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Leaf absorptance of photosynthetically active radiation in relation to chlorophyll meter estimates among woody plant species

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Abstract

The quantum yield of photosystem II, determined by chlorophyll fluorescence and the quantum yield of CO_2 uptake, determined from gas exchange, are two physiologically important measurements in clarifying the response to environmental stress. Both measurements, however, require an accurate assessment of leaf light absorption in the photosynthetically active radiation wavelength range (400–700 nm). To date, integrating sphere and field-portable spectroradiometer measurements of leaf reflectance, transmittance, and absorptance are time consuming, costly, and cumbersome. It is therefore desirable to determine if SPAD meter chlorophyll concentration estimates could be used in lieu of an integrating sphere and field-portable spectroradiometer for determining leaf reflectance, transmittance, and absorptance in woody plant species.

An integrating sphere and field-portable spectroradiometer were used to measure reflectance, transmittance, and absorptance of leaf samples at 2 nm intervals between 400 and 700 nm. A paired SPAD 502 hand-held chlorophyll estimate was also determined for each sample. Regression analysis revealed a strong relationship between the SPAD estimate and leaf transmittance and absorptance. The reflectance relationship, although still present, was not as accurate. The study indicates that the

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SPAD meter could be used to provide a rapid estimate of leaf absorbance and transmittance in the 400–700 nm wavelength range in woody plant species.

Keywords: Absorptance; Chlorophyll; Reflectance; Transmittance

1. Introduction

Measurement of the quantum yield of photosynthesis is important when evaluating both the ability of a plant to tolerate environmental stresses and the extent to which those stresses have damaged the photosynthetic apparatus (Maxwell and Johnson, 2000). Quantification of the quantum yield of photosystem II can be determined by chlorophyll fluorescence (Genty et al., 1989), and the quantum yield of CO_2 uptake can be determined from gas exchange (Ehleringer and Björkman, 1977). Both measurements, however, require an accurate assessment of leaf light absorption. Currently, the nature of light-absorptance measurement requires the use of two bulky, expensive, and potentially time consuming instruments—namely an integrating sphere and field-portable spectroradiometer. It has recently been demonstrated, however, that leaf chlorophyll concentrations are linked to spectral characteristics (Carter and Knapp, 2001). The SPAD meter, a non-destructive, relatively inexpensive chlorophyll estimate meter, can provide a rapid estimate of extractable chlorophyll in leaves of several species (Marquard and Tipton, 1987; Monje and Bugbee, 1992; Sibley et al., 1996), and thus has the potential to significantly reduce the time and cumbersome nature of leaf absorptance measurements.

Ontogenic and stress factors can alter leaf chlorophyll concentrations in response to environmental cues, altering leaf light absorption. For example, chlorophyll and Rubsico contents decline as the leaf remobilizes resources in preparation for abscission. With respect to photosynthetically active radiation (PAR) absorption, chlorophyll and accessory pigments absorb strongly in the visible range, minimizing diffuse reflectance (Carter et al., 1992; Knipling, 1970). Characterizing leaf absorptance in response to chlorophyll degradation is important when chlorophyll concentrations are potentially altered in response to both natural ontogenic and/or stress factors. Carter and Knapp (2001) described a consistent stress alteration of leaf reflectance at visible wavelengths (∼400–720 nm). A possible explanation within these wavelengths, where chlorophyll is the major absorber in the leaf, may be the metabolic disturbance brought about by stress that alters the leaf chlorophyll concentrations (Knipling, 1970).

With respect to water stress, radiation absorbed by the leaf tends to decrease due to lower leaf H_2O content. Although water absorbs most strongly in the wavelengths of the infrared region of the spectrum from approximately 1300 to 2500 nm (Curcio and Petty, 1951), radiation absorbed by water still occurs at lower wavelengths. As water is lost from a leaf, reflectance increases and absorption decreases primarily as a result of water's radiative properties (e.g., Bowman, 1989; Hunt and Rock, 1989). Even after accounting for the radiative characteristics of water, secondary effects of water content on absorption by leaf pigments or other internal substances often occur (Carter, 1991). When Massantini et al. (1990) looked at *Amaranthus hypochondriacus* L. exposed to acute water stress at the leaf level, alteration of reflectance, absorptance, and total transmittance permitted precise detection of plant response to water stress. A relationship between chlorophyll content, spectral properties, and SPAD estimates of extractable chlorophyll, especially one that holds among genotypes and woody species, might enable the detection of water stress under field conditions.

The purpose of this study was to: (1) determine the degree to which reflectance, transmittance and absorptance responses to water stress may be related to SPAD meter chlorophyll concentration estimates in woody species; (2) characterize reflectance, transmittance, and absorptance responses to stress and chlorophyll degradation using the range of SPAD chlorophyll estimates found in water-stressed and unstressed leaves of maple genotypes, as well as chlorophyll-degraded and undegraded leaves of woody species; (3) determine if measurement of the adaxial versus abaxial leaf surface affects the relationship between SPAD readings and reflectance, transmittance, or absorptance estimates; and (4) determine if SPAD readings could be used in lieu of spectroradiometry.

2. Materials and methods

2.1. Water deficit experiment

2.1.1. Plant material

To compare the within-species response to water deficit, four genotypes of red maple were selected: 'Summer Red', October Glory®, 'Autumn Flame', and 'Franksred' (Red Sunset®), as well as one hybridized Freeman maple genotype, 'Jeffersred' (Autumn Blaze®) to represent a narrow range in spectral diversity and because basic information on chlorophyll concentrations and SPAD estimates already exist (Sibley et al., 1996). The five maple genotypes were transplanted into 56.7 l spin-out treated plastic pots containing a mixture of 20 pine bark:1 sand (by volume), fertilized with 8.3 kg m^{-3} of Nutricote™ 20N–3.0P–8.3K type 360 (Chiso-Asahi, Japan), and placed on an outdoor pad. Once the genotypes were transplanted, they grew outdoors under natural photoperiod and irradiance at a local SC nursery. Plants were irrigated four times daily to container capacity with pressure-compensating drip emitters (ML Irrigation, Laurens, SC). Plants were shipped to Clemson University on 7 August 2001, transferred to an outdoor gravel pad, and fitted with identical pressure-compensating drip emitters. Initially, all pots were watered to saturation and permitted to drain for 18 h. Plants were irrigated six times daily to container capacity prior to imposing drought. Pots were spaced 1.5 m center-to-center. For each genotype, treatments consisted of a well-watered control ($n = 6$) and a drought treatment where water was withheld to approximately 0.09 $m^3 \cdot m^{-3}$ ($n = 6$). To eliminate evaporation from the substrate surface or water penetration in case of rain, white plastic bags were cut and sealed to the stem with Parafilm (American National Can™, Greenwich, CT). The bottom ends of the bags were left open and secured to the pots with an elastic fit. Wrapping the exterior of each container with aluminum foil reduced radiation load on containers.

2.1.2. Water measurements

After drainage and thereafter on alternate days, bulk volumetric water content of each container was measured in four locations with a Theta Probe type ML2 (Delta-T Devices, Cambridge, England) at 10 and 20 cm below the rooting medium surface. The readings were taken in pre-drilled locations on opposite sides of the pot. Drilled holes were large enough to allow the probe adequate movement and contact with the substrate surface within the container. The readings were then averaged in order to estimate bulk volumetric water content for each container. In order to minimize the chances of leaf abscission and variation in bulk volumetric water content, a preliminary experiment ($n = 6$) was conducted to derive non-lethal bulk volumetric water content over time (Bauerle et al., 2003).

2.1.3. *Measurements of leaf absorptance and SPAD readings*

Leaf optical responses to drought stress were examined at two extreme substrate moisture conditions. The substrate moisture status of each plant was assessed individually. When an individual replicate of a given cultivar reached ~0.070 $m^3 \cdot m^{-3}$, a spectroradiometer (LI-1800 with 1800-12S integrating sphere attachment; LI-COR, Lincoln, NE) was used to measure leaf reflectance and transmittance on the first fully expanded non-damaged leaf of the first lateral from the terminal tip. A leaf was clamped into position over the sample port on the sphere wall and a 1.65 cm^2 leaf area was irradiated by the beam from a tungsten halogen lamp.

Reflectance and transmittance were measured for each of the six replicates per genotype per treatment. Each leaf remained attached to the stem until immediately before reflectance and transmittance determinations. Immediately upon excision, a reference scan and a sample scan were made from 400 to 700 nm at 2 nm intervals for both reflectance and transmittance. The sample scan was multiplied by 100 and divided by the reference scan to yield percentage units. These values were integrated over the 400–700 nm wavelength range and divided by the number of spectroradiometer channels to obtain spectral averages. Percentage leaf absorptance (400–700 nm average) was computed as: $100 - (\text{reflectance} + \text{transmittance})$.

Upon completion of spectral estimates, leaf chlorophyll concentrations were estimated with a Minolta SPAD 502 chlorophyll meter (Minolta Camera, Ramsey, NJ). The SPAD reading, which is correlated with leaf chlorophyll concentration in red maple cultivars (Sibley et al., 1996), uses a silicon photodiode to derive the ratio of transmittance through the leaf tissue for spectral bands at 650 and 940 nm wavelengths. For each leaf, the leaf area sampled for spectral properties was designated and also used for SPAD measurements.

2.1.3.1. Chlorophyll-degraded experiment. To compare species responses to simulated chlorophyll degradation, three species of woody plants (forest production, landscape ornamental, and fruit production) were chosen to represent across-commodity long-lived perennials. Specifically, *Populus trichocarpa* × *P. deltoids* F_1 hybrid clone 15–29 (hybrid poplar), *Acer rubrum* L. 'Summer Red' (red maple), and orchard selection *Prunus persica* 'Redhaven' on BY520-9 rootstock (peach) were used from an existing nursery and orchard block. Hybrid poplar and red maple were transplanted into containers during June 2002 following protocols of the water deficit experiment. The other species, peach, was part of an established in-ground orchard located at the Clemson University Musser Farm. Leaves were harvested from hybrid poplar and red maple (50 each) and peach (100) over a 3-week period (1–21 August 2002). As in the water deficit experiment, a spectroradiometer with the1800-12S integrating sphere attachment was used to measure leaf reflectance and transmittance on the first fully expanded non-damaged leaf on the terminal tip. Integrating sphere and SPAD meter protocols followed those of experiment 1 unless otherwise noted. Reflectance and transmittance were measured for each of the 50 replicate leaves on hybrid poplar and red maple under non-chlorophyll-degraded conditions. Once the reflectance and transmittance measurements were completed, five SPAD estimates were taken and averaged within the leaf area measured by the spectroradiometer. To manipulate the chlorophyll concentration in vitro, we submersed the leaf in 99% methanol for 1 h and identical measurements were again taken (Carter and Knapp, 2001). Identical measurements were taken on 100 replicate peach leaves without chlorophyll degradation. Methanol was not used on the peach due to midrib instability after the application of methanol. Overall, 100 paired spectroradiometer and SPAD meter estimates were taken on each of these three species. Lastly, reflectance and transmittance were measured for each of the 10 and 9 replicate leaves with and without 99% methanol on *Quercus shumardii* (Shumard Oak) and *Prunus serotina* (black cherry), respectively. These plants were part of an existing nursery stock block and were used to probe for possible deviations in the relationship between SPAD and spectroradiometer estimates among woody species.

2.2. Experimental design and data analysis

The two irrigation treatments (control and drought) were randomly assigned to five red maple genotypes that were arranged on a gravel pad in a completely randomized design with six replications. The relationship between spectral measurements (reflectance, transmittance, and absorptance) and SPAD readings of sampled leaves was characterized by fitting appropriate exponential models using nonlinear least squares. The 'extra sum of squares' principle was employed to provide the necessary information for making comparisons among fitted response curves (Draper and Smith, 1966). Hypothesis testing was performed using the 5% probability level.

3. Results

Fig. 1 illustrates the relationship of spectrally-averaged reflectance, transmittance, and absorptance with SPAD readings for 60 non-randomly chosen leaf samples of red maple genotypes. Transmittance and absorptance were found to be closely correlated with SPAD values across the range of observations. Water stress did not appear to alter the nonlinear relationship for reflectance ($P = 0.115$), transmittance ($P = 0.357$), or absorptance ($P = 0.232$). In addition, the relationship between leaf chlorophyll estimates and spectroradiometer measures did not appear to vary among genotypes (Fig. 1). Fig. 2a and b illustrates the percent of light reflected in the 400–850 nm wavelengths that corresponded with water stress in red maple genotypes. Differences in percent reflectance in response to stress was determined by subtracting the control reflectance from reflectance curves representing the stressed states. The resulting difference curves indicate the wavebands in which reflectance changed most greatly with stress (Fig. 2b). Although increased reflectance was observed, it was less than 1% throughout the wavelength range.

Relationships between instrument values similar to those in Fig. 1 were observed for the data presented in Fig. 3; these include measurements taken from leaf samples on five

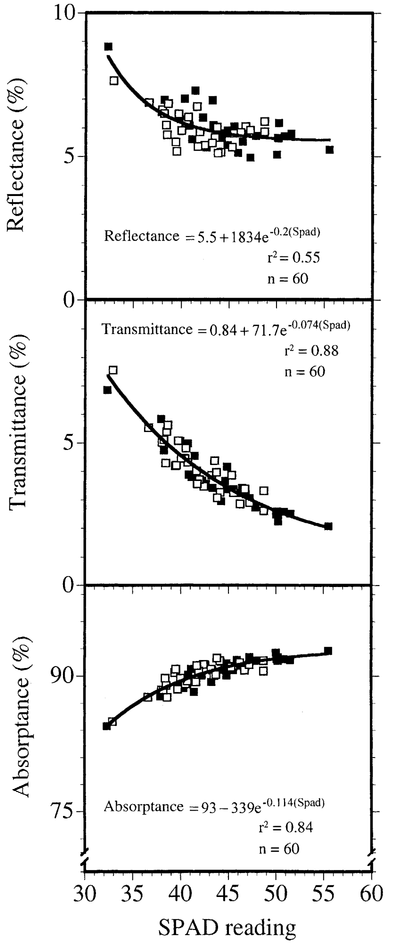

Fig. 1. Relationships between spectrally-averaged (400–700 nm) leaf reflectance, transmittance, and absorptance to SPAD readings in well watered (■) and drought stressed (□) maple genotypes.

species and both sides of the leaf. We looked at the statistical difference in the relationship at the species level for red maple and hybrid poplar. Relationships for reflectance, transmittance, and absorptance were determined to be statistically different, however, the differences were not considered to be biologically meaningful and were attributed to the extreme sensitivity achieved with the large data set. We also tested the difference between measurements taken on the adaxial versus abaxial sides of the leaf. Statistically different relationships ($P < 0.001$) were found between the adaxial and abaxial for all three parameters, i.e. reflectance, transmittance, and absorptance. These statistical differences are illustrated by shifts in reflectance and absorptance magnitude. Reflectance increased and absorptance decreased on the abaxial as compared with adaxial surfaces. Although values differed between leaf sides, the results suggest that SPAD readings could be used to provide

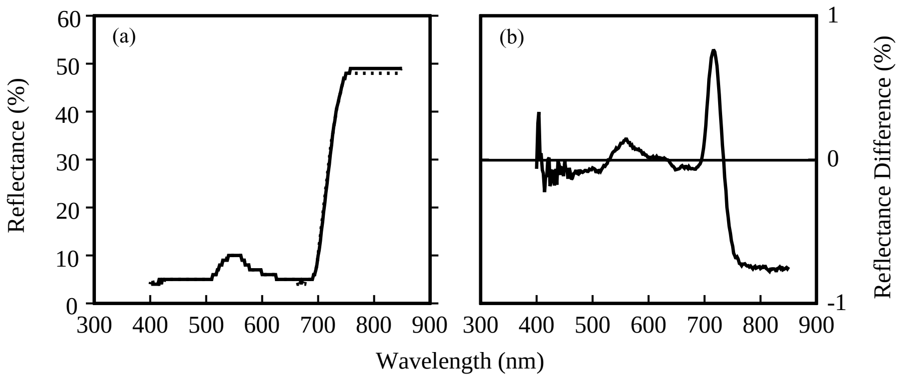

Fig. 2. Mean responses of leaf spectral reflectance to drought stress. The solid line represent mean leaf reflectance, whereas the broken line represents the water stress treatment (a). A reflectance difference curve (b) was computed by subtracting mean reflectance of the control state from that of the stressed state. Note the different vertical axis scales in (a) and (b).

a rapid and reasonably accurate estimate of leaf transmittance and absorptance. However, separate curves should be developed per leaf side.

4. Discussion

Leaf chlorophyll content is often highly correlated with leaf N status, photosynthetic capacity, and RuBP carboxylase activity (Evans, 1983; Seemann et al., 1987). This study provides evidence that SPAD values, which are estimates of leaf chlorophyll content, are nonlinearly correlated to leaf reflectance, transmittance, and absorptance. Moreover, our experiments show constancy within and among species subjected to two different treatments. SPAD values and leaf absorptance, transmittance, and reflectance presented a closely correlated relationship across a broad range of values. The relationship did not differ between well irrigated and water-stressed red maple genotypes and among five species of woody plants. Together, these results suggest that SPAD readings could be used to provide a rapid and reasonably accurate estimate of woody plant leaf absorptance and transmittance under a variety of stress related responses. SPAD estimates, however, although related to leaf reflectance, are not as accurate in predicting leaf reflectance on either the adaxial or abaxial side of woody plant leaves. Although a statistical difference was found between measurements from the adaxial versus the abaxial side of the leaf, it is unlikely that that the difference is biologically meaningful, but rather is a result of an increase in reflectance on the abaxial side of the leaf. Overall, the relationships are consistent with respect to either the adaxial or abaxial side of the leaf, but sampling should correspond to the side of concern.

Chlorophyll content is a sensitive indicator of plant stress (Palta, 1990). Carter et al. (1992) hypothesized that increase in leaf reflectance in response to environmental conditions may be a result of decreased chlorophyll content, which provides a link between chlorophyll content and leaf spectral characteristics. In addition, reflectance response to environmental

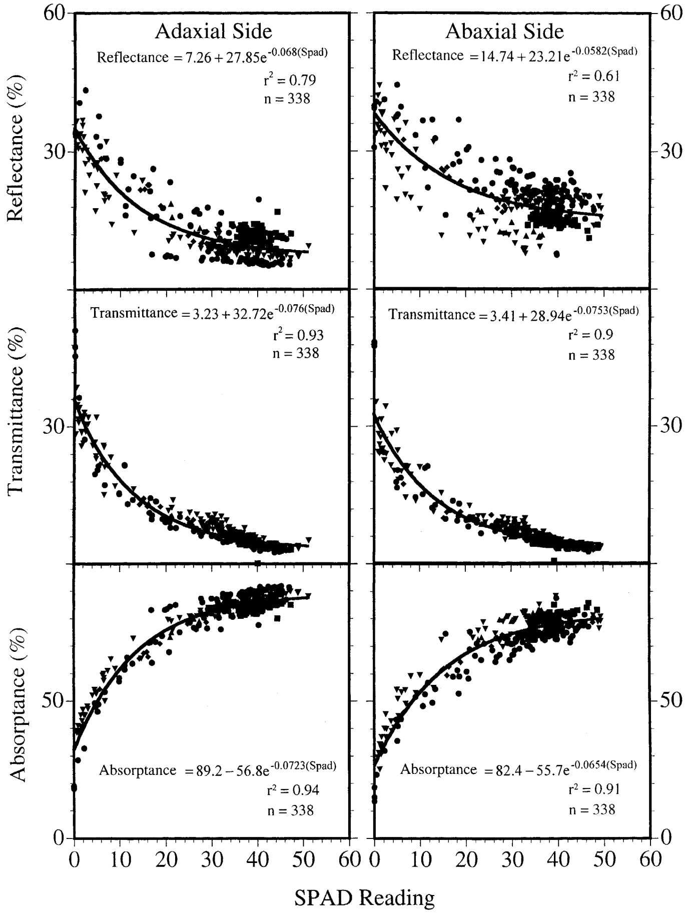

Fig. 3. Relationship between spectrally-averaged (400–700 nm) leaf reflectance, transmittance, and absorptance to SPAD readings in red maple (●), hybrid poplar (▼), peach (■), Shumard Oak (◆), and black cherry (▲) and for adaxial and abaxial sides of the leaf.

conditions does not appear to be unique among species, supporting the notion that plant physiological responses to stress are similar regardless of the cause of stress (Chapin, 1991; Carter et al., 1992). A small change in chlorophyll concentration could, therefore, have a large effect on leaf absorptance, and thus reflectance and transmittance, due to the fact that absorption is an exponential function. Carter (1993) found that leaf spectral reflectance is most likely to indicate plant stress within the PAR wavebands, specifically 535–640 and 685–700 nm. Our data support these wavelength ranges, however, the 1% effect observed in Fig. 2 may not be enough to diagnose water stress.

Leaf spectral properties are more consistently altered in response to stress in the visible wavelengths rather than in the remainder of the incident solar spectrum (Carter, 1993, 1994). This alteration of spectral properties in the visible wavelengths is more likely a result of a loss in chlorophyll. Alternatively, the arrangement of cells within a leaf could increase and/or decrease transmitted light by adjustment of the optical pathlength through the leaf (Vogelmann, 1986). Recently, Field et al. (2001) explored the role of anthocyanins in senescing leaves of *Cornus stolonifera*. The study indicates that anthocyanins are screening pigments that reduce light capture of chloroplasts by optically masking chlorophyll. If so, the potential anthocyanin accumulation could bring into question the validity of the SPAD meter/spectroradiometer relationship. However, Merzylak et al. (1999) illustrated that optical changes during leaf senescence are primarily confined to the 400–500 nm wavelength range, which is outside the spectral range to which the SPAD meter is sensitive.

One of the objectives of this study was to determine the degree to which reflectance, transmittance and absorptance responses may be related to SPAD meter chlorophyll concentration estimates in the leaves of woody species. Our findings indicate that the SPAD meter could accurately predict leaf transmittance and absorptance. The SPAD absorbance estimate is very important because it can then be used to aid in quantification of the quantum yield of photosystem II determined by chlorophyll fluorescence, and in the quantum yield of CO_2 uptake from gas exchange. The accuracies of the relationships between SPAD meter readings and absorptance estimates, however, are dependent on the accuracy with which the reflectance reference of the integrating sphere is known (Earl and Tollenaar, 1997). We performed a preliminary experiment to verify that our reference was 1.00 in the 400–700 nm range. The relationship between the two instruments appears to be good as long as attention is given to accurate sampling and measurement techniques.

In conclusion, the SPAD meter could be used in lieu of an integrating sphere and field-portable spectroradiometer to accurately estimate leaf absorptance and transmittance in a rapid and non-destructive fashion. Caution should be exercised when using different individual SPAD 502 units because readings can vary between units (Earl and Tollenaar, 1997). A relationship between SPAD readings and absorptance, transmittance, and reflectance should be determined on an individual meter basis. In addition to variation among SPAD meters, caution should also be taken when extrapolating measurements to species that do not have a documented relationship between chlorophyll concentration and SPAD values.

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