Can. J. Remote Sensing, Vol. 32, No. 6, pp. 405–416, 2006

Estimation of daytime net ecosystem CO_2 exchange over balsam fir forests in eastern Canada: combining averaged tower-based flux measurements with remotely sensed MODIS data[1]

Quazi K. Hassan, Charles P.-A. Bourque, and Fan-Rui Meng

Abstract. The focus of this paper is to develop a practical approach for estimating daytime net CO_2 fluxes (i.e., daytime net ecosystem exchange or NEE) generated over balsam fir (*Abies Balsamea* (L.) Mill.) dominated forest ecosystems in the Atlantic Maritime ecozone of eastern Canada. The approach establishes empirical relationships between daytime NEE and absorbed photosynthetically active radiation (APAR) for the May–September period in 2004 and 2005 using flux measurements obtained at one of four flux towers in west-central New Brunswick, Canada. Our analysis reveals that the seasonally averaged daytime NEE and APAR values are strongly correlated. A linear regression fitted to the data explains more than 97% of the variation in the averaged daytime fluxes. Application of this linear relationship to data collected from a second New Brunswick flux site with higher measured NEE produces an equally high r^2 value (~99%) when a linear fit is applied to the observed versus predicted values. Spatial calculations of APAR are obtained by multiplying the moderate resolution imaging spectroradiometer (MODIS) derived fraction of photosynthetically active radiation and digital elevation model corrected calculations of photosynthetically active radiation. This information and the relationship between daytime NEE and APAR provide the basis for the calculation of NEE across a balsam fir dominated region in northern New Brunswick, where it constitutes more than 50% of the forest cover.

Résumé. L'objectif de cet article est de développer une approche pratique pour l'estimation des flux nets diurnes de carbone (c.-à-d. échanges nets diurnes dans les écosystèmes; ENE) générés au-dessus des écosystèmes forestiers dominés pas les sapins baumiers (*Abies Balsamea* (L.) Mill.) dans l'écozone Maritime Atlantique de l'est du Canada. L'approche établit des relations empiriques entre les valeurs diurnes de ENE et le rayonnement photosythétiquement actif absorbé (RPAA) pour la période de mai à septembre 2004 et 2005, à l'aide de mesures de flux obtenues à l'une des quatre tours de flux situées dans le centre-ouest du Nouveau-Brunswick, au Canada. Notre analyse révèle que les valeurs diurnes moyennes saisonnières de ENE et de RPAA sont fortement corrélées. Une régression linéaire ajustée aux données explique plus de 97 % de la variation dans les flux diurnes moyennés. L'application de cette relation linéaire aux données acquises à partir d'un second site de mesures de flux au Nouveau-Brunswick montrant une valeur plus élevée de ENE produit une valeur également élevée de r^2 (~99 %) lorsqu'un ajustement linéaire est appliqué aux données observées par rapport aux données prédites. Des estimations spatiales de RPAA sont obtenues en multipliant la fraction de rayonnement photosynthétiquement actif dérivée des données MODIS (« moderate resolution imaging spectroradiometer ») et les estimations corrigées à l'aide d'un modèle numérique d'altitude de rayonnement photosynthétiquement actif. Cette information utilisée conjointement avec la relation entre les valeurs diurnes de ENE et de RPAA sert de base au calcul de ENE dans une région dominée par des forêts de sapins baumiers dans le nord du Nouveau-Brunswick, où les sapins baumiers constituent plus de 50 % du couvert forestier. [Traduit par la Rédaction]

Introduction

Unprecedented rises in atmospheric carbon dioxide (CO_2) and associated transformations in global climate have drawn a great deal of attention from scientists, policy-makers, and the general public globally. Carbon dioxide, a prominent greenhouse gas, absorbs outgoing terrestrially emitted long-

---

Received 26 September 2006. Accepted 11 January 2007.

Q.K. Hassan, C.P.-A. Bourque,[2] and F.-R. Meng. Faculty of Forestry and Environmental Management, University of New Brunswick, Fredericton, NB E3B 6C2, Canada.

[1] This paper was submitted in response to a request for papers arising from the 27th Canadian Symposium on Remote Sensing, Denver, Colorado, 31 July – 4 August 2006, and was guided through the review process by Dr. Monique Bernier, Guest Editor.

[2] Corresponding author (e-mail: cbourque@unb.ca).

wave energy as part of its role in the greenhouse effect. Increased absorption of long-wave energy has been responsible for an observed increase in the earth's mean temperature since industrialization in the late 1800s.

Forests play an important role in transforming and storing atmospheric CO_2 in the live and dead biomass. About 87% of total world CO_2 emissions during the period 1850–1990 have been directly attributable to human activity in global forests through deforestation and burning (Houghton, 1999). Well-thought-out forest management plans have been demonstrated to be valuable in offsetting industrial production of CO_2 (Meng et al., 2003). As Canada possesses about 10% of the global forests, it is important for Canada to study how its forest ecosystems take part in the global carbon budget.

Our focus in this paper is to develop a practical methodology to estimate daytime net CO_2 fluxes (i.e., daytime net ecosystem exchange (NEE)) generated over balsam fir (*Abies balsamea* (L.) Mill.) dominated forest ecosystems in eastern Canada by combining tower-based flux measurements with remotely sensed moderate resolution imaging spectroradiometer (MODIS) data. Daytime NEE is defined as the difference between the uptake of atmospheric CO_2 through photosynthesis (defined as a positive flux in this paper) and the release of CO_2 through plant and soil respiration (defined as a negative flux).

Over the past two decades, flux towers have been made operational around the world for acquiring information about the magnitude of biospheric fluxes of CO_2, water vapour, and energy for many of the world's biomes. Central to the operation of these networks is the eddy-covariance technique. This technique monitors ecosystem function with respect to climate variation and disturbance at temporal scales ranging from a few minutes to several decades (Baldocchi et al., 2001; Baldocchi, 2003). Since 2003, four eddy-covariance towers have been operational in New Brunswick, Canada, as the Atlantic Canada contribution to the Fluxnet-Canada Research Network project (FCRN) (Coursolle et al., 2006). Although the towers acquire very useful temporally enriched information about ecosystems, they only integrate over spatial areas of a few hundreds of hectares and, as a result, fail to give the spatial data (extent) needed for forest management applications. Since remote sensing offers near-continuous spatial information at large spatial extents, the integration of flux measurements with remotely sensed data is a viable approach to understanding the carbon cycle (and tree productivity) across a multitude of spatial scales (e.g., Ruimy et al., 1996; Running et al., 1999; Veroustraete et al., 2002; Hunt et al., 2002; 2004; Gilmanov et al., 2005; Maselli et al., 2006). For instance, Holifield et al. (2003) have used a water deficit index derived from satellite images to estimate instantaneous CO_2 fluxes over grassland ecosystems. Kelly et al. (2002) have employed airborne-based remote sensing measurements to relate daytime NEE to absorbed photosynthetically active radiation (APAR) over mixed coniferous forests, mixed short-grass prairie, and sagebrush shrubland. Hassan et al. (2006a) have demonstrated the potential of using an empirical relation between daytime NEE and APAR to calculate net daytime CO_2 fluxes over forests in New Brunswick using four MODIS images obtained from the May–September period of 2004.

In this paper, our objectives are to (*i*) characterize the light use efficiency (i.e., the capacity of vegetation to convert APAR into living biomass) and ecosystem respiration for young to intermediate-aged balsam fir forest ecosystems in New Brunswick, (*ii*) relate tower-based measurements of NEE to APAR, (*iii*) use a digital elevation model (DEM) of the province to enhance spatial calculations of daily photosynthetically active radiation (PAR) and APAR under cloud-free conditions, and (*iv*) generate a spatial calculation of daytime NEE for a balsam fir dominated region in northwestern New Brunswick.

Study area

Canada is divided into 15 terrestrial ecozones (i.e., generalized zonal groupings based on similar types of soil formation, climate, and land-use cover) as described by the National Ecological Framework for Canada (Ecological Stratification Working Group, 1996). The Atlantic Maritime ecozone in eastern Canada (**Figure 1a**) is characterized by its temperate evergreen–deciduous mix (transitional) forest cover type, of which the Acadian forest forms a significant component. The climate is largely influenced by the proximity of the region to the Atlantic Ocean. The area experiences a cool–moist climate with mean annual temperature and annual precipitation ranges of 3.5–6.5 °C and 900–1500 mm, respectively. New Brunswick occupies about 35% of the Atlantic Maritime ecozone.

New Brunswick has a total land area of 73 440 km^2. The northern area is dominated by the Appalachian Mountains, sloping into a rolling plateau in the interior. The eastern portion of New Brunswick is mostly flat, and the southern portion of the province is significantly more rugged. Here, mixed forests occupy about 85% of the land base (Natural Resources Canada; available from http://www.nrcan-rncan.gc.ca/cfs-scf/national/what-quoi/sof/sof06/profilesNB_e.html). The dominant deciduous species are red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh), white birch (*Betula papyrifera* Marsh), yellow birch (*Betula alleghaniensis* Britton), and beech (*Fagus grandifolia* Ehrh.). The dominant coniferous species are balsam fir (*Abies balsamea* (L.) Mill.), black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss), red spruce (*Picea rubens* Sarg.), eastern white cedar (*Thuja occidentalis* L.), and eastern hemlock (*Tsuga canadensis* (L). Carr.). Among these species, balsam fir is one of the most important commercial species for the production of pulp, as it occupies about 19% of New Brunswick forests. The average age of forests in New Brunswick is between 20 and 40 years old for about 80% of the forest land (including balsam fir forest land) due to the province's extensive harvesting history.

The province is further subdivided into the following seven distinct ecoregions according to topography, climate, soil, and

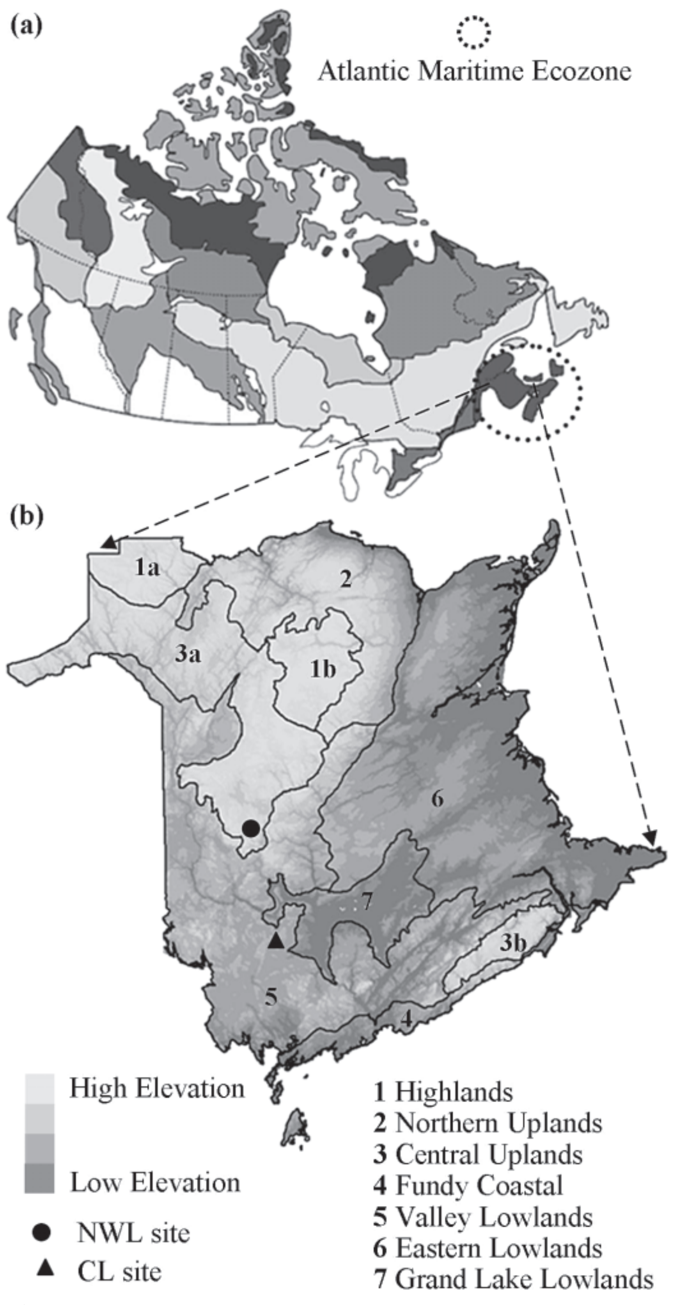

Figure 1. (a) Location of the Atlantic Maritime ecozone in Canada. (b) Flux sites used in this study and delineation of ecological regions of the province of New Brunswick, as shown over the digital elevation model.

vegetation types: (1) highlands (representing about 6.7% of New Brunswick), (2) northern uplands (12.0%), (3) central uplands (16.5%), (4) Fundy coastal zone (3.1%), (5) valley lowlands (27.7%), (6) eastern lowlands (28.8%), and (7) Grand Lake lowlands (5.2%). **Figure 1b** shows the boundaries of the ecoregions as a function of elevation.

In this study we make use of flux data acquired at two tower sites situated in high balsam fir content stands near Nashwaak Lake (balsam fir making up ~90% of the total site volume; Xing et al., 2005) and Charlie Lake (~95%; Xing et al., 2005). The Nashwaak Lake (NWL) and Charlie Lake (CL) sites fall in the central uplands and valley lowlands ecoregions, respectively (**Figure 1b**). According to Godin and Roberts (1994), balsam fir is the dominant species (with >50% species make up) over the relatively cold and wet highlands of northern New Brunswick, i.e., the highlands, northern uplands, and central uplands ecoregions (ecoregions 1a, 1b, 2, and 3a; **Figure 1b**). These ecoregions together make up about 33.2% of the total land area of New Brunswick.

Data requirements

Table 1 lists the data used in this study. Main inputs to the calculation of daytime NEE include digital number (DN) from the MODIS satellite sensor and fluxes of CO_2 and PAR acquired from the NWL flux tower. Among the 36 available bands (channels) of the MODIS images, the visible and near-infrared bands (optical bands 1 and 2) are used in this research. The visible and near-infrared bands capture visual detail of the earth's surface appropriate for estimating surface variables, such as normalized difference vegetation index (NDVI; a measure of vegetation greenness) and surface albedo (surface reflectivity). The optical bands acquire detail at comparatively fine spatial resolutions, at least once every day. In this paper, we use 12 almost cloud-free MODIS level 1B images of calibrated radiances (MOD02QKM) for identifying the potential of employing MODIS data in mapping daytime NEE. We prefer using level 1B data over other MODIS products, such as MOD43B3 (surface albedo), MOD15A2 (leaf area index fraction of PAR), and MOD17A2 (gross primary production), because of the obvious relationship of the data with the forest management unit level at 250 m. Derived MODIS products are generally undesirable in most forest management applications because (*i*) at 1 km resolution, the resolution is far too coarse to be practical; and (*ii*) the derived products are mostly comprised of 8–16 day composites. In addition, tower-based measurements of NEE, APAR, and above-canopy temperature are generally presented as 20–60 min averages. Air temperature is included here to examine its relation to ecosystem respiration. The DEM of the province provides a terrain correction to the calculation of PAR and, subsequently, APAR.

Methodology

Figure 2 is a flow diagram of the calculation procedure for daytime NEE and intermediate variables, such as daily PAR, fraction of PAR (fPAR), and APAR. The calculations are carried out in four separate steps: (1) an empirical expression relating point (tower) measurements of daytime NEE to APAR (>0.0) is developed from data collected at NWL; (2) daily photosynthetically active radiation (incident PAR) is spatially estimated using the LanDSET model of Bourque and Gullison (1998); (3) MODIS-based values of NDVI are used to estimate fPAR, which in turn are used to calculate APAR (**Figure 2**); and (4) average daytime values of NEE are spatially estimated for

Table 1. Tower and MODIS data specifications.

Data type	Description	Acquisition time
Optical satellite data (MODIS data from NASA)	Visible and near-infrared bands at 0.62–0.67 and 0.841–0.876 µm, respectively; satellite revisits sites at least once every day; acquired at 250 m spatial resolution	8 May, 10 June, 12 July, 25 August, and 15 and 26 September 2004; 11 May, 9 June, 16 July, 8 August, and 2 and 28 September 2005
CO_2 fluxes (i.e., net ecosystem exchange, NEE) and PAR fluxes	Acquired at NWL and CL flux-tower sites; acquired at half-hourly resolutions; PAR fluxes have two components, namely incident PAR above canopy and above-canopy reflected PAR	May–September period, 2004 and 2005
Air temperature	Acquired from the NWL site at every half hour; measured above the forest canopy	May–September period, 2004 and 2005

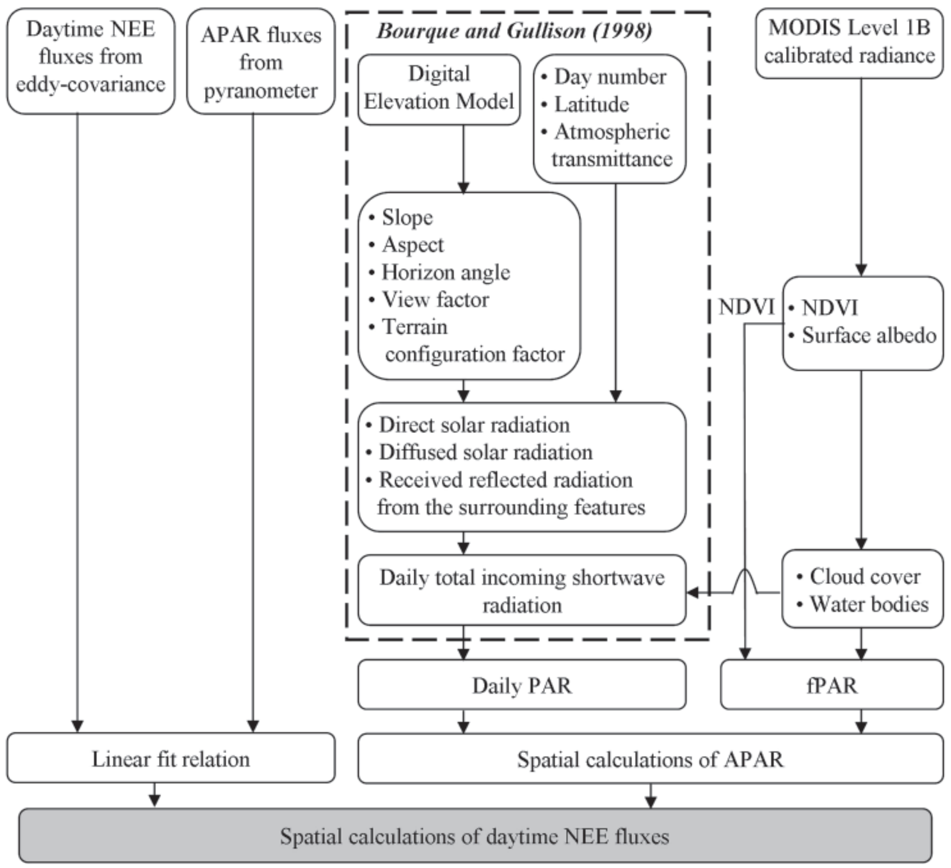

Figure 2. Flow chart of procedures for mapping the spatial distribution of daytime NEE and intermediate variables, such as PAR, fPAR, and APAR.

balsam fir dominated forests in northern New Brunswick by applying the linear relation derived in step 1 with the spatial calculation of APAR (in step 3) as input.

Relating daytime NEE with APAR

Theoretically, daytime NEE should be strongly correlated with APAR, as plants use APAR to convert CO_2 and H_2O to plant biomass. We use the following expression to capture this dependency:

$$\text{daytime NEE} = \text{LUE} \times \text{APAR} - R_E \qquad (1)$$

where daytime NEE is in µmol·m^{-2}·s^{-1}, APAR is in µmol·m^{-2}·s^{-1}, LUE is the light use efficiency (equation slope) in mol·mol^{-1}, and R_E is the ecosystem respiration (equation intercept) in µmol·m^{-2}·s^{-1} (e.g., Hunt et al., 2004). As LUE and R_E are ecosystem specific, we use flux data from the NWL softwood-dominated site to estimate LUE and R_E for balsam fir. Although estimates from Equation (1) are based on point data, the values of LUE and R_E are expected to remain constant in similarly composed, similarly aged forest ecosystems (e.g., Veroustraete et al., 2002; Chiesi et al., 2005). This uniformity facilitates scaling up of NEE point calculations to cover entire regions dominated by balsam fir.

Data processing

Prior to generating an empirical expression linking average daytime NEE to APAR (by means of Equation (1)), the flux data are preprocessed as follows: (*i*) measurements are taken from a time window from 6 am to 9 pm (local time), when PAR > 0.0, to ensure that only daytime NEE values are used in the analysis; (*ii*) since the quality of NEE measurements is routinely affected by excessive precipitation (due to sensor wetting), low wind velocities, and sensor malfunctioning, NEE values collected during periods of rain, low wind speeds, or sensor or system malfunctioning are eliminated from the dataset; and (*iii*) point calculation of APAR is based on tower measurements of PAR, i.e.,

$$\mathrm{APAR} = \mathrm{PAR}\downarrow - \mathrm{PAR}\uparrow \tag{2}$$

where PAR↓ represents the incident PAR in $\mu\mathrm{mol}\cdot\mathrm{m}^{-2}\cdot\mathrm{s}^{-1}$, and PAR↑ is the PAR reflected from the canopy in $\mu\mathrm{mol}\cdot\mathrm{m}^{-2}\cdot\mathrm{s}^{-1}$.

From this information, seasonally averaged daytime values of NEE and APAR are derived by averaging their respective half-hourly values over the May–September growing periods for 2004 and 2005, regardless of sky cloudiness. Estimates of LUE and R_E are generated by least-squares fitting of Equation (1) to the seasonally averaged 30 min mean values.

Estimating daily PAR

Terrain-corrected estimates of daily PAR are calculated with the LanDSET model of Bourque and Gullison (1998). A key input to the model is a 250 m resolution DEM of New Brunswick from which all of the following are computed (Bourque and Gullison, 1998): (*i*) slopes; (*ii*) slope orientation; (*iii*) horizon angles (minimum angle at which direct sunlight can reach to a particular point at a given sun position angle without being obstructed by the surrounding terrain); (*iv*) view factors (proportion of the sky that is unobstructed from one's view from every direction (360° field of view)); and (*v*) terrain configuration factors, which determine the amount of reflected radiation that can be received from the surrounding terrain. Together with variables like day of year (DOY), time of solar noon, latitude, and atmospheric transmittance (set at 0.70), daily total cloud-free incoming solar radiation is modelled over variable terrain (Bourque and Gullison, 1998; Bourque et al., 2000). In the LanDSET model, incoming solar radiation is composed of a direct and diffused component and a reflected component representing radiation streaming from the surrounding terrain. Available PAR is assumed to make up approximately 45% of incoming solar energy (Goldberg and Klein, 1977).

MODIS data processing

The radiance values of the MODIS level 1B data for both the visible and near-infrared bands are converted as top of atmosphere (TOA) reflectance values using the reflection scales specified in the header file and solar zenith angle. The TOA reflectance is used here in the calculation of NDVI and the albedo at TOA (i.e., α^{TOA}) (Valiente et al., 1995):

$$\mathrm{NDVI} = \frac{r_2^{\mathrm{TOA}} - r_1^{\mathrm{TOA}}}{r_2^{\mathrm{TOA}} + r_1^{\mathrm{TOA}}} \tag{3}$$

and

$$\alpha^{\mathrm{TOA}} = 0.035 + 0.545 r_1^{\mathrm{TOA}} + 0.32 r_2^{\mathrm{TOA}} \tag{4}$$

where NDVI and α^{TOA} are dimensionless quantities; and r_1^{TOA} and r_2^{TOA} are the TOA reflectances from the visible and near-infrared bands (also dimensionless), respectively. Surface albedo, α_s (dimensionless), is then estimated from α^{TOA} by applying a simple atmospheric correction described, for example, in Chen and Ohring (1984) and Bastiaanssen et al. (1998), i.e.,

$$\alpha_\mathrm{s} = \frac{\alpha^{\mathrm{TOA}} - a}{b} \tag{5}$$

where a is the mean albedo at the top of a clear atmosphere above a nonreflecting surface, and b is the mean effective "two-way" transmittance through a clear atmosphere (both dimensionless). Values of a and b are set to 0.0587 and 0.73 after Chen and Ohring (1984).

The combination of NDVI and surface albedo is then used to delineate water bodies (i.e., when NDVI < 0 and surface albedo < 10%) and cloud cover (i.e., when NDVI > 0 and surface albedo > 30%) to exclude the associated information from further analysis. **Figure 3** provides sample scatterplots illustrating the relationship between α_s and NDVI for 2 days during the May–September period, namely 12 July 2004 and 2 September 2005.

The NDVI is also used to calculate a simple ratio (SR), from which fPAR is estimated, specifically

$$\mathrm{SR} = \frac{1 + \mathrm{NDVI}}{1 - \mathrm{NDVI}} \tag{6}$$

$$\mathrm{fPAR} = \frac{[\mathrm{SR} - \mathrm{SR}_{\mathrm{min}}] \cdot \mathrm{fPAR}_{\mathrm{range}}}{\mathrm{SR}_{\mathrm{range}}} + \mathrm{fPAR}_{\mathrm{min}} \tag{7}$$

where $\mathrm{SR}_{\mathrm{range}} = \mathrm{SR}_{\mathrm{max}} - \mathrm{SR}_{\mathrm{min}}$, and $\mathrm{fPAR}_{\mathrm{range}} = \mathrm{fPAR}_{\mathrm{max}} - \mathrm{fPAR}_{\mathrm{min}}$ (and $\mathrm{fPAR}_{\mathrm{range}} = 0.95 - 0.01 = 0.94$) (Sellers et al., 1996). To define $\mathrm{SR}_{\mathrm{max}}$ and $\mathrm{SR}_{\mathrm{min}}$, we use estimates of NDVI from Equation (3) to derive SR values at NWL (by means of Equation (6)). We find that a value of $\mathrm{NDVI} \geq 0.66$ gives $\mathrm{SR}_{\mathrm{max}} = 4.80$, and a value of NDVI = 0.03 gives $\mathrm{SR}_{\mathrm{min}} = 1.06$ with

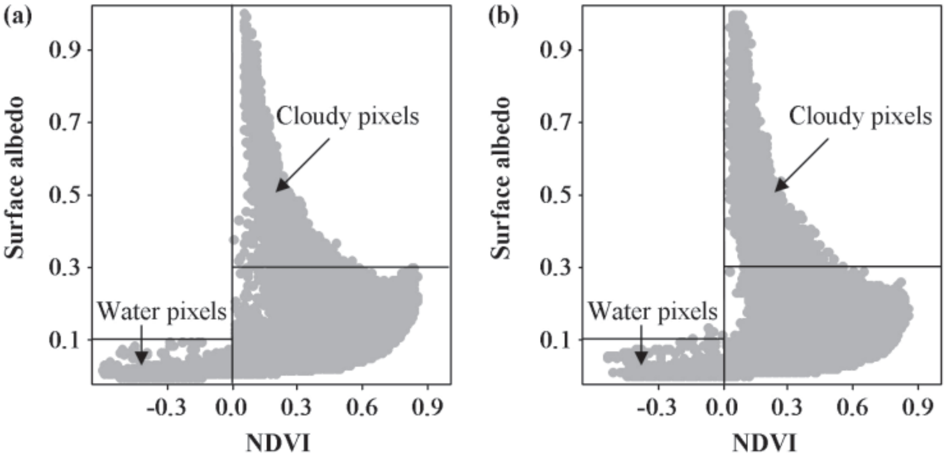

Figure 3. Scatterplot of surface albedo as a function of NDVI for (a) 25 August 2004, and (b) 2 September 2005. Thresholds for delineating water bodies and cloud patches are specified as horizontal lines for surface albedo and vertical lines for NDVI.

Equation (6). The SR values determined here are very similar to those reported in Sellers et al. (1996).

The spatial calculations of APAR are obtained from estimates of fPAR (based on Equation (7)) and daily total estimates of PAR as follows:

$$\mathrm{APAR} = \mathrm{fPAR} \times \mathrm{PAR} \tag{8}$$

Estimating average daily NEE

Spatial estimates of daytime NEE for the May–September period in 2004 and 2005 (incorporating 12 near-cloud-free MODIS images descriptive of the sampling period) are then calculated with Equation (1) and values of APAR, LUE, and R_E predetermined in steps 1 and 3 in the Methodology.

Results and discussion

Relating daytime NEE with APAR

Figure 4a provides the May–September average variation in daytime NEE and APAR as a function of local time for the 2004 and 2005 sampling periods. It reveals that the peak of daytime NEE occurs earlier than the peak of APAR, mostly related to the gradual closing of the stomates when temperatures exceed the optimum temperature (around 17 °C for balsam fir) as solar heating increases. It is interesting to note that the average May–September period daytime patterns and values of APAR for both years are nearly identical. There is a slight decrease in peak daytime NEE during 2005, however, compared with the peak value in 2004 (~2 $\mu\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$ reduction; an explanation for this reduction is addressed in the next paragraph). **Figures 4b** and **4c** provide the linear regressions between daytime NEE and APAR for the May–September period for both 2004 and 2005. They reveal extremely strong relationships, with r^2 values ≥97%. Calculated regression slopes and intercepts (representing LUE and R_E, respectively) are listed in **Table 2**. LUE values for both years are very similar (i.e., 0.0114 $\mathrm{mol \cdot mol^{-1}}$ for 2004 compared with 0.0103 $\mathrm{mol \cdot mol^{-1}}$ for 2005) and agree reasonably well with values derived from other high-latitude forest ecosystems in North America (e.g., LUE ≈ 0.010 $\mathrm{mol \cdot mol^{-1}}$ for forests at 40°–56° N latitude; Still et al., 2004). Coursolle et al. (2006) report an LUE value of about 0.011 $\mathrm{mol \cdot mol^{-1}}$ for the NWL site for NEE measurements collected over a 3-week period in 2003, very much in agreement with our 2004 and 2005 LUE values.

As the APAR values for the May–September periods of 2004 and 2005 are quite similar, CO_2 uptake during the day should be nearly identical. The difference in net CO_2 uptake is therefore largely a function of the variation in R_E (1.637 $\mu\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$ for 2005 versus 1.475 $\mu\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$ for 2004; **Table 2**). **Figure 5** shows R_E to vary exponentially, largely as a function of temperature. Soil moisture in this study did not differ greatly between years to make a significant difference in R_E (data not shown). Empirical work by others has shown similar relationships between soil respiration (an element of R_E) and soil temperature (e.g., Singh and Gupta, 1977; Raich and Schlesinger, 1992; Lloyd and Taylor, 1994). Because surface temperature is relatively easy to assess with remote sensing techniques under cloud-free conditions, R_E can be reasonably modelled with above-canopy air temperature (or surface temperature, in well-ventilated, vegetation-free areas). About 63% of the variation in nighttime R_E is explained by air temperature alone (Hassan et al., 2006b) (**Figure 5a**). It is shown that the above-canopy air temperatures in the May–September period of 2005 were generally higher (i.e., greater propensity for higher temperatures) than those of 2004 (**Figure 5b**), resulting in an increase in R_E (**Table 2**) and a subsequent decrease in average (and peak) daytime NEE for the May–September period in 2005. As R_E is generally low compared with daytime uptake of carbon (~15 $\mu\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$), young to immature balsam fir ecosystems in New Brunswick have the potential to be significant CO_2 sinks.

Daytime NEE values from a selection of forest ecosystems across North America show that the NEE values from the NWL

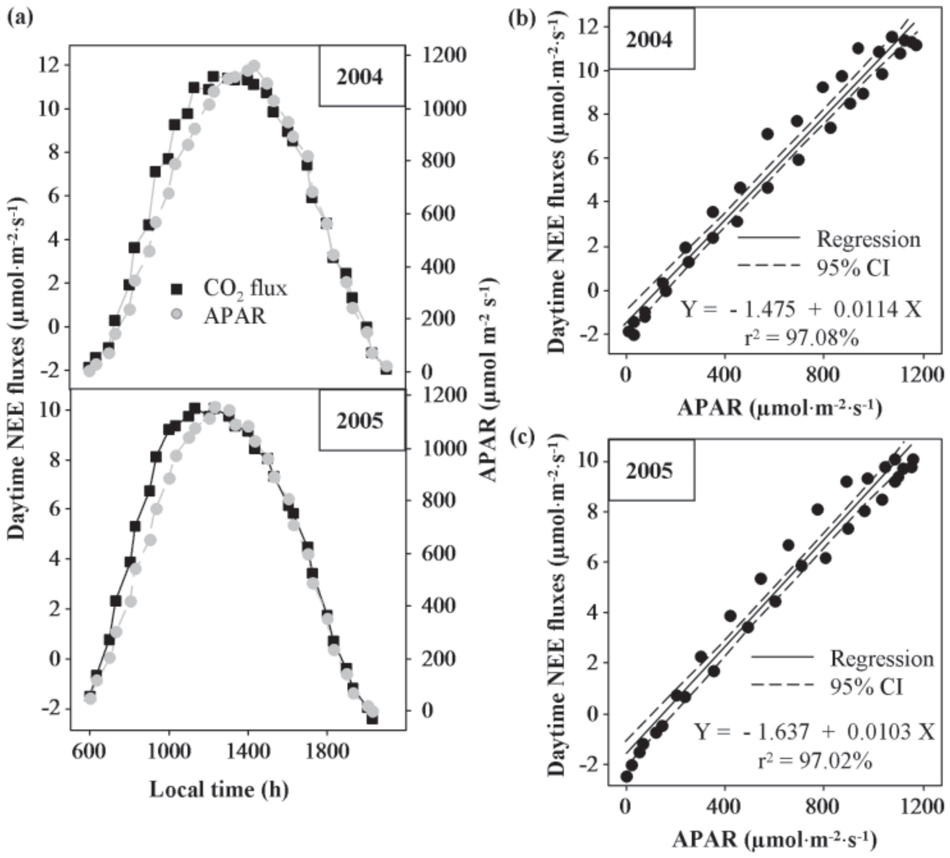

Figure 4. Relation between daytime NEE and APAR at NWL. (a) Averaged May–September period daytime NEE as a function of local time for 2004 and 2005. (b, c) Linear fits applied to plots of daytime NEE as a function of APAR. CI, confidence interval; r^2, regression coefficient.

site (i.e., 1.2–12.8 µmol·m^{-2}·s^{-1}) are significantly higher than values measured at other forest sites in North America, e.g., 3.5–9.7 µmol·m^{-2}·s^{-1} for lodgepole pine (*Pinus contorta* Dougl.), engelmann spruce (*Picea englemannii* Parry), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) (Kelly et al., 2002); 2.2–6.8 µmol·m^{-2}·s^{-1} for jack pine (*Pinus banksiana* Lamb.) (Desjardins et al., 1997); and 0–8.4 µmol·m^{-2}·s^{-1} for black spruce (*P. mariana*) (Desjardins et al., 1997). This difference is most likely due to the fact that the other sites are composed of older forests, which over the long term tend not to sequester as much CO_2 as young to immature forests. Older forests are at a point where uptake of CO_2 for photosynthesis approaches the level of CO_2 released from stem and soil respiration, resulting in a zero net uptake of CO_2 (e.g., Kimmins, 1997; Coursolle et al., 2006).

Table 2. Regression coefficients derived from fitting Equation (1) to the May–September period averaged NEE and APAR measurements from NWL for 2004 and 2005.

Year	LUE (mol·mol^{-1})	R_E (µmol·m^{-2}·s^{-1})
2004	0.0114	1.475
2005	0.0103	1.637

Note: LUE, light use efficiency and equation slope; R_E, ecosystem respiration and equation intercept.

Verification

Figure 6 provides comparisons between daily measured and modelled PAR (**Figure 6a**) and APAR (**Figure 6b**) using the LanDSET model for both the NWL and CL sites. Reasonable agreement exists between observed and predicted values (i.e., root mean square error (RMSE) = 22.25 µmol·m^{-2}·s^{-1} and r^2 = 95.9% for PAR, and RMSE = 19.61 µmol·m^{-2}·s^{-1} and r^2 = 96.7% for APAR, with calculated slopes close to ~0.90), producing a slight overprediction. Differences between modelled and measured values may be related to instrumentation calibration and levelling inaccuracies, the presence of thin cloud layers, and model inaccuracies. Defining which of these variables (or combination of variables) contribute to the unexplained portion of the variation (4%–5%) is fairly difficult.

Applying Equation (1) to the CL site produces strong correlations between tower-based measurements and model predictions of NEE, when both actual and modelled APAR values from the site are used as input, i.e., RMSE = 0.49 µmol·m^{-2}·s^{-1} and r^2 = 99% with actual APAR values

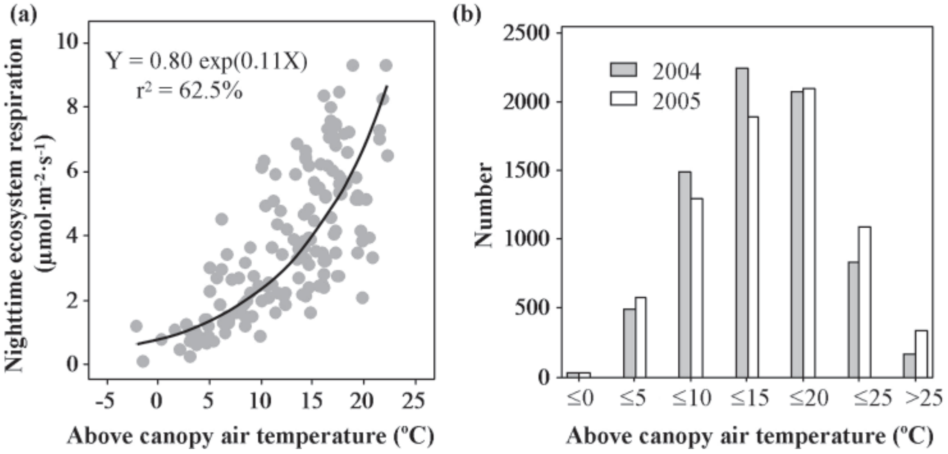

Figure 5. (a) Exponential relation between average nighttime ecosystem respiration and above-canopy air temperature at the NWL site (adopted from Hassan et al., 2006b). (b) Comparison of air temperature occurrence frequencies for temperature groupings incremented by 5 °C for 2004 and 2005.

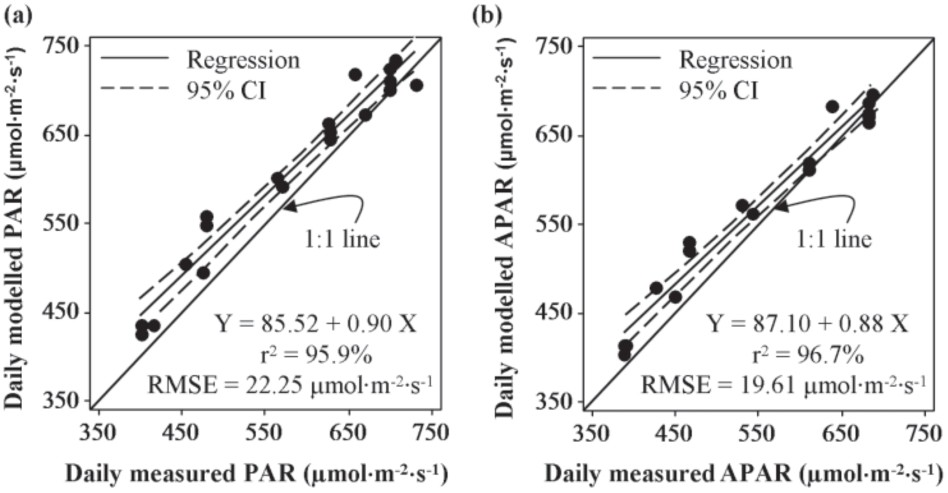

Figure 6. Comparison between daily measured and LanDSET-modelled values of (a) PAR and (b) APAR, where APAR = fPAR × PAR, and fPAR is derived from MODIS data and application of Equations (6) and (7) at both NWL and CL sites.

(**Figure 7a**), and RMSE = 0.55 µmol·m^{-2}·s^{-1} and r^2 = 99% with modelled APAR values (**Figure 7b**). The values of equation coefficients in Equation (1) are based on the coefficients generated by fitting Equation (1) to the NWL site data (**Figure 4b**). Despite strong correlations in both cases, NEE predictions using modelled APAR values as input provide a slightly better fit. The deviation from the 1:1 correspondence line in **Figures 7a** and **7b** suggests that the forest at CL, on average, tends to sequester more CO_2 than the forest at NWL during 2004.

As soil water controls NEE (Suyker and Verma, 2001) and thus plant growth, differences in soil water content (SWC) are hypothesized to be responsible for the increased carbon uptake and stand growth at CL for the 2004 period. The mean difference between SWC measurements (i.e., the average values taken at four different soil depths of 5, 10, 20, and 50 cm) at both CL and NWL is about 30% during the July–September 2004 period, as shown in **Figure 8**. The CL site, because of its physiographic position within a prominent landscape depression, is observed to have a more favourable SWC regime compared to the NWL site, found in an active drainage zone, despite the fact that NWL received more precipitation (+11%). Another variable, such as the projected area of green leaves on the ground (i.e., leaf area index, LAI), can also influence NEE. The higher LAI value at CL (~9.4) compared with that at NWL (~8.4) (Chen et al., 2006) can also be considered responsible for the increased carbon uptake at CL. Examination of annual increment growth of selected harvested trees and site index ranking data from the two sites and several ancillary sites nearby reinforces this conclusion (Bourque et al., 2006). Further research on this matter is being contemplated by referring to long-term meteorological and site

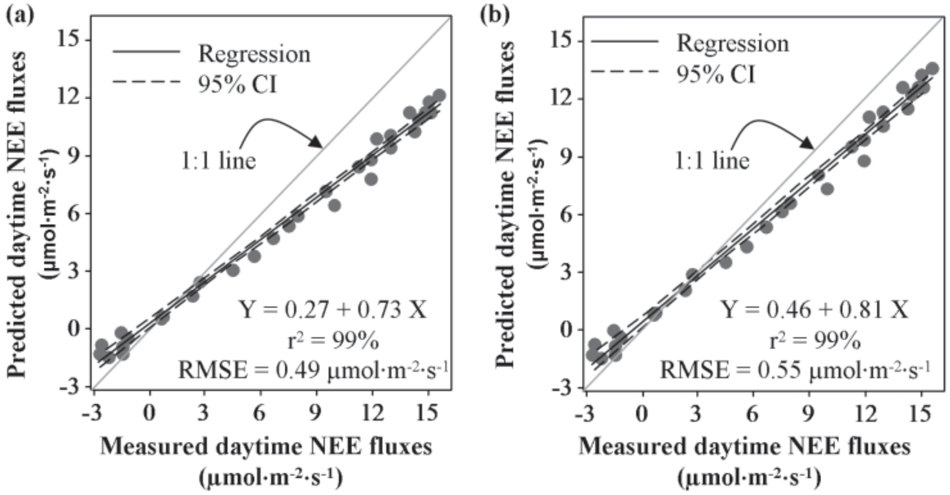

Figure 7. Predicted versus measured daytime NEE for the July–September period in 2004 for the CL site using (a) tower-based APAR measurements and (b) modelled APAR as input to Equation (1).

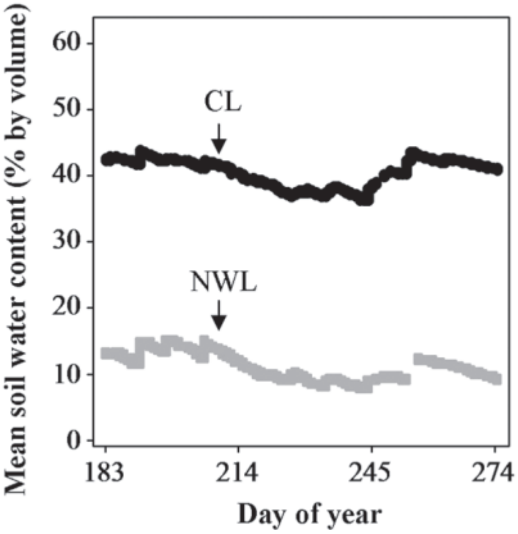

Figure 8. Mean soil water content (SWC; % by volume) at both CL and NWL sites during the July–September period, 2004. The mean values are obtained by averaging SWC measurements taken at four different soil depths (5, 10, 20, 50 cm). The breaks in the SWC lines occur because of gaps in the data.

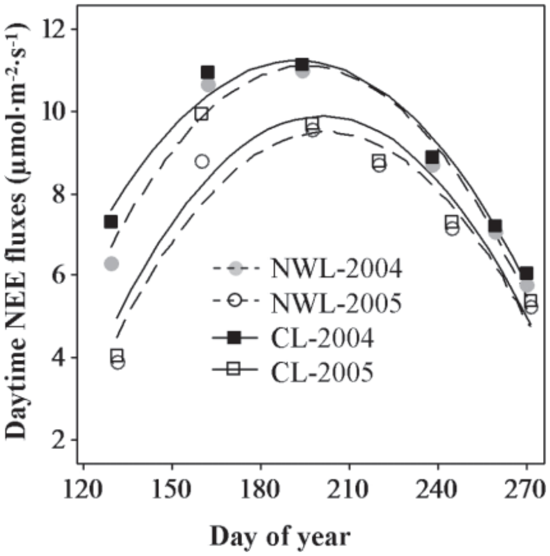

Figure 9. MODIS-derived average daytime NEE for the NWL and CL flux sites for the May–September period in 2004 and 2005.

records and available ecophysiological models to assess cause-and-effect relationships.

Spatiotemporal variation of NEE

Figure 9 provides the May–September variation of daytime NEE for 2004 and 2005 for NWL and CL based on the analysis of 12 MODIS images. Also shown are quadratic fits applied to the site-specific NEE values as a function of DOY. As we have related NEE to APAR based on seasonally averaged daytime values, this approach is clearly unable to capture the day-to-day variation inherent in 30 min NEE values. The approach reveals that for both years (2004 and 2005), however, the CL site sequesters a greater amount of CO_2 compared with the NWL site. These observations are consistent with our understanding of the trends observed in **Figure 7**.

Figure 10a provides a spatial distribution of daily average daytime NEE for the balsam fir dominated region of northern New Brunswick for 10 June 2004 and reveals that average NEE values mostly fall in the range of 8–12 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (**Figure 10b**).

Limitations

As May–September period trends are used to determine the average daytime NEE, our methodology fails to address daily variations in CO_2 exchange. The methodology could potentially be useful for understanding the seasonal carbon

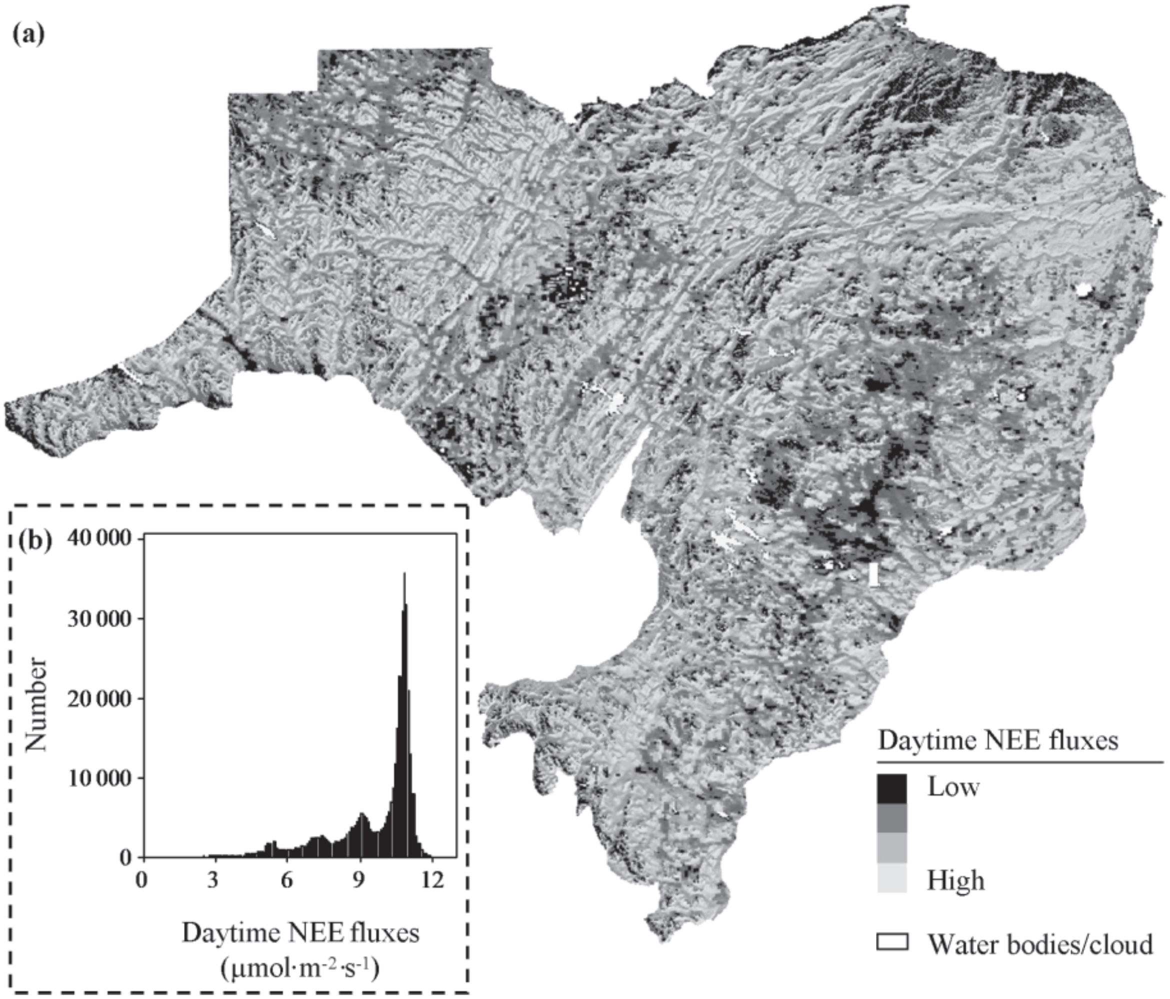

Figure 10. (a) Spatial and (b) frequency distribution of average daytime NEE over a balsam fir dominated region (i.e., ≥50% balsam fir) in northern New Brunswick (involving ecoregions 1a, 1b, 2, and 3a; see **Figure 1b**) based on MODIS data acquired on 10 June 2004.

uptake, which should in theory reflect the average annual growth rate in aboveground biomass in balsam fir dominated forests. As daytime NEE is affected by species composition, stand age, and variable climatic conditions, addressing these variations would involve installing additional flux towers (or implementing a roving-tower system) to capture local variations in ecosystem functioning and carbon exchange in a multitude of ecosystems.

Concluding remarks

This study demonstrates an approach of integrating site-specific flux measurements with remotely sensed MODIS data to capture net CO_2 exchange in balsam fir dominated regions of eastern Canada. Ninety-seven percent of the variability in the averaged May–September daytime values of NEE measured at the NWL site could be explained by averaged estimates of APAR alone. Coefficient values determined in the analysis provide important ecological information concerning light-use efficiency of balsam fir and ecosystem respiration with respect to the spatial calculation of daytime NEE for young to intermediate-aged (20–40 years old) balsam fir forests.

Estimates of daytime NEE founded on (*i*) the combination of MODIS data and the daytime NEE–APAR relation (via Equation (1)) and (*ii*) tower-based measurements are consistent when applied to the NWL and CL sites. MODIS-based estimates of NEE indicate that the CL site is more productive and absorbs a greater amount of CO_2 for 2004 and 2005 than the NWL site. A similar conclusion is drawn when tower-based estimates of NEE for 2004 for CL and NWL are compared.

In this research, we introduce the concept of using an average periodic diurnal trend analysis applied to measured fluxes of NEE and APAR, which is not common in carbon cycling research. It is interesting to note that the described approach assists us to understand a significant portion of the growing-season variation (i.e., >97%) in averaged NEE, despite the simplicity of the approach. Although not viable for assessing daily variation in NEE, averaging schemes like this have a role in assessing mean diurnal patterns spatially and over seasonal time frames and as such have a significant part in the study of carbon exchange. Being able to differentiate NEE between sites from satellite imagery is critical to the advancement of carbon cycling science and to the development of site productivity ranking methodologies for forest management applications.

Acknowledgments

This study was partially funded by the FCRN project and funds from a Discovery Grant awarded to CPAB from the Natural Sciences and Engineering Research Council of Canada (NSERC). We would like to acknowledge the National Aeronautics and Space Administration (NASA) for providing the MODIS data free of charge. We would also like to thank the participants of the New Brunswick component of the FCRN project for acquiring and processing the flux data required for the research, in particular Zisheng Xing (University of New Brunswick Ph.D. student), Yanlin Zhang and Junhui Yuan (visiting scientists and Ph.D. candidates at the Beijing Forestry University of the People's Republic of China), and Tim Dodson and Daniel Rogers (research technicians). Lastly, we would like to acknowledge the participation of three anonymous reviewers in providing helpful suggestions in improving the manuscript.

References

Baldocchi, D. 2003. Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. *Global Change Biology*, Vol. 9, No. 4, pp. 179–492.

Baldocchi, D., Falge, E., Gu, L.H., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, C., Davis, K., Evans, R., Fuentes, J., Goldstein, A., Katul, G., Law, B., Lee, X.H., Malhi, Y., Meyers, T., Munger, W., Oechel, W., Paw U, K.T., Pilegaard, K., Schmid, H.P., Valentini, R., Verma, S., Vesala, T., Wilson, K., and Wofsy, S. 2001. FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. *Bulletin of the American Meteorological Society*, Vol. 82, No. 11, pp. 2415–2434.

Bastiaanssen, W.G.M., Menenti, M., Feddes, R.A., and Holtslag, A.A.M. 1998, A remote sensing surface energy balance algorithm for land (SEBAL). 1. Formulation. *Journal of Hydrology*, Vol. 212–213, pp. 198–212.

Bourque, C.P.-A., and Gullison, J.J. 1998. A technique to predict hourly potential solar radiation and temperature for a mostly unmonitored area in the Cape Breton Highlands. *Canadian Journal of Soil Science*, Vol. 78, No. 3, pp. 409–420.

Bourque, C.P.-A., Meng, F.R., Gullison, J.J., and Bridgland, J. 2000. Biophysical and potential vegetation growth surfaces for a small watershed in northern Cape Breton Island, Nova Scotia, Canada. *Canadian Journal of Forest Research*, Vol. 30, pp. 1179–1195.

Bourque, C.P.-A., Lehnert, S., Xing, Z., Meng, F.R., and Swift, D.E. 2006. Site influences on net ecosystem productivity in managed *Abies balsamea* stands. In *Proceedings of the International Conference on Regional Carbon Budget*, 16–18 August 2006, Beijing. Chinese National Committee for the International Geosphere–Biosphere Programme (CNC–IGBP), Beijing. pp. 25–31.

Chen, T.S., and Ohring, G. 1984. On the relationship between clear-sky planetary and surface albedos. *Journal of the Atmospheric Sciences*, Vol. 41, No. 1, pp. 156–158.

Chen, J.M., Govind, A., Sonnentag, O., Zhang, Y., Barr, A., and Amiro, B. 2006. Leaf area index measurements at Fluxnet-Canada forest sites. *Agricultural and Forest Meteorology*, Vol. 140, Nos. 1–4, pp. 257–268.

Chiesi, M., Maselli, F., Bindi, M., Fibbi, L., Cherubini, P., Arlotta, E., Tirone, G., Matteucci, G., and Seufert, G. 2005. Modelling carbon budget of Mediterranean forests using ground and remote sensing measurements. *Agricultural and Forest Meteorology*, Vol. 135, Nos. 1–4, pp. 22–34.

Coursolle, C., Margolis, H.A., Barr, A.G., Black, T.A, Amiro, B.D, McCaughey, J.H., Flanagan, L.B., Lafleur, P.M., Roulet, N.T., Bourque, C.P-A., Arain, M.A., Wofsy, S.C., Dunn, A., Morgenstern, K., Orchansky, A.L., Bernier, P.Y., Chen, J.M., Kidston, J., Saigusa, N., and Hedstrom, N. 2006. Late-summer carbon fluxes from Canadian forests and peatlands along an east–west continental transect. *Canadian Journal of Forest Research*, Vol. 36, No. 3, pp. 783–800.

Desjardins, R.L., MacPherson, J.I., Mahrt, L., Schuepp, P., Pattey, E., Neumann, H., Baldocchi, D., Wofsy, S., Fitzjarrald, D., McCaughey, H., and Joiner, D.W. 1997. Scaling up flux measurements for the boreal forest using aircraft-tower combinations. *Journal of Geophysical Research*, Vol. 102, No. D24, pp. 29 125 – 29 134.

Ecological Stratification Working Group. 1996. *A national ecological framework for Canada*. Research Branch, Centre for Land and Biological Resources Research, Agriculture and Agri-Food Canada, Ottawa, and State of Environment Directorate, Environment Canada, Ottawa–Hull. 125 pp.

Gilmanov, T.G., Tieszen, L.L., Wylie, B.K., Flanagan, L.B., Frank, A.B., Haferkamp, M.R., Meyers, T.P., and Morgan, J.A. 2005. Integration of CO_2 flux and remotely sensed data for primary production and ecosystem respiration analyses in the Northern Great Plains: potential for quantitative spatial extrapolation. *Global Ecology and Biogeography*, Vol. 14, No. 3, pp. 271–292.

Godin, B., and Roberts, M.R. 1994. *Part I. Ecological land classification for New Brunswick: the ecoprovince, ecoregion and ecodistrict levels*. Mimeographed Report, Provincial Legislative Library, Fredericton, N.B. 99 pp.

Goldberg, B., and Klein, W.H. 1977. Variations in the spectral distribution of daylight at various geographical locations on the Earth's surface. *Solar Energy*, Vol. 19, No. 1, pp. 3–13.

Hassan, Q.K., Bourque, C.P.-A., Meng, F.R., Arp, P., MacLean, D., and Zhang, Y. 2006a. Net daytime carbon dioxide fluxes over eastern Canadian forests: an application of MODIS imagery. In *IGARSS'06, Proceedings of the 2006 IEEE International Geoscience and Remote Sensing Symposium and the 27th Canadian Symposium on Remote Sensing*, 31 July – 4 August 2006, Denver, Colo. The Institute of Electrical and Electronics Engineers, Inc. (IEEE), New York. Vol. 4, pp. 1717–1720.

Hassan, Q.K., Bourque, C.P.-A., Meng, F.R., Clowater, C., and Xing, Z. 2006b. Nighttime ecosystem respiration modelling for balsam fir (*Abies balsamea*) forests in eastern Canada. In *Proceedings of the Eastern CANUSA Forest Science Conference*, 19–21 October 2006, Québec City, Que. 4 pp.

Holifield, C.D., Emmerich, W.E., Moran, M.S., Bryant, R., and Verdugo, C.L. 2003. Estimating regional daytime net carbon dioxide flux using remotely sensed instantaneous measurements. In *Proceedings of the 1st Interagency Conference on Research in the Watersheds*, 27–30 October 2003, Benson, Ariz. Edited by K.G. Renard, S.A. McElroy, W.J. Gburek, H.E. Canfield, and R.L. Scott. Agricultural Research Service, US Department of Agriculture, Benson, Ariz. pp. 517–521.

Houghton, R.A. 1999. The annual net flux of carbon to the atmosphere from changes in land use 1850–1990. *Tellus B*, Vol. 51, No. 2, pp. 298–313.

Hunt, E.R., Jr., Fahnestock, J.T., Kelly, R.D., Welker, J.M., Reiners, W.A., and Smith, W.K. 2002. Carbon sequestration from remotely sensed NDVI and net ecosystem exchange. In *From laboratory spectroscopy to remotely sensed spectra of terrestrial ecosystems*. Edited by R.S. Muttiah. Kluwer Academic Publishers, Dordrecht, The Netherlands. pp. 161–174.

Hunt, E.R., Jr., Kelly, R.D., Smith, W.K., Fahnestock, J.T., Welker, J.M., and Reiners, W.A. 2004. Estimation of carbon sequestration by combining remote sensing and net ecosystem exchange data for northern mixed-grass prairie and sagebrush-steppe ecosystems. *Environmental Management*, Vol. 33, No. 1, pp. S432–S441.

Kelly, R.D., Hunt, E.R., Jr., Reiners, W.A., Smith, W.K., and Welker, J.M. 2002. Relationships between daytime carbon dioxide uptake and absorbed photosynthetically active radiation for three different mountain/plains ecosystems. *Journal of Geophysical Research*, Vol. 107, No. D14, pp. 19.1–19.8.

Kimmins, J.P. 1997. *Forest ecology*. 2nd ed. Prentice Hall, Inc., Upper Saddle River, N.J. 596 pp.

Lloyd, J., and Taylor, J.A. 1994. On the temperature dependence of soil respiration. *Functional Ecology*, Vol. 8, No. 3, pp. 315–323.

Maselli, F., Barbati, A., Chiesi, M., Chirici, G., and Corona, P. 2006. Use of remotely sensed and ancillary data for estimating forest gross primary productivity in Italy. *Remote Sensing of Environment*, Vol. 100, No. 4, pp. 563–575.

Meng, F.R., Bourque, C.P.-A., Oldford, S.P., Swift, D.E., and Smith, H. 2003. Combining carbon sequestration objectives with timber management planning. *Mitigation and Adaptation Strategies for Global Change*, Vol. 8, No. 4, pp. 371–403.

Raich, J.W., and Schlesinger, W.H. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tullus*, Vol. 44B, No. 2, pp. 81–99.

Ruimy, A., Kergoat, L., Field, C.B., and Saugier, B. 1996. The use of CO_2 flux measurements in models of the global terrestrial carbon budget. *Global Change Biology*, Vol. 2, No. 3, pp. 287–296.

Running, S.W., Baldocchi, D.D., Turner, D.P., Gower, S.T., Bakwin, P.S., and Hibbard, K.A. 1999. A global terrestrial monitoring network integrating tower fluxes, flask sampling, ecosystem modeling and EOS satellite data. *Remote Sensing of Environment*, Vol. 70, No. 1, pp. 108–127.

Sellers, P.J., Los, S.O., Tucker, C.J., Justice, C.O., Dazlich, D.A., Collatz, G.J., and Randall, D.A. 1996. A revised land surface parameterization (SiB2) for atmospheric GCMs. Part II: The generation of global fields of terrestrial biophysical parameters from satellite data. *Journal of Climate*, Vol. 9, No. 4, pp. 706–737.

Singh, J.S., and Gupta, S.R. 1977. Plant decomposition and soil respiration in terrestrial ecosystems. *Botanical Review*, Vol. 43, No. 4, pp. 449–528.

Still, C.J., Randerson, J.T., and Fung, I.Y. 2004. Large-scale plant light-use efficiency inferred from the seasonal cycle of atmospheric CO_2. *Global Change Biology*, Vol. 10. No. 8, pp. 1240–1252.

Suyker, A.E., and Verma, S.B. 2001. Year-round observations of the net ecosystem exchange of carbon dioxide in a native tallgrass prairie. *Global Change Biology*, Vol. 7, No. 3, pp. 279–289.

Valiente, J.A., Nunez, M., Lopez-Baeza, E., and Moreno, J.F. 1995. Narrow-band to broad-band conversion for Meteosat-visible channel and broad-band albedo using both AVHRR-1 and -2 channels. *International Journal of Remote Sensing*, Vol. 16, No. 6, pp. 1147–1166.

Veroustraete, F., Sabbe, H., and Eerens, H. 2002. Estimation of carbon mass fluxes over Europe using the C-Fix model and Euroflux data. *Remote Sensing of Environment*, Vol. 83, No. 3, pp. 376–399.

Xing, Z., Bourque, C.P.-A., Swift, D.E., Clowater, C.W., Krasowski, M., and Meng, F.R. 2005. Carbon and biomass partitioning in balsam fir (*Abies balsamea*). *Tree Physiology*, Vol. 25, No. 9, pp. 1207–1217.