Modeling spatially distributed ecosystem flux of boreal forest using hyperspectral indices from AVIRIS imagery

Abdullah F. Rahman, John A. Gamon, David A. Fuentes, Dar A. Roberts, and Dylan Prentiss

Abstract. Correct estimation of spatially distributed CO$_2$ flux is of utmost importance for regional and global carbon balance studies. Tower-based instruments provide flux data from a small footprint area and may not be suitable for spatial extrapolation over areas not represented by the towers. In this study we developed a method of combining optical indices from remotely sensed hyperspectral images with flux data from towers covering different vegetation types to make spatially continuous maps of gross CO$_2$ fluxes. Using a simple light-use efficiency model, we tested the ability of spectral indices derived from Airborne Visible Infrared Imaging Spectrometer (AVIRIS) imagery to estimate photosynthetic fluxes of several boreal forest stands. Because CO$_2$ flux from terrestrial ecosystems is dependent on both vegetation cover and physiological state, we hypothesized that measures of both forest structure and physiology were important for flux estimation. Consequently, the modeled fluxes considered both the normalized difference vegetation index (NDVI) and a scaled value of the photochemical reflectance index (PRI), both derived from narrowband reflectance. NDVI alone was of limited use in describing the variation in ecosystem fluxes ($R^2 = 0.26$). Addition of the PRI, which is related to xanthophyll cycle pigment activity and unrelated to NDVI, improved the agreement between modeled and measured fluxes ($R^2 = 0.82$). Our results also indicated that simple extrapolation of point-based flux tower data to represent the large-area fluxes of boreal forest may lead to an underestimation of the spatially distributed fluxes, at least for the vegetation types studied in this analysis.

1. Introduction

The boreal forest represents ~11% of the Earth’s total land area [Bonan and Shugart, 1989] and contains more than 30% of all forest soil carbon [Schlesinger, 1991] and ~13% of the total carbon in the terrestrial biosphere [Schlesinger, 1977]. Global climate simulations suggest that the boreal region will undergo significant warming in response to increasing atmospheric CO$_2$ [Houghton et al., 1990]. Because of the large contribution of these forests to the global carbon budget, warming in these northern regions could have large implications for the global carbon cycle and climate regulation.

The need to better understand how the boreal forest will respond to climate change has been the main driving force behind a large-scale study of the Canadian boreal region, named the “Boreal Ecosystem-Atmosphere Study” (BOREAS) [Sellers et al., 1995]. One goal of this study was to improve our current understanding of boreal carbon fluxes. Recently, there has been an ongoing debate about whether the boreal forest is a net sink or source of terrestrial carbon [Wang and Polglase, 1995]. Some studies have suggested that it is a source [Quay et al., 1992]. Other studies have suggested the opposite, that it is a sink, thus helping to offset the rising atmospheric CO$_2$ concentration [Keeling et al., 1996]. A major focus of the BOREAS project was to examine the exchange of CO$_2$ between the boreal ecosystems and the atmosphere to clarify the spatial and temporal patterns of carbon flux.

This study explores a simple method for mapping the photosynthetic component of the CO$_2$ flux based on a combination of Airborne Visible Infrared Imaging Spectrometer (AVIRIS) imagery and flux tower data. First, we used a semiempirical statistical modeling approach to correlate hyperspectral remotely sensed surface characteristics to CO$_2$ fluxes from different vegetation types. On the basis of this correlation we then derived maps of CO$_2$ fluxes that depict the midday peak photosynthetic rates for these boreal landscapes consisting of old aspen, old and young jack pine, old black spruce, and fen. We then compared the fluxes collected at the tower sites to the modeled fluxes of the same vegetation types outside the tower footprint area.

2. Modeling Approach

There are three main types of modeling approaches used to estimate the ecosystem CO$_2$ fluxes and productivity [Ruiný et al., 1994]. These are (1) statistical models, which correlate the fluxes to various climate variables [Lith, 1975]; (2) parametric models that utilize the light-use efficiency (LUE) concept to decompose the fluxes into various components [Kumar and Moneth, 1981]; and (3) process models, which take into account the basic processes of photosynthesis and respiration [Esser, 1992]. Statistical and parametric models are semiemp-
empirical by nature and generally biome specific. Process models are the most sophisticated, but some require multiple parameters that are generally not available for global ecosystems [Ruiny et al., 1994; Liu et al., 1999].

Remote sensing provides one method of exploring spatial patterns of CO₂ flux. Multiple studies have shown that the optically based normalized difference vegetation index (NDVI) can be used to estimate CO₂ fluxes of vegetation [Goward et al., 1985; Whiting et al., 1991]. NDVI is related to the fraction of photosynthetically active radiation (PAR) absorbed by green vegetation (or, f_{APAR}). Myneni and Williams [1994] have used canopy radiative transfer models to show that both NDVI and f_{APAR} are sensitive to the amount of leaf area in a green vegetation canopy. Tucker and Sellers [1986] have related biophysical and scattering properties of plant canopies to show that NDVI and f_{APAR} are functionally related. There is also substantial empirical evidence to suggest that in general, a relationship exists between these two optical properties of plant canopies [Kumar and Monteith, 1981; Daughtry et al., 1983; Asrar et al., 1984; Choudhury, 1987; Goward et al., 1994]. Modeling efforts [Asrar et al., 1984; Shu, 1991; Goward and Huenemrich, 1992] and empirical studies [Bartlett et al., 1991; Pinter, 1993] have indicated that the relationship between NDVI and f_{APAR} is also relatively insensitive to changes in solar zenith angle.

Kumar and Monteith [1981] have shown that f_{APAR} can be multiplied by an efficiency factor (ε) to derive the net primary productivity (NPP), or the net photosynthetic carbon gain, of a vegetation stand:

\[ NPP = (\varepsilon \times \Sigma f_{APAR}) \]

where NPP is usually estimated by aboveground biomass (kg) accumulated in a growing season, Σf_{APAR} is the annual integral of photosynthetically active radiation (PAR) (400–700 nm, in μmol m⁻² s⁻¹) absorbed by vegetation, and ε is defined as the efficiency with which absorbed PAR is converted to biomass. [Kumar and Monteith, 1981; Heimann and Keeling, 1989; Potter et al., 1993].

Given the fact that NDVI can be expressed as a function of f_{APAR} and the relationship between these two terms are not affected by solar zenith angle, (1) can be rewritten in terms of a function:

\[ NPP = f(\varepsilon \times NDVI). \]

Usually, ε is not derived directly from remote sensing. According to Monteith [1977], ε is a relatively constant value among plants of the same metabolic type but can vary depending on the phenologic stage, climate conditions, and water stress [Jarvis and Leverenz, 1983]. However, some recent studies have shown that an optically based index derived from hyperspectral (narrowband) reflectance, called the photochemical reflectance index (PRI), has considerable promise as a measure of vegetation light-use efficiency [Gamon et al., 1992, 1995b; Peñuelas et al., 1995; Fillela et al., 1996; Nichol et al., 2000]. This link to efficiency occurs because this index detects the response of xanthophyll cycle pigments to changing light conditions [Gamon et al., 1990, 1997; Gamon and Surfus, 1999].

Under conditions of excess light when PAR exceeds the capacity of photosynthetic reactions, certain foliar carotenoids, known as xanthophyll cycle pigments, provide a means of dissipating the excess light through the production of heat, thus protecting the photosynthetic apparatus [Demmig-Adams and Adams, 1996; Horton et al., 1996]. This happens through the activation of a deepoxidase enzyme present in the leaf chloroplasts. Deepoxidase converts violaxanthin, a xanthophyll that transfers light energy to the photosynthetic apparatus into zeaxanthin, a xanthophyll that directs light energy away from the photosynthetic apparatus and dissipates it as heat [Yamamoto, 1979; Pfundel and Bilger, 1994; Demmig-Adams and Adams, 1996]. This reaction is readily reversed under low light conditions, and zeaxanthin is converted back to violaxanthin through the activation of an epoxidase enzyme in leaf chloroplasts [Demmig-Adams and Adams, 1996].

The interconversion of the xanthophyll cycle pigments can be detected through a change in reflectance at 531 nm [Gamon et al., 1990, 1992]. Because these pigments are responsible for regulating absorbed light energy within the leaf, their reflectance characteristics provide a useful optical indicator of changing photosynthetic activity. On the basis of this premise, Gamon et al. [1992] formulated the PRI incorporating the narrowband vegetation reflectance at 531 nm and a reference wavelength. Originally, this reference wavelength was 550 nm [Gamon et al., 1992]. However, more recent studies have adopted 570 nm as a reference wavelength [Peñuelas et al., 1995; Gamon et al., 1997; Gamon and Surfus, 1999; Nichol et al., 2000].

The relationship between vegetation reflectance at 531 nm and photosynthetic light-use efficiency (LUE) has been studied for leaf and small vegetation plots showing that the PRI provides a widely applicable index of vegetation LUE across species, functional types, and nutrition levels [Gamon et al., 1997]. Recently, Stylinski [2000] has demonstrated that the PRI-LUE relationship is maintained across seasons for evergreen scrub vegetation. Also, Nichol et al. [2000] have shown that PRI can be effectively used as an indicator of photosynthetic LUE at stand levels of boreal ecosystems.

On the basis of these findings we hypothesize that the LUE parameter of a vegetation stand can be expressed in terms of PRI. Equation (2) then can be rewritten to incorporate PRI as an efficiency factor for an instantaneous estimate of ecosystem photosynthetic rates (or CO₂ uptake):

\[ CO₂ \text{ uptake} = f(\text{PRI} \times NDVI). \]

3. Problem Statement

Even though the relationship between PRI and LUE has been studied at leaf, plant, and stand levels, tests of this index as an indicator of photosynthetic flux at the landscape scale have rarely been attempted. To our knowledge, only one other study published by Nichol et al. [2000] has been directed toward relating these two parameters at stand levels in the boreal forest. The lack of landscape-level "PRI versus LUE" studies is, in part, because of the shortage of appropriate data sets. To validate PRI as a LUE indicator, it is helpful to have an independent set of carbon flux (photosynthesis) measurements, which is often unavailable at the landscape scale. Recently, eddy covariance flux towers have been deployed in different biomes worldwide as a means of sampling net carbon fluxes over large landscapes. By integrating the high-frequency covariance between CO₂ concentration and vertical velocity, this method provides a direct means of sampling instantaneous landscape-level fluxes [Balchcchi et al., 1988; Verma, 1990].

Although the establishment of worldwide eddy covariance flux towers has opened up opportunities of testing the hypo-
esis that PRI can detect the LUE at landscape level, an additional challenge remains in this effort. The fact that remote sensing typically samples in the spatial domain, whereas flux towers sample a limited footprint area in the temporal domain, makes it difficult to compare these two data types. There are airborne hyperspectral sensors, such as AVIRIS [Vane et al., 1993; Green et al., 1998] or CASI (Compact Airborne Spectrographic Imager) (Itres Research Ltd., Alberta, Canada), which acquire images covering different flux-tower sites. These images are snapshots in time but spatially continuous, and they cover areas larger than the immediate footprint areas of the flux towers. On the other hand, eddy covariance, which is typically expressed at half hourly to daily intervals, can provide flux measurements suitable for comparison with a small portion of a remotely sensed image. In other words, images are spatially continuous at their pixel scales, and eddy fluxes are temporally continuous at their recording intervals. They only interact at a point in time and at a small area of footprint coverage and hence render intercomparison difficult.

Ideally, to develop or validate a map of CO2 fluxes with PRI derived from a hyperspectral image such as AVIRIS, it would be best to have multiple flux towers sampling across a landscape covered by an image, or temporally continuous images of a tower footprint. Currently, both of these scenarios are unavailable, so we developed an alternative approach. The data set used in this study was derived from a number of AVIRIS images and multiple eddy covariance flux towers from across the BOREAS study region, thus providing a unique opportunity to explore the relationships between hyperspectral indices and CO2 fluxes.

4. Materials and Methods

4.1. Study Sites

In 1993 the BOREAS project was undertaken in the boreal forest of central Canada called the BOREAS modeling region (~500,000 km²). Two 50 x 50 km intensive study areas were selected at the north and south ends of the modeling region (see Sellers et al. [1995] for details). The northern study area (NSA) and the southern study area (SSA) were located near Thompson, Manitoba, and Prince Albert, Saskatchewan, respectively. They were about 500 km apart, and each region contained flux towers located on relatively homogeneous vegetation and soil patches to measure water, vapor, heat, and CO2 fluxes using eddy covariance techniques. Our study utilized the CO2 data collected during spring and fall seasons of 1994 from the SSA region flux towers. There were six flux towers in that region, representing black spruce, jack pine, aspen, and herbaceous-species-dominated fen patches (Table 1). Each flux site was relatively level, and the forest stand was horizontally homogeneous throughout the area deemed as the flux footprint, a region extending ~1 km upwind. An estimated aerial proportion of these vegetation types across the SSA was fen 6.9%, black spruce 27.4%, jack pine 13.6%, and aspen 13.5% [Hall et al., 1997]. The rest of the SSA areas were covered by water bodies, mixed forests, roads, urban areas, burned patches, and grass.

4.2. Remotely Sensed Data

AVIRIS is a hyperspectral sensor that collects data in 224 continuous spectral channels (also called bands) each with a wavelength-sensitive range (also known as spectral bandwidth) of ~10 nm, allowing it to cover the spectral range between 380 nm and 2500 nm. This instrument, administered by the Jet Propulsion Laboratory of NASA, flies aboard a NASA ER-2 airplane at ~20 km above the sea level. AVIRIS produces 614 pixels for the 224 channels each scan. Each pixel produced by the instrument covers an ~20 m x 20 m square area on the ground (with some overlap between pixels), thus yielding a ground swath about 11 km wide (for more details, see Vane et
Table 2. Southern Study Area Data Availability Matrix Based on the Dates of AVIRIS Overflight

<table>
<thead>
<tr>
<th></th>
<th>4/19/94</th>
<th>7/21/94</th>
<th>9/16/94</th>
<th>Biome</th>
</tr>
</thead>
<tbody>
<tr>
<td>TF-2</td>
<td>NF, Ref</td>
<td>Ref</td>
<td>Ref</td>
<td>OA</td>
</tr>
<tr>
<td>TF-4</td>
<td>Ref</td>
<td>Ref</td>
<td>NF, GF, Ref</td>
<td>YJP</td>
</tr>
<tr>
<td>TF-5</td>
<td>NF, GF, Ref</td>
<td>NF, GF, Ref</td>
<td>OJP</td>
<td></td>
</tr>
<tr>
<td>TF-7</td>
<td>Ref</td>
<td>NF, Ref</td>
<td>NF, GF, Ref</td>
<td>OJS</td>
</tr>
<tr>
<td>TF-9</td>
<td>Ref</td>
<td>Ref</td>
<td>Ref</td>
<td>OBS</td>
</tr>
<tr>
<td>TF-11</td>
<td>Ref</td>
<td>NF, GF, Ref</td>
<td>NF, GF, Ref</td>
<td>FEN</td>
</tr>
</tbody>
</table>

*NF stands for net CO2 flux (from flux towers), GF stands for gross photosynthetic flux (respiration corrected), and Ref stands for reflectance data. TF followed by a number represents the flux tower designated by that number. Bold lettered points are the ones that had both AVIRIS image and gross photosynthetic flux data available and were used for the present study. The biome abbreviations are as follows: OA, old aspen; YJP, young jack pine; OJP, old jack pine; OBS, old black spruce; and FEN, fen site.

AVIRIS was flown over the BOREAS study areas in 1994 and 1996. Images were available from April 19, July 21, and September 16, 1994, covering all six tower sites. However, since most of the flux towers reported data sporadically during the 1994 season, there were only nine cases when both AVIRIS image and concurrent CO2 flux data were available from the tower sites. Gross CO2 flux could not be derived for two of these nine points (see section 4.5). Consequently, the useful data for this study were limited to seven points in July and September (Table 2).

The image acquisition time was ~1130 LT. Original radiance images were corrected for atmospheric degradation and converted to surface reflectance values using algorithms developed by Green et al. [1993]. Atmospherically corrected images were then georeferenced, using a geocorrected Landsat TM image of the area as a base map. These atmospheric- and geocorrected AVIRIS images were then used to produce NDVI and PRI images using the following equations:

\[
\text{NDVI} = \frac{R_{47} - R_{30}}{R_{47} + R_{30}} \tag{4}
\]

\[
\text{PRI} = \frac{R_{17} - R_{21}}{R_{17} + R_{21}} \tag{5}
\]

where \( R \) represents reflectance, and the subscript \( B \) followed by a number represents the AVIRIS band represented by that number. AVIRIS bands 30, 47, 17, and 21 represent reflectance at wavelengths 660, 800, 531 and 570 nm, respectively. The 660 nm band was considered "red" and the 800 nm band was considered "near infrared."

PRI is a normalized index similar to NDVI, and its values fall between -1 and +1. Since our goal was to use PRI as an efficiency factor, we derived a scaled value of PRI (\( s\text{PRI} \)) to represent an adjusted range of 0 to 1:

\[
\text{sPRI} = \frac{(\text{PRI} + 1)}{2}. \tag{6}
\]

A very low \( s\text{PRI} \) value would indicate that the photosynthetic light use efficiency is very low. On the other hand, a high \( s\text{PRI} \) value would mean that photosynthesis is happening at its maximum efficiency.

4.3. Footprint Area

The footprint areas of the flux towers were determined on the basis of the prevailing wind direction during the image acquisition time, as recorded by the tower instruments. Following the theoretical discussion of Kaharabata et al. [1997], a 300 m × 900 m rectangular area toward the upwind direction from each tower site was selected as an optimal footprint area (Figure 1). Average values of NDVI and PRI of those footprint areas were calculated for this study. Since flux towers sense the...
Table 3. Schematic Diagrams of the Footprint Areas for the Data Use in This Studya

<table>
<thead>
<tr>
<th>Date</th>
<th>Flux Tower Site</th>
<th>Wind Direction (From North)</th>
<th>Footprint Area (in Relation to the Tower)</th>
</tr>
</thead>
<tbody>
<tr>
<td>04/19/1994</td>
<td>old aspen</td>
<td>130°</td>
<td></td>
</tr>
<tr>
<td>07/21/1994</td>
<td>fen</td>
<td>250°</td>
<td></td>
</tr>
<tr>
<td>07/21/1994</td>
<td>old black spruce</td>
<td>300°</td>
<td></td>
</tr>
<tr>
<td>07/21/1994</td>
<td>old jack pine</td>
<td>250°</td>
<td></td>
</tr>
<tr>
<td>09/16/1994</td>
<td>old aspen</td>
<td>300°</td>
<td></td>
</tr>
<tr>
<td>09/16/1994</td>
<td>fen</td>
<td>120°</td>
<td></td>
</tr>
<tr>
<td>09/16/1994</td>
<td>old black spruce</td>
<td>180°</td>
<td></td>
</tr>
<tr>
<td>09/16/1994</td>
<td>old jack pine</td>
<td>230°</td>
<td></td>
</tr>
<tr>
<td>09/16/1994</td>
<td>young jack pine</td>
<td>270°</td>
<td></td>
</tr>
</tbody>
</table>

*aColumn 4 shows the areas in a rectangular shape, with the towers depicted as circles at the middle of the downwind edges. Average wind directions from 1 hour before to 1 hour after the AVIRIS overflight were taken as the representative wind directions.

area-averaged flux data originating from the footprint area [Horst and Weil, 1992; Schmid, 1994], we compared an area-averaged spectral value of the footprint area with the flux data collected by the tower instruments.

Flux towers recorded wind direction data in a half-hourly interval. However, the wind was not always blowing from exactly east-west or north-south directions. To be able to resample the footprint areas in a rectangular fashion, we devised a procedure of averaging wind direction. The AVIRIS scenes that included the tower sites in them were cut in rectangular shapes such that the top of these rectangular images represented north. Two imaginary straight lines, perpendicular to each other, were drawn on the images at “east-west” and “north-south” directions, respectively. The intersection point of these two lines represented the flux tower location. The east-west line was considered the x axis, and the north-south line was considered the y axis.

Wind blowing from +45° to −45° of the positive x axis was considered to be blowing from the east. Similarly, winds from +45° to −45° of the negative x axis, positive y axis, or negative y axis were considered to be blowing from the west, north, or south, respectively (Table 3). Given that the flux tower sites were established on relatively homogeneous patches, we assumed that the error induced by approximating the footprint area with this method would be small. Furthermore, it simplified the image processing and the resampling of the footprint areas significantly.

4.4. CO2 Flux Data

The BOREAS “Tower Flux” science group collected CO2 and other fluxes from both SSA and NSA sites (http://eosims.esd.ornl.gov/BOREAS/bhs/Science_Groups.html). The eddy flux densities were determined by calculating the covariance between vertical velocity and scalar fluctuations [Baldocchi et al., 1988; Wofsy et al., 1994]. Scalar fluctuations of CO2 were computed in real time, using a running mean removal method [McMillen, 1988]. These data were then averaged and stored at half-hour intervals. Negative flux values indicated net carbon uptake (i.e., photosynthesis) by the vegetation, and positive values indicated carbon loss to the atmosphere (i.e., respiration). We used CO2 flux data from flux towers 2, 4, 5, 7, 9, and 11 for this study (Table 2), obtained through the courtesy of the respective “Tower Flux” teams (http://eosims.esd.ornl.gov/BOREAS/boreas_home_page.html).

These half-hourly-averaged CO2 flux data showed considerable short-term fluctuation even on a totally clear day, which confounded interpretation over short periods. Further averaging of the half-hourly data to a 2-hour running mean produced a pattern smooth enough to show a clear diurnal trend (Figure 2). For comparison with AVIRIS imagery, we took an average value of CO2 flux data from 1 hour before to 1 hour after the AVIRIS image acquisition time from the smoothed data as a representative instantaneous flux value for the tower region.

4.5. Photosynthetic Flux

The daytime flux data, collected using eddy covariance, provided the net CO2 flux from the footprint area, i.e., the combination of gross photosynthetic plus respiratory fluxes. To obtain gross photosynthetic rates, net fluxes were corrected by estimates of daytime ecosystem respiration as functions of air temperature [Goulden et al., 1996].

We calculated ecosystem respiration assuming an exponential dependence of respiration on air temperature. Following Goulden et al. [1997], nighttime half-hourly CO2 flux data at relatively high wind speeds (when the friction velocity was 0.2 ms⁻¹ or higher) were plotted against air temperature, using bins of flux data at an interval of 1°C (Figure 3). This was done using the nighttime data from the months of April, June, and September 1994 from the tower sites. The rationale of this approach was that nighttime fluxes were composed of respiration, and friction velocity of 0.2 ms⁻¹ or higher ensured a proper mixing of the flux from the footprint area for the eddy covariance system. The relationship between air temperature and respiration for the 3 months of data produced an exponential function of the form

$$R = 1.0371 \times e^{0.01127T_a},$$

where $R$ is the respiration (µmol m⁻² s⁻¹), $T_a$ is the air temperature (°C), and $e$ is the base of natural logarithm. The

Figure 2. Representative tower flux data from the old black spruce tower site on July 21, 1994, showing fluctuation in CO2 flux data at half-hourly average (solid line) as it was collected. A two-hourly running average (dashed line) smoothes the fluctuation and shows the diurnal trend better. The vertical dashed line shows the approximate time of AVIRIS overflight.
would mean an increased confidence that the relation is sta-
value" (also called Fisher's "r to z transformation). It tests the
variable. Hence all the R^2 values mentioned in this paper refer
to the adjusted R^2 values.

The coefficients a and b were derived from linear regression
fitting between the respiration-corrected gross CO2 flux and
the independent variables included in the regression equation
(8).

gross CO2 uptake = a + b \times (sPRI \times NDVI) \quad (8)

The coefficients a and b were derived from linear regression
fitting between the respiration-corrected gross CO2 flux and
the hyperspectral product (sPRI x NDVI).

For the regression analyses employed in this study, we used
the adjusted R^2, rather than the simple R^2 (coefficient
of determination), because it takes into account the number of
independent variables included in the regression equation
[Zar, 1984]. Since we had only seven data points for this study,
the adjusted R^2 provided a more unbiased estimate of the
dependent variable’s variability explained by the independent
variable. Hence all the R^2 values mentioned in this paper refer
to the adjusted R^2 values.

Another measure of correlation between dependent and
independent variables used in this study was the Fisher’s “p
value” (also called Fisher’s “r to z transformation”). It tests the
null hypothesis that the correlation between the dependent and
the independent variables is equal to zero. When used with
regression analysis, a high R^2 value and a relatively low p value
would mean an increased confidence that the relation is sta-
tistically significant.

4.7. Representativeness of the Tower Sites

Since our modeling approach allowed us to make maps of
CO2 flux of the area covered by the AVIRIS images, we fur-
ther examined if a tower site located in a specific vegetation
type were typical of the fluxes from the same vegetation type
lying outside the footprint areas. For this purpose we used a
land cover map developed by Fuentes et al. [this issue]. Using
this map, we first masked out the areas occupied by different
vegetation types. Then we used those mask maps to cut areas
of a specific vegetation type from the gross photosynthetic CO2
flux maps. A histogram of the flux values was created for each
of the four vegetation types to show the frequency distribution
patterns of the fluxes from the areas under each type. Fluxes
were grouped into categories that differed by 0.1 \( \mu\text{mol m}^{-2}
\text{s}^{-1} \) of gross CO2 fluxes.

We used the modified Shannon-Weiner diversity index \( J \),
also called the evenness index [Pielou, 1966], to measure the
distribution patterns of flux data from each vegetation type
[Zar, 1984; Shannon, 1948]:

\[
J = \frac{H}{H_{\text{max}}},
\]

where \( H \) is the original Shannon diversity index:

\[
H = \frac{n \log n - \sum_{i=1}^{k} f_i \log f_i}{n},
\]

and \( H_{\text{max}} \) is the maximum diversity index:

\[
H_{\text{max}} = \log k.
\]

In (10) and (11), \( k \) is the number of categories, \( n \) is the total
number of data points, and \( f_i \) is the number of data points in
the ith category.

The value of \( J \) has a range from 0 to 1 [Zar, 1984]. A \( J \) value
of 1 would mean that the flux values were evenly distributed
between the mean and the tails for the histogram distribution
in each category. In other words, a higher \( J \) would produce a
more platykurtic distribution, and this would mean that the
fluxes are coming from heterogeneous sources. On the other
hand, a smaller \( J \) value means the flux distribution would be
more leptokurtic, indicating that most of the fluxes are coming
from a functionality uniform stand.

To test how well the tower-based flux measurements repre-
sented the spatially distributed fluxes from their respective
vegetation types outside the footprint areas and the boreal
biome in general, we used a "weighted aerial coverage" ap-
proach. We derived the average flux values of each vegetation
type from the masked-out maps of gross CO2 flux. We then
compared these mean flux values with their respective tower
flux values to find out if the towers agreed with the average
fluxes for these vegetation types. Using the aerial estimation of
SSA vegetation cover estimates by Hall et al. [1997], we mul-
tiplied the percent cover of a vegetation type with the percent
underestimation or overestimation of the fluxes by the tower
from that vegetation. Adding up these weighted values of dis-
crepancies for the four vegetation types used in this study
resulted in an estimation of how well the boreal forest towers
represented the larger regions outside the footprint areas.

5. Results

NDVI showed a weak relationship with gross CO2 flux from
the seven study sites, with a low \( R^2 \) value of 0.26 and a rela-
Figure 4. Comparison of photosynthetic CO$_2$ with (a) NDVI and (b) PRI shows $R^2$ values of 0.26 and 0.77 and $p$ values of 0.9 and 0.0001, respectively. (c) NDVI and PRI were weakly related with an $R^2$ value of 0.07 and a high $p$ value of 0.17. Data points are labeled using month and site names separated by a hyphen. The solid straight lines represent the regression trend lines.

Figure 5. Relationships between ($s$PRI x NDVI) versus net CO$_2$ flux (a) and gross CO$_2$ flux (b). Net CO$_2$ flux showed a relatively low correlation with ($s$PRI x NDVI) with an $R^2$ value of 0.49 and a $p$ value of 0.48, while gross CO$_2$ flux showed a significant correlation, with an $R^2$ value of 0.82 and a $p$ value of 0.002. Similar to Figure 5, data points are labeled using month and site names separated by a hyphen, and the solid straight lines represent the regression trend lines.

resulting $R^2$ was 0.49, and the $p$ value was 0.48 (Figure 5a), not a significant correlation.

A comparison of gross CO$_2$ flux with the product ($s$PRI x NDVI) showed a significant correlation, with an $R^2$ value of 0.82 and a $p$ value of 0.002 (Figure 5b). The linear relation derived using (8) with the gross CO$_2$ flux resulted in the following equation:

$$\text{CO}_2 \text{ uptake} = -4.3833 - 15.018 \times (s\text{PRI} \times \text{NDVI}).$$

(12)

Using (12), we made gross CO$_2$ flux maps of different areas of the boreal forest which were covered by the AVIRIS images. Flux maps of two areas, which included the black spruce and the fen tower sites, are shown in Plate 1. In these maps the roads (on the left-hand side of Plate 1a, extending from the bottom to the top, and on the right-hand side of Plate 1b, slanted from the top to the bottom) had low photosynthetic fluxes. The deforested areas (next to the lower part of the road in Plate 1a) showed the lowest fluxes. The fluxes from the old black spruce tower site (marked by an asterisk on the top middle part of Plate 1a) and its vicinity were more homoge-
Plate 1. Maps of gross CO$_2$ flux from the BOREAS-SSA (a) old black spruce and (b) fen sites on July 21, 1994. The flux tower sites are shown by the asterisk marks on each image. Flux units are in $\mu$mol m$^{-2}$ s$^{-1}$.

The comparison of tower flux values with the modeled flux values for larger regions of the same vegetation types revealed that the aspen tower site was recording 16% less photosynthetic flux than the larger aspen region outside the tower footprint. The fen tower was recording 11% more flux, and black spruce and jack pine were recording 8.5 and 5% less fluxes than their respective vegetation areas outside the tower footprints (Table 4).

Our "weighted aerial coverage" approach shows that the use of tower data alone to estimate an aerial total of flux rates from the four SSA vegetation types would result in an $\sim$10% underestimation of the gross photosynthetic flux for these portions of the SSA. Since the towers were established only in the four vegetation types and the rest ($\sim$40% of SSA land cover) was not represented by these tower sites, we were not able to fully assess how well the tower sites represented the gross CO$_2$ fluxes of the boreal biome as a whole.

6. Discussion

6.1. CO$_2$ Flux Versus Hyperspectral Indices

Equation (8) described a simple model that incorporates the statistical and parametric approaches of modeling ecosystem fluxes. The statistical part of this model is based on the cali-
bration of the hyperspectral data to tower flux data, and also the relating of respiratory flux to air temperature. The parametric part of it, i.e., the depiction of $s_{PRI}$ as the efficiency parameter, is based on the spectral response to changes in plant photosynthetic processes. In this sense, this simple model encompasses all three types of approaches (i.e., statistical, parametric, and process based) which have been traditionally used in ecosystem flux modeling. Presumably, the LUE term in this model (i.e., $s_{PRI}$) is dynamic over a short interval, dependent upon the spectral response of xanthophyll cycle pigments, rather than having fixed values assumed for a given vegetation type. The other term, NDVI, is dynamic over a longer timescale and dependent on vegetation structure and the amount of green leaf area. Since both NDVI and PRI (and hence $s_{PRI}$) can vary pixel to pixel, this model is suitable for making CO$_2$ maps of large areas for estimating spatially distributed photosynthetic flux.

The results from this study show that only 26% of the variation in photosynthetic flux can be explained by NDVI, whereas PRI alone would be able to explain 77% of the variation in the same flux (Figures 4a and 4b). This finding is in agreement with previous research results that show NDVI to

<table>
<thead>
<tr>
<th>Vegetation Type</th>
<th>Mean CO$_2$ Flux of Tower Footprint ($\mu$mol m$^{-2}$ s$^{-1}$)</th>
<th>Modeled CO$_2$ Flux of Tower Footprint ($\mu$mol m$^{-2}$ s$^{-1}$)</th>
<th>Mean CO$_2$ Flux From Masked Areas ($\mu$mol m$^{-2}$ s$^{-1}$)</th>
<th>“J” Values of Masked Areas</th>
<th>Percent Difference in Flux Values Between Towers and Areas Outside the Footprint</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fen</td>
<td>-11.08</td>
<td>-10.13</td>
<td>-9.87</td>
<td>0.66</td>
<td>11</td>
</tr>
<tr>
<td>Black spruce</td>
<td>-9.16</td>
<td>-9.81</td>
<td>-9.93</td>
<td>0.64</td>
<td>-8.5</td>
</tr>
<tr>
<td>Jack pine</td>
<td>-9.01</td>
<td>-9.22</td>
<td>-9.44</td>
<td>0.81</td>
<td>-5</td>
</tr>
<tr>
<td>Aspen</td>
<td>-6.88</td>
<td>-7.62</td>
<td>-7.97</td>
<td>0.50</td>
<td>-16</td>
</tr>
</tbody>
</table>

*Fen, black spruce, and jack pine data are taken from 07/21/1994. Aspen data are from 09/16/1994.
be highly sensitive to structural elements of green vegetation [Goward et al., 1994; Myneni and Williams, 1994] but insensitive to short-term variation in photosynthetic rates [Gamon et al., 1992]. Consequently, NDVI can be a poor indicator of variation in CO₂ flux, particularly for evergreen species [Running and Nemani, 1988; Gamon et al., 1995c]. On the other hand, PRI responds to the changing photosynthetic status of leaves and canopies, so it could largely explain the day-to-day and site-to-site variation in the photosynthetic flux. This observation is consistent with the recent results of Nichol et al. [2000], who demonstrated that PRI derived from a helicopter-mounted spectrometer and simulated AVIRIS data corresponded well to the photosynthetic light-use efficiency of boreal forest stands. Our results (Figure 4) confirm that the fine spectral signals contained in the AVIRIS images were suitable for extracting PRI, which could be used to follow the photosynthetic flux of different vegetation types in the boreal biome.

In some cases [e.g., Gamon et al., 1995a], PRI has also been found to be sensitive to the same changes in canopy structure that affect NDVI. However, in this study the poor relationship between NDVI and PRI suggests that in the boreal biome, these two spectral indices detect different aspects of green vegetation (Figure 4c). Combining the physiological information in PRI with the structural vegetation index NDVI, also from AVIRIS images, explained most of the spatial and temporal variation in CO₂ flux from the boreal forest (Figure 5b).

As a qualitative validation of this approach, we observed that during the summer month of July the photosynthetic fluxes were higher for all biomes than in September, the onset of winter, and both the tower-based flux data and the hyperspectral product conformed to this fact (Figure 5b). The fen site had undergone a large change in flux rates during these three months. During summer, the shrubs in the fen site were green and photosynthesizing at a high rate. At the onset of winter, most of the fen shrub canopies senesced [Sukker et al., 1997], and photosynthesis declined significantly. NDVI of the fen site also followed this seasonal trend (Figure 4a). The photosynthetic activity of old jack pine site exhibited a similar decline, but to a lesser extent, presumably because it was dominated by evergreens. Baldocchi et al. [1997] stated that during 1994 the old jack pine stand had a new flush of needles in early June, while in September, needle yellowing started, and there was appreciable loss of 2-, 3-, and 4-year-old needles, coincident with the September decline in photosynthetic flux. Because PRI also responds to carotenoid/chlorophyll ratios [Gamon et al., 1995a; 2001], which can scale with photosynthetic activity in evergreen species, this yellowing may be an additional reason why the sPRI × NDVI product successfully tracked that trend (Figure 5b).

The higher NDVI values of old jack pine in September relative to July (Figure 4a) may be due to the fact that NDVI is affected by multiple factors, including shade, vegetation structure, and soil wetness. Consequently, the use of NDVI alone to predict flux values would have been misleading. In this case, the use of sPRI as an efficiency factor minimized the ambivalence of NDVI in predicting the flux values. Since we had only one season's data for young jack pine, old black spruce, and old aspen, the impact of seasonal variation on fluxes of those vegetation types could not be tested here.

6.2. Limitations and Suggestions

A number of limitations must be overcome if the method described in this paper is to be used for routine mapping of CO₂ fluxes. The primary limitation derives from the semiparametric nature of this method, which requires the availability of flux tower data for calibration of hyperspectral-imagery-based indices. To develop a process-based model of CO₂ flux assessment using hyperspectral imagery, there is a need of more coordinated flux and optical data collection from different biome types. This problem of lack of hyperspectral data from the tower regions can be solved by increased aircraft-based image acquisition. Images from the recently launched MODIS sensor should also be tested for this purpose. Meanwhile, it is important to remember that our modeled fluxes are based on an empirical calibration with tower fluxes rather than on a fully independent model.

Another weakness of this method might arise from errors in interpreting two-band indices derived from remotely sensed images of complex scenes. In our study, pixels contained mixes of vegetation with nonvegetation cover types, which may lead to problems in the interpretation of indices. Use of spectral mixture models [Adams et al., 1993; Roberts et al., 1993] may help solve that problem. Although the vegetation map used here was based partly on spectral mixture analysis, we did not directly apply this technique in our study. Further difficulties of interpreting remotely sensed data, including the effects of view and solar zenith angles (bidirectional reflectance distribution function), and atmospheric degradation of the reflectance signal, all deserve further study because they pose formidable challenges to routine applications of this approach. Despite these limitations, the strong correlation between our simple two-parameter model and tower flux data indicates that considerable potential exists for mapping photosynthetic fluxes over large landscapes using narrowband optical indices.

Since the flux images provided in this study (Plate 1) provided instantaneous maps of gross CO₂ fluxes, there is also a need to extend these maps to daily values of carbon uptake. This way, the daily values can be integrated throughout the year, and spatially distributed NPP values of different biomes can be derived. There is evidence that the daily trends in xanthophyll cycle pigments, and hence PRI, can be estimated from diurnal changes in incident sunlight [Adams and Demmig-Adams, 1992; Schindler and Lichtenhaver, 1996; Adams et al., 1999]. Most of the established flux towers around the globe record half-hourly values of diurnal incident sunlight. A weekly or biweekly measurement of NDVI and PRI from an aerial- or satellite-based sensor, combined with estimated daily variations in PRI at a half-hourly interval, could be utilized to achieve the goal of mapping spatially distributed NPP of different biomes.

A thorough error analysis is also needed. Tower fluxes have a number of inherent errors that have been well discussed [Moncrieff et al., 1996]. Some of these tower flux errors would necessarily be incorporated into our regional flux estimates. On the other hand, the calibration against multiple towers may have reduced random tower errors, which may be why the regional flux estimates for the individual vegetation types agreed more closely with the modeled fluxes than with the measured fluxes (arrows in Figure 6). Further errors in our regional estimates could arise from inaccuracies in the vegetation map, which have been partly discussed by Fuentes et al. [this issue]. Additionally, the optically based model presented here undoubtedly has its own inherent limitations and error sources, some of which have also been discussed before [Gamon et al., 2001]. Thus a full error analysis for our approach would require consideration of multiple types and sources of
error and would probably require more than the seven tower data points available here.

### 6.3. Spatially Distributed Flux

Despite these limitations, some conclusions regarding regional fluxes may be made. Because the model was calibrated against flux towers, it provided a means to extrapolate the tower flux measurements to a regional scale. Even if absolute measures are in error due to the reasons discussed above, the comparison of tower fluxes with regional estimates provides valuable insight into the degree to which flux towers were representative of the larger region. This comparison indicates that with the exception of the fen site, most towers reported flux values that were less than the modeled values for larger regions of the same vegetation types (Table 4). If this comparison is valid, a simple accounting, based on these differences and the areas of each vegetation type, suggests that errors due to nonrepresentative tower locations alone would be on the order of 10% for the four vegetation types in this study. The annual carbon budgets from tower flux sites in the boreal forest range from a net source to a net sink and have not conclusively resolved the carbon balance of this biome [Sellers et al., 1997]. Consequently, a 10% underestimate of gross fluxes for these vegetation types could be significant in terms of the regional carbon balance and suggests that the vegetation types included in this analysis comprise a slight net carbon sink. Although not conclusive, this conclusion is consistent with several recent studies suggesting that the boreal forest has been a net carbon sink in recent years [e.g., Keeling et al., 1996].

The apparent underestimation of gross carbon flux rates may be due, in part, to the fact that most of the BOREAS flux towers were located in mature stands. Recent studies suggest that mature forest stands often show age-related declines in photosynthetic rates and NPP [Yoder et al., 1994; Ryan and Yoder, 1997; Magnani et al., 2000], and this may be true for the boreal forest. The BOREAS flux towers also avoided mixed stands, which often were located on relatively productive sites. Although not explicitly part of this study, the extent and productivity of mixed and aggregating stands should be more carefully considered in any regional analysis. Additionally, the disagreement between tower fluxes and larger regional fluxes could simply be due to the patchiness of boreal stands (clearly visible in Plate 1), which could lead to an accumulation of random errors that could cause a particular set of tower measurements to disagree with regional estimates for the same stands. The use of Shannon-Weiner J statistics showed that the spatial distribution patterns of boreal forest gross photosynthetic flux vary depending upon vegetation types. Consequently, the “representativeness” of these tower sites appears to be a complex issue, varying with vegetation types.

The approach presented in our study offers a way of overcoming the limitations of point sources by mapping spatially distributed fluxes from combining tower data with remotely sensed hyperspectral images. A semiempirical equation, as shown in (8), can be used to track the spatial and temporal flux trends of a biome using hyperspectral images acquired over that biome. The techniques described in this paper can then be used to map spatially distributed CO₂ fluxes over areas much larger than flux tower footprints. Spatial heterogeneity of fluxes from different global vegetation types could be studied using these spatially continuous flux maps. Since there are operational flux towers in many of the forest and rangeland biomes around the world, establishing equations to solve the “a” and “b” parameters for several representative biomes in (8) might be a reasonable goal, particularly if the appropriate hyperspectral imagery were to become more available.

### 7. Conclusions and Future Directions

The primary conclusion of this study is that a simple, two-parameter model based on narrowband NDVI (a function of \( f_{\text{APAR}} \)) and a dynamic efficiency factor \( (s_{\text{PRI}}) \) can capture most of the variations in photosynthetic CO₂ fluxes across the boreal forest landscape. To our knowledge, this is the first time that a direct correlation between hyperspectral indices and landscape-level fluxes has been shown. Thus this may provide an alternative to more complex models (e.g., SiB2 [Sellers et al., 1996]) which require far more extensive parameterization.

On the basis of an empirical calibration against flux tower data, our study suggests that the BOREAS-SSA flux towers may be underestimating the spatially distributed fluxes by ~10%, at least for the vegetation types covered in this analysis. The fact that the towers represented only 60% of the land cover in SSA, and missed the remaining 40%, increases the possibility of total uncertainty in boreal biome flux estimation if only the tower-based information were used for this purpose. This observation has a larger implication in the sense that flux tower data are routinely used to estimate regional and global carbon balances. If the towers were not properly representing larger regions outside their footprint areas and not covering all constituent land covers and age classes of that region, then the estimation of spatially distributed fluxes based on flux towers would most likely be erroneous. Our study illustrates that combining hyperspectral remote sensing and flux tower data can provide further tools for estimating spatially distributed photosynthetic fluxes from large regions, providing one way to scale up point tower measurements to the regional scale.

Since AVIRIS images are not available for all seasons or all vegetation types, and atmospheric correction poses a problem due to lack of ground truthing during AVIRIS flight, our next goal is to use tram- and light aircraft-based hyperspectral data collection platforms for the further development of this model. We are currently testing a hardware system and protocol for collecting hyperspectral data from a chaparral stand near San Diego, California, and arctic tundra in Barrow, Alaska, where operational flux towers are available for collecting CO₂ and other flux data continuously. We plan to fly the aircraft and set up movable trams along the tower footprint areas throughout different seasons to further compare our model outputs with tower flux data and to test the error propagation and sensitivity of the model parameters. Our future research is also geared toward deriving daily gross CO₂ values of boreal and other biomes using hyperspectral imagery and tower-based solar radiation measurements.

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**References**


Adams, J. B., M. O. Smith, and A. R. Gillespie, Imaging spectroscopy:
Gamon, J. A., C. B. Field, M. L. Goulden, and K. L. Griffin, Rela-
Gamon, J. A., L. Serrano, and J. S. Surfus, The photochemical reflec-
energy dissipation and photosystem II efficiency in two vines,
Stephania japonica and Smilax australis, growing in the understory of

Agrar, G., M. Fučka, E. T. Kanemasu, and J. H. Hatfield, Estimating
absorbed photosynthetic radiation and leaf area index from spectral

Baldocchi, D. D., B. B. Hicks, and T. P. Meyers, Measuring biosphere-
atmosphere exchanges of biologically related gases with microme-

Baldocchi, D. D., C. A. Vogel, and B. Hall, Seasonal variation of
energy and water vapor exchange rates above and below a boreal

Bartlet, D. S., G. J. Whiting, and J. M. Hartman, Use of vegetation
indices to estimate intercepted solar radiation and net carbon dioxi-
dioxide exchange of a grass canopy, Remote. Sens. Environ., 30, 115–128,
1989.

Bonan, G. B., and H. H. Shugart, Environmental factors and ecological

Choudhury, B. J., Relationships between vegetation indices, radiation
absorption, and net photosynthesis evaluated by a sensitivity analy-

Daughtly, C. S. T., K. P. Gallo, and M. E. Bauer, Spectral estimates of solar
radiation intercepted by corn canopies, Agron. J., 75, 527–531,
1983.

Demmg-Adams, B., and W. Adams, The role of xanthophyll cycle carotenoids in the protection of photosynthesis, Trends Plant Sci., 1,
21–26, 1996.

Esser, G., Implications of climate change for production and decom-
position in grassland and coniferous forests, Ecol. Appl., 2(1), 47–54,

Fillela, I., J. L. Amaro, and J. Penuelas, Relationship between photo-
synthetic radiation-use efficiency of barley canopies and the photo-

and O. Williams, Imaging spectroscopy and the Airborne Visible/Infrac-
tered signal from the Airborne Visible-Infrared imaging Spectrometer (AVIRIS) using MODTRAN2, in Imaging Spectrometry of the Terrestrial Environment,

Hall, F. G., D. E. Knapp, and K. F. Huenrmich, Physically based classi-
cation and satellite mapping of biophysical characteristics in the
southern boreal forest, J. Geophys. Res., 102, 29,567–29,580,
1997.

Heimann, M., and C. D. Keeling, A three dimensional model of at-
mospheric CO2 transport based on observed winds, 2, Model de-
scription and simulated tracer experiments, in Aspects of Climate Variability in the Pacific and the Western Americas, Geophys. Monog.
Ser., vol. 55, edited by D. H. Peterson, pp. 237–274, AGU, Wash-
ington, D. C., 1989.


Horst, T. W., and J. C. Weil, Footprint estimation for scalar flux
measurements in the atmospheric surface layer, Boundary Layer Meteorol.,


Houghton, J. T., G. J. Jenkins, and J. J. Ephraums, Climate Change:
The IPCC Scientific Assessment, 366 pp., Cambridge Univ. Press,

Jarvis, P. G., and J. W. Leverenz, Productivity of temperate, deciduous
and evergreen forests, in Encyclopedia of Plant Physiology, vol. 12d,
edited by O. L. Lange, P.S. Nobel, C. B. Osmond, and H. Ziegler,


Kaharabata, S. K., P. H. Scheupp, S. Ogunjemiyo, S. Shen, M. Y. Leclecre, R. L. Desjardins, and J. I. MacPherson, Footprint consid-

Keeling, C. D., J. F. S. Chin, and T. F. Whorl, Increased activity of
northern vegetation inferred from atmospheric CO2 measurements,

Kumar, M., and J. L. Monteith, Remote sensing of crop growth, in
Plants and the Daylight Spectrum, edited by H. Smith, pp. 133–144,

Lieth, H., Modeling the primary productivity of the world, in Primary
Production of the Biosphere, edited by H. Leithand and R. H. Whit-

Liu, J. M. Chen, J. Cihlar, and W. Chen, Net primary productivity

Margolis, H. F., M. Mencuccini, and M. Grace, Age-related decline in stand productivity: The role of structural acclimation under hydrau-

McMillen, R. T., An eddy correlation technique with extended appli-
cability to non-simple terrain, Boundary Layer Meteorol., 45(3), 231–

Moncrieff, J. B., Y. Malhi, and R. Leuning, The propagation of errors


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