

# Influence and predictive capacity of climate anomalies on daily to decadal extremes in canopy photosynthesis

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**Abstract** Significant advances have been made over the past decades in capabilities to simulate diurnal and seasonal variation of leaf-level and canopy-scale photosynthesis in temperate and boreal forests. However, long-term prediction of future forest productivity in a changing climate may be more dependent on how climate and biological anomalies influence extremes in interannual to decadal variability of canopy ecosystem carbon exchanges. These exchanges can differ markedly from leaf level responses, especially owing to the prevalence of long lags in nutrient and water cycling. Until recently, multiple long-term (10+ year) high temporal frequency (daily) observations of canopy exchange were not available to reliably assess this claim. An analysis of one of the longest running North American eddy covariance flux towers reveals that single climate variables do not adequately explain carbon exchange anomalies beyond the seasonal timescale. Daily to weekly lagged anomalies of photosynthesis positively autocorrelate with daily photosynthesis. This effect suggests a negative feedback in photosynthetic response to climate extremes, such as anomalies in evapotranspiration and maximum temperature. Moisture stress in the prior season did inhibit photosynthesis, but mechanisms are difficult to assess. A complex interplay of integrated and lagged productivity and moisture-limiting factors indicate a critical role of seasonal thresholds that limit growing season length and peak productivity. These results lead toward a new conceptual framework for improving earth system models with long-term flux tower observations.

**Keywords** Eddy covariance · Canopy photosynthesis · Spectral analysis · Carbon cycle

## Introduction

Every year in modern times, photosynthetic organisms on land and in the ocean assimilate around 120,000,000,000,000 kg of carbon dioxide from the atmosphere, a process which drives the entire cycle of biosphere metabolism, production, and decomposition (Beer et al. 2010). Variation of photosynthetic rates across space is strongly a function of adaptation of species to climatic, geological, and biological limiting factors of temperature, light, soil nutrients, moisture, disturbance, and competition. These adaptations are often manifested in differences in plant functional form, such as leaf shape, leaf longevity, tree heights, root depths, etc. Similarly, variation of photosynthesis in time is governed by how species in an ecosystem respond and adapt to diurnal, seasonal, and inter-annual changes in limiting factors.

Today, society faces a grand challenge as feedbacks between carbon dioxide uptake by photosynthetic organisms and the climate system are a leading source of uncertainty in the magnitude and severity of future climatic change, on the same order as scenarios of future anthropogenic emissions and aerosol or cloud feedbacks (Booth et al. 2012). Coupled carbon-climate models show a large range of future climate states depending on assumptions built into models about biospheric uptake, particular in the terrestrial biosphere (Friedlingstein et al. 2006). Extreme interannual anomalies in biospheric uptake have been linked to large-scale climate features like El Niño Southern Oscillation (ENSO), and recent increasing trends in the fraction of fossil fuel emissions that remain in the atmosphere point to troubling

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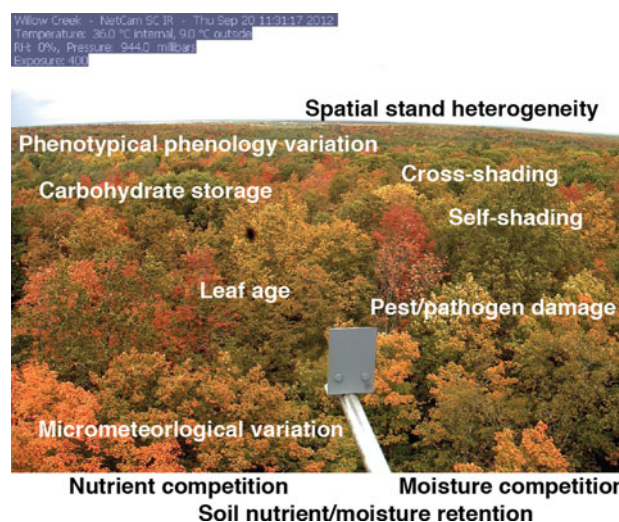
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concerns about the state of the biospheric carbon sink (Le Quéré et al. 2009).

Quantifying these variations and improving predictive ecosystem models at the scale of regions to the globe over time periods of days to decades requires careful lab experimentation and long-term field observations (Moorcroft 2006). Early experiments in the late 1970s and into the 1980s that included careful monitoring of leaf photosynthesis and isotopic discrimination in controlled environments along with theoretical thermodynamic and biochemical arguments led to the first successful representation of leaf photosynthesis through the simplified equations for C3 (and later C4) assimilation as reviewed in Farquhar and Sharkey (1982) and co-occurring development of leaf-atmosphere canopy conductance coupling as reviewed in Collatz et al. (1991). While major advances have been made on understanding the biochemistry of photosynthesis at the genomic, cellular, and leaf level, many reported in this journal, most of these have not significantly altered these equations and similar formulations that are prevalent in most sophisticated ecosystem models (Schaefer et al. 2012).

The reason for the lack of more sophisticated leaf-level photosynthesis models is partly a question of computational resources in that models can not simulate every leaf in an ecosystem, let alone every cell. But a larger source of uncertainty rests in how one goes from the leaf-level model to an ecosystem patch or grid box. Early attempts focused on the issue of scaling of canopy radiative transfer, given that the variation of light through a canopy is the dominant mode of variability of limiting factors within an ecosystem patch to be simulated. Original models include the “big-leaf” representation of the average semi-transparent leaf (e.g., Sellers 1985), partly owing its success to the ability to characterize vegetation fraction and photosynthesis through satellite remote sensing of visible and infrared canopy reflectance (Kumar and Monteith 1981). However, field observations noted that canopy radiative transfer may not necessarily scale so neatly (Baldocchi et al. 1985), leading to development of multiple canopy layer models (e.g., De Pury and Farquhar 1997). At the minimum, sunlit/shaded fractions of the canopy have to be treated separately in models for accurate simulation of photosynthesis (Sprintsin et al. 2012). More sophisticated models now allow for multiple cohorts of interactively competing and shading species with varying plant functional types (Medvigy et al. 2009).

The primary production model in most ecosystem models now consists of a leaf-level photosynthesis mechanism, embedded within a leaf boundary-layer coupling, leaf energy balance model, canopy-scaling algorithm, a soil water and humidity-sensitive transpiration model, and sometimes a nutrient transformation and transport model,



**Fig. 1** Examples of processes that affect photosynthesis in the environment that make canopy-scale photosynthesis differ from leaf-level photosynthesis, superimposed on a photo taken from an eddy covariance flux tower overlooking a temperate hardwood forest

primarily for nitrogen. Despite the apparent complete description of canopy photosynthesis, interactions, and small changes in parameters of these components cause ecosystem models to predict widely divergent estimates of the sensitivity of canopy photosynthesis to climatic and biotic changes, even when they’re using the same equations (Schaefer et al. 2012). Differences in parameters that control rates of leaf respiration, canopy architecture, or microclimate variation have large effects on canopy photosynthesis rates and sensitivity.

Uncertainties also arise in our understanding of variation in radiation quality and sun flecks, multiple interacting species, age-dependent changes in photosynthesis and transpiration, moisture and nitrogen availability in soil, transformation of assimilated carbon into storage pools, and canopy-scale stomatal and photosynthetic rate responses to atmospheric CO<sub>2</sub> enrichment (e.g., Fig. 1). Models tend to underestimate variability in canopy photosynthesis in response to climatic anomalies, but overestimate threshold responses to climate and biospheric state shifts. On the one hand, ecosystems, as an assemblage of species, and hence composed of species that are adapted to have compensating responses to environmental change are more conservative than the single “model” species represented by the typical plant functional type approach in models. On the other hand, overall ecosystem variance is large and since species present on the landscape are partly a function of local climate and soils, they may show additive effects in response to climate anomalies that exceed the threshold (i.e., an extreme).

Consequently, there is a role for long-term canopy-scale observations of photosynthesis toward evaluating and

improving these kinds of model responses. The rise of canopy-scale observations of net ecosystem exchange of CO<sub>2</sub> (NEE) and inference of gross primary productivity (GPP) through tower-based eddy covariance methods (Baldocchi 2008) and other canopy-scale experiments have expanded our ability to make claims of model fidelity and sensitivity. For example, recent articles have focused on dryness (Yi et al. 2010), temperature (Niu et al. 2012), light response (Schaefer et al. 2012), phenology (Richardson et al. 2012), short-term climate fluctuations (Medvigy et al. 2010), interannual variations (Keenan et al. 2012a), disturbance (Amiro et al. 2010), and CO<sub>2</sub> enrichment (Norby and Zak 2011). Still, many of these studies are limited by short time series at most sites. Advanced methods to link anomalies of environmental drivers to fluxes have only been applied in limited cases.

In this manuscript, I focus on the value of longer-term observations of high-frequency photosynthetic flux observations at the canopy scale. Are there effects of lagged environmental drivers that are masked at shorter time scales? Can ecosystem adaptation and community reorganization responses from extremes be detected? Hypotheses have been put forward suggesting that canopy-scale productivity may be linked to prior season carbon storage of non-structural or labile carbohydrates (Carbone et al. 2007) and also antecedent moisture availability in mesic forests (Ricciuto et al. 2008; Desai et al. 2010). These lagged responses would not be seen at the leaf level, where direct controls of moisture availability and leaf carbon content influence photosynthesis strongly by limiting rates of light harvesting and total leaf area.

The purpose of the analysis here is not to put forth brand new models of canopy photosynthesis, but rather to highlight the path forward with long-term observations. As such, my goals are twofold: (1) to demonstrate advanced statistical methods to evaluate modes of variation of long-term environmental data and (2) observe how these methods provide new insight into lags and switches of canopy photosynthesis that make it so hard to model and so different from leaf-level responses. In particular, I use a 15-year record of regional NEE from a very tall tower in the north central US to test which of antecedent soil moisture availability and prior productivity most influence canopy productivity. Moisture lags likely represent the accumulation and storage of available water that allows a canopy to respond to periods of high water demand or physiological stress. Similarly, prior carbon accumulation influences current carbon uptake both in changes in allocation and development of carbohydrate reserves. Can these effects be seen in observations and if so, which is the most relevant to include in models?

I hypothesize that short-term (daily) drivers of photosynthesis are primarily light and temperature, but longer-

term (weekly to annual) is limited primarily by moisture and internal storage of prior photosynthate. These hypotheses are tested against the landscape-scale observations of net carbon uptake and associated surface and meteorological forcing.

## Methods

### Analysis framework

Many of the analyses described in the prior section attempted to use many short-term (2–5 year) ecosystem flux observations to improve prediction or modeling by substituting space for time (e.g., Yi et al. 2010). Many sites each with a few years of data are analyzed to make inferences about long-term evolution of biosphere to climate and environmental drivers. However, there is some evidence that predictions made in this form across sites do not necessarily map well onto long-term predictions at a single site (Desai 2010; Keenan et al. 2012a). The limiting factor is the lack of long-term high-frequency observation of the state of the biosphere.

Short-term measurements are difficult to use for diagnosing anomalies and extremes. Short-term multi-site studies can diagnose mean state and mean variability of carbon fluxes, but may underestimate the true level of variability over years and how extremes in climate and biotic disturbance (including both large short-term pulse and long-term press (steady pressure) disturbances) can drive carbon assimilation differently than short-term responses. For example, many eddy covariance flux tower studies focus on a few years of data to identify particular climate responses (e.g., wet versus dry year), but are likely to have confounded co-variability among climate factors, to miss multi-year responses, or have low probability of capturing extreme climate events and the role of pre-conditioning of ecosystem states. Community-scale response from changes in resource availability and competitive advantages to these can occur in forest ecosystems at timescales of years to decades (Gellesch et al. 2013).

While some processes like photosynthetic acclimation have been well captured in lab experiments, they are harder to diagnose with short-term environmental data, even with a decade long record from enriched CO<sub>2</sub> experiments (Norby and Zak 2011). The statistical sample for environmental observations of low probability, high impact events is too small.

A benefit of an evolving measurement network is that over time there are sites that start having long records where one can look closely at features like memory effects (long-lag relationships), decadal trends, and state shifts that would not be easily noted across space. Instead, the

challenge is addressing the data deluge. A decade long flux tower record of half-hourly NEE observations and related climate drivers can easily exceed  $10^6$  observations. Moreover, the data are strongly auto-correlated and may suffer from harmonization issues related to changes in instruments, measurement height, and so forth. As a consequence, many analyses, even at long-term tower sites, limit their analyses to subsets of the data. For example, Keenan et al. (2012b) found no suitable combination of parameters of a simple model could adequately explain three separate 5-year periods in NEE observed over the 18-year record at Harvard forest.

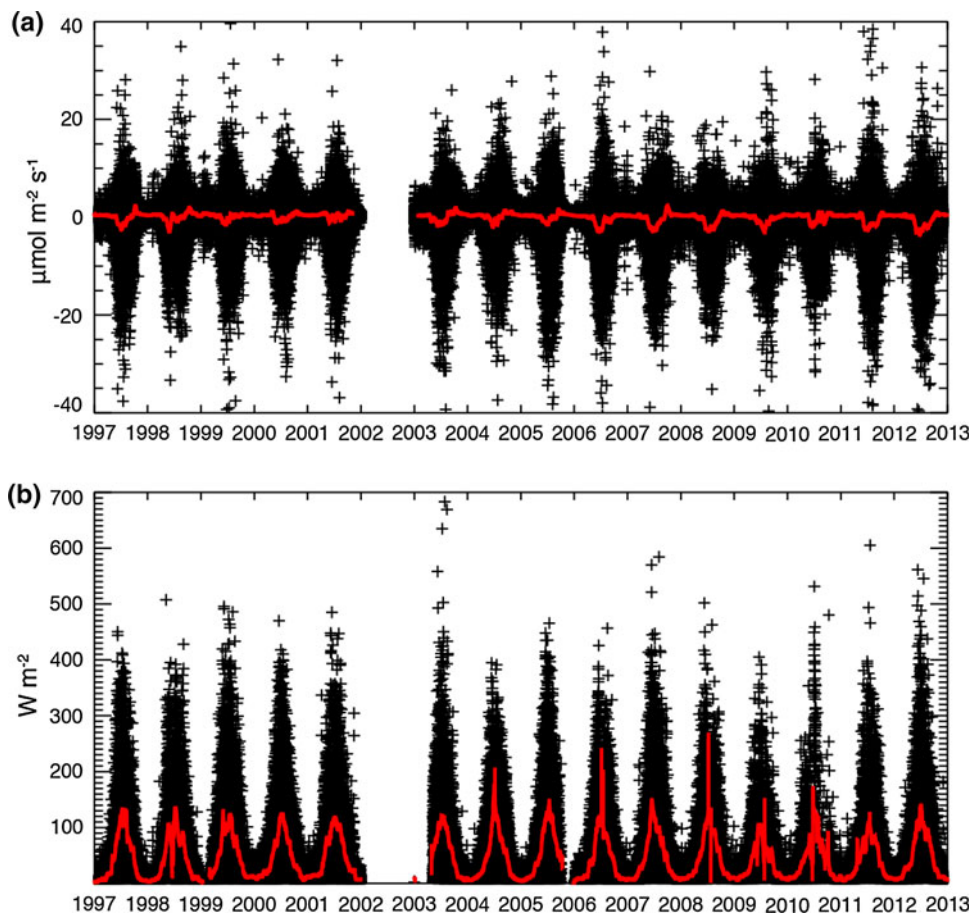
There is ongoing work on improving harmonization of long-term datasets like decadal eddy covariance and the evolving National Ecological Observatory Network (NEON), which will include nearly 60 sites across North America with eventually 30+ years of carbon cycle and biological observations. These observations provide a suitable data tested if and only if the community first develops reliable and usable statistical metrics and model-data evaluation. Therefore, in this study, I specifically focus on the more than 15-year record of eddy covariance carbon and water regional flux observations at a forested site in the north central US (Figs. 2, 3).

#### Site description and data

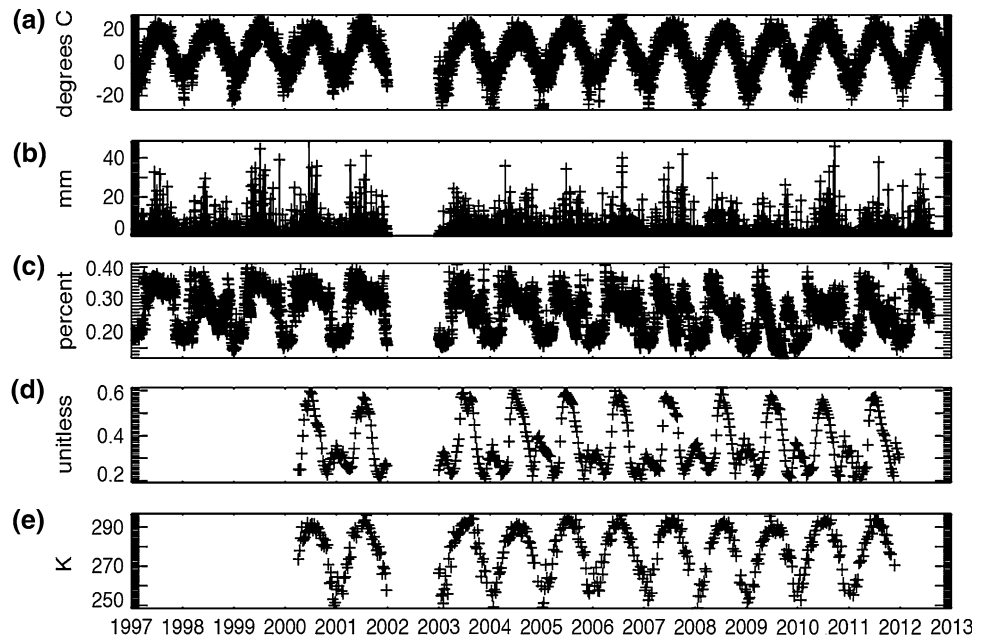
I analyzed 15-years of flux tower observations of  $\text{CO}_2$  and  $\text{H}_2\text{O}$  flux from one of the longest continuously running eddy covariance flux towers in the U.S., the WLEF Park Falls tower (US-PFa) (Davis et al. 2003), where fluxes have been measured since late 1996 with minimal disruptions, except in 2002 (Fig. 2). Meteorological variables were also observed at the site (Fig. 3; Table 1). WLEF is unique for being the tallest flux tower across the Fluxnet network, allowing us to observe the impact of patchy landscapes and canopy interactions on carbon assimilation. My collaborators and I have observed fluxes at three heights (30, 122, 396 m) and use these to develop a single “preferred” flux product (Davis et al. 2003), based on boundary-layer turbulence conditions. The tower samples a fetch on the order of 1–5 km depending on atmospheric stability and wind speed.

Unlike canopy-scale towers, tall-towers sample fluxes that represent many species and many soil types. However, an advantage of these observations is they are at a similar scale to that which ecosystem models represent canopies and plant functional types (10–100 s of km). Schaefer et al. (2012) noted that ecosystem model estimates of daily GPP were surprisingly well simulated at this site in a large flux

**Fig. 2** Nearly 15-year time series of **a** net ecosystem exchange of  $\text{CO}_2$  (NEE), and **b** evapotranspiration flux (ET) at hourly (black crosses) and biweekly (red line) timescales as observed from the WLEF Park Falls, WI very tall eddy covariance flux tower from 1997 to 2012. Long-term datasets like these on canopy-scale carbon and water fluxes are starting to be made available in the eddy covariance community. The large variability at multiple timescales presents a significant opportunity and challenge for improving predictions of ecosystem fluxes



**Fig. 3** Time series of daily **a** air temperature ( $T_{air}$ ), **b** precipitation ( $P_{recip}$ ), **c** soil moisture ( $Q_{soil}$ ) and biweekly, **d** MODIS-enhanced vegetation index (EVI), and **e** MODIS land surface temperature (LST). To allow comparisons to the quality-controlled flux data, 2002 was also removed from these data



**Table 1** Abbreviations used in this paper

Abbreviation	Description	Source
NEE	Net ecosystem exchange of CO <sub>2</sub>	Flux tower
GPP	Gross primary production	Flux tower
$P_d$	Photosynthetic drawdown	Flux tower
EVI	Enhanced Vegetation Index, 8-day average	MODIS TERRA/AQUA
ET	Evapotranspiration	Flux tower
WUE	Water use efficiency ( $P_d/ET$ )	Flux tower
$P_{recip}$	Daily precipitation	NCDC + NARR reanalysis
$Q_{soil}$	10 cm soil moisture	NARR reanalysis
$T_{mean}$	Daily temperature	Flux tower + NCDC
$T_{min}$	Minimum daily temperature	Flux tower + NCDC
$T_{max}$	Maximum daily temperature	Flux tower + NCDC
$T_{range}$	Daily temperature range (max–min)	Flux tower + NCDC
LST	Land surface temperature, 8-day day/night average	MODIS TERRA/AQUA

tower-model intercomparison of GPP, either because modelers have used this site significantly for calibration, or, that the fluxes better represent the “model organism” being represented by the single plant functional types used in most models.

The site samples carbon and water fluxes from a temperate mixed forest landscape that consists of approximately 3/4 forest equal parts young to intermediate age commercially harvested aspen, mature northern hardwood (sugar maple, ash, basswood), and red pine plantations (Desai et al. 2007). The remaining 1/4 is primarily a mosaic

of wetlands and shrub areas, including black spruce and peat bogs, cedar swamps, sedge wetlands, and shrub fens. Spatial variability occurs in relatively small scales, driven by microtopography and land management, while the overall landscape topography is flat and density of human settlement in the tower footprint is minimal.

#### Estimating canopy-scale photosynthesis

Eddy covariance towers observe the *net* exchange of trace gases, heat, and momentum from the surface to atmosphere, based on well-established micrometeorological theory (Baldocchi 2008). Turbulence properties of the atmospheric surface layer allows one to take the 30–60 min mean covariance of high-frequency (>10 Hz) observations of vertical wind and the flux tracer of interest (e.g., carbon dioxide, water, temperature) summed with below-sensor net tracer storage and vertical flux divergence to represent the net surface flux. Sonic anemometry (measuring vertical and horizontal wind components with sound pulses) and infrared gas analyzers sampling air near the anemometer are typically used to measure this net covariance. Contributions from low-frequency transport (advection) are usually neglected, but tend to be small, of the same magnitude as the 10–20 % inherent random flux error (Yi et al. 2000). Over the years, researchers have instrumented nearly 500 of these sites for carbon and water cycle observations and general quality control approaches have been identified for instrument noise, lag, and spectral corrections, coordinate geometry rotation for wind velocity, low turbulence screening, and other turbulence statistics, which are applied here (Berger et al. 2001; Foken et al. 2012).

The focus of this analysis of the effect of climate anomalies on photosynthesis, not net exchange (which includes respiration and decomposition processes). Therefore, I developed a method to represent this photosynthesis from net ecosystem exchange of CO<sub>2</sub> (NEE). Unfortunately, there is no single accepted method for doing so, and all require some level of empirical assumptions or statistical inference that partly takes advantage of the lack of GPP at night. Consequently, methods diverge on estimates of GPP by more than 20 % and can include artifacts from fitting NEE to respiration models (Desai et al. 2008).

Since I want to focus on the value of NEE to models, I developed an alternate metric of the effect of canopy photosynthesis on NEE, termed net photosynthetic drawdown ( $P_d$ ), a daily metric of canopy photosynthesis that removes assumptions used in many GPP models.  $P_d$  was estimated at a daily timescale from the hourly flux data as the difference in nighttime to daytime NEE. Maximum nighttime NEE was identified at night when more than 4 h of good observations were available. Maximum is used over mean since it has been shown to be closer to the advection corrected observations at night (Van Gorsel et al. 2009). This estimate of nighttime NEE is then differenced with the mean daytime gap-filled NEE between 10 and 14 local time if there are more than 4 h of good observations during that day (when the sun is up). Here I use gap-filled NEE to avoid biasing the mean NEE, which exhibits a strong diurnal cycle. Gap-filling errors tend to be much smaller than GPP uncertainty (Moffat et al. 2007). The  $P_d$  time series is shown in Fig. 4a. The  $P_d$  time series has 5,490 days of data, with 37 % of data missing.

Further analysis showed that use of  $P_d$  instead of GPP does not significantly change the results or conclusions of this study and presents a novel way to understand the effect of climate on photosynthesis. The correlation of  $P_d$  to GPP is high, particularly for maximum daily GPP ( $r^2 = 0.81$ ) and greater at the monthly timescale ( $r^2 = 0.96$ ). The fit is linear for GPP, with an intercept of 0 (Fig. 5). Since  $P_d$  is a detector of maximum daily photosynthetic uptake and has a greater dynamic range than GPP, it is likely that  $P_d$  is better at detecting extreme photosynthesis responses to climate anomalies. While this method is conceptually analog to atmospheric CO<sub>2</sub> “drawdown” (e.g., Desai et al., 2010), it is different as the flux drawdown does not include covariation with boundary-layer depth and represents a much smaller footprint.

#### Statistical analysis

I tested the hypotheses mentioned above by testing for both direct and lagged relationships between  $P_d$  and climate forcing factors (Table 1) at multiple time scales and compared them to the autocorrelation of  $P_d$ . A number of

studies have identified characteristic timescales of variability in flux data using wavelet, single spectrum, or Fourier time-series analysis (e.g., Baldocchi et al. 2001; Mahecha et al. 2007; Stoy et al. 2009), which have all noted characteristic peaks of variability in NEE especially at the diurnal, synoptic (3–4 day), seasonal, and interannual timescale. Similarly, frequency-dependent model-data comparisons (e.g., Dietze et al. 2011; Mahecha et al. 2010; Keenan et al. 2012a) have all found deficiencies of models in representing many of these modes of variability.

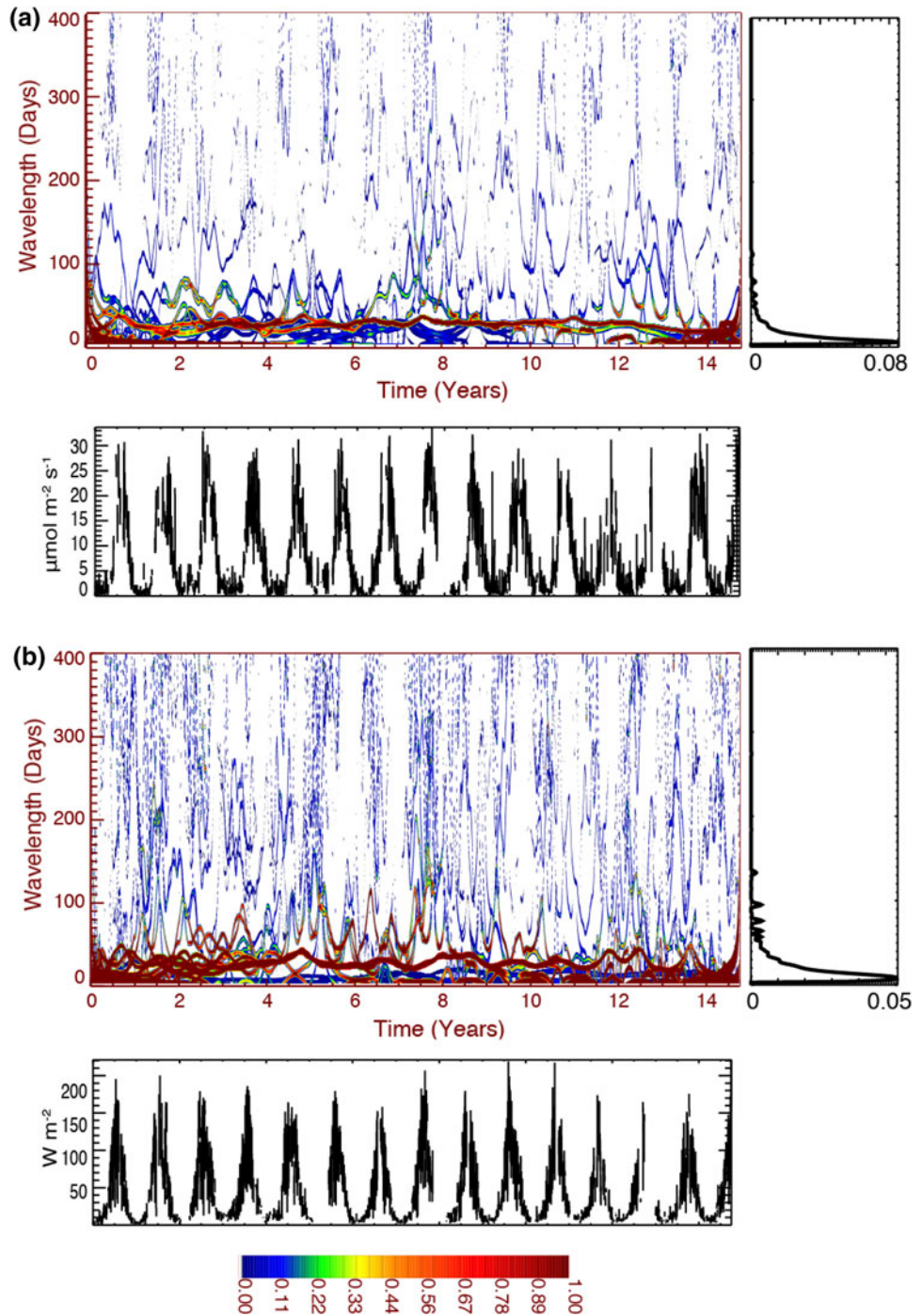
I identified these scales in daily  $P_d$  and evapotranspiration (ET) flux using a similar analysis of empirical model decomposition (EMD), whose results are fed into the Hilbert–Huang spectral transformation (HHT) (Huang and Wu 2008). EMD is an empirical approach to time series deconvolution that does not require assumptions of cyclical behavior (as needed by Fourier) or stationarity and does not require determination of the shape of the weighting kernel or wavelet. The discontinuous EMD (Barnhart et al. 2012) further extends the application to time series with missing data by applying a mirroring approach to fill the data gaps. EMD decomposes a time series into a series of intrinsic mode functions (IMF) also in the time dimension, which when fed to the HHT algorithm that outputs a time by frequency power spectrum.

Timescales for analysis were determined from the HHT of  $P_d$  and ET (Fig. 4). Both signals have a number of similar modes of variability, especially at the synoptic, monthly, and seasonal timescale. ET has greater temporal variations in these modes and greater signal on long-time scales (>100 days). Longer timescale variability is present in the growing season more than outside of it. HHT identified strong monthly peaks that were not previously identified and suggests that interannual variability explains less of the signal than other methods have previously shown (e.g., Baldocchi et al. 2001). Methodologically, I used this analysis to select averaging timescales of 1, 3, 8, 15, 30, 90, 180, 360, 720, and 1440 day, as described next.

The HHT analysis also identified the importance of normalizing variability across timescale to best identify climatic and internal controls on  $P_d$ . For example, there is a variety of literature that will show high correlation of GPP to other variables, solely because the main modes of variability (e.g., the annual solar cycle) are strong in both, not because one truly explains the other. This method of analysis is disingenuous when it comes to the question I seek to answer here.

One of the benefits of long-term data is the ability to remove much of this co-variability and look at how anomalies or extremes manifest themselves in the data and how they are correlated to anomalies or extremes in another variable. If a daily time series signal  $X(\text{day}, \text{year})$  is

**Fig. 4** Hilbert–Huang power spectral transformation of **a** net canopy carbon uptake ( $P_d$ ), and **b** daily evapotranspiration (ET) derived from empirical mode decomposition of the tall tower fluxes. Raw daily time series are shown below each transformation and marginal power spectrum on the right. To improve clarity of higher frequency variation, the transform is cut-off at 400-day wavelength. The time–frequency decomposition reveals that both carbon and water exchange exhibit a number of characteristic timescales of variability, including substantial peaks at the monthly and seasonal timescale. Longer-term variability is much weaker, especially for carbon, but growing season signals of variability on the 100–200 day wavelength exist and strong coherence among water and carbon are also noted



stationary (as it mostly appears to be in this case and discussed more in the discussion), then an anomaly time series  $X_{an}(\text{day}, \text{year})$  can be simply constructed by removing the ensemble mean:

$$X_{an}(\text{day}, \text{year}) = X(\text{day}, \text{year}) - \overline{X(\text{day})}_{\text{year}}, \quad (1)$$

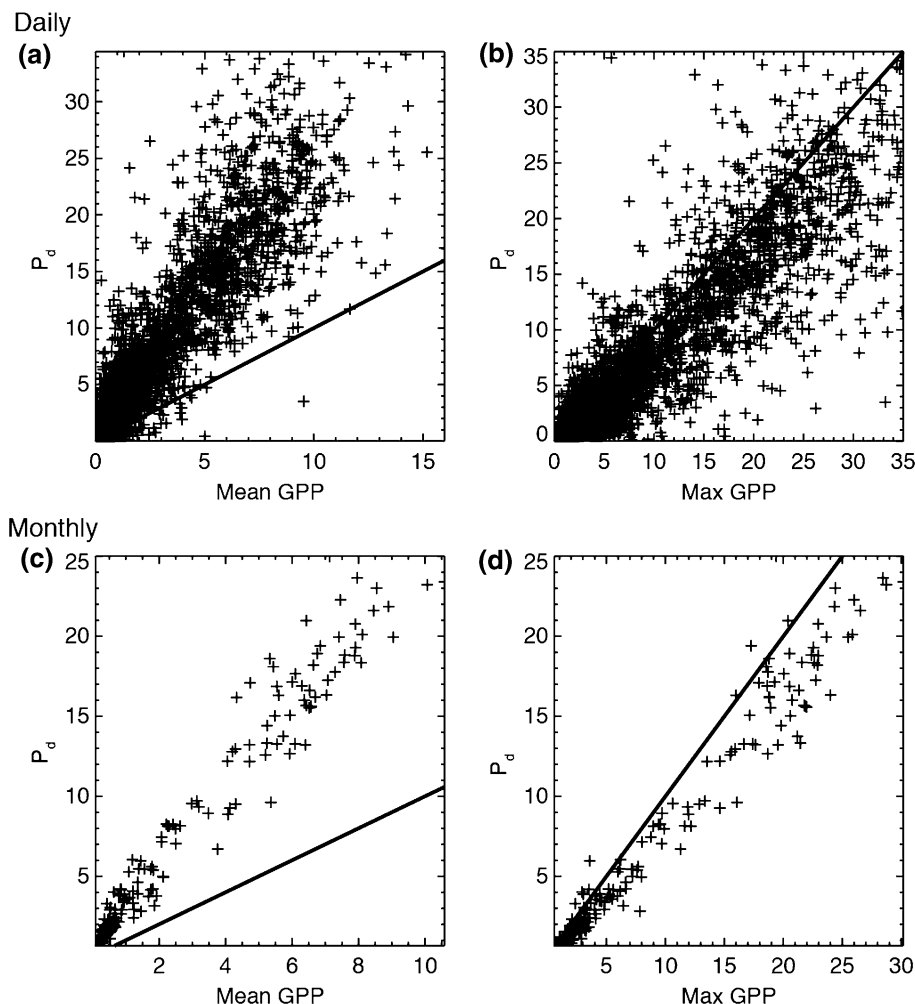
where  $X(\text{day})|_y$  is the daily time series of variable  $X$  ensemble averaged across all years. To test across multiple timescales, I applied a forward averaging filter across the

time series (e.g., Fig. 6b), avoiding forecasting by removing the end of the data series:

$$X_{an}(\text{day}, \text{year})|_{\text{timescale}} = \frac{1}{\text{timescale}} \sum_{t=\text{day}}^{t=\text{day}+\text{timescale}} X_{an}(t, \text{year}), \quad (2)$$

where timescale is the number of days to average. One issue that arises when analyzing this variable across seasonal to interannual timescales is the need for averages to

**Fig. 5** Scatterplot of flux tower-derived GPP (based on fit of nighttime NEE to temperature to estimate respiration) to  $P_d$  for **a** mean daily GPP, **b** maximum daily GPP, **c** mean monthly GPP, and **d** mean monthly maximum daily GPP. 1:1 fit line shown on all four and shows that  $P_d$  is closely related to maximum daily GPP. Correlation at daily scale is  $r^2 = 0.81$  and monthly  $r^2 = 0.96$



stay aligned with the solar orbital forcing cycle, so that averages in any 1 year can be comparable to other years. To do this, I reduced each year to 360 day length by removing the first few and last few days of data for each year and choosing averaging scales which share divisors with 360. The choice of timing has relatively minimal effect and the choice of winter, where carbon fluxes are near zero is ideal. A second issue involves gaps in the data. For gaps, I sampled the data with replacement, filling gaps linearly across small gaps (days) and taking long-term means for longer gaps (weeks).

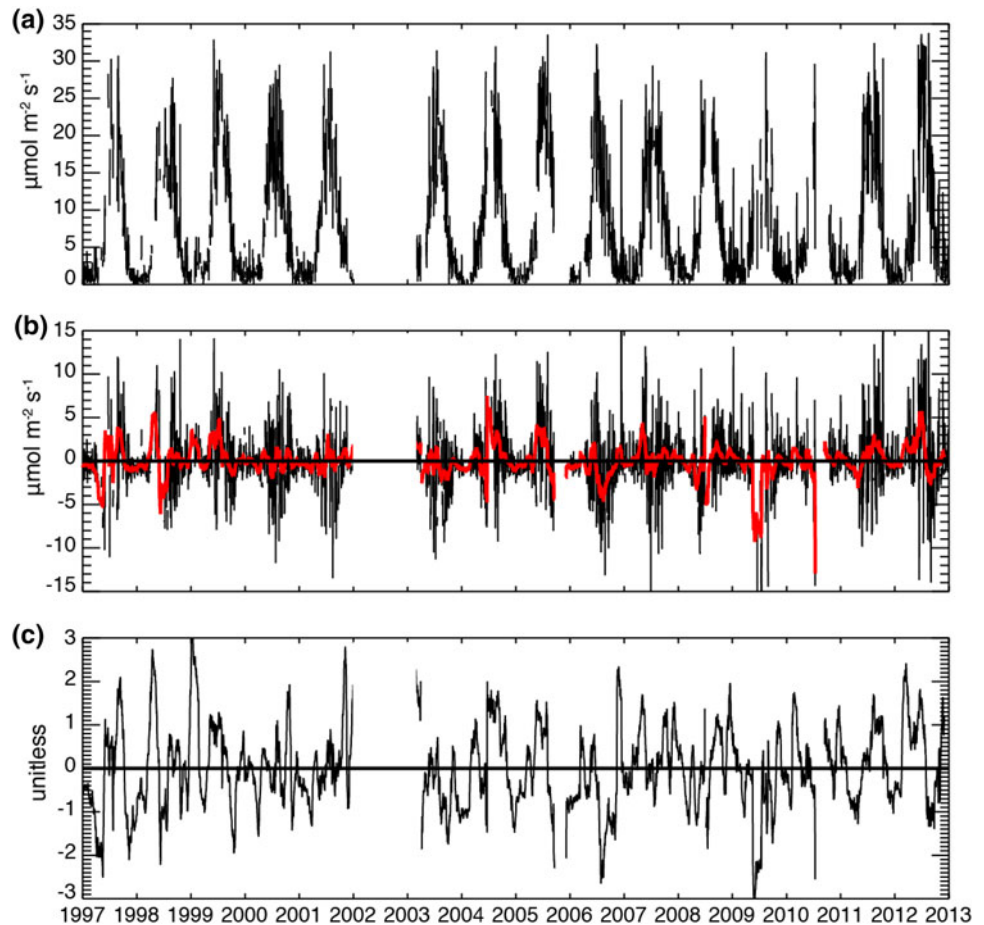
To remove the previously discussed solar forcing driven artificial correlation among variables, I normalized the time series. Flux anomalies (e.g., Fig. 6c) display a strong seasonality given the change in variability from winter to summer (Fig. 3). Relative anomalies  $X_{rel,an}(\text{day,year})|_{\text{timescale}}$  were derived from averaged anomalies by dividing the time series by the ensemble average standard deviation across all years for a given averaging timescale:

$$X_{rel,an}(\text{day, year})|_{\text{timescale}} = \frac{X_{an}(\text{day, year})|_{\text{timescale}}}{\sigma(X_{an}(\text{day, year})|_{\text{timescale}}|_{\text{year}}}. \tag{3}$$

The remaining time series appears stationary and random (Fig. 6c), and reflects a statistically defensible view of relative anomalies of the time series as a function of averaging filter. Relative anomalies in this fashion were computed for  $P_d$  (Fig. 6) and a variety of observations to test hypotheses including variables related to canopy physiology and structure such as remotely sensed vegetation index (EVI) and minimum, maximum, mean, and diurnal range of air temperature, remotely sensed land surface temperature (LST), and variables related to canopy moisture availability including ET, water use efficiency (WUE, GPP divided by ET), precipitation, and soil moisture, as noted in Table 1 and shown in Fig. 3. Remotely sensed variables were derived from the NASA MODIS TERRA and AQUA reflectance properties and downloaded from the ORNL MODIS land product subset server



**Fig. 6** Example of generating relative anomalies for lag-correlation analysis. Raw daily time series of **a** net photosynthetic drawdown ( $P_d$ ), were **b** de-seasonalized by removal of the ensemble average daily time series and then averaged to the appropriate averaging timescale, in this example, monthly (*red line*), and finally **c** normalized to relative values. The final signal represents the true anomalies of variation across time and has successfully removed the seasonal variability of solar forcing



(<http://daac.ornl.gov/MODIS/>), while other variables were directly observed by the tower with gaps filled from harmonized daily climate data downloaded from the National Climatic Data Center archive of National Weather Service co-operative observer stations and weather forecast reanalysis from the NOAA North American Regional Reanalysis (NARR).

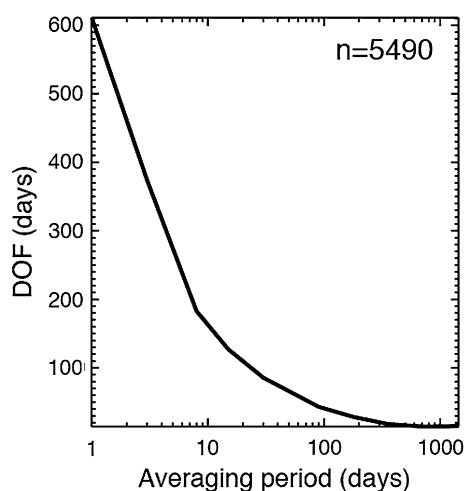
I compared relative anomalies of all variables to relative anomalies of  $P_d$  at all averaging timescales both with direct linear correlation and with lagged correlation where climate factors were lagged against  $P_d$  at a range of lags equivalent to the averaging timescales. A two-tailed  $t$  test for significance was applied to all correlation coefficients and only those coefficients that were significant at the 90 % level were saved.

The significance test was modified to account for the autocorrelation present in all environmental time series. Consequently, the degrees of freedom to apply to significance tests should be much smaller than the total number of samples. I reduced the degrees of freedom using a modified effective degrees of freedom (EDOF) approach of Bretherton et al. (1999):

$$N_* = \frac{N}{\sum_{t=N/2}^N \left[ \left(1 - \frac{t}{N}\right) \rho_t^X \rho_t^Y \right]}, \quad (4)$$

where  $N^*$  is the reduced degrees of freedom for significance testing of correlation of two time series  $X$  and  $Y$  with  $N$  samples.  $\rho_t^X$  represents the autocorrelation of time series  $X$  at lag  $t$ . Though most of the autocorrelation is in the first few lags, I included all lags to  $N/2$  to account for long-lead correlations. Further, only those correlations of variables to  $P_d$  that exceeded the lagged autocorrelation of  $P_d$  are used as a test to compare moisture versus carbon storage control as predictors of current  $P_d$ .

The EDOF of  $P_d$  (Fig. 7) reveals that while daily  $P_d$  has over 3400 observations, the EDOF at daily scale is only slightly above 600, and decreases nearly linearly with logarithmic increases in averaging timescale, such that interannual analysis is limited to EDOF in the few tens to single digits. As shown in the results, this limits the ability of this analysis to diagnose correlations of anomalies at multi-year timescales and highlights how even a 15 year time series may be unreliable for detecting interannual and longer trends and correlations. The results here shows that



**Fig. 7** Degree of freedom analysis for daily net photosynthetic drawdown from the tall tower fluxes. The total record has 5,490 observation periods (with 37 % of observations missing), but the full autocorrelation analysis reveals an exponentially declining true degree of freedom from slightly over 600 for no-averaging, to near zero above 360 day smoothing of the time series. This reduced  $N$  is used for all correlation significance tests

**Table 2** Granger causality analysis for  $P_d$  as a function of averaging period reveals best predictive models generally include temperature and transpiration observations for daily to weekly averages but precipitation, soil moisture, and water use efficiency for monthly time scales, primarily within the first or two lags

Variable/averaging period (days)	1	3	8	15	30	90	360
EVI						90	
$T_{\text{mean}}$	1	3	8				
LST	1	3					
ET	1–3	3	8				360
WUE	1–3	3		15–360			
$P_{\text{recip}}$							
$Q_{\text{soil}}$							

No variables could exceed  $P_d$  autoregression in explaining longer averaging scales (>30 days)

a few time series were able to meet significance threshold, but multi-year correlation analysis with flux tower data requires sufficiently long data sets because of high autocorrelation.

A second test was also applied for comparing predictive ability of variables against inherent autocorrelation of  $P_d$ , known as the Granger causality analysis (Detto et al. 2012). The method originated from economics, but has recently gained popularity in geophysical time series analysis. The analysis builds a multiple linear regression of lagged values of a time series  $X$  to predict current values of  $X$ . This regression is then compared iteratively to including an increasing number of lagged values of time series  $Y$  that are significantly (two-tailed  $t$  test at 90 % level) correlated to

$X$  to predict current values of  $X$ . When the new regression significantly improves upon (tested with an  $F$  test) the autocorrelation regression, those lags of  $Y$  are retained and the terminology is that  $Y$  “Granger causes”  $X$ , or prior values of  $X$  and  $Y$  at certain lags explains a significantly larger fraction of  $X$  than the prior values of  $X$  does by itself. A minor modification was made here to include the reduced degrees of freedom for significance testing and the replacement of the  $F$  test with the more empirical Akaike Information Criterion, which incorporates both the likelihood of the regression and penalties for number of parameters. Here, I tested Granger causality for all variables against  $P_d$  (Table 2).

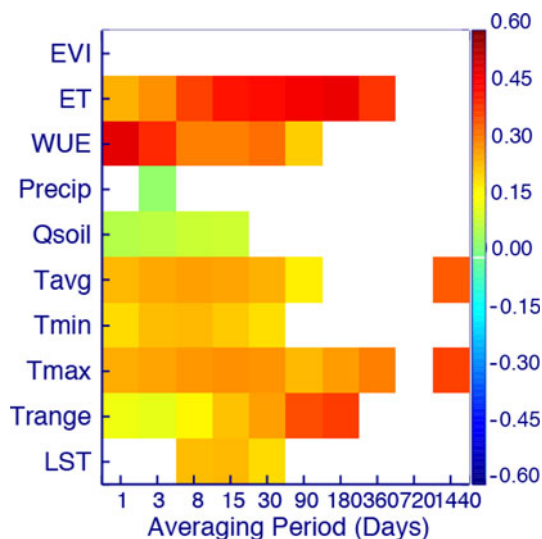
Though all these methods are relatively standard time series analysis, they have only recently been applied to carbon flux data, mostly because long-time series of flux data are only now becoming common. The results show how the lagged correlation, spectral, and causality analysis together provide insight on how canopy photosynthesis is different from leaf photosynthesis and how it can be leveraged to improve canopy photosynthesis models.

## Results

### Modes of variability in observations

Large variability exists in hourly flux data of NEE and ET (Fig. 2). Outliers exist in most years, but positive anomalies in ET and NEE decreased after 2005. Diurnal and seasonal variability dominate the signal and trends. The decrease in NEE uptake from 2006 to 2010 is visually evident, but difficult to discern quantitatively against the variability at the hourly scale (Desai et al. 2010). Not surprising, hourly data can be challenging when it comes to statistical data assimilation approaches to constraining ecosystem models (Zobitz et al. 2011), as these methods tend to force model parameters toward the dominant modes of variability (diurnal and seasonal) and limit excursions away from the mean (over-fitting the mean at the expense of the extremes) (Desai 2010) especially when data uncertainty is large, as it is the case for hourly flux observations (Raupach et al. 2005). Not surprisingly, models have great difficulty simulating other temporal modes of variability in photosynthesis (Dietze et al. 2011; Keenan et al. 2012a). Moreover, many of the anomalies of photosynthesis that are related to climate anomalies may exist only at longer timescales.

The EMD analysis directly shows the importance of weekly to seasonal variability in  $P_d$  and ET (Fig. 3), counter to previous wavelet-based analyses. For example, Baldocchi et al. (2001) found a spectral gap in flux tower NEE at the 3–4-week scale. The transformed data and the more empirical approach of HHT reveal that there are variations present at this scale,



**Fig. 8** Direct correlation coefficients of standardized anomalies of climate variables to net photosynthetic drawdown ( $P_d$ ) anomalies at daily to multi-year filter scales. Temperature variables explain a small fraction of weekly to monthly anomalies in  $P_d$ , while moisture variability explains a greater fraction of long-term seasonal variability in anomalies of  $P_d$ . Interestingly, remotely sensed vegetation index anomalies do not significantly explain  $P_d$  anomalies at any timescale

perhaps more so than at longer scales, and not consistently at a fixed value. Longer-term variability (90–360 day) is more present in the growing season (summer) and more distributed across frequency for ET compared to  $P_d$ , suggesting more coherence in interannual variability of ET than  $P_d$ .

#### Direct relationships

Given the range of variability in flux tower observations and a general overlap of modes of variability in ET and  $P_d$  anomalies at the daily to seasonal timescales, it should be expected that some level of correlation exists among these factors. The strongest direct linear significant correlations between ET and  $P_d$  anomalies exist at scales between 30 and 360 days, but persist down to 1 day, where ET explains around 10 % of the variability in  $P_d$  at short timescales and approaches 40 % at seasonal scales (Fig. 8). Longer-term correlations are not significant, but this may partly be the result of insufficient length of time series and the strict degree of freedom constraint. A similar level correlation is seen for WUE, but not at annual time scales. This correlation partly stems from self-correlation since GPP, which goes into the WUE calculation, and  $P_d$  are both derived from NEE.

Temperature is a well-known factor influencing leaf-level photosynthesis. Even though solar forcing leads to a strong correlation between temperature and NEE or GPP at diurnal and seasonal scales, when the ensemble average is removed and the variables compared as standardized anomalies, the relationship is much weaker, though it

remains significant from 1 day out to 30 day, with  $r$  around 0.15. None of the temperature factors (average, maximum, minimum, mean, range, or land surface temperature) are particularly better than others at explaining variation in  $P_d$ , though stronger correlations exist for maximum daily temperature especially at longer timescales, including a particular strong correlation at the 1,440 day scale. It should be noted that  $LST$  is provided at 8-day intervals, so 1 and 3 days average correlations are not included. For the purpose of the lag analysis, given similar relationships, only  $T_{\text{mean}}$  is further analyzed.

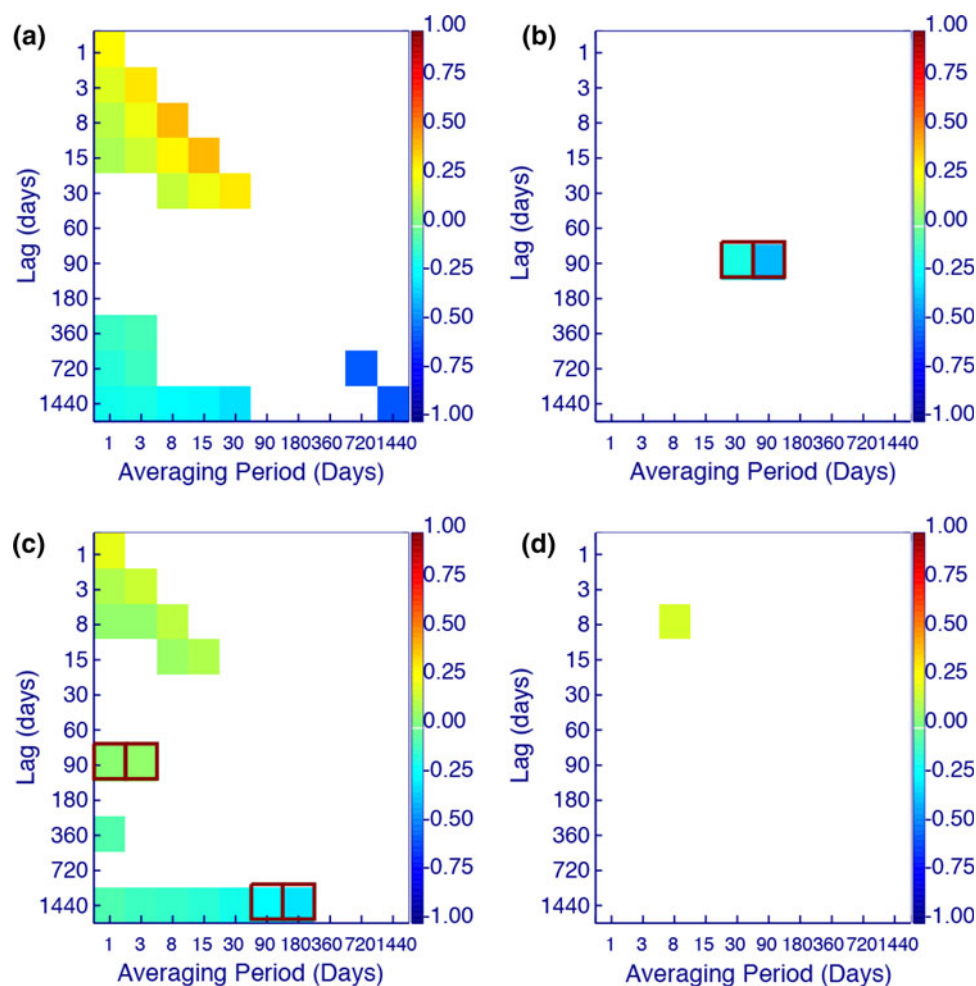
For direct correlation, the results are weaker for soil moisture than for temperature, but do provide some evidence to the importance of seasonal moisture budgets on net carbon assimilation, even in mesic forest/wetland systems. This result is partly consistent with an earlier model calibration study that showed interannual variability in NEE at WLEF was best explained by soil moisture (Ricciuto et al. 2008), but when lags are taken into account, the results change, as shown below. Though not shown, results with atmospheric humidity variables were similar to those of  $Q_{\text{soil}}$ . Precipitation anomalies only weakly  $P_d$  at 3-day averages. This result may be caused by the intermittent nature of precipitation, the greater error in short-term precipitation, and the importance of soil percolation processes prior to plant water uptake. Finally, EVI anomalies are found to have no correlation to  $P_d$  anomalies at any timescale.

#### Lagged analysis

Lagged analysis (Figs. 9, 10) further supports results shown in Fig. 8, but also reveals subtleties regarding moisture. The non-moisture-specific variables support both a strong autocorrelation of  $P_d$  as previously shown in Fig. 6 and lack of correlation at many timescales for EVI anomalies. Lagged EVI (Fig. 9b) does have some weak, but significant negative correlation to  $P_d$  for monthly averaging timescales and 3 month lag, and this correlation exceeds the autocorrelation. This signal represents both the impact of summer vegetation stress (low EVI) on autumn photosynthesis (reduced) (Wu et al. 2013) and the impact of phenology (late spring = low EVI) on net carbon uptake (reduced). Spring flush is typically a 2-week process and the growing season is around 3 months.

The autocorrelation of  $P_d$  (Fig. 9a) is persistent at AR-1 and AR-2 out to 30 days. For any given lag, some amount of autocorrelation exists for all averaging times up to the lag, increasing as the lag approaches the averaging timescale (i.e., AR-1). Some out of phase (180 day) negative correlation exists as it also does at the very long timescale (1,440 day), the latter of which is difficult to explain. At one level, ecosystem models incorporate this autocorrelation through the “memory effect” of labile carbon pools, but

**Fig. 9** Analysis of lagged standardized anomalies of **a**  $P_d$ , **b** EVI, **c**  $T_{\text{mean}}$ , and **d** LST to  $P_d$  at a range of averaging times and lag times. Only significant correlations are displayed, after correction of autocorrelated degrees of freedom. *Red squares* indicate significant correlations that exceed  $P_d$  autocorrelation at that averaging and lag scale. Strong AR-1 correlation persist in  $P_d$  at lags up to 1 month and averaging periods to 1 month, while small negative correlations show predictive ability for temperature at lags exceeding 1 year and EVI at the 2-month lag



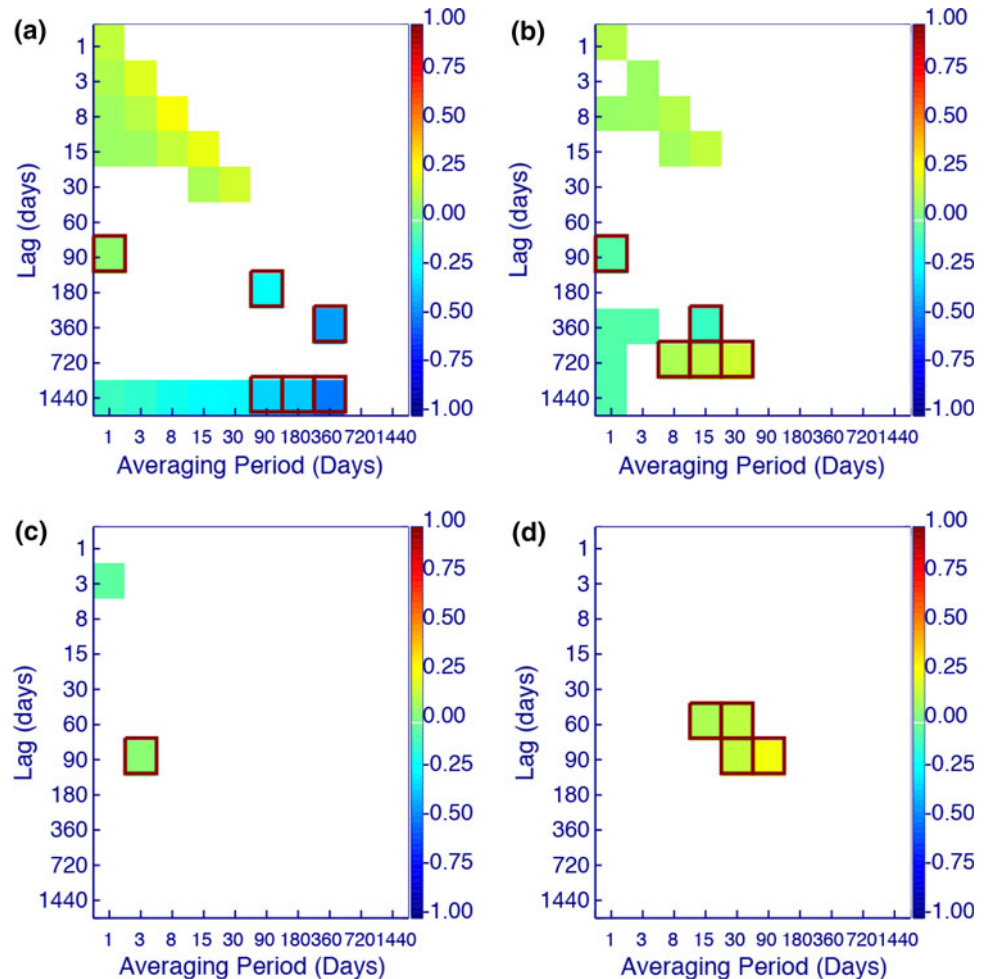
these are probably not responsible for the observed longer timescale correlations, possibly tied to other non-structural carbohydrate pools (e.g., Carbone et al. 2007) or signals of community reorganization, ecosystem dynamics, or climate oscillations. However, the lack of long autocorrelations in  $P_d$  do not provide much evidence here for strong long-term internal control through non-structural carbohydrates, shifts in plant allocation, or community reorganization.

Lagged temperature is predictive for  $P_d$  anomalies at short lags and averaging times out to a few weeks (Fig. 9c, d), with a positive correlation (warm anomalies lead to increased  $P_d$  1–2 weeks out), but these are much weaker than the autocorrelation. An interesting weak, but stronger than autocorrelation, relationship exists with 90-day prior daily mean temperature and current  $P_d$ , hinting at possible long-lag effects, where a short early season warm spell (e.g., false spring), can enhance growth. There is also a weak but significant negative relationship of seasonal average temperature from 4 years past, once again difficult to explain.

Moisture anomalies (ET, WUE,  $P_{\text{recip}}$ , and  $Q_{\text{soil}}$ ) also have some predictive ability for  $P_d$  anomalies and most all positive—increased ET or precipitation enhances carbon assimilation. Correlations of lagged ET to  $P_d$  (Fig. 9a) exist at short timescales and the first two lags for each timescale, but they are surprisingly weak compared to the strong direct correlation (Fig. 8). Similar to temperature, a 4-year lag negative correlation of ET on  $P_d$  is found for seasonal averaging.

Relationships also exist in weekly to seasonal average precipitation and soil moisture at the 2–3 month lag. Positive anomalies in soil moisture are more predictive for future weekly to seasonal  $P_d$  than  $P_d$  itself, suggesting a long-term moisture control. For example, early season weekly to seasonal moisture deficits inhibit end of season carbon assimilation. This effect is of slightly greater magnitude and correlation as the effect of direct moisture deficits on  $P_d$ . Unlike the direct correlation, these results more strongly support both the work of Ricciuto et al. (2008) and the second hypothesis of long-term moisture control on  $P_d$ .

**Fig. 10** Same as Fig. 9 but for moisture variables of **a** ET, **b** WUE, **c**  $P_{\text{recip}}$ , and **d**  $Q_{\text{soil}}$ . While ET and WUE have significant direct correlations as shown in Fig. 5, lagged correlations are small. Stronger positive correlations exist for precipitation and soil moisture at the weekly to seasonal timescale for seasonal scale lags



### Causality analysis

The findings of the Granger causality analysis (Table 2) are consistent with the lag analyses for most except the moisture variables. Daily to weekly temperature and ET both Granger cause  $P_d$ , with additional longer-term control by seasonal EVI and annual ET. Interestingly,  $Q_{\text{soil}}$  does not Granger cause  $P_d$  at any timescale. Only ET anomalies have predictive ability at long-time scales and highlights the difficulty of dissecting the causes of seasonal to interannual variability even with 15 years of flux tower data.

### Discussion

#### Role of lagged forcing in photosynthesis

Internal control (carbon assimilation rates related to prior carbon assimilation rates) is a strong predictor on canopy carbon assimilation at timescales up to a week, while the key direct climatic modifier of this are temperature and

available moisture, but primarily on longer timescales and longer lag times. Clearly, this differs from the primarily direct relationships one finds for leaf photosynthesis controls and highlights the complexity of modeling canopy photosynthesis and the value of long-term data.

The analysis here is unable to directly identify mechanisms. I assumed that a strong autocorrelation at long-time scales implies carbohydrate storage or other mechanisms of buffering that limits ecosystem response to climate extremes. However, the evidence that such occurs here is weak and instead long-lead short-term moisture stress and prior season temperature anomalies appear to have the strongest effects, suggesting that moisture control is stronger than expected. A number of biotic interactions are likely in response to climate anomalies, in addition to changes in internal storage of sugars and starches, there are possible shifts in allocation in response to extremes or aging or community reorganization from shifts in competitive pressure. There was very limited management in the region over the study period and no evidence for a shift in age structure or dominance of certain ecosystems (Gellesch et al. 2013; Scheffer et al. 2001), which allowed this

analysis to assume stationary conditions. In addition, it is unclear from the analysis if any state shifts from multiple or repeating stress, dubbed “ecological stress memory” (Walter et al. 2013), was observed here. Instead, the analysis suggests that modeling and experimental studies should look and evaluate carbon cycle shifts over long-time scales (seasons to years) in response to relatively short-term drought manipulation or prior season temperature anomalies. Further, multi-year anomalies that may be related to patterns and oscillations in biology or climate warrant more investigation. For example, the negative autocorrelation of  $P_d$  at interannual timescales for annual and longer averages suggests potential biological oscillations, cycles of herbivory, or species successional processes.

Further evidence on the lack of a strong negative feedback or “internal control” is the surprising lack of correlation between relative anomalies of  $P_d$  to EVI. Anomalies of  $P_d$  do not appear to relate to anomalies of EVI at any timescale, calling into question how well remote sensing can be used to evaluate how climate anomalies drive productivity anomalies. Many applications have been developed around the ability to apply differences in infrared and visible reflectance of canopies to estimate global photosynthesis from space, ever since early work showed the strong link of absorbed radiation to plant carbon assimilation (e.g., Kumar and Monteith 1981). For example, remarkably strong monthly to seasonal correlations exist between NASA MODIS-derived monthly GPP against flux tower estimated GPP (Heinsch et al. 2006). However, many of these papers find that while satellites can sense large-scale latitudinal variation, significant unexplained variability exists across smaller regions and across longer timescales.

It appears that EVI and similar metrics of remotely sensed vegetation greenness or absorbed radiation capture processes like phenology, leaf area, or canopy development, though they likely do not readily capture the anomalies or extremes as formulated in this analysis. Though anomalies do not correlate, EVI does explain approximately 75 % of the biweekly variation of  $P_d$ . EVI has also been argued as a good proxy for carbon uptake phenology, but at this site, dates of start and end of carbon uptake period (period when mean daily smoother  $P_d$  is positive) do not correlate strongly to dates of start and end of the “greenness” period as identified in EVI. However, I did find that growing season length as defined by its carbon uptake period has a strong correlation with average growing season EVI ( $r = -0.88$ ), though with a negative relationship and a small effect size, suggesting that short- and long-term EVI have opposing effects and may partially explain the lack of correlation of anomalies. The strongest relationship with mean growing season EVI is with correlation of the end date of this uptake period ( $r = -0.92$ ), consistent with some recent work that many temperate

forest systems have interannual variability in NEE driven by end of season signals (Wu et al. 2013). The analysis here does suggest caution is warranted when analyzing anomalies in broadband satellite vegetation indices.

Finally, it is apparent that both at the direct timescale, through the high correlation of ET to  $P_d$  and at the lagged timescale, through the positive association of seasonal soil moisture to  $P_d$  and the long lag relationships of temperature to  $P_d$ , all imply a variety of moisture retention and moisture use processes influence photosynthesis at a number of timescales. Some of these maybe related to summer droughts influence late season photosynthesis and others may be related the dynamics of the snowpack on soil moisture. The existence of moisture control on plant biogeochemistry in a mesic temperate forest and wetland landscape in and of itself is surprising and opens up a number of new avenues for analysis.

#### Toward a canopy photosynthesis-modeling framework

Compared to lab experiments, both uncontrolled and controlled field observations require greater explicit consideration of time and spatial scale, and the extent to which variability expressed in one dimension truly reflects the signal one seeks to estimate. This paper, like others (e.g., Stoy et al. 2009), demonstrate that frequency dependent analysis is essential for identifying processes over long-time periods or large regions. Otherwise, conclusions can be drawn from short-term or small-scale data that have very limited application to how photosynthesis actually responds to the environment.

Statistical analyses for large environmental data sets are still in development. Modern computational speeds, open source libraries for advanced programming languages, and new models of graduate student training have led to continued improvement in these (Zobitz et al. 2011). Of course, whether the methods presented here are useful ultimately depend on the interpretation of results.

Moorcroft (2006) asked if we have reached a predictive ability for the biosphere. Progress has been made, especially with advanced coupled dynamic vegetation and carbon cycling models (e.g., Medvigy et al. 2009), but the community may have reached a standstill until we seriously reconsider how we confront models with data. Dietze et al. (2011) found among more than a dozen ecosystem models, very little confidence is present in our ability to simulate both the diurnal cycle and interannual variability, with the latter finding confirmed by Keenan et al. (2012a, b). New research further finds even short-term environmental variability can strongly affect long-term carbon cycling (Medvigy et al. 2010).

The analysis here suggests that models need to be evaluated on the temporal memory of moisture and carbon

storage mechanisms. Advances have been made in applying data assimilation or Bayesian inference methods to sift through data and models (Williams et al. 2009). Large model-data syntheses as mentioned in the introduction have contributed to our ability to diagnose consistent model errors. Data uncertainty, machine readability, and archival have also gotten greater attention. Uncertainty, in particular, is essential to collect with all these data, given how sensitive model-data comparisons can be to them (Raupach et al. 2005). Finally, recent progress has been made on making modeling and model-data comparisons a routine exercise, or at least, more user-friendly and across a wider range of data sources (LeBauer et al. 2013).

Multiple lag and time filtering should be applied to climate extreme experiments conducted with ecosystem models in the soil moisture and carbon storage domains. Various model structures and parameters (e.g., root exudates, labile carbohydrate storage, community shifts, or soil moisture storage rates) can be investigated not for merely how well they simulate NEE or even  $P_d$ , but rather how well they simulate the observed relationships among variables across time. Some of these responses span over multiple years. Further, comparisons should be made in anomaly space if we really want to test how climate extremes influence photosynthesis.

## Conclusion

I found that neither the carbon storage control or moisture control hypotheses could be falsified with long-term data, once seasonal cycle was removed. The extent to which the hypotheses could be falsified was strongly dependent on the scale of the averaging filter and the lags analyzed. Using Hilbert spectra to identify relevant lags, I found a short-term carbon storage link on the order of weeks and a longer-term seasonal positive soil moisture influence on photosynthesis anomalies. Daily to weekly lagged positive anomalies of photosynthesis positively influence current photosynthesis, inhibiting photosynthetic response to direct climate extremes, primarily anomalies on evapotranspiration and maximum temperature. Moisture stress or surplus in the prior season did inhibit or promote photosynthesis, respectively, but mechanisms are difficult to assess.

These results support prior suppositions that spring moisture anomalies and autumn carbon uptake anomalies influence future carbon assimilation rates, not just length of growing season or phenology. Further, the results highlight the difficulty that some commonly used indicators of plant growth such as remotely sensed vegetation indices, can reliably detecting anomalies in net carbon uptake. Finally, multi-year lagged negative relationships of temperature and evapotranspiration anomalies on

current photosynthesis are intriguing and suggest new avenues of exploration for the role of long-lead ecosystem responses to extremes.

These findings are not necessarily detectable with shorter-term data or leaf-level analysis, as they involve subtle relationships and canopy- and soil-level processes. The results are similar to, for example, recent work by Niu et al. (2012) who argued that thermal acclimation of NEE (a flux made up of many interacting processes) can occur on interannual timescales in canopies. Also interesting was the lack of relationship between spectral indices and  $P_d$ , once converted to anomaly space, similar to some of the results of Heinsch et al. (2006) that remotely sensed GPP is adequate for large spatial scale variation but poor for single pixel interannual variability.

The results here demonstrate the importance of long-term environmental observation of canopy photosynthesis but caution has to be taken regarding the high temporal autocorrelation that exists in flux and climate data. Strong covariance of these signals to seasonal orbital forcing requires careful evaluation of spurious correlation. A disconcerting finding was the lack of strong statistical power at detecting many correlations at long timescales, beyond interannual, even with >15 years of data. Methods that seek complementary use of short-term field manipulations, lab observations, and long-term datasets like Fluxnet and the evolving NEON observatory will require continued evolution of model-data comparison tools. Other papers in this special issue point to a number of intriguing new ways to look at photosynthesis in models (Dietze et al., this issue; Rogers et al., this issue; Sitch et al., this issue; Tholen et al., this issue). Here, I have shown that a spectral anomaly framework and long-term flux observation network contribute to their evaluation and improvement.

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## References

- Amiro B, Barr AG, Barr JG et al (2010) Ecosystem carbon dioxide fluxes after disturbance in forests of North America. *J Geophys Res* 115:G00K02. doi:[10.1029/2010JG001390](https://doi.org/10.1029/2010JG001390)
- Baldocchi DD (2008) Breathing of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems. *Aust J Bot* 56:1–26
- Baldocchi DD, Hutchison BA, Matt DR, McMillen RT (1985) Canopy radiative transfer models for spherical and known leaf

- inclination distribution angles: a test in an Oak-Hickory forest. *J Appl Ecol* 22:539–555
- Baldocchi DD, Falge E, Wilson K (2001) A spectral analysis of biosphere-atmosphere trace gas flux densities and meteorological variables across hour to year time scales. *Agric For Meteorol* 107:1–27
- Barnhart BL, Eichinger WE, Preuger JH (2012) Introducing an Ogive method for discontinuous data. *Agric For Meteorol* 162:58–62
- Beer C et al (2010) Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate. *Science* 329:834–838. doi:10.1126/science.1184984
- Berger BW, Zhao CL, Davis KJ, Yi C, Bakwin PS (2001) Long-term carbon dioxide fluxes from a very tall tower in a northern forest: flux measurement methodology. *J Atmos Ocean Technol* 18:529–542
- Booth BB et al (2012) High sensitivity of future global warming to land carbon cycle processes. *Environ Res Lett* 7:024002. doi:10.1088/1748-9326/7/2/024002
- Bretherton CS, Widman M, Dymnikov VP, Wallace JM, Blade I (1999) The effective number of spatial degrees of freedom of a time-varying field. *J Climate* 12:1990–2009
- Carbone MS, Czimczik CI, McDuffee KE, Trumbore SE (2007) Allocation and residence time of photosynthetic products in a boreal forest using a low-level  $^{14}\text{C}$  pulse-chase labeling technique. *Glob Change Biol* 13:466–477
- Collatz GJ, Ball JT, Grivet C, Berry JA (1991) Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer. *Agric For Meteorol* 54:107–136
- Davis KJ, Bakwin PS, Yi C, Berger BW, Zhao C, Teclaw RM, Isebrands JG (2003) The annual cycles of  $\text{CO}_2$  and  $\text{H}_2\text{O}$  exchange over northern mixed forest as observed from a very tall tower. *Glob Change Biol* 9:1278–1293
- De Pury DGG, Farquhar GD (1997) Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. *Plant Cell Environ* 20:537–557
- Desai AR (2010) Climatic and phenological controls on coherent regional interannual variability of carbon dioxide flux in a heterogeneous landscape. *J Geophys Res* 115:G00J02. doi:10.1029/2010JG001423
- Desai AR, Moorcroft PR, Bolstad PV, Davis KJ (2007) Regional carbon fluxes from a biometrically constrained dynamic ecosystem model: impact of disturbance,  $\text{CO}_2$  fertilization and heterogeneous land cover. *J Geophys Res* 112:G01017. doi:10.1029/2006JG000264
- Desai AR, Richardson AD, Moffat AM, Kattge J, Hollinger DY, Barr A, Falge E, Noormets A, Papale D, Reichstein M, Stauch VJ (2008) Cross site evaluation of eddy covariance GPP and RE decomposition techniques. *Agric For Meteorol* 148:821–838. doi:10.1016/j.agrformet.2007.11.012
- Desai AR, Helliker BR, Moorcroft PR, Andrews AE, Berry JA (2010) Interannual variability in regional carbon fluxes from top-down and bottom-up perspectives. *J Geophys Res* 115:G02011. doi:10.1029/2009JG001122
- Detto M, Molini A, Katul G, Stoy P, Palmroth S, Baldocchi DD (2012) Causality and persistence in ecological systems: a nonparametric spectral granger causality approach. *Am Nat* 179:524–535
- Dietze MC et al (2011) Identifying the time scales that dominate model error: a North American synthesis of the spectral properties of ecosystem models. *J Geophys Res* 116:G04029. doi:10.1029/2011JG001661
- Farquhar GD, Sharkey TD (1982) Stomatal conductance and photosynthesis. *Annu Rev Plant Physiol* 33:317–345
- Foken T, Aubinet M, Leuning R (2012) The eddy-covariance method. In: Aubinet M et al (eds) *Eddy covariance: a practical guide to measurement and data analysis*. Springer, Dordrecht, pp 1–19
- Friedlingstein P, Cox P, Betts R et al (2006) Climate—carbon cycle feedback analysis, results from the C4MIP model intercomparison. *J Clim* 19:3337–3353
- Gellesch E, Hein R, Jaeschke A, Beierkuhnlein C, Jentsch A (2013) Biotic interactions in the face of climate change. *Prog Bot* 74:321–349. doi:10.1007/978-3-642-30967-0\_12
- Heinsch FA, Zhao M, Running SW et al (2006) Evaluation of remote sensing based terrestrial productivity from MODIS using Ameriflux tower eddy flux network observations. *IEEE Trans Geosci Remote* 44:1908–1925. doi:10.1109/TGRS.2005.853936
- Huang NE, Wu Z (2008) A review on Hilbert–Huang transform: method and its applications to geophysical studies. *Rev Geophys* 46:RG2006. doi:10.1029/2007RG000228
- Keenan TF et al (2012a) Evaluation of terrestrial biosphere model performance for land-atmosphere  $\text{CO}_2$  exchange on inter-annual time scales: results from the North American Carbon Program interim site synthesis. *Glob Change Biol*. doi:10.1111/j.1365-2486.2012.02678.x
- Keenan TF, Davidson E, Moffat A, Munger W, Richardson AD (2012b) Using model-data fusion to interpret past trends, and quantify uncertainties in future projections, of forest ecosystem carbon cycling. *Glob Change Biol* 18:2555–2569
- Kumar M, Monteith JL (1981) Remote sensing of crop growth. In: Smith H (ed) *Plants and the daylight spectrum*. Academic Press, London, pp 133–144
- Le Quéré C, Raupach MR, Canadell JG et al (2009) Trends in the sources and sinks of carbon dioxide. *Nat Geosci*. doi:10.1038/ngeo689
- LeBauer DS, Wang D, Richter KT, Davidson CC, Dietze MC (2013) Facilitating feedbacks between field measurements and ecosystem models. *Ecol Monogr* 83:133–154. doi:10.1890/12-0137.1
- Mahecha MD, Reichstein M, Lange H, Carvalhais N, Bernhofer C, Grünwald T, Papale D, Seufert G (2007) Characterizing ecosystem-atmosphere interactions from short to interannual time scales. *Biogeosciences* 4:743–758
- Mahecha MD, Reichstein M, Jung M, Seneviratne SI, Zaehle S, Beer C, Braakhekke MC, Carvalhais N, Lange H, Le Maire G, Moors E (2010) Comparing observations and process-based simulations of biosphere-atmosphere exchanges on multiple time scales. *J Geophys Res* 115:G02003. doi:10.1029/2009JG001016
- Medvigy D, Wofsy SC, Munger JW, Hollinger DY, Moorcroft PR (2009) Mechanistic scaling of ecosystem function and dynamics in space and time: the Ecosystem Demography model version 2. *J Geophys Res* 114:G01002. doi:10.1029/2008JG000812
- Medvigy D, Wofsy SC, Munger JW, Moorcroft PR (2010) Responses of terrestrial ecosystems and carbon budgets to current and future environmental variability. *Proc Natl Acad Sci USA* 107:8275–8280
- Moffat AM, Papale D, Reichstein M et al (2007) Comprehensive comparison of gap-filling techniques for eddy covariance net carbon fluxes. *Agric For Meteorol* 147:209–232. doi:10.1016/j.agrformet.2007.08.011
- Moorcroft PR (2006) How close are we to a predictive science of the biosphere? *Trends Ecol Evol* 21:400–407
- Niu S et al (2012) Thermal optimality of net ecosystem exchange of carbon dioxide and underlying mechanisms. *New Phytol* 194:775–783. doi:10.1111/j.1469-8137.2012.04095.x
- Norby RJ, Zak DR (2011) Ecological lessons from free-air  $\text{CO}_2$  enrichment (FACE) experiments. *Annu Rev Ecol Evol Syst* 42:181–203
- Raupach MR, Rayner PJ, Barrett DJ, DeFries RS, Heimann M, Ojima DS, Quegan S, Schimmlius CC (2005) Model-data synthesis in terrestrial carbon observation: methods, data requirements and data uncertainty specifications. *Glob Change Biol* 11:378–397
- Ricciuto DM, Butler MP, Davis KJ, Cook BD, Bakwin P, Andrews A, Teclaw RM (2008) Causes of interannual variability in



- ecosystem-atmosphere CO<sub>2</sub> exchange in a northern Wisconsin forest using a Bayesian model calibration. *Agric For Meteorol* 148:309–327
- Richardson AR et al (2012) Terrestrial biosphere models need better representation of vegetation phenology: results from the North American Carbon Program Site Synthesis. *Glob Change Biol* 18:566–584. doi:[10.1111/j.1365-2486.2011.02562.x](https://doi.org/10.1111/j.1365-2486.2011.02562.x)
- Schaefer K et al (2012) A model-data comparison of gross primary productivity: results from the North American Carbon Program Site Synthesis. *J Geophys Res* 117:G03010. doi:[10.1029/2012JG001960](https://doi.org/10.1029/2012JG001960)
- Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. *Nature* 413:591–596
- Sellers PJ (1985) Canopy reflectance, photosynthesis and transpiration. *Int J Remote Sens* 6:1335–1372. doi:[10.1080/01431168508948283](https://doi.org/10.1080/01431168508948283)
- Sprintsin M, Chen JM, Desai AR, Gough CM (2012) Evaluation of leaf-to-canopy upscaling methodologies against carbon flux data in North America. *J Geophys Res* 117:G01023. doi:[10.1029/2010JG001407](https://doi.org/10.1029/2010JG001407)
- Stoy PC, Richardson AD, Baldocchi DD, Katul GG, Stanovick J, Mahecha MD, Reichstein M, Detto M, Law BE, Wohlfahrt G, Arriga N, Campos J, McCaughey JH, Montagnani L, Paw UKT, Sevanto S, Williams M (2009) Biosphere-atmosphere exchange of CO<sub>2</sub> in relation to climate: a cross-biome analysis across multiple time scales. *Biogeosciences* 6:2297–2312
- Van Gorsel E, Delpierre N, Leuning R et al (2009) Estimating nocturnal ecosystem respiration from the vertical turbulence flux and change in storage of CO<sub>2</sub>. *Agric For Meteorol* 149:1919–1930. doi:[10.1016/j.agrformet.2009.06.020](https://doi.org/10.1016/j.agrformet.2009.06.020)
- Walter J, Beierkuhnlein C, Jentsch A, Kreyling J (2013) Ecological stress memory and cross stress tolerance in plants in the face of climate extremes. *Environ Exp Bot*. doi:[10.1016/j.envexpbot.2012.02.009](https://doi.org/10.1016/j.envexpbot.2012.02.009)
- Williams M, Richardson AD, Reichstein M, Stoy PC, Peylin P, Verbeeck H, Carvalhais N, Jung M, Hollinger DY, Kattge J, Leuning R, Luo Y, Tomelleri E, Trudinger C, Wang Y-P (2009) Improving land surface models with FLUXNET data. *Biogeosciences* 6:1341–1359
- Wu C, Chen JM, Black TA et al (2013) Interannual variability of net ecosystem productivity in forests is explained by carbon flux phenology in autumn. *Glob Ecol Biogeogr*. doi:[10.1111/geb.12044](https://doi.org/10.1111/geb.12044)
- Yi C, Davis KJ, Bakwin PS, Berger BW, Marr L (2000) The influence of advection on measurements of the net ecosystem-atmosphere exchange of CO<sub>2</sub> from a very tall tower. *J Geophys Res* 105:9991–9999
- Yi C, Ricciuto DM, Li R et al (2010) Climate control of terrestrial carbon exchange across biomes and continents. *Environ Res Lett* 5:034007. doi:[10.1088/1748-9326/5/3/034007](https://doi.org/10.1088/1748-9326/5/3/034007)
- Zobitz J, Desai AR, Moore DJP, Chadwick MA (2011) A primer for data assimilation with ecological models using Markov Chain Monte Carlo (MCMC). *Oecologia* 167:599–611. doi:[10.1007/s00442-011-2107-9](https://doi.org/10.1007/s00442-011-2107-9)