ESTIMATION OF CANOPY PHOTOSYNTHETIC AND NONPHOTOSYNTHETIC COMPONENTS FROM SPECTRAL TRANSMITTANCE

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Abstract. Spectral transmittance signatures (expressed as absorbances) were studied as a potential indicator of photosynthetic and nonphotosynthetic contributions to the canopy-absorbed photosynthetically active radiation (PAR). An analytical approach was made under laboratory conditions using synthetic canopies in an integrating sphere. This approach provided the basis for identifying spectral (absorbance-based) features and indices to estimate green (photosynthetic) and nongreen (structural and dead materials) contributions to canopy absorbance. A strong relationship was found between the amplitude of the first derivative of the absorbance (Aᵣₑ) and green area, while the integrated absorbance in the PAR region (Aᵣₑ / Aᵣₑ PAR) mainly responded to variations in total area. The ratio Aᵣₑ / Aᵣₑ PAR was closely correlated to the fraction of photosynthetic area to total area (i.e., the canopy green fraction). Similarly, the ratio and normalized difference of the absorbances at 680 and 900 nm (Aₛᵣ and Aₑᵣₑₑₑ) closely tracked variations in the canopy green fraction. Subsequently, these indices were tested in field plots with contrasting structural characteristics. Under field conditions, Aᵣₑ was a good indicator of green biomass. The indices Aₛᵣ and Aₑᵣₑₑₑ were also reliable indicators of green biomass but were affected by changes in sampling conditions. As in the lab study, Aᵣₑ / Aᵣₑ PAR was a good indicator of canopy green fraction. Thus, ground-based measurements of canopy spectral transmittance provided a tool for determining the photosynthetic contribution to canopy-absorbed PAR by correcting for nonphotosynthetic canopy components. Moreover, Aᵣₑ showed a strong correlation with conventional vegetation indices derived from spectral reflectance measurements. This technique could be a useful tool for plant ecophysiology studies and a field-validation method for remote-sensing studies.

Key words: absorbed photosynthetically active radiation; Beer-Lambert law; field methods, plant ecophysiology; green vegetation biomass; green vegetation fraction; leaf area index; light transmittance; Mediterranean-climate vegetation; spectral absorbance; spectral vegetation indices.

INTRODUCTION

Leaf area index (LAI), the one-sided total leaf area per unit ground area, is an important canopy structural parameter linked to a number of ecophysiological processes such as evapotranspiration and photosynthesis (Jarvis and Leverenz 1983). LAI is related to light interception which, in turn, is linked to productivity for a variety of ecosystems and, thus, is a key parameter for monitoring plant development and stress and for modeling studies (Norman 1993).

Direct LAI measurements are difficult and time consuming due to the great spatial variability in natural ecosystems. Destructive harvest of leaves is labor intensive and often impracticable. Thus, methods based on allometry, litterfall, and optical techniques are currently used to estimate leaf area. Allometric equations are typically site specific and, thus, error prone (Burton et al. 1991, White et al. 1997). Litterfall collection approaches are slow and require estimates of specific leaf area (SLA, cm²/g; Vose et al. 1995). Furthermore, this methodology is not useful for evergreen forests where the litterfall may be weakly related to new growth. Moreover, with these methods it is difficult to follow the spatial and temporal dynamics of leaf area development (Chason et al. 1991). By contrast, indirect procedures based on the measure of light transmittance through plant canopies allow rapid and low-cost measurements (Pierce and Running 1988).

Ground measurements of photosynthetically active radiation (PAR) transmittance have been used to derive LAI values based on the Beer-Lambert law for exponential light extinction in plant canopies. Accordingly,

\[ I/I_o = \exp(-K \times \text{LAI}) \]

where \( I \) is the irradiance at the depth \( z \) from the top of the canopy, \( I_o \) is irradiance at the top of the canopy, LAI is the projected Leaf Area Index, and \( K \) the leaf
extinction coefficient for PAR (Jarvis and Leverenz 1983).

The term \((1 - [I/If])\) represents the fraction of intercepted PAR (f\(\text{PAR}\)). Fractional intercepted PAR differs from the fraction of absorbed PAR (f\(\text{APAR}\)) due to PAR being reflected from the soil or litter surface and from the canopy. In open canopies, f\(\text{PAR}\) underestimates f\(\text{APAR}\), particularly when LAI < 1 (Prince 1991), because a fraction of PAR reflected from the ground may be reabsorbed by the canopy. In contrast, in dense canopies, f\(\text{PAR}\) slightly overestimates f\(\text{APAR}\) because a small fraction of PAR is reflected by canopy elements, but the differences are small as long as full green canopies are present (Gallo and Daughtry 1986).

Most ground-transmittance-based measurements involve broadband PAR sensors which cannot readily distinguish absorption by photosynthetic (green) material from absorption by dead or nonphotosynthetic (nongreen) material (Gholz et al. 1991, Gamon et al. 1995, White et al. 1997). Thus, when the contribution of nongreen components to the canopy f\(\text{APAR}\) is large, the relationships between LAI and f\(\text{PAR}\) or f\(\text{PAR}\) become more complex and can lead to an overestimation of either LAI or f\(\text{APAR}\) based on absorbance of photosynthetic material. Moreover, f\(\text{PAR}\) yields a good estimation of LAI in uniform canopies provided that the spatial distribution of leaves is random and the distribution of leaf angles is spherical (Goudriaan 1977). To account for deviations from these assumptions most of the current models of radiation attenuation through canopies (e.g., Li and Strahler 1985, Myneni and Asrar 1993) incorporate a geometrical component that characterizes the spatial distribution of canopy elements.

Broadband PAR (light bars or ceptometers) sensors have been used to derive LAI values in coniferous forests (Pierce and Running 1988, Lathrop and Pierce 1991) and in broad-leaved stands (Vose et al. 1995). However, unless the extinction coefficient is well-known and calibrated to exclude the absorption from branches and stems, the derived values represent the total surface area of all the plant components (Plant Area Index, PAI) instead of the LAI (Larsen and Kershaw 1996). In several studies the extinction coefficients have been derived by inverting the equation and using direct measurements of LAI or allometric equations. However, the light extinction coefficient has been reported to be both site and species dependent (Boldstad and Gower 1990, Vose et al. 1995) and LAI dependent within species (Sampson and Smith 1993). Thus, the selection of an appropriate \(K\) is a topic of debate especially in those situations where there is great species diversity and plant density.

Other methods based on differential measurements of light above and below the canopy for LAI estimation require measurements at two or more zenith angles. One of the more commonly used instruments is the LAI-2000 Plant Canopy Analyzer (LI-COR, Lincoln, Nebraska, USA) for it provides immediate LAI estimates, provided certain key assumptions are met (Welles 1990). This instrument measures transmittance of blue diffuse light (400–490 nm) and has been used to estimate leaf area index in conifer (Gower and Norman 1991, Chen 1996) and broad-leaved stands (Cutini et al. 1998). Recently, LAI estimates in grasslands have also been obtained using the LAI-2000 (White et al. 1997). However, corrections for foliage clumping (Gower and Norman 1991, Chen 1996) need to be done in order to obtain reliable LAI values. Moreover, since the instrument sees not only leaves but also branches and stems, its estimates often correspond more closely to the PAI (Smolander and Stenberg 1996), further confounding estimation of photosynthetic canopy material. Thus, in making optical measurements, the contribution of nonphotosynthetic materials has to be removed. Correction factors for woody to total area ratio are obtained through labor-intensive destructive sampling and entail a major workload in making optical measurements (Chen 1996). Optical measurements might be also corrected using allometrically estimated LAI, but errors in site allometry should be taken into account when applying a single clumping coefficient (White et al. 1997).

Remotely sensed vegetation indices provide another way to estimate LAI and f\(\text{PAR}\). Furthermore, vegetation indices have been found to primarily respond to green LAI and to f\(\text{APAR}\) by green vegetation (Hall et al. 1992, Goward et al. 1994, Gamon et al. 1995). There are, however, large uncertainties in the estimates of either LAI or f\(\text{APAR}\) with remote sensing. Several studies have indicated variations in the relationship between vegetation indices and LAI caused by phenology, woody parts, or litter (Bartlett et al. 1990, van Leeuwen and Huete 1995). Significant scatter in the relationship between vegetation indices and f\(\text{PAR}\) may arise from a number of factors, including poor characterization of background contributions to scene reflectance and inadequate characterization of interception by nonphotosynthetic elements of the canopy (Goetz and Prince 1996). As most ground validation methods involve indirect estimation based on allometric or optical methods described above, inaccurate estimates of green and nongreen fraction may be a primary reason for continued uncertainties. The development of field methods based on simple and fast measurements would enable improved estimates of LAI and f\(\text{APAR}\) by green leaves. For remote sensing and modeling studies, this information is crucial to derive and validate the relationships of vegetation indices and the canopy biophysical variables.

Because spectral signatures respond distinctly to photosynthetic (hereafter “green”) and nonphotosynthetic (“nongreen”) canopy materials, and because of the coupled behavior of reflectance, transmittance, and absorbance, we hypothesized that spectral transmittance measurements could be used to characterize amounts of green and nongreen materials in vegetation
canopies. In this article, we explore this possibility by measuring spectral transmittance (expressed as spectral absorbance) instead of a single integrated discrete band of PAR or blue diffuse light. A first approach to this technique was conducted by synthesizing artificial canopies in the laboratory under controlled conditions to establish the validity of the hypothesis. Subsequently, we conducted a field study using natural canopies with varying structural characteristics and phenology to assess the capabilities of this technique under actual field conditions. Finally, we studied the relationships of these absorbance measures with reflectance indices obtained in the same fieldplots with the final aim of testing absorbance measures as a field validation tool for remote sensing studies.

**METHODS**

**Lab experiment on synthetic canopies**

The study was conducted with *Pseudotsuga menziesii* (Douglas fir) branch tips in a cardboard integrating sphere (~30 cm diameter) with a spectroradiometer as a detector. The inside of the sphere was sealed with several layers of barium sulfate suspension (white reflectance coating #6080, Eastman Kodak, Rochester, New York, USA). Illumination was provided by a diffuse light source (Osram halogen 64488, Osram Sylvania, Danvers, Massachusetts, USA) placed at the top of the sphere.

The experiment followed a factorial design, combining various numbers of green and nongreen branch tips to create synthetic canopies. Twig samples were obtained from the current year’s live branches containing live needles (green) and from dead branches containing brown-colored dead needles from previous years’ growth (nongreen). Measurements were taken by progressively increasing the number of green branch tips (from 0 to 5) and by combining them with an increasing number of brown branch tips (0–5). Branch tip samples were ~5–10 cm long, and were placed side by side on a transparent tape medium and positioned inside the integrating sphere.

Absorbance of the samples was measured using a spectroradiometer (SE 590 WB-R, Spectron Engineering, Denver, Colorado, USA) fitted with a cosine head sensor placed on a port at the bottom of the integrating sphere. This instrument measures 252 bands from ~390 to 1100 nm every 3 nm, with 11 nm spectral resolution. To minimize the potential effect of temperature drifts on lamp output, irradiance spectra for each canopy configuration were taken 5 s after turning on the light. Each final irradiance spectrum was the mean of four scans. Absorbance values were obtained as follows:

\[
\text{Absorbance} = \log \left( \frac{I_e}{I} \right)
\]

where \(I_e\) is the irradiance within the empty sphere, and \(I\) is the irradiance with the sample in the sphere.

Absorbance was calculated both as a function of wavelength (spectral absorbance) and as a broadband absorbance in the red and near infrared. To simulate a broadband sensor, absorbances in the PAR \((A_{PAR})\) and the near infrared \((A_{NIR})\) regions were calculated by integrating absorbances at single narrowbands between 400 and 700 nm and between 700 and 1000 nm, respectively.

After the irradiance measurements were completed, projected leaf and stem measured areas were determined with a flatbed scanner (Scannaker IXF, Microtek Lab, Torrance, California, USA). Images were digitized using Adobe Photoshop (Adobe Systems, Mountain View, California, USA) and analyzed for area using IPLab Spectrum (Signal Analytics, Vienna, Virginia, USA). Per branch areas were then summed up according to the arrangement of the green and brown branches in the sphere allowing the determination of the spectral absorbance as a function of green, nongreen, and total area.

**Field study on natural vegetation**

**Study area.**—The field study was conducted during 1995 and 1996 in the Santa Monica Mountains (34°5' N, 118°40' W) and near the San Gabriel Valley (34°5' N, 117°45' W) in Los Angeles County, California, USA. Vegetation was typical of California chaparral and coastal sage scrub (Munz and Keck 1959) and included grassland and chaparral species representing different stages of postfire succession (Table 1).

In the Santa Monica Mountains, plots were located at Stunt Ranch Reserve and the adjacent Cold Creek Canyon watershed, managed by the University of California, Los Angeles and the Santa Monica Mountains Restoration Trust, respectively. This region was selected for its low biomass, resulting from a fire occurring three years earlier. Twelve plots were measured at Cold Creek Canyon, six in spring 1995 and six during fall 1995 with pronounced differences in canopy green fraction between seasons. At Stunt Ranch, a total of seven plots were measured: three north-oriented plots and four south-oriented plots providing a clear contrast of biomass and phenology due to differential successional patterns on north and south slopes.

In the San Gabriel Valley, plots were located at Bernard Field Station, a natural reserve of the Claremont Colleges. In this field site vegetation was composed of grasslands (mixed forbs and grasses) and shrubs characteristic of coastal sage scrub (Munz and Keck 1959). Four plots were sampled.

**Absorbance.**—Light transmittance was measured using a spectral radiometer that consisted of a hemispheric cosine-corrected fore-optic (1800-11 remote cosine receptor, LI-COR, Lincoln, Nebraska, USA) attached to a spectroradiometer (Spectron SE-590 with a CE390 WB-R detector; Spectron Engineering, Denver, Colorado, USA) with a 1.5 m long custom-made fiber optic. The fiber optic allowed the sensing fore-
Table 1. Vegetation types and species considered in this study.

<table>
<thead>
<tr>
<th>Species</th>
<th>Phenology</th>
<th>Field site</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Amsinckia menziesii</em> (var. intermedia)</td>
<td>annual</td>
<td>BFS</td>
</tr>
<tr>
<td><em>Erodium botrys</em></td>
<td>annual</td>
<td>BFS</td>
</tr>
<tr>
<td><em>Lupinus sp.</em></td>
<td>annual</td>
<td>BFS</td>
</tr>
<tr>
<td><em>Vicia sp.</em></td>
<td>annual</td>
<td>BFS</td>
</tr>
<tr>
<td><em>Arabis glabra</em></td>
<td>perennial</td>
<td>BFS</td>
</tr>
<tr>
<td><em>Bromus sp.</em></td>
<td>annual</td>
<td>SR</td>
</tr>
<tr>
<td>Post-fire species</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Lotus scoparius</em></td>
<td>perennial</td>
<td>SR</td>
</tr>
<tr>
<td><em>Calystegia macrostegia</em></td>
<td>perennial</td>
<td>SR, CCC</td>
</tr>
<tr>
<td>Chaparral shrubs/Coastal sage scrub</td>
<td>drought-DECIDUOUS</td>
<td>BFS</td>
</tr>
<tr>
<td><em>Artemisia californica</em></td>
<td>evergreen</td>
<td>CCC</td>
</tr>
<tr>
<td><em>Adenostoma fasciculatum</em></td>
<td>evergreen</td>
<td>SR</td>
</tr>
<tr>
<td><em>Ceanothus cuneatus</em></td>
<td>evergreen</td>
<td>BFS</td>
</tr>
<tr>
<td><em>Eriodictyon crassifolium</em></td>
<td>evergreen</td>
<td>CCC</td>
</tr>
<tr>
<td><em>Malosma laurina</em></td>
<td>evergreen</td>
<td>SR</td>
</tr>
<tr>
<td><em>Quercus dumosa</em></td>
<td>evergreen</td>
<td></td>
</tr>
</tbody>
</table>

*Note:* Species nomenclature is consistent with Hickman (1993). Abbreviations: BFS, Bernard Field Station; SR, Stunt Ranch; CCC, Cold Creek Canyon.

optic to be inserted well into the canopy avoiding edge effects and ensuring that measurements were not contaminated by the presence of the operator. The instrument was held in a horizontal position using a bubble level. In 1995 we took measurements in Cold Creek Canyon on 20 May and 20 October, and in 1996 measurements were taken on 24 April at Bernard Field Station and on 30 May at Stunt Ranch. Table 2 summarizes the absorbance and reflectance sampling conditions.

To overcome the small dimensions of the sensor, a large number of below-canopy measurements were made at each plot. One hundred measurements were taken at 10-cm intervals along two perpendicular axes of a 1-m² area, except at Cold Creek Canyon, where there were 10 below-canopy measurements per sampled area. Each measurement consisted of eight scans averaged to reduce instrument noise. For every 10 measurements underneath the canopy ($I_1$) a measurement was taken at the top of the canopy or at the nearest canopy gap to record the above-canopy irradiance ($I_0$). Canopy light transmittance was expressed as absorbance ($A$):

$$A = \log \left( \frac{I_0}{I_1} \right).$$

Results are presented as plot-averaged single-absorbance measurements.

Reflectance.—Canopy reflectance was measured on the same plots where absorbance was determined using a pair of attached spectrometers (S590 Spectron) mounted on a self-leveling plate attached to a tripod boom. Radiance data were acquired using a detector fitted with a 15° field of view foreoptic in a nadir orientation -1 m above the canopy. Nine or ten radiance spectra and two irradiance spectra were taken at each plot; each spectrum consisted of eight scans automatically averaged. Irradiance spectra were taken with a second identical detector outfitted with a hemispheric, cosine-corrected fore-optic oriented towards the sky. In order to calculate reflectance, the two detectors were cross-calibrated by comparing the upward-looking sensor to the downward-looking sensor positioned above a white standard (Spectralon, Labsphere, North Dutton, New Hampshire, USA). At Cold Creek Canyon reflectance measurements were taken on 20 May and 20 October. At Bernard Field Station measurements were taken on 15 April and at Stunt Ranch on 25 April. Reflectance and absorbance measurements were taken at comparable times and sun conditions, facilitating comparison of spectral absorbance to spectral reflectance. Dates and times of all measurements are summarized in Table 2.

Biomass and ceptometer readings.—Aboveground biomass was determined by destructive sampling in the

Table 2. Field sampling protocol for absorbance and reflectance measurements at Cold Creek Canyon (CCC), Bernard Field Station (BFS), and Stunt Ranch (SR).

<table>
<thead>
<tr>
<th>Field site</th>
<th>Plots†</th>
<th>Harvest area</th>
<th>Absorbance measurements</th>
<th>Reflectance measurements</th>
</tr>
</thead>
<tbody>
<tr>
<td>CCC (spring)</td>
<td>6</td>
<td>0.28 m²</td>
<td>20 May 1995 1136–1544 10</td>
<td>20 May 1995 1136–1544 10</td>
</tr>
<tr>
<td>CCC (fall)</td>
<td>6</td>
<td>0.28 m²</td>
<td>20 October 1995 1210–1441 10</td>
<td>20 October 1995 1206–1426 10</td>
</tr>
<tr>
<td>BFS</td>
<td>5</td>
<td>1 m²</td>
<td>24 April 1996 1115–1312 100</td>
<td>24 April 1996 1115–1312 9</td>
</tr>
<tr>
<td>SR</td>
<td>7</td>
<td>1 m²</td>
<td>30 May 1996 1130–1500 100</td>
<td>24 May 1996 1139–1317 9</td>
</tr>
</tbody>
</table>

† Number of plots sampled.
‡ Number of scans/plot.
TABLE 3. Green and total biomass and green fraction (green biomass/total biomass; G/T) in field plots.

<table>
<thead>
<tr>
<th>Field site</th>
<th>Green biomass</th>
<th>Total biomass</th>
<th>G/T</th>
<th>IPAR</th>
</tr>
</thead>
<tbody>
<tr>
<td>BF</td>
<td>9.2</td>
<td>3538.9</td>
<td>0.00</td>
<td>0.78</td>
</tr>
<tr>
<td>CCC (fall)</td>
<td>0</td>
<td>385.0</td>
<td>0.00</td>
<td>0.65</td>
</tr>
<tr>
<td>CCC (fall)</td>
<td>0</td>
<td>562.2</td>
<td>0.00</td>
<td>0.91</td>
</tr>
<tr>
<td>CCC (fall)</td>
<td>5.1</td>
<td>344.8</td>
<td>0.01</td>
<td>0.71</td>
</tr>
<tr>
<td>BF</td>
<td>124.5</td>
<td>4715.6</td>
<td>0.03</td>
<td>0.91</td>
</tr>
<tr>
<td>CCC (fall)</td>
<td>21.8</td>
<td>403.4</td>
<td>0.05</td>
<td>0.68</td>
</tr>
<tr>
<td>SR</td>
<td>17.8</td>
<td>301.2</td>
<td>0.06</td>
<td>0.85</td>
</tr>
<tr>
<td>CCC (fall)</td>
<td>48.8</td>
<td>717.2</td>
<td>0.07</td>
<td>0.73</td>
</tr>
<tr>
<td>CCC (fall)</td>
<td>37.1</td>
<td>419.2</td>
<td>0.09</td>
<td>0.61</td>
</tr>
<tr>
<td>BF</td>
<td>350.2</td>
<td>3253.0</td>
<td>0.11</td>
<td>0.88</td>
</tr>
<tr>
<td>CCC (spring)</td>
<td>300.1</td>
<td>1746.8</td>
<td>0.17</td>
<td>0.63</td>
</tr>
<tr>
<td>SR</td>
<td>181.5</td>
<td>936.7</td>
<td>0.19</td>
<td>0.81</td>
</tr>
<tr>
<td>SR</td>
<td>91.8</td>
<td>299.4</td>
<td>0.31</td>
<td>0.84</td>
</tr>
<tr>
<td>CCC (spring)</td>
<td>224.6</td>
<td>548.8</td>
<td>0.41</td>
<td>0.74</td>
</tr>
<tr>
<td>CCC (spring)</td>
<td>305.0</td>
<td>750.2</td>
<td>0.41</td>
<td>0.62</td>
</tr>
<tr>
<td>CCC (spring)</td>
<td>312.1</td>
<td>726.7</td>
<td>0.43</td>
<td>0.67</td>
</tr>
<tr>
<td>SR</td>
<td>1101.5</td>
<td>2370.7</td>
<td>0.47</td>
<td>0.98</td>
</tr>
<tr>
<td>CCC (spring)</td>
<td>219.4</td>
<td>459.2</td>
<td>0.48</td>
<td>0.61</td>
</tr>
<tr>
<td>SR</td>
<td>1382.2</td>
<td>2783.3</td>
<td>0.50</td>
<td>0.98</td>
</tr>
<tr>
<td>SR</td>
<td>143.8</td>
<td>283.4</td>
<td>0.51</td>
<td>0.92</td>
</tr>
<tr>
<td>CCC (spring)</td>
<td>463.4</td>
<td>808.5</td>
<td>0.57</td>
<td>0.91</td>
</tr>
<tr>
<td>BF</td>
<td>299.3</td>
<td>378.6</td>
<td>0.79</td>
<td>0.59</td>
</tr>
<tr>
<td>SR</td>
<td>1664.9</td>
<td>1953.9</td>
<td>0.85</td>
<td>0.87</td>
</tr>
</tbody>
</table>

Notes: Each row shows data for one plot. Biomass is expressed in grams per square meter. Nongreen biomass included senescent leaves and brown branches and stems. IPAR is the mean fraction of incoming photosynthetically active radiation intercepted by the canopy. Abbreviations: BF, Bernard Field Station; SR, Stunt Ranch; CCC, Cold Creek Canyon.

same area where radiometric measurements were taken. However, in some cases (south-facing plots at Stunt Ranch) harvests were made in adjacent plots of matched height, species composition, and appearance. In 1995, cylindrical sections were harvested by mounting a 30 cm diameter ring on a vertical rod. In spring 1996, square sections were harvested by mounting a square frame, 1 m on a side, attached to two vertical rods. The ring or frame was gradually lowered and all plant material falling within was clipped and put in a plastic bag for transport to the lab. Green (leaves and stems) and nongreen (brown stems and branches and senescing material) biomass were manually separated and dried in an oven at 60°C until their mass was constant to determine dry weight biomass. Table 3 summarizes the amounts of green and total biomass in each plot.

Canopy PAR interception was determined using a ceptometer (Decagon SF-80, Pullman, Washington, USA). Ten below-canopy \( (I_a) \) and ten above-canopy \( (I_s) \) incident PAR readings were taken on each plot while holding the ceptometer level. Fractional interception of PAR \( (f_{IPAR}) \) was calculated as follows:

\[
\text{Fractional Interception} = \frac{(I_a - I_s)}{I_s} \quad (4)
\]

Data analysis.—To evaluate changes in absorbance due to canopy structure we analyzed the correlation between absorbance at certain wavelengths and canopy structural variables (green, nongreen, and total biomass). The absorbances at four narrow wavebands, namely 430 nm \( (A_{430}) \), 550 nm \( (A_{550}) \), 680 nm \( (A_{680}) \), and 900 nm \( (A_{900}) \) and the integrated absorbances over the PAR \( (400-700 \text{ nm}; A_{PAR}) \) and NIR \( (700-1100 \text{ nm}; A_{NIR}) \) regions were tested as candidate indicators of canopy structure. These wavelengths were chosen for their sensitivity to changes in pigment content and canopy structure based on reflectance studies (Peñuelas and Filella 1998). Indices formulated by combining two absorbance bands and absorbance-based first derivative indices were also studied.

Derivative spectra were obtained using commercial plotting software (Igor, WaveMetrics, Lake Oswego, Oregon, USA). A smoothing filter (box smoothing) that consisted of replacing the absorbance value at a given wavelength by the mean absorbance in the adjacent bands was applied. Five bands were averaged in accordance with the instrument bandpass characteristics (Goward et al. 1994).

Statistical analysis, including Pearson correlation and linear regression, were conducted with commercial software (StatView 4.5, Abacus Concepts, Berkeley, California, USA).

RESULTS

Lab experiments on synthetic canopies

Area estimation.—Increasing the number of branch tips within the integrating sphere, and thus the absorbing area, resulted in increases in absorbance, both in the visible and near infrared regions (Figure 1A). To explore the relative effects of green and nongreen components on spectral absorbance, we experimentally manipulated the numbers of green and nongreen canopy elements in the integrating sphere. For those arrangements containing only brown branch tips, absorbance showed a steady decrease from visible to near infrared regions with a relatively shallow slope in the red edge region, i.e., the transition between the red and near infrared regions (Fig. 1A). In contrast, arrangements with only green branch tips showed a sharper transition (Fig. 1A). When brown and green branch tips were combined, the response was intermediate with pronounced variations in the shape of the red edge: an increase in the proportion of photosynthetic area was associated with a slope increment in the red edge region (Fig. 1A).

A correlation spectrum was calculated to highlight statistically significant relations between the canopy structural variables (green, nongreen, and total area) and absorbance data (Fig. 1B). In the visible region, green area was highly correlated with absorbance. Total area showed the highest degree of correlation with absorbance at any of the visible wavelengths, while in the NIR region variations in absorbance were mostly driven by changes in nongreen area.

Integrated absorbance in the PAR region \( (A_{PAR}) \) and
in the NIR region ($A_{\text{NIR}}$) were better correlated with total area ($r = 0.98$, $P < 0.0001$, and $r = 0.83$, $P < 0.0001$, PAR and NIR, respectively) than with green area ($r = 0.90$, $P < 0.0001$, and $r = 0.61$, $P = 0.0003$, PAR and NIR, respectively). A significant scatter appeared in the relationships between green area and $A_{\text{PAR}}$ due to the contribution of nongreen area to $A_{\text{PAR}}$ (Fig. 2). As the number of brown branch tips in the composite canopy increased (Fig. 2), the relationship between $A_{\text{PAR}}$ and green area was upshifted, resulting in different linear relationships with similar slopes but higher $y$-intercepts. When considering both green and brown areas, $A_{\text{PAR}}$ yielded a close relationship with total area (Fig. 2). In the NIR, and when considering green area, increases in nongreen area promoted changes in $A_{\text{NIR}}$ similar to those observed in the visible region (data not shown); however, the relationship between total area and $A_{\text{NIR}}$ had a larger scatter. A similar response was observed when correlating absorbance at single wavelengths in the PAR and NIR regions against the canopy variables (data not shown).

Green fraction estimation.—Changes in spectral absorbance had distinct patterns for equivalent increases in area depending on whether branch tips were green or brown. For a given green (solid line) or brown (dotted line) area, adding similar amounts of either brown or green area (thicker lines), respectively, resulted in almost equivalent increases in $A_{\text{PAR}}$ (Fig. 3A). However, $A_{\text{NIR}}$ increased approximately twice as much when adding brown to green than when adding green to brown area. This illustrated that the transition between the red and near infrared region was a key to understanding spectral responses to green and nongreen canopy components. Consequently, we explored this red edge region as an indicator of canopy structure by calculating the first derivatives of absorbance spectra.

The absorbance changes with varying green to nongreen ratios were more evident in the absorbance derivatives. For a given combination of green and nongreen branch tips, increases in the green area contributions to the scene absorbance resulted in a deepening of the spectral trough in the red edge region (increases in the amplitude of the minimum) and in a shift of the first derivative of this minimum position towards longer wavelengths (Fig. 3B). The proportion of woody area added some variability to this relation, in the sense that there were slight decreases in the amplitude (the depth of the spectral trough diminished) due to the increasing contribution of nongreen area to the primary canopy scene (Fig. 3B). However, these decreases were much less than those produced by similar increases of green area in the scene, illustrating the relative insensitivity of the red edge to brown canopy material. The position of the first derivative absorbance minimum ($A_{\text{ARE}}$) for those arrangements containing only brown material was ~690 nm, while for combinations of only

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**Fig. 1.** (A) Absorbance spectra of *Pseudotsuga menziesii* nongreen branches (dashed line), *P. menziesii* green branches (dotted line) and a combination of nongreen and green branches (dotted–dashed line). The boxed key indicates the ratio of green area to total area, and the numbers near the data lines show the total area of plant material in the scene for each arrangement. (B) Correlation spectra for green, nongreen, and total area in each of the spectroradiometer wavebands for combinations of green and brown *Pseudotsuga menziesii* branch tips within the integrating sphere. Data are for synthetic canopies in an integrating sphere ($n = 32$).

**Fig. 2.** Relationships of integrated absorbance over the PAR region ($A_{\text{PAR}}$) with green area (open symbols) and total area (solid symbols). Open symbols increase in size with increases in the number of nongreen branches in the scene (from 1 to 5). Data are for synthetic canopies in an integrating sphere ($r = 0.90$, $P < 0.0001$ for green area; $r = 0.98$, $P < 0.0001$ for total area; $n = 29$).
green branch tips this minimum was located at ~720 nm (data not shown).

The amplitude \((A_{RE})\) and position \((A_{ARE})\) of the first derivative absorbance minimum in the red edge region were then tested as green area estimators. \(A_{RE}\) showed a close correlation with green area \((r = -0.99, P < 0.0001; \text{Fig. 4})\), while the correlation of \(A_{ARE}\) against green area, although significant, was slightly weaker \((r = 0.85, P < 0.0001)\) due to the \(A_{RE}\) displacement towards shorter wavelengths when adding nonphotosynthetic components (data not shown).

While \(A_{PAR}\) closely tracked changes in area, whether it was green or brown, \(A_{RE}\) solely responded to changes in green area. Consequently, we formulated an estimator of the ratio green area:total area (green fraction) by dividing \(A_{RE}\) over \(A_{PAR}\). The ratio \(A_{RE}/A_{PAR}\) showed a strong correlation with green fraction \((r = -0.96, P < 0.0001; \text{Fig. 5A})\).

Since the contribution of brown and green components resulted in contrasting responses in the red and near infrared regions, we considered the possibility of applying vegetation indices that are typically used with spectral reflectance to spectral absorbance. The reflectance-based vegetation indices NDVI and SR have been recently reviewed in Peñuelas and Filella (1998) and Gamon and Qiu (1998) and are known to be good estimators of canopy structure (green biomass, LAI, and fAPAR). However, since the relative contributions of green and nongreen areas modulated the changes in the red edge, and there was a similarity between the vegetation indices and the ratio \(A_{RE}/A_{PAR}\) formulated above, we expected to obtain an estimator of green fraction. The analogous absorbance indices were called \(A_{SR}\) (absorbance simple ratio) and \(A_{NDVI}\) (absorbance normalized difference vegetation index) and were calculated as follows:

\[
A_{SR} = A_{680}/A_{900},
\]

\[
A_{NDVI} = (A_{680} - A_{900})/(A_{680} + A_{900}).
\]

\(A_{NDVI}\) showed significant correlation with green area \((r = 0.74, P < 0.0001)\) and with green area fraction (green area/total area; \(r = 0.96, P < 0.0001; \text{Fig. 5B})\). Thus, \(A_{NDVI}\) had a lower aptitude for tracking changes in green area than \(A_{RE}\), but was similar to the ratio \(A_{RE}/A_{PAR}\) in estimation of green fraction. Compared with \(A_{NDVI}\), correlations of \(A_{SR}\) with green area and with the ratio green area:total area were weaker \((r = 0.54, P = 0.002, \text{and } r = 0.79, P < 0.0001, A_{SR} \text{ and } A_{NDVI}, \text{respectively})\).

Field studies

To test the ability of spectral absorbance and spectral vegetation indices to distinguish green from nongreen components, we conducted a series of measurements in natural canopies.

FIG. 4. Relationship between green area and the minimum amplitude of the first derivative of spectral absorbance at the red edge \((A_{RE}; n = 29)\). Data are for synthetic canopies in an integrating sphere.
Absorbance values in the visible portion of the spectra increased in response to the amount of total biomass (green and nongreen). A similar but less striking response was observed in the near infrared region (Fig. 6). Spectral absorbance signatures in Figure 6 were chosen to be representative of a range of canopy biomasses and of contrasting amounts of green and nongreen biomass (photosynthetic and nonphotosynthetic components). As in the laboratory study, the absorbance signature showed a clear contrast in the red edge region (~700 nm) varying with the amount of green biomass: canopies with evergreen species showed a sharp transition between the red and near infrared regions (Fig. 6) while canopies with senescing plants showed a roughly linear transition (Fig. 6).

All narrowband absorbances and the integrated absorbance in the visible region showed highly significant correlation with green biomass (Table 4). From all the narrowbands considered in the visible region, $A_{430}$, where carotenoids and chlorophyll pigments absorb, showed the highest degree of correlation with green biomass ($r = 0.75, P < 0.0001$; Table 4). Absorbances at 550 nm and 680 nm, the peak and the absorption wavelength of the in vivo chlorophyll pigments, respectively, also showed highly significant correlations with green biomass (Table 4). Absorbances at selected wavelengths were better correlated with log-transformed total biomass than with total biomass per se (data not shown). Correlations of log-transformed total biomass with $A_{430}$, $A_{550}$, and $A_{680}$ were significant (Table 4). In the NIR region, $A_{900}$ was better correlated with log-transformed total biomass than with green biomass (Table 4). However, correlations of both green and total biomass with the spectral absorbance at selected wavelengths were weaker than in the laboratory study where we considered areas instead of biomass.

When considering integrated absorbances, the results partially agree with those obtained in the sphere study.

### Table 4. Correlation coefficients (and significance) of absorbance at selected wavelengths and absorbance-based indices with green biomass and log of total biomass ($n = 22$).

<table>
<thead>
<tr>
<th>Absorbance</th>
<th>Green biomass</th>
<th>Log total biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A_{430}$</td>
<td>0.75***</td>
<td>0.60**</td>
</tr>
<tr>
<td>$A_{550}$</td>
<td>0.72***</td>
<td>0.64**</td>
</tr>
<tr>
<td>$A_{680}$</td>
<td>0.72***</td>
<td>0.67**</td>
</tr>
<tr>
<td>$A_{900}$</td>
<td>0.38NS</td>
<td>0.57**</td>
</tr>
<tr>
<td>$A_{PAR}$</td>
<td>0.73***</td>
<td>0.64**</td>
</tr>
<tr>
<td>$A_{NIR}$</td>
<td>0.45*</td>
<td>0.60**</td>
</tr>
<tr>
<td>$A_{RE}$</td>
<td>-0.76***</td>
<td>-0.40NS</td>
</tr>
<tr>
<td>$A_{ARE}$</td>
<td>0.55**</td>
<td>0.74***</td>
</tr>
</tbody>
</table>

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, not significant.
Correspondingly, absorbances in the NIR ($A_{\text{NIR}}$) mainly responded to changes in nongreen biomass, resulting in closer correlations with log-transformed total biomass than with green biomass (Table 4). In contrast, and when considering biomass instead of area, absorbances in the visible region ($A_{\text{PAR}}$), were better correlated with green than with total biomass (Table 4).

Absorbance derivatives provided more information on canopy structure. The position (wavelength) of the absorbance first derivative minimum in the red edge region ($A_{\text{RE}}$) was influenced by the amount of non-photosynthetic biomass (data not shown). A close correlation between $A_{\text{RE}}$ and log of nongreen biomass ($r = 0.70, P < 0.0001$) and log of total biomass was found (Table 4). As in the laboratory study, the amplitude of the first derivative of absorbance in the red edge region was a good estimator of green biomass (Table 4).

Our results showed, despite a notable scatter, a significant relationship between the integrated absorbance in the PAR region ($A_{\text{PAR}}$) and log-transformed total biomass (Fig. 7A). The amplitude of the first derivatives of spectral absorbance in the red edge ($A_{\text{RE}}$) was also significantly related to log-transformed green biomass (Fig. 7B). When comparing data from 1996 sampled plots with those plots sampled in 1995 (Fig. 7B), an apparent shift in the relationship was observed. However, a covariance analysis considering either vegetation type or sampling conditions as sources of variation did not yield any significant effect on the $A_{\text{RE}}$ log vs. green biomass relationship (data not shown). Consequently, a single relationship for the whole data set was considered (Fig. 7B). Thus, the ratio $A_{\text{RE}}/A_{\text{PAR}}$ was tested as a potential indicator of green fraction. The relationships of $A_{\text{RE}}/A_{\text{PAR}}$ with green fraction were significant and linear, although weaker than in the laboratory study. However, and as the results of the covariance analysis indicated (data not shown), differences in the regression line between sampling dates were statistically significant, yielding separate relationships for 1995 and 1996 sampled plots (Fig. 8A).

$A_{\text{RE}}$ closely tracked variations in green biomass, while $A_{\text{NIR}}$ mainly responded to changes in total biomass. As in the laboratory study, we formulated the

![Figure 7](image_url)

**Fig. 7.** Relationships between two absorbance-based indices and the canopy variables for the field plots studied. (A) Relationship between integrated absorbance over the PAR region ($A_{\text{PAR}}$) and log-transformed total biomass ($n = 22$). (B) Relationship between the absorbance first derivative amplitude ($A_{\text{RE}}$) and log-transformed green biomass ($n = 20$). Open and solid symbols indicate 1995 and 1996 field campaigns, respectively. Correlation coefficients ($r$) and significance ($P$) are indicated in the figure.

![Figure 8](image_url)

**Fig. 8.** Relationships between green fraction (green biomass/total biomass) and (A) the absorbance based indices $A_{\text{RE}}/A_{\text{PAR}}$ and (B) $A_{\text{NIR}}$. Open and solid symbols indicate 1995 and 1996 field data, respectively. Regression lines and correlation coefficients ($r$) and significance ($P$) are for 1995 data ($n = 12$; dashed line, lightface type) and 1996 data ($N = 10$; solid line, boldface type).
vegetation indices derived from the absorbance at these wavelengths ($A_{280}$ and $A_{340}$). $A_{SR}$ and $A_{NDVI}$ yielded a significant, although weak, relationship with log-transformed green biomass. The correlation coefficients of log-transformed green biomass with $A_{SR}$ and $A_{NDVI}$ were $r = 0.48$ ($P = 0.03$) and $r = 0.54$ ($P = 0.01$), respectively. However, the results of the covariance analysis indicated that the relationships between either $A_{SR}$ or $A_{NDVI}$ and the canopy variables varied significantly between 1995 and 1996 data sets. When considering separately both data sets, $A_{SR}$ and $A_{NDVI}$ yielded more significant relationships with log-transformed green biomass. The correlation coefficients between $A_{NDVI}$ and log-transformed green biomass were $r = 0.92$ ($P < 0.0001$) and $r = 0.81$ ($P = 0.003$) for 1995 and 1996 data sets, respectively. A significant relationship between $A_{NDVI}$ and canopy green fraction emerged when considering separately data sets from 1995 ($r = 0.82$, $P = 0.005$) and from 1996 ($r = 0.85$, $P = 0.001$; Fig. 8B). The relationships between $A_{SR}$ and green fraction were also significant. The correlation coefficients between $A_{SR}$ and green fraction for 1995 and 1996 data sets were $r = 0.81$ ($P = 0.003$) and $r = 0.86$ ($P = 0.0003$), respectively.

Absorbance–reflectance relationships.—Narrowband vegetation indices (SR and NDVI) derived from reflectance measurements were significantly correlated with log of green biomass ($r = 0.84$, $P < 0.0001$, and $r = 0.88$, $P < 0.0001$, respectively). Fig. 9A illustrates the relationship between log green biomass and NDVI. The maximum amplitude of the first derivative reflectance (at the red edge) also showed, despite considerable scatter, significant correlation with log-transformed green biomass ($r = 0.49$, $P = 0.03$).

When examining the relationships between reflectance and absorbance data, correlations between absorbance and reflectance values at selected wavelengths were not significant (data not shown). In some plots, reflectance and absorbance measurements were conducted in different dates and hours and, thus, lack of relationship could reflect differences due to changing illumination conditions. Despite some variability probably due to differences between herbaceous and shrub canopies, the relationship was consistent for those data sets measured under similar light intensities, whereas no relationship emerged from the data set collected at Stunt Ranch (data not shown), where absorbance and reflectance data were taken in different days.

In spite of those disparities, the minimum amplitude of the first derivative of spectral absorbance ($A_{RE}$), an absorbance-based indicator of green biomass (Fig. 7A), was significantly correlated with the reflectance-based red edge amplitude (first derivative reflectance maximum; $r = -0.70$, $P = 0.0001$). $A_{RE}$ also showed significant correlations with the vegetation indices SR ($r = -0.86$, $P < 0.0001$) and NDVI ($r = -0.83$, $P < 0.0001$; Fig. 9B) derived from reflectance measurements.

**Discussion**

Spectral absorbance measurements provided a number of potential indicators of green and nongreen canopy structure. $A_{PAR}$ was a good indicator of total biomass, $A_{RE}$ of green biomass and the ratio $A_{RE}/A_{PAR}$ of green fraction or proportion of photosynthetic material. Nongreen canopy components contributed significantly to $A_{PAR}$, in agreement with previous studies using integrating spheres (Oquist et al. 1978, Serrano et al. 1997). Furthermore, the relative contribution of nongreen components to $A_{PAR}$ was larger at lower green areas. These results emphasize the need for optically separating green and nongreen contributions to PAR absorbance, or other expressions of canopy absorbed PAR, particularly in grasslands, shrublands and other...
ecosystems with typically low LAI values and large proportion of nonphotosynthetic components.

Nongreen contribution to the canopy structure also increased the magnitude of NIR absorbance. In the NIR region leaves exhibit large scattering (they reflect and transmit light in great amounts). In contrast, nongreen components and even senescing leaves show negligible NIR transmittance values (van Leeuwen and Huete 1996) reducing the radiation levels in below-canopy readings. Asner (1998) indicated that the effects of woody material are enhanced in the NIR because the photons penetrate the canopy more effectively in that spectral region, allowing maximum interaction of stem material in the radiation field. Thus, due to the unconstrained radiation path through the leaves, changes in transmittance in the NIR were mostly driven by nonphotosynthetic components. In reflectance-based studies, the contribution of nonphotosynthetic (nongreen) components to the scene reflectance has been shown to decrease the magnitude of the NIR plateau (Asner 1998).

The reflectance index NDVI is a widely accepted indicator of green vegetation amount and fAPAR by green vegetation (Hall et al. 1992, Goward et al. 1994, Gamon et al. 1995). Similarly, absorbance based spectral indices (ASR and A NDVI ) were sensitive to green rather than to total vegetation amount. However, ASR and A NDVI were affected by the presence of nongreen components. This situation was highlighted when plotting A NDVI vs. green area for the lab data set: the relationship between A NDVI and green area was down-shifted as nongreen contribution to the scene absorbance increased. The assumption made in the formulation of vegetation indices is that the canopy spectral signature has a spectrally flat background (a gray component) and a green component from photosynthetic vegetation, so that spectral indices only respond to changes in green biomass (Goward et al. 1994). There is some evidence, though, that this approximation is not appropriate: leaves and other materials in the canopy (branches, bark) and standing litter show important variations in their spectral signature (Stoner and Baumgardner 1981, Williams 1991, Goward et al. 1994). This variability has shown to have a significant impact when reflectance vegetation indices are formulated using two different wavelengths (Bartlett et al. 1990, van Leeuwen and Huete 1996). In both field and lab studies, A NDVI showed a higher degree of correlation with canopy attributes than ASR. Since A NDVI is normalized, correcting for differences in brightness could have contributed to the improvement of the relationship.

The amplitude of the absorbance first derivative (A ΔR ) was a good predictor of green vegetation amount. To our knowledge, there are no previous studies where A ΔR , derived from spectral absorbance data, has been used as an indicator of green biomass, but the results obtained are consistent with previous findings based on reflectance spectra. Amplitude of the reflectance red edge has been reported to be a good indicator of green area and biomass (Guyot et al. 1992, Filella and Peñuelas 1994). Since nongreen branch tips in the sphere and nongreen components of vegetation in field plots yielded absorbance spectral signatures with near-linear decreases as a function of wavelength, they had derivative values close to zero, thus allowing an estimate of green biomass even in complex field situations. Therefore, in our study, derivatives reduced artifacts due to differences in canopy architecture and other background effects, as has been previously suggested by Shah (1985). This is supported by the fact that, despite disparities in sampling conditions and canopy attributes related to functional type and phenology, a unique relationship emerged for the whole field data set. In contrast, when considering indices derived from single wavelengths (i.e., A SR and A NDVI ) different relationships had to be considered.

The ratio A RG/A PAR was a good indicator of the proportion of photosynthetic area. Similarly, A SR and A NDVI closely tracked changes in green fraction. The divergence in the relationships between A RG/A PAR, A SR and A NDVI and the canopy attributes between the two field data sets (1995 and 1996) could be attributed to various factors. Reflectance-based vegetation indices have been reported to be affected by changes in chlorophyll content (Yoder and Waring 1994). However, since we covered a wide range of phenological stages and, thus, of chlorophyll contents within a data set, we believe that differences were primarily due to other factors. Vegetation types sampled in 1995 had green herbaceous stems, while, in their majority, 1996 sampled plots had woody brown stems. Thus, expressing the canopy attributes as biomass could also have contributed to the detachment of the relationship between field data sets. Variability could have been also introduced by canopy structure and architecture. However, since 1996 sampled plots included a diversity of vegetation types (grasslands, fire-follower species, and chaparral and coastal sage scrubs), divergence in the relationships between the data sets of the two years was probably related to differences in sampling conditions between field campaigns.

Correlations between A RG and vegetation indices derived from spectral reflectance were significant. Vegetation indices (ratios and linear combinations of reflected or absorbed radiance at different wavelengths) are intended to reduce the effects of changing irradiance (Jackson and Huete 1991). This might explain why single narrowband absorbance and reflectance values did not show significant relationships, especially for those data sets collected under different light conditions, while significant correlation arose when using ratios and derivatives.

The ratio A RG/A PAR provided a reliable tool for assessing green fraction under lab and field conditions, as well as A SR and A NDVI . These indices could be used to correct the fAPAR estimates obtained with broad-
band optical sensors (e.g., ceptometers) to determine the fraction of photosynthetic active radiation absorbed by green leaves. To determine the canopy green fraction, \( A_{\text{GFDV}} \) could be advantageous since it uses two single wavelengths which could simplify the instrument design compared to \( A_{\text{RE}} \) which needs high spectral resolution measurements along the red edge region. However, a unique relationship between \( A_{\text{RE}} \) and green biomass emerged for the whole field data set which substantiates the prospective power of this indicator of green area. Furthermore, \( A_{\text{RE}} \) was more closely correlated with conventional reflectance-based estimators of green biomass and LAI, thus, providing a closer link with data obtained from satellites and airborne sensors.

LAI values derived from optical measurements are affected by multiple scale, nonrandom self-shading effects (White et al. 1997) and by projected nongreen area seen by the sensor (Smolander and Stenberg 1996). While optical techniques have been developed to remove the effects of foliage clumping on LAI measurements (Gower and Norman 1991, Fassnacht et al. 1994, Chen and Cihlar 1995), the contribution of nongreen elements has to be estimated by destructive methods. Thus, \( A_{\text{RE:PAR}} \) and \( A_{\text{GFDV}} \) may provide a tool to correct for nongreen area contribution.

Although we did not consider in this study canopy architecture issues, and we mainly assessed dense shrub canopies (\( f_{\text{PAR}} > 50\% \)), the results obtained were robust in the sense that we covered a broad range of canopy green fractions and species at different successional stages. Recently, Larsen and Kershaw (1996) simulated the effects of varying canopy horizontal and vertical foliage distributions on predictions from Beer’s law. Their results indicated that mean light extinction for the entire canopy was equivalent for all canopy organizations, which might explain the validity of the relationships between canopy variables and absorbance data across a range of growth forms and functional groups. A number of factors undoubtedly contributed to the weaker relationships under field conditions. Comparison of harvests to optical sampling assumes that the harvested material was representative of the canopy region viewed by the optical detector. Since the study was conducted in canopies of complex, heterogeneous structures, this assumption must have been violated to some extent (particularly in south-facing plots at Stunt Ranch), which must have contributed to the scatter in Figs. 7, 8, and 9. Discrepancies between field and laboratory studies must be also related to different light conditions (direct sunlight vs. diffuse radiation, respectively). We found that diffuse light conditions greatly reduces the signal-to-noise ratio at the detector in below-canopy readings, decreasing the reliability of the data. Improvement in detector sensitivity could allow improved data quality under diffuse light conditions and this might improve agreement with lab results. Additionally, cross-calibrating the sensors between campaigns and standardizing sampling protocols would have probably improved the relationships.

While this simple analysis has been found to accurately predict green vegetation amount and canopy green fraction, its applicability to other vegetation canopies (particularly forests and discontinuous canopies with large gaps) will need to be evaluated by further field experiments. In our study we have not addressed critical issues such as leaf and stem spatial distribution which are important factors controlling light attenuation through canopies (Ross 1981). More complicated procedures might be required to account for deviations from Beer’s law caused by foliage clumping at the various scales in other vegetation types. To further test the reliability of these indices under field conditions, expression of the canopy attributes in terms of area instead of biomass, and assessment of the canopy architecture must be done.

Spectral absorbance measurements might provide an accurate and efficient way to quantitatively assess vegetation structure attributes. Assessing canopy structure (photosynthetic and nonphotosynthetic vegetation amount) is of particular interest to determine above-ground allocation and phenology in developmental and disturbance studies. The photosynthetic:nonphotosynthetic vegetation ratio provides information on pasture productivity to land managers (Asner et al. 1998) and on fire fuel load to assess fire risk (Piñol et al. 1998). Seasonal and long-term trends in live and dead tissues are also needed for planning prescribed fires (Asner et al. 1998).

LAI plays an important role in the exchange of CO\(_2\), water vapor, and trace gases between the biosphere and the atmosphere. Thus, this approach might be also useful in ecophysiological studies where LAI measurements are necessary such as in determining ecosystem productivity and evapotranspiration. The determination of LAI is especially important in the context of large-scale intensive studies attempting to link remotely sensed data to ground-based measurements (White et al. 1997). Improvement in the accuracy of the estimated structural parameters and biophysical attributes could also provide an improved parameterization of biogeochemical cycle models (Running et al. 1994, Fiel et al. 1995). This absorbance technique may be of particular use in remote sensing field validation studies (over large areas) where leaf area measurements are notoriously difficult and the existing optical methods lack the ability to discriminate green from nongreen components.

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LITERATURE CITED


Ross, J. K. 1981. The radiation regime and architecture of plant stands. Kluwer, Boston, Massachusetts, USA.