THE REFLECTION OF VISIBLE RADIATION FROM LEAVES OF SOME WESTERN AUSTRALIAN SPECIES

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Summary

A spectrophotometer with an integrating sphere-reflectance attachment was used to determine total reflectances of leaves after irradiation with visible light of wavelengths ranging from 340 to 620 mμ. Reflectance measurements were made at 20-mμ intervals in this range. The leaves of 32 Western Australian plant species were studied, and where upper and lower surfaces were different these were considered separately. No significant differences were found between the reflectances of leaves from different topographic areas.

Additional experiments were carried out to ascertain the effect of different treatments upon reflectance values. A decrease in water content was found to increase reflectances and intercellular infiltration caused decreased reflectances. This is discussed in terms of the anatomical structure of the leaf. Surface hairs and surface wax were found to increase reflection.

I. Introduction

The extensive literature on the light-absorbing and light-reflecting properties of leaves has been reviewed by Rabinowitch (1951) and Geiger (1965). Recently attention has been directed towards the factors that affect these properties. For example, the influences of geographical position, xeromorphy and succulence, seasons, soil moisture, fertilizers, and leaf structure have been investigated (Billings and Morris 1951; Kleshnin and Shul'gin 1959; Tageeva, Brandt, and Derevyanko 1961; Shul'gin 1961; Shul'gin, Khazanov, and Kleshnin 1961; Dadykin and Bedenko 1960,1961). The present paper presents, for comparison, data concerning reflectances of certain Western Australian species, and forms part of a general investigation into the absorption and dissipation of energy by leaves.

II. Materials and Methods

A Bausch and Lomb Spectronic 20 colorimeter with an integrating sphere-reflectance attachment was used for measuring total reflected radiation from leaves. The colorimeter unit produced wavelengths ranging from 340 to 620 mμ, in bands of 20 mμ width, and these were directed onto the leaf with an angle of incidence of 0°. The total reflected radiation was collected by the integrating sphere and measured with a photomultiplier (Fig. 1).

The leaf material was collected from plants growing in the six areas listed in Table 1. A total of 32 different species was studied, of which 10 had upper and lower surfaces with similar reflection properties. One species was collected in two areas and thus 56 types of leaf surface were considered. From 10 leaves of each species,

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2·3-cm diameter disks were punched. Five of these were used for upper-surface and five for lower-surface determinations. Each disk was fixed with two pins onto a rubber mat 4·5 cm square, which acted as a support for the specimens and served to prevent stray light entering the sphere. The reflectivity of the rubber was less than 10% at all wavelengths, and as the transmissivity of these leaves was probably always less than 20% (cf. Rabinowitch 1951), it follows that the error due to the reflection of the transmitted light from the rubber was less than 0·5%. The instrument was set at a given wavelength, all 10 replicates measured, and then reset to the next wavelength, and so on.

In addition to these determinations, several experiments were carried out on the effect of different treatments upon the reflectance values. Firstly measurements were performed on the upper surface of leaves of *Arctotheca nivea* before and after the removal of surface hairs. This species was ideal for this experiment because of the ease with which the hairs could be removed without damage to the leaf. *Dryandra*

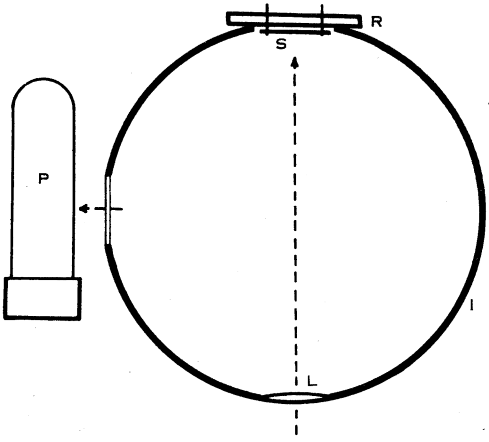

Fig. 1.—Schematic representation of the Spectronic 20 reflectance attachment, consisting of an integrating sphere (*I*), a lens (*L*), a rubber mat (*R*) onto which the sample (*S*) is attached with two pins, and a photomultiplier (*P*).

sessilis leaves were investigated before and after the upper surface had been wiped with a damp cloth to partially remove the waxy layer. Measurements were made on leaves of *Pisum sativum* before and after the infiltration of the intercellular spaces with water. *Pisum sativum* leaves were used because they were easier to infiltrate than the xeromorphic native plants being studied. Infiltration was obtained by immersing the leaves in water under vacuum, and then restoring the pressure. Reflectances of leaves of *Acacia cyanophylla* were measured immediately after collection (water content 68·4%), and then when the water content had fallen to 61·9% and finally to 50·3% after suspending the leaves in a current of air.

III. Results

The average reflectances for all the species considered are plotted in Figure 2(*a*), together with the averages for the King's Park and Stirling Mountain species. Results for the sand-dune plants (from City Beach, Perth) are given in Figure 2(*b*). Figures 2(*c*) and 2(*d*) illustrate results for two typical species. Data showing the effects of different treatments upon reflectance values are given in Figures 3(*a*)–3(*d*).

All points plotted in Figures 2(*c*) and 2(*d*) and in Figures 3(*a*)–3(*d*) are averages for five replicates. Standard errors are not included because of the lack of variation that occurred between replicates.

IV. Discussion

(*a*) *The Reflectance Spectrum*

Although the magnitude of reflection was found to vary greatly between species, the same spectral pattern always occurred. This consisted of a reflection minimum at about 380 mμ and a maximum at 540 mμ. This type of spectrum is similar

Table 1

Species collected and their localities

Locality	Species Collected	Locality	Species Collected
City Beach, near Perth (sand dunes)	*Acacia cyclops* A. Cunn. ex G. Don *Arctotheca nivea* (Less.) Lewin. *Lepidosperma gladiatum* Labill. *Myoporum insulare* R. Br. *Scaevola crassifolia* Labill. *Spinifex hirsutus* Labill. *Tetragonia zeyheri* Fenzl. ex Harv. & Sond.	Stirling Plain, 210 miles south-east of Perth (sand-plain)	*Acacia myrtifolia* Willd. *Banksia coccinea* R. Br. *Eucalyptus tetragona* (R.Br.) F. Muell. *Isopogon cuneatus* R.Br.
National Park, 15 miles east of Perth	*Hovea trisperma* Benth. *Dryandra sessilis* (Knight) Domin.	Exposed slope of Bluff Knoll, Stirling Mountains, 200 miles south-east of Perth	*Banksia petiolaris* F. Muell. *Dryandra cuneata* R.Br. *Eucalyptus marginata* Sm. *Grevillea oleifolia* Brogn. & Gris. ex Guillaumin *Hakea baxteri* R.Br. *Isopogon attenuatus* R.Br. *Synaphea favosa* R.Br.
King's Park, Perth	*Acacia cyanophylla* Lindl. *Banksia grandis* Willd. *Eucalyptus gomphocephala* DC. *Eucalyptus marginata* Sm. *Hakea prostrata* R.Br. *Hardenbergia comptoniana* (Andr.) Benth. *Helichrysum cordatum* DC. *Kennedya prostrata* R.Br.	Porongorup Mountains, 230 miles south-east of Perth	*Leucopogon verticillatus* R.Br. *Myoporum serratum* R. Br. *Oxylobium lanceolatum* (Vent.) Druce *Thomasia tenuivestita* F. Muell. *Trymalium spathulatum* (Labill.) Ostf.

to those reported in the literature (e.g. Billings and Morris 1951; Kleshnin and Shul'gin 1959; Dadykin and Bedenko 1960). Detailed analysis of the shape of the reflection curves was not made, but it is considered that the slight peak or plateau of reflection at about 460 mμ is a result of an absorption minimum of chlorophyll *a* at this wavelength. The reflection maximum at 540 mμ is probably related to the low absorption of carotenoids and phytocyanins in this wavelength. The magnitude of the reflection was comparable with that recorded by Rabideau, French, and Holt (1946) and Billings and Morris (1951). The variation that occurred between species is demonstrated by the extent of the standard error limits in Figure 2(*a*). The average reflectance over all the wavelengths may be seen to lie between 10 and 25%.

(*b*) *Influence of Surface Structures*

Two of the plants examined showed a marked divergence from the normal pattern. These were the extremely hairy sand-dune species *Arctotheca nivea* and *Spinifex hirsutus*, both of which are early colonizers of bare beach sands. The lower surface of *Arctotheca nivea* reflected by far the most light, having an average reflectance of 67·1%. The importance of surface hairs in these studies was demonstrated by their removal from the upper surface of *Arctotheca nivea* [Fig. 3(*d*)] which resulted in

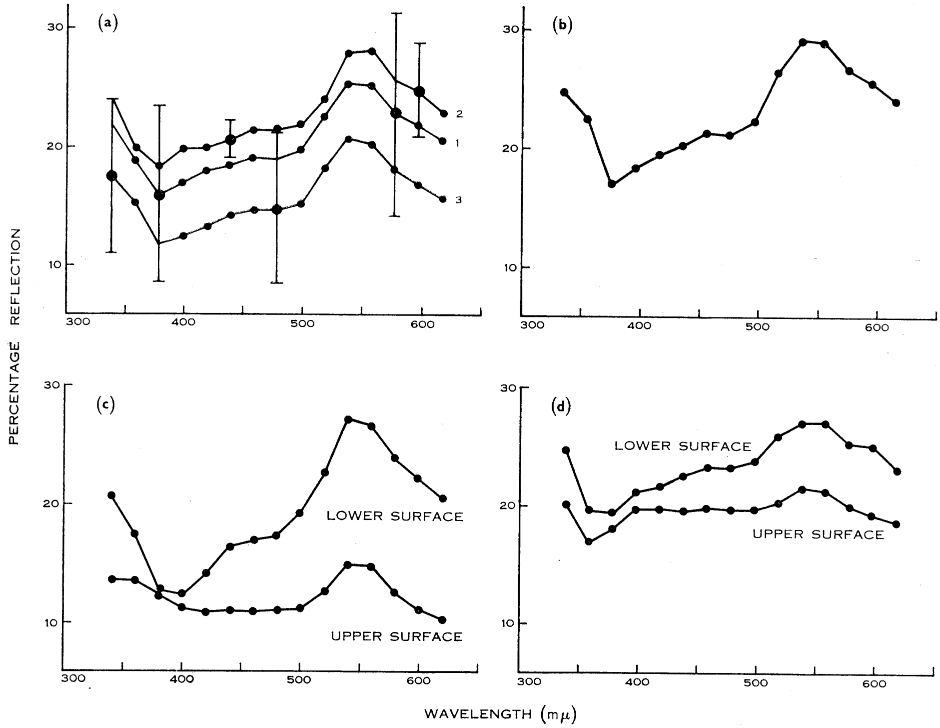

Fig. 2.—(*a*) Average percentage reflection of upper and lower surfaces of 32 Western Australian plant species (curve 1), of the seven Stirling Mountain species (curve 2), and of the eight King's Park species (curve 3). The vertical bars show the standard error for that curve at the point marked by the larger symbol. (*b*) Average reflectance for the seven City Beach (sand-dune) species. (*c*) Reflectance of upper and lower surfaces of *Eucalyptus marginata* leaves. (*d*) Reflectance of upper and lower surfaces of *Hovea trisperma* leaves.

the reduction of the average reflectance from 31·7 to 15·0%. Presumably the hairs present to the incoming radiation many interfaces that scatter the light, decreasing the amount entering the leaf and thus being absorbed. Shull (1929) also found that the curves for species with high reflectance were less markedly contoured. Our results are in general agreement with this. A further example of the way in which surface structures can influence reflection is given by *Dryandra sessilis* [Fig. 3(*b*)]. Here when the powdery, waxy layer on the upper surface of the leaf was partially removed, the average reflectance fell from 26·3 to 22·7%.

(c) *Internal Reflection*

Although surface reflection may account for an appreciable proportion of the total reflection of visible light from a leaf, in most species the majority of the reflection takes place internally. The fact that the reflection spectra are clearly influenced by the chlorophyll and carotenoid absorption maxima and minima suggests that the

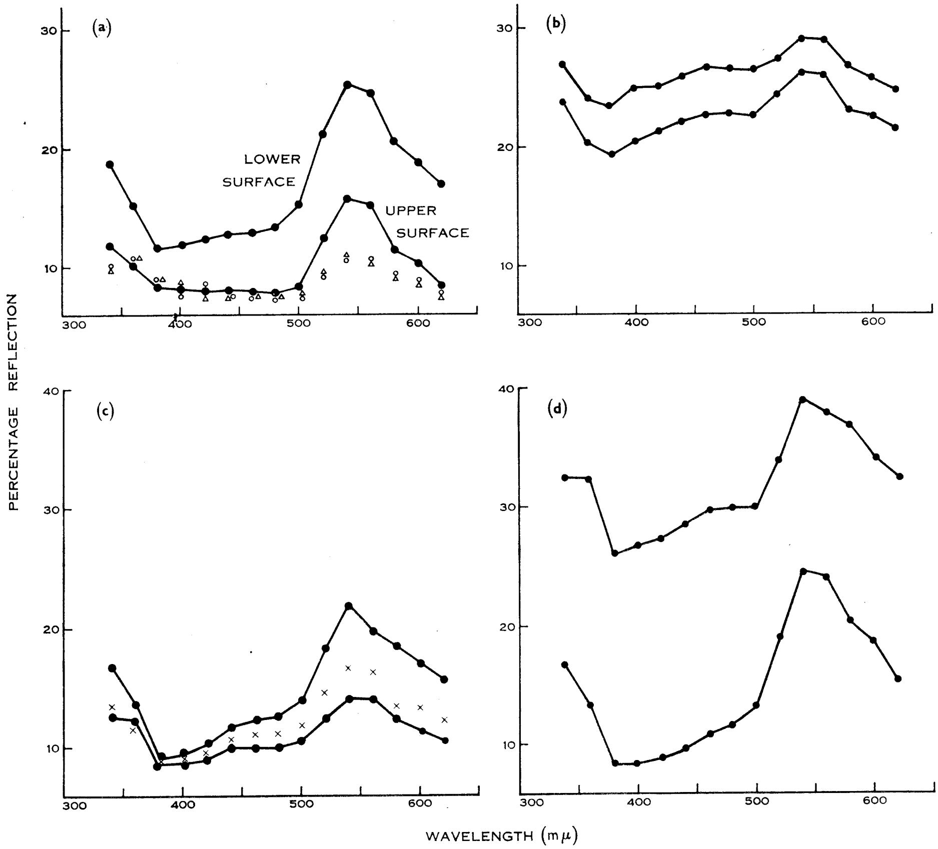

Fig. 3.—(*a*) Reflectances before infiltration of the intercellular spaces of *Pisum sativum* leaves with water (●) and of the lower (○) and upper (△) leaf surfaces after infiltration. (*b*) Reflectance of *Dryandra sessilis* leaves before (upper curve) and after (lower curve) the partial removal of the powdery surface layer. (*c*) Reflectances of *Acacia cyanophylla* leaves as collected—water content 68·4% (lower curve), after partial drying to a water content of 61·9% (×), and after drying to a water content of 50·3% (upper curve). (*d*) Reflectances of *Arctotheca nivea* leaves before removal (upper curve) and after removal (lower curve) of the hairs of the upper surface of the leaf.

reflected light has come from the interior of the leaf. The way in which the many cell interfaces within the leaf act as multiple reflectors, increasing the possibility of absorption and utilization, has been examined by Tageeva, Brandt, and Derevyanko (1961). They also indicated that infiltration of the intercellular spaces with water reduced the effectiveness of these reflectors. Figure 3(*a*) illustrates results from the author's experiments on the influence of intercellular infiltration with water.

From these results it is apparent that firstly there was an obvious reduction in the reflection percentage with infiltration. This, together with the fact that the leaves appeared to the naked eye to be more transparent after infiltration, supports the idea that infiltration does decrease internal scattering of light. Secondly these data show a marked difference between upper and lower surfaces before infiltration but not after. This suggests that the difference between the two surfaces is associated with or due to the amount of scattering light undergoes when entering the leaf from one surface or the other. In a dorsiventral leaf such as *Pisum sativum,* light entering the upper surface passes through the relatively closely packed palisade cells and is strongly absorbed by the chlorophyll before reaching the loosely packed mesophyll cells. This explains why over most of the spectrum the upper-surface reflectance is unaffected by infiltration. On the other hand, light entering the leaf from the lower surface must traverse the mesophyll region before reaching the palisade layer. This may be one explanation for the high reflectances commonly found for lower surfaces of leaves. Dadykin and Bedenko (1961) demonstrated that *Quercus robur* plants grown in soils of low moisture content reflected more light from their leaves than did those grown in soils of higher water content. The author obtained similar results [Fig. 3(*c*)] by allowing leaf material to dry out. It thus appears probable that the turgidity of the cells influences the number and extent of the internal reflecting surfaces. From this it seems possible that seasonal changes in water stress may significantly influence the amount of light reflected from leaves in the field.

The dependence of reflection on the water status of the leaves also means that special care must be taken to minimize water loss from leaves after collection and during experiments. In this connection all material collected was enclosed in plastic bags for as short a time as possible prior to measurement. The actual measurement period was reduced from 60 to 30 min for each species by recording results verbally on a tape recorder. The technique of using punched disks for measurements was found to be satisfactory under these conditions, there being no significant difference between readings taken at the same wavelength at the beginning and at the end of the 30-min measuring period.

The above measurements were made on leaves collected in the middle of winter when water content was high. Further measurements on leaves collected in the drier periods of the year are envisaged.

(*d*) *Geographic Position*

No significant differences were recorded between the reflectances of groups of plants from different areas. The greatest deviation from the normal pattern occurred in the sand-dune group, but these results must be treated with reserve since they include the two species *Arctotheca nivea* and *Spinifex hirsutus* which had exceptionally high reflectances. The samples were fairly small in number and the climatic conditions not very extreme. Because of the difficulty of aligning smaller surfaces in the instrument, the leaves of the specimens chosen for examination had widths greater than $2 \cdot 3$ cm. Selection of this type excludes the use of a very large number of southern Western Australian species, since many of them show xeromorphic modification in the reduced size of the leaf laminae.

V. Acknowledgments

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