Spatial analysis of growing season length control over net ecosystem exchange

GALINA CHURKINA*, DAVID SCHIMEL†, BOBBY H. BRASWELL‡ and XIANGMING XIAO‡

*Max-Planck Institute for Biogeochemistry, Hans Knöll Str. 10, 07745 Jena, Germany, †NCAR, 1850 Table Mesa Dr., Boulder, CO 80307, USA, ‡Institute for the Study of Earth, Oceans and Space, Morse Hall, University of New Hampshire, Durham, NH 03824, USA

Abstract

Using data from 28 flux measurement sites, we performed an analysis of the relationship between annual net ecosystem exchange (NEE) and the length of the carbon uptake period (CUP) (the number of days when the ecosystem is a net carbon sink). The observations suggest a linear correlation between the two quantities. The change in annual carbon exchange per day of the CUP differs significantly between deciduous and evergreen vegetation types. The sites containing vegetation with short-lived foliage (less than 1 year) have higher carbon uptake and respiration rates than evergreen vegetation. The ratio between mean daily carbon exchange rates during carbon uptake and release periods is relatively invariant (2.73 ± 1.08) across different vegetation types. This implies that a balance between carbon release and uptake periods exists despite different photosynthetic pathways, life forms, and leaf habits. The mean daily carbon sequestration rate for these ecosystems never exceeds the carbon emission rate by more than a factor of 3. Growing season lengths for the study sites were derived from the normalized difference vegetation index (NDVI) of advanced very-high-resolution radiometer and from the enhanced vegetation index (EVI) of VEGETATION SPOT-4. NDVI and EVI were found to be closely related to the CUP, and consequently they also can be used to approximate annual carbon exchange of the ecosystems. This approach has potential for allowing extrapolation of NEE over large areas from remotely sensed data, given a certain amount of ancillary information. This method could complement the currently existing techniques for extrapolation, which rely upon modeling of the individual gross fluxes.

Keywords: carbon uptake period, growing season length, net carbon exchange, phenology, vegetation index

Introduction

Despite significant progress in estimating global carbon fluxes from large-scale observations (Gurney *et al.*, 2002), a large amount of uncertainty about the magnitude, spatial pattern, and causes of terrestrial ecosystem carbon uptake remains. New methods, such as eddy covariance, provide measures of net fluxes from a wide range of ecosystems, and when combined with models, they can constrain the likely mechanisms controlling carbon exchange (Thornton *et al.*, 2002;

Correspondence: Galina Churkina, fax + 49 3641 577300, e-mail: churkina@bgc-jena.mpg.de

Churkina *et al.*, 2003). However, even the globally distributed network of eddy flux stations samples only a small subset of the Earth's biomes, disturbance regimes, and land management systems. Further, eddy flux techniques are currently limited to relatively flat terrain (Schimel *et al.*, 2002). Thus, estimation of net ecosystem exchange (NEE) over large heterogeneous areas remains challenging. Remote sensing is a potentially powerful tool, providing spatially comprehensive measures of ecosystem activity. Most extant satellite algorithms estimate gross primary productivity, net primary productivity (NPP), or woody biomass from satellite measurements (Myneni *et al.*, 2001), and rely on models to complete the carbon balance (Running *et al.*,

2000; Potter *et al.*, 2001). Here, we propose an alternative approach to regional estimation of NEE by synthetic analysis of flux measurements with satellite remote sensing.

Carbon exchange measurements based on the eddy correlation technique provide extremely valuable information about carbon and water fluxes for the region immediately surrounding the towers ($\sim$ 100 m–5 km). The carbon flux footprint, or source distribution function, depends on the height of the tower (sensor) relative to the zero plane displacement of the vegetation, on the surface roughness, on the wind speed, and on the atmospheric stability (Baldocchi *et al.*, 1996). Given the typical footprint sizes, and the limited number of measurement points, the carbon flux network alone provides samples of fluxes and their controls from a wide range of systems, but cannot be simply averaged to obtain regional-to-global estimates with any precision.

Longer time series of data, and improving representation of different ecosystems in various climate conditions, improve our understanding of the causes and mechanisms lying behind carbon exchange variability. They allow investigation of correlations of NEE with environmental variables, the spatial distribution and temporal variability of which can be obtained over large areas using different measurement techniques.

Because of the variation in controls over competing gross fluxes throughout the course of a year, the length of the growing season is a key control over net uptake. This critical time interval can, in principle, be inferred from remotely sensed measurements that are sensitive to plant canopy changes. A number of studies have pointed to a major role for growing season length (GSL) in the terrestrial carbon cycle (Black *et al.*, 1996, 2000; Myneni *et al.*, 1997; White *et al.*, 1999). For centuries, the positive relationship between vegetation productivity and GSL has been used in agriculture to optimize crop yields. In areas with extended warm summers, farmers can produce up to three crop rotations per year. Lieth (1975) noticed a similar relationship in forests, when he found a correlation between annual NPP and the length of the photosynthetic period for deciduous broadleaved forests of the Eastern United States. Valentini *et al.* (2000) analyzed net ecosystem productivity (NEP, the difference between NPP and heterotrophic respiration) of European forests and found a significant increase in net carbon uptake with decreasing latitude, which is a surrogate for increasing GSL. A more detailed study of assimilatory and respiratory processes of the world forests (Falge *et al.*, 2002) showed that not only NEP, but also gross carbon assimilation increases with decreasing latitude. The increase in the latter is, however, greater than the increase in NEP, indicating a larger

contribution of respiratory processes in boreal systems (the total amount of respiration in the boreal system is lower than in the rain forest). Eddy flux data allow determination of a carbon uptake period (CUP), or the number of days on which the net carbon flux is negative (the ecosystem is a sink of carbon). The CUP is controlled by GSL, but is not identical because growth will typically commence for some time before the carbon flux changes sign, and drought-stressed systems might even show carbon release periods in the middle of the growing season. Thus, CUP is defined by NEE rather than by NPP or plant activity.

A strong correlation between measured NEE and the length of CUP was reported for temperate broadleaved forests (Baldocchi & Wilson, 2001). Barr *et al.* (2004) showed that annual NEE was positively correlated with the canopy duration and the annual maximum LAI for deciduous boreal forest. Based on model simulation results White & Nemani (2003) suggested that there is a strong relationship between NEE and CUP, but a very weak relationship between NEE and canopy duration. The latter study implies that detection of patterns of NEE variation with remote observations of GSL is not possible.

Using data from a large number of flux measurement sites, we analyzed the relationship between NEE and CUP, as well as the ratio between net exchange rates during carbon release and uptake periods for different vegetation types, including forests and grasslands. To test the capabilities of remote observations, we relate the length of the CUP from tower measurements to the GSL from remotely sensed data. This analysis allows discussion of the advantages and shortcomings of the remote sensing approach to estimate NEE values over large areas.

Methods

We define the CUP as the number of days per year when the ecosystem is a net sink of carbon. During this period, daily ecosystem carbon uptake exceeds carbon release. The CUP is related, but not identical, to the GSL of plants, which is defined as the time between budburst (greenness onset) and cessation of plant growth (greenness termination). In tropical rain forests, however, plant development continues throughout the year, so the length of the growing season is approximately equal to the length of the year. Multiple factors can control the length of the growing season, although it is most often thought of in terms of temperature (White *et al.*, 1997; Menzel, 2003). The leaf onset or termination timing is triggered by a combination of daylength, spring warming/fall cooling, winter chilling, and soil moisture. In arid and semiarid

climates, plant growing season is often dominated by moisture and may be bi- or multimodal. The time of leaf onset does not usually indicate the beginning of the CUP, which starts later, when the leaves are large enough to photosynthesize at a rate higher than respiration rate. The CUP ends when ecosystem respiration becomes larger than photosynthesis, but plant growth may continue. During drought, vegetation may be a net source of carbon for a few weeks, which does not imply the end of the growing season. Also alpine and boreal sites may experience carbon loss on cloudy days during summer (Monson *et al.*, 2002). The GSL, however, would most likely stay unchanged as long as this unfavorable period is short. The resulting discrepancy would be within the uncertainty range of GSL–CUP relationship. The mechanisms behind the leaf-shedding process are complex, and most likely associated with physiological, whole-tree, and ecosystem processes (Royer *et al.*, 2003). The growing season in most cases will be longer than the CUP because the balance between total ecosystem respiration (autotrophic and heterotrophic) and photosynthesis defines CUP.

Description of CO_2 flux sites and data

The eddy covariance technique offers an exceptional opportunity to assess net carbon and water fluxes between terrestrial ecosystems and the atmosphere at the ecosystem level. The fluxes of CO_2 and H_2O are monitored by sampling their concentrations in the air at a point located near a sonic anemometer, which makes high-frequency (10 Hz) measurements of vertical wind speed variations. In general, the daytime flux footprints extend about 100 m for every meter measured above the reference level and can cover areas located as far as 100–1000 m from the tower (Baldocchi *et al.*, 1996). The flux footprint is generally smaller in daytime and larger at night because of the diurnal cycle of the boundary layer.

The eddy covariance method is not free from uncertainty. A number of errors of atmospheric, surface, and instrumental origins contribute to uncertainty in flux estimation (Moncrieff *et al.*, 1996). In addition, instrument failure associated with adverse weather conditions can result in a large number of data gaps (sometimes greater than 40% of the time series). Various methods for filling the data gaps exist, but they can yield substantially different annual NEE (Falge *et al.*, 2001). Systematic overestimation of NEE is also possible using eddy covariance techniques, because nonturbulent atmospheric phases occur more often during the respiration-dominated (nighttime) periods.

In our analysis, we used annual sums of carbon exchange from 28 sites (Table 1) that are part of the EUROFLUX (Aubinet *et al.*, 2000) and AMERIFLUX

(Baldocchi *et al.*, 2001) networks. The sums were from different years during 1990s and 2000s. Multiple years of data were available for several sites. For consistency, data gaps, if any, were filled using the lookup table method (Falge *et al.*, 2001) in all data sets, except for the Hainich data. The Hainich data were received directly from the site investigators and were gap filled as described in Knohl *et al.* (2003). The sites were divided into four groups depending upon the leaf habit: evergreen needleleaf forests (ENF), deciduous broadleaf forests (DBF), evergreen broadleaf forests (EBF), and grasslands/crops (GRC). With the exception of five sites (Norunda, Tharandt, Hainich, Manaus, and Wind River), most of the forests were younger than 100 years, and consequently still regrowing in a 'linear acceleration' phase. Most of the forests appeared to be sinks of carbon during the years considered in this study.

The CUP was calculated as the number of days when the ecosystem was a net sink of carbon. Average daily values of carbon exchange rate were computed separately for carbon uptake and release periods for each site and each year, so that the ratio between the two absolute mean rates for each site could be analyzed. We calculated this ratio to find out if emission rates during the carbon uptake and release periods are related. The above-mentioned average daily carbon exchange rates were also used to test the assumption that vegetation with short-lived foliage has higher carbon uptake and release rates than evergreen vegetation.

Description of remotely sensed data

Phenological changes in vegetation can, in principal, be detected from remotely sensed data and used to infer GSL, and possibly the CUP. This phenologically based analysis is fundamentally different from those based upon traditional ground-based observations. The capacity of satellite sensors to detect such events as budburst or flowering is limited, because of the ground resolution of the sensors and the effects of other vegetation and soil background characteristics. Despite these limitations, satellite sensors are capable of measuring broad-scale phenological changes in the landscape, which may not be associated with phenological events of specific plants, but are descriptive of the ecosystem condition.

An efficient and objective description of phenological signals over large areas can be derived from the temporal profiles of vegetation indices. These empirical measures have been developed using data from broadband optical sensors over the last few decades. To infer the GSL in this study, we used two vegetation indices: normalized difference vegetation index (NDVI) and enhanced vegetation index (EVI). NDVI is a normalized

Table 1 Sites considered in this study have been divided into four groups depending on the leaf habit: ENF, DBF, GRC, and EBF

Site, Country	Abbreviation	Vegetation type	Latitude	Longitude	Years of flux data	Age (years)	Reference
Flakaliden, Sweden	FL	ENF	64.113	19.457	1997–1998	31	Lindroth *et al.* (1998)
Hyytiala, Finland	HY	ENF	61.847	24.295	1997–1999	30	Markkanen *et al.* (2001), Vesala *et al.* (1998)
Norunda, Sweden	NO	ENF	60.086	16.220	1996–1997	100	Lindroth *et al.* (1998)
Aberfeldy, UK	AB	ENF	56.606	−03.797	1997–1998	14	Valentini (2003)
North Boreas, Canada	NB	ENF	55.905	−98.524	1995–1998	53–155	Goulden *et al.* (1998)
Loobos, Netherlands	LO	ENF	52.167	05.744	1997–1998	80	Valentini (2003)
Brasschaat, Belgium	BR	ENF	51.309	04.520	1998	67	Apps *et al.* (2003)
Tharandt, Germany	TH	ENF	50.964	13.567	1997–2000	100	Valentini, (2003)
Weiden Brunnen, Germany	WB	ENF	50.161	11.882	1998	40	Valentini (2003)
WLEF, USA	WL	ENF	45.945	−90.272	1997–1999	60–80	Berger *et al.* (2001)
Wind River, USA	WR	ENF	45.820	−121.952	1999–2000	Old growth	Chen *et al.* (2002)
Howland, USA	HL	ENF	45.204	−68.740	1996–1997	90	Hollinger *et al.* (1999)
Metolius, USA	ME	ENF	44.499	−121.622	1996–1997	50–250	Law *et al.* (2000), Law *et al.* (2001b)
Niwot Ridge, USA	NR	ENF	40.032	−105.546	2000	95	Monson *et al.* (2002)
Blodget Forest, USA	BL	ENF	38.895	−120.633	1999	12	Law *et al.* (2001a)
Duke Forest, USA	DU	ENF	35.978	−79.094	1998–1999	17	Law *et al.* (2002), Lai *et al.* (2002)
Soroe, Denmark	SO	DBF	55.487	11.646	1997–1999	78	Pilegaard *et al.* (2001)
Hainich, Germany	HN	DBF	51.079	10.452	2000–2001	Old growth	Knohl *et al.* (2003)
Vielsalm, Belgium	VI	DBF/ENF	50.308	05.998	1996, 1998	60–90	Valentini (2003)
Hesse, France	HE	DBF	48.674	07.065	1997–1999	30	Valentini (2003), Granier *et al.* (2000)
Willow Creek, USA	WC	DBF	45.808	−90.079	1999–2000	55	Law *et al.* (2002)
Harvard Forest, USA	HV	DBF	42.537	−72.171	1992–1999	70	Goulden *et al.* (1996), Barford *et al.* (2001)
Bondville , USA	BV	GRC	40.006	−88.292	1997–2000	1	Meyers (2001)
Shidler, USA	SH	GRC	36.933	−96.683	1997	1	Suyker & Verma (2001)
Ponka, USA	PO	GRC	36.766	−97.133	1997	1	Law *et al.* (2002)
Little Washita, USA	LW	GRC	34.960	−97.979	1997–1998	1	Meyers (2001)
Castelporziano, Italy	CP	EBF	41.705	12.377	1997–1998	30	Valentini (2003)
Manaus, Brazil	MA	EBF	−02.589	−60.115	1996	Old growth	Malhi *et al.* (1999)

Most of evergreen needleaf and deciduous broadleaf forests were still maturing and actively sequestering carbon. ENF, evergreen needleaf forest; DBF, deciduous broadleaf forest; GRC, grasslands/crop; EBF, evergreen broadleaf forest.

ratio between red (RED) and near infrared (NIR) bands (Tucker, 1979) as follows:

$$\mathrm{NDVI} = \frac{\mathrm{NIR} - \mathrm{RED}}{\mathrm{NIR} + \mathrm{RED}}.$$

The EVI is calculated using reflectance in the RED, NIR, and blue (BLUE) spectral bands (Huete *et al.*, 1997) as follows:

$$\mathrm{EVI} = G \frac{\mathrm{NIR} - \mathrm{RED}}{\mathrm{NIR} + (C1 \times \mathrm{RED} - C2 \times \mathrm{BLUE}) + L},$$

where $G = 2.5$, $C1 = 6$, $C2 = 7.5$, $L = 1$.

The advantage of EVI over NDVI is that it includes a blue band, which allows accounting for residual atmo-

spheric contamination, and weight *L*, which compensates for variable soil background reflectance.

The NDVI was calculated from the National Oceanic and Atmospheric Administration's advanced very-high-resolution radiometer (AVHRR) data, which have just two spectral bands (red and NIR) that are used for vegetation study, but which provide a very long time series of data. From NOAA-AVHRR, there are currently over 15 years of data available, but we focused on the more reliable post-Pinatubo period of 1996–2001 (Gutman, 1999) at 1 km spatial resolution, which also corresponds well with the period of eddy flux tower measurements.

The EVI was derived from data collected by the VEGETATION (VGT) sensor onboard the SPOT-4

satellite, which was launched in March 1998. The VGT has four spectral bands: blue (0.43–0.47 μm), red (0.61–0.68 μm), NIR (0.78–0.89 μm), and shortwave infrared (1.58–1.75 μm). The VGT sensor provides daily global observations at 1 km spatial resolution. The standard 10-day composite data (VGT-S10) are produced and available to the public (http://free.vgt.vito.be). The temporal compositing method for generating standard 10-day synthetic products (VGT-S10) is to select an observation with the maximum NDVI value within a 10-day period. There are three 10-day composites within a month: days 1–10, days 11–20, and day 21 to the end of the month.

We acquired the VGT-S10 data over the period of April 1–10, 1998 to December 21–31, 2002 for the globe (a time-series data of 135 VGT-S10 images). EVI (Huete *et al.*, 1997; Xiao *et al.*, 2003) was calculated for all the 10-day composite images (VGT-S10). A detailed description of the preprocessing and calculation of vegetation indices from VGT-S10 data are given elsewhere (Xiao *et al.*, 2003). For a time series of vegetation index, we used a simple gap-filling method (Xiao *et al.*, 2003) to fill vegetation index values of those cloudy pixels identified by the quality flag in the VGT-S10 reflectance files.

EVI and NDVI time series over the available years were averaged into a single composite year for each site in order to minimize the effects of clouds and aerosols. We selected the 1 km × 1 km pixel with a center point closest to the respective eddy flux tower coordinates. Because of potential satellite data geo-registration issues, we also extracted the eight pixel neighbors of the center pixel for the comparison of results. After initial analysis, by shifting the data in all eight possible directions, no consistent linear spatial bias was found. The spatial noise, however, was decreased by averaging the reflectance values of nine pixels prior to performing the analysis. As a result we had a 10% improvement in the overall comparison between CUP and GSL. This is likely because of the existence of random geolocation error (≤1 pixel), rather than a consistent offset, which is not uncommon for data that span a very large region such as in this study (Hagen *et al.*, 2002).

The vegetation index time series are available at a time interval of 10 days, so there were 36 points per site used to describe the seasonal cycle of the vegetation canopy at each location. We interpolated the data linearly to form a daily time series with 365 points. As result we had available for each FLUXNET site an average annual temporal profile at daily temporal resolution. Linearly interpolated moderate temporal resolution data depict actual forest phenological changes better than the finer resolution version of the same data (e.g., 8–30 days vs. 1 day). The reason is that the observed day-to-day variations of data of this type

(e.g., AVHRR, SPOT, MODIS) are dominated by atmospheric and view geometry effects. Furthermore, linear interpolation of moderate temporal resolution data also appears to be adequate for this purpose, especially for deciduous forests (Jenkins *et al.*, 2003). We believe that (1) the composited data represent a very good estimate of reflectance for the associated period, and (2) because vegetation dynamics do not vary in a complex non-linear way on week-to-week time scales, the linear interpolation is an adequate way to estimate the most likely reflectance value at an intermediate interval.

The GSL was computed for each data set, and defines the number of days the vegetation index was greater than a given threshold. A single threshold value was used for all sites and is meant to indicate the EVI or NDVI value that best corresponds to the phenological transitions that we discuss in this paper. Instead of using an arbitrary value, we selected the threshold that yielded GSL values most correlated across sites with CUP estimates from eddy flux data. Two different threshold values of 0.02 and 0.05 were selected for EVI and NDVI, respectively. The resulting mean and range of GSL onset and termination days for each site corresponded well with the CUP interval, indicating that the GSL was indeed an acceptable indicator of canopy seasonality.

Statistical analysis of data

For testing the inequality of regression slopes between CUP and NEP for two different vegetation types, we calculated t^* as $t^* = (b_1 - b_2)/\sqrt{(s_1^2 + s_2^2)}$, where b_1 and b_2 are regression slopes, and s_1 and s_2 are the standard errors of regression slopes for the two vegetation types. The null hypothesis that the regression slopes b_1 and b_2 are the same was rejected if $t^* > t$, where t was derived from the Student's t test given $n_1 + n_2 - 4$ degrees of freedom (df) (n_1 and n_2 are the number of points in regressions for two vegetation types), based upon an $\alpha = 0.05$ confidence level.

We used cluster analysis to test the assumption that vegetation, with short-lived foliage, exhibited higher carbon uptake and respiration rates than evergreen vegetation. The clustering was applied to the daily values of carbon exchange rate, computed separately for carbon uptake and release periods for each site and each year. We used two clustering methods, which produced somewhat different results and helped to highlight borderline cases. The first partitioning method was the *k*-means algorithm. In this approach, the observations were classified as belonging to one of the *k* groups. Group membership was determined by calculating the centroid for each group (the multidimensional mean), and assigning each observation to the

closest centroid. The centroids were calculated using least squares, and the observations were assigned to the closest centroid, also based on their minimum squared distance. This use of a least-squares criterion makes *k*-mean less resistant to outliers than the medoid-based method, which we also used for analysis. The partitioning around medoids algorithm is similar to *k* means, but uses medoids rather than centroids. The method computes *k* representative objects, called medoids, which together determine a cluster. Each observation was assigned to the cluster corresponding to the nearest medoid. Both methods are described in more detail in Kaufman & Rousseeuw (1990).

Cross-validation analysis was used for checking the capability of the GSL from satellite data to predict CUP. For each vegetation index we have randomly removed 10% of the data and fit the model to the remaining 90% of data. Then we calculated the mean-squared prediction error (MSPE), while predicting the 10% of originally removed data.

Results and discussion

From our analysis of data from the FLUXNET network, we found linear correlations between annual NEE and the CUP, with different slopes for different vegetation types (Fig. 1). The relationship exists in part because the variability in mean daily flux rates is low (less than a factor of 10) compared with the variability on annual sums (two orders of magnitude) and, thus, much of the variability in annual NEE is because of CUP. From carbon exchange measurements, ENFs had the lowest annual gain of carbon per CUP-day of $3.4\,g\,C\,m^{-2}$, DBFs had higher carbon uptake of $5.8\,g\,C\,m^{-2}$, and the carbon gain of grass/crop was even higher at $7.9\,g\,C\,m^{-2}$. A similar analysis was not possible for EBFs because of the very few observations available (three site years of data). For temperate broadleaf forests the increased annual rate for each additional CUP day was comparable with the results by Baldocchi & Wilson (2001) of $5.72\,g\,C\,m^{-2}$ and slightly lower than those reported by Barr *et al.* (2004) of $6.9\,g\,C\,m^{-2}$, probably because the latter result was for one site only. Although coniferous forests and deciduous vegetation (deciduous broadleaf forest and grasslands) had significantly different regression slopes ($t^* = 3.09$ and $t^* = 2.37$, $t^* > t$ with 49 and 37 df at 95% confidence level), the difference between DBF and grasslands was not statistically significant ($t^* = 1.06$, $t^* < t$ with 24 df at
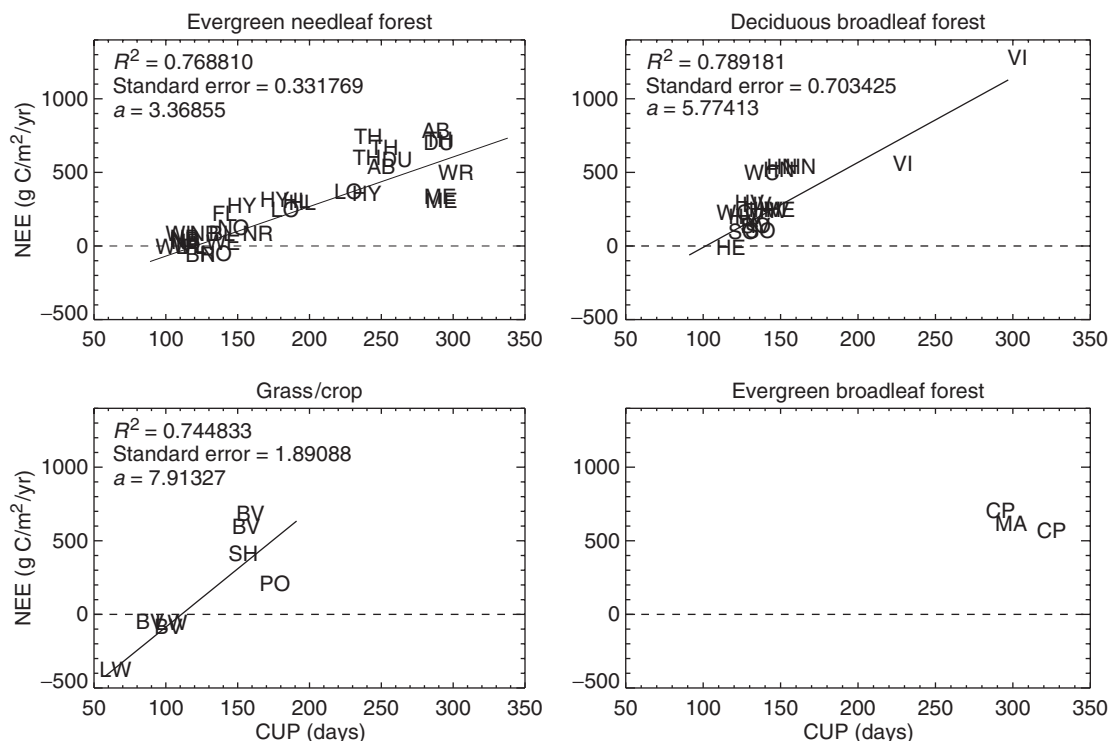

Fig. 1 Correlations between carbon uptake period from eddy covariance measurements and annual cumulative net ecosystem exchange (NEE) for different vegetation types. The statistical test of the equality of two slopes showed that the regression slopes for evergreen needleaf and deciduous forests are different, while the slopes of the deciduous broadleaf forest (DBF) and grass/crops are the same with 95% confidence level. The correlation plot for the DBF includes one mixed forest (VI). Each data point represents a site from EUROFLUX or AMERIFLUX data sets.

95% confidence level). The ENFs included a couple of old growth forest stands and on average were slightly older than deciduous broadleaf ones. Older forests normally have lower carbon gain per day than the younger ones. Therefore, the difference in the annual gains of carbon per each additional CUP day between deciduous broadleaf and ENF may stem from slightly different ages of the forests in these two groups and not the species. The caveat here is that we do not know if this relationship would hold between years at a single site, although some studies (Barr et al., 2001; White & Nemani, 2003) suggest that it does.

We suggest that CUP represents a measure of water/energy availability and the regressions represent the adjustment of carbon gain to the typical amount of water and energy available, balanced against other resources (Schimel et al., 1997). Burke et al. (1997) showed that empirical relationships between site-level interannual precipitation and NPP were substantially smaller than spatial relationships between mean annual precipitation and NPP. The spatial pattern approximates the steady-state response, with factors such as nutrient availability and species composition that have response times longer than a year adjusted to the mean climate. Because nutrient availability, species composition, and other processes cannot adjust instantaneously to year-to-year variability in precipitation, the interannual response to rain is much smaller than the regional spatial correlation would suggest. Following Burke et al.'s (1997) argument we predict that the interannual response to CUP should be much smaller than the spatial, because species composition (especially in forests) and nutrient availability cannot respond as fast as weather from year to year. In fact not only is the nutrient constraint slower to change, and possibly in equilibrium with average CUP, the species on a site may even be evolutionarily tied to mean climate and CUP. Mean and maximum daily flux rates reflect the ecosystem physiological possibilities of the species present at a site. Because the variability of mean daily flux rates is so much lesser than that of annual exchange (a factor of 10 compared with a factor of 1000), the physiological variability between species and life forms controls only a part of the variability in net exchange, with climate constraints also playing a large role. This analysis can help sort out how much detail in the understanding of physiological variability is needed to understand regional scale flux variability.

Analysis of mean daily carbon exchange rates during carbon uptake and release periods for different sites showed that it is possible to separate vegetation types with different leaf habits (Fig. 2) according to their mean daily fluxes. Depending on their leaf habit, plants acquire their net gain of carbon per unit of time in
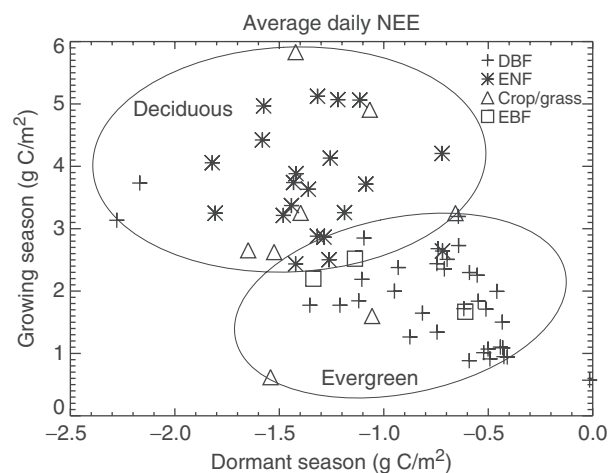

Fig. 2 Relationship between average net ecosystem exchange (NEE) rates during carbon uptake (NEE > 0) and carbon release (NEE ≤ 0) periods. The lines are drawn around two groups corresponding to evergreen and deciduous life forms as derived from cluster analysis. During both periods, coniferous forests tend to have lower mean daily carbon exchange rates than deciduous broad-leaved forests. Evergreen broadleaf forests have a comparable daily mean NEE rate with coniferous forests. For each site, average daily NEE rate was calculated separately for carbon uptake and release periods.

different ways. Vegetation with short-lived foliage (less than 1 year) has high carbon uptake rates and high respiration rates. Vegetation with long-lived foliage (more than 1 year) has lower photosynthetic rates and lower decomposition rates (more lignin, compounds, which are difficult to decompose).

Both methods used for clustering clearly distinguished between two clusters characterizing evergreen and deciduous vegetation. The evergreen needleaf and broadleaf forests formed the first cluster (center: −0.79, 1.79 g C m^{-2} day^{-1}), while most crops and grasslands were grouped together with deciduous forests in the second cluster (center: −1.37, 3.64 g C m^{-2} day^{-1}). An exception was one dry grassland site (Little Washita), which fell into the cluster with evergreen vegetation. Among forests, there was one outlier case (the evergreen forest in Norunda) as well as a few borderline cases, which fell into the deciduous or evergreen cluster depending on the clustering method. The ENF in Norunda was classified together with deciduous vegetation because of its very high carbon uptake and release rates. The Aberfeldy and Tharandt sites were borderline cases among ENFs. Conversely, Hesse, Vielsalm, and Soroe were borderline cases among the deciduous forests. It is possible that high carbon uptake and release rates in Norunda were related to special soil conditions of the site (drained soils) and fertilization. The borderline cases can be at least partially explained

by mixed vegetation in the flux measurements footprint (Vielsalm), indirect or direct site fertilization (Tharandt and Aberfeldy), or climatic limitations (Soroe and Hesse).

The ratio between mean daily exchange rates during the carbon uptake and carbon release periods was relatively conservative for different vegetation types and averaged around 2.73 ($\pm$ 1.08). This value varied rather little between vegetation types (2.65 $\pm$ 1 for ENF, 2.96 $\pm$ 1 for DBF, 2.65 $\pm$ 1.7 for crop/grass, and 2.2 $\pm$ 0.5 for EBF), suggesting that a balance between carbon release and uptake rates existed despite varying emissions, uptake periods, different photosynthetic pathways, life forms, and leaf habits. The average daily ecosystem carbon sequestration rate was found to exceed the carbon emission rate by less than a factor of three. Existence of this balance explains the correlation between CUP and NEE, and why we do not observe situations with low carbon sequestration rates and long CUP, or with high carbon sequestration rates and short CUP.

Our comparison with the satellite data suggests that the length of the CUP can be inferred from the length of a vegetation activity period from NDVI AVHRR and/or EVI VGT (Fig. 3). The GSL derived from EVI provided better estimates of CUP than the one derived from NDVI, as indicated by the fact that MSPE for EVI (MSPE = 2818) was significantly lower than for NDVI (MSPE = 4125). Within a 15-day deviation from CUP, there were 11 sites with accurate GSL estimates derived from EVI and eight sites with accurate GSL estimates derived from NDVI. Among them were estimates of GSL in which both indices were relatively close to each other and to CUP of five coniferous forests (Loobos, Hyytiala, Flakaliden, Aberfeldy, Metolius) and one mixed forest (Vielsalm).

The CUP of 15 sites was overestimated by GSL derived from NDVI by between 15 days and 3 months. There were, however, only 10 sites with GSL derived from EVI falling into this category. The GSL of two coniferous forests (WLEF, Weiden Brunnen), two broad-leaf deciduous (Soroe, Willow Creek), two broadleaf evergreen forests (Castelporziano, Manaus), and one site in the prairie (Shidler) was overestimated by GSL derived from both indices. The discrepancies in CUP estimates may be related to the use of a single threshold for extracting GSL from vegetation indices. When longer time series of data for concurrent time periods are available from EUROFLUX, AMERIFLUX, and remote sensing, we can test whether using different threshold values for broadleaf, needleaf forests, and grasslands/croplands would improve CUP estimates.

Both correlation analyses contained outlier sites, with CUP overestimated by more than 3 months. One group of outliers represented sites in arid climates (Little Washita – grassland, Blodget forest – needleaf ever-green forest). The vegetation indices at these sites do not necessarily drop during the summer drought as long as the vegetation stays green, although the carbon balance may switch from positive to negative. Although CUP for the forest site was undetectable from both sets of remotely sensed data, GSL of the grassland site was
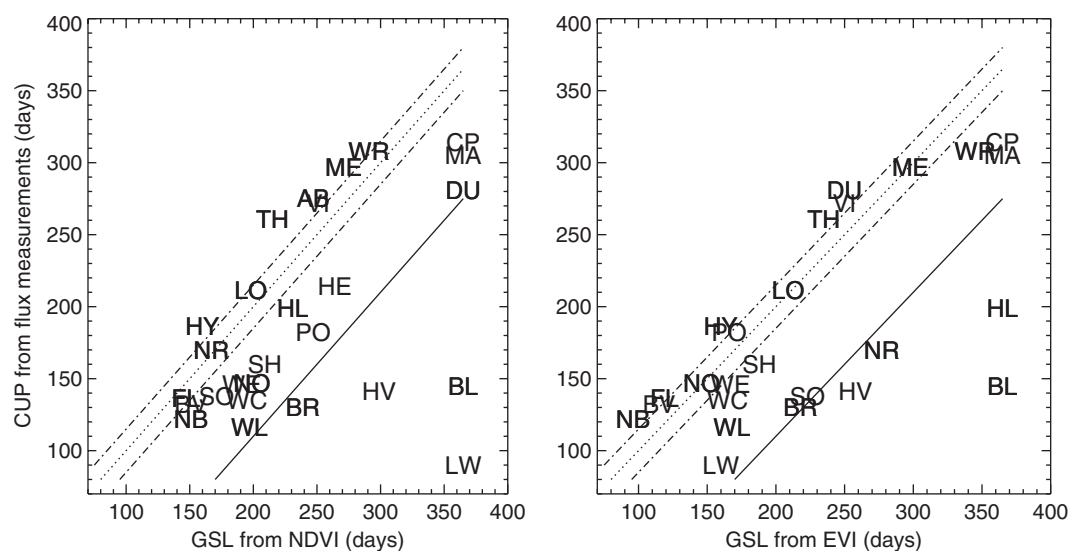

Fig. 3 Correlation between carbon uptake period (net ecosystem exchange, NEE > 0) from eddy flux observations and growing season length from normalized difference vegetation index (NDVI) and EVI. The dotted line represents 1 : 1 relationship. The dash-dot lines show the 15-day deviation from the 1 : 1 line. The dash-dot-dot line shows three month deviation from the 1 : 1 line. Each data point represents one site from AMERIFLUX of EUROFLUX network. The sites with coniferous forests are marked in black.

just at the limits of the 3-month range from EVI, and undetectable from NDVI profiles. The second group of outliers (coniferous forests at Niwot Ridge and Howland) can be explained by the sensitivity of EVI to snow cover. Even residual snow cover under the canopy may increase EVI values in the late fall or early spring (Xiao et al., 2004). These two coniferous forests were outliers on the plot of CUP and GSL from EVI. Nevertheless, GSLs of these sites were within a 15-day deviation from CUP, when derived from NDVI profiles. It was more difficult to ascertain why the CUPs of deciduous (Harvard forest) and coniferous (Braschaat) forests were greatly overestimated by GSL from both indices. Most likely it can be attributed to the high heterogeneity of vegetation in the pixel.

Conclusions

Our analysis of eddy covariance data from 28 EUROFLUX and AMERIFLUX sites, covering multiple years, suggests that the length of the CUP has potential to be used for extrapolation of annual NEE for many types of terrestrial ecosystems. This extrapolation will apparently need to be refined by inclusion of land management and disturbance information, where available, in order to stratify the data into age classes. This finding could eventually greatly simplify the estimation of carbon sinks and sources over large land areas, through application of tower data together with the remotely sensed observations that provide GSL of vegetation over large surface areas. The GSL from satellite data often closely approximate the CUP of temperate and boreal coniferous forests, but overestimate the CUP of the broadleaf forests. The method does not currently produce good results for arid climates, at least with the vegetation indices we used. Perhaps indices based on sensitivity to canopy moisture (Xiao et al., 2004) should be considered.

We are not yet in the position to make spatially explicit estimates of NEE based on the length of the growing season derived from the vegetation indices. To apply this method may require more complete sampling of vegetation types of the world by the flux data and of course, improved proxies for CUP from the remotely sensed data. The correlation between CUP and annual NEE from eddy covariance measurements should be investigated further, once longer time series of flux data from more sites and vegetation types become available. It would also help to better identify the domain of the application of this method. It would be useful to investigate if these relationships hold for other vegetation types and to find out if the correlation is valid for multiple years at the same site. For instance, we would not expect to find the same relationship

between NEE and CUP in very young or old stands as are found in mid-aged aggrading systems.

More work also has to be done for a more accurate definition of GSL from the remotely sensed data. Improved remotely sensed data from the next generation of remote sensors are needed as are vegetation indices accounting for water stress. Vegetation indices (e.g. photochemical reflectance index) from hyperspectral data may provide better results as well, because they give a better proxy for the physiological capacity of plants (Rahman et al., 2003), but will be more limited spatially.

The ratio between mean daily carbon exchange rates during carbon uptake and release periods, or coefficient of absorption, appears to be consistent across different vegetation types, implying that a balance between carbon release and uptake periods exists despite different photosynthetic pathways, life forms, and leaf habits.

References

Apps MJ, Artaxo P, Barrett D et al. (2003) Science Statement on Current Scientific Understanding of the Processes Affecting Terrestrial Carbon Stocks and Human Influences Upon Them. IPCC, Geneva.

Aubinet M, Grelle A, Ibrom A et al. (2000) Estimates of the annual net carbon and water exchange of forests: the EUROFLUX methodology. Advances in Ecological Research, 30, 113–175.

Baldocchi DD, Falge E, Gu L et al. (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 American Meteorologocal Society, 82, 2415–2434.

Baldocchi DD, Valentini R, Running SW et al. (1996) Strategies for monitoring and modeling CO_2 and vapor fluxes over terrestrial ecosystems. Global Change Biology, 2, 159–168.

Baldocchi DD, Wilson KB (2001) Modeling CO_2 and water vapor exchange of a temperate broadleaved forest across hourly to decadal time scales. Ecological Modelling, 142, 155–184.

Barford CC, Wofsy SC, Goulden ML et al. (2001) Factors controlling long- and short-term sequestration of atmospheric CO_2 in a mid-latitude forest. Science, 294, 1688–1691.

Barr AG, Black TA, Hogg EH *et al.* (2004) Long-term carbon diozide fluxes from a very tall tower in a northern forest: flux measurement methodology. *Journal of Atmospheric and Oceanic Technology*, **18**, 529–542.

Berger BW, Davis KJ, Bakwin PS *et al.* (2001) Long-term carbon dioxide fluxes from a very tall tower in a northern forest: flux measurement methodology. *Journal of Atmospheric and Oceanic Technology*, **18**, 529–542.

Black TA, Chen WJ, Barr AG *et al.* (2000) Increased carbon sequestration by a boreal deciduous forest in years with warm spring. *Geophysical Research Letters*, **27**, 1271–1274.

Black TA, den Hartog G, Neumann HH *et al.* (1996) Annual cycles of water vapor and carbon dioxide fluxes in and above a boreal forest. *Global Change Biology*, **2**, 219–229.

Burke IC, Lauenroth WK, Parton WJ (1997) Regional and temporal variability in aboveground net primary productivity and net N mineralization in grasslands. *Ecology*, **78**, 1330–1340.

Chen JM, Falk M, Euskirchen E *et al.* (2002) Biophysical controls of carbon flows in three successional Douglas-fir stands based on eddy-covariance measurements. *Tree Physiology*, **22**, 169–177.

Churkina G, Tenhunen J, Thornton PE *et al.* (2003) Analyzing the ecosystem carbon dynamics of four European coniferous forest using a biogeochemistry model. *Ecosystems*, **6**, 168–184.

Falge E, Baldocchi D, Olson R *et al.* (2001) Gap filling strategies for defensible annual sums of net ecosystem exchange. *Agricultural and Forest Meteorology*, **107**, 43–69.

Falge E, Baldocchi DD, Tenhunen J *et al.* (2002) Seasonality, ecosystem respiration and gross primary production as derived from FLUXNET measurements. *Agricultural and Forest Meteorology*, **113**, 53–74.

Goulden ML, William MJ, Fan S-M *et al.* (1996) Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. *Science*, **271**, 1576–1578.

Goulden ML, Wofsy SG, Harden JW *et al.* (1998) Sensitivity of boreal forest carbon balance to soil thaw. *Science*, **279**, 214–217.

Granier A, Ceschia E, Damesin C *et al.* (2000) The carbon balance of a young beach forest. *Functional Ecology*, **14**, 312–325.

Gurney KR, Law RM, Denning AS *et al.* (2002) Towards robust regional estimates of CO_2 sources and sinks using atmospheric transport models. *Nature*, **415**, 626–630.

Gutman G (1999) On the use of long-term global data of land reflectances and vegetation indices derived from the AVHRR. *Journal of Geophysical Research*, **104**, 6241–6255.

Hagen SC, Braswell BH, Frolking SE *et al.* (2002) Determination of sub-pixel fractions of non-forested area in the Amazon using multi-resolution satellite data. *Journal of Geophysical Research*, **107**, 8049.

Hollinger DY, Goltz SM, Davidson EA *et al.* (1999) Seasonal patterns and environmental controls of carbon dioxide and water vapor exchange in an ecotonal boreal forest. *Global Change Biology*, **5**, 891–902.

Huete AR, Liu HQ, Batchily K *et al.* (1997) A comparison of vegetation indices over a global set of TM images for EOS-MODIS. *Remote Sensing of Environment*, **59**, 440–451.

Jenkins JP, Braswell BH, Frolking SE *et al.* (2003) Detecting and predicting spatial and interannual patterns of temperate forest springtime phenology in the eastern U.S. *Geophysical Research Letters*, **29**, 54–56.

Kaufman L, Rousseeuw PJ (1990) *Finding Groups in Data: An Introduction to Cluster Analysis*. John Wiley & Sons Inc, New York.

Knohl A, Schulze ED, Kolle O *et al.* (2003) Large carbon uptake by unmanaged 250-year-old deciduous forest in Central Germany. *Agricultural and Forest Meteorology*, **118**, 151–167.

Lai C-T, Katul G, Butnor J *et al.* (2002) Modelling night-time ecosystem respiration by a constrained source optimization method. *Global Change Biology*, **8**, 124–141.

Law BE, Falge E, Baldocchi DD *et al.* (2002) Carbon dioxide and water vapor exchange of terrestrial vegetation in response to environment. *Agricultural and Forest Meteorology*, **113**, 97–120.

Law BE, Goldstein AH, Anthoni PM *et al.* (2001a) CO_2 and water vapor exchange by young and old ponderosa pine ecosystems during a dry summer. *Tree Physiology*, **24**, 299–308.

Law BE, Thornton PE, Irvine J *et al.* (2001b) Carbon storage and fluxes in ponderosa pine forests at different developmental stages. *Global Change Biology*, **7**, 755–777.

Law BE, Williams M, Anthoni PM *et al.* (2000) Measuring and modeling seasonal variations of carbon dioxide and water vapor exchange of a *Pinus ponderosa* forest subject to soil water deficit. *Global Change Biology*, **6**, 613–630.

Lieth H (1975) Modeling primary productivity of the world. In: *Primary Productivity of the Biosphere*, **Vol. 14** (eds Lieth H, Whittaker RH), pp. 237–263. Springer-Verlag, New York.

Lindroth A, Grelle A, Moren AS (1998) Long-term measurements of boreal forest carbon balance reveal large temperature sensitivity. *Global Change Biology*, **4**, 443–450.

Malhi Y, Baldocchi DD, Jarvis P (1999) The carbon balance of tropical, temperate and boreal forests. *Plant Cell and Environment*, **22**, 715–740.

Markkanen T, Rannik Ü, Keronen P *et al.* (2001) Eddy covariance fluxes over a boreal Scots pine forest. *Boreal Environment Research*, **6**, 65–78.

Menzel A (2003) Plant phenological anomalies in Germany and their relation to air temperature and NAO. *Climatic Change*, **57**, 243–263.

Meyers TP (2001) A comparison of summertime water and CO_2 fluxes over rangeland for well watered and drought conditions. *Agricultural and Forest Meteorology*, **106**, 205–214.

Moncrieff JB, Mahli Y, Leuning R (1996) The propagation of errors in long-term measurements of land–atmosphere fluxes of carbon and water. *Global Change Biology*, **2**, 231–240.

Monson RK, Turnipseed A, Sparks JP *et al.* (2002) Carbon sequestration in a high-elevation, subalpine forest. *Global Change Biology*, **8**, 459–478.

Myneni RB, Dong J, Tucker CJ *et al.* (2001) A large carbon sink in the woody biomass of Northern forests. *Proceedings of the National Academy of Sciences USA*, **98**, 14784–14780.

Myneni RB, Keeling CD, Tucker CJ *et al.* (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, **386**, 698–702.

Pilegaard K, Hummelshoej P, Jensen NO *et al.* (2001) Two years of continuous CO_2 eddy-flux measurements over a Danish beech forest. *Agricultural and Forest Meteorology*, **107**, 29–41.

Potter CS, Wang S, Nokolov NT *et al.* (2001) Comparison of boreal ecosystem model sensitivity to variability in climate and forest site parameters. *Journal of Geophysical Research*, **106**, 33671–33675.

Rahman AF, Gamon JA, Sims DA *et al.* (2003) Optimum pixel size for hypospectral studies of ecosystem function in southern California chaparral and grassland. *Remote Sensing of Environment*, **84**, 192–207.

Royer DL, Osborne CP, Beerling DJ (2003) Carbon loss by deciduous trees in a CO_2-rich ancient polar environment. *Nature*, **424**, 60–62.

Running SW, Thornton PE, Nemani RR *et al.* (2000) Global terrestrial gross and net primary productivity from the Earth observing system. In: *Methods in Ecosystem Science* (eds Sala OE, Jackson RB, Mooney HA, Howarth RW), pp. 44–57. Springer-Verlag, New York.

Schimel DS, Braswell RH, Parton WJ (1997) Equilibration of the terrestrial water, nitrogen, and carbon cycles. *Proceedings of the National Academy of Sciences*, **94**, 8280–8283.

Schimel DS, Kittel TGF, Running SW *et al.* (2002) Carbon sequestration studies in Western US Mountains. *Eos, Transactions, American Geophysical Union*, **83**, 445–449.

Suyker A, Verma S (2001) Year-round observations of the net ecosystem exchange of carbon dioxide in a native tallgrass prairie. *Global Change Biology*, **7**, 279–289.

Thornton PE, Law BE, Gholz HL *et al.* (2002) Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. *Agricultural and Forest Meteorology*, **113**, 185–222.

Tucker CJ (1979) Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sensing of Environment*, **8**, 127–150.

Valentini R (2003) *Fluxes of carbon, water and energy of European forests.* Springer Verlag, Berlin.

Valentini R, Mateucci G, Dolman AJ *et al.* (2000) Respiration as the main determinant of carbon balance in European forests. *Nature*, **404**, 861–865.

Vesala T, Haataja J, Aalto P *et al.* (1998) Long-term field measurements of atmosphere–surface interactions in boreal forest combining forest ecology, micrometeorology, aerosol physics and atmospheric chemistry. *Trends in Heat, Mass and Momentum Transfer*, **4**, 17–35.

White MA, Nemani RR (2003) Canopy duration has little influence on annual carbon storage in the deciduous bread leaf forest. *Global Change Biology*, **9**, 967–972.

White MA, Running SW, Thornton PE (1999) The impact of growing-season length variability on carbon assimilation and evapotranspiration over 88 years in the eastern US deciduous forest. *International Journal of Biometeorology*, **42**, 139–145.

White MA, Thornton PE, Running SW (1997) A continental phenology model for monitoring vegetation responses to interannual climatic variability. *Global Biogeochemical Cycles*, **11**, 217–234.

Xiao X, Braswell RH, Zhang Q *et al.* (2003) Sensitivity of vegetation indices to atmospheric aerosols: continental-scale observations in Northern Asia. *Remote Sensing of Environment*, **84**, 385–392.

Xiao X, Hollinger DY, Aber JD *et al.* (2004) Satellite-based modeling of gross primary production in an evergreen needleaf forest. *Remote Sensing of Environment*, **89**, 519–534.