

Spectral Properties of Plants

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The spectral properties of plant leaves and stems have been obtained for ultraviolet, visible, and infrared frequencies. The spectral reflectance, transmittance, and absorptance for certain plants is given. The mechanism by which radiant energy interacts with a leaf is discussed, including the presence of plant pigments. Examples are given concerning the amount of absorbed solar radiation for clear sky and overcast conditions. The spectral properties of desert plants are compared with those of more mesic plants. The evolution of the spectral properties of plant leaves during the early growing season is given as well as the colorimetric behavior during the autumn.

Introduction

Plants depend upon radiant energy for the energy necessary to carry on photosynthesis and other physiological processes. The green plant has been called the converter of solar energy. In the presence of sunlight it synthesizes complex organic compounds such as sugars, fats, proteins, etc., from simple inorganic compounds such as water, carbon dioxide, minerals, salts, etc. The interaction of plants with radiant energy is of interest to the botanist, forester, geographer, biophysicist, biochemist, ecologist, hydrologist, agronomist, photogrammetrist, and others. Naturally, the perspective will be dramatically different as viewed by these various scientists. The biochemical perspective dealing with the photochemistry of plant pigments may be the most complex and has been treated extensively in the scientific literature, see French,¹ and Calvin and Andros.² The quantum chemistry of photosynthesis and the photosynthetic process will not be treated in this article. The primary purpose here is to describe the interaction of radiant energy with the plant leaf as seen from the classical optics viewpoint.

Leaf Morphology

The leaf of a plant is the primary photosynthesizing organ with photosynthesis occurring in the chloroplasts where the chlorophyll pigment is located. The cross section of a leaf is shown in Fig. 1(a), where the chloroplasts are readily seen located along the walls of the parenchyma cells comprising the mesophyll or middle

section of the leaf. The parenchyma cells are filled with cell sap and protoplasm. The cell structure of leaves is strongly variable depending upon species and environmental conditions during growth. Most leaves have a distinct layer of long palisade parenchyma cells in the upper part of the mesophyll and more irregular-shaped, loosely arranged spongy parenchyma cells in the lower part of the mesophyll. The palisade cells tend to form in the portion of the mesophyll toward the side from which the light enters the leaf. In most horizontal leaves the palisade cells will be toward the upper surface, except in leaves which grow nearly vertical in which case the palisade cells may form from both sides. In some leaves the elongated palisade cells will be entirely absent and only spongy parenchyma will exist within the mesophyll.

The cellular structure of the leaf is large compared to the wavelengths of light. Typical cell dimensions will be $15\ \mu \times 15\ \mu \times 60\ \mu$ for palisade cells and $18\ \mu \times 15\ \mu \times 20\ \mu$ for spongy parenchyma cells. The epidermal cells are of the same order of dimension as the spongy parenchyma cells, and these have a thin waxy cuticle overlay which is highly variable in thickness but often is only $3\text{-}\mu$ to $5\text{-}\mu$ thick. Clements³ has given an excellent discussion of the physical dimensions and relationships of leaf structure. The chloroplasts suspended within the cellular protoplasm are generally $5\ \mu$ to $8\ \mu$ in diameter and about $1\ \mu$ in width. As many as 50 chloroplasts may be present in each parenchyma cell. Within the chloroplast are long slender strands called grana within which the chlorophyll is located. The grana may be $0.5\ \mu$ in length and $0.05\ \mu$ in diameter. Clearly, the grana are of the dimension of the wavelength of light and may produce a considerable scattering of light entering the chloroplast. The chloroplasts are generally more abundant towards the upper side of the leaf in the palisade cells and hence account for the darker appearance of the upper leaf surface compared with the lower lighter surface.

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Leaf anatomies typically have a great deal of open structure in the form of intercellular spaces, which contain moisture-saturated air. The materials of the leaf which are important from the standpoint of light and radiation are: cellulose of the cell walls, water containing solutes (ions, small and large molecules such as protein and nucleic acid) within the cells, and intercellular air spaces and pigments within the chloroplasts. The pigments generally found in chloroplasts are chlorophyll (65%), carotenes (6%), and xanthophylls (29%), although the percentage distribution is highly variable. Chlorophyll *a* and chlorophyll *b* are most frequent in higher plants, but altogether about ten forms have been identified, each with a unique absorption spectrum. The role in photosynthesis of pigments other than chlorophyll has been questioned, but there is evidence that energy transfer can take place from accessory pigments to chlorophyll, see French and Young⁴ who have given a review of the spectra of photosynthetic pigments.

Radiant energy interacts with the leaf structure by absorption and by scattering. The energy absorbed selectively at certain wavelengths by chlorophyll will be converted into heat or fluorescence, and converted photochemically into stored energy in the form of organic compounds through photosynthesis. The absorption spectra of chlorophyll *a*, chlorophyll *b*, α -carotene, lutein (xanthophyll), and liquid water are shown in Fig. 1(b). Chlorophyll *a* is found in all photosynthesizing plants and chlorophyll *b* in most plants but not all. It should be noticed in Fig. 1(b) that the predominant pigments absorb in the same region, in the vicinity of $445\text{ m}\mu$ ($22,500\text{ cm}^{-1}$) in the blue, but only chlorophyll absorbs in the red in the vicinity of $645\text{ m}\mu$ ($15,500\text{ cm}^{-1}$). Liquid water absorbs strongly in the far infrared at wavelengths greater than $2.0\ \mu$ (5000 cm^{-1}) and only weakly at shorter wavelengths. The materials comprising leaves are moderately transparent in the green, around $540\text{ m}\mu$ ($18,500\text{ cm}^{-1}$), and highly transparent in the near infrared from $700\text{ m}\mu$ ($14,300\text{ cm}^{-1}$) to nearly $2.0\ \mu$ (5000 cm^{-1}).

Energy Environment

Plants are magnificently adapted to the radiation environment in which they live. Figure 1(c) shows the spectral distribution of the energy of sunlight, cloud light, sky light, and light transmitted through vegetation plotted as a function of wavenumber in cm^{-1} . The wavenumber is the reciprocal of the wavelength and is proportional to the frequency of the radiation. The advantage of a wavenumber plot rather than a wavelength plot is that the full frequency span of the solar radiation distribution is readily accommodated by the graph without the long wavelength tail being cut off. The infrared part of the spectrum is not given a disproportionate amount of graph. The ultraviolet portion of the spectrum is terminated by the atmospheric absorption and hence the graph need not extend indefinitely on the high-frequency end. The energy scale used in Fig. 1(c) is energy per unit area per unit

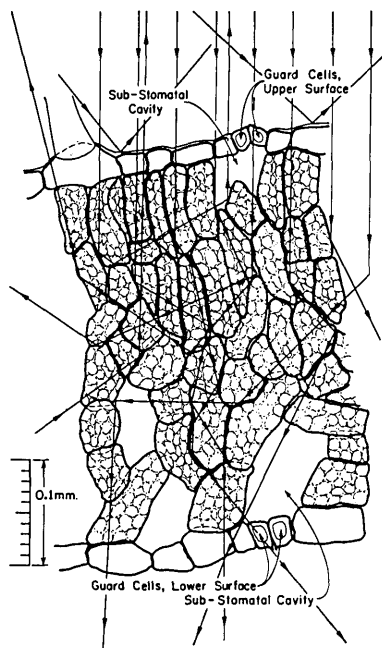
time per wavenumber increment. It will be noticed the solar energy distribution has its peak at $1.0\ \mu$ in the infrared and approximately 50% of the energy received from the sun is in the infrared beyond $0.7\ \mu$ ($14,300\text{ cm}^{-1}$).

Previous Spectral Measurements

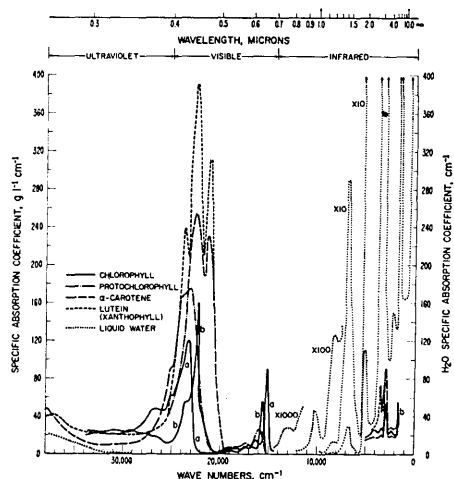
A relatively small amount of research has been done on the spectral properties of plants and most of that work has concerned itself with the visible and very near infrared portions of the spectrum. Only a few primary references will be mentioned here and these will contain extensive reference to earlier work. Rabideau *et al.*⁵ using an Ulbricht integrating sphere grating spectrophotometer reported on the absorption and reflection spectra of leaves and chloroplasts. Some of the earliest work was done by Shull⁶ and by McNicholas.⁷ Clark⁸ reviews most of the earlier work pertaining to the photographic region of the infrared. Krinov⁹ reviews a large volume of data collected by himself and the Russian workers including field data pertaining to stands of vegetation, and a more recent paper by Kleshnin and Shulgin¹⁰ is important. Interesting papers concerned with some of the ecological implications of plant reflectivity were by Billings and Morris¹¹ and by Obaton.¹² The visible spectral property of leaves was also investigated by Moss and Loomis.¹³ The infrared specular reflection spectrum from $1.5\ \mu$ to $25\ \mu$ of many plants was reported by Gates and Tantraporn.¹⁴ They showed that the far-infrared reflectance was generally less than 5% for 65° angle of incidence and less than 3% for 20° incidence angle. At far-infrared wavelengths the upper surface reflects more than the lower, old leaves more than young, and shade leaves more than sun leaves. In each instance the inverse is true in the visible and near infrared.

Recently, Kuiper¹⁵ has studied the action spectrum of stomatal movement and shown that maximum opening was caused by light of $432\text{ m}\mu$ and $675\text{ m}\mu$. Stomata remained closed for light of $525\text{ m}\mu$ to $580\text{ m}\mu$. The action spectrum showed photosynthesis within guard cell chloroplasts to be responsible for maintenance of stomatal opening. The action spectrum of stomatal movement is very similar to the action spectrum of photophosphorylation by ATP-formation within the guard cells.

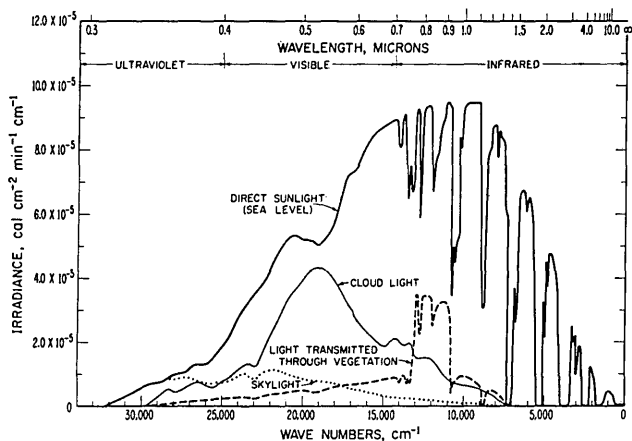
Plant pigments fluoresce, and the study of fluorescence provides valuable information concerning the process of energy transfer from one pigment to another. French¹ has reviewed the entire subject in detail. The following quote from French should serve to summarize the subject of fluorescence. "Chlorophyll and its derivatives have a brilliant red fluorescence when dissolved in organic solvents. About 25% to 30% of the incident light quanta may come out as fluorescence from chlorophyll solutions. However, in the plant, chlorophyll is only about one-tenth as efficient a fluorescing material as it is in solution. The maximum fluorescence intensity is at a slightly longer wavelength than the red peak of the absorption curve and the fluorescence intensity drops rapidly to zero on the short wavelength side of



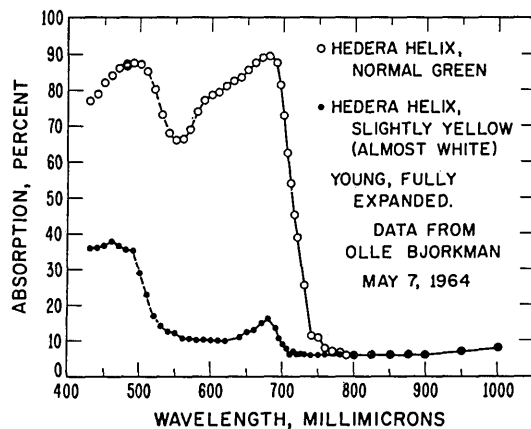
A



B



C



D

Fig. 1. (a) Cross section of a *Mimulus cardinalis* leaf showing possible paths for light rays which are critically reflected at cell walls within the leaf. The chloroplasts can be seen within the mesophyll cells. (b) Specific absorption versus frequency of the principal plant pigments and liquid water. (c) Spectral distribution of direct sunlight on a horizontal surface, cloud light, skylight, and a representative curve for light transmitted through vegetation. (d) The spectral absorption of a green *Hederia helix* leaf and of an albino leaf from the same plant. Data supplied by Olle Bjorkman, Carnegie Institution of Washington (private communication).

the peak. On the long wavelength side there is a prolonged tail extending out toward the near infrared with a secondary minor maximum at about 730 m μ . The amount of light lost to the plant by emission as fluorescence is negligible from an energy balance point of view, since it amounts at most to a few per cent."

Present Spectral Measurements

The spectral reflectance and transmittance of plants were measured with an integrating sphere attachment to the Hardy (General Electric) recording spectrophotometer, see Gibson and Keegan,¹⁶ on a Cary 14

spectrophotometer with a Cary 1411 reflectance attachment (see Keegan *et al.*¹⁷). Both instruments were carefully calibrated as to wavelength and photometric scales by means of filters and standard test surfaces (see Keegan *et al.*¹⁸). The sample was irradiated by monochromatic dispersed radiation incident at an angle of 6° in the GE spectrophotometer, and specular and diffuse reflected radiation was detected in the integrating sphere. In the Cary 14, intense, undispersed radiation was incident on the sample by diffuse reflectance from the wall of the integrating sphere. The sample was viewed at approximately 60°. The

intense radiation dried the sample, and frequent replacement of the irradiated area was necessary in order to get a valid measurement. For transmittance measurements with both instruments the incident radiation is normal to the surface. Slits of approximately 10 $m\mu$ and 20 $m\mu$ of spectral width were used with the GE over the spectral ranges 400 $m\mu$ to 750 $m\mu$ and 730 $m\mu$ to 1080 $m\mu$, respectively. Slits with the Cary 14 ranged from approximately 1 $m\mu$ at 700 $m\mu$ to approximately 9 $m\mu$ at 2.0 μ . The results of the spectral measurements are shown in Figs. 2(a)–4(a).

For transmittance measurements on the GE spectrophotometer the specimens were placed against the entrance port of the integrating sphere and illuminated with dispersed radiant energy. This arrangement allowed the measurement of the transmittance of the leaf plus all forward scattered energy. On the Cary 14 spectrophotometer, the specimen is placed at the exit port of the integrating sphere and illuminated diffusely by nondispersed radiant energy.

Absorptance, A_λ , was computed by the following expression

$$A_\lambda = 1 - (T_\lambda + R_\lambda),$$

where T_λ is the spectral transmittance and R_λ is the spectral reflectance of the specimen.

Plants absorb very efficiently throughout the ultraviolet and the visible regions of the spectrum where the energy is required for photosynthesis. However, immediately to the long wavelength side of the red chlorophyll absorption band the reflectance and transmittance of plant leaves increases dramatically, resulting in the absorptance falling to a very low value. This occurs precisely throughout the frequency range where the direct sunlight incident on plants has the bulk of its energy. If the plants absorbed this energy with the same efficiency as they do in the visible they would frequently become much too warm and the proteins would be irreversibly denatured. Gates¹⁹ has reported the temperatures of sunlit leaves frequently to be from 10°C to 20°C above air temperature; leaf temperatures often reach 50°C, which is very close to the denaturation temperature for most plant proteins. A few degrees higher will destroy the proteins. However, at wavelengths greater than 2.5 μ (4000 cm^{-1}) plants become nearly black once again absorbing the far infrared very efficiently. At the longer wavelengths there is not sufficient solar energy remaining in the spectrum to influence substantially the plant temperature. However, a good absorber is a good emitter at the same frequency. Since objects at ambient temperatures in the vicinity of 20°C radiate energy in the far infrared with a spectral distribution maximum near 10 μ , this makes plants efficient radiators of these long wavelengths and in turn permits them to cool themselves substantially by reradiation. In fact, as shown by Gates and Benedict,²⁰ of the total energy absorbed by plants approximately 75% is reradiated and 25% is dissipated by convection and transpiration. Hence, plants absorb efficiently where they require the energy, absorb poorly the near infrared to keep from becoming

overheated, and absorb the far infrared in order to be efficient radiators.

Mechanism

The light entering the leaf as shown in Fig. 1(a) has been proved by Willstätter and Stoll²¹ to be critically reflected internally at the cell walls where there is a change in the index of refraction from 1.33, for liquid water, to 1.00 for air in the intercellular spaces. This provides an efficient internal reflection at each interface. Although a ray may encounter several reflections before leaving the leaf, if there is very little absorption then most of the light will be returned.

There are two regions of the spectrum where relatively little absorption will occur as can be seen in Fig. 1(b). A region from 500 $m\mu$ (20,000 cm^{-1}) to 600 $m\mu$ (16,660 cm^{-1}) and a region from 700 $m\mu$ (14,300 cm^{-1}) to 1200 $m\mu$ (8280 cm^{-1}). At wavelengths longer than 1200 $m\mu$ or 1.2 μ water vapor absorption rises very steeply, and in the red and the blue regions of the visible spectrum pigment absorption is very strong. Because of several factors the attenuation of light in a leaf occurs throughout a much broader spectral region in the visible than would be indicated by the fairly sharp absorption bands. This is primarily due to scattering which depends upon anomalous dispersion in the vicinity of an absorption band and was shown by Latimer²² to produce a considerable broadening and distortion of the absorption spectrum of a leaf. The presence of pigments other than chlorophyll tends to broaden the domain of absorption throughout the visible region as can be seen in Fig. 1(b). Scattering is also caused by structures within the leaf which are of the dimension of a wavelength of light. Such structures may include mitochondria, ribosomes, nuclei, starch grains, and other plastids.

A lack of chlorophyll pigmentation can be shown to reduce drastically the absorption of visible light by a leaf. Figure 1(d) shows the absorption spectrum of a green leaf of *Hedera helix* and of a white leaf lacking chlorophyll taken from the same plant. The white leaf exhibits very little absorption through the green and red spectral regions and only increases in the blue due to the absorption by protochlorophyll. The carotenoid and chlorophyll pigments are partially lacking in the white leaf.

Further indication of the role of pigmentation on the spectral properties of plant tissue is shown in Fig. 2(a), which is a comparison of the reflectance and transmittance properties of a red rose petal, a magnolia petal, and a cottonwood leaf. The pigmentation of the red rose is caused by carotene and shows up as strong absorption in the green. The red rose is not a pure red since a small blue component shows up in the reflectance and transmittance curves. The spectral reflectance for red felt is very similar to that of the red rose except it lacks the blue component (see Evans²³). The magnolia blossom is lacking most pigments and absorbs only at the blue end of the visible spectrum and appears white in color.

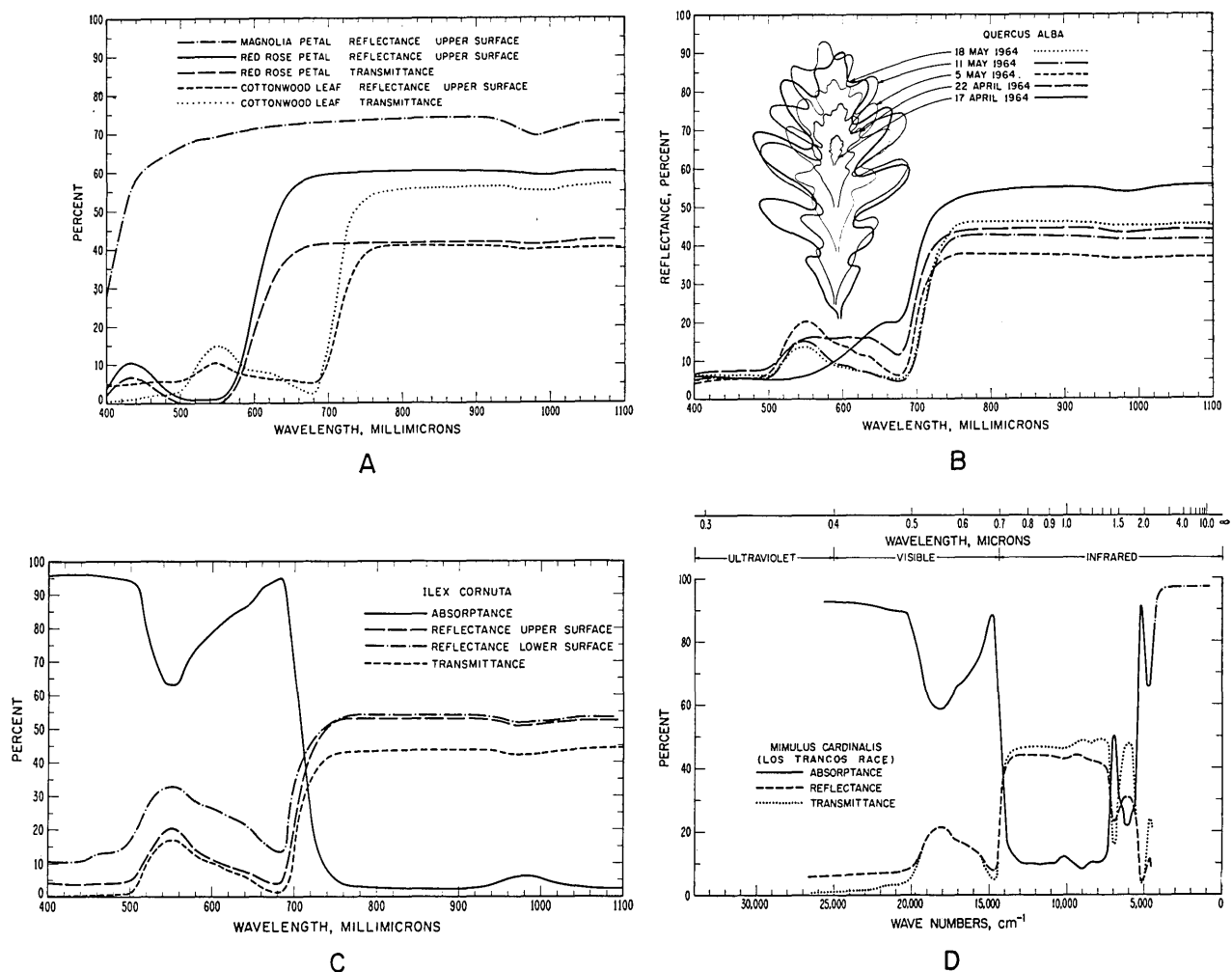


Fig. 2. (a) Spectral reflectance and transmittance as a function of the wavelength of a red rose petal and a cottonwood leaf, and spectral reflectance of a magnolia petal to show the influence of pigmentation of the spectral properties of the plant. (b) Evolution of the spectral reflectance of a leaf during the growing season for the dates shown. The corresponding leaf expansion can be seen by the leaf outlines shown. Changes in leaf pigmentation are evident from the curves. (c) The spectral reflectance, transmittance, and absorptance of leaves of *Ilex cornuta* which appear very shiny when illuminated with visible light. (d) The spectral reflectance, transmittance, and absorptance of leaves of *Mimulus cardinalis* (Los Trancos) race. These leaves are thin and light green in color.

The evolution of the spectral properties of a leaf during the growing season is shown in Fig. 2(b) for *Quercus alba*. Several features seen in Fig. 2(b) are interesting. Initially the reflectance of the small young leaf on 17 April 1964 exhibited primarily protochlorophyll and very little chlorophyll absorption. Comparison with Fig. 1(b) will show there to be a displacement of the red protochlorophyll band towards shorter wavelengths from the red chlorophyll band. This same shift is evident in Fig. 2(b) as the young leaf develops chlorophyll, comparing the red absorption on 17 April 1964 with that on 22 April 1964. The growth of the chlorophyll pigmentation shows up as a deepening of the absorption band at 680 $m\mu$ and at first an increase in the green reflectance at 550 $m\mu$ and a decrease in the infrared reflectance beyond 740 $m\mu$. Then after 5 May 1964 the green pigmentation darkened, the reflectance at 550 $m\mu$ diminished, and the reflectance at

infrared wavelengths increased. It should be noted that the absorption edge of the reflectance curves at 700 $m\mu$ shifted progressively and systematically toward longer wavelengths. The position of this edge may be a good measure of the amount of chlorophyll within the leaf. As the chlorophyll content reaches its maximum value the strong chlorophyll absorption bands in the blue and the red begin to absorb in the green, and the reflectance of the mature, dark leaf is reduced at 550 $m\mu$. Smith and Young²⁴ review the knowledge concerning chlorophyll development in etiolated leaves. Experiments show that the rate of conversion of protochlorophyll to chlorophyll is an extremely rapid process but that the subsequent accumulation of chlorophyll is a very slow process. The initial chlorophyll formed acts as an autocatalyst and then the process slows down to reach a steady state. The rate of formation of chlorophyll

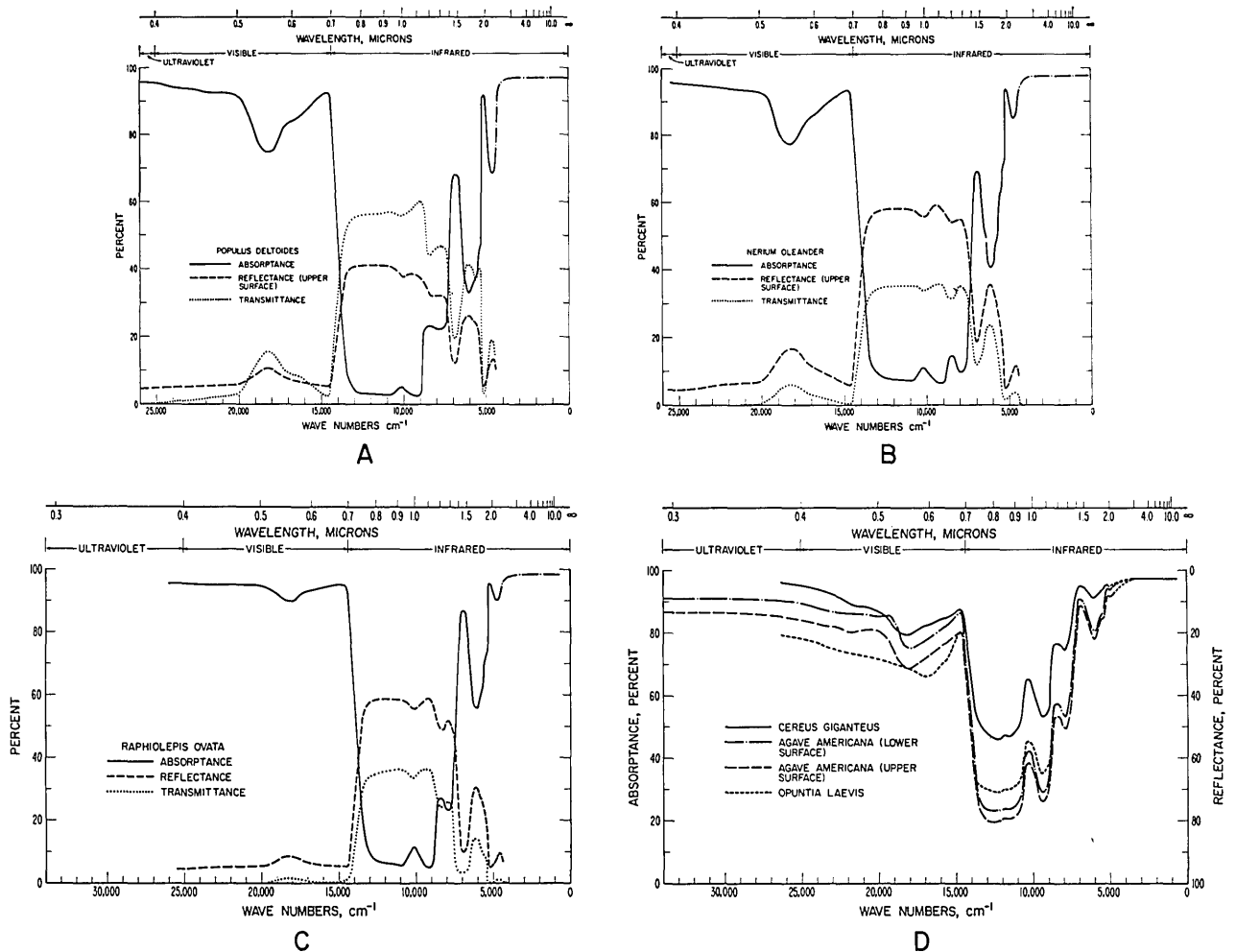


Fig. 3. (a) The spectral reflectance, transmittance, and absorbance of leaves of *Populus deltoides*, a moderately thin, light colored leaf. (b) The spectral reflectance, transmittance, and absorbance of leaves of *Nerium oleander*, a thick green leaf. (c) The spectral reflectance, transmittance, and absorbance of leaves of *Raphiolepis ovata*, a thick dark green leaf. (d) The spectral absorbance and reflectance of the stems of desert succulent plants. The transmittance is zero.

is directly proportional to the light intensity. Chlorophyll production is also temperature dependent and the optimum temperature is somewhat dependent on time.

The near-infrared reflectance behavior of the maturing leaf is less easy to understand. It is probable that the near-infrared reflectance is a function of the cell shape and size as well as the amount of intercellular space. Initially the mesophyll of the very young leaf consists primarily of spongy parenchyma with considerable air spaces which are favorable to the mechanism of internal reflection. Then as the leaf matures the cells enlarge, crowding together, and reducing the intercellular space and reducing the reflectance. It would then appear that during the final maturing the cell structure and intercellular space relationship becomes favorable for increased reflectance. In order to establish this relationship careful experiments will need to be done relating the reflectance to the leaf morphology.

Ilex cornuta, Chinese holly, possesses leaves which are very shiny, highly reflecting. The reflectance, transmittance, and absorbance curves for this plant are

shown in Fig. 2(c). As with most leaves the lower surface or dorsal reflects more than the upper surface or ventral. However, the distinction is only notable at visible wavelengths, and in the near infrared the reflectance is approximately equal for the two surfaces. This may be caused by the pigment containing chloroplasts being located more densely toward the upper part of the mesophyll and producing greater absorbance to the light entering the ventral side, or it may be caused by a more waxy cuticle on the upper surface. The distribution of the chloroplasts is probably the more likely explanation.

Concerning the mechanism of reflectance of light within a leaf there is no doubt that some scattering or diffraction takes place by the interaction of the light with structures whose dimensions are comparable with the wavelength. The cell dimensions are generally too large, but the chloroplast and grana dimensions are such as to create some scattering. Whatever scattering does exist, it is evident from the spectral reflectance and transmittance curves that the scattering phe-

nomena is not strongly wavelength dependent. Whatever scattering does exist is probably more of the Mie type than the Rayleigh type.

Spectral Properties

Figures 2(d)–3(c) show the reflectance, transmittance, and absorptance of plants whose leaves are progressively darker and thicker. The visible absorptance substantially increases from the lighter to the darker leaves and the near infrared absorptance is the highest for the thinner leaf. The most striking feature in the near infrared is the fact that the transmittance of the thinner leaves is greater than the reflectance, but for the thicker leaves the reflectance drastically increases, more than compensating for the drop in transmittance and keeping the absorptance low in the near infrared. Figures 2(d)–3(c) certainly demonstrate that, although qualitatively all green leaves have similar spectral characteristics, quantitatively they differ considerably and from the heat transfer standpoint the differences are significant. The water absorption bands in the far infrared are clearly recognized in each of the curves.

Desert Plants

A great deal of speculation has always ensued concerning the spectral properties of desert plants and their adaptation to intense heat and light. Figures 3(d) and 4(a) show the spectral absorptance and reflectance of some desert plants which are succulents. Most of these plants consist of enlarged fleshy stems and do not exhibit leaves in the usual popular conception of a leaf. The fleshy stems are green and do contain chlorophyll within chloroplasts. The transmittance of the fleshy stems is zero and hence these plants have only one mechanism for controlling their degree of coupling to the radiation environment, that is, by means of reflectance. It is clear from Figs. 3(d) and 4(a) that these desert plants reflect substantially more radiation at all wavelengths than do the more mesophytic types considered earlier.

Reference to Table I shows the mean absorptance of the desert plants to solar radiation to be greater than the thin-leaved mesophytic type plants, but not substantially different than the thicker darker leaves of *Nerium* and *Raphiolepis*, both being plants from fairly xeric environments.

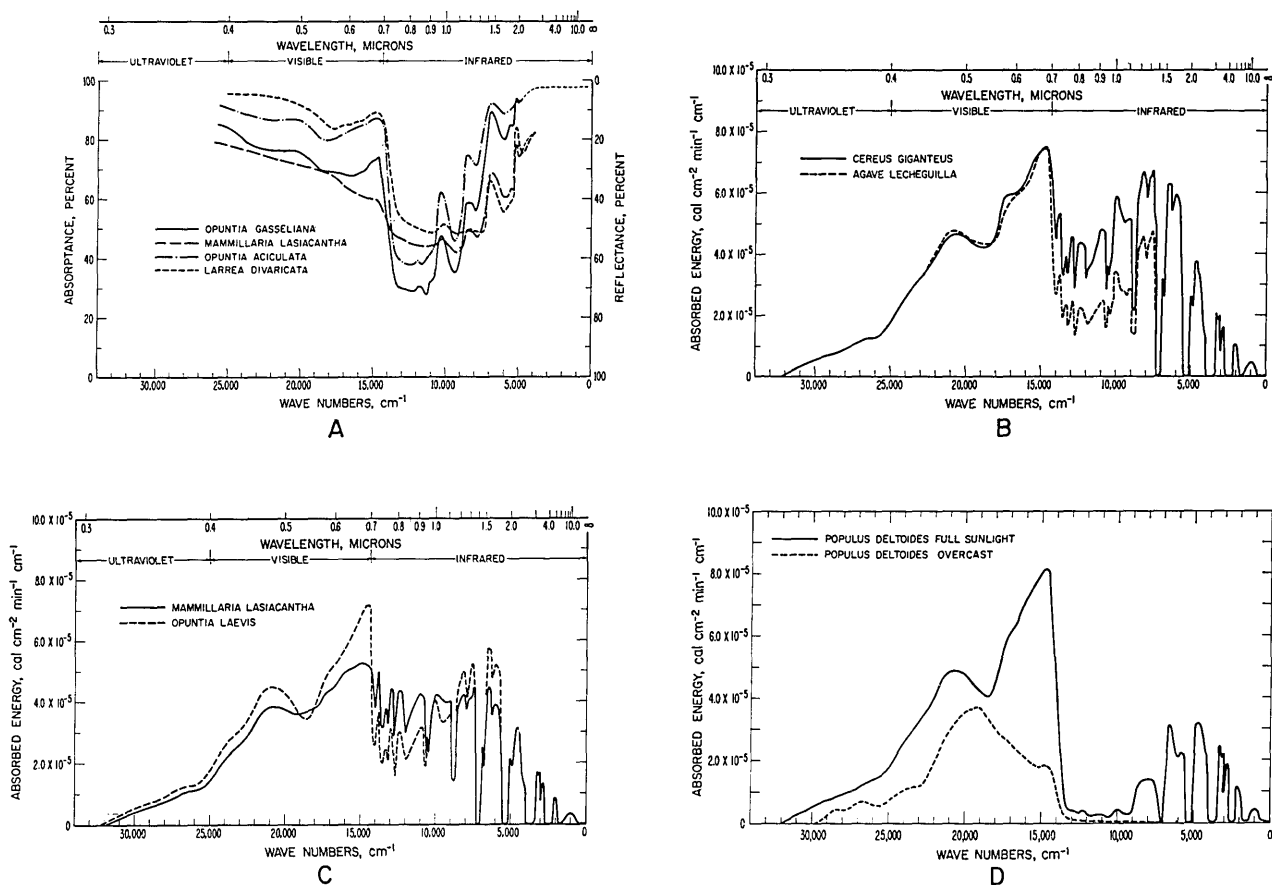
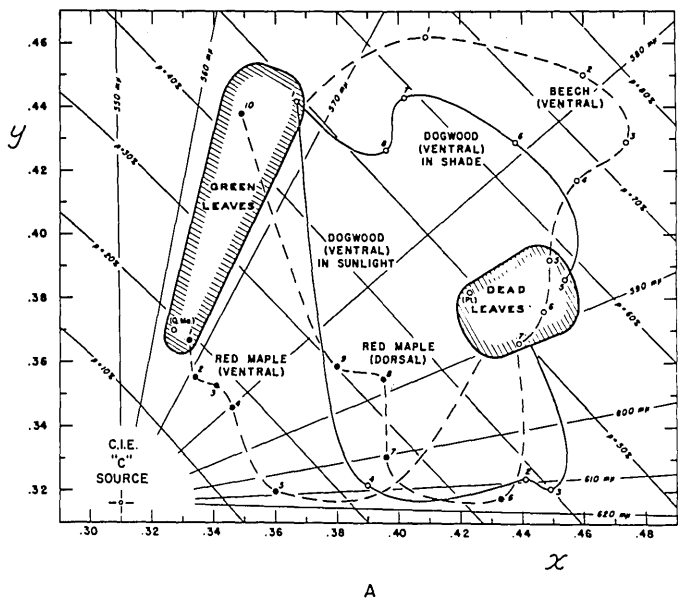
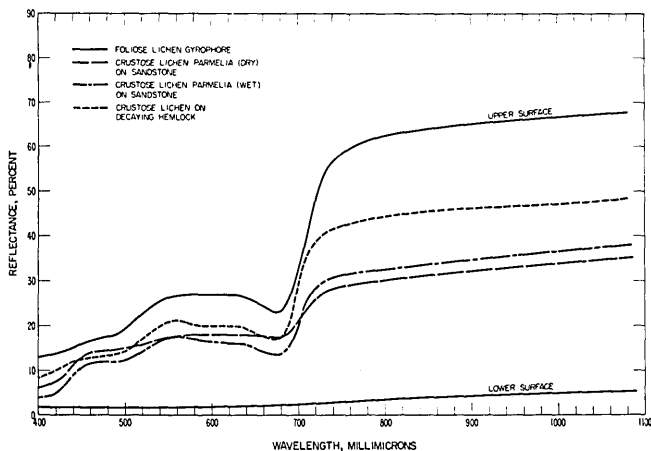


Fig. 4. (a) The spectral absorptance and reflectance of the stems and leaves of desert plants. *Opuntia* is the prickly pear cactus without an abundance of thorns. The *Mammillaria* is a cushion cactus completely covered with a dense layer of thorns. The *Larrea* is the creosote bush with small dark opaque leaves. The transmittance of all plants is zero. (b) The spectral distribution of absorbed incident solar radiation by two desert species of plants. (c) The spectral distribution of absorbed incident solar radiation by two desert species of plants. The *Opuntia laevis* has very few thorns and the *Mammillaria lasiocantha* has a dense covering of thorns. (d) The spectral distribution of absorbed incident solar radiation by *Populus deltoides* (cottonwood) for clear sky and overcast sky.



A



B

Fig. 5. (a) Chromaticity diagram of the International Commission on Illumination (CIE) for the colors of autumn leaves for CIE Source C (representative of average daylight). (b) The spectral reflectance of selected lichens as a function of the wavelength. Each specimen was in its normally dry state as collected in the field. The change in the spectral reflectance of the lichen when soaked in water is shown for one example.

Considerable speculation has existed concerning the role thorns may play in the heat balance of a desert plant. In order to ascertain if there might be a possible effect, a cactus possessing a dense covering of fine thorns was selected, namely *Mammillaria lasiacantha*. The over-all effect was to reduce the absorptance throughout the visible, increase it slightly in the near infrared, and substantially reduce it in the far infrared. However, the advantage gained is small and the loss in long wave emittance is serious, rendering the plant hotter than a thornless variety under the same conditions of light and radiation. It can be stated from the heat transfer standpoint that a dense covering of thorns offers no strong advantage over the thornless or sparsely thorned varieties of desert plants. It is possible that thorns

extending out a considerable distance from the surface and casting a shadow on the surface, as do the large thorns of *Cereus giganteus*, reduce slightly the heat load without obstructing the flow of air.

Reflectance measurements were made of the cuticle stripped from the *Agave americana* plant. The reflectance was nearly neutral with wavelength values of about 30% throughout the visible and falling to 22% at 2.1μ . At wavelengths less than $500 m\mu$ the cuticle reflectance drops off steeply. The water bands were extremely weak in the cuticle reflectance and transmittance curves.

Coniferous Plants

The reflectance curves for *Pinus strobus* needles and *Thuja occidentalis* awns were obtained by forming mosaic samples. It was necessary, in working with the pine needles, to place two layers of needles running at right angles and illuminate them with the slit image at 45° to either line of needles in order to reduce polarization effects on the GE spectrophotometer. The reflectance values for these two coniferous species are very similar to one another. These coniferous plants have higher absorptances throughout the visible and near-infrared spectrum than any other plants measured, including all of the desert species. At visible wavelengths they had absorptances as high as 97.4% and in the infrared as high as 57.8%. As seen from Table I their mean absorptance is strikingly higher than any of the other plants. This is based on the assumption that needles do not transmit radiation, a measurement which is very difficult to obtain. This high absorptance

Table I. Absorbed Energy and Mean Absorptance Values for Various Plants Exposed to Incident Solar Energy of $1.20 \text{ cal cm}^{-2} \text{ min}^{-1}$ and to Cloudy Day Sunlight of $0.38 \text{ cal cm}^{-2} \text{ min}^{-1}$ with the Spectral Distributions Shown in Fig. 1(c)

Plant	Sunny		Cloudy	
	Energy abs. ($\text{cal cm}^{-2} \text{ min}^{-1}$)	Mean abs.	Energy abs. ($\text{cal cm}^{-2} \text{ min}^{-1}$)	Mean abs.
<i>Populus deltoides</i>	0.72	0.60	0.26	0.70
<i>Mimulus cardinalis</i> (Los Trancos)	0.68	0.57	0.25	0.66
<i>Mimulus cardinalis</i> (Priest's Grade)	0.62	0.51	0.22	0.57
<i>Nerium oleander</i>	0.76	0.64	0.28	0.74
<i>Raphiolepis ovata</i>	0.81	0.68	0.30	0.79
<i>Cereus giganteus</i>	0.88	0.74	0.28	0.75
<i>Agave americana</i>	0.88	0.73	0.27	0.72
<i>Agave lecheguilla</i>	0.76	0.63	0.28	0.74
<i>Opuntia gasseliana</i>	0.84	0.70	0.25	0.67
<i>Opuntia laevis</i>	0.74	0.62	0.26	0.69
<i>Opuntia aciculata</i>	0.98	0.82	0.29	0.76
<i>Mammillaria lasiacantha</i>	0.71	0.59	0.25	0.66
<i>Larrea divaricata</i>	1.00	0.83	0.30	0.81
<i>Ilex cornuta</i>	0.69	0.57	0.26	0.69
<i>Agropyron repens</i>	0.72	0.60	0.28	0.73
Bamboo	0.72	0.60	0.27	0.72
<i>Thuja occidentalis</i>	1.06	0.88	0.33	0.88
<i>Pinus strobus</i>	1.07	0.89	0.33	0.88

does not imply that coniferous plants become substantially warmer than deciduous and succulent types under the same conditions. A single pine needle is tightly coupled to the air temperature through a large convection coefficient. However, a cluster of pine needles on a branch is much less tightly coupled to the air temperature than is a single needle. The cylindrical geometry of a needle changes the angle of incidence with the surface so that the effective absorbing area for sunlight is reduced. The detailed heat transfer for a pine branch has been discussed by Gates *et al.*²⁵

Lichens

The spectral reflectances of selected lichens are shown in Fig. 5(b). Within the wavelength region for which the measurements were made, there would appear to be no prominent features of the spectral reflectance of lichens distinguishing them from higher plants. One possible exception is the absence with the lichens of a strong green peak of spectral reflectance around $550\text{ m}\mu$ which occurs for the higher plants.

Each lichen spectrum was of the natural dry lichen in the condition as collected in the field. The lichen was then soaked in water and a comparison reflectance spectrum was obtained. Such a comparison is shown for the crustose lichen *Parmelia* on sandstone in Fig. 5(b). The absorption of water reduced the reflectance in the visible and increased the reflectance in the near infrared.

Absorbed Energy

The amount of solar radiation absorbed by a leaf or a plant depends not only on the intensity and the spectral distribution of the energy but also on the angle of incidence on the plant surface. This requires knowledge concerning the angular dependence of the specular component of the reflectance. This information is not readily available. Providing the angle of incidence is not extremely large the reflectance values obtained here should be reasonably useful. In Fig. 1(c) a fairly typical solar curve for sea level is shown. This could be taken as the direct sunlight incident normally to a leaf surface and has a total integrated value of $1.20\text{ cal cm}^{-2}\text{ min}^{-1}$. Figures 4(b)–4(d) show the product of the solar energy spectral values with the spectral absorptances to give the distribution of the energy absorbed by the plant.

The mean value of the absorptance is the radiation absorbed by the plant divided by the total incident radiation. Table I gives these values for some of the plants studied here for the solar curve and the cloudy day curve of Fig. 1(c). The mean value of the absorptance will change with the spectral distribution of the incident radiation. The mean absorptance of a plant can be described as the degree of coupling between the plant and the radiation of the environment. Because of the relatively high absorptance values in the visible the plant is tightly coupled to radiation of visible wavelengths. The plant is strongly decoupled from the near-infrared radiation and very tightly coupled to the far infrared.

The total radiant energy absorbed by a plant in a given environment is important to the plant from the heat transfer and plant temperature standpoint. The temperature of the various parts of a plant determines the rate at which certain physiological processes are carried on within the plant, other factors being equal. Many physiological processes become very critical as high leaf temperatures, 40°C to 50°C , are approached. Gates¹⁹ has discussed the heat transfer process in detail. In addition, the quantum processes of photosynthesis are involved with the selective absorption of visible wavelengths. This complex interaction with the ever-changing radiation environment requires that the spectral absorptance, the coupling factor, be known in detail for each species of plant if the interaction of the plant with the environment is to be understood.

Colorimetric Properties

The colorimetric properties of plant leaves have been studied extensively by H. J. Keegan and associates of the National Bureau of Standards (private communication) (see references under Keegan¹⁸). This work includes the spectral directional reflectance measurements of leaves from many different deciduous trees or shrubs in the eastern part of the United States. Leaves were selected for various stages of color change. Chromaticity coordinates were determined in each case.

A particularly interesting set of data was obtained concerning the color changes of autumn leaves. These are illustrated in Fig. 5(a) which shows the complete gamut of colors from the green leaf in transition to the brown, dead leaf. Each series of leaf colors was obtained from leaves on the same branch which were removed from the tree at a time when nearly the complete gamut of colors was represented. The families of spectrophotometric curves indicate pigment changes of three types: (1) disappearance of green pigment (chlorophyll) followed by development of a temporary red pigment, followed by development of a permanent brown, (2) disappearance of green pigment followed by development of permanent brown, and (3) disappearance of green pigment and simultaneous development of red pigment giving an isosbestic point. The associated color sequences are: (1) green, yellow, red, brown; (2) green, yellow (or yellowish green), brown; and (3) green, olive, red.

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overleaf

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