A Satellite-Based Biosphere Parameterization for Net Ecosystem CO₂ Exchange: Vegetation Photosynthesis and Respiration Model (VPRM)

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Abstract

We present the Vegetation Photosynthesis and Respiration Model (VPRM), a satellitebased assimilation scheme that estimates hourly values of Net Ecosystem Exchange of CO_2 (*NEE*) for 12 North American biomes using the Enhanced Vegetation Index (*EVI*) and Land Surface Water Index (LSWI), derived from reflectance data of the Moderate Resolution Imaging Spectroradiometer (MODIS), plus high resolution data for sunlight and air temperature. The motivation is to provide reliable, fine-grained first-guess fields of surface CO₂ fluxes for application in inverse models at continental and smaller scales. An extremely simple mathematical structure, with minimal numbers of parameters, facilitates optimization using *in situ* data, with finesse provided by maximal infusion of observed *NEE* and environmental data from networks of eddy covariance towers across North America (AmeriFlux, Fluxnet Canada). Cross validation showed that the VPRM has strong prediction ability for hourly to monthly time scales for sites with similar vegetation. The VPRM also provides consistent partitioning of *NEE* into Gross Ecosystem Exchange (GEE, the light dependent part of NEE) and ecosystem Respiration (*R*, the light independent part), half-saturation irradiance of ecosystem photosynthesis, and annual sum of NEE at all eddy flux sites for which it is optimized. The capability to provide reliable patterns of surface flux for fine scale inversions is presently limited by the number of vegetation classes for which NEE can be constrained by the current network of eddy flux sites, and by the accuracy of MODIS data and data for sunlight.

1. Introduction

A primary goal of studying the terrestrial carbon cycle is to determine the magnitude of Net Ecosystem Exchange (*NEE*) of carbon dioxide between the terrestrial biosphere and the atmosphere, and to understand the main drivers for hourly, seasonal and inter-annual variations of NEE [*Wofsy and Harriss,* 2002]. Particular interest attaches to time-resolved measurements of fluxes on regional and continental scales, too small to be reliably resolved by global inverse models, but too large for direct measurement.

Inverse ("top-down") analyses of CO₂ budgets on regional scales utilize measurements of atmospheric CO₂ concentrations on towers and by aircraft within the regions where sources and sinks are most active [*Tans*, 1980; *Fung*, 1993; *Tans et al.*, 1993; *Bakwin et al.*, 1998; *Lin et al.*, 2004; *Gerbig et al.*, 2005]. These data are influenced by small scale, near field fluxes as well as by continental and global sources and sinks, and the analysis therefore requires fine scale spatial and temporal resolution for both transport fields and for distributions of surface fluxes [*Gerbig et al.* 2003 a-b; *Baket et al.*, 2006]. Fluxes must be resolved on timescales including hourly, seasonal and annual, and on spatial scales as small as 1-10 km, a difficult challenge because NEE represents the difference between uptake (photosynthesis) and loss (respiration) processes that vary on a wide range of timescales [*Goulden et al.*, 1996; *Katul et al.*, 2001].

Since the inception of inverse modeling of CO₂, it has been recognized that surface flux sub-models must accurately represent relevant spatio-temporal variations of NEE [*Fung et al*, 1987; *Ruimy et al.*, 1995; *Sellers et al*, 1996; *Goetz and Prince* 1999; *Xiao et al.*, 2002; 2004a-b]. *A priori* surface flux models must have a low order of

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parameterization, so that the optimization process is well constrained [*Denning et al.*, 1995; *Lin et al.*, 2004], while retaining the required fine spatial and temporal resolution.

The present paper addresses the need to reliably represent surface fluxes at fine time/space scales with minimal parameters, into which we infuse the maximum information from observations.

We use remotely sensed data to define vegetation properties with t fine spatial resolution. Unfortunately temporal resolution is poor and direct information on NEE is lacking. We use measurements of NEE from eddy flux towers [Baldocchi et al., 2001] for direct flux data at high temporal resolution, capturing ecosystem functional responses to the environment at sites in North, Central, and South America, but, unfortunately, only small spatial scales (1 km²).

The Vegetation Photosynthesis Respiration Model (VPRM) presented here assimilates remote sensing, meteorological, and tower flux data for a large number of sites in order to represent surface fluxes with the highest possible fidelity. Model structure is made very simple to facilitate subsequent inverse analysis.

Formulation of the VPRM starts from the Vegetation Photosynthesis Model (*VPM*) of *Xiao et al.* [2004a-b], which estimates Gross Ecosystem Exchange (*GEE*) using satellitebased vegetation indices and environmental data, adding respiration (*R*) to provide NEE and a nonlinear function to account for the response of GEE to light. The Enhanced Vegetation Index (*EVI*) [*Huete et al.*, 1997, 2002] estimates of the Fraction of Photosynthetically Active Radiation (*PAR*) absorbed by photosynthetically active parts of the vegetation (*FAPAR*_{*PAV*}) [*Xiao et al.*, 2004a-b], and the Land Surface Water Index (*LSWI*) helps capture the effects of water stress and leaf phenology [*Xiao et al.* [2004a-b], especially for vegetation that becomes dormant in summer (e.g. grasslands). The VPRM shares many features of earlier models for surface CO₂ fluxes (e.g., NASA-CASA [Potter et al., 1993, 1999], SiB2 [Sellers et al., 1996], and TURC [Lafont et al., 2002]) developed for, and most appropriate to, global-scale inverse analysis, but it returns to the simpler functional representation introduced by *Fung et al.* [1987]. As summarized schematically in Fig. 1, the VPRM systematically incorporates data from eddy flux towers, spanning dominant vegetation types over North America, plus MODIS data and high-resolution meteorological fields, to provide a much finer representation of surface fluxes than in previous simple models. VPRM NEE fields are thus optimally consistent with eddy flux data, and t

he model is readily exported to potential users and optimized using atmospheric data. Inversion of the VPRM is intended to enable it to capture seasonal and spatial variations of NEE not explicitly represented *a priori*.

2. Model Framework

Monteith [1972] showed that ecosystem production correlates with the fraction of Absorbed Photosynthetically Active Radiation (FAPAR). FAPAR is often estimated as a linear or nonlinear function of the Normalized Difference Vegetation Index (*NDVI*) [*Prince and Goward*, 1995; *Running et al.*, 2000], the normalized ratio between satellite-derived reflectance in the red (ρ_{red}) and near infrared (ρ_{nir}) bands [*Tucker*, 1979],

$$NDVI = \frac{\rho_{nir} - \rho_{red}}{\rho_{nir} + \rho_{red}} , \qquad (1)$$

using NDVI from the Advanced Very High Resolution Radiometer (AVHRR) to compute rates of terrestrial photosynthesis [e.g. *Fung et al.*, 1987; *Potter et al.*, 1993].

Recent studies [*Xiao, et. al.,* 2004a-b & 2005] showed that MODIS *EVI* [*Huete et al.,* 1997 & 2002] is more closely correlated with photosynthesis [*Xiao et al.,* 2004a-b] across a larger range of leaf area index, and more closely follows phenology:

$$EVI = G \times \frac{(\rho_{nir} - \rho_{red})}{\rho_{nir} + (C_1 \times \rho_{red} - C_2 \times \rho_{blue}) + L}$$
(2)

where G=2.5, C₁=6, C₂=7.5, and *L*=1. Inclusion of the blue band helps account for atmospheric contamination, and *L* helps compensate for soil background reflectance. The VPRM also utilizes the LSWI [*Xiao et al.*, 2004a-b] to help capture effects of water stress and phenology on plant photosynthesis:

$$LSWI = \frac{\rho_{nir} - \rho_{swir}}{\rho_{nir} + \rho_{swir}}$$
(3)

where NIR refers to the 841-876 nm band and SWIR to 1628-1652 nm).

2.1 Gross Ecosystem Exchange

We divide *NEE* into a light-dependent term, Gross Ecosystem Exchange (*GEE*), and a light-independent part, ecosystem respiration (*R*), where NEE = -GEE

+ R, following the sign convention that uptake of CO₂ by plants is a negative flux (removal from the atmosphere). *GEE* is represented by:

$$GEE = \varepsilon \times \frac{1}{(1 + PAR/PAR_0)} \times PAR \times FAPAR_{PAV}$$
(4)

where $FAPAR_{PAV}$ is the fraction of Photosynthetically Active Radiation (*PAR*, µmol m⁻² s⁻¹) absorbed by the photosynthetically active portion of the vegetation (*PAV*), *PAR*₀ is the half saturation value, and ε is the light use efficiency (µmol CO₂ / µmol PPFD) at low light levels. We decompose ε into the product of the maximum quantum yield, ε_0 , and factors ranging between 0 and 1 that reduce light use efficiency,

$$\boldsymbol{\varepsilon} = \boldsymbol{\varepsilon}_0 \times T_{scale} \times W_{scale} \times P_{scale} \tag{5}$$

On average ε_0 has a value around 1/6 for well-watered, C3 plants at optimal temperatures.

The parameter T_{scale} in Eq. (5) represents the temperature sensitivity of photosynthesis, calculated at each time step using the equation developed for the Terrestrial Ecosystem Model [*Raich et al.*, 1991]:

$$T_{scale} = \frac{(T - T_{\min})(T - T_{\max})}{[(T - T_{\min})(T - T_{\max}) - (T - T_{opt})^{2}]},$$
(6)

where T_{\min} , T_{\max} , and T_{opt} are minimum, maximum and optimal temperatures (°C) for photosynthesis, respectively [*Aber & Federer*, 1992; *Raich et al.*, 1991]. If air temperature falls below T_{\min} , T_{scale} is set to be zero [*Xiao et al.*, 2004a-b].

Since temperature and PAR are correlated on a daily basis, inclusion of T_{scale} in Eq. 5 modifies values of PAR₀ inferred from tower flux data. Moreover, were the parameters in Eq. 6 to be fit to eddy flux data along with PAR_0 , parameter values would be unstable; therefore T_{min} , T_{max} , and T_{opt} were fixed at literature values. The role of T_{scale} in the VPRM is explored in a sensitivity analysis below.

The function P_{scale} accounts for effects of leaf age on canopy photosynthesis, using EVI and LSWI to identify the green-up (leaf expansion) and senescence phases [*Xiao et al.*, 2002, 2004a; *Boles et al.*, 2004]. For evergreen classes, P_{scale} is assumed to be 1 for

the whole year. For deciduous vegetation and grasslands, we computed P_{scale} as a linear function of LSWI from bud burst to leaf full expansion ("phase 1") by:

$$P_{scale} = \frac{1 + LSWI}{2} \tag{7}$$

After leaf full expansion (phase two) P_{scale} was set to 1, and Eq. (7) was adopted again during senescence (phase 3). The dates for the three phases of phenology (bud burst, full canopy, senescence) were obtained using an EVI seasonal threshold similar to that of the MODIS phenology product MOD12Q2 [*Friedl et al.*, 2003]. Thus, for large-scale application of the VPRM across North America, MOD12Q2 dates can be used directly.

The effect of water stress on *GEE* is a complex function of soil moisture and VPD [e.g. *Field et al.*, 1995; *Running et al.*, 2000]. These are not available for the VPRM, since they cannot be derived directly from weather or remote sensing data [*Pathmathevan et al.*, 2003].

Following Xiao et al., [2004a], we set

$$W_{scale} = \frac{1 + LSWI}{1 + LSWI_{max}} \tag{8}$$

where $LSWI_{max}$ is the maximum LSWI within the plant growing season for each site (or pixel). LSWI has been shown to capture drought-induced changes in plant canopies for ecosystems that senesce during dry periods, such as grasslands, but not for other vegetation. Hence effects of water stress are a principal source of variance to be captured in an inverse analysis via adjustments to the VPRM parameters.

The complete expression for GEE in the VPRM is thus given by:

(10)

Here λ_{PAR} replaces ε_0 , in order to aggregate into one parameter empirical adjustments to P_{scale} , T_{scale} , and W_{scale} ; λ_{PAR} and PAR_0 are the only adjustable parameters for description of the light-dependent part of NEE, with values derived below from tower flux data.

PAR is measured at all flux tower sites, but not across the continent. At large scales, the VPRM will be driven using shortwave (*SW*) radiation, available for almost all of North America from Geostationary Operational Environmental Satellite (*GOES*) data [e.g. *Diak et al.*, 2004] and from assimilated meteorological products. *SW* is very closely correlated with PAR, $SW \cong 0.505 \times PAR$ (units: SW, Watts/m²; PAR, µmolm⁻²s⁻¹).

2.2 Ecosystem Respiration

Plant and soil respiration rates generally increase as temperatures rise [*Grace and Rayment*, 2000; *Piovesan and Adams*, 2000], and we therefore represented *R* as:

$$R = \alpha \times T + \beta . \tag{11) We}$$

set $T=T_{low}$ in Eq. (11) when $T \le T_{low}$, to account for the persistence of soil respiration in winter, when air temperatures are very cold but soils remain warm. Values for α , β , and T_{low} were derived from tower flux data for each vegetation type (Table 2).

2.2.3 Net Ecosystem Exchange

The full VPRM model equation is:

$$NEE = -\lambda_{PAR} \times T_{scale} \times P_{scale} \times W_{scale} \times \frac{1}{(1 + PAR/PAR_0)} \times EVI \times PAR + \alpha \times T + \beta$$
(12)

There are four basic parameters per vegetation type, λ_{PAR} , PAR_0 , α and β , which can be adjusted in an inverse model application to provide an accurate representation for the distribution NEE in space and time across North America, with *a priori* estimates from flux towers data. We assess transferability across the landscape by examining data from sites not used in deriving the prior estimates ("validation sites").

3. Study sites and data

3.1 Vegetation and tower flux data

Tower measurements of NEE and water fluxes are made at numerous sites in North America and worldwide [*Baldocchi et al.*, 2001]. We assembled a large subset of these data to calibrate and test VPRM surface fluxes, classified by vegetation type based on the 1-km International Geosphere Biosphere Programme (*IGBP*) classification [*Belward et al.*, 1999].

Since tower flux data are not available for each of the 17 IGBP vegetation classes, we grouped North American ecosystems into 9 major classes

for which eddy flux data are available are: evergreen forests, deciduous forest, mixed forest, shrubland (including open and closed shrubland), savannas (savannas and woody savannas), cropland, grassland (grassland, cropland/natural vegetation mosaic, and barren or sparsely vegetated), permanent wetlands, and others (especially the water bodies).

Two of these 9 large classes needed to be subdivided to account for major biophysical differences within them. The IGBP class "evergreen needleleaf forests" (~6.751% of land area) is broadly distributed, from boreal boggy black spruce to subtropical slash pine. We combined this class with "evergreen broadleaf forests", which have negligible occurrence in North America (~0.5%), and then subdivided into 4 classes (boreal (e.g., black spruce), wet temperate/montane (e.g., Douglas fir, western white pine), dry temperate (e.g., ponderosa pine) and subtropical (e.g., slash pine, with strong summertime droughts)) by climate zone, using Holdridge Life Zone data [*Leemans and Cramer*, 1991]. Similarly, "cropland" was divided into soy and corn (to be expanded to include wheat when data become available). Fortunately, suitable eddy flux data are available for these subdivisions.

We designated 11 tower sites to calibrate the four parameters for each vegetation class (except water, snow and ice, where fluxes are assumed zero), and identified 11 other sites for testing ("validation") as listed in Table 1. More details and data of the 22 test sites can be obtained from network websites, (http://public.ornl.gov/ameriflux/) and (http://www.fluxnet-canada.ca/), and from the original references in Table 1.

The calibration sites for evergreen forests are the Northern Old Black Spruce (NOBS/BOREAS) site in Manitoba (boreal fores), Niwot Ridge in Colorado (subalpine coniferous forest) and Metolius Forest in Oregon (ponderosa pine) for Wet and Dry Temperate Evergreen, respectively, and Donaldson (Florida Slash pine) for Subtropical Dry Evergreen forest. We would like additional evergreen classes for cool non-montane pines (e.g white pine) and for hemlock, but flux data are unavailable.

Harvard Forest was the calibration site for deciduous broadleaf forests (~1.976%), which also included IGBP class "deciduous needleleaf forests" (e.g. larch) that do not occur extensively in North America. IGBP mixed forest (~7.29%) was calibrated using

Howland, (Maine). IGBP closed (~0.54%) and open shrubland (~8.6%) were combined into "Shrubland", and calibrated using Lucky Hills. IGBP woody savannas (~1.3%) and savannas (~0.14%) were combined ("Savannas") and calibrated using Tonzi Ranch.

The IGBP class of croplands (~3.77%) was adopted as-is, and calibrated using data from Mead-S2 (Nebraska) for both irrigated maize and soybeans, planted in rotation.

IGBP "grasslands" (~3.3%), "crop/natural vegetation mosaic" (~3.9%) and "barren or sparsely vegetated lands" (~1.8%) were combined into VPRM "Grasslands" and calibrated at the Vaira range site. This class may be affected by significant representation errors when the grassland calibration is applied to crop/natural mosaics, which in the northern tier are often dairy farms interspersed with woodlands. But there are no data to allow subdivision of these categories. The IGBP "permanent wetlands" (~0.7%) was calibrated at the Eastern Peatland site in Canada. IGBP classes for water bodies (~59%), urban and built-up (~0.18%) and snow and ice (~0.27%) were combined into our last class, for which vegetation-derived fluxes are assigned as zeros.

Tower data sets provide several versions of NEE: with and without filtering by turbulent intensity (u*), and with or without gap filling. Some sites also provide GEE and R, separated using various approaches. To avoid possible biases and inconsistencies from filling or separating *GEE* and *R*, VPRM parameters were optimized against <u>unfilled</u> to eliminate unrepresentative observations.

The current VPRM is intended to cover vegetation from 11N to 65N and 50W to 145W, including the continental United States, Mexico, and most of Canada. For large-scale applications, the 1–km IGBP vegetation data was classified into these types and regridded to 10 x 10 km, or $1/4^{\circ}$ x $1/6^{\circ}$, retaining information on the fractional coverage for each vegetation type. These data are provided to the public with the VPRM distribution.

3.2Satellite data

We analyzed multi-year satellite images from the MODIS sensor aboard the Terra satellite (2000-2003/04), crossing the equator at 10:30 a.m. MODIS views the entire surface of the Earth every 1 - 2 days measuring 36 spectral bands at 250 or 500 m resolution between 0.405 and 14.385 µm.

We acquired 8-day mean MODIS surface reflectances (MOD09A1) for our calibration and validation sites from the Oak Ridge Distributed Active Archive Center (http://www.modis.ornl.gov/modis/index.cfm), which provides time series data for most flux towers in ASCII format. We had to process MODIS subsets directly (Hierarchical Data Format (*HDF*); http://landval.gsfc.nasa.gov) for sites where the MODIS ASCII subsets were unavailable (e.g., Lucky-Hill).

The MOD09A1 products give data for 9 MODIS pixels covering 1.5 km \times 1.5 km, centered on each flux tower. We averaged the 8-day mean surface reflectance data for red (620-670 nm), NIR (841-876 nm), blue (459-479 nm), and SWIR (1628 -1652 nm) to calculate EVI and LSWI, then applied a low-order smoothing algorithm ("lowess", Locally-weighted least squares) [Cleveland, *1981*] to the time series for each to reduce noise associated with imperfect atmospheric corrections in MOD09A1 data.

4. Results

We optimized model parameters (λ , PAR₀, α , and β ; Table 2) via non-linear least squares (Newton-Raphson, tangent linear approximation), and estimated confidence intervals assuming Gaussian errors for both model and tower data. For each calibration

site, we generated hourly data from the smoothed time series of vegetation indices (EVI, LSWI), and obtained measurements of air temperature and PAR from the tower sites.

Examples of observed and modeled *NEE* are shown in Fig. 2a. The VPRM provides consistent partitioning of tower NEE data into light-dependent and lightindependent parts for all calibration sites, and it thus provides an independent tool for filling missing data (see Fig. 2a). (Note that T_{scale} is assumed to define the temperature dependence of photosynthesis.) VPRM has the advantage of incorporating satellite data into the process, and it can be applied to any tower site. It yields consistent, independent estimates of annual net exchange for all sites where the optimization procedure is run.

When driven by high-resolution data sets, the VPRM equations are able to reproduce one to four years of data with remarkable fidelity, including both diurnal cycles (Fig. 2b) and aggregation to monthly time scales (Fig. 3), despite their ultra-simple doem. Inputs of accurate solar irradiance and temperatures allow the VPRM to closely track hourly variations; inputs from remote sensing data enable the VPRM to also track the seasonal course of NEE. The model even captures a significant amount of inter-annual variability, driven by variations in *T*, *PAR*, and *EVI*, (Fig. 2a, *right panels*).

Values of λ for forests and crops range from 0.17 to 0.27 (Table 2), consistent with the expectation that optimum light use efficiency at low light should be ~1:6 for a dense vegetation canopy. Values are lower for semi-arid grasslands and shrublands, again as expected. Values of r^2 range from 0.6 to 0.9 for calibration sites; correlations are almost as good at many validations sites. Note the high value of PAR_0 (Table. 2) for corn, suggesting a high LUE [*Gower et al.*, 1999]. PAR_0 values in Table 2 are higher at cropland xeric sites than would be found in conventional analysis of a light curve, where NEE is fit to a hyperbolic function of PAR. Midday summer temperatures often exceed T_{opt} , and hence the VPRM infers high R and low GEE, attributing the decrease in photosynthetic efficiency to excessive heat rather than to light saturation.

The upper panels in

4.1

Figure 3 show the relationship between the seasonal dynamics of *NEE* and the VPRM photosynthesis factors. As expected, croplands and grasslands respond strongly to phenology (P_{scale}) and the amount of photosynthetically active vegetation (*EVI*). Likewise, variations in P_{scale} and *EVI*, as well as light (PAR), strongly modulate the uptake of CO₂ at deciduous and mixed sites (Harvard, Howland), whereas the temperature dependence of photosynthesis (T_{scale}) is the primary factor limiting uptake of CO₂ by well-watered evergreen forests (NOBS, Metolius/Oregon, Niwot). Intra-seasonal trends sometimes captured by water stress and changes in EVI.

There are a few surprises. Harvard and Howland forests both include significant evergreen conifers, as typical for "deciduous" and "mixed" forests, and T_{scale} is thus also critically important in limiting uptake at these sites in winter. Donaldson is warm and evergreen, but in winter it is not actually very green at all, and the very low values of EVI limit uptake. The notably poor fit at Donaldson in summer may be particular to the 2001-2002 interval used for calibration; this was the end of a severe, extended drought and remotely sensed indices might not have captured the associated aftereffects.

Other discrepancies appear to be associated with the inability of remotely-sensed data to detect water stress and/or conductance limitations during summer at sites with strong coniferous representation (Donaldson, Metolius, Howland). Thus the VPRM overpredicts uptake at these sites in mid- and late-summer, when photosynthesis rates decline steeply but EVI and LSWI change only modestly. At some sites the model does a surprisingly good job in capturing declines in net uptake due to increased respiration in mid- and late summer, for example, NOBS/BOREAS [*Dunn et al*, 2006].

The shrubland site (Lucky-Hill) had the worst fit. Carbon dioxide exchanges at this site derive from both organic and inorganic pools [*Emmerich*, 2003]. Separation of the carbon fluxes from these two pools is beyond the scope of a model like the VPRM.

4.2

We carried out VPRM simulations for 11 different validation sites (SOBS, B1850, EOBS, DUKE-PP, INDIANA, DUKE-HW, WCREEK, LCREEK, WLEF, BOND, and ANLGRASS) using derived model parameters from calibration sites in the same vegetation classes, without any adjustment. SOBS, B1850 and EOBS were classified as old-growth evergreen boreal forests and model parameters were taken from NOBS. DUKE-PP was classified as evergreen dry temperate forest and model parameters were taken from Metolius. INDIANA and DUKE-HW were classified as deciduous forest and model parameters were taken from Harvard Forest. WCREEK, LCREEK and WLEF were classified as mixed forest and model parameters were taken from Howland Forest. Soy and corn at BOND and ANLGRASS were validated using Mead-S2 soy and corn and VAIRA model parameters, respectively. We were not able to test the VPRM independently for other vegetation classes due to lack of tower data.

Most validation simulations were very successful. Figure 4 shows that the diurnal variation of NEE was slightly underestimated at B1850, DUKE-HW and ANLGRASS and slightly overestimated at BOND-soy and LCREEK. ANLGRASS nighttime

respiration was notably underestimated. Figure 5 shows the seasonal variation of NEE at validation sites, and associated VPRM functions, as in Fig. 3. Seasonal peaks of NEE were slightly overestimated at DUKE-PP, INDIANA, ANLGRASS, and BOND-SOY.

Overall, when model parameters from calibrated sites were applied to similar ecosystems for validation (Table 3), r^2 values were almost as high as at calibration sites, demonstrating strong predictive ability for sites with similar vegetation. WLEF was an outlier. Several studies have noted [*Desai et al.*, 2006; *Wang et al.*, 2006] the sharp differences between WLEF fluxes versus WCREEK and LCREEK, which lie in very similar vegetation. Mackay et al. [2002] compared WLEF stand types to IGBP classes and suggested that 4 distinct stand types are needed to characterize the region's evapotranspiration fluxes. Possibly the great tower height affects resolution of surface fluxes, extends the area influencing the tower, or introduces measurement artifacts.

The VPRM provides excellent prediction of monthly NEE for most calibration and validation sites (Figure 6), excluding WLEF. Since the optimization exclusively used hourly data, the excellent agreement between VPRM and observations at the monthly time scale (Table 3), representing aggregation by factor ~600 in time, indicates successful elimination of bias in the nonlinear optimized functions. Only one calibration site (Donaldson/slash pine) and two of the validation sites (ANL-grassland, Duke Ponderosa pine) fail to scale up in time. These are the sites are likely affected by water stress, which we already noted may not be accurately captured in the VPRM.

The VPRM validations did not capture the seasonal cycle as well at boreal evergreen forests (SOBS, B1850 and EOBS; see Table 3) as at other sites. These biomes exhibit an especially strong strong seasonal cycle of ecosystem respiration, controlled by subsurface processes such as slow thawing and draining of snowmelt-saturated soils [*Dunn et al.*, 2006] that are not remotely sensible. Thus the VPRM cannot distinguish the late summer trends at these sites from the trend fit to the NOBS data.

We quantified the role of satellite vegetation indices and of the temperature function for photosynthesis (T_{scale}) using a series of reduced models. Each was optimized independently using NEE data for Harvard and NOBS, then compared to the VPRM:

$$NEE_{model-2} = -\lambda' \times T_{scale} \times \frac{1}{(1 + PAR/PAR_{0}')} \times EVI \times PAR + \alpha' \times T + \beta'$$
(13)

$$NEE_{model-l} = -\lambda'' \times T_{scale} \times \frac{1}{(1 + PAR/PAR_{0}'')} \times PAR + \alpha'' \times T + \beta''$$
(14)

$$NEE_{model-0} = -\lambda^{'''} \times \frac{1}{(1 + PAR/PAR_0^{'''})} \times PAR + \alpha^{'''} \times T + \beta^{'''}$$
(15)

Model-2 deletes the water and phenology scaling factors using *LSWI*, Model-1 deletes all satellite information (*LSWI* and *EVI*), and Model-0 deletes these and also drops T_{scale} .

Figure 7 compares GEE from the VPRM to GEE from these reduced models, and to GEE partitioned from eddy flux data. At Harvard, the shaping of the uptake curve by P_{scale} plays a role, and inter- and intra-seasonal changes of *EVI* are very important (Figure 7a). The role of T_{scale} is surprisingly significant, as noted above, and omitting T_{scale} ruins the seasonal fit at Harvard.

Data inputs from *LSWI* and *EVI* are much less important for representing fluxes from boreal evergreens (Figure 7b), as expected. However, inter-annual variations of *EVI* appear significant in capturing inter-annual variations of GEE. At this site also, no good fit can be obtained unless T_{scale} is included to limit photosynthesis in cold weather.

5. Discussion

This paper develops and validates the VPRM, a satellite-based vegetation photosynthesis and respiration model intended to provide NEE over North America with fine temporal and spatial resolution. The model has very simple structure and few adjustable parameters. It was tested using observations from all across the AmeriFlux and Fluxnet-Canada networks. When combined with maps of vegetation type, meteorological data for temperature, and satellite-derived shortwave radiation, it provides an excellent *a priori* representation of surface CO_2 fluxes, with hourly time resolution and spatial resolution equal to that of the vegetation data (1-km for the IGBP).

The are many process-based biogeochemical models (e.g., SiB2 or Biome-BGC) that simulate the storage and fluxes of water, carbon, and nitrogen by vegetation, litter and soil. They can provide estimates of net primary production (*NPP*) or gross primary production (*GPP*), and in some cases, NEE, with hourly resolution. However, these models require complex parameter specification. For example, 47 parameters were spatially interpolated for regional simulations of SiB2 [*Denning et al.*, 2001]. In many cases, model parameters need frequent recalibration within short time periods, and the models may incur significant computational effort.

The data-driven approach of the VPRM is capable of reproducing spatial and temporal variations of NEE using simple equations plus a compact database derived from MODIS. There are only 4 parameters per vegetation type that persist for the whole annual cycle, with spatial and temporal variations rendered by high-resolution meteorological and remote sensing data.

Statistical uncertainties in the VPRM are given in Tables 2 and 3. Important additional systematic errors arise in part from the

model structure. The lack of a soil moisture component and inability to remotely sense water stress are discussed above.

Errors also arise due to limited resolution in the vegetation classification. Calibration and validation sites do not have identical vegetation assemblages, and the landscape includes assemblages not represented at all in present networks (e.g. northern white pine forests, loblolly pine plantations). Differences in vegetation functional responses are also associated with climate, soil properties and soil moisture, canopy structure, and tree ages and distribution, none of which can currently be resolved using tower site data. Related errors arise from misclassification by the IGBP.

Noise in MODIS data also introduce significant errors in EVI and LSWI, and the noisy time series of MODIS data lead to errors in phenology. Notably large errors in model NEE accrue due to deficiencies in the driver data (sunlight, temperature), affecting CO₂ flux predictions from all surface flux models. Detailed studies of errors in driver data will be described in a subsequent paper.

6. Conclusions

The VPRM assimilates large amounts of data from remote sensing, meteorology, and flux towers, and compresses the acquired knowledge into just four parameters in each vegetation class. Vegetation indices (EVI, LSWI) from the MODIS sensor, representation of the temperature dependence of photosynthesis, and accurate driver data are all required to describe the hourly and seasonal dynamics of NEE across the landscape. When coupled to accurate data sets for these factors, the VPRM partitions NEE into GEE (light-dependent) and R (light independent) without complex algorithms, sub-models, or arbitrary assumptions, and the 4 parameters of the VPRM have strong predictive ability for NEE from hourly to monthly timescales.

The selected calibration and validation sites provide a minimal representation of the vegetation of North America. At present, over 200 eddy flux tower sites make up a global FLUXNET network (http://www.daac.ornl.gov/FLUXNET). Data for CO₂, H₂O and energy flux for numerous ecosystem types have been accumulated; but availability of quality-assured data has not kept pace. Once multi-year data from more eddy flux tower sites are available, the VPRM can be refined and extended across a wider range of ecosystem and climate and soil conditions, and to other continents..

The VPRM can be applied at the scale of North American, providing a detailed representation of the spatiotemporal variation of CO₂ fluxes across the landscape, with a low dimensional parameter space for optimization in an inverse model framework. The calibrated model coefficients (λ , *PAR*₀, α and β) represent *a priori* parameter estimates, to be re-optimized at any local, regional, or continental scale in top-down analyses of carbon fluxes. The model and underlying databases are publicly available at (http://www-as.harvard.edu/data/).

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Abbreviation	Site	Data Year	LAT(N)	LON(W)	Country	Reference
NOBS	NSA Old black Spruce Forest	2000-2003	55.879	98.480	MB, Canada	Goulden et al., [1998]; Dunn et al., [2006]
NIWOT	Niwot Ridge Forest (NWT1)	2000-2003	40.033	105.546	CO, USA	Monson et al., [2002]; Yi et al., [2004]
METOLIUS	Metolius-intermediate (69Yrs) ponderosa pine Forest	2002-2004	44.452	121.557	OR, USA	Coops et al., [2005]
DONALDSON	Donaldson mid-rotation (12 Yrs) Slash pine Forest	2001-2002	29.755	82.163	FL, USA	Clark et al., [1999]; Clark et al., [2004];
HARVARD	Harvard Forest (main)	2000-2003	42.538	72.171	MA, USA	Wofsy et al., [1993]; Davidson et al., [2002a]
HOWLAND	Howland Forest (main)	2000-2003	45.204	68.740	ME, USA	Hollinger et al., [1999]; Davidson et al., [2002a-b]
LUCKY-HILL	Walnut-Gulch Lucky Hills Shrub lands	2000-2003	31.744	110.052	AZ, USA	Emmerich et al., [2003]
TONZI	Tonzi Range Savannas	2002-2004	38.432	120.966	CA, USA	Xu et al., [2003]; Baldocchi et al., [2004]
MEAD-S2	Irrigated maize-soybean rotation site (2)	Soy-2002 Corn-2003	41.099	96.281	NE, USA	Verma et al., [2005]
VAIRA	Vaira Range Grassland	2001-2003	38.407	120.951	CA, USA	Xu et al., [2004]; Baldocchi et al., [2004]
PEATLAND	Eastern Peatland, Permanent wetland	2002	45.409	75.520	ON, Canada	Lafleur et al., [2001] Lafleur et al., [2003]
ANLGRASS	Walnut River Watershed, Grassland	2002-2003	37.521	96.855	KS, USA	Song et al., [2003; 2006] Coulter et al., [2005]
WLEF	Park Falls / WLEF	2000-2001	45.946	90.272	WI, USA	Davis et al., [2003]; Ricciuto et al., [2006]
WCREEK	Willow Creek	2000-2004	45.806	90.080	WI, USA	Desai et al., [2005] Cook et al., [2004]
LCREEK	Lost Creek	2001-2004	46.083	89.979	WI, USA	Desai et al., [2006] Wang et al., [2006]
SOBS	SSA Old black Spruce Forest	2000-2004	53.987	105.118	SK, Canada	Turner et. al., [2003]; Griffis et al., [2003]
B1850	NSA 1850 Burn site	2001-2004	55.880	98.480	MB, Canada	Goulden et al., [2006]
EOBS	Quebec Mature Boreal Forest	2004	49.693	74.342	PQ, Canada	Bergeron et al., [2006]
BOND	Bondville maize-soy Cropland	Soy-2000 Corn-2001	40.006	88.292	IL, USA	Hollinger et al., [2004] Meyers et al., [2004]
INDIANA	Morgan Monroe State Forest	2000-2003	39.323	86.413	IN, USA	Schmid et al., [2000] Su et al., [2004]
DUKE_PP	Duke Forest - loblolly pine	2001-2004	35.971	79.093	NC, USA	Oren et al., [2006]
DUKE HW	Duke Forest - Hardwoods	2001-2004	35.974	79.100	NC, USA	Stoy et al., [2005]

Tables:

Table 1. Carbon Flux and MODIS Data from these 22 AmeriFlux and Fluxnet-Canada sites used in this study.

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Site	T _{min}	T _{opt}	T _{max}	T _{low}	PAR ₀	λ	α	β	σ- PAR ₀	σ-λ	σ-α	σ-β
HARVARD	0	20	40	5	570	0.127	0.271	0.25	14	0.002	0.006	0.06
HOWLAND	0	20	40	2	629	0.123	0.244	24	17	0.002	0.004	0.03
NOBS	0	20	40	1	262	0.234	0.244	0.14	5	0.004	0.002	0.01
NIWOT	0	20	40	1	446	0.128	0.250	0.17	13	0.003	0.003	0.01
METOLIUS	0	20	40	2	1206	0.097	0.295	43	39	0.002	0.003	0.02
SOY_MEADS2	5	22	40	2	2051	0.064	0.209	0.20	137	0.002	0.005	0.05
CORN_MEAD	5	22	40	2	11250	0.075	0.173	0.82	1746	0.002	0.006	0.08
TONZI	2	20	40	-	3241	0.057	0.012	0.58	293	0.002	0.002	0.03
VAIRA	2	18	40	-	542	0.213	0.028	0.72	23	0.006	0.002	0.03
DONALDSON	0	20	40	1	790	0.114	0.153	1.56	18	0.002	0.004	0.07
LUCKY-HILLS	2	20	40	-	321	0.122	0.028	0.48	14	0.004	0.001	0.01
PEATLAND	0	20	40	3	558	0.051	0.081	0.24	23	0.002	0.002	0.01

Site	Calibration		r ^{2 §}	r ²	Mean Mean Mean Mean Mean Mean Mean Mean	NEE-all $m^{-2}s^{-1}$)	Growing seas.: (µmole m ⁻² s ⁻¹)		
	Site		mon	hrly	Obs	VPRM	Obs	VPRM	
HARVARD	-	4	0.96	0.83	-1.64	-1.70	-7.24	-7.50	
HOWLAND	-	4	0.33	0.65	-0.59	-0.59	-1.32	-2.61	
NOBS	-	4	0.83	0.72	-0.54	-0.59	-1.75	-1.96	
NIWOT	-	4	0.25	0.56	-0.19	-0.19	-0.85	-1.13	
METOLIUS	-	3	0.55	0.63	-0.99	-0.99	-1.66	-1.31	
SOY MEADS2	-	1	0.61	0.66	0.08	0.05	-2.32	-2.05	
CORN_MEADS2	-	1	0.94	0.83	-1.54	-1.58	-8.13	-9.42	
TONZI	-	3	0.57	0.43	-0.59	-0.59	-1.22	-0.81	
VAIRA	-	3	0.44	0.55	-0.42	-0.43	-1.33	-2.43	
DONALDSON	-	2	-1.04	0.82	-1.49	-1.52	-1.15	-2.12	
LUCKY-HILLS	-	4	0.36	0.46	0.02	0.01	0.31	0.74	
PEATLAND	-	1	0.50	0.71	-0.04	-0.04	-0.77	-1.06	
SOBS	NOBS	5	0.81	0.69	-0.88	-1.23	-2.04	-2.83	
EOBS	NOBS	1	0.88	0.74	-0.51	-0.29	-1.91	-1.70	
B1850	NOBS	4	0.84	0.62	-0.66	-0.57	-1.97	-1.69	
DUKE_PP	METOLIUS	4	-0.43	0.58	-1.01	-2.63	-1.66	-4.89	
DUKE HW	HARVARD	4	0.64	0.58	-1.00	0.47	-3.59	-1.80	
INDIANA	HARVARD	4	0.59	0.65	-0.70	-0.40	-4.35	-4.94	
WCREEK	HOWLAND	5	0.77	0.77	-0.87	-1.78	-5.36	-7.95	
LCREEK	HOWLAND	4	0.53	0.66	-0.27	-0.18	-2.12	-2.68	
WLEF	HOWLAND	2	-11.0	0.46	0.26	-0.37	-0.52	-3.94	
SOY_BOND	SOY_MEAD	1	0.80	0.72	0.31	0.85	-2.62	-3.02	
CORN_BOND	CORN_MEAD	1	0.76	0.63	-1.27	-0.53	-7.02	-9.03	
ANLGRASS	VAIRA	2	040	0.57	-0.34	-0.80	-0.52	-1.32	

Table 3: Correlation coefficients (r^2) for monthly and hourly NEE, and means for all seasons and for the growing season hourly data (April to June for VAIRA and ANLGRASS; June to August for all other sites) of tower flux and VPRM calculations at

calibration and cross validation sites. Only intersection data (available in both observation and model columns) were used.

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