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CORRELATES OF LEAF OPTICAL PROPERTIES IN TROPICAL FOREST SUN AND EXTREME-SHADE PLANTS¹

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ABSTRACT

Thirteen shade-adapted rain forest species were compared with twelve sun-adapted tropical forest species for correlates to leaf optical properties (described previously in Amer. J. Bot. 73: 1100-1108). The two samples were similar in absorptance of quanta for photosynthesis, but the shade-adapted taxa: 1) had significantly lower specific leaf weights, indicating a more metabolically efficient production of surface for quantum capture; 2) synthesized less chlorophyll per unit area; and 3) used less chlorophyll for capturing the same quanta for photosynthesis. The anatomical features that best correlate with this increased efficiency are palisade cell shape and chloroplast distribution. Palisade cells with more equal dimensions have more chloroplasts on their abaxial surfaces. This dense layer of chloroplasts maximizes the light capture efficiency limited by sieve effects. The more columnar palisade cells of sun-adapted taxa allow light to pass through the central vacuoles and spaces between cells, making chloroplasts less efficient in energy capture, but allowing light to reach chloroplasts in the spongy mesophyll. Pioneer species may be an exception to these two groups of species. Three pioneer taxa included in this study have columnar palisade cells that are extremely narrow and packed closely together. This layer allows little penetration of light, but exposure of the leaf undersurface may provide illumination of spongy mesophyll chloroplasts in these plants.

PLANTS from different environments may vary in their capacity to capture radiant energy. Leaves absorb electromagnetic radiation in the visible wavelengths (primarily with chlorophyll pigments) and reflect and transmit most quanta of wavelengths beyond 700 nm (Seybold, 1933; Rabideau, French, and Holt, 1946; Gates et al., 1965; Loomis, 1965; Gausman and Allen, 1973; Woolley, 1971). The leaves of desert plants frequently have less absorption (Ehleringer, 1981; Lee et al., 1986), as may those from high altitude shrubs (Ehleringer,

1988). Leaf epidermises may also absorb more ultraviolet wavelengths in plants naturally receiving more radiation of these wavelengths, particularly tropical alpine species (Robberecht and Caldwell, 1980). Extreme shade-adapted plants should more efficiently capture light for photosynthesis (Osborne and Raven, 1986), using less metabolic energy per unit area. Although leaf absorptions in some extreme shade-adapted tropical forest species were greater, the means of samples of shade and sun plants were not significantly different (Lee and Graham, 1986). The present paper examines the influence of pigment composition and anatomical features on leaf absorption in the same taxa.

Although surface features, such as scales and hairs, reduce absorption (Ehleringer, Björkman, and Mooney, 1976; Ehleringer et al., 1981; Eller and Willi, 1981), it is not clear how other leaf features affect leaf optical properties. Total pigment concentration should be the overriding factor determining absorption, but simple comparisons of the absorption of pigments and whole leaves indicates that other factors play very important roles (Shul'gin, Khazanov, and Kleshnin, 1960; Loomis, 1965; Fig. 1)

Three approaches have been employed in

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previous research on the determinants of leaf optical properties. The utility of optical models (Willstätter and Stoll, 1918; Kubelka and Munk, 1931; Allen, Gausman, and Richardson, 1973; Hemenger, 1977; Tucker and Garratt, 1977; Fukshansky, 1981; Seyfried and Fukshansky, 1983) has been limited by the complexity and diversity of leaf structure. The greatest success has been with thick and compact tissue, such as developing cotyledons, where scattering is less complicated (Allen et al., 1969; Seyfried and Schafer, 1983; Vogelmann, 1986). Changes in reflectance might be used to deduce the status of vegetation through remote sensing, such as a diseased or water-stressed condition (Gausman et al., 1969; Pinter et al., 1981; Gausman, 1985), but this research has added little to an understanding of how leaf structure affects optical properties.

Experimental research on intact leaves and leaf components has been more helpful. The contribution of pigments to absorption in the leaf is affected by their distribution in plastids. Pigment extracts have transmittance spectra very different from their absorptions *in vivo* (Loomis, 1965; Shul'gin et al., 1977; Fig. 1). Plastids provide a discontinuous distribution of pigments in the leaf, so that attenuation consistent with the Lambert-Beer law is not observed. At wavelengths of stronger absorbance, as 650–680 nm, spectra are notably flattened (Duysens, 1956; Kirk, 1975; Kirk and Goodchild, 1972), due to the sieve effect (Das et al., 1967; Fukshansky, 1981): the probability that some light will not be absorbed by the discontinuous distribution of chlorophyll. Chloroplasts distributed uniformly throughout the leaf thickness would maximize the degree of flattening, while chloroplasts arranged in a discrete layer within the leaf would minimize it. At wavelengths of weaker absorbance, as at around 550 or 700 nm, quanta within the leaf are more likely to be absorbed because of the path-lengthening effect (Butler, 1964; Kirk and Goodchild, 1972). Light is scattered because of the differing refractive indices of cell walls, intercellular spaces and chloroplast membranes, relative to surrounding media. Scattered light is more likely to be absorbed by a chlorophyll molecule, even though the pigments absorb weakly at these wavelengths. Any structure within the leaf that enhances light scattering would increase the effect of path-lengthening, including the frequency and distribution of intercellular spaces and chloroplasts (Ruhle and Wild, 1979; Terashima and Saeki, 1983). Differences in the compactness of the palisade and spongy mesophyll affect the degree of scattering and explain the differences

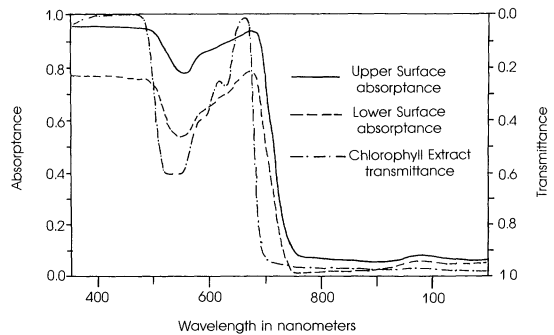


Fig. 1. Spectra of leaf optical characteristics for *Bras-sia actinophylla* (BA; Lee and Graham, 1986).

in absorption between adaxial and abaxial surfaces of bifacial leaves (Fig. 1).

Leaf anatomy influences chloroplast distribution. In bifacial leaves the palisade layer provides a concentration of chloroplasts exposed to intense radiation. The long central vacuole and intercellular spaces should allow light to illumine chloroplasts in the spongy mesophyll (Sharkey, 1985; Lee, 1987). Thus, decrease in spaces between palisade cells, decrease in palisade cell diameter, or change in cell shape would alter light distribution within the leaf and affect its optical properties. Palisade cells with a much smaller height to diameter ratio accumulate chloroplasts on the abaxial as well as lateral walls, creating a denser layer of chloroplasts (see Roth, 1984). Tree architecture provides a useful analogy of light capture strategies, in the monolayer and multilayer understory canopies of Horn (1971). A monolayer distributes chloroplasts for greater efficiency in light capture, while a multilayer is able to take advantage of higher fluence rates by exposing more chloroplasts. The effect of chloroplast distribution on leaf optical properties has been confirmed by reports of small transient changes in transmittance due to chloroplast movement in leaves (Seybold, 1956; Zurzycki, 1961; Inoue and Shibata, 1974), as well as changes in absorption from acclimation to different light regimes (Tsel'niker, 1975).

Additional factors affect leaf optical properties. Leaf surface, aside from scales and pubescence, may 1) alter patterns of reflectance (McClendon, 1984); 2) reduce the reflectance of diffuse radiation through convex cell curvature (Bone, Lee, and Norman, 1985); and 3) selectively interfere with light through thin film interference (Héban and Lee, 1984). Internal structures also selectively interfere with light (Graham and Lee, 1988), and convex epidermal cell curvature may locally increase light

intensity within the leaf (Bone et al., 1985), as may scattering within the leaf (Vogelmann and Bjorn, 1984; Vogelmann, 1986). Pigments other than chlorophylls influence leaf optical properties. Anthocyanins increase absorptance, particularly in rapidly developing leaves, senescing leaves, and the undersurfaces of leaves of many extreme-shade species (Lee, Lowry, and Stone, 1979; Lee, 1986; Lee, Brammeier, and Smith, 1987).

The purpose of the present study was to determine which leaf structures best correlate with previously published optical properties of 13 extreme-shade adapted understory species and 12 sun-tolerating tropical forest species (Lee and Graham, 1986). Additional measurements of these taxa have made it possible to determine if 1) chlorophyll content is an important determinant of absorptance; 2) chloroplast distribution has a significant effect; 3) whether the effect is through flattening or path-lengthening; and 4) whether other variables, as thickness, palisade parenchyma, cell dimensions, the extent of air spaces, and epidermal cell curvature, affect leaf absorptance. This comparative approach has been well justified by Givnish (1987).

MATERIALS AND METHODS—The plants studied in this research (Table 1) are the same as those described by Lee and Graham (1986). Their sites of collection and analysis are as follows: La-Selva, Costa Rica (AC, DN, GC, LD, PS, TH, ZS, CL); Barro Colorado Island (BCI), Panama (BC, IP, PS, CP, OP); and Miami (BM, HR, RM, BJ, BA, BS, CI, CU, HT, MI, SM, TC). Leaves of BC, IP and PS were dried and measured for specific weight at BCI in May of 1987. These values were, respectively, 1.98 ± 0.30 , 4.62 ± 0.57 and 1.98 ± 0.48 mg cm⁻². The leaves of each species were kept fresh under moist conditions and analyzed for optical properties and chlorophyll content within 2 hr of collection. Diffuse transmittance and reflectance were measured with a Li-1800 spectroradiometer (Li-Cor Instruments, Lincoln, NE) attached by a fiber optic cable to an integrating sphere (Lee and Graham, 1986). These measurements allowed the calculation of absorptance as $1 - \text{reflectance} - \text{transmittance}$. Optical properties were also measured of six species (BA, BJ, BM, HR, RM, TC) whose leaves had been infiltrated with water under partial vacuum, complete infiltration defined as a uniformly dark leaf color. Infiltration removes most light scatter from intercellular spaces, since the refractive index of water is close to that of the hydrated cell wall. Only those sun species were used that

could be completely infiltrated by these methods, and an equal number of shade species available in Miami were infiltrated for comparison. Chlorophyll content, measured from 80% acetone extracts (Arnon, 1949), permitted estimations of chlorophyll per unit area ($\mu\text{g cm}^{-2}$). Chlorophyll absorbance in intact leaves (called attenuation: Ruhle and Wild, 1979; Terashima and Saeki, 1983) was estimated by analysis of absorptance data (Lee and Graham, 1986). A calculation of log-absorptance at 652 or 700 nm, minus that at 800 nm, provided estimates of the in vivo absorbance of chlorophyll. The wavelength of 652 nm (where the extinction coefficients of chlorophylls a and b in vitro are equal) was used to detect flattening effects, and a second wavelength of 700 nm was chosen as a region where chlorophyll absorbs weakly, and effects of path-lengthening could be detected. The wavelength of 550 nm was not used because of possible interference by anthocyanins; Ruhle and Wild (1979) showed comparable results at both wavelengths. The absorbance of chlorophyll in vitro in the leaves at these wavelengths could be calculated from estimations of chlorophyll content per unit area, using an extinction coefficient of 34.5 l mg^{-1} for chlorophylls a and b at 652 nm (Arnon, 1949), and 0.4 l mg^{-1} for chlorophyll a at 700 nm (determined by measurement with a Beckman Acta V spectrophotometer, Beckman Instruments, Fullerton, CA). The absolute values are meaningless because of differences in the chlorophyll absorbance maxima in vitro (in 80% acetone) vs. those in vivo, but are useful for comparing differences between species. The extent of sieve and path-lengthening effects was estimated from differences in ratios of attenuation/absorbance at 652 and 700 nm, in a procedure similar to that of Ruhle and Wild (1979) and Terashima and Saeki (1983). Relatively higher ratios would suggest the importance of path lengthening and lower ratios of sieve effects.

Optical properties of chloroplast suspensions and corresponding concentrations of chlorophyll extracts in 80% acetone were measured in one species, *Begonia mazae* (BM). The chloroplasts were prepared by standard methods (Roberts and Whitehouse, 1976) using a suspension medium of 50 mM tricine, pH 7.8 with 400 mM sucrose, 10 mM NaCl and 1 mM MgCl₂ (Glick, McCauley, and Melis, 1985). Chloroplast suspension absorptances were measured as for leaves through use of a flat cuvette with a path length of 1.8 mm. The comparative concentration of chloroplasts was determined by chlorophyll measurement and comparison with concentration in the leaf.

TABLE 1. Species names, species codes, results of optical, pigment, and anatomical measurements of the 25 taxa. Absorptances of photosynthetically active radiation (PAR) and leaf specific weights were taken from Lee and Graham (1986). Significance values for the Student's *t* distribution are given for comparisons of the two samples: ns = not significantly different, * = *P* < 0.05, and ** = *P* < 0.01

Species	Code	PAR absorptance	Chlorophyll µg cm ⁻²	Air space	Chloroplast distribution SD in µm	Attenuance/absorbance	
						652 nm	700 nm
Shade species							
<i>Alternanthera costaricensis</i>	AC	0.920 ± 0.002	50 ± 10	0.235 ± 0.043	48 ± 7	0.68 ± 0.01	39.7 ± 1.7
<i>Blechnum costaricensis</i>	BC	0.813 ± 0.021	25 ± 1	—	—	1.08 ± 0.04	31.6 ± 1.7
<i>Begonia mazae</i>	BM	0.948 ± 0.012	41 ± 5	0.091 ± 0.057	15 ± 4	0.92 ± 0.09	56.3 ± 2.0
<i>Danaea nodosa</i>	DN	0.889 ± 0.004	47 ± 2	0.248 ± 0.057	37 ± 5	0.64 ± 0.04	37.5 ± 2.8
<i>Geonema cuneata</i>	GC	0.899 ± 0.011	55 ± 12	0.048 ± 0.019	21 ± 2	0.62 ± 0.02	37.5 ± 2.5
<i>Hoffmania refulgens</i>	HR	0.938 ± 0.013	48 ± 4	0.215 ± 0.044	21 ± 4	0.69 ± 0.05	38.3 ± 3.6
<i>Ischnosciphon pruinosis</i>	IP	0.923 ± 0.010	42 ± 6	—	—	0.72 ± 0.02	37.4 ± 1.5
<i>Leandra dichotoma</i>	LD	0.870 ± 0.011	37 ± 2	0.157 ± 0.020	12 ± 2	0.92 ± 0.02	52.7 ± 2.4
<i>Philodendron scandens</i>	PS	0.928 ± 0.003	48 ± 2	—	—	0.72 ± 0.02	37.4 ± 1.5
<i>Psychotria surrensis</i>	PU	0.928 ± 0.005	48 ± 2	0.301 ± 0.035	21 ± 4	0.63 ± 0.03	38.4 ± 1.3
<i>Ruellia makoyana</i>	RM	0.906 ± 0.009	36 ± 4	0.164 ± 0.048	16 ± 4	0.86 ± 0.02	49.5 ± 2.7
<i>Triolena hirsuta</i>	TH	0.903 ± 0.048	38 ± 2	0.141 ± 0.026	38 ± 7	0.84 ± 0.01	45.2 ± 7.2
<i>Zamia skinnerei</i>	ZS	0.864 ± 0.015	38 ± 7	0.384 ± 0.050	90 ± 10	0.81 ± 0.03	42.9 ± 3.0
Mean ± SD		0.902 ± 0.037	42 ± 8	0.198 ± 0.100	32 ± 24	0.78 ± 0.14	41.9 ± 7.1
Sun species							
<i>Bischofia javanica</i>	BJ	0.917 ± 0.004	51 ± 2	0.177 ± 0.034	80 ± 4	0.70 ± 0.01	43.0 ± 2.3
<i>Brassaia actinophylla</i>	BA	0.893 ± 0.019	64 ± 12	0.244 ± 0.047	32 ± 15	0.51 ± 0.03	26.3 ± 1.8
<i>Bursera simaruba</i>	BS	0.902 ± 0.008	67 ± 6	—	—	0.48 ± 0.01	29.4 ± 2.6
<i>Calophyllum inophyllum</i>	CI	0.878 ± 0.013	52 ± 4	—	—	0.73 ± 0.03	46.7 ± 5.6
<i>Calathea lutea</i>	CL	0.924 ± 0.007	47 ± 11	—	—	0.60 ± 0.02	32.3 ± 3.7
<i>Cecropia peltata</i>	CP	0.896 ± 0.017	50 ± 6	0.232 ± 0.038	—	0.67 ± 0.04	38.7 ± 3.7
<i>Coccoloba wifera</i>	CU	0.870 ± 0.009	60 ± 12	—	—	0.47 ± 0.01	27.9 ± 1.5
<i>Hibiscus tiliaceus</i>	HT	0.885 ± 0.014	54 ± 5	—	—	0.56 ± 0.02	35.4 ± 3.3
<i>Mangifera indica</i>	MI	0.868 ± 0.014	52 ± 6	—	—	0.55 ± 0.05	29.6 ± 4.2
<i>Ochroma pyramidale</i>	OP	0.897 ± 0.010	34 ± 3	0.269 ± 0.033	—	0.95 ± 0.02	57.6 ± 2.2
<i>Swietenia mahogany</i>	SM	0.861 ± 0.039	78 ± 5	—	—	0.35 ± 0.04	21.1 ± 2.1
<i>Terminalia catappa</i>	TC	0.842 ± 0.016	58 ± 6	0.137 ± 0.023	75 ± 7	0.49 ± 0.02	22.1 ± 2.6
Mean ± SD		0.886 ± 0.023	56 ± 11	0.194 ± 0.065	62 ± 26	0.59 ± 0.16	34.2 ± 10.1
<i>t</i> =		1.28	3.66	0.08	1.87	3.17	2.21
		ns	**	ns	ns	**	*

Transmission spectra of chlorophyll extracts were made in the same manner.

Anatomical features of most species were measured from color transparency photomicrographs of sectioned material projected on a rear screen. Portions of 5 leaves of each taxon were fixed with 3% glutaraldehyde in 0.08 M phosphate buffer at pH 6.8. Tissue was embedded in JB-4 resin, sectioned at 5 µm and stained with toluidine blue. Anatomical measurements of six species (BS, CI, CU, HT, MI, SM) were made with fresh hand sections. Ten sections (two per leaf) were examined for each taxon. Measurements included 1) total leaf thickness; 2) thickness of individual tissue layers; 3) number of cell layers; and 4) height and width of palisade cells, measuring the adaxial cell layer where the palisade layer consisted of more than one cell layer. Thirteen taxa (AC, BA, BJ, BM, DN, GC, HR, LD, PS, RM, TC,

TH, ZS) were examined for the vertical distribution of chloroplasts, measuring the distance from the adaxial surface of the first 50 chloroplasts in a transect along the transverse sections, and calculating the standard deviation. The proportion (v/v) of intercellular spaces in these taxa, including CP and OP, was also estimated by use of stereological techniques (Parkhurst, 1982).

Multiple regression analysis was performed by SAS Version 5 (SAS Institute, 1985) to determine the variables which were most closely correlated with each other. Principal components analysis, using the 8 variables with no missing data, was performed on a correlation matrix of the 25 taxa to determine relationships among the species. Pairwise sample comparisons were evaluated with Student's *t* test.

Light refraction and concentration by convexly curved leaf epidermal cells was estimated

TABLE 2. Leaf, cell layer thicknesses, palisade height to width ratios, and numbers of cell layers for the 25 taxa. Means and standard deviations for each taxon, as well as the sun and shade groups, are given. Significance limits for the Student's *t* distribution are given as in Table 1

Species code	Thicknesses (μm)			Palisade height/width	No. of cells
	Leaf	Palisade	Spongy		
Shade species					
AC	230 \pm 11	50 \pm 7	138 \pm 16	1.93 \pm 0.36	7.0 \pm 0.0
BM	423 \pm 30	36 \pm 4	61 \pm 12	1.50 \pm 0.16	7.1 \pm 0.3
BC	129 \pm 25	31 \pm 5	46 \pm 16	1.44 \pm 0.36	5.5 \pm 0.5
DN	246 \pm 15	74 \pm 8	119 \pm 26	1.21 \pm 0.35	6.9 \pm 1.4
GC	87 \pm 12	14 \pm 2	62 \pm 12	0.51 \pm 0.11	8.3 \pm 0.5
HR	182 \pm 26	44 \pm 5	69 \pm 5	1.45 \pm 0.16	6.6 \pm 0.5
IP	137 \pm 24	29 \pm 3	46 \pm 12	3.99 \pm 0.59	9.1 \pm 0.6
LD	100 \pm 15	27 \pm 4	16 \pm 5	1.19 \pm 0.16	4.2 \pm 0.4
PS	236 \pm 27	53 \pm 5	43 \pm 7	1.65 \pm 0.34	9.0 \pm 0.0
PU	137 \pm 11	34 \pm 3	51 \pm 7	1.58 \pm 0.14	6.2 \pm 0.4
RM	106 \pm 18	30 \pm 5	28 \pm 5	1.23 \pm 0.15	5.2 \pm 0.4
TH	160 \pm 28	53 \pm 10	68 \pm 16	1.69 \pm 0.24	6.2 \pm 0.8
ZS	345 \pm 12	43 \pm 4	279 \pm 11	1.07 \pm 0.30	12.2 \pm 0.6
Mean \pm SD	194 \pm 100	40 \pm 15	79 \pm 69	1.57 \pm 0.81	7.2 \pm 2.1
Sun species					
BJ	350 \pm 26	123 \pm 15	157 \pm 14	3.98 \pm 0.48	11.2 \pm 0.9
BA	360 \pm 28	115 \pm 20	178 \pm 14	3.27 \pm 0.54	17.2 \pm 0.4
BS	260 \pm 34	84 \pm 18	109 \pm 20	9.88 \pm 1.33	6.8 \pm 0.6
CL	181 \pm 30	62 \pm 6	49 \pm 7	12.80 \pm 3.10	10.8 \pm 0.9
CI	320 \pm 18	83 \pm 7	186 \pm 12	4.74 \pm 0.66	11.4 \pm 1.2
CU	457 \pm 28	130 \pm 14	194 \pm 18	9.18 \pm 1.35	12.1 \pm 0.5
CP	126 \pm 45	54 \pm 3	55 \pm 1	9.10 \pm 1.23	8.9 \pm 0.6
HT	198 \pm 45	84 \pm 10	66 \pm 12	9.96 \pm 2.09	8.4 \pm 0.5
MI	260 \pm 18	60 \pm 7	151 \pm 17	5.80 \pm 0.74	9.1 \pm 0.6
OP	159 \pm 18	60 \pm 9	66 \pm 8	9.34 \pm 2.51	6.0 \pm 0.0
SM	194 \pm 10	58 \pm 5	112 \pm 9	5.79 \pm 3.7	7.3 \pm 0.5
TC	277 \pm 16	96 \pm 11	152 \pm 14	6.43 \pm 1.43	10.4 \pm 0.8
Mean \pm SD	262 \pm 97	84 \pm 27	128 \pm 54	7.52 \pm 0.91	10.0 \pm 3.0
<i>t</i> =	1.72	5.09	1.96	17.29	2.72
	ns	**	ns	**	*

for 4 taxa with this feature (BM, PS, PU, RM) by a ray-tracing program described by Bone et al. (1985). The program allows an estimation of concentration factors at the level of the chloroplasts, and at the level of maximum focus, within each leaf for diffuse and direct radiation.

RESULTS—Leaf anatomical measurements, pigment concentrations, and calculations based on these and earlier reported measurements (Lee and Graham, 1986) are reported in Tables 1 and 2. Attenuance/absorbance ratios of infiltrated leaves, and the ratios of normal to infiltrated leaves, are presented for six species in Table 3. For those species with convexly curved upper epidermal cells, concentration factors are reported in Table 4.

To clarify the interpretation of these results, we will briefly describe the values for a typical sun-adapted species, *Brassaia actinophylla* (BA) and an extreme shade-adapted one, *Begonia mazaе* (BM). Anatomically, BA develops rather

thick leaves (360 μm), with a distinct palisade layer of 2–3 cells, 115 μm thick (Fig. 2, Table 2). The palisade cells are highly columnar, with a height/width ratio of 3.27. The leaves consist of approximately 17 layers of cells. A consequence of this structure is that the chloroplasts are concentrated in the palisade mesophyll, but distributed vertically throughout most of the leaf (Fig. 2, 3; Table 1) with a moderate standard deviation from the mean in vertical distribution of 32 μm . Air spaces, almost entirely in the spongy mesophyll, occupy 0.244 of leaf volume. Mean leaf absorptance of 0.893, coupled with a rather high chlorophyll concentration, results in an attenuance/absorbance ratio of 0.51 at 652 nm, and 26.3 at 700 nm. For leaves infiltrated with water, the attenuance/absorbance ratios at 652 and 700 nm were lower, 0.43 and 20.0, indicating that intercellular spaces contribute slightly to path-lengthening effects at these wavelengths (Table 3). The differences between

TABLE 3. Attenuance/absorbance ratios at 652 and 700 nm for leaves of six species infiltrated with water, and comparisons of those ratios with normal leaves. Means and standard deviations of shade and sun species are given

Species code	Infiltrated attenuance/absorbance		Normal/infiltrated	
	652 nm	700 nm	652 nm	700 nm
Shade species				
BM	0.94 ± 0.05	43.1 ± 2.2	0.98	1.31
HR	0.51 ± 0.03	25.1 ± 2.4	1.53	1.53
RM	0.92 ± 0.02	37.4 ± 1.4	0.93	1.32
	0.79 ± 0.24	35.2 ± 9.2	1.15 ± 0.33	1.39 ± 0.12
Sun species				
BA	0.43 ± 0.03	20.0 ± 1.6	1.19	1.31
BJ	0.64 ± 0.03	32.7 ± 1.3	1.16	1.40
TC	0.52 ± 0.03	18.3 ± 2.7	0.94	1.22
	0.53 ± 0.10	23.7 ± 7.9	1.10 ± 0.14	1.34 ± 0.10

leaf absorptance and transmittance of an equivalent concentration of chlorophyll in 80% acetone is shown in Fig. 1.

In contrast, the extreme shade-adapted species, BM, has a strikingly different leaf anatomy (Fig. 4). Although the leaves are also quite thick (423 μm), the palisade layer is extremely thin, 36 μm (Table 2), and the entire mesophyll represents less than a quarter of leaf thickness. The leaf is composed of 7 cell layers, the thickest of which are the ad- and abaxial hypodermis. The palisade cells are conical, with a small height/width ratio of 1.50. Consequently, the chloroplasts are more highly concentrated in the palisade layer; the standard deviation of chloroplast vertical distribution (15 μm) is substantially smaller than that of BA or any other sun taxa (Fig. 4, 5; Table 1). Chlorophyll concentration (41 μg cm⁻², Table 1) is much lower than BA. Yet leaf absorptance of 0.948 is much higher. Although this difference is partly due to the presence of anthocyanins in BM and greater absorptance at 500–550 nm, the efficiency of absorbance by chlorophyll (attenuance/absorbance, Table 1) is much higher at both 652 and 700 nm. Water-infiltrated leaves have similar attenuance/absorbance ratios at 652 nm, and differences between normal and infiltrated ratios at 700 nm are smaller than BA, consistent with the smaller scattering by reduced air cell contacts for BM (air/cell volume = 0.091, Table 3). The differences in spectra for normal absorptance, infiltrated absorptance, and transmittance by an equivalent concentration of chlorophyll extract is shown in Fig. 6. Leaves of this species develop convexly curved epidermal cells (Fig. 4), which give them a velvety appearance. The level from the adaxial surface of optimum light concentration is 11 μm for diffuse radiation and 28 μm for direct radiation, inside of the large

hypodermal cells. These cells do not significantly concentrate light at the level of the chloroplasts (Table 4). Since the palisade cells are strongly conical in shape, their most significant function may be to increase absorptance of diffuse light at oblique angles (Bone et al., 1985).

Several statistically significant differences between the samples of sun and extreme-shade plants stand out. The shade-adapted plants have lower chlorophyll concentrations, yet have higher attenuance/absorbance ratios than the sun plants (Table 1). In addition the leaves of extreme-shade plants tend to be thinner, with fewer cell layers, less columnar palisade mesophyll cells, and a more stratified chloroplast distribution (Tables 1, 2).

DISCUSSION—The two samples of extreme shade- and sun-adapted taxa absorbed approximately the same portions of quanta for photosynthesis, although individual shade species absorbed significantly more. Yet the much low-

TABLE 4. The degree of light concentration in leaves of taxa with convexly curved upper epidermal cells. Levels within the leaf are presented as distance in μm from the leaf surface, and include the level at optimal concentration and at the upper edge of the dense layer of chloroplasts characteristic of these taxa. These values were estimated by a ray tracing program (Bone et al., 1985)

Species code	Concentration factor (CF) at levels (μm)			
	Diffuse radiation		Direct radiation	
	CF/chloroplast	CF/optimal	CF/chloroplast	CF/optimal
BM	0.95/65	2.32/11	1.00/65	19.00/28
PS	1.92/49	1.97/66	3.91/49	19.00/266
PU	1.79/66	1.96/35	5.10/66	21.80/150
RM	1.62/26	2.34/4	6.56/26	7.35/34

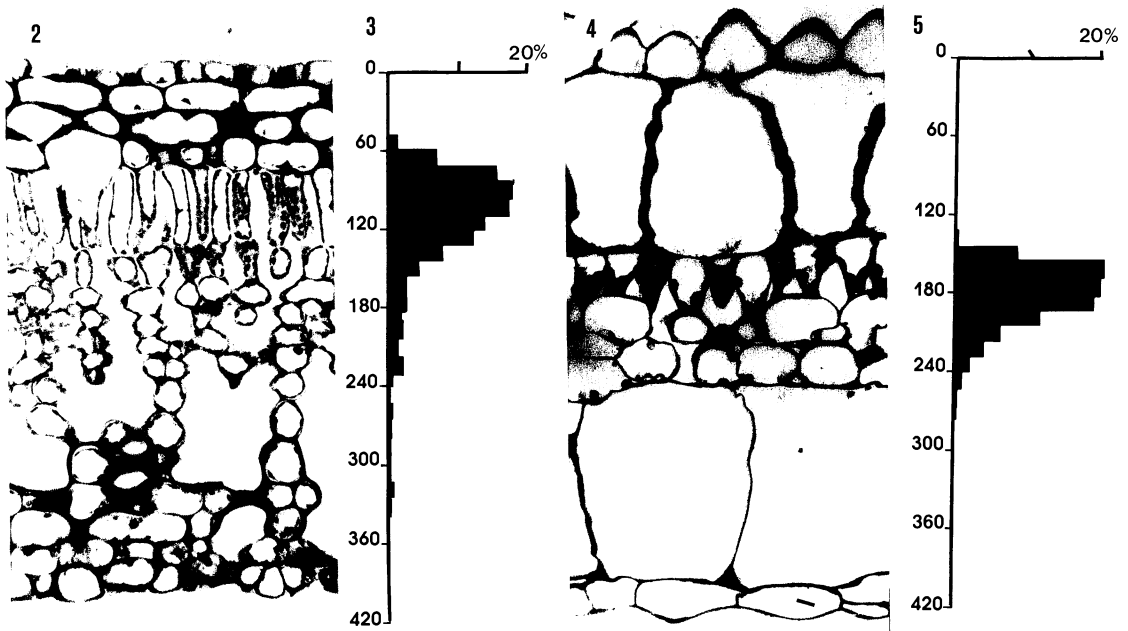


Fig. 2-5. Leaf transverse sections and bar graphs of chloroplast distributions of representative sun and extreme-shade species. 2. *Brassia actinophylla*. 3. Chloroplast distributions within leaves of *B. actinophylla*. 4. *Begonia mazaе*. 5. Chloroplast distributions within leaves of *B. mazaе*. Values are in μm .

er leaf specific weights of the extreme-shade species suggest that they are capable of producing surfaces for energy capture at lower metabolic cost (Lee and Graham, 1986). Results of the present study also show that the shade plants capture energy for photosynthesis with significantly lower chlorophyll content per unit area, and that their ratios of attenuation/absorbance at 652 and 700 nm are also higher (Table 1). How might they achieve this? Greater efficiency of absorbance could be achieved through reducing the flattening effect at peak chlorophyll absorbance (Duysens, 1956), and/or by increasing path-lengthening effects, principally at more weakly absorbed wavelengths (Butler, 1964). Higher ratios of attenuation/absorbance_{652nm} would be due to the reduction of the sieve effect.

Sun and shade taxa have high attenuation/absorbance_{700nm} (Table 1), which is moderately reduced by infiltration (Table 3). These large values are mainly due to the low extinction coefficient of extracted chlorophyll at 700 nm. Absorbance maxima of chlorophyll *in vivo* will be shifted towards longer wavelengths, increasing this ratio. The results still document the strong path-lengthening effect of cells in normal and infiltrated leaves. Some of this may be caused by scatter between and within chloroplasts (Bialek et al., 1977), but most is by cell walls. That scatter and path lengthening

may be important at wavelengths of strong chlorophyll absorbance is shown by the difference in attenuation/absorbance_{652 nm} for infiltrated vs. normal leaves (Table 3) and the difference between the leaf and chloroplast spectrum (Fig. 6), but the effects may be similar in extreme-shade and sun plants. Thus both groups benefit from path-lengthening effects, and intercellular spaces do not affect one group more than the other. The degree of intercellular spaces was not significantly different between the sun and shade taxa (Table 1), and it was not significantly correlated with attenuation/absorbance_{700 nm} (Table 5).

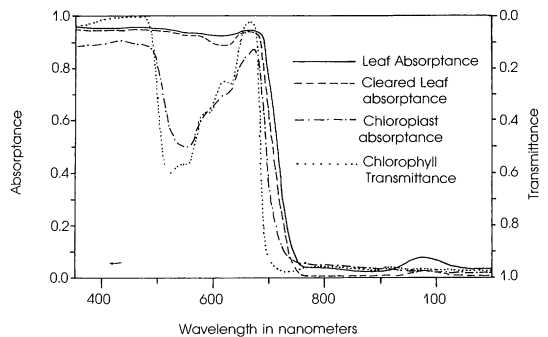


Fig. 6. Spectra of leaf optical characteristics for *Begonia mazaе* (BM).

TABLE 5. Pearson product correlation matrix of ten of the leaf variables described in the text. Specific leaf areas and absorptances are from Lee and Graham (1986). Coefficients for chloroplast standard deviations (CLP) and the degree of air spaces (AIR) are from reduced samples (Table 1). One asterisk indicates a level of significance below 0.05; two asterisks, below 0.01

Variable (symbol)	CLA	AAA	AAB	THI	PHW	CEL	AIR	CLP	ABS	SWT
Chlorophyll $\mu\text{G cm}^{-2}$ (CLA)	—	-0.950 **	-0.707 **	0.380	0.369	0.408 *	-0.137	0.193	-0.021	0.591 **
Absorbance/attenuance 652 nm (AAA)		—	0.771 **	-0.347	-0.370	-0.446 *	-0.033	-0.290	0.064	-0.608 **
Absorbance/attenuance 700 nm (AAB)			—	-0.232	-0.176	-0.413 *	-0.104	-0.377	-0.488 *	-0.528 **
Leaf thickness μm (THI)				—	0.047	0.632 **	-0.009	0.477 **	0.099	0.632 **
Palisade height/ width (PHW)					—	0.276	-0.082	0.551 *	-0.089	0.432 *
No. cell layers thick (CEL)						—	0.226	0.558 *	-0.077	0.734 **
% Air spaces (AIR)							—	0.406	-0.191	0.074
Chloroplast distribution (CLP)								—	-0.479	0.314
PPFD absorptance (ABS)									—	-0.256
Leaf specific weight (SWT)										—

The most important contribution to reduction of the sieve effect in shade plants, increasing their efficiency of quantum capture, is the distribution and structure of chloroplasts. In shade plants chloroplasts should be arranged in a more continuous layer. Such a compact layer should decrease the sieve effect by decreasing the probability of quanta passing through the leaf. The layer is partly achieved through regulation of the shape of palisade cells. Columnar cells allow the passage of light through the central vacuole (Lee, 1987) and intercellular spaces (Sharkey, 1985; Fig. 2). Cells more equal in dimension tend to distribute chloroplasts on abaxial surfaces, or may be small and packed with chloroplasts (Fig. 5; Roth, 1984). Conical cells may also effectively channel light towards the chloroplasts at the narrow end.

A test of the contribution of chloroplast distribution to efficiency of light absorptance is to be seen in the matrix of correlations among anatomical and optical characteristics (Table 5). Many of the significant correlations in this matrix are obvious, as between leaf thickness and numbers of cell layers, or either of these with specific leaf weight. Chlorophyll content would also be expected to be negatively correlated with attenuance/absorbance. However, palisade height/width and chloroplast standard deviations are not significantly correlated with attenuance/absorbance at 652 nm or with

absorptance, although they are obviously correlated with each other. The prediction is not confirmed.

An examination of the species selected for this study explains the discrepancy. One shade species is clearly an anomaly. A cycad, *Zamia skinnerei* (ZS), belongs to a genus primarily adapted to sunny and dry environments. Its leaves are thick and tough, with the highest specific weight among the shade taxa ($7.5 \mu\text{g cm}^{-2}$; Lee and Graham, 1986). Even though the palisade cells have low height/width ratios (Table 2), they allow considerable light to pass through and illuminate the numerous chloroplasts in the extensive spongy mesophyll. The removal of ZS from the comparisons reduced the standard deviation of chloroplast distribution to $21 \pm 15 \mu\text{m}$ and made the shade sample significantly smaller than the sun sample ($P < 0.01$). Among the sun-adapted species are three taxa with high attenuance/absorbance_{652 nm}: *Calathea lutea* (CL), *Cecropia peltata* (CP), and *Ochroma pyramidale* (OP). These are rain forest pioneers, whose leaf undersurfaces are exposed to bright sunlight. Leaves of these taxa have the lowest specific weights of the sun species. Closer examination of their leaf anatomy showed that their highly columnar palisade cells are compact and extremely narrow (less than $10 \mu\text{m}$ wide). Thus, these cells lack a large central vacuole that would allow light to pass through this layer, and chlo-

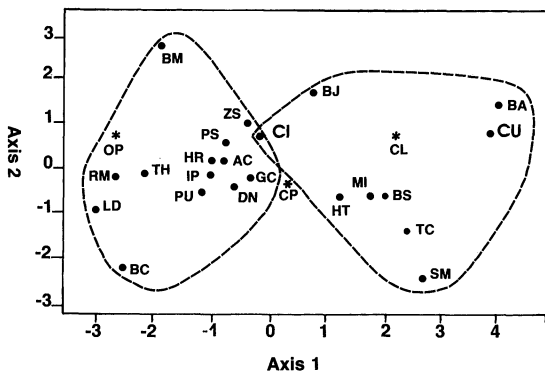


Fig. 7. Principal components analysis of the 25 taxa based on the Pearsonian correlation coefficients of the eight variables for which there were no missing data. Dashed lines encircle the clusters of extreme shade-adapted (left) and sun-adapted taxa (right). Asterisks designate the three pioneer species: CP, CL, and OP.

roplasts in the spongy mesophyll would be more exposed to light from the undersurface. No other taxa studied had such narrow and compact palisade cells, or such ecological requirements.

The relationships of the above four taxa to the rest are revealed by principal components analysis (Fig. 7). ZS is seen at the contact between the groups of sun and shade plants, and OP and CP are clustered among the shade taxa. When multiple correlation was performed without the data from these taxa, the r values for attenuation/absorbance_{652 nm} with palisade height/width and chloroplast distribution were increased to -0.70 ($P < 0.01$) and -0.62 ($P < 0.05$), respectively. The level of significance for chloroplast distribution is limited by the smaller sample size, $N = 11$.

Neither chlorophyll content nor any of the anatomical measurements were significantly correlated with absorbance. Only attenuation/absorbance_{700 nm} was correlated. For the reduced sample, palisade height/width ($r = -0.56$, $P > 0.01$) was also negatively correlated with absorbance.

Four of the extreme shade taxa (BM, PS, PU, RM) developed convexly curved adaxial epidermal cells (Table 4). Ray tracing analysis indicated that they all significantly concentrated light within the leaf. If this refraction directed light on clusters of chloroplasts, the sieve effect would be reduced and attenuation/absorbance_{652 nm} should be greater for these taxa. However, the chloroplasts appeared to be evenly distributed and attenuation/absorbance ratios are not higher than the other shade plants. Only PS, PU, and RM significantly concentrated light in ways that could theoretically

increase photosynthetic efficiency. At the level of chloroplasts this concentration varied from 1.92 to 6.56, and was close to the optimal for diffuse radiation. Its potential physiological significance has been discussed by Bone et al. (1985).

These results indicate that leaf structure strongly influences the efficiency of light absorbance in plants, and that shade plants possess a suite of features (low specific weight, low chlorophyll content per area, equidiameter palisade cells, and narrow chloroplast distribution) that contribute to a greater efficiency of light capture. Such plants would have a selective advantage in energy-poor extreme-shade environments. On the other hand, such a dense layer of chloroplasts would be disadvantageous to plants adapted to higher light conditions. The compact layer of chloroplasts would limit rates of CO_2 diffusion, and carbon fixation (Sharkey, 1985). It would reduce the total number of chloroplasts exposed to light, and increase the number of chloroplasts exposed to intensities above light saturation levels for photosynthesis, increasing the probability of photosynthetic inhibition or photochemical damage (Björkman, 1981; Osmond, 1987). A greater vertical distribution of chloroplasts, especially in cells surrounded by air spaces, would enhance CO_2 diffusion rates, expose more chloroplasts to radiation (but fewer chloroplasts to the most intense radiation), and result in higher light-saturated levels of photosynthesis. Such interception by the palisade layer would limit the intensity of light available to spongy mesophyll chloroplasts (Terashima and Saeki, 1983), which should be acclimated to extreme shade conditions. Confirming evidence has been shown in leaves of *Camellia japonica* (Terashima and Inoue, 1984), spinach (Terashima and Inoue, 1985a, b), and in the fluorescence properties of chloroplasts from adaxial and abaxial leaf faces (Schreiber, Fink, and Vidaver, 1977; Kulandaivelu et al., 1983).

Reduced chlorophyll content and Calvin cycle enzyme levels would contribute to lower specific leaf weights in these shade-adapted plants (Björkman, 1981), along with thinner leaves, fewer cell layers, thinner cell walls, and reduced lignification. Reduced metabolic allocation per unit of absorbing surface would also mean lowered maintenance costs, and reduced dark respiration rates. Leaves of extreme-shade plants may also optimize the efficiency of biomass allocation in other ways (Givnish, 1987). Most of the shade-adapted taxa studied here have comparatively thick epidermal or hypodermal cell layers. Flexural rigidity of shade leaves may be primarily due

to the turgor pressure of these cells, providing a metabolically inexpensive mode of mechanical support, but one more susceptible to water stress.

Results of this study provide further evidence for the importance of leaf structure in controlling the photosynthetic properties of plants in different environments. The next phase in this research should include controlled experiments on the effect of light levels (and quality: Smith, 1982; Lee, 1988) on leaf anatomy, optical properties, pigment composition, and photosynthesis within individual species. Thinner sections (less than 1 μm) would also make possible the estimation of chloroplast densities, cross-sectional areas and area indices (Tsel'niker, 1975), as well as vertical distribution. The results of our study suggest the potential of this approach in understanding the relationship of leaf structure to function.

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