# Optical Parameters of Leaves of 30 Plant Species ${ }^{1}$ 

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#### Abstract

Optical parameters (absorption coefficient $k$, infinite reflectance $R_{\infty}$, scattering coefficient $s$ ) are tabulated for seven wavelengths and analyzed for statistical differences for 30 plant species. The wavelengths are: 550 nm (green reflectance peak), 650 nm (chlorophyll absorption band), 850 nm (infrared reflectance plateau), 1450 nm (water absorption band), 1650 nm (reflectance peak following water absorption band at 1450 nm ), 1950 nm (water absorption band), and 2200 $\mathbf{n m}$ (reflectance peak following water absorption band at 1950 nm). Thick, complex dorsiventral (bifacial mesophyll) leaves such as rubber plant, begonia, sedum, and privet had lower $\boldsymbol{R}_{\infty}$ values than thinner, less complex dorsiventral leaves (i.e., soybean, peach, bean, rose) or essentially centric (undifferentiated mesophyll) sorghum and corn leaves. Infinite reflectance was negatively correlated with leaf thickness ( $-0.734^{* *}$ ). Thick, complex dorsiventral leaves (crinum, oleander, privet, rubber plant, sedum) had higher ( $p$ 0.01) $k$ values than thinner, less complex dorsiventral leaves (i.e., soybean, rose, peach) or essentially centric sorghum, sugarcane, and corn leaves. A coefficient of $0.718^{* *}$ was obtained for the correlation of $\boldsymbol{k}$ values with leaf thickness values. Complex dorsiventral oleander, orange, and crinum leaves had higher ( $\boldsymbol{p} 0.01$ ) $s$ values than less complex dorsiventral (i.e., onion, begonia, banana) or centric leaves (i.e., corn and sugarcane). The scattering coefficient was not correlated with leaf thickness.


Reflectance and transmittance of a plant leaf have been explained on the basis of critical reflection of light at the cell wall-air interface of the spongy mesophyll tissue (22). A hypothesis has been advanced that leaf reflectance derives from the diffuse characteristics of plant cell walls (19). Light reflectance from a leaf is generally reduced over all wavelengths when the leaf is infiltrated with water $(14,16)$ or with an oil mixture (23). Most of the reflectance, therefore, originates internally and is reduced when the cell wall-air interfaces are eliminated. Reflectance at 680 and 1950 nm is relatively unchanged by infiltrations, however, so most of it must originate from the

[^0]cuticle or surface of the leaf. The structure of light beams reflected from plant leaves has also been studied (17).

Near infrared light reflectance ( $750-1350 \mathrm{~nm}$ ) usually increases with an increase in number of intercellular air spaces $(7,8)$ because light is scattered in passing from hydrated cell walls with a refractive index of 1.47 (23) to intercellular air with a refractive index of 1.0 . For example, maturation of a cotton leaf is characterized by development of intercellular air spaces in the mesophyll; consequently light reflectance increases and light transmittance of the leaf decreases (8). Internal refractive index discontinuities other than air-cell interfaces are responsible for some of the near infrared light reflected by a leaf $(6,19,23)$.

Diffuse reflectance and transmittance of a compact leaf such as corn, a leaf impregnated with water, and an immature cotton leaf immediately after it unfolds (9) can be predicted from a plate theory (4). Generalization of the plate theory (flat plate model) to include the effect of intercellular air spaces (4) leads to the concept of void area index of a leaf. When a leaf is regarded as a pile of $N$ compact layers separated by infinitesimal air spaces, the $\mathrm{VAI}^{2}$ is given as $N-1$. The VAI of a compact leaf is zero. The VAI is roughly the average number of air spaces penetrated by a ray passing through the leaf. Parameters that emerge from the flat plate theory $(1,13)$ include a measure of the water and air in the leaf and the effective index of refraction $n$ and absorption coefficient $k$ (3$5,8,9)$. The effective index of refraction of a typical leaf is not inconsistent with the refractive index of epicuticular wax. The effective absorption coefficient of a typical leaf is a superposition of the absorption coefficients of chlorophyll and pure liquid water. The plate model of a leaf is used to determine moisture content from reflectance and transmittance measurements. The absorption of a compact leaf can be simulated closely over the 1350 - to $2500-\mathrm{nm}$ wavelength interval by absorption of an equivalent water thickness.

Reflectance against a soil background increases as number of leaf layers in the plant canopy increases until a stable value of reflectance called infinite reflectance $R_{\infty}$ is attained (1). In the visible and in the 1500 - to $2500-\mathrm{nm}$ WLI, $R_{\infty}$ is reached when plants reach a leaf area index (LAI) of 2 . Leaf area index is the cumulative one-sided leaf area per unit ground area measured from the canopy top to a plane at a given distance above ground (15). In the 750 - to $1350-\mathrm{nm}$ WLI, a LAI of about 8 is required to reach $R_{\infty}$ because of the transparency of the leaves (4). Infinite reflectance can be calculated if the reflectance and transmittance of a single leaf are known.

The experimental and theoretical spectral reflectance and transmittance from two, four, six, and eight stacked leaves

[^1]have been presented $(1,15)$. In the 750 - to $1350-\mathrm{nm}$ WLI, plant leaves absorb very little electromagnetic radiation. The leaf reflects about half and transmits the other half of the incident solar radiation in this interval to leaves lower in the plant canopy (21). Multiple transmission and reflection from leaves in a plant canopy result in a maximum reflectance of about $40 \%$ of the energy incident on a mature crop canopy in the 750 - to $1350-\mathrm{nm}$ WLI.

The purpose of this study is to present significant differences among optical parameters (absorption coefficient $k$, infinite reflectance $R_{\infty}$, scattering coefficient $s$ ) for 30 plant species at the 550 nm (green reflectance peak), 650 nm (chlorophyll absorption band), 850 nm (on infrared reflectance plateau), 1450 nm (water absorption band), 1650 nm (reflectance peak following water absorption band at 1450 nm ), 1950 nm (water absorption band), and 2200 nm (reflectance peak following water absorption band at 1950 nm ) wavelengths. The optical constants can be used to predict the response of a leaf to radiation. These constants are valuable for researchers doing light-canopy and photosynthesis studies.

## MATERIALS AND METHODS

Ten fully grown and healthy appearing leaves were harvested from each of 30 plant species listed in Table I. All plants were field-grown, except that lettuce and onions were purchased in a fresh condition at a local market, and soybeans and pinto beans were grown in a greenhouse. Immediately

Table I. Common and Latin Names of 30 Plant Species Used in This Study

| Common Name | Latin Name |
| :---: | :---: |
| Avocado | Persea americana Mill. |
| Banana | Musa paradisiaca L. |
| Bean | Phaseolus vulgaris L. |
| Begonia | Begonia semperflorens Link and Otto |
| Cantaloupe | Cucumis melo L. var. reticulatus Naud. |
| Corn | Zea mays L. |
| Cotton | Gossypium hirsutum L. |
| Crinum | Crinum fimbriatulum Baker |
| Eucalyptus | Eucalyptus camaldulensis Dehnh |
| Rubber plant | Ficus elastica Roxb. |
| Hyacinth | Eichhornia crassipes (Mart.) Solms |
| Lettuce | Lactuca sativa L. |
| Privet | Ligustrum lucidum Ait. |
| Okra | Hibiscus esculentus L. |
| Oleander | Nerium oleander L. |
| Onion | Allium cepa L. |
| Orange | Citrus sinensis (L.) Osbeck |
| Peach | Prunus persica (L.) Batsch |
| Pepper | Capsicum annuum L. and other spp. |
| Pigweed | Amaranthus retroflexus L. |
| Pumpkin | Cucurbita pepo L. |
| Rose | Rosa L. (var. unknown) |
| Sedum | Sedum spectabile Boreau |
| Sorghum | Sorghum bicolor (L.) Moench |
| Soybean | Glycine max (L.) Merr. |
| Sugarcane | Saccharum officinarum L. |
| Sunflower | Helianthus annuus L. |
| Tomato | Lycopersicon esculentum Mill. |
| Watermelon | Citrullus lanatus (Thunb.) Mansf. |
| Wheat | Triticum aestivum L . |

after excision, leaves were wrapped in Saran ${ }^{3}$ or Glad-Wrap to minimize moisture loss. Leaves were wiped with a slightly dampened cloth preceding spectrophotometric measurements to remove surface contaminants. Only one-half (split longitudinally) of the tubular onion leaf was used for spectrophotometric measurements.

A Beckman Model DK-2A spectrophotometer, equipped with a reflectance attachment, was used to measure spectral diffuse reflectance and transmittance on the adaxial (upper) surface of single leaves. Data were recorded at discrete $50-\mathrm{nm}$ intervals over the continuously measured 500 - to $2500-\mathrm{nm}$ WLI. The basic design of the instrument allows illumination of the leaf surface with a beam of monochromatic light of a desired wavelength. The reflected or transmitted light is collected by an integrating sphere, and the intensity is measured by a photoelectric cell. The integrating sphere is coated with a nearly perfect diffusive reflector of light. When an elementary area of the sphere is illuminated with light, the diffusing material reflects the light, omnidirectionally, to other parts of the sphere. A detector in the sphere surface measures the amount of light being reflected in the sphere.

Data have been corrected for decay of the MgO standard (18) to give absolute radiometric data (2).

Leaf thickness was measured with a linear transducer and digital voltmeter (12). Percentage of leaf water content was determined on an oven-dry weight basis by drying leaves at 68 C for 72 hr and cooling in a desiccator before final weighing. Leaf thickness and water content determinations were not made on wheat leaves.

Leaf thickness and diffuse reflectance and transmittance measurements were completed within 6 hr , after leaves were obtained for each species.

Infinite reflectance $R_{\infty}$ and the absorption $k$ and scattering $s$ coefficients were calculated by the methods of Allen and Richardson (1). Equations used were

$$
\begin{align*}
R_{x} & =1 / a  \tag{1}\\
k & =[(a-1) /(a+1)] \log b  \tag{2}\\
s & =\left[2 a /\left(a^{2}-1\right)\right] \log b  \tag{3}\\
a & =\left(1+r^{2}-t^{2}+\Delta\right) / 2 r  \tag{4}\\
\mathrm{~b} & =\left(1-r^{2}+t^{2}+\Delta\right) / 2 t \tag{5}
\end{align*}
$$

$R_{\infty}=$ infinite reflectance, $t=$ transmittance, $k=$ absorption coefficient, $a=$ optical constant, $s=$ scattering coefficient, $b=$ optical constant, $r=$ reflectance. The quantity $\Delta$ is defined by the relation

$$
\begin{equation*}
\Delta^{2}=(1+r+t)(1+r-t)(1-r+t)(1-r-t) \tag{6}
\end{equation*}
$$

The quantities $a$ and $b$ (equations 4 and 5) are constants at a given wavelength. Since $r$ and $t$ vary with wavelength, the quantities $a$ and $b$ are also functions of wavelength. Light passing through a leaf model is absorbed and scattered in direct proportion to a nondimensional differential distance, $d n$, traversed and in direct proportion to the amplitude of the light at that point. The quantity $n$ is the leaf area index. Absorbed radiation disappears from the model. Scattered radiation is merely changed in direction. Since the model is onedimensional, the scattering must be either forward or backward. The forward scattered component is indistinguishable from the incident light but the backward scattered compo-

[^2]nent adjoins the light moving in the opposite direction. The absorption coefficient $k$ (equation 2) and the scattering coefficient $s$ (equation 3) are associated with the leaf area index. The coefficients $s$ and $k$ correspond to fractions of light which are scattered and absorbed respectively per unit of leaf area index.

Variance analysis and Tukey's $w$ procedure (20) were used on the spectrophotometric data for the selected wavelengths at $550-$ - $650-$, $850-, 1450-$, $1650-, 1950-$, and $2200-\mathrm{nm}$ wavelengths.

## RESULTS AND DISCUSSION

Leaf Thickness and Water Content. Table II gives leaf thicknesses and water contents for 29 plant species (data unavailable for wheat). Table II is included to show the wide range of leaf thickness ( $0.140-0.978 \mathrm{~mm}$ ) and water content ( $60.1-97.0 \%$ ) values represented by the plant species. These data are used for descriptive and correlative purposes. The optical parameters (infinite reflectance $R_{\infty}$, absorption coefficient $k$, and scattering coefficient $s$ ) represent the optical differences among leaves of the plant species.

Infinite Reflectance $\boldsymbol{R}_{\infty}$. Table III contains infinite reflectances $R_{\infty}$ for 30 plant species at seven wavelengths of light. The interaction of plant species with the wavelengths was highly significant ( $p 0.01$ ). The significant variance was primarily caused by low $R_{\infty}$ values of onion, sedum, and lettuce

Table II. Leaf Thickness and Water Content of Leaves for 29 Plant Species (Data Unavailable for Wheat) Arranged in Descending Order of Magnitude

| Plant | Leaf Thickness | Plant | Water Content |
| :---: | :---: | :---: | :---: |
|  | $m m$ |  | \% |
| Onion | 0.978 | Lettuce | 97.0 |
| Sedum | 0.816 | Sedum | 94.9 |
| Lettuce | 0.720 | Begonia | 94.8 |
| Crinum | 0.665 | Onion | 93.5 |
| Rubber plant | 0.606 | Bean | 93.5 |
| Privet | 0.527 | Crinum | 90.1 |
| Begonia | 0.468 | Banana | 87.7 |
| Cantaloupe | 0.468 | Hyacinth | 86.9 |
| Oleander | 0.442 | Cantaloupe | 85.8 |
| Sunflower | 0.407 | Pepper | 85.0 |
| Hyacinth | 0.375 | Tomato | 83.4 |
| Sorghum | 0.274 | Watermelon | 82.4 |
| Eucalyptus | 0.272 | Cotton | 81.7 |
| Bean | 0.263 | Pigweed | 81.7 |
| Tomato | 0.262 | Soybean | 81.4 |
| Avocado | 0.255 | Okra | 80.6 |
| Sugarcane | 0.248 | Pumpkin | 78.0 |
| Orange | 0.245 | Sunflower | 76.9 |
| Banana | 0.241 | Rubber plant | 75.8 |
| Watermelon | 0.232 | Sorghum | 74.9 |
| Cotton | 0.209 | Corn | 74.8 |
| Pepper | 0.203 | Sugarcane | 72.4 |
| Corn | 0.200 | Rose | 70.6 |
| Okra | 0.198 | Oleander | 68.4 |
| Pigweed | 0.170 | Privet | 66.6 |
| Pumpkin | 0.157 | Peach | 65.8 |
| Peach | 0.152 | Orange | 63.7 |
| Rose | 0.150 | Avocado | 60.6 |
| Soybean | 0.140 | Eucalyptus | 60.1 |
| Mean | 0.357 |  | 79.6 |
| SD | 0.219 |  | 10.6 |

Table III. Infinite Reflectance $R_{\infty}$ of 30 Plant Species at Seven Wavelengths of Light

| Plant | Wavelength |  |  |  |  |  |  | Mean ${ }^{1}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 550 | 650 | 850 | 1450 | 1650 | 1950 | 2200 |  |
|  | $n m$ |  |  |  |  |  |  |  |
| Onion | 12.0 | 8.2 | 71.2 | 6.8 | 18.7 | 4.4 | 8.1 | 18.5 a |
| Rubber plant | 8.1 | 5.1 | 74.0 | 7.8 | 27.3 | 3.7 | 10.3 | 19.5 ab |
| Begonia | 13.2 | 6.6 | 77.3 | 6.2 | 24.2 | 3.9 | 8.6 | 20.0 ab |
| Sedum | 20.4 | 8.4 | 78.1 | 5.2 | 18.8 | 3.3 | 6.3 | 20.1 b |
| Privet | 10.3 | 5.4 | 74.0 | 9.0 | 29.2 | 4.1 | 11.2 | 20.5 bc |
| Oleander | 10.8 | 6.8 | 67.1 | 13.0 | 34.4 | 5.5 | 16.3 | 22.0 cd |
| Crinum | 15.8 | 7.2 | 74.4 | 10.0 | 30.5 | 5.3 | 13.7 | 22.4 d |
| Banana | 10.7 | 6.0 | 73.9 | 12.3 | 35.9 | 5.1 | 17.3 | 23.0 de |
| Hyacinth | 12.1 | 7.0 | 75.4 | 11.8 | 35.0 | 4.8 | 15.7 | 23.1 de |
| Tomato | 11.0 | 8.6 | 68.7 | 14.6 | 36.8 | 6.0 | 18.0 | 23.4 def |
| Eucalyptus | 12.8 | 9.2 | 71.8 | 16.6 | 35.6 | 7.0 | 16.5 | 24.2 efg |
| Sunflower | 11.1 | 8.5 | 75.2 | 14.6 | 37.0 | 6.5 | 17.0 | 24.3 efgh |
| Lettuce | 40.2 | 27.6 | 63.0 | 9.1 | 18.7 | 5.6 | 9.7 | 24.8 fgh |
| Sugarcane | 19.0 | 11.5 | 69.8 | 14.9 | 36.5 | 6.3 | 17.6 | 25.1 ghi |
| Cantaloupe | 12.8 | 9.9 | 75.5 | 15.0 | 37.7 | 6.9 | 18.4 | 25.2 ghi |
| Cotton | 12.0 | 7.7 | 75.9 | 15.9 | 39.8 | 6.0 | 19.3 | 25.2 ghi |
| Watermelon | 14.6 | 9.9 | 70.3 | 17.2 | 40.1 | 7.0 | 20.3 | 25.6 ghij |
| Avocado | 8.9 | 7.3 | 74.9 | 20.0 | 40.9 | 7.6 | 21.0 | 25.8 hij |
| Pigweed | 12.5 | 9.0 | 78.6 | 16.5 | 41.2 | 5.8 | 19.9 | 26.2 ijk |
| Okra | 13.1 | 9.2 | 74.9 | 18.9 | 42.8 | 7.0 | 22.0 | 26.8 jk |
| Pumpkin | 11.9 | 8.7 | 73.3 | 20.2 | 44.1 | 7.5 | 23.1 | 27.0 jk |
| Corn | 16.4 | 9.3 | 77.5 | 17.6 | 41.9 | 7.2 | 21.9 | 27.4 kl |
| Orange | 10.2 | 7.1 | 75.0 | 22.7 | 44.7 | 8.6 | 24.5 | 27.5 kl |
| Wheat | 13.5 | 7.7 | 75.5 | 22.6 | 45.7 | 9.0 | 26.2 | 28.61 |
| Pepper | 17.1 | 9.3 | 83.3 | 18.2 | 44.5 | 6.7 | 23.1 | 28.9 lm |
| Rose | 10.6 | 7.3 | 81.1 | 25.2 | 50.0 | 9.7 | 29.1 | 30.4 mn |
| Bean | 18.8 | 10.7 | 86.9 | 18.7 | 47.0 | 6.1 | 25.0 | 30.5 n |
| Peach | 10.9 | 8.7 | 78.4 | 26.2 | 50.4 | 10.7 | 29.0 | 30.6 n |
| Soybean | 13.5 | 7.9 | 80.3 | 24.0 | 51.0 | 8.3 | 29.5 | 30.6 n |
| Sorghum | 17.4 | 11.3 | 77.3 | 27.1 | 50.8 | 12.3 | 30.2 | 32.3 o |
| Mean | 14.1 | 8.9 | 75.1 | 15.9 | 37.7 | 6.6 | 19.0 |  |
| SD | 5.8 | 3.9 | 4.7 | 6.1 | 9.4 | 2.1 | 6.7 |  |

${ }^{1}$ Means followed by a common letter are not significantly different, $p 0.01$, according to Tukey's $w$ procedure.
at the $1650-\mathrm{nm}$ wavelength; and high $R_{\infty}$ values of lettuce at the 550 and 650 nm , of bean at the 850 nm , and of peach and sorghum at the $1950-\mathrm{nm}$ wavelengths. Lettuce was considerably different from the other species in the visible region because its leaves were pale green (low chlorophyll content) and, hence, very transparent. The application of Tukey's $w$ procedure to the means of the seven wavelengths for each species divides the 30 species into many significantly different groups with like means within each group. However, thick (Table II), complex dorsiventral (bifacial mesophyll) leaves such as those of rubber plant, begonia, sedum, and privet generally had lower $R_{\infty}$ values than thinner, less complex dorsiventral leaves (i.e., soybean, peach, bean, rose) or essentially centric (undifferentiated mesophyll) sorghum and corn leaves. Sorghum leaves had significantly higher average $R_{\infty}$ values than leaves of all other species. This indicates that sorghum leaves had a finer divided mesophyll structure than leaves of the other species that was conducive to short path lengths of light and subsequently less light absorptance (5). Coefficients for the linear correlations of $R_{\infty}$ values with $k$ values for the 30 species were $-0.654^{* *},-0.613^{* *},-0.837^{* *},-0.802^{* *},-0.899^{* *}$, $-0.819^{* *}$, and $-0.861^{* *}$ for the $550-, 650-, 850-, 1450-$, $1650-, 1950-$, and $2200-\mathrm{nm}$ wavelengths, respectively. Considering the means of all wavelengths, $R_{\infty}$ was negatively correlated with leaf thickness ( $-0.734^{* *}$ ).

Absorption Coefficient $\boldsymbol{k}$. Table IV shows the absorption coefficients $k$ for 30 plant species at the seven wavelengths of light. The interaction of plant species with wavelengths was highly significant ( $p 0.01$ ). The significant variance was pri-

Table IV. Absorption Coefficients $k$ of 30 Plant Species at Seven Wavelengths of Light

| Plant | Wavelength |  |  |  |  |  |  | Mean ${ }^{1}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 550 | 650 | 850 | 1450 | 1650 | 1950 | 2200 |  |
|  |  |  |  | $n m$ |  |  |  |  |
| Soybean | 1.408 | 2.483 | 0.023 | 0.749 | 0.179 | 1.875 | 0.500 | 1.031 a |
| Sorghum | 1.697 | 3.139 | 0.033 | 0.690 | 0.184 | 1.649 | 0.493 | 1.126 ab |
| Rose | 1.911 | 3.327 | 0.025 | 0.744 | 0.203 | 1.823 | 0.554 | 1.227 bc |
| Peach | 2.234 | 3.004 | 0.032 | 0.747 | 0.208 | 1.827 | 0.579 | 1.233 bc |
| Pumpkin | 1.863 | 2.932 | 0.046 | 0.945 | 0.260 | 2.216 | 0.694 | 1.279 bc |
| Okra | 1.746 | 2.652 | 0.044 | 1.106 | 0.313 | 2.594 | 0.810 | 1.324 cd |
| Pigweed | 1.831 | 3.025 | 0.027 | 1.034 | 0.280 | 2.392 | 0.735 | 1.332 cd |
| Cotton | 1.587 | 2.716 | 0.036 | 1.168 | 0.332 | 2.762 | 0.847 | 1.350 cde |
| Sugarcane | 1.423 | 2.553 | 0.064 | 1.286 | 0.390 | 2.862 | 0.953 | 1.362 cde |
| Pepper | 1.461 | 2.904 | 0.022 | 1.213 | 0.306 | 2.879 | 0.822 | 1.372 cde |
| Watermelon | 1.761 | 3.369 | 0.064 | 1.198 | 0.348 | 2.776 | 0.877 | 1.485 def |
| Bean | 1.497 | 2.689 | 0.014 | 1.450 | 0.334 | 3.571 | 0.943 | 1.500 def |
| Eucalyptus | 2.033 | 3.005 | 0.054 | 1.209 | 0.406 | 2.860 | 1.064 | 1.519 ef |
| Sunflower | 1.917 | 2.515 | 0.042 | 1.401 | 0.402 | 3.340 | 1.070 | 1.527 ef |
| Corn | 1.682 | 4.658 | 0.030 | 1.097 | 0.286 | 2.625 | 0.742 | 1.589 fg |
| Avocado | 2.706 | 3.657 | 0.046 | 1.058 | 0.349 | 2.434 | 0.881 | 1.590 fg |
| Cantaloupe | 1.890 | 3.076 | 0.040 | 1.463 | 0.397 | 3.424 | 1.032 | 1.617 fg |
| Lettuce | 0.317 | 0.627 | 0.076 | 2.464 | 0.811 | 5.570 | 1.713 | 1.654 fg |
| Banana | 1.701 | 4.413 | 0.039 | 1.379 | 0.366 | 3.390 | 0.911 | 1.743 gh |
| Wheat | 2.227 | 5.286 | 0.048 | 1.050 | 0.304 | 2.528 | 0.792 | 1.748 gh |
| Tomato | 2.352 | 4.241 | 0.077 | 1.561 | 0.451 | 3.666 | 1.112 | 1.923 h |
| Hyacinth | 1.978 | 4.774 | 0.047 | 1.886 | 0.499 | 4.535 | 1.289 | 2.144 i |
| Orange | 3.264 | 6.001 | 0.061 | 1.254 | 0.386 | 3.081 | 1.006 | 2.150 i |
| Begonia | 1.425 | 3.043 | 0.031 | 2.441 | 0.670 | 6.399 | 1.658 | 2.238 i |
| Onion | 1.308 | 2.311 | 0.043 | 2.870 | 0.845 | 6.328 | 1.968 | 2.239 i |
| Crinum | 2.026 | 5.795 | 0.063 | 3.290 | 0.855 | 5.809 | 2.121 | 2.851 j |
| Oleander | 3.930 | 6.028 | 0.120 | 2.425 | 0.708 | 5.216 | 1.773 | 2.886 j |
| Privet | 2.656 | 6.196 | 0.065 | 2.655 | 0.801 | 6.360 | 1.992 | 2.961 j |
| Rubber plant | 3.743 | 6.239 | 0.060 | 3.059 | 0.862 | 6.408 | 2.186 | 3.222 k |
| Sedum | 1.490 | 5.008 | 0.037 | 5.861 | 1.301 | 6.414 | 3.212 | 3.332 k |
| Mean | 1.969 | 3.722 | 0.047 | 1.691 | 0.468 | 3.654 | 1.178 |  |
| SD | 0.726 | 1.409 | 0.021 | 1.078 | 2.895 | 1.610 | 0.629 |  |

[^3]marily caused by low $k$ values of sorghum at 2200 nm and of lettuce at 550 and 650 nms ; and high $k$ values of oleander at the 550 and 850 nm , or rubber plant at 550 nm , and of sedum at 1450,1650 , and 2200 nm . Lettuce leaves were low and oleander and rubber plant leaves were high in chlorophyll content. Sorghum leaves had a finer divided mesophyll structure than the oleander, sedum, and rubber plant leaves. As indicated previously, a finely divided mesophyll structure, compared with a coarsely divided structure is conducive to short path lengths of light within the mesophyll and subsequently there is less light absorption. This is also evident when comparisons are made with Tukey's $w$ procedure (Table IV) among the means of the seven wavelengths for each species. Thick, complex dorsiventral leaves (crinum, oleander, privet, rubber plant, sedum) had significantly higher ( $p 0.01$ ) $k$ values than thinner, less complex dorsiventral leaves (i.e., soybean, rose, peach) or essentially centric sorghum, sugarcane, and corn leaves (Table II).

The absorption coefficient $k$ in the Kubelka-Munk representation (1) is a number that expresses the amount of water over the port of the spectrophotometer. If all leaves have the same water content, as is approximately true from Table II, then $k$ must correlate well with leaf thickness. A coefficient of
$0.718^{* *}$ was obtained for the correlation of absorption coefficients with leaf thicknesses.

Scattering Coefficient $\boldsymbol{s}$. Table V shows the scattering coefficient $s$ for 30 plant species at seven wavelengths of light. The interaction of plant species with wavelengths was highly significant ( $p 0.01$ ). The significant variance was primarily caused by low $s$ values of begonia at $1450-\mathrm{nm}$, of lettuce at $1650-\mathrm{nm}$, and of pigweed and soybean at $1950-\mathrm{nm}$ wavelengths; and by high $s$ values of corn at $650-\mathrm{nm}$, of orange at $1450-$, $1650-$, and $2200-\mathrm{nm}$, and of oleander at 550 - and $850-\mathrm{nm}$ wavelengths. Mean comparisons with Tukey's test show that complex dorsiventral oleander, orange, and crinum leaves had significantly higher ( $p 0.01$ ) $s$ values than less complex dorsiventral (i.e., onion, begonia, banana) or centric leaves (i.e., corn and sugarcane). Complex dorsiventral leaves have more air-cell interfaces than simpler dorsiventral leaves that are conducive to light scattering, particularly at the $850-\mathrm{nm}$ wavelength $(9,10)$. The values of $s$ were correlated with $k$ values at the $650-\mathrm{nm}$ wavelength $\left(r 0.663^{* *}\right)$ and at the $1950-\mathrm{nm}$ wavelength ( $r 0.590^{* *}$ ). The $650-$ and $1950-\mathrm{nm}$ wavelengths correspond to chlorophyll and water absorption bands, respectively. Coefficients of variation for the $650-$ and $1950-\mathrm{nm}$ wavelengths were 17.6 and $24.6 \%$, respectively. Values of $s$ were also cor-

Table V. Scattering Coefficients s of 30 Plant Species at Seven Wavelengths of Light

| Plant | Wavelength |  |  |  |  |  |  | Mean ${ }^{1}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 550 | 650 | 850 | 1450 | 1650 | 1950 | 2200 |  |
|  | $n m$ |  |  |  |  |  |  |  |
| Onion | 0.407 | 0.449 | 0.716 | 0.452 | 0.476 | 0.615 | 0.378 | 0.499 a |
| Begonia | 0.497 | 0.459 | 0.859 | 0.342 | 0.564 | 0.539 | 0.341 | 0.514 a |
| Banana | 0.456 | 0.602 | 0.830 | 0.441 | 0.636 | 0.382 | 0.460 | 0.544 ab |
| Lettuce | 0.633 | 0.586 | 0.662 | 0.535 | 0.446 | 0.703 | 0.397 | 0.566 bc |
| Pigweed | 0.598 | 0.655 | 0.866 | 0.488 | 0.664 | 0.313 | 0.456 | 0.577 bcd |
| Cotton | 0.493 | 0.491 | 0.943 | 0.523 | 0.726 | 0.374 | 0.501 | 0.579 bcd |
| Soybean | 0.508 | 0.467 | 0.894 | 0.607 | 0.739 | 0.360 | 0.597 | 0.593 cd |
| Sunflower | 0.541 | 0.511 | 0.954 | 0.561 | 0.747 | 0.501 | 0.528 | 0.620 de |
| Pumpkin | 0.573 | 0.617 | 0.922 | 0.598 | 0.732 | 0.389 | 0.541 | 0.625 de |
| Eucalyptus | 0.679 | 0.669 | 0.922 | 0.574 | 0.691 | 0.467 | 0.499 | 0.643 ef |
| Rose | 0.506 | 0.565 | 0.985 | 0.670 | 0.810 | 0.431 | 0.640 | 0.658 efg |
| Sugarcane | 0.818 | 0.749 | 0.968 | 0.528 | 0.706 | 0.408 | 0.492 | 0.667 efgh |
| Okra | 0.604 | 0.595 | 1.033 | 0.629 | 0.811 | 0.418 | 0.581 | 0.667 efgh |
| Avocado | 0.581 | 0.616 | 1.088 | 0.655 | 0.810 | 0.431 | 0.582 | 0.680 fghi |
| Cantaloupe | 0.638 | 0.750 | 0.966 | 0.608 | 0.771 | 0.546 | 0.568 | 0.692 ghij |
| Watermelon | 0.705 | 0.826 | 0.978 | 0.597 | 0.770 | 0.447 | 0.557 | 0.697 ghij |
| Hyacinth | 0.614 | 0.770 | 1.072 | 0.577 | 0.829 | 0.482 | 0.575 | 0.703 ghijk |
| Corn | 0.788 | 1.051 | 0.900 | 0.564 | 0.708 | 0.437 | 0.529 | 0.711 hijkl |
| Peach | 0.615 | 0.623 | 1.025 | 0.719 | 0.851 | 0.489 | 0.662 | 0.712 hijkl |
| Pepper | 0.719 | 0.655 | 1.099 | 0.656 | 0.881 | 0.442 | 0.642 | 0.728 ijkl |
| Tomato | 0.652 | 0.871 | 1.065 | 0.624 | 0.827 | 0.498 | 0.594 | 0.733 jklm |
| Rubber plant | 0.711 | 0.702 | 1.302 | 0.563 | 0.888 | 0.517 | 0.562 | 0.749 klmn |
| Sorghum | 0.860 | 0.898 | 0.943 | 0.699 | 0.768 | 0.523 | 0.610 | 0.757 lmn |
| Privet | 0.674 | 0.749 | 1.395 | 0.572 | 0.928 | 0.570 | 0.564 | 0.779 mn |
| Sedum | 0.958 | 0.986 | 1.254 | 0.672 | 0.739 | 0.449 | 0.458 | 0.788 n |
| Wheat | 0.800 | 0.949 | 1.166 | 0.784 | 0.943 | 0.547 | 0.757 | 0.849 o |
| Bean | 0.850 | 0.726 | 1.331 | 0.819 | 1.110 | 0.490 | 0.834 | 0.880 o |
| Crinum | 0.900 | 0.973 | 1.409 | 0.809 | 1.074 | 0.689 | 0.781 | 0.948 p |
| Orange | 0.832 | 0.982 | 1.407 | 0.956 | 1.131 | 0.640 | 0.863 | 0.973 p |
| Oleander | 1.007 | 0.938 | 1.476 | 0.824 | 1.129 | 0.645 | 0.814 | 0.976 p |
| Mean | 0.674 | 0.716 | 1.047 | 0.622 | 0.797 | 0.558 | 0.578 |  |
| SD | 0.154 | 0.176 | 0.210 | 0.128 | 0.169 | 0.098 | 0.137 |  |

Means followed by a common letter are not significantly different, $p 0.01$, according to Tukey's $w$ procedure.
related with $R_{\infty}$ at the 1450- ( $r 0.463^{* *}$ ), 1650- ( $r 0.386^{* *}$ ), and 2200- ( $r$ 0.519**) nm wavelengths. The scattering coefficient $s$ is a function of the matter associated with a single leaf. If leaves of all plant species have essentially the same internal structure, the scattering coefficient should be strongly correlated with leaf thickness. However, this was not true ( $r 0.035$ ), so it can be concluded that structure must play an important role in light scattering.

Acknouledgments-The laboratory and computer assistance of A. J. Richardson and D. E. Escobar are gratefully acknowledged.

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[^0]:    ${ }^{1}$ This study was supported in part by the National Aeronautics and Space Administration under Contract No. R-09-038-002.
    $* *$ Significance of the correlation coefficient for the 0.01 level of significance.

[^1]:    ${ }^{2}$ Abbreviations: VAI: void area index; WLI: wavelength interval; LAI: leaf area index.

[^2]:    ${ }^{3}$ Trade and company names are for the convenience of the reader and do not imply endorsement or preferential treatment by the United States Department of Agriculture.

[^3]:    ${ }^{1}$ Means followed by a common letter are not significantly different, $p 0.01$, according to Tukey's $w$ procedure.

