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Epidermis effects on spectral properties of leaves of four herbaceous species

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The spectral properties of the leaves of the herbaceous species *Brassica oleracea* L. var. *botrytis* L., *Cerastium tomentosum* L., *Petunia hybrida* Vilm., and *Talinum paniculatum* (Jacq.) Gaertn. were examined to see what effect the epidermis had on leaf absorptance, reflectance and transmittance. Removal of the epidermis from the side of the leaf surface being illuminated resulted in increases in leaf absorptance and transmittance, and a decrease in reflectance in the 400–800 nm waveband. Removal of the epidermis from the opposite side of an illuminated leaf (effect was similar in both abaxial and adaxial surfaces) resulted in small decreases in both absorptance and reflectance, and corresponding increases in transmittance. Removal of both the upper and lower epidermis resulted in a marked increase in transmittance, while both leaf reflectance and absorptance were decreased. The results suggest that the presence of the epidermis significantly increases leaf absorptance in the photosynthetic wavebands.

Additional key words – Epidermis, leaf absorptance.

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Introduction

The spectral characteristics of intact green leaves in the photosynthetically active wavelengths (440–700 nm) are well established (Moss and Loomis 1952, Gates et al. 1965, Loomis 1965, Woolley 1971). The upper surfaces of green leaves normally absorb approximately 85% of the sunlight in the 400–700 nm waveband (Gates et al. 1965, Ehleringer 1981). Epidermal structures such as hairs and salt bladders on the upper leaf surface can result in large changes in leaf spectral characteristics, specifically decreased leaf absorptance and increased leaf reflectance (Eller and Willi 1977, Mooney et al. 1977, Ehleringer and Björkman 1978, Ehleringer 1981). Similar changes in leaf spectral characteristics can result from waxes secreted onto the leaf surface (Sinclar and Thomas 1970, Clark and Lister 1975, Reicosky and Hanover 1978, Mulroy 1979). In many cases the epidermal modification is not equal on upper and lower leaf surfaces, resulting in divergent spectral characteristics for upper and lower leaf surfaces (Eller and Willi 1977).

Relatively little is known about the role of the epidermis in leaf absorptance characteristics. Gausman et al. (1975) investigated the role of the epidermis in absorbing ultraviolet (UV) radiation, and found that UV absorptance was a function of epidermis thickness. Effective UV absorption by the leaf epidermis has also been reported for a variety of plant species (Robberecht and Caldwell 1978, Robberecht et al. 1980).

The purpose of this study was to determine the effects of the upper and lower epidermis on the spectral characteristics of leaves over the photosynthetically active wavelengths (400–700 nm).

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Materials and methods

Four species (*Brassica oleracea* L. var. *botrytis* L., *Cerastium tomentosum* L., *Petunia hybrida* Vilm. and *Talinum paniculatum* (Jacq.) Gaertn. were chosen for study, largely on the basis of having an epidermis that could be easily removed. Plants were greenhouse grown. Natural sunlight was supplemented with high intensity discharge (HID) lamps to create incident total daily photon irradiances in the 400–700 nm waveband of 30–50 mol m^{-2} day^{-1}. The HID lamps were also used to create a constant 14 h/10 h day/night photoperiod. Leaf absorptance, reflectance and transmittance measurements were determined as a function of wavelength using a Bausch and Lomb high intensity grating monochromator and light source in conjunction with an Ulbricht integrating sphere (Ehleringer 1981). Readings were taken at 25 nm intervals in the 400–800 nm waveband. A complete spectrum could be obtained in approximately four min. In these spectral measurements, the direct beam from the monochromator was incident on the leaf at an angle perpendicular to the leaf surface. Light from the monochromator was supplied by a tungsten filament lamp; the bandwith from the monochromator was 9.6 nm. After the spectrum of a leaf with an intact upper or lower epidermal surface had been measured, the epidermis was removed with a dissecting needle and forceps from the same leaf disk and the spectral characteristics again measured. Sample size in the experiments was 3–4, and the data presented are averages of these readings. Standard errors for data point replicates were 0.53% for *B. oleracea,* 0.60% for *C. tomentosum,* 0.45% for *P. hybrida* and 0.88% for *T. paniculatum.*

Results

The effect of epidermis removal on leaf spectral characteristics

Figure 1 shows the effect of removal of the upper epidermis on leaf absorptance and reflectance for the upper leaf surface (illumination incident on this side of the leaf) of *Talinum paniculatum,* a thick-leaved species. Leaf absorptance increased and reflectance decreased by about 3% each over the 400–700 nm waveband. No change in either reflectance or absorptance was observed in the 700–800 nm waveband.

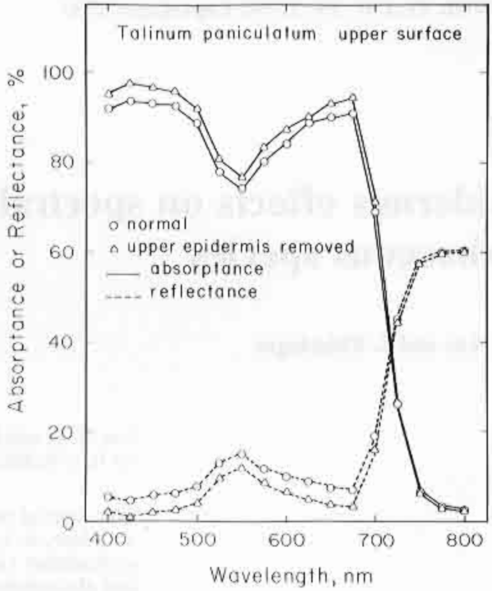

Fig. 1. Absorptance and reflectance spectra of intact leaves of *Talinum paniculatum* measured with upper leaf surface facing the light source and also with the upper epidermis removed.

When light was incident on the lower leaf surface, removal of the lower epidermis had similar effects on both leaf absorptance and reflectance as when the upper leaf surface had been illuminated and the upper epidermis removed (Fig. 2). In *Petunia hybrida,* leaf absorptance of the lower surface in the 400–700 nm waveband was increased by 5% and leaf reflectance was decreased by a similar amount when the lower epider-

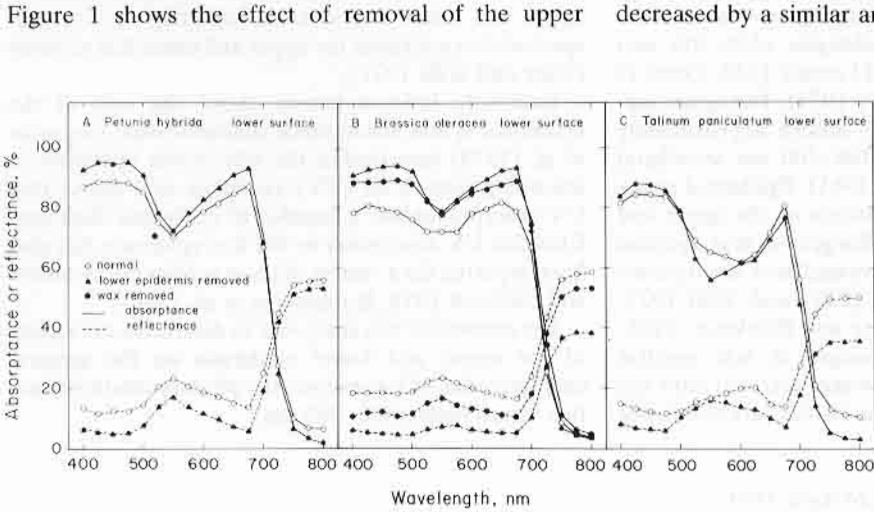

Fig. 2. Absorptance and reflectance spectra of intact leaves of *Petunia hybrida* (A), *Brassica oleracea* (B) and *Talinum paniculatum* (C), measured with the lower leaf surface facing the light source and also with the lower epidermis removed.

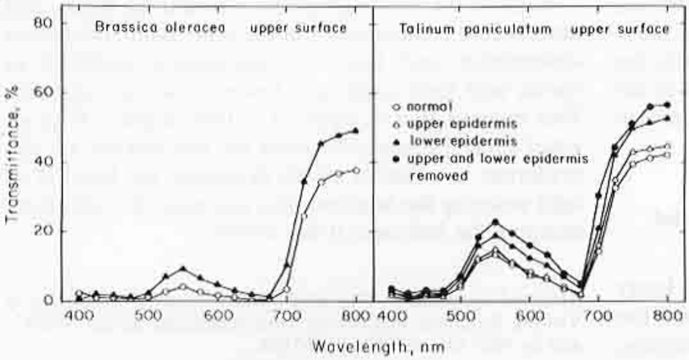

Fig. 3. Transmittance spectra of intact leaves of *Brassica oleracea* (A) and *Talinum paniculatum* (B), measured with the upper leaf surface facing the light source and then with the upper epidermis removed, the lower epidermis removed, or with both upper and lower epidermis removed.

mis was removed. The lower epidermis of leaves of *Brassica oleracea* is covered with a waxy layer. When absorptance and reflectance spectra of the lower side of intact leaves of this species were compared with *P. hybrida,* leaf absorptances were lower and reflectances higher. Removal of the wax from the lower epidermis by rubbing with tissue paper and then removal of the lower epidermis resulted in leaf absorptance increases of approximately 7–15% (Fig. 2). Associated with these changes were similar decreases in leaf reflectance.

The leaf absorptance curve of the underside of leaves (abaxial surface) of *T. paniculatum* was different from the other two species measured. The absorptance in the 650–700 nm waveband exhibited a pronounced peak

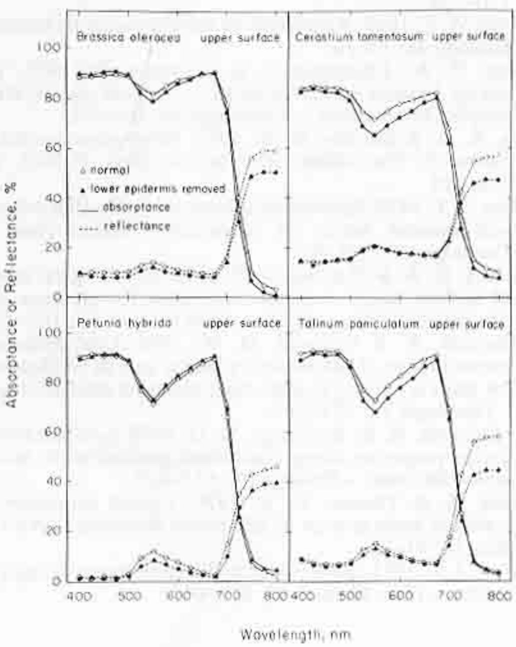

Fig. 4. Absorptance and reflectance spectra of intact leaves of *Brassica oleracea* (A), *Cerastium tomentosum* (B), *Petunia hybrida* (C), and *Talinum paniculatum* (D), measured with the upper leaf surface facing the light source and then with the lower epidermis removed.

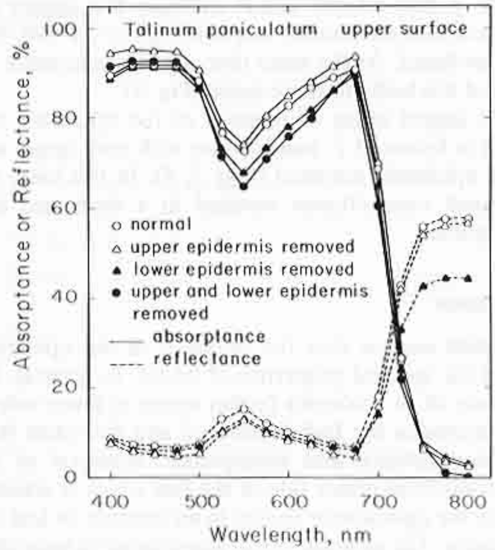

Fig. 5. Absorptance and reflectance spectra of intact leaves of *Talinum paniculatum* measured with the upper leaf surface facing the light sources, then with the upper epidermis removed, the lower epidermis removed, and with both upper and lower epidermis removed.

(Fig. 2). Additionally, the trough of the leaf absorptance curve was flat from 525 to 625 nm. The reflectance peak between 400 and 700 nm, which is notally at 550 nm, was shifted to 625 nm. However, when the lower epidermis was removed and the spectral characteristics of the lower leaf surface again measured, the absorptance and reflectance curves appeared more typical.

Changes in the leaf transmittance were also observed when the epidermis was removed (Fig. 3). When the upper leaf surface was illuminated, removal of the upper epidermis had little effect on leaf transmittance. However, when the upper leaf surface was illuminated and the lower epidermis removed, there was a substantial increase in leaf transmittance. With both upper and lower epidermis removed, there was a further increase in leaf transmittance. The leaf absorptance decreased in leaves with both upper and lower epidermis removed and was due to a decrease in the upper leaf reflectance and by increased leaf transmittance. In other words, the increase in absorptance expected by the removal of the upper epidermis was more than offset by the increased transmittance through the leaf.

Interactions between the upper and lower surface on leaf spectral characteristics

When the upper surface of a leaf from which the lower epidermis had been removed was illuminated, both the leaf reflectance and absorptance decreased slightly, suggesting an increase in leaf transmittance. Figure 4 shows this pattern for leaves of *B. oleracea, C. tomentosum, T. paniculatum* and *P. hybrida.* The largest decrease in leaf reflectance was observed in the 700–800 nm waveband. At the same time, leaf transmittance increased markedly in these cases (Fig. 3).

The largest effect of removal of the epidermis was found in leaves of *T. paniculatum* with both upper and lower epidermis removed (Figs 3, 5). In this case, the increased transmittance resulted in a decreased leaf absorptance.

Discussion

Our data suggest that the presence of the epidermis adjust the spectral properties of leaves. In general, the presence of an epidermis (either upper or lower side of leaf) increases the leaf reflectance and decreases both the transmittance and absorptance. Removal of the epidermis from either side of the leaf *which is oriented toward the light source* results in an increase in leaf absorptance. The increase in leaf absorptance is associated with a decrease in reflectance in this situation.

Much less change in leaf absorptance was observed by removing the epidermis from the side of the leaf *opposite to the light source.* Although the leaf reflectance decreased, the leaf transmittance increased markedly. Relative to this, Sinclair et al. (1970) pointed out that the combination of a high degree of internal scattering at the cell-air interference and within cells and also the presence of strongly absorbing pigments determined the final values of reflection, transmission and absorption. In our experiments, the internal scattering should have remained constant since we used the same leaf disk. Our data suggest that the presence of a light barrier (epidermis) on the abaxial surface of the leaf reduces leaf transmittance. The abaxial surface epidermis reduces transmittance by enhancing the internal reflectance.

Without the upper epidermis (toward the light), leaf absorptance is increased. On the other hand, the lowest absorptance and highest transmittance occurred in leaves with both upper and lower epidermis removed. This suggests that in addition to their similar effect on water vapor exchange between the leaf and the air, the epidermis is a barrier which decreases the fraction of light entering the leaf and also prevents the light from escaping the leaf once it has entered.

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