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David W. Lee; Rita Graham

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## LEAF OPTICAL PROPERTIES OF RAINFOREST SUN AND EXTREME SHADE PLANTS<sup>1</sup>

DAVID W. LEE AND RITA GRAHAM

Department of Biological Sciences, Florida International University, Miami, Florida 33199

### ABSTRACT

The optical properties of the leaves of twelve tropical sun species and thirteen tropical extreme shade species were examined with an integrating sphere attached to a spectroradiometer. Measurements of diffuse reflectance and transmittance allowed calculations of absorptance, 350–1,100 nm. Although some shade species absorbed higher percentages of quantum flux densities for photosynthesis (400–700 nm, PPFD) than the mean for the sun species, the sun and shade species as groups were not significantly different from each other: 90.2, S.D. 3.6% for shade species and 88.6, S.D. 2.4% for the sun species. The groups of species did not differ in total absorptance of energy 350–1,100 nm. Furthermore, the sun and shade species were identical in their shift of absorptance at wavelengths between 650 and 750 nm. The anthocyanic coloration of the leaf undersurfaces of two species polymorphic for this characteristic (*Trionela hirsuta* and *Ischnosciphon pruinosis*) is correlated with increased absorptance at the upper end of the action spectrum of photosynthesis. Although sun and shade species have similar optical properties, the energy investment (as documented by dry wt per unit area of leaf surface) is much less for the shade species.

LEAF OPTICAL PROPERTIES are frequently neglected in studies on photosynthesis or plant productivity, yet it is only possible to determine the efficiency of these processes when the amount of radiation usable in photosynthesis (photosynthetic photon flux density = PPFD) absorbed by the leaf is known. Studies on leaf optical properties go back over fifty years (Willstatter and Stöll, 1918; Shull, 1929; Seybold, 1933; Billings and Morris, 1951; Loomis, 1965). Much of the impetus in studying leaf optics has been its relevance to remote sensing (Gausman, Escobar and Rodriguez, 1981; Smith, 1981), with a continuing interest in the effect of leaf surface features, as pubescence, on the absorptance of radiation. Several studies (Ehleringer, Björkman and Mooney, 1976; Eller and Willi, 1981; Ehleringer, 1981) have demonstrated that surface features can significantly reduce absorptance of radiant energy, reduce leaf temperatures, and thus reduce water loss from transpiration. Other than the work of Billings and Morris (1951) along an elevation gradient in the Sierra Nevada and that of Ehleringer (1981) in the Mohave and Sonoran deserts, there have been no comparisons of leaf optics from plants from different ecosystems—and none of tropical forest plants—despite the relevance of such properties for photosynthe-

sis, and energy and water relations (Mooney et al., 1980). In this study we compared the optical properties of leaves from extreme shade and sun-adapted plants of tropical forests to determine if shade-adapted plants absorb more energy, and if differences in absorptance occur at specific wavelengths.

Although all leaves have similar optical properties (Gates et al., 1965; Loomis, 1965; Wooley, 1971; Gausman and Allen, 1973; Ehleringer, 1981; Fig. 1), it is important to consider the precise optical properties of leaves in relationship to the light environments in which the plants live. Because of the selective filtering of light through foliage, plants of extreme shade encounter a drastically different light environment than those to full sunlight (Chazdon and Fetcher, 1984a, b; Lee, 1986a). Full sunlight near solar zenith on a clear day has a PPFD in excess of  $2,200 \mu \text{mol s}^{-1} \text{m}^{-2}$  and a total irradiance of over  $1,000 \text{w m}^{-2}$  (Fig. 2). Because wavelengths of radiant energy in the red and far-red wavelengths affect the equilibria of phytochrome, which may have profound effects on plant development (Smith, 1981, 1982), it is useful to describe the spectral distribution of this radiation in terms of the quantum ratio at 660 compared to 730 nm (the red : far-red ratio or R:FR in the sense of Smith, 1982). For sunlight the R:FR is approximately 1.25 (Tasker and Smith, 1977; Holmes, 1981; Lee, 1986a; Fig. 2). In contrast, the light climates of rainforest understory are deficient in total radiant energy, especially in PPFD, and have a much lower R:FR (Lee, 1986a; Fig. 2).

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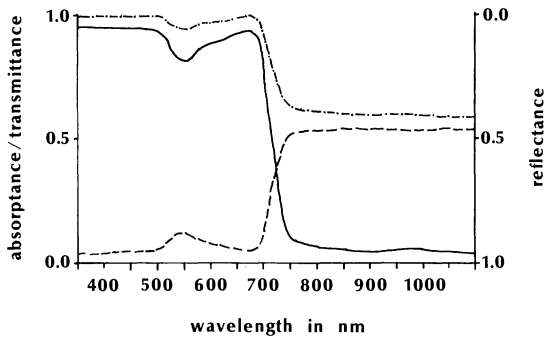


Fig. 1. Leaf optical properties of *Bursera simaruba* (Lee, 1986b). (---) denotes diffuse reflectance and (-·-) diffuse transmittance. Since leaves scatter light and are only approximately described by Beer's law, the term "absorbance" is used rather than "absorbance." Absorbance equals 1-reflectance-transmittance, and is denoted by (—).

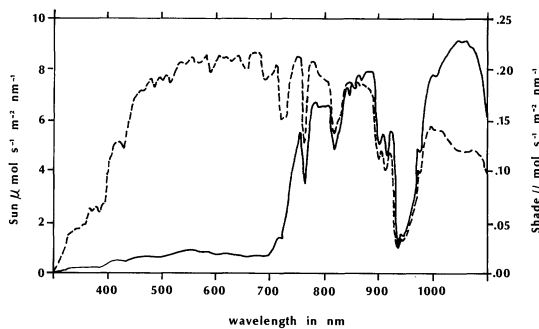


Fig. 2. Quantum spectral distribution of light environments at La Selva, Costa Rica (Lee, 1986a). (---) is of solar radiation near solar zenith under a clear sky; PPFD is 2,280  $\mu\text{mol s}^{-1} \text{m}^{-2}$  and R:FR is 1.25. (—) is of radiation under forest shade; PPFD is 5.46  $\mu\text{mol s}^{-1} \text{m}^{-2}$  (0.3% full sunlight) and R:FR is 0.31. Note that the vertical legends on either side differ by a factor of 40.

A logical prediction is that extreme shade plants, under the strong selective constraints of a deficiency of energy for photosynthesis and growth, should absorb significantly more PPFD than sun plants, which must balance absorbance of PPFD with requirements of temperature regulation (Givnish, 1984). Plants of the extreme shade of rainforests display the same characteristics that have been described in temperate region shade plants, such as thinner leaves and lower chlorophyll a/b ratios (Goodchild, Björkman and Pyliotis, 1972). Responses of leaf morphology to extreme shade manifest phenotypically, genotypically and as differences between species (Larcher, 1980). Extreme shade adaptations of leaves have been characterized on morphological, anatomical, ultrastructural, physiological and biochemical levels (Björkman, 1973; Boardman, 1977; Björkman, 1981). There are definite limits to biochemical responses in the photosynthetic machinery to low light levels in vascular plants (Richardson, Beardall and Raven, 1983), and extreme shade plants do not have greater quantum efficiencies than sun plants (Björkman,

1981). In addition, many plants from the extreme shade environments of tropical rainforests develop leaves markedly different in appearance to an observer familiar with temperate zone vegetation. These characteristics may contribute to different absorbances in some extreme shade plants. The upper leaf surfaces are frequently velvety, due to convexly curved, or papillose, epidermal cell walls (Haberlandt, 1913; Lee and Bone, 1983; Bone, Lee and Norman, 1985). The leaf undersurfaces are frequently red or violet, due to the presence of anthocyanins in a discrete layer in the mesophyll (Lee, Lowry and Stone, 1979). In a few species the leaves have a striking iridescent blue sheen (Lee, 1977).

Extreme shade plants may also have different optical properties as evolutionary responses to the spectral distribution of light in their native environments. A typical plant photosynthetic action spectrum shows an abrupt

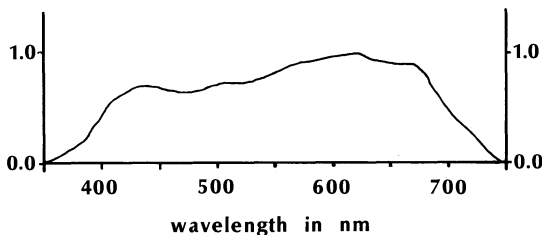


Fig. 3. Relative quantum efficiency, after McCree (1972). Data are from crop species grown under field conditions, and have been extrapolated beyond 730 nm. Values are in relationship to highest efficiencies at 620 nm.

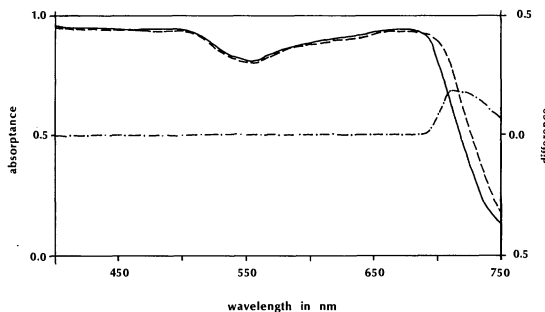


Fig. 4. Leaf absorbance of *Bursera simaruba* (—); Lee, 1986b). An imaginary leaf with optical properties above 650 nm shifted 10 nm towards the far-red has also been plotted (---). Increased absorbance by such a leaf above 700 nm is shown by the difference spectrum (-·-).

TABLE 1. Names of taxa analyzed for leaf optical properties. Abbreviations for study sites are: LS = La Selva, BCI = Barro Colorado Island, FTU = Tamiami Campus of Florida International University in Miami, and FTG = Fairchild Tropical Garden in Miami. Leaf characteristics are abbreviated as: a = red-violet undersurface, b = papillose upper epidermis, c = blue iridescence, and d = variegation

Scientific name	Code	Family	Origin	Location studied	Comments
<b>Sun species</b>					
<i>Bischofia javanica</i> Bl.	BJ	Euphorbiaceae	Southeast Asia	FTU	
<i>Brassia actinophylla</i> Endl.	BA	Araliaceae	Queensland	FTU	
<i>Bursera simaroba</i> (L.) Sarg.	BS	Burseraceae	South Florida, Central America	FTU	
<i>Calathea lutea</i> (Aubl.) Schultes		Marantaceae	Central America	LS	
Upper surface	CLU				
Lower surface	CLL				
<i>Calophyllum inophyllum</i> L.	CI	Guttiferae	Southeast Asia	FTU	
<i>Cecropia peltata</i> L.	CP	Moraceae	Central America	BCI	
<i>Coccoloba wifera</i> (L.) L.	CU	Polygonaceae	Central Amer., So. Florida	FTU	
<i>Hibiscus tiliaceus</i> L.	HT	Malvaceae	Panropical	FTU	
<i>Mangifera indica</i> L.	MI	Anacardiaceae	India	FTU	
<i>Ochroma pyramidale</i> (Cav. ex Lam.) Urban	OP	Bombacaceae	Central America	BCI	
<i>Swietenia mahogany</i> (L.) Jacq	SM	Meliaceae	So. Florida, Caribbean Basin	FTU	
<i>Terminalia catappa</i> L.	TC	Combretaceae	Southeast Asia	FTU	
<b>Shade species</b>					
<i>Alternanthera costaricensis</i> O. Kuntze	AC	Amaranthaceae	Central America	LS	a, b, c
<i>Begonia mazaе</i> ('Joe Hayden') Zeisenhenne	BM	Begoniaceae	Mexico	FTG	
<i>Blechnum costaricense</i> Oerst	BC	Acanthaceae	Central America	BCI	
<i>Danaea nodosa</i> (L.) J. Sm.	DN	Marattiaceae	Central & So. America	LS	c
<i>Geonema cuneata</i> H. Wendl ex Spruce	GC	Arecaceae	Central & So. America	LS	
<i>Hoffmania refulgens</i> (Hook.) Hemsl.	HR	Rubiaceae	Central America	FTG	a, b
<i>Ischnosiphon pruinosus</i> (Reg.) O. G. Peterson		Marantaceae	Central America	BCI	
Green under-surface	IPG				a
Red under-surface	IPR				c
<i>Leandra dichotoma</i> Cogu.	LD	Melastomataceae	Central America	LS	
<i>Philodendron scandens</i> C. Koch & Sell		Araceae	Central America	BCI	
Juvenile	PSJ				a, b
Adult	PSA				a, b, d
<i>Psychotria suerrensii</i> J. D. Sm.		Rubiaceae	Central America	LS	
Juvenile	PJT				
Adult	PUA				
<i>Ruellia makoyana</i> Hort.	RM	Acanthaceae	South America	FTG	a, b, d
<i>Triolena hirsuta</i> Triana		Melastomataceae	Central America	LS	
Green under surfaced	THG				
Red under surfaced	THR				
<i>Zamia skinneri</i> Warsz.	ZS	Zamiaceae	Central America	LS	a

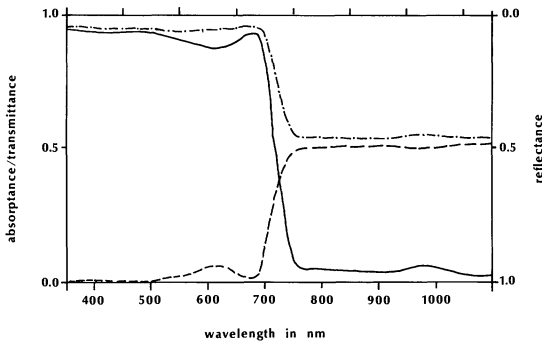


Fig. 5. Leaf optical properties of *Alternanthera costaricensis*. The leaves appear almost black in the forest understory, as can be seen by the low diffuse reflectance (— · —) in the visible wavelengths. Little diffuse transmittance in the visible (— — —) contributes to very high absorbance (—) in the visible wavelengths.

drop at 700 nm, and the quanta available for photosynthesis (PPFD) have thus been defined as the range of 400–700 nm (McCree, 1981). This abrupt cut-off is correlated with a decrease in leaf absorbance about 700 nm. McCree (1972) and Inada (1978) have shown that plants can use quanta beyond 700 nm in photosynthesis, revealed by a spectrum of relative quantum efficiency (Fig. 3). Given the spectral quality of extreme shade (as exemplified by Fig. 2) and a strong selection pressure for using light efficiently in these environments, it is reasonable to predict that extreme shade plants should be able to absorb more efficiently at wavelengths beyond 700 nm (Björkman, 1973). McCree (1981) estimated that as much as 7% of photosynthetic radiation available to a leaf within a tree canopy might be in wavelengths beyond 700 nm. The classical example of an altered action spectrum in an extreme-shade environment is that of the green alga *Ostreobium* which resides beneath encrusting dinoflagellates and within a large coral (Halldal, 1968). The following example (from Lee, 1986b) demonstrates the significance of slightly altered optical properties. Leaves of *Bursera simaruba* (Fig. 1) are typical in their spectral absorbance of radiation, with a drop at 550 nm and little above 750 nm. The wavelength-dependent product of this absorbance spectrum and that of extreme shade (Fig. 2), times the relative quantum efficiency spectrum of McCree (1972, Fig. 3) will indicate the wavelengths available for photosynthesis, assuming the data of McCree are relevant to the example. Quantum integration of this product reveals that the interval of 700–750 nm contributes 4.9% of the interval 400–700 for photosynthesis. If there were a shift in optical properties of just 10 nm (Fig. 4), the region of 700–750

nm would contribute 6.0% relative to that for 400–700 nm. Although these percentages are low, they may be evolutionarily significant in contributing to the efficiency of productivity in an extreme shade environment.

The purpose of this study was to compare the optical properties of a sample of 12 tropical species, native to full sunlight, to a sample of 13 species adapted to the extreme shade of tropical forests. Absorbances of these species were compared to determine if the shade species captured a greater percentage of PPFD incident on the leaf surface, more total energy 350–1,100 nm, and if they absorbed relatively more quanta at 700–750 nm. Shade species with blue iridescence, papillose epidermis and pigmented undersurface were also included in the sample. Dry/wet wts and wt per area of blade were also determined for the sun and shade plants, to estimate the relative costs of producing a surface for absorbance.

**MATERIALS AND METHODS**—The species analyzed in this investigation are listed in Table 1. Leaves were freshly collected and kept in water and plastic bags to prevent water loss; they were analyzed within 2 hr of removal from plants. Plants were studied from the following locations: La Selva Forest Reserve, Costa Rica (Frankie, Baker and Opler, 1974) in April of 1983 and 1984; Barro Colorado Island, Panama (Leigh, Rand and Windsor, 1983) in June of 1983; and in Miami from March to October during 1983 and 1984. The exotic shade plants studied in Miami were collected from natural shade conditions in Fairchild Tropical Garden. Five healthy mature leaves from each species were analyzed for diffuse reflectance and diffuse transmittance, allowing calculation of total absorbance. For optical analysis a Li-Cor integrating sphere attached by a fiber optic cable to a Li-Cor 1800 spectroradiometer was used in all measurements. The leaf sample was placed against an outside port of the sphere, and diffuse reflectance or transmittance was compared to a barium sulfate standard (Kodak #6084). The calculations used a control measurement of reflectance of the standard with the leaf surface in place. The experimental setup provided a spectral range of 350–1,100 nm, scanning at intervals of 2 nm with a half-peak bandwidth of 6 nm. Programs in the instrument's microcomputer made the following presentations of data possible: 1) calculation of absorbance for each leaf; 2) quantum integration 400–700, using shade light (Fig. 2) for % PPFD calculations; 3) integration of 350–1,100 nm using sunlight (Fig. 2) for % energy absorbance; 4) multiplication of individual

TABLE 2. Summary of leaf optical characteristics for the 12 sun and 13 extreme-shade species. Species symbols are given in Table 1. Each value is the mean of five measurements, and the S.D. are given where appropriate. \* denotes that leaves were not utilized in the statistical comparisons between groups

Species code	SHFC		% PPFD	% 350-1,100	% absorbance at 620 nm	% reflectance at 620 nm	Dry wt/area mg cm <sup>-2</sup>	Dry wt/fresh wt
	700-750/400-700	700-750/400-700						
<b>Sun species</b>								
BJ	0.048 ± 0.002	0.048 ± 0.002	0.917 ± 0.004	0.621	0.926 ± 0.005	0.058	17.9 ± 1.7	0.386 ± 0.019
BA	0.047 ± 0.007	0.047 ± 0.007	0.893 ± 0.019	0.614	0.894 ± 0.022	0.071	32.5 ± 2.6	0.374 ± 0.013
BS	0.049 ± 0.004	0.049 ± 0.004	0.902 ± 0.008	0.617	0.904 ± 0.009	0.071	16.1 ± 1.1	0.412 ± 0.011
CLU	0.055 ± 0.003	0.055 ± 0.003	0.924 ± 0.007	0.637	0.932 ± 0.006	0.049	6.6 ± 1.2	0.332 ± 0.035
*CLL	—	—	0.615 ± 0.045	0.388	0.616 ± 0.047	0.363	—	—
CI	0.041 ± 0.004	0.041 ± 0.004	0.878 ± 0.013	0.596	0.884 ± 0.018	0.074	22.5 ± 3.1	0.412 ± 0.048
CP	0.043 ± 0.002	0.043 ± 0.002	0.896 ± 0.017	0.598	0.907 ± 0.018	0.052	7.8 ± 0.3	0.357 ± 0.012
CU	0.045 ± 0.013	0.045 ± 0.013	0.870 ± 0.009	0.602	0.870 ± 0.007	0.092	29.4 ± 1.8	0.383 ± 0.014
HT	0.044 ± 0.004	0.044 ± 0.004	0.885 ± 0.014	0.591	0.891 ± 0.012	0.068	18.0 ± 1.3	0.429 ± 0.020
MI	0.045 ± 0.003	0.045 ± 0.003	0.868 ± 0.022	0.609	0.864 ± 0.032	0.084	21.0 ± 7.7	0.368 ± 0.113
OP	0.046 ± 0.002	0.046 ± 0.002	0.897 ± 0.010	0.607	0.901 ± 0.007	0.057	7.5 ± 0.2	0.375 ± 0.019
SM	0.045 ± 0.002	0.045 ± 0.002	0.861 ± 0.039	0.589	0.859 ± 0.034	0.059	11.1 ± 2.0	0.365 ± 0.023
TC	0.031 ± 0.005	0.031 ± 0.005	0.842 ± 0.016	0.561	0.838 ± 0.022	0.085	13.5 ± 1.8	0.320 ± 0.020
All sun species	0.045 ± 0.006	0.045 ± 0.006	0.886 ± 0.023	0.604 ± 0.019	0.889 ± 0.028	0.068 ± 0.014	17.0 ± 8.3	0.376 ± 0.032
<b>Shade species</b>								
AC	0.043 ± 0.014	0.043 ± 0.014	0.920 ± 0.002	0.619	0.895 ± 0.005	0.047	3.5 ± 0.4	0.149 ± 0.014
BC	0.037 ± 0.003	0.037 ± 0.003	0.813 ± 0.021	0.547	0.812 ± 0.025	0.079	—	—
BM	0.044 ± 0.001	0.044 ± 0.001	0.948 ± 0.012	0.635	0.933 ± 0.013	0.038	5.0 ± 0.7	0.070 ± 0.006
DN	0.045 ± 0.003	0.045 ± 0.003	0.889 ± 0.004	0.605	0.894 ± 0.002	0.047	3.4 ± 0.4	0.167 ± 0.028
GC	0.048 ± 0.002	0.048 ± 0.002	0.899 ± 0.011	0.610	0.906 ± 0.012	0.033	6.2 ± 0.4	0.388 ± 0.046
HR	0.045 ± 0.002	0.045 ± 0.002	0.938 ± 0.013	0.637	0.909 ± 0.017	0.028	5.4 ± 0.5	0.120 ± 0.013
IPG	0.046 ± 0.004	0.046 ± 0.004	0.923 ± 0.010	0.621	0.920 ± 0.014	0.053	—	—
IPR	0.040 ± 0.007	0.040 ± 0.007	0.861 ± 0.048	0.583	0.861 ± 0.048	0.068	—	—
LD	0.040 ± 0.010	0.040 ± 0.010	0.870 ± 0.011	0.587	0.882 ± 0.012	0.047	3.0 ± 0.5	0.183 ± 0.016
PSJ	0.043 ± 0.001	0.043 ± 0.001	0.928 ± 0.003	0.632	0.898 ± 0.010	0.043	—	—
*PSA	0.044 ± 0.002	0.044 ± 0.002	0.888 ± 0.013	0.601	0.893 ± 0.005	0.062	—	—
PUJ	0.045 ± 0.009	0.045 ± 0.009	0.928 ± 0.005	0.626	0.904 ± 0.007	0.058	2.2 ± 0.4	0.133 ± 0.023
*PUA	0.051 ± 0.001	0.051 ± 0.001	0.914 ± 0.016	0.617	0.923 ± 0.005	0.049	5.1 ± 0.2	0.402 ± 0.018
RM	0.041 ± 0.002	0.041 ± 0.002	0.906 ± 0.009	0.604	0.895 ± 0.011	0.062	5.0 ± 0.8	0.154 ± 0.051
THR	0.044 ± 0.003	0.044 ± 0.003	0.903 ± 0.048	0.622	0.871 ± 0.053	0.082	3.0 ± 0.2	0.162 ± 0.006
*THG	0.040 ± 0.003	0.040 ± 0.003	0.825 ± 0.032	0.564	0.821 ± 0.046	0.074	3.4 ± 0.7	0.178 ± 0.016
ZS	0.045 ± 0.002	0.045 ± 0.002	0.864 ± 0.015	0.598	0.865 ± 0.015	0.067	7.5 ± 0.6	0.259 ± 0.038
All shade species	0.044 ± 0.003	0.044 ± 0.003	0.902 ± 0.037	0.611 ± 0.024	0.891 ± 0.030	0.060 ± 0.016	4.4 ± 1.7	0.178 ± 0.088

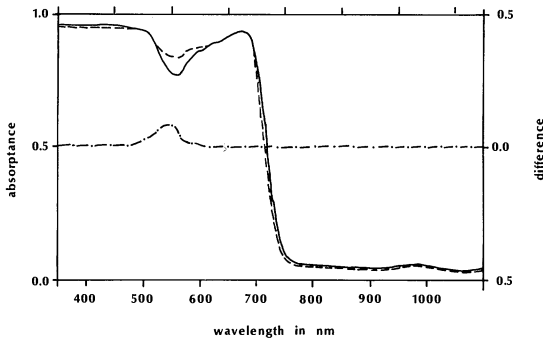


Fig. 6. Mean leaf absorbances of the twelve sun species (—) and the thirteen extreme shade species (---). Similarity between the two samples is shown by the difference spectrum (-·-), with only a slight increase in absorbance by the shade species at around 550 nm.

absorbance spectra and determination of mean spectra; 5) multiplication of leaf absorbance by the mean relative quantum efficiency spectrum of McCree (Fig. 3) times the shade environment (Fig. 2) and subsequent quantum integration to determine the ratios of wavelengths 700–750/400–700 nm available for photosynthesis.

Individual species, as well as the sample of sun and shade species, were statistically compared by student's *t* test and distribution, at a level of significance of  $P = 0.05$ . A minimum of five freshly collected leaf blades of each species, collected at La Selva and in Miami in 1984 and weighed with an electronic balance, were compared to the same samples dried for 48 hr at 60 C to allow calculation of % fresh wt and leaf specific area (wt per unit leaf area in  $\text{mg cm}^{-2}$ ). Leaf areas were measured with a Li-Cor leaf area meter.

**RESULTS**—Leaf optical properties of an extreme shade plant, that of *Alternanthera costaricensis* growing in the forest understory at La Selva, are typical of all plants in the strong absorbance of radiation 400–700 nm and lack of absorbance at wavelengths beyond 750 nm (Fig. 5). However, the leaves absorb more efficiently at 400–700 nm than other taxa described (Loomis, 1965; Ehleringer, 1981). Analysis of these optical properties is seen in Table 2, after AC. Percentage absorbance of PPFD is significantly greater than that of *Bursera simaruba* (BS) described earlier. Absorbance is almost identical at 620 nm, but reflectance is lower for AC. However, the product of absorbance times the quantum efficiency spectrum and shade spectrum (700–750/400–700 nm) is less for AC (0.043) than for BS (0.049). The lower value for AC is partly due

to greater absorbance in visible wavelengths from the presence of anthocyanins (with an absorbance peak of 525 nm) in the mesophyll. Thus, the leaves of this plant do not absorb differently than those of BS at wavelengths of 700–750 nm. Despite these overall similarities in optical properties, the leaves of AC have a much lower percentage dry wt (14.9% S.D. 1.4) than BS (41.2% S.D. 1.1). The lower percentage is reflected in the reduced leaf specific area for AC compared to BS ( $3.5 \text{ mg cm}^{-2}$ , S.D. 0.4 vs.  $16.1 \text{ mg cm}^{-2}$ , S.D. 1.1).

The leaves of all species were analyzed identically as for *Alternanthera costaricensis* (Table 2). The samples of sun and extreme shade species were very similar in their optical properties. Mean absorbance spectra for sun and shade plants are identical except for an increase in absorbance by the shade plants at approximately 550 nm (Fig. 6). However, shade plants reflected less, and transmitted more, radiant energy. Differences in reflectance at 620 nm are not statistically significant, but are at wavelengths above 750 nm. The most significant differences between the two samples are their dry/fresh wts and leaf specific wts, both significantly lower in the shade species. Thus, the shade plants produce a surface for absorbance that is lighter, and presumably metabolically less expensive to produce, than the sun plants.

**DISCUSSION**—The samples of sun and extreme shade plants analyzed in this study have similar optical properties. The spectral similarities are consistent with the lack of a known biochemical basis for a chromatic shift of absorbance into the far-red wavelengths for land plants. However, given standard relative quantum efficiency spectra (McCree, 1972; Fig. 3), quanta beyond 700 nm may contribute 4% or more of the visible spectrum in a typical forest shade environment. Such percentages may be evolutionarily significant for extreme shade species. We need to measure the action spectra of extreme shade plants with precision to know the contribution of these wavelengths with any certainty. Although the species in each sample are typical of plants in the respective environments, two species in the shade sample, *Zamia skinneri* and *Blechnum costaricense* also grow in more open environments, as near gaps. These species absorb the least of the group; if they are removed from the calculations the shade plants have significantly greater mean absorbance of PPFD than the sun species.

Eight of the extreme shade species develop leaves with red-violet undersurfaces, pigmented by anthocyanins. Their mean absorbance of PPFD is significantly greater (0.927

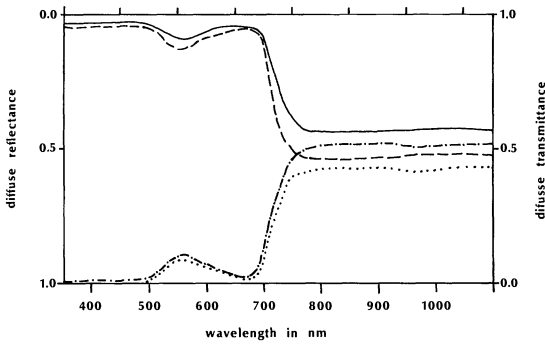


Fig. 7. Comparisons of diffuse reflectances and diffuse transmittances of the twelve sun (· · · ·) and thirteen shade (— —) species. Upper lines are diffuse reflectance, and lower lines are diffuse transmittance.

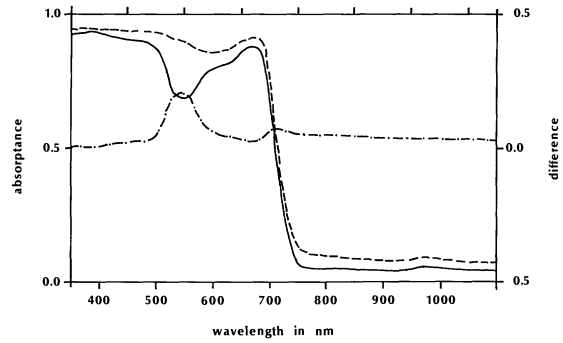


Fig. 8. Leaf absorbances of red (— —) and green (—) undersurfaced forms of *Trionela hirsuta*. The difference spectrum between the two forms (— · —) indicates greater absorbance for the red form at 550 nm and at around 700 nm.

S.D. 0.017), but their absorbance of quanta 700–750/400–700 nm (0.044) is not. Enhanced absorbance by anthocyanins (peaking at approximately 525 nm) contributes to this difference. This increase does not affect photosynthetic efficiency, since there is no evidence that quanta captured by these pigments contribute to photosynthesis (McClure, 1975; Lee et al., 1986). Lee et al. (1979) hypothesized that the backscattering by this layer may contribute to increased absorbance at higher wavelengths. Although these data do not support the hypothesis, other factors may independently affect optical properties. The best test of the hypothesis is to compare leaves of species that appear to be polymorphic only for the undersurface pigmentation. Two such species, *Ischnosciphon pruinosus* and *Trionela hirsuta*, were included in the sample of shade species. With the additional pigmentation, both absorb higher percentages of PPF than the green forms. Since this increase in absorbance would lower the ratio of quanta at 700–750/400–700 nm (Table 2), the ratios should not be greater for the red-undersurfaced leaves. A more realistic test is to compare the relative absorbance at 700–750 nm from both forms to that of 400–700 nm for the green forms. The ratio is then significantly higher for IPR (4.9%) and THR (4.8%). The absorbance spectra of the red forms are different (Fig. 8, 9), with more absorbance at 550 nm and 700–750 nm. How this pigmentation contributes to increased absorbance at 700 nm remains unknown (Lee, 1986b).

Three species in the shade sample also produce iridescent blue coloration, such as the striking young leaves of *Danaea nodosa*. Although these data do not show enhanced absorbance at higher wavelengths for blue-leaved plants, as has been shown for *Selaginella* (Lee

and Lowry, 1975; Héban and Lee, 1984; Lee, 1986b), the contribution of other factors to absorbance makes it difficult to isolate the contribution of iridescence in these plants. The same is true for the papillose epidermis present in six of the shade species.

Leaf radiation balances of the two groups of species, as documented by the percent absorbance of solar energy at 350–1,100 nm, are not significantly different. The spectral response of the measurements does not include the wavelengths of 1,100–3,000 nm, which include 25% of energy of the solar spectrum, and which are strongly absorbed by leaves (Gates et al., 1965). However, Ehleringer (1981) has shown a strong correlation between percent absorbance of PPF and radiant energy 400–3,000 nm in a sample of desert plants. His regression line predicts 52% absorbance 400–3,000 nm for leaves with 88% absorbance of PPF. None of the species studied here have waxy coverings or pubescence that might significantly reduce absorbance of radiant energy. However, *Calathea lutea* (CLU and CLL, Table 2) produces a thick waxy coating on leaf undersurfaces and orientates its leaves in relationship to solar elevation and water stress (Herbert and Larsen, 1985). The difference in energy absorbance between upper and lower surfaces is large, 0.637 vs. 0.388, approximately 0.54 and 0.35 for total radiant energy using the regression equation of Ehleringer (1981).

Although the leaf absorbances of sun and extreme shade species are similar, there are a number of important differences in the optical properties of these plants. Shade species reflect less radiation, and transmit more, than the sun species. In addition, the shade species are more lightly constructed (much lower in leaf specific wts). These differences may be explained by a



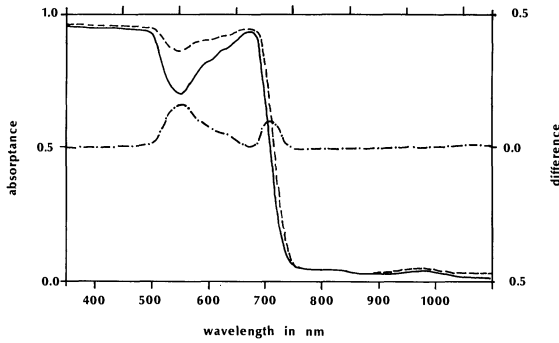


Fig. 9. Leaf absorbances of red (— —) and green (—) undersurfaced forms of *Ischnosciphon pruinosis*. The difference spectrum between the two forms (· · ·) indicates greater absorbance for the red form at 550 nm and at 700–750 nm.

number of important anatomical differences. The leaves of these shade species appear to have fewer intercellular spaces, particularly at the level of the palisade parenchyma (Lee, unpubl. results). Fewer spaces near the upper surface should result in less backscatter. What may be important for extreme shade plants are anatomical and ultrastructural configurations that maximize the effective path lengths of a beam of radiation within the leaf. In such a leaf a given amount of chlorophyll will more effectively absorb radiation (Ramus, 1978; Ruhle and Wild, 1979; Larkum and Barrett, 1983; Terashima and Saeki, 1983). It will be important to make quantitative comparisons of leaf anatomy, using techniques of stereology (Parkhurst, 1982) as well as measure chlorophyll contents to resolve the discrepancy between these differences and their over-all optical similarity.

Thus, the most important difference in the leaves between these extreme shade and sun species is not their total absorbance, but it is the greater efficiency with which shade species produce foliar surfaces for absorbance of energy, giving them a selective advantage in an energy-poor environment.

#### LITERATURE CITED

- BILLINGS, W. D., AND R. J. MORRIS. 1951. Reflection of visible and infra-red radiation from leaves of different ecological groups. *Amer. J. Bot.* 38: 327–331.
- BJÖRKMAN, O. 1973. Comparative studies of photosynthesis in higher plants. *Photophysiol.* 7: 1–163.
- . 1981. Responses to different quantum flux densities. In *Physiological plant ecology I*, Encyclopedia of plant physiology, Series 2, pp. 57–107. Springer-Verlag, Heidelberg.
- BOARDMAN, N. K. 1977. Comparative photosynthesis of sun and shade plants. *Ann. Rev. Pl. Physiol.* 128: 355–377.
- BONE, R. A., D. W. LEE, AND J. N. NORMAN. 1985. Epidermal cells functioning as lenses in leaves of tropical rainforest shade plants. *Appl. Optics* 24: 1408–1412.
- CHAZDON, R. L., AND N. FETCHER. 1984a. Photosynthetic light environments in a lowland tropical rainforest in Costa Rica. *J. Ecol.* 72: 553–564.
- , AND ———. 1984b. Light environments of tropical forests. In E. Medina, H. A. Mooney, and C. Vásquez-Yanes [eds.], *Physiological ecology of plants of the wet tropics*, pp. 27–36. W. Junk, The Hague.
- EHLERINGER, J. 1981. Leaf absorbances in Mohave and Sonoran desert plants. *Oecologia* 49: 366–370.
- , O. BJÖRKMAN, AND H. A. MOONEY. 1976. Leaf pubescence: effects on absorbance and photosynthesis in a desert shrub. *Science* 192: 376–377.
- ELLER, B. M., AND P. WILLI. 1981. The significance of leaf pubescence for the absorption of global radiation by *Tussilago farfara* L. *Oecologia* 49: 179–187.
- FRANKIE, G. F., H. G. BAKER, AND P. A. OPLER. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 62: 881–919.
- GATES, D. M., H. J. KEEGAN, J. C. SCHLETER, AND V. R. WEIDNER. 1965. Spectral qualities of plants. *Appl. Optics* 4: 11–20.
- GAUSMAN, H. W., AND W. A. ALLEN. 1973. Optical parameters of leaves of 30 plant species. *Pl. Physiol.* 52: 57–62.
- , D. E. ESCOBAR, AND P. R. RODRIGUEZ. 1981. Effects of stress and pubescence on plant leaf and canopy reflectance. *Int. Arch. Photogrammetry* 12: 719–749.
- GIVNISH, T. J. 1984. Leaf and canopy adaptations in tropical forests. In E. Medina, H. A. Mooney, and C. Vásquez-Yanes [eds.], *Physiological ecology of plants of the wet tropics*, pp. 51–84. W. Junk, The Hague.
- GOODCHILD, D. J., O. BJÖRKMAN, AND N. A. PYLIOTIS. 1972. Chloroplast ultrastructure, leaf anatomy, and content of chlorophyll and soluble protein in rainforest species. *Carnegie Institution Yearbook* 71: 102–107.
- HABERLANDT, G. 1913. *Physiological plant anatomy*, 4th ed. McMillan, London.
- HALLDAL, P. 1968. Photosynthetic capacities and photosynthetic action spectra of endozoic algae of the massive coral *Favia*. *Biol. Bull.* 134: 411–424.
- HÉBANT, C., AND D. W. LEE. 1984. Ultrastructural basis and developmental control of iridescence in *Selaginella* leaves. *Amer. J. Bot.* 71: 216–219.
- HERBERT, T. J., AND P. B. LARSEN. 1985. Leaf movement in *Calathea lutea* (Marantaceae). *Oecologia* 67: 238–243.
- HOLMES, M. G. 1981. Spectral distribution of radiation within plant canopies. In H. Smith [ed.], *Plants and the daylight spectrum*, pp. 147–158. Academic Press, London.
- INADA, K. 1978. Spectral dependence of photosynthesis in crop plants. *Acta Hort.* 87: 177–185.
- LARCHER, W. 1980. *Physiological ecology*, 2nd ed. Springer-Verlag, Heidelberg.
- LARKUM, A. W. D., AND J. BARRETT. 1983. Light harvesting processes in algae. *Adv. Bot. Res.* 10: 3–219.
- LEE, D. W. 1977. On iridescent plants. *Gard. Bull. Singapore* 3: 21–29.
- . 1986a. The spectral distribution of radiation in two neotropical rain forests. *Biotropica*: (In press).
- . 1986b. Unusual strategies of light absorption in rainforest herbs. In T. Givnish [ed.], *The economics of plant form and function*, pp. 105–131. Cambridge University Press, New York.

- , AND J. B. LOWRY. 1975. Physical basis and ecological significance of iridescence in blue plants. *Nature* 254: 50–51.
- , ———, AND B. C. STONE. 1979. Abaxial anthocyanin layer in leaves of tropical rainforest plants: enhancer of light capture in deep shade. *Biotropica* 11: 70–77.
- , AND R. A. BONE. 1982. Optical refraction by leaf epidermal cells of extreme shade plants: quantitative analysis and implications for photosynthesis. *Bot. Soc. America Misc. Public.* 262: 38–39.
- , S. BRAMMEIER, AND A. P. SMITH. 1986. The selective advantages of anthocyanins in developing leaves of mango and cacao. *Biotropica*. (In press).
- LEIGH, E. G., A. S. RAND, AND D. M. WINDSOR [EDS.] 1983. The ecology of a neotropical forest: seasonal rhythms and longer-term fluctuations. Smithsonian Institution Press, Washington.
- LOOMIS, W. E. 1965. Absorption of radiant energy by leaves. *Ecology* 46: 14–17.
- MCCLURE, J. W. 1975. Physiology and functions of flavonoids. In J. B. Harborne, T. J. Mabry, and H. Mabry [eds.], *The flavonoids*, pp. 971–1055. Chapman and Hall, London.
- MCCREE, K. J. 1972. The action spectrum, absorptance and quantum yield of photosynthesis in crop plants. *Agric. Meteorol.* 9: 191–216.
- . 1981. Photosynthetically active radiation. *Physiological plant ecology 1*, *Encyclopedia of Plant Physiology*, Series 2, pp. 41–55. Springer-Verlag, Heidelberg.
- MOONEY, H. A., O. BJÖRKMAN, A. E. HALL, E. MEDINA, AND P. B. TOMLINSON. 1980. The study of the physiological ecology of tropical plants—current status and needs. *BioScience* 30: 22–26.
- PARKHURST, D. 1982. Stereological methods for measuring internal leaf structure variables. *Amer. J. Bot.* 69: 31–39.
- RAMUS, J. 1978. Seaweed anatomy and photosynthetic performance: the ecological significance of light guides, heterogenous absorption and multiple scatter. *J. Phycol.* 14: 352–362.
- RICHARDSON, K., J. BEARDALL, AND J. A. RAVEN. 1983. Adaptation of unicellular algae to irradiance: an analysis of strategies. *New Phytol.* 93: 157–191.
- RUHLE, W., AND A. WILD. 1979. The intensification of absorbance changes in leaves by light dispersion-differences between high-light and low-light leaves. *Planta* 146: 551–557.
- SHULL, C. A. 1929. A spectrophotometric study of reflection of light from leaf surfaces. *Bot. Gaz.* 87: 583–607.
- SEYBOLD, A. 1933. Über die Optischen Eigenschaften der Laubblätter. III. *Planta* 18: 479–485.
- SMITH, H. [ED.] 1981. *Plants and the daylight spectrum*. Academic Press, London.
- . 1982. Light quality, photoreception and plant strategy. *Ann. Rev. Pl. Physiol.* 33: 481–518.
- TASKER, R., AND H. SMITH. 1977. The function of phytochrome in the natural environment. V. Seasonal changes in radiation energy quality. *Photochem. Photobiol.* 26: 487–491.
- TERASHIMA, I., AND T. SAEKI. 1983. Light environments within a leaf I. Optical properties of paradermal sections of *Camellia* leaves with special reference to differences in the optical properties of palisade and spongy tissues. *Pl. Cell. Physiol.* 24: 1493–1501.
- WILLSTATTER, R., AND A. STÖLL. 1918. *Untersuchungen über die Assimilation der Kohlensäure*. Springer-Verlag, Berlin.
- WOOLLEY, J. T. 1971. Reflectance and transmittance of light by leaves. *Pl. Physiol.* 47: 656–662.