SPECTRAL ENERGY RELATIONS OF ISOBILATERAL LEAVES

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Summary

Reflectance and transmittance have been studied for eucalypts in the spectral range from 4000 to 9500 Å at varying angles of incidence. Spectral reflectance and spectral transmittance were observed to be high in the infrared. All leaf surfaces were found to be highly diffusing and not to reflect white light in accordance with the sine law.

Transmittance of light in the visible spectrum through a single leaf was observed to be insignificant, and reflectivity in the infrared increased but slightly with mats in excess of four leaves. From the spectral data, absorptance values were calculated for single leaves of each species.

I. Introduction

The primary objective of the overall study was directed towards providing a fundamental understanding of some aspects of interpretation of aerial photographs of the eucalypt environment, particularly the reflection of light by vegetation. To the photo-interpreter the eucalypt environment presents its own distinct and challenging problems. It may be sufficient to say that up to the present time most research relating to photo-interpretation has been confined to the temperate deciduous and coniferous forests of the Northern Hemisphere (e.g. Backstrom and Wellander 1953; Olson 1964) and the amount of fundamental research directed towards the environment of the indigenous, evergreen, broad-leaved species of both the Southern Hemisphere and the tropics has been negligible.

In this paper, the optical and spectral properties of the leaves of four eucalypt species from the wet sclerophyllous forest near Mount Disappointment, south-central Victoria, will be considered, not from the aspect of interpretation of aerial photographs, but as being important in the study of the energy relations of plants. Unless otherwise stated, the examination and discussion refers to sun leaves which have recently attained maturity in size. It is intended to publish later details of the reflectance and reflectivity of a further 41 species, including 6 species from Western Australia (e.g. *E. marginata*, *E. diversicolor*), 10 from New South Wales (e.g. *E. crebra*, *E. melanophloia*), 6 from the Northern Territory (e.g. *E. tetradonta*), and 4 from South Australia (e.g. *E. dumosa*).

The reflective properties of the leaves of the four species have been examined in that part of the solar spectrum in which it is normal practice to take aerial photographs, i.e. from c. 4500 to 9500 Å. As light-scattering in the atmosphere increases

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rapidly towards the blue end of the visible spectrum in accordance with Rayleigh's law, the shorter wavelengths are excluded for aerial photography by using a minus-blue filter (e.g. Wratten 12). However, in the present paper, the lower limit of measurement has been extended to 4000 Å to include the peaks of chlorophyll a and chlorophyll b absorption of higher plants in the blue band of the solar spectrum. This band and the chlorophyll a and chlorophyll b absorption bands between 6100 and 7000 Å have conspicuous influences on the reflectance curves in the visible spectrum (i.e. 4000 to approx. 7200 Å). The spectral range between 4000 and 9500 Å covers about 65% of the solar flux at sea level.

II. Material and Methods

(a) Plant Materials

The four species studied in relation to their spectral and optical properties were *Eucalyptus goniocalyx* F. Muell. (mountain grey gum), *E. obliqua* L'Hérit. (messmate), *E. radiata* Sieb. (narrow-leaved peppermint), and *E. regnans* F. Muell. (mountain ash). The first species belongs to the section Macrantherae and the remainder to the Renantherae. Blakely's classification (1955) has been followed.

When collecting in the field, two samples were obtained from two pole-size or sawlog-size trees of each species, and represented twigs and leaves considered to be visible to an observer in an aircraft. The samples were stored in sealed polythene bags overnight at 34–38°F. Storage under these conditions was satisfactory for at least 14 days; but dehydration could be rapid and affect the reflectance, particularly in the infrared, if precautions were not taken. For example, a detached seedling leaf of *E. regnans* held at room temperature (70°F) for 25 min wilted and the reflectance in the infrared increased by approximately 4%.

(b) Methods

The majority of the recordings of reflectance, reflectivity, transmittance, and transmissivity were made with a Beckman DK-2 spectrophotometer, which had a monochromatic reflectance attachment. For each species, measurements were taken according to elevation, site, tree age, leaf ontogeny, and locum on the leaf. Additional studies of the reflection and transmission at various angles were recorded in a Dunkle–Gier spectrophotometer, because readings in a Beckman spectrophotometer can only be made with the light normal (0°) to the leaf surface or at 5° to the normal. Recordings of the same sample at the two angles in the Beckman provide measurements of the total reflectance and diffuse reflectance; and their difference represents a specular component.

An essential part of both the Beckman and Dunkle–Gier spectrophotometers is a magnesium oxide coated integrating sphere (Ulbricht sphere). In the Dunkle–Gier spectrophotometer, the magnesium oxide coating must be 2 mm thick for satisfactory working in the infrared spectrum beyond 20,000 Å (Dunkle, personal communication 1965). Spectral reflection and transmission is recorded on either a photo-multiplier cell or a lead sulphide detector at the side of the sphere. In the Dunkle–Gier spectrophotometer, the sample is mounted on a rod within the sphere, whilst the sample is
placed on the external periphery of the Beckman integrating sphere. Both instruments were calibrated against magnesium oxide, and the reflection and transmission of light by leaf samples were expressed as a percentage of light reflected from fully illuminated magnesium oxide.

Magnesium oxide is to be preferred to other surfaces as a standard reference, since it has been most widely used internationally in similar work and thereby provides a means for direct comparison of graphs of other workers. Also magnesium oxide has the highest reflectivity of several surfaces examined. A Watson No. 1 filter paper also provides uniform spectral reflectance, but the reflectivity is about 10% less than magnesium oxide.

**Table 1**

SPECTRAL REFLECTANCES OF LEAVES OF FOUR EUCALYPT SPECIES

Values given are means for six leaves and their standard deviations, and are expressed as a percentage of the reflection of a magnesium oxide surface at each wavelength

<table>
<thead>
<tr>
<th>Species</th>
<th>Wavelengths (Å):</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>4500*</td>
</tr>
<tr>
<td><strong>E. regnans</strong></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>4.2</td>
</tr>
<tr>
<td>S.D.</td>
<td>0.32</td>
</tr>
<tr>
<td><strong>E. radiata</strong></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>4.5</td>
</tr>
<tr>
<td>S.D.</td>
<td>0.49</td>
</tr>
<tr>
<td><strong>E. obliqua</strong></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>3.0</td>
</tr>
<tr>
<td>S.D.</td>
<td>0.45</td>
</tr>
<tr>
<td><strong>E. goniocalyx</strong></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>3.4</td>
</tr>
<tr>
<td>S.D.</td>
<td>0.2</td>
</tr>
</tbody>
</table>

* Visible spectrum.  † Infrared.

All samples were backed with black matt paper of predetermined low reflectivity. This precaution was taken because the black matt painted platten of the Beckman sample holder had a high spectral reflectance in the infrared (40–60%). Curves for a single leaf, with and without black matt paper, differed markedly from each other in the infrared, but were similar in the visible spectrum.

A Gossens Lunasix light-meter was used to measure quantitatively the direction of white light reflected from leaves of each species. The light-meter was mounted on a metal arm, which could be rotated in a semicircle about the incident light on the leaf. The leaf, mounted against black matt paper, was also rotated at varying angles to the normal of the incident light. The light source comprised a 500-W bulb of a 35-mm projector behind an aperture of 1.5 mm diameter. Between the source and the leaf, a suitable collimating lens was interposed to provide parallel light rays. This part of the study is now being repeated and extended with more sophisticated equipment.
III. RESULTS

For 22 mesophytic eucalypt species from eastern, western, and northern Australia, the characteristic shapes of the reflectance curves were remarkably similar and in accordance with observations reported by other workers for other families, genera, and species (e.g. Billings and Morris 1951; Moss and Loomis 1952; Spurr 1960; Gates 1962; Olson 1964). Reflectance in the visible spectrum was found to be highest in the youngest anthocyanin-pigmented leaves (13–20% at 5350 Å), and to increase with leaf age in the infrared spectrum. Anthocyanin-pigmented leaves were associated with high reflectance in the orange and red bands of the visible spectrum (cf. Pokrowski 1925; Shull 1929). Particularly in young leaves, the reflectance could be reduced by removing the wax, but in old leaves the differences were small (e.g. 1–2%).

![Graph of spectral reflectance curves for different number of leaves](image)

Fig. 1.—Spectral reflectance curves for a single leaf and mats of two, three, and four leaves of *E. regnans*. Reflectances are expressed as a percentage of the reflected energy per unit area of leaf compared with the reflected energy per unit area of a magnesium oxide surface.

Spectral data relating to the reflectance of the four species are summarized in Table I and the characteristic curves for an individual leaf of *E. regnans* and for mats of two to four leaves are shown in Figure 1. In the visible spectrum (Fig. 1) there is a minimum reflectance and reflectivity in the vicinity of chlorophyll absorption in the blue and red bands and a peak in between at c. 5350 Å. Chlorophyll extracts in 80% acetone provided maxima transmittances for each species at c. 4250 and 6550 Å.

In the infrared, there is a rapid rise to 50% in the reflectance of intact leaves at about 7500 Å, and this is followed by a plateau which continues until 9500 Å. Usually there is a slight depression of the curve at 9500 Å resulting from the presence of a hydroxyl-absorbing band. Beyond 9500 Å, the plateau continues until about 12,500 Å, when the reflectance commences to fall off. Eventually at about 25,000 Å, the leaf is behaving virtually as a black body. Experiments indicated that 10–18% of normally incident white light between 4000 and 7200 Å is reflected.

Reflectance curves were also recorded for mats of four to eight leaves. It was observed that in the infrared the reflectance increased considerably up to four leaves...
and above this number the reflectance usually depended more on the reflective properties of the top leaf than on an increase in the number of leaves in the mat. For example, for *E. goniopteryx* at 8500 Å, the percentage reflectances were 51, 68, 75, 79, and 80 for one, two, three, four, and five leaves, respectively, and 81 for a mat of eight leaves. By changing the top leaf of a mat of four leaves, the range in reflectivity varied between 78 and 80%, and was found to vary between 79 and 81% for a mat of eight leaves.

Comparable studies were carried out relating to the transmission of light through the leaf, and as would be expected in accordance with photometrical principles the characteristic shape of the transmittance curve resembles the reflectance curve for a leaf of the same species. Transmittance curves for one, two, three, and four leaves of *E. regnans* are given in Figure 2. Experimental results showed that 2–3% of normally incident white light was transmitted between 4000 and 7000 Å. Transmittance for a single leaf was minimal at 4250 Å and at 6550 Å was 1.2% (Fig. 2).

A peak occurred at 5350 Å (5.8% transmittance) and at 9000 Å 41% transmittance was attained. For a mat of two leaves only 1% transmittance occurred at 5350 Å and reached only 9% in the infrared for a mat of four leaves. The fall off in transmittance with increasing thickness is in accordance with Lambert’s law. Similar curves were obtained for the other three species.

The Dunkle–Gier spectrophotometer was used to check the Beckman readings and to extend the angles of incident energy for reflectance to 60° and transmittance readings to 40°, which were about the maximum angles that could be recorded accurately. At 30° incidence in the visible spectrum transmittance was observed to decrease by only about 1% but in the infrared the transmittance had decreased by up to 5%. Spectral reflectance curves for 0, 30, 45, and 60° incidence for single leaves of *E. regnans* are shown in Figure 3. The curves were similar for the other three species. Up to 30° incident light, irrespective of the quality of light in the visible spectrum,
the reflectance was approximately the same and the difference was only 1–2% in the infrared. No differences were detected for angles of incidence of 5 and 15°. The dotted line in Figure 3 provides the cosine corrected curve for incident energy of 60°, and illustrates the fall off in energy per unit area of leaf which occurs with increasing angles of incident solar radiation. In the spectrophotometer, the fall off in the intensity of the incident energy per unit area of the leaf is compensated for by increasing the area of the reflective surface.

As mentioned in Section II(b), a Lunasix light-meter was used to determine quantitatively the direction of reflected white light from leaves of each species. Readings of brightness were taken at 5, 15, 30, 45, 60, and 75° to the normal subtended by the leaf and with the incident light at angles of 0, 30, 60, 70, and 75°. The meter readings indicated that the incident light at 0° is scattered in all directions, as indicated schematically in Figure 4(b); and that a specular component (in accordance with the sine law for mirror surfaces) was not conspicuous until an angle of about 60° was attained [Fig. 4(d)]. Between 30 and 60°, spread reflection becomes conspicuous [Fig. 4(c)]. Specular reflection is illustrated diagrammatically in Figure 4(a).

**IV. DISCUSSION**

Several interesting conclusions were formulated from the experimental results relating to the characteristics of reflectance, transmittance, and absorptance. Of considerable interest is the diffused pattern of reflected light by the leaf, as given above. It was thought initially that a strong specular component would exist at acute angles of incidence, since in published diagrams of light incident on leaves, the light is usually shown as being reflected specularly [Fig. 4(a)] in accordance with the sine law (cf. Bomberger and Dill 1960; Kriedeman, Neales, and Ashton 1964). When on a macroscopic scale there is no mirror-like reflection from a reflecting surface, then the reflection is said to be diffused (International Commission on Illumination 1957).
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It will be observed from Figure 4(b) that the arrows representing the intensity of the reflected light provide an elongated envelope rather than a true hemisphere in accordance with Lambert's cosine law. Any unit area on the periphery of the envelope is assumed to contain the same light energy as a similar area on a hemisphere. In the same diagram, a hemisphere is represented by the solid line.

The divergence of the reflection pattern of normally incident light on a leaf does not appear to exceed too greatly the diffusing pattern of well-known matt surfaces. Bouguer in 1760 suggested matt surfaces to be made of innumerable elementary surfaces, each acting as a mirror, and the theory as developed by Berry (see Wood 1934), assumed that the elementary surfaces are distributed in space according to the Gaussian probability law. It is suggested that for some purposes relating to the study of light on and within foliage, the reflected light may be assumed initially to be dispersed in accordance with Lambert's cosine law and the Gaussian probability law;

![Diagram](image)

Fig. 4.—(a) Specular reflectance, as occurs when the incident light ($E_i$) is reflected ($E_r$) by a mirror. (b) Diffused reflectance from a leaf of *E. regnans* with the incident light normal to the surface. The length of each arrow represents the intensity of the reflected light. (c), (d) As in (b) but with the incident light at 30 and 60°, respectively.

and at larger angles of incidence the reflectance pattern can usually be assumed to be of the spread reflection type. Reflected incident light continues to be diffused in all directions even at very oblique angles.

Under no circumstances were the leaves observed to behave as highly specular (i.e. glass-type) surfaces in accordance with Fresnel's law. At 75° to the normal, the reflectance in the neighbourhood of specular reflection was only 100–200% greater than at 30°. This may be compared with the true specular component for non-polarized light reflected from a glass surface using the formula:

$$\rho = \frac{1}{2} \left[ \frac{\sin^2(i-r)}{\sin^2(i+r)} + \frac{\tan^2(i-r)}{\tan^2(i+r)} \right],$$

where $i$ and $r$ are the angles of incidence and refraction, respectively, and $\rho$ the fraction of incident light reflected at the surface. For a glass of refractive index 1·5
and at angles of incidence of 30 and 75°, \( \rho = 0.083 \) and 0.506, respectively. That is an increase of 6.1 times in the specular component between 30 and 75°.

When the incident angle exceeds 45° (Fig. 3), the total spectral reflectance, as recorded in an integrating sphere, increases conspicuously. This is supported by the results of Shulgin, Kasanov, and Kleshnin (1960), who obtained increasing reflectance with increasing angles of incidence for Begonia pelata. Above 45°, as indicated by light-meter readings, there is a considerable increase of spread reflection in the visible spectrum. It will be appreciated, however, as mentioned earlier, that on applying the cosine correction, the total reflection per unit area of leaf is considerably less at 60° than for light normally incident on the leaf. Leaf orientation in relation to the incident solar flux would seem to be an exceedingly efficient and also simple method of adjustment by a plant to prolonged or intense irradiation.

The curves for the transmission of light suggest that in the visible spectrum the transmittance is so small after passing through one leaf that it does not require further consideration even on becoming incident on a second leaf. Gates (1962) has given similar-shaped curves for single leaves of Ficus elastica, but the transmittance was lower, both in the visible and near infrared spectra. The luminance factor of the second leaf in the shadow of the first leaf is so small that the space between the two leaves is virtually a black cavity for the visible spectrum; and the surface provided by the first layer of leaves may be considered as a mosaic of reflectors, absorbers, and black cavities, when viewed from above. As transmitted light is extremely deficient in "photosynthetic light" (Fig. 2), it would seem that leaves, other than those in the first surface on the tree, are relatively inefficient as absorbers.

In the infrared, for the sun leaves of the four eucalypts, transmittance requires to be taken into account up to about the eighth leaf; but in relation to reflectance it needs to be considered only up to the fourth leaf, as then the nature of the surface of the top leaf may be more important in influencing total reflectance. It will also be appreciated that, as might be expected of leaf tissue, the transmittance falls off as the angle of incidence is increased; but in the visible spectrum the difference in transmittance for angles of incidence of 0 and 30° was not more than 0.6%.

### Table 2

**Spectral Absorptance of Normally Incident Light \( (E_a) \) by Single Leaves**

Values are given as percentages of incident light \( E_i \) [see equation (2)]

<table>
<thead>
<tr>
<th>Species</th>
<th>Wavelength (Å)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>4000</td>
</tr>
<tr>
<td>E. regnans</td>
<td>97</td>
</tr>
<tr>
<td>E. radiata</td>
<td>94</td>
</tr>
<tr>
<td>E. obliqua</td>
<td>94</td>
</tr>
<tr>
<td>E. goniocalyx</td>
<td>95</td>
</tr>
</tbody>
</table>
Rabinowitch (1951) expressed the energy balance in the visible spectrum for a leaf by the formula:

\[ E_a = E_t - E_t - E_r, \]  

where

- \( E_a \) = absorbed energy,
- \( E_t \) = total energy,
- \( E\text{t} \) = transmitted energy, and
- \( E_r \) = reflected energy.

If these are now expressed as percentages, of which \( E_t = 100\% \), then we may write

\[ E_a = 100 - (E_t + E_r). \]  

As \( E_t \) and \( E_r \) are known from experimental studies, the absorptance \( (E_a) \) can be determined. The absorptance of a second leaf \( (E_{a2}) \) receiving only transmitted light from the first leaf may be determined from reflectance values only since \( E_t \to 0 \) and therefore

\[ E_{a2} = 100 - E_{r2}. \]

The total absorptance in the visible spectrum for an indefinite number of overlapping leaves is approximately

\[ E_a = 100 - (E_{t1} + E_{r1} + E_{r2} + E_{r3} + E_{r4}). \]

The total absorptance in the visible spectrum (4000–7200 Å) was calculated to be between 80 and 88% for single sun leaves of the species studied, and between 8 and 13% in the infrared. Spectral absorptances for each species have been summarized in Table 2.

V. Acknowledgments

The author is indebted to Professor A. Buchanan, Chemistry Department, and Dr. T. F. Neales, Botany School, University of Melbourne, for helpful discussion and for kindly reading the manuscript. The provision of facilities by the Divisions of Dairy Research and Building Research, CSIRO, Highett, and particularly the assistance given by Mr. F. Horwood of the former division, is greatly appreciated.

VI. References


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