example nimbus clouds may transmit 15%, altostratus 40%, and cirrus clouds 80% of sunlight (Coulson 1975), so the values given in this paper must not be regarded as constants. Eqs. A.4a, b can be modified to account for this by adding $f_i q_i(\lambda)$ terms for predetermined

cloud brightness classes. If necessary, penumbral effects (sun partially covered by cloud) can also be included by modifying the first term in the equation.

Ambient light in the forest

The relationship between the forest shade spectrum and its sources can also be obtained from Eq. A.2. Let $q_i(\lambda)$ be the radiance of light that has been transmitted through and reflected from leaves (ignoring for heuristic reasons the differences among species), and $q_k(\lambda)$ be the radiance reflected from bark, branches, and other parts of the vegetation (also ignoring differences in their spectra). Let f_i and f_k be the total solid angles of the sources, respectively. If there are no gaps, then $f_i + f_k = 2\pi$. Therefore, from Eq. A.2 the resulting irradiance spectrum is:

$$Q(\lambda) = f_i q_i(\lambda) + f_k q_k(\lambda). \quad (\text{A.5})$$

Clearly, the greater the proportion of ambient light originating from leaves (f_i) the more similar the ambient light [$Q(\lambda)$] will be to the saturated (high chroma) leaf radiance [$q_i(\lambda)$] and the more dissimilar to the relatively less saturated light reflected from the rest of the vegetation [$q_k(\lambda)$].

Consider first gap environments, where the solar disk is entirely within one of the canopy holes, or would be if not obstructed by a cloud. From Eq. A.2 the ambient light spectrum will be

$$Q(\lambda) = f_s q_s(\lambda) + f_b q_b(\lambda) + f_c q_c(\lambda) + f_d q_d(\lambda) \quad (\text{A.6a})$$

when the sun is not blocked by a cloud, and

$$Q(\lambda) = C f_s q_s(\lambda) + f_b q_b(\lambda) + f_c q_c(\lambda) + f_d q_d(\lambda) [Q_c(\lambda)/Q_s(\lambda)] \quad (\text{A.6b})$$

when the sun is blocked by a cloud. Unlike Eqs. A.4a, b, $f_b + f_c = f_s - f_s$, rather than $2\pi - f_s$; we are specifically concerned with the solid angles of blue sky and cloud within the gap solid angle f_g (Eq. A.7a, b). The quantity [$Q_c(\lambda)/Q_s(\lambda)$] in Eq. 6b corrects for the fact that the irradiance of the sky above the forest changes whenever the sun is blocked by a cloud: $Q_c(\lambda)$ is the sky irradiance spectrum when the sun is obstructed by clouds (Eq. 6b) and $Q_s(\lambda)$ is the sky irradiance when the sun is unobstructed (Eq. 6a). Adjustments could be made for penumbral effects arising from (a) the sun partially blocked by a cloud, and (b) the sun partially blocked by leaves or other vegetation, or both.

Now consider the shade environments, where the solar disk is entirely obstructed by the vegetation, or would be if not obstructed by a cloud. From Eq. A.2 the ambient light spectrum will be

$$Q(\lambda) = f_b q_b(\lambda) + f_c q_c(\lambda) + f_d q_d(\lambda) \quad (\text{A.7a})$$

when the sun is not blocked by a cloud, and

$$Q(\lambda) = f_b q_b(\lambda) + f_c q_c(\lambda) + f_d q_d(\lambda) [Q_c(\lambda)/Q_s(\lambda)] \quad (\text{A.7b})$$

when the sun is blocked by a cloud. Eqs. 7a, b differ from Eqs. 6a, b in that they lack the direct solar component, and $f_b + f_c = f_g$, rather than $f_s - f_s$. As in the gap calculations, the percentage contribution of each source i depends upon the product of its solid angle (f_i) and radiance spectrum (q_i).