

Leaf Absorptances of Mohave and Sonoran Desert Plants

James Ehleringer

Department of Biology, University of Utah, Salt Lake City, Utah 84112, USA

Summary. Leaf absorptances to solar radiation in the 400–700 nm (photosynthetically useful wavelengths) are presented for a diversity of species in the Mohave and Sonoran Deserts of North America. As a life form shrubs are shown to have the widest range of absorptance, with perennial herbs and cacti exhibiting a smaller range, and very little variation in leaf absorptances among trees and annuals. The measurement of leaf absorptance at 625 nm is shown to be the same as the leaf absorptance to solar radiation over the 400–700 nm. Over a wide range of species and absorptances, the total solar leaf absorptance (400–3,000 nm) is shown to be closely related to the 400–700 nm leaf absorptance.

Introduction

The spectral characteristics of leaves are an important feature in both the energy relations and photosynthesis of plants. Measurements of leaf absorptances and reflectances for a number of species have been reported by a number of investigators (e.g., Shull 1929; Billings and Morris 1951; Pearman 1966; Sinclair and Thomas 1970; Ehleringer and Björkman 1978; Gates 1980). While decreases in leaf absorptance are known to significantly affect leaf temperature, transpiration, and photosynthesis (Ehleringer and Mooney 1978; Smith and Geller 1980), few studies have considered seasonal variations in spectral characteristics and their consequences. Most investigations have been limited to the measurement of leaf absorptances or reflectances of single species in a single season.

A number of studies have considered the spectral characteristics of the dominant species that comprise a community or a vegetation type. Billings and Morris (1951) measured reflectances of four predominant species in desert, pine forest, and subalpine vegetation types of Nevada. They found that the average community leaf reflectance was positively correlated with habitat aridity. In contrast, Pearman (1966) determined the leaf reflectance characteristics of plants in three community types in Western Australia and found no significant reflectance differences between communities. However, Pearman (1966) excluded many species from his analyses because the leaves were too small to measure. In a similar study, Sinclair and Thomas (1970) measured reflectance in a number of species in South Australia. They found a wide range of reflectances for arid land species. As a result of this variation, there was no significant difference in the average leaf reflectance of plants from arid land and non-arid land habitats. What these Australian studies indicate

is that while increased leaf reflectance occurs in some species from dry habitats, it is by no means characteristic of all.

The purpose of this study was to measure the spectral characteristics of a number of common plant species in the Mohave and Sonoran Deserts of North America to determine 1) what the variation was between species, 2) what the seasonal variation was within species, and 3) what the variation was within life forms.

Methods

Leaf absorptance to solar radiation over the 400–700 nm waveband was measured with an Ulbricht integrating sphere (Fig. 1), that had been coated on the inside with a thin layer of magnesium oxide. Monochromatic light was provided by a lamp attached to a grating monochromator (Bausch and Lomb). This light passes through a diaphragm, condensing lens, and off a front surface mirror (at base of integrating sphere) before it is focused onto the sample within the integrating sphere. A silicon cell attached from the outside to the inside wall was used to measure the absorptance at different wavelengths. A small barrier located above the sample prevents the sensor from seeing the sample directly, but does not interfere with the reflectance and transmittance from the leaf. In this way the sensor detects light only after it has bounced off the walls of the integrating sphere. Absorptances for the 400–700 nm waveband were measured by directing midday sunlight into the integrating sphere using a mirror attached to a heliostat (replacing monochromator and lens) through the same opening that was used for the monochromatic beam. A quantum sensor (model 190-SR, Lambda Instruments, Lincoln, Nebraska) replaced the silicon cell for leaf absorptance measurements in the 400–700 nm waveband.

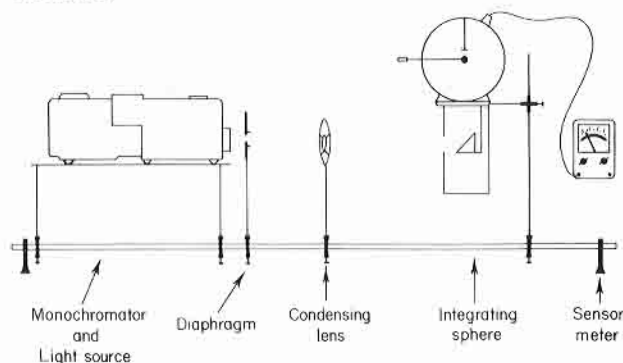


Fig. 1. Setup of integrating sphere. Monochromatic light is supplied by a light source-monochromator and focused onto the sample inside the integrating sphere with a condensing lens. The base of the integrating sphere is covered with a black velvet material to reduce stray light

Leaf absorbance was measured by first placing the sample within the beam, recording the sensor signal and then pulling the sample out of the beam to get the signal when light is reflected off the magnesium oxide coated barrier. The leaf absorbance is then calculated as

$$\text{absorbance} = 1 - \frac{\text{sample in beam}}{\text{sample out of beam}} \quad (1)$$

Leaf absorbances to the entire solar spectrum (400–3,000 nm) were measured with a magnesium oxide coated Taylor integrating sphere (13 cm diameter) similar to the one described by Birkebæk and Birkebæk (1964). The difference between their sphere and the one used in this study was that the reference standard (magnesium oxide) and samples were placed in the same port manually rather than with a rotational device. The Taylor integrating sphere was insulated with 2.5 cm of rubber foam on the outside to dampen any thermal gradients. A sensitive thermopile (model BI-6, Hy-Cal Engineering, Santa Fe Springs, Calif.) was used as the sensor. Reflectance and transmittance are measured individually relative to the reference standard. Since our reflectance standard (magnesium oxide) has a flat 97–99% reflectance over the 400–3,000 nm waveband, our absorbance estimates are very close to the absolute values. Absorbance over the 400–3,000 nm waveband is calculated as

$$\text{Absorbance} = 1 - \text{reflectance} - \text{transmittance} \quad (2)$$

Unless otherwise mentioned, leaf absorbances as used in this study are the absorbance by the leaf to solar radiation in the 400–700 nm waveband.

Leaf absorbances were measured on fresh tissues in the field. For monochromatic measurements, samples were stored in plastic bags on ice for the one or two days before the measurements could be made. Plants were sampled at various Mohave and Sonoran Desert locations at several time periods during the year. For plants whose leaf absorbance changed seasonally, this allowed an opportunity to determine the annual leaf absorbance range.

Results

The monochromatic absorbance spectra between 400 and 700 nm of leaves of different species show the same basic pattern, although the absolute absorbances may differ greatly (Fig. 2). There are two broad absorption peaks at 400–500 nm and 600–700 nm, with a decreased absorbance or trough at 550 nm. Leaves of *Prosopis juliflora* are glabrous and exhibit an absorption spectra typical for green leaved species. Transmittance between 400 and 700 nm ranges 2–6%.

The reduction in absorbance at all wavelengths in the leaves of other species is because of an increased surface reflectance, and is achieved in a number of different ways. Leaves of *Brickellia incana* and *Encelia farinosa* are covered with dense mats of hairs (pubescence). In *Opuntia polycantha*, the cactus cladode (leaves are absent) is covered with white waxes and spines. Still different, the epidermal surface of *Atriplex hymenelytra* is covered with sodium chloride filled bladders. Though the mechanisms may differ, one factor is common. The reduced absorbance results from epidermal modifications resulting in increased reflectance; reduced absorbance is not achieved through increased transmittance.

A much faster and more useful measurement of leaf absorbance in many cases is the total integrated leaf absorbance to sunlight between 400 and 700 nm. This is the leaf absorbance to the photosynthetically useful wavelengths and is thus a measure of the fraction of solar radiation incident on the leaf that is available for photosynthesis.

The dominant plant species in the Mohave and Sonoran Deserts were surveyed for their 400–700 nm leaf absorbance

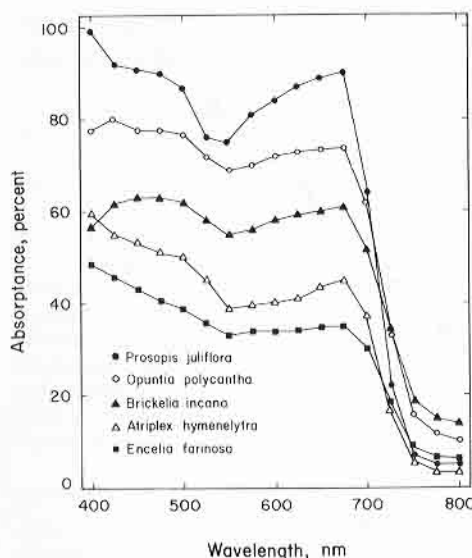


Fig. 2. Absorbance spectra between 400 and 800 nm for several common species in the Mohave and Sonoran Deserts

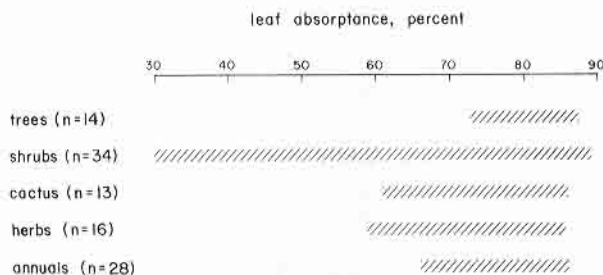


Fig. 3. Ranges of leaf absorbances to solar radiation (400–700 nm) measured for different life forms in the Mohave and Sonoran Deserts. N is the sample size. A complete species list appears in the appendix

characteristics. The results are summarized into different life form categories in Fig. 3 and a complete summary appears as an appendix. The widest range of leaf absorbances, 60 percent, is found within the shrub species, and includes both deciduous and evergreen types. Both intraspecific (seasonal) and interspecific variation contribute to this high range. The lowest ranges occur in the trees (14 percent) and in annuals (20%) where the variation is completely interspecific. The annual, *Dicoria canescens*, is unusual in that it has an absorbance of 66%, lower than any of the other annuals. Without *D. canescens*, the range of absorbances in annuals would be only 13%.

It is often desirable to measure leaf absorbances quickly at times when direct sunlight is not readily available (hazy or cloudy conditions). For such situations, an artificial light source could be substituted for sunlight if there was a close agreement between the 400–700 nm solar waveband leaf absorbance and the absorbance at a specific wavelength. To determine if there was such a single wavelength, the leaf absorbance was first measured monochromatically between 400 and 700 nm using a silicon cell sensor and then measured with sunlight as the light source using a quantum sensor. The results presented in Fig. 4 suggest that over a wide range of absorbances, the leaf absorbance at 625 nm is the same as the 400–700 nm leaf absorbance to solar radiation ($r^2 = 0.995$, $p < 0.01$).

For energy and heat balance studies it is necessary to know the leaf absorbance over the entire solar radiation waveband,

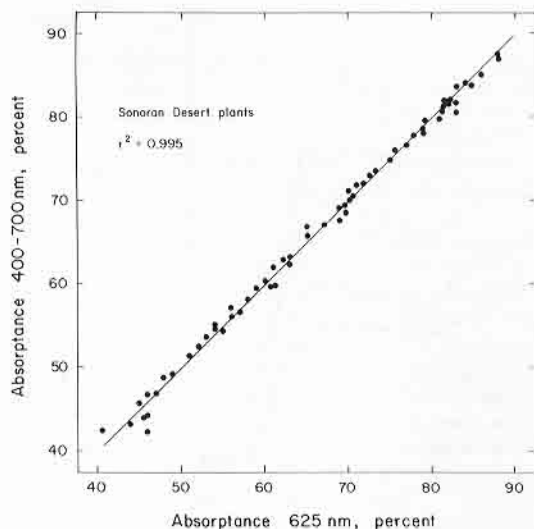


Fig. 4. Relationship between leaf absorbance to solar radiation (400–700 nm) and the leaf absorbance at 625 nm for a diversity of desert species

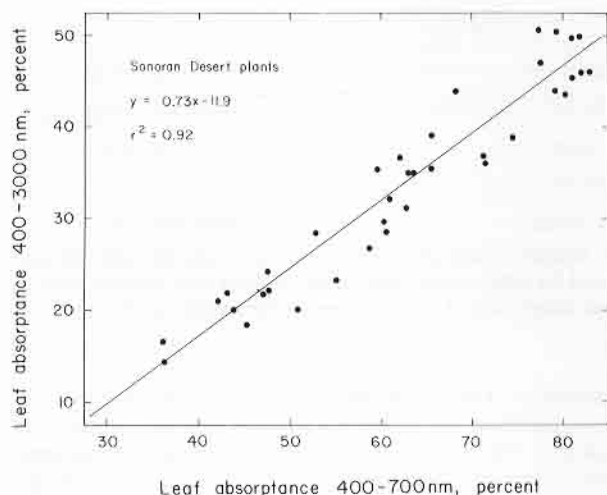


Fig. 5. Relationship between leaf absorbance to total solar radiation (400–3,000 nm) and leaf absorbance to photosynthetically useful solar radiation (400–700 nm) for a diversity of desert species

effectively 400–3,000 nm. Since the solar radiation in the 400–700 nm waveband represents nearly 50% of the total solar energy, the leaf absorbance to visible wavelengths (400–700 nm) should be closely related to the absorbance to total solar radiation (400–3,000 nm).

The leaf absorbances to visible and total solar radiation were measured on the same sample for a diversity of species in the field. Figure 5 shows the results, and as expected, there is a strong relationship between the two absorbances ($r^2=0.92$, $p<0.01$). This relationship can be quantified as

$$A_{400-3,000} = 0.73 A_{400-700} - 11.9 \quad (3)$$

where $A_{400-3,000}$ and $A_{400-700}$ are the leaf absorbances to solar radiation for the 400–3,000 nm (total solar) and 400–700 nm (visible) wavebands, expressed as percentages.

Discussion

Leaf temperature and energy balance depend on leaf absorbance over the total solar spectrum (400–3,000 nm), while photosynthesis depends on leaf absorbance in the visible wavelengths (400–700 nm). However, the two absorbances are tightly correlated. The current study shows that typical leaf absorbances for green leaves to solar radiation in the 400–700 nm waveband are 85% and for the 400–3,000 nm waveband are 50%, which is in agreement with other studies (Birkebak and Birkebak 1964; Gates et al. 1965; Ross 1975). Through the use of epidermal modifications though, absorbances can be reduced to 29% and 9%, respectively.

The advantage of a reduced leaf absorbance as an adaptive feature in arid environments is reductions in leaf temperature, transpiration, and metabolic rate. If the total solar leaf absorbance is reduced from 50% to 20% leaf temperature may drop as much as 6–10°C (Ehleringer and Mooney 1978; Smith 1978; Smith and Geller 1980; Gates 1980). The disadvantage to a reduced leaf absorbance is a reduction in the quanta available for photosynthesis. In the pubescent leaved *Encelia farinosa*, the photosynthetic rate is greatly depressed by light reflected from the leaf surface (Ehleringer et al. 1976; Ehleringer and Mooney 1978).

The use of reduced leaf absorbance as an adaptation to hot, arid conditions is best developed in shrubs, occurs to a lesser extent in cacti and perennial herbs, and is rare or absent in trees and annuals. Within the shrub life form, several species are capable of varying leaf absorbance depending on environmental conditions (Mooney et al. 1977; Ehleringer and Björkman 1978). There is a tendency for herbaceous and shrub species with reduced leaf absorbances to occur on drier, exposed bajadas and rocky slopes and not in ravine bottoms or along water courses where glabrate leaved species usually predominate. Just exactly what this means in terms of interspecific competition, or extending growth activity into drought periods is unknown. Within trees and annuals, much of the variation in leaf absorbances results from differences in leaf thickness (transmittance) and not reflectance. The absence of reduced leaf absorbances in these two groups is not surprising, since trees occur primarily along water courses and annuals have such an ephemeral life history.

Although Billings and Morris (1951) showed that desert plants had lower absorbances than other more mesic vegetation types, studies by Pearman (1966) and Sinclair and Thomas (1970) found no significant differences between arid and more mesic vegetation types. This study has indicated that leaf spectral characteristics are highly dependent on both life form and season, which may explain the differences in conclusions of the previous studies. It is perhaps more appropriate to restrict inter-vegetation comparisons to similar life forms.

Leaf absorbance measurements are not routinely made in ecological or ecophysiological studies for a variety of reasons. This study has pointed out though that by knowing the leaf absorbance at a single wavelength, 625 nm, two important parameters can be reliably calculated: the leaf absorbance to photosynthetically useful wavelengths (400–700 nm) and the total solar leaf absorbance (400–3,000 nm). This should greatly facilitate the determination of leaf absorbance characteristics for use in future studies.

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Appendix. Leaf absorptances to solar radiation (400–700 nm) for species appearing in Fig. 3. Data are averages. For species whose leaf absorptance changed seasonally, ranges are presented

Trees ($n=14$)

<i>Acacia greggii</i>	82
<i>Bursera odorata</i>	79
<i>Celtis reticulata</i>	79
<i>Cercidium floridum</i>	73
<i>C. microphyllum</i>	87
<i>Chilopsis linearis</i>	76
<i>Dodonea viscosa</i>	77
<i>Gossypium thurberi</i>	81
<i>Nicotiana glauca</i>	83
<i>Prosopis juliflora</i>	85
<i>Quercus emoryi</i>	84
<i>Salix laesiolepis</i>	83
<i>Sambucus mexicana</i>	83
<i>Tecoma stans</i>	83

Shrubs ($n=34$)

<i>Ambrosia ambrosoides</i>	83
<i>A. deltoidea</i>	80
<i>A. dumosa</i>	75–82
<i>Amphipappus fremontii</i>	74
<i>Atriplex hymenelytra</i>	41–76
<i>A. lentiformis</i>	78
<i>A. parryi</i>	59
<i>Brickellia incana</i>	65
<i>Bursera hindsiana</i>	69
<i>Caespalina pumila</i>	79
<i>Encelia asperifolia</i>	75
<i>E. californica</i>	85
<i>E. farinosa</i>	29–81
<i>E. frutescens</i>	79
<i>E. halimifolia</i>	79
<i>E. palmeri</i>	45–82
<i>E. phenicodonta</i>	40–80
<i>E. radians</i>	79
<i>E. virginensis</i>	79
<i>Fouquieria splendens</i>	80
<i>Hibiscus denudatus</i>	72
<i>Hymenoclea salsola</i>	79
<i>Hyptis emoryi</i>	74
<i>Jatropha cinerea</i>	80
<i>Larrea divaricata</i>	83
<i>Peucephyllum schottii</i>	89
<i>Rhus integrifolia</i>	84
<i>Salvia apiana</i>	56
<i>Simmondsia chinensis</i>	68
<i>Suaeda torreyana</i>	78
<i>Vaqueria californica</i>	78
<i>Viguiera deltoidea</i>	65
<i>V. reticulata</i>	71
<i>V. tomentosa</i>	82

Cactus ($n=13$)

<i>Carnegiea gigantea</i>	86
<i>Echinocereus engelmannii</i>	77
<i>Ferocactus viridescens</i>	84
<i>Mammillaria dioica</i>	84
<i>Opuntia acanthocarpa</i>	61
<i>O. basilaris</i>	78
<i>O. bigelovii</i>	61
<i>O. echinocarpa</i>	70
<i>O. fulgida</i>	71
<i>O. megacarpa</i>	82
<i>O. occidentalis</i>	78
<i>O. polyantha</i>	73
<i>O. prolifera</i>	69

Herbs ($n=16$)

<i>Abutilon parvulum</i>	81
<i>Asclepias erosa</i>	73
<i>Astragalus lentiginosus</i>	77
<i>Boerhaavia annulata</i>	78
<i>Cassia bahinioides</i>	81
<i>Cucurbita digitata</i>	86
<i>C. palmata</i>	77
<i>Datura meteloides</i>	84
<i>Enceliopsis argophylla</i>	66
<i>Eriogonum inflatum</i>	76
<i>Euphorbia parishii</i>	75
<i>Marrubium vulgare</i>	82
<i>Psathyrotes ramosissima</i>	59–70
<i>Sphaeralcea ambigua</i>	77
<i>Tidestromia oblongifolia</i>	67–81
<i>Vaseyanthus brandegei</i>	79

Annuals ($n=28$)

<i>Abronia villosa</i>	78
<i>Allionia incarnata</i>	77
<i>Amaranthus palmeri</i>	85
<i>Atrichoseris platyphylla</i>	75
<i>Boerhaavia spicata</i>	77
<i>B. wrightii</i>	84
<i>Calandrinia ambigua</i>	75
<i>Camissonia claviformis</i>	81
<i>Chorizanthe rigida</i>	78
<i>Dicoria canescens</i>	66
<i>Euphorbia glyptosperma</i>	75
<i>Geraea canescens</i>	78
<i>Gilia latifolia</i>	76
<i>Kallstroemia grandiflora</i>	79
<i>Lupinus arizonicus</i>	74
<i>Malvastrum rotundifolium</i>	83
<i>Mentzelia albicaulis</i>	75
<i>Mohavea breviflora</i>	71
<i>Oxystylis lutea</i>	86
<i>Palafoxia linearis</i>	81
<i>Phacelia calthifolia</i>	77
<i>P. crenulata</i>	73
<i>P. fremontii</i>	76
<i>Plantago insularis</i>	73
<i>Proboscidea parviflora</i>	84
<i>Salvia pachyphylla</i>	79
<i>Trianthema portulacastrum</i>	80
<i>Tribulus terrestris</i>	79

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