Changes in Spectral Properties of Leaves as Related to Chlorophyll Content and Age of Papaya*

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Abstract

Both leaf absorptance and reflectance changed with leaf age in three cultivars of *Carica papaya* L. These spectral changes were associated with changes in leaf chlorophyll (Chl) content and Chl a/b ratio. Between Chl $(a+b)$ contents of 10 to 50 µg cm^{-2}, the leaf absorptance increased from 50 to 88%. Chl content declined in concert with maximum net photosynthetic rate as the leaves aged.

Spectral characteristics of leaves over the visible wavelengths result from the interactions of the absorbing photosynthetic pigments and reflecting epidermal features (Rabideau *et al.* 1946, Moss and Loomis 1952, Gates *et al.* 1965, Loomis 1965, Sinclair *et al.* 1971, Wooley 1971, Thomas and Barber 1974, Ehleringer and Björkman 1978, Ehleringer 1981). In general, green leaves absorb 85% of the visible wavelengths from the sun, and reflect approximately 10% of this radiation (Moss and Loomis 1952). Changing chlorophyll (Chl) content (for review see Šesták 1977) should affect the absorptance (% of visible radiation absorbed), but very few studies exist to show this. Gabrielson (1948) measured photosynthetic efficiency of plants as a function of total Chl content. He demonstrated that for most plants no further change in net photosynthetic rate (P_N) could be obtained when Chl content exceeded 40 µg cm^{-2}. However, Šesták (1963) found that P_N and Chl content were strongly correlated in both tobacco and cabbage up to chlorophyll contents of 50 µg cm^{-2}.

The purpose of this study was to measure the spectral characteristics of three cultivars of papaya over the lifetime of individual leaves in order to determine the relationships between Chl content and leaf absorptance. P_N was measured on the same leaves to see if changes in P_N and Chl content occurred in concert or independently.

MATERIALS AND METHODS

Papaya (*Carica papaya* L.) cultivars 4 × 2, 2 × 0.7, and South China were grown in a greenhouse at a 30/18 °C (day/night) air temperature, a 13/11 h photoperiod, and a midday irradiance (400–700 nm) of 1.2 mmol m^{-2} s^{-1}. Leaf age series were obtained by sampling leaves from different positions on single plants.

Leaf absorptance, transmittance and reflectance were measured on the upper leaf surface using a *Bausch and Lomb* high intensity grating monochromator with an Ulbricht integrating sphere (Ehleringer 1981). The leaf absorptance [%] was calculated as:

Absorptance = 100% − (Transmittance + Reflectance) %

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Leaf Chl contents and Chl *a*/*b* ratios were determined by extracting Chl in 90% acetone according to the method of Arnon (1949). The absorbances were measured with a *Beckman* Model *25* spectrophotometer. After individual leaf spectra had been measured, the same leaf disc was used for Chl analysis. Each sample was replicated 3–4 times.

Net photosynthetic rates were measured on intact, attached leaves using an open gas exchange system as described by Ehleringer and Björkman (1977).

RESULTS AND DISCUSSION

Absorptance spectrum: The shapes of absorptance spectra of mature leaves of three papaya cultivars were similar (Fig. 1): there were two broad peaks at 475 nm and 675 nm and a trough at 550–575 nm. The curves declined markedly beyond 700 nm with only a slight absorptance between 750 and 800 nm (about 5%). The absorptance maxima at 650–675 nm corresponded with the strongest absorption waveband of Chl *a*. The absorptance spectra when integrated with the solar spectrum at the earth's surface resulted in solar absorptance values of 84.7% (South

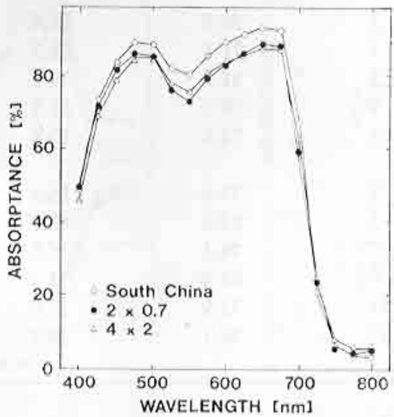

Fig. 1. Absorptance spectra of mature leaves of three cultivars of papaya between 400 and 800 nm.

Table 1

Chlorophyll (Chl) content, net photosynthetic rate (P_N) and leaf absorptance to solar radiation in the 400–700 nm waveband in three cultivars of papaya. Data are means ±1 standard error.

Cultivar	Chl content [$\mu g\ cm^{-2}$]	Chl *a*/*b* ratio	P_N [$\mu mol\ m^{-2}\ s^{-1}$]	Leaf absorptance [%]
South China	50.7 ± 2.3	3.27	8.2 ± 0.4	84.7 ± 0.1
4 × 2	46.7 ± 3.0	3.29	7.3 ± 0.6	82.2 ± 1.8
2 × 0.7	39.1 ± 2.7	3.22	6.6 ± 0.4	80.1 ± 1.3

China), 82.2% (4 × 2), and 80.1% (2 × 0.7). The higher absorptance in the visible region of cultivar South China suggested greater Chl contents. As expected there was agreement with solar absorptance and Chl content for the three cultivars (Table 1). Additionally, P_N of the cultivars was closely correlated with Chl content.

The leaf absorptance spectra changed with age (Fig. 2, *top*). The calculated leaf absorptance to solar radiation ranged from 82 to 59% in cv. South China (11 leaves) and 83 to 56% in cv. 2 × 0.7 (13 leaves) (Table 2). Unexpanded leaves (first, second) absorbed only 55–60% of the

Table 2

The relationship between leaf position (from the youngest leaf), leaf absorptance (400–700 nm), and chlorophyll (Chl) content in two cultivars of papaya.

Cultivar	Leaf position	Leaf absorptance [%]	Chl content [μg cm^{-2}]	Chl a/b ratio
South China	1	59.2	15.4	1.99
	3	71.1	28.7	3.62
	7	81.8	39.5	3.64
	9	79.2	31.7	3.81
	11	78.1	30.4	3.64
2 × 0.7	2	55.9	16.1	2.21
	5	82.6	42.7	3.44
	7	78.5	36.5	3.69
	9	81.4	33.3	3.86
	11	75.9	28.6	3.70
	13	76.1	22.7	3.06

visible solar radiation. The absorptance between 500 and 600 nm was lowest in the youngest leaves, and increased as leaves matured. Middle-aged leaves (fifth-seventh) had the highest leaf absorptance and appeared to also have the highest P_N (Lin and Ehleringer 1982). Older leaves exhibited a gradual decrease in leaf absorptance, but no significant changes in the shape of the absorptance spectrum.

These absorptance results are similar to those found for cotton leaves (Gausman *et al.* 1971) and Norway maple leaf (Malkina 1976). Gausman *et al.* (1971) reported that leaves from a variety of growth conditions (growth chamber, greenhouse, and field) showed an increase in leaf absorptance at 550 nm from node 2 to 8, followed by a gradual decrease to the older leaves at nodes 13 and 16. They concluded that middle-aged leaves had maximum leaf absorptance, although they were not able to measure leaf absorptance over the entire visible band. Malkina (1976) found that the greatest difference in leaf absorptance was in the green region. Our data also demonstrate that the effects of leaf age appear greatest in the 500 to 650 nm waveband (green-red region).

Reflectance spectrum. The highest reflectances were in the 725 to 800 nm portion of the spectrum (Fig. 2, *bottom*). Between 450 and 700 nm reflectances were approximately 15%, except for a small peak at 550 nm. The reflectance curves were essentially mirror images of absorptance spectra, suggesting that transmittance was low at all wavelengths. No reflectance differences were found among the three papaya cultivars. Leaf position had an effect on reflectance (Fig. 2, *bottom*) with the youngest leaves showing the greatest reflectance between 400 and 700 nm, but the lowest reflectance above 700 nm.

Gupta and Woolley (1971) reported that between 450 and 1800 nm, young soybean leaves reflected more than old leaves. The greatest difference in reflectance between young and old leaves was at about 550 nm. In contrast, an earlier study by Moss and Loomis (1952) found that yellow and orange leaves (older) had greater reflectances in the green region. A similar result was reported by Gausman *et al.* (1971) with greenhouse grown cotton leaves.

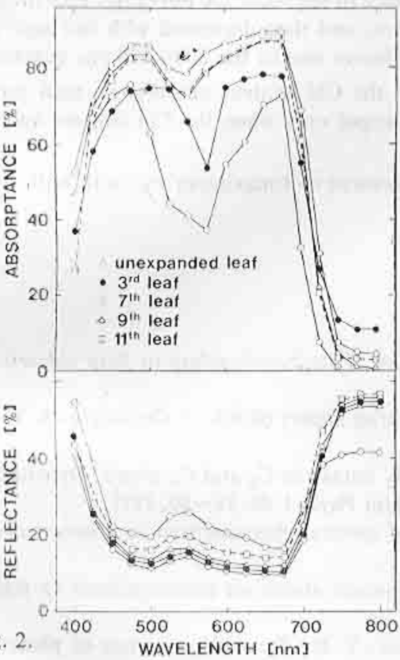

Fig. 2.

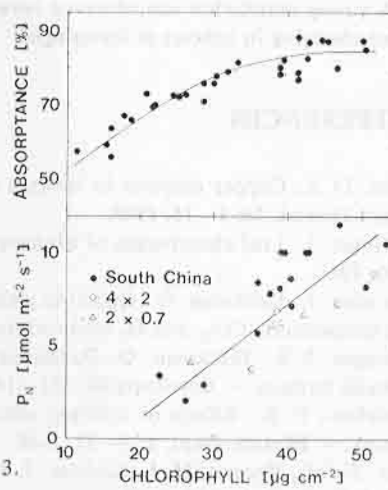

Fig. 3.

Fig. 2. Absorptance and reflectance spectra of leaves of different ages in papaya (cv. South China) between 400 and 800 nm.

Fig. 3. The relationship between leaf absorptance to solar radiation in the 400–700 nm waveband (*top*) or radiant energy saturated net photosynthetic rate, P_N (*bottom*) and chlorophyll content in papaya.

Chlorophyll content and absorptance: The leaf absorptance to solar radiation and the Chl content were strongly correlated (Fig. 3, *top*). The linear correlation coefficient was 0.89. Chl contents below 30 μg cm^{-2} resulted in a sharp decrease in leaf absorptance. The differences in optical properties were the result of using leaves of different age. The youngest papaya leaves had the lowest Chl content (15–16 μg cm^{-2}) and Chl *a*/*b* ratio (2-2.2). These values were only about half those of middle aged leaves. When compared with mature leaves, older leaves contained 54–70% of the Chl, and the Chl *a*/*b* ratio had decreased from 3.7 to 3.0.

The great changes in absorptance spectra between 500 and 625 nm in both unexpanded and senescent leaves demonstrated that this region was the most sensitive region of the spectrum to changes in pigment content.

A strong linear relationship was found between Chl content and P_N, regardless of the leaf age or cultivar (Fig. 3, *bottom*). By this relationship, we do not want to infer that photosynthetic capacity is limited by Chl content, but that as leaves age the P_N and Chl content decrease in concert.

Conclusions:

(*1*) The absorptance spectra over the visible waveband of three cultivars of papaya were similar. The leaf absorptances to solar radiation ranged between 80 and 84%. Differences among three cultivars can be accounted for by Chl content.

(*2*) Leaf age had an effect on absorptance and reflectance in the 400—700 nm range. Leaf absorptance increased to reach a maximum in mature leaves, and then decreased with leaf age. The great change in the absorptance spectra of different leaves was in the 500—625 nm waveband.

(*3*) Absorptance values were closely correlated with the Chl content of different aged leaves. However, the shape of the absorptance spectrum changed only when the Chl content and *a/b* ratio declined greatly.

(*4*) A strong correlation was observed between Chl content and maximum P_N, with both parameters changing in concert as leaves aged.

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