Assessing forest structure and function from spectral transmittance measurements: a case study in a Mediterranean holm oak forest

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\textbf{Summary} Annual changes in structural attributes and seasonal dynamics in water content, photosynthetic rate and light-use efficiency (LUE) were assessed by spectral transmittance for 4 years (1999–2003) in six stands of a Mediterranean holm oak forest. Green biomass, total biomass and leaf area index (LAI) were determined. In 1999, seasonal dynamics of net carbon dioxide (CO\textsubscript{2}) exchange and water content were measured. We recorded photosynthetically active radiation (PAR) transmittance and hyperspectral transmittance in the 400–1100 nm region and derived reflectance-based vegetation indices.

Transmittance over the PAR region derived from either cepitometer or spectroradiometer measurements (PAR\textsubscript{T} and T\textsubscript{PAR}, respectively) was related to green and total biomass. Both PAR\textsubscript{T} and T\textsubscript{PAR} were also related to LAI (r = 0.79 and r = 0.70, respectively, \(P < 0.001\)) and were appropriate for comparison among stands, whereas subtle changes in LAI within a stand were better assessed by the transmittance amplitude in the red edge region (T\textsubscript{RE}) (within a stand, \(r = 0.77–0.99, P < 0.001\)).

Spectral transmittance-based indices successfully captured physiological processes that occurred on temporal (seasonal) and spatial scales. The transmittance-based water index (T\textsubscript{WI}) was related to both foliage and canopy water content (r = 0.69, \(P < 0.001\)). Estimates of foliage and canopy water content improved in dense (closed) stands (r = 0.84 and r = 0.87, respectively, \(P < 0.001\)) compared with low-density stands. Under non-drought conditions, transmittance-based photochemical reflectance index (T\textsubscript{PRI}) was related to LUE (r = 0.58, \(P < 0.05\)) and net CO\textsubscript{2} exchange (r = 0.72, \(P < 0.01\)), and the combined T\textsubscript{PAR} × T\textsubscript{PRI} index greatly improved these relationships (r = 0.93 and r = 0.84, respectively, \(P < 0.01\)), indicating that both structural and physiological adjustments modified CO\textsubscript{2} fixation capacity in these forest stands. Our novel approach to the study of transmitted radiation provides a tool for estimating structural and functional variables such as LAI, LUE and water content, which are key determinants of terrestrial productivity.

\textbf{Keywords:} growth, leaf area index, light-use efficiency, net CO\textsubscript{2} exchange, remote sensing, water content.

\textbf{Introduction} Ground estimates of forest canopy structural properties are important for monitoring plant growth and site condition and for validating remote sensing data, and are crucial for studies aimed at linking ecosystem structure and function.

Both leaf area index (LAI) and non-photosynthetic vegetation area index (NPVAI) are robust structural indicators of aboveground allocation, phenological state and seasonal growth (net primary production (NPP)) and, thus, have critical links to carbon and nutrient cycles (Running et al. 1994, Shugart 1997, Asner et al. 1998). Moreover, LAI influences the exchange of energy, water vapor and carbon dioxide between terrestrial ecosystems and the atmosphere (Sellers et al. 1997), and is currently used in process-based models to simulate ecosystem carbon (Goetz and Prince 1998, Gower et al. 1999) and water (Canadell et al. 2000) cycles. In addition, LAI can be determined for terrestrial ecosystems from satellite-borne sensors. Thus, assessing LAI and NPVI is important for validating remote sensing data (White et al. 2000).

In forest stands, estimating LAI and NPVIAI is particularly challenging because of the heterogeneity in vegetation structural characteristics and functional groups that occurs on large spatial scales. Because direct procedures (e.g., allometric equations) for describing canopy structure are time consuming and laborious (Lang et al. 1985, Weiss et al. 2004), indirect radiometric methods are currently used to facilitate field estimation of forest growth and canopy structure (Hyer and Goetz 2004).

Estimation of LAI by radiometric inversion of light transmission through a canopy allows rapid nondestructive sampling over large areas. However, most ground transmittance measurements involve broadband photosynthetically active radiation (PAR) sensors that do not distinguish absorption by green components from absorption by non-photosynthetic material. Jordan (1969) proposed estimating LAI from the quality of light transmission based on the ratio of light transmitted at 800 nm to that at 675 nm. More recently, methods based on the analysis of spectral light transmission have been used to estimate the fractions of green and non-green compo-
nents within a canopy (Kucharick et al. 1998, Serrano et al. 2000a). Estimates of LAI based on light transmission are affected by nonrandom distribution of foliage (clumping). Several methods for correcting clumping have been proposed (Chen et al. 1997, Kucharick et al. 1997) (see Bréda 2003 and Jonckheere et al. 2004 for recent reviews); however, they are inappropriate for routine measurements because of their complexity (Gower et al. 1999).

Although monitoring PAR transmittance cannot entirely resolve changes in vegetation structure, this approach is appealing because, under certain assumptions, the fraction of intercepted PAR (i.e., 1 – PAR transmittance) relates to the fraction of absorbed PAR. Thus, NPP can be estimated indirectly by measuring seasonal or annual absorbed PAR (APAR) by vegetation canopies and assuming a light-use efficiency (LUE) value that accounts for the efficiency with which APAR is converted to NPP (Monteith 1972, 1977). This simple LUE model has been the basis for many evaluations of photosynthesis and primary production from canopy to global scales (Runyon et al. 1994, Waring et al. 1995, Nichol et al. 2000), but its power is limited by the variability in LUE (Ruimy et al. 1994). Several studies indicate that reduced LUE can significantly impact whole-system carbon gain (Joel et al. 1997, Nichol et al. 2000), particularly in seasonally dry evergreen ecosystems where significant diurnal and seasonal fluctuations in net CO2 uptake occur (Running and Nemani 1988, Gamon et al. 1995, Stylinski et al. 2002). This finding highlights the need for a direct measure of spatial and temporal variations in LUE (Barton and North 2001). Thus, although APAR is theoretically linked to LAI, APAR may not necessarily be linked to photosynthetic function if LUE is a dominant term.

From the remote sensing perspective, it is well established that hyperspectral reflectance data provide information from which canopy structural and functional attributes can be inferred. Vegetation indices primarily respond to green LAI and to fractional APAR by green vegetation (Gamon et al. 1995). Furthermore, several indices based on reflectance data have been proposed to assess physiological status (Peñuelas and Filella 1998). For instance, the photochemical reflectance index (PRI) is linked to LUE and net CO2 uptake (Gamon et al. 1992, 1997, Peñuelas et al. 1995). Similarly, the water index (WI) is an indicator of vegetation water content at the leaf, canopy and landscape scales (Peñuelas et al. 1993, 1996, Serrano et al. 2000b).

Because vegetation structure largely determines the radiation regime within a canopy (Panferov et al. 2001) and because of the coupled behavior of reflectance, transmittance and absorption, spectral transmittance measurements could be used to characterize amounts of green and non-green materials in vegetation and to derive physiological indices as tools for assessing canopy structure and function. Serrano et al. (2000a) found that narrow-band spectral transmittance measurements in the 400–1100 nm region were closely related to reflectance measurements and were successfully applied to assess canopy structure in continuous shrub canopies.

We have now evaluated the usefulness of spectral transmittance measurements to estimate canopy structural attributes in a complex holm oak forest by considering several stands differing in stem density, tree height and LAI. In addition, we tested the capability of this technique to track seasonal changes in canopy function by considering two widely used reflectance indicators of physiological status (WI and PRI) derived from spectral transmittance measurements. Furthermore, we tested the feasibility of using a simple LUE model based on spectral transmittance measurements to estimate photosynthetic function and net primary production.

Materials and methods

Study site

The experimental area is located in Solana dels Torneros, Serra de Prades (Catalonia, Spain) (41°13’ N, 0°55’ E, 990 m a.s.l., 25° slope and 150° aspect). The soil is a Typic xerochrept on a bedrock of metamorphic sandstone with a depth between 35 and 90 cm. Temperature, rainfall, relative air humidity, wind speed and radiation measurements were recorded at the experimental area with a data logger (Campbell CR10X, Campbell Scientific, Logan, UT). Climatic conditions are typical of montane Mediterranean climates with a mean annual precipitation of 658 mm and a mean annual temperature 12 °C over the study period.

The study area is characterized by a dense (16,616 trees ha–1) sclerophyllous holm oak forest dominated by Quercus ilex L. (8633 trees ha–1) and Phyllirea latifolia L. (3600 trees ha–1), which represent, on average, 88% of the total basal area. Other Mediterranean species present include Arbutus unedo L., Erica arborea L., Juniperus oxycedrus L. and Cistus albidus L. Tree height was about 5 to 7 m and mean diameter at 50 cm height in 1999, 2000, 2001 and 2003. We derived LAI greater than 2 cm were tagged and their diameters measured at 50 cm aboveground was 6.03 ± 3.69 cm (basal area 33.87 m2 ha–1) and 3.26 ± 0.95 cm (basal area 3.46 m2 ha–1) for Q. ilex and P. latifolia, respectively. In February 1999, six adjacent stands (10 × 15 m2) differing in stem density were delimited. Table 1 summarizes the initial structural characteristics of each stand.

Biomass assessment

Green (GB) and total biomass (TB) and LAI were determined annually during 1999–2003. The annual production of GB and TB in each stand was estimated from annual radial increment and allometric equations derived from Q. ilex and P. latifolia trees growing adjacent to the experimental site at the beginning of the experiment (February 1999) (Ogaya et al. 2003). All living stems of Q. ilex and P. latifolia with diameters greater than 2 cm were tagged and their diameters measured at 50 cm height in 1999, 2000, 2001 and 2003. We derived LAI from GB and specific leaf area (SLA; m2 g–1) for each species and year.

Radiometric measurements

Radiation was measured under cloudless skies with a spectroradiometer (Spectron SE-590, Spectron Engineering, Denver, CO) (400–1100 nm) equipped with a cosine corrected hemispherical fore-optic. At each stand, a fixed location was selected and five measurements were made (one at the center and
one in each of the cardinal directions at 1 m from the center) with the instrument fore-optics pointing toward the canopy zenith. At each position, four scans were internally averaged. Below-canopy measurements were conducted at 0.5 m above ground, and care was taken so that the operator was outside the field of view of the optical sensor. Above-canopy irradiance measurements were taken several times during the sampling period in the nearest canopy gap. According to Monsi and Saeki’s formulation (1953) of the Beer Lambert law, radiometric measurements are related to leaf area index (LAI) as:

\[
LAI = -\frac{1}{k} \ln T
\]  

where \(\ln T\) is the natural logarithm of radiation transmittance (the ratio of below- to above-canopy irradiance) and \(k\) is the extinction coefficient. At each fixed location, \(\ln T\) was calculated as the logarithmic mean of five measurements (Lang et al. 1991). To allow comparison of measurements taken at different times (i.e., at different solar zenith angles), each transmittance measurement was multiplied by the cosine of the solar zenith angle. Reflectance-based indices were derived from \(-\ln T\) spectra (hereafter simply denoted as transmittance). Transmittance water index (\(T_{WI}\)) and transmittance photochemical reflectance index (\(T_{PRI}\)) were calculated as:

\[
T_{WI} = \frac{T_{970}}{T_{900}}
\]  

\[
T_{PRI} = \frac{T_{570} - T_{531}}{T_{570} + T_{531}}
\]

where subscripts indicate the wavelength in nm.

These indices were formulated to show increasing values in response to increasing water content and LUE. Integrated transmittance over the PAR region (\(T_{PAR}; 400–700\) nm) was also calculated.

Derivative spectra were approached as first difference spectra and smoothed using a three-band window running mean. Transmittance amplitudes in the red edge region (\(T_{RE}\)) were computed from these spectra. Unlike the \(T_{WI}\) and \(T_{PRI}\) indices, \(T_{RE}\) decreased with increasing green biomass and LAI.

Transmitted PAR (\(\text{PAR}_T\)) was measured with a ceptometer (SF-80, Decagon, Pullman, WA) following the same sampling scheme as used for spectral transmittance measurements and corrected for differences in solar zenith angle as described previously. To allow comparison with spectral transmittance data, \(\text{PAR}_T\) was calculated as:

\[
\text{PAR}_T = -\ln \frac{\text{PAR}_a}{\text{PAR}_b}
\]  

where subscripts a and b denote above- and below-canopy readings, respectively.

Radiometric measurements were made on March 4, 1999, February 25, 2000, February 1, 2001 and March 4, 2003 for biomass assessment. In addition, in 1999, measurements were also taken on May 13, September 2 and November 24 to assess seasonal changes in water content and photosynthetic function (see below).

Water content measurements

In 1999, leaf water content was determined for each stand and species on the same day as the transmittance measurements. Water content was determined on five samples of foliage collected in different trees of each species from the upper and lower layers of each tree crown. Leaf water content was determined in leaf disks cut with a cork borer or in entire leaves. Disks (or leaves) were immediately placed in a pre-weighed vial filled with water, sealed and kept in an ice chest until taken to the laboratory. The mass of the vial containing the sample was determined, and the difference between the final and initial vial mass was recorded as fresh mass (FM). Disks (or leaves) were then removed from the vial and oven-dried at 70 °C to constant dry mass. Water content (WC) was calculated as a fraction of dry mass (DM). Canopy water content (WC\_CAN) was calculated as the product of foliage dry mass and species-specific foliage water content.

Gas exchange measurements

In 1999, gas exchange was measured in four stands over 2 to 6 consecutive days within 2 weeks of the radiometric measurements made under a clear sky in each of the four seasons of the year.

Net CO₂ exchange and incident PAR were measured with a portable gas exchange system ADC4 equipped with a PLC4B.
chamber (ADC BioScientific, Hoddesdon, Hertfordshire, U.K.) and were expressed on a projected leaf area basis measured with a Li-Cor 3100 area meter (Li-Cor, Lincoln, NE). One current-year leaf of four trees per species and two canopy positions (i.e., sun and shade leaves) was measured in the morning and at midday. Mean leaf values of net CO₂ exchange and incident PAR were calculated for each stand and season, and LUE was calculated as the ratio of mean net CO₂ exchange to mean PAR (moles of carbon fixed per mole of incident PAR).

Statistical analyses

The relationships between structural (GB, TB and LAI) and functional traits (WC, WC_CAN, LUE and net CO₂ exchange) and spectral indices (PAR, T_PAR, T_RE, T_WI and T_PRL) were studied by correlation analysis. All statistical analyses were conducted with the statistical software SPSS 11.5 (SPSS, Chicago, IL).

Results and discussion

Assessing forest structure

Optical measurements were related to allometric estimates of LAI, GB and TB. Across stands, PAR/T was a good estimator of GB (r = 0.75, P < 0.001), LAI (r = 0.76, P < 0.001) and TB (r = 0.79, P < 0.001). Similarly, the integrated T_PAR was a good estimator of GB (r = 0.69, P < 0.001), LAI (r = 0.70, P < 0.001) and TB (r = 0.72, P < 0.001). When data were split by year, the correlation between these variables significantly improved (Figure 1), particularly when using T_PAR data. Although T_RE was not significantly related to GB or to LAI across stands and years, it was closely related to within-stand variation in LAI (Figure 2). In contrast, PAR/T and T_PAR failed to track subtle changes in LAI (i.e., within-stand variation across years).

The good agreement between PAR transmittance-based indices (PAR_T and T_PAR) and structural attributes across stands and years could be partially associated with the sampling strategy; standardizing the distance and orientation from a subject tree reduces variability and is as effective and accurate as standard strategies based on transect measurement (López-Serrano et al. 2000). Moreover, because structural attributes were derived from measurements at the stand level, good agreement between transmittance-based indices and structural attributes indicates that sampling locations were representative of the whole stand.

Radiation transmittance through a canopy is influenced by solar zenith angle, amount of diffuse radiation and nonrandom foliage distribution (clumping) (Bréda 2003, Weiss et al. 2004). In particular, changes in solar zenith angle over long data acquisition times affect LAI estimates significantly (Hyer and Goetz 2004). Although we corrected for variation in solar zenith angle across years and seasons, changes in solar zenith angle during data acquisition were not fully accounted for because an open area was distant from some stands. Therefore, we used the midpoint solar zenith angle between the beginning and end of the data acquisition time. Concurrent measurements of above- and below-canopy radiation would probably have improved the agreement between our optical and LAI estimates. Changes in the proportion of direct and diffuse radiation might be another source of error, particularly when LAI is estimated from measurements over the PAR region (Hyer and Goetz 2004), which may explain the within-year improvement in the relationships between optical measurements and LAI.

In addition, accurate estimates of LAI require determination of the light extinction coefficient k, which accounts for nonrandomness in foliage distribution and must be calibrated to exclude absorption from branches and stems (Bréda 2003). We assumed a constant k because we could not provide an independent estimate of k. However, by inversion of the regression of LAI against PAR_T within stands (data not shown), k was found to vary by ~45% among stands. Previous studies have reported that k varies as a result of the effects of canopy architecture and stand structure (Dufrêne and Bréda 1995, Vose et al. 1995), and is LAI-dependent within species (Sampson and Voie et al. 1995).
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Serrano et al. (2000) the transition between the red and near infrared regions of green and non-green canopy components modulate (Kucharick et al. 1998). Because variations in the relative proportion of canopy elements occurs at several scales: between branches or shoots within plants, and between plants within a stand (Chen et al. 1997). Thus, the existence of local light flecks and canopy gaps in sparse canopies may have increased bias in radiation estimates (Hyer and Goetz 2004).

Unlike our previous study (Serrano et al. 2000a), which was based on continuous shrub canopies, this study was conducted on forest canopies of complex and heterogeneous stand structure. In forest stands, branch area is largely covered by leaves; however, stems may not be preferentially shaded by leaves (Kucharick et al. 1998). Because variations in the relative proportion of green and non-green canopy components modulate the transition between the red and near infrared regions (Serrano et al. 2000a), the lack of a relationship between \( T_{RE} \) and LAI across our stands may be attributed, in part, to differences in structure among stands. However, the use of \( T_{RE} \) when compared with \( T_{PAR} \) and \( T_{PAR} \), significantly improved within-stand LAI estimates, even in sparse canopies. Thus, \( T_{RE} \) might be useful for assessing relative changes in LAI within a stand.

Assessing water content

We found that \( T_{W1} \) was correlated with WC \( (r = 0.69, P < 0.001) \) as well as with WC \( _{CAN} \) \( (r = 0.69, P < 0.001) \) (Figure 3). Several studies have shown the capability of water index derived from reflectance data to assess water content at the leaf, canopy and landscape scales (Peñuelas et al. 1993, 1996, Serrano et al. 2000b, among others), but this is the first time that the approach has been validated for transmittance data. When the data set was split according to stand density, the correlation coefficient between \( T_{W1} \) and WC improved for both high \( (r = 0.84, P < 0.001) \) and low \( (r = 0.76, P < 0.01) \) density stands (Figure 3A). Similarly, the correlation coefficient between \( T_{W1} \) and WC \( _{CAN} \) \( (in \ g \ m^{-2}) \) improved in high density stands \( (r = 0.87, P < 0.001) \) and was marginally significant in low density stands \( (r = 0.58, P = 0.05) \) (Figure 3B). Thus, in agreement with previous results based on reflectance data (Dawson et al. 1999, Serrano et al. 2000b), \( T_{W1} \) responded to both LAI and leaf water content. In reflectance studies, poor estimates of vegetation water content in non-continuous canopies by the water band index are attributed to the contributions of soil reflectance (Gao 1996, Ustin et al. 1998) and non-photosynthetic components (van Leeuwen and Huete 1996) to canopy reflectance. In our study, non-photosynthetic components may have also contributed to the scatter in the relationships, and local light flecks and canopy gaps may have contributed to the scatter in our low density stands.

Assessing light-use efficiency and photosynthetic function

We found that \( T_{PRI} \) was correlated with both net CO\(_2\) uptake and LUE. Across seasons, \( T_{PRI} \) was slightly correlated with LUE \( (r = 0.46, P = 0.07) \); however, when we excluded the summer data (when net CO\(_2\) uptake was negative because of low photosynthetic rates and high respiratory rates), \( T_{PRI} \) was significantly correlated with LUE \( (r = 0.58, P < 0.05) \) (Figure 4A). Although similar results at the canopy level have been obtained in reflectance studies (Gamon et al. 2001, Stylniski et al. 2002, Filella et al. 2004), this is the first time that a consistent relationship has been reported for spectral transmittance data. In addition, \( T_{PRI} \) was significantly correlated with net CO\(_2\) uptake \( (r = 0.72, P < 0.01) \) (Figure 4B). Several studies

Figure 2. Relationships between the transmittance amplitude in the red edge (\( T_{RE} \)) and leaf area index (LAI) measured over 4 years in six holm oak forest stands (each stand is denoted by a different symbol). The coefficients of determination for stand data sets are indicated \( (P < 0.001) \). See Materials and methods for derivation of these indices.

Figure 3. (A) Relationship of the transmittance-based water index \( (T_{W1}) \) and mean leaf water content and (B) relationship between \( T_{W1} \) and canopy water content measured in six holm oak forest stands across seasons in 1999. Solid and open symbols correspond to high and low density stands, respectively. The coefficients of determination and significance are indicated in each panel \( (n = 12) \).
have reported significant relationships between PRI and net
CO₂ uptake (Peñuelas et al. 1995, Gamon et al. 1997), al-
though these relationships appear to be weaker during drought
stress (Peñuelas et al. 1994, 1997). In our study, summer
drought conditions were severe (predawn water potential was
about –5.0 MPa; L. Serrano, unpublished results). Reduction
in the correlation between PRI and net CO₂ uptake has been
attributed to a drought-induced uncoupling between PSII activ-
ity and photosynthetic down-regulation and also to seasonal
changes in the total carotenoid pool (Stylinski et al. 2002).

The \( T_{\text{PAR}} \times T_{\text{PRI}} \) index was even more closely correlated with
canopy LUE \((r = 0.93, P < 0.01)\) and mean net CO₂ uptake \((r =
0.84, P < 0.01)\) (Figures 4C and 4D) than were separate mea-
surements of \( T_{\text{PAR}} \) and \( T_{\text{PRI}} \). In contrast with previous studies
based on reflectance data (Barton and North 2001), there was
no correlation \((r = 0.26, P = 0.42)\) between \( T_{\text{PRI}} \) and \( T_{\text{PAR}} \), indicat-
ing that these indices were largely independent over the
temporal and spatial scales of our study. These results, to-
gether with the observed enhancement of the relationships be-
tween \( T_{\text{PAR}} \times T_{\text{PRI}} \) and net CO₂ uptake, indicate that both
structural and physiological adjustments were responsible for
modifying CO₂ fixation capacity in our forest stands. Other
studies in chaparral evergreen species indicated that changes
in CO₂-fixation capacity are driven primarily by physiological
adjustments rather than by structural changes during periods
of photosynthetic down-regulation (Stylinski et al. 2002).

Because \( T_{\text{PAR}} \times T_{\text{PRI}} \) provided a reliable estimate of net CO₂
uptake, we tested the ability of a simple LUE model based on
transmittance data to estimate growth (NPP). Integrated \( T_{\text{PAR}} \times
T_{\text{PRI}} \) \((\Sigma T_{\text{PAR}} \times T_{\text{PRI}})\) was calculated by summing the individual
seasonal values (including summer data). Growth was calcu-
lated on the basis of aboveground TB increment between
March 1999 and March 2000 in each stand. We found a close
relationship between \( \Sigma T_{\text{PAR}} \times T_{\text{PRI}} \) and total biomass increment
\((r = –0.85, P = 0.11)\). This approach was quite successful con-
sidering the time lag between gas exchange and spectral trans-
mittance measurements and the small sample sizes. Further re-
search is needed to assess this response in a wider range of for-
est structures. Nevertheless, these data provide further evi-
dence that canopy structure does not necessarily scale with
physiological activity, and that the combined \( T_{\text{PAR}} \) and \( T_{\text{PRI}} \)
information is required to adequately assess photosynthetic ac-
tivity in this Mediterranean forest. In addition, the close agree-
ment between growth and \( \Sigma T_{\text{PAR}} \times T_{\text{PRI}} \) suggests that seasonal
estimates of LUE and fractional intercepted PAR (i.e., \( 1 – \text{PAR}
transmittance) might be sufficient to estimate carbon balance
in this forest.

Conclusions
Spectral transmittance measurements were related to allo-
metric estimates of LAI and green and total biomass. Measure-
ments of \( T_{\text{PAR}} \) and \( T_{\text{PAR}} \) provided information on gross
changes in total biomass and LAI and were appropriate for
comparing stands, although subtle changes within a stand
were better assessed by \( T_{\text{RE}} \). Although we did not consider the
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effects of non-random foliage distribution or the contribution of non-green canopy elements (the relationships between LAI and \( T_{\text{Bas}} \) were affected by stand structure), our results indicate that, in long-term studies of fixed plots, changes in LAI can be estimated from \( T_{\text{Pri}} \) measurements with a high degree of confidence. In addition, indices based on spectral transmittance were successful in capturing physiological processes that occur on fine temporal and spatial scales, such as changes in photosynthetic function and water content through measurements of \( T_{\text{Pri}} \) and \( T_{\text{Bas}} \). Moreover, by estimating LUE through \( T_{\text{Pri}} \), we obtained accurate estimates of net CO₂ uptake and growth, providing a tool to assess canopy photosynthetic function and NPP.

This novel approach might provide a powerful tool for studying ecosystem carbon and water budgets and might also be useful as a validation technique for remote sensing studies. More studies of transmitted radiation through canopies are needed to explore the capabilities of this approach.

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