Original Research Article

Disentangling the confounding effects of PAR and air temperature on net ecosystem exchange at multiple time scales

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Net ecosystem exchange of CO₂ (NEE) in temperate forests is modulated by multiple microclimatic factors. The effects of these factors vary across time scales, with some correlated to produce confounding effects. Photosynthetically active radiation (PAR) and air temperature (Ta) are among the two most important drivers of NEE in temperate forests and are highly correlated because of their similar diel and annual cycles. In this study, we attempted to disentangle the confounding effects of them on NEE at multiple time scales. We applied innovative spectral analysis techniques, including the continuous wavelet transformation (CWT), cross wavelet transformation (XWT), wavelet coherent (WTC), and partial wavelet coherence (PWC), on a seven-year time series (2004–2010) of PAR, Ta, and NEE from the Ohio Oak Openings Ameriflux site (N 41.5545°, W 83.8438°), USA. We found that PAR was the primary driver at short time scales (e.g., multi-hour and daily), while Ta dominated NEE at long time scales (e.g., seasonal to annual). At the daily scale, PAR co-varied with NEE without time lag, while Ta lagged PAR for 2–3 h during growing seasons, which could be explained by the strong dependence of NEE on photosynthesis, which has a similar time lag of 2–3 h of Ta to PAR. At the daily scale, during the non-growing seasons, NEE varied little and co-varied with Ta and PAR with no high common power. At the annual scale, Ta co-varied with NEE with no time delay, but PAR led NEE by about one month. This can be explained by the strong dependence of leaf area index (LAI) on Ta as well as the lag between the LAI/biomass development and the progress of sunlight. We also found that NEE distributes most of its variation at seasonal and annual scales, suggesting that Ta is more important than PAR in determining the annual and long-term carbon budget.

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1. Introduction

Our knowledge about the variability of the net ecosystem exchange (NEE) of CO₂ in terrestrial ecosystems at multiple time scales remains poor; yet, it is critical to global modeling analyses for quantifying the terrestrial carbon cycle (Stoy et al., 2009). NEE is simultaneously modulated by multiple physical and biological forcing factors that constantly change over time with unique magnitudes and frequencies (Baldocchi et al., 2001; Baldocchi and Wilson, 2001; Stoy et al., 2005, 2009). The daily and seasonal progressions of sunlight and temperature, precipitation events, the seasonal changes of plant structure, and the decadal successions of plants are obvious examples. Ecosystem functions (e.g., NEE) respond to these forcing factors and their variability is the transferred variability of these drivers.

The response of NEE to each environmental driver varies by time scale. At the hourly scale, NEE variations are likely to be forced by changes in photosynthesis, stomatal conductance, and respiration that are controlled by sunlight and temperature (Baldocchi et al., 2001) as well as precipitation events (Stoy et al., 2005). At the daily scale, they are forced mostly by daily rhythms of solar radiation, air and soil temperature, humidity, and atmospheric CO₂ concentration (Baldocchi et al., 2001; Jarvis et al., 1997). Weather patterns/changes associated with the passages of high- and low-pressure systems, fronts, and precipitation can cause weekly fluctuations in NEE (Baldocchi and Wilson, 2001; Stoy et al., 2005). At
monthly, seasonal, and annual scales, NEE experiences the effects of seasonal changes in sunlight, temperature, soil water balance, leaf dynamics, phenology, drought/wet events, and growing season duration (Baldocchi et al., 2001; Goulden et al., 2004; Stoy et al., 2005, 2009). At multi-year scales, long-term climatic changes (e.g., El Nino, La Nina cycles) and ecological dynamics (e.g., succession) and environmental changes (e.g., N deposition, CO2 fertilization) may be more responsible for the NEE variations (Baldocchi et al., 2001; Stoy et al., 2005). Despite this general knowledge, few efforts have been made to thoroughly examine the changes of variations in NEE and its drivers across multiple time scales.

Ecosystem models that synthesize terrestrial carbon exchange often represent an explicit hypothesis on how an ecosystem transfers variability from microclimatic drivers to ecological responses, such as NEE and energy fluxes. However, Stoy et al. (2013) evaluated the wavelet coherence between measurements and several NEE models at multiple time scales and found that the mechanisms for diurnal and annual NEE variability require further improvement to correctly simulate the magnitudes of fluxes. This suggests that some of the explicit hypotheses might be wrong or not accurate enough, partially due to the fact that the modulating effects of the microclimatic drivers may vary across time scales and drivers might be correlated to produce confounding effects. Temperature (e.g., Ta), radiation (e.g., PAR), and water (e.g., precipitation) are among the most important microclimatic drivers that modulate the magnitude and frequency of carbon fluxes in temperate forests (van Dijk et al., 2005) and have always been important variables in ecosystem models (Liu et al., 1997; Urbanski et al., 2007; Xiao et al., 2004). However, among the three, PAR and Ta are highly correlated at multiple time scales because they have similar diurnal and seasonal cycles and thus may produce strong confounding effects. This inspired us to further confirm, refine, and adjust the effects of Ta and PAR on NEE across time scales (especially daily, seasonal, and annual scales). Here, we collected seven years of meteorological and flux measurements at the Oak Openings site in northwest Ohio with the objectives to explore the variability of NEE at multiple temporal scales and to disentangle the effects of Ta and PAR on regulating NEE. We excluded precipitation in our analysis because: (1) its effects have been reported in our previous studies (Noormets et al., 2008; Xie et al., 2014), (2) it is a stochastic event and lacks regular daily and seasonal patterns, and (3) it is weakly correlated to Ta and PAR. However, we included leaf area index (LAI) to assist our analysis because it is the most important biological driver of NEE and is highly correlated with PAR and Ta at seasonal to annual scales (Chen et al., 2002).

A spectral analysis of NEE and its driving force are especially well-adapted to achieve our study objective. The Fourier transform (FT) technique can be applied to analyze the frequency spectrum of the time series and determine the magnitude of frequencies, but not on the timing of particular frequency components (Massel, 2001). Thus, the FT is only appropriate for stationary signals with constant frequency components present throughout the records. The non-stationary nature of the flux measurements requires time-varying statistics that can decompose signals into the time-scale domain. A recently developed method, the Hilbert–Huang transform (HHT), does a good job tackling non-stationary and nonlinear data (Huang and Wu, 2008), but it is only empirically based and is at its early stage with difficulties in dealing with two or more time series simultaneously. Alternatively, a suite of wavelet analysis tools is ideally suited to the analysis of multiple non-stationary signals (Cazelles et al., 2008; Grinsted et al., 2004; Torrence and Compo, 1998). The continuous wavelet transform (CWT) that employs a finite basis function, a.k.a. “mother wavelet”, which is translated (shifted) and dilated (expanded and contracted) across a signal, can quantify the time series signal variance across both time and frequency. In addition, a cross-wavelet analysis (XWT) is able to expose the common power and relative phase in the time-frequency space of two time series. The wavelet coherence transform (WTC), a measure of wavelet coherence, can detect the significant coherence against noise, even when the common power is low between the two time series. The partial wavelet coherence (PWC), a technique similar to partial correlation, can identify the resulting wavelet coherence between two time series after eliminating the influence of a third common dependence (Ng and Chan, 2012). Because of these unique features, we employed them in this study to achieve our study objectives. We hypothesized that PAR is the major driver at short scales (e.g., 12-h, day) and Ta is the major driver at long scales (season, year). Specifically, we: (1) quantified the variability of NEE across multiple time scales and (2) investigated the scale-dependent relationships between Ta/PAR and NEE.

2. Methods

2.1. Site characteristics

Our study site is located in a 70-year-old oak-dominated forest within Oak Openings Preserve Metropark near Toledo (N 41.55’, W 83.84’) in northwest Ohio, USA. The forest comprises a mosaic of oak (Quercus spp.) woodlands, maple (Acer spp.) floodplains, remnants of oak savanna, and barrens and prairie (Brever and Vankat, 2004). The topography is flat with an elevation range of 200–205 m. The long-term mean annual air temperature is 9.2 C and the annual total precipitation is 840 mm (Noormets et al., 2008). The height of the dominant trees is ~24 m, with an average canopy height of ~20 m. An open-path eddy-covariance (EC) system was mounted on the top of a 34-m tower surrounded by uniform canopy in all directions with similar species and age composition (Xie et al., 2014).

2.2. Flux measurement

Turbulent exchanges of CO2 (Fc) between the forest and the atmosphere were measured using the EC method (Lee et al., 2004) since November, 2003. The EC system consists of a LI-7500 infrared gas analyzer (IRGA; LI-COR Biosciences, Lincoln, NE, USA) that measures high-frequency CO2 densities and a 3-dimensional sonic anemometer (CSAT3; Campbell Scientific, Inc. (CSI), Logan, UT, USA) that measures wind speed/direction. Raw data spikes (>6 standard deviations) were removed; wind coordinates were rotated to mean streamline plane calculated from wind data over an entire year (Wilczak et al., 2001) and temperature was corrected for changes in atmospheric humidity and pressure (Schotanus et al., 1983). Each 30-min mean flux value was then calculated as the covariance of vertical wind speed, air temperature, and CO2 densities using the Webb–Pearson–Leuning correction (Massman and Lee, 2002; Webb et al., 1980). The warming of the IRGA above air temperature was corrected to 30-min fluxes (Grelle and Burba, 2007). The 30-min NEE (µmol CO2 m−2 s−1) was calculated as the sum of turbulent flux and the CO2 storage was estimated as mean rate of 30-min change in CO2 concentrations measured within the canopy.

To exclude outliers and bad data, all 30-min flux data from the EC tower was quality checked, including stationarity, integral turbulence characteristics, and friction velocity thresholds (Noormets et al., 2008). As a result, gaps exist for long time series NEE (Table 1). The gaps were filled using a dynamic
parameter process model (Moffat et al., 2007). First, a respiration model was parameterized from nighttime data to fill nighttime NEE (e.g., ER, respiration):

$$ER = R_{10}e^{A/R(1/T_{ref} - 1/T_{a} + 273.15)}$$

where $R_{10}$ is the reference respiration ($\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$), normalized to a base temperature ($T_{ref} = 283.15$ K), $E_a$ is the activation energy (kJ mol$^{-1}$ K$^{-1}$), $R$ is the universal gas constant (8.3134) mol$^{-1}$ K$^{-1}$, and $T_a$ is the air temperature above the canopy (°C). Daytime ER was then estimated from Eq. (1), assuming the consistency of temperature sensitivity between nighttime and daytime gas exchanges. The daytime NEE was then filled with:

$$NEE = ER + \alpha \cdot PAR \cdot P_{max}$$

where $\alpha$ is the apparent quantum yield ($\mu$mol CO$_2$ cm$^{-2}$ PAR), PAR has a unit of $\mu$mol m$^{-2}$ s$^{-1}$, and $P_{max}$ is the maximum apparent photosynthetic capacity of the canopy ($\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$).

2.3. Meteorological and vegetation measurements

Ta (°C) was measured by a HMP45AC probe (Vaisala, Finland) and PAR ($\mu$mol m$^{-2}$ s$^{-1}$) by a LI-190SB Quantum sensor (LI-COR) above the canopy at the same height as the IRGA with every 20 s, which were then used to calculate the 30-min means. The original Ta and PAR 30-min series also included gaps due to sensor failure (Table 1). Short gaps (<1.5 h) were filled by linear interpolation and longer gaps (>1.5 h) were filled using the Mean Diurnal Variation method (Falge et al., 2001). The LAI 8-day composite as a proxy of vegetation (m$^2$ m$^{-2}$) was obtained from the 1-km resolution MODIS LAI/FPAR Collection 5 (http://daac.ornl.gov/MODIS/modis.shtml) with an online subset output of a 3 km × 3 km pixel matrix centered on the flux tower.

2.4. The continuous wavelet transform (CWT)

The wavelet transform analyzes time series that contain non-stationary power at many different frequencies (Daubechies, 1990). A wavelet is a function with a zero mean localized in both frequency and time and characterized by localized time (\(\Delta t\)) and frequency (\(\Delta w\) or the bandwidth). According to the classical Heisenberg uncertainty principle, there is always a tradeoff between localization in time and frequency. One particular wavelet, the Morlet wavelet (with $w_0=6$), provides a good balance between the localization of time and frequency. We applied it as the mother wavelet in our analyses. The Morlet, consisting of a plane wave modulated by a Gaussian, is defined as:

$$\psi_0(t) = \pi^{-1/4} e^{j\omega_0 t} e^{-t^2/2}$$

where $\omega_0$ is dimensionless frequency and $\eta$ is dimensionless time.

The idea behind the CWT is to apply the wavelet as a band pass filter to a time series. The mother wavelet is stretched in time by varying its scale and normalizing it to have unit energy. Therefore, the CWT can be thought of as a consecutive series of band-pass filters applied to a time series. The CWT of time series $X (x_n, n = 1, \ldots, N)$ with uniform time steps ($\delta t$) is defined as the convolution of $X$ with the scaled and normalized mother wavelet:

$$W_n^X(s) = \sum_{j=-\infty}^{\infty} X_n \psi_{j, s}$$

where $s$ is the set of scales used. The wavelet power is defined as $|\hat{W}_n^X(s)|^2$. Because the mother wavelet cannot be completely localized in time, the CWT has edge artifacts. It is therefore a cone of influence (CI) that was introduced as the area where errors will occur to the wavelet power at the beginning and end of the wavelet power spectrum (Torrence and Compo, 1998). Many geophysical time series have distinct red noise characteristics; thus, a 5% significance level against red noise needs to be tested. The methods for significance tests were described in Grinsted et al. (2004). We adopted the ecosystem spectral transfer (EST) form Stoy et al. (2009), which is defined as:

$$EST_{x_1, x_2} = \log \frac{W_{x_1}^X(s)}{W_{x_2}^Y(s)}$$

where $x_1$ is “amplified” ("dampened") by $x_2$ if $EST_{x_1, x_2}$ is positive (negative). The concepts of amplifying and dampening come from signal processing literature, which need not imply causality in systems that respond to many factors (Stoy et al., 2009) but are useful to ascertain or deduce the simplest driver-response relationships across scales of time.

2.5. The cross wavelet transform (XWT)

The XWT of two time series $X$ and $Y$ is defined as $W_{XY} = W_XW_Y^*$, where * denotes complex conjugation. The cross wavelet power is defined as $|W_{XY}|$. The XWT reveals areas with high common power for two time series but does not necessarily suggest a high coherent or cause and effect relationship unless the two time series are phase-locked. The complex argument arg $W_{XY}$ can be interpreted as the local relative phase between $X$ and $Y$ and drawn in the time frequency space of XWT (e.g., Figs. 2-4) as arrows. Arrows pointing down are interpreted as $X$ leading $Y$ by 90° or lagging $Y$ by 270°. Arrows pointing up are interpreted as $X$ lagging $Y$ by 90° or leading $Y$ by 270°. Arrows pointing left and right can be interpreted as anti-phase and in-phase, respectively.

2.6. The wavelet coherence (WTC)

We used the WTC to quantify the coherence of the two time series of XWT in time–frequency/scale plane. High coherence between two time series can happen at frequencies and time periods where their common wavelet power is not necessarily high. The WTC is a tool for identifying possible relationships between two processes by searching frequency bands and time intervals during which they co-vary (Ng and Chan, 2012). The WTC square of two time series $X$ and $Y$ is defined as (Grinsted et al., 2004):

$$R_n^2(x, y) = \frac{|S(s^{-1}W^X_{n}(s)|^2}{S(s^{-1}W^X_{n}(s)|^2)} \cdot \frac{|S(s^{-1}W^Y_{n}(s)|^2}{S(s^{-1}W^Y_{n}(s)|^2)^2}$$

where $S$ is a smoothing operator, $s$ is the set of scales used as in Eq. (4), and $W$ is the WTC operator. This definition closely resembles the traditional correlation coefficient and it is useful to think of the WTC as a localized correlation coefficient in time.
frequency space (Grinsted et al., 2004). When there is a real significant relationship between two phenomena, it is shown in the WTC time frequency space. The $S$ operator can have varying forms and produce a large impact on a significant level. We followed the form of Torrence and Webster (1998) for the Morlet wavelet.

2.7. The partial wavelet coherence (PWC)

The PWC is a new wavelet analysis technique recently introduced by Mihanovic et al. (2009) to the field of marine science together with another new wavelet tool of multiple wavelet coherence (MWC). The idea of the PWC is to calculate the resulting WTC for two time series after removing their common dependent factors. The PWC is a technique similar to partial correlation that helps find the resulting WTC between two time series $Y$ and $X_1$ after eliminating the influence of the time series $X_2$ when $X_1$ and $X_2$ are not independent (Ng and Chan, 2012). The PWC square is defined as:

$$RP^2(y,x_1,x_2) = \frac{|R(y,x_1) - R(y,x_2) - R(y,x_1)^2|}{[1 - R(y,x_2)]^2[1 - R(x_1,x_2)]^2}$$

(7)

where $R$ is the WTC operator.

2.8. Wavelet analysis

We used non-gap-filled data for the wavelet analysis because gap-filling can bring artificial correlations that will contribute to wavelet common power or coherence. However, a tradeoff is that we will lose information at time scales shorter than the length of the gaps during periods with the gaps; gaps will sometimes bias wavelet calculation at scales longer than the length of the gaps. Additionally, when three time series were analyzed together by the PWC, gaps are more likely to cause problems and confound the results. Therefore, the WTC was also used on gap-filled data for the interpretation and PWC was only applied to the gap-filled data. The WTC analysis related LAI to NEE, PAR, and $Ta$ was also conducted to clarify the effects of PAR and $Ta$ at seasonal scales. Each time series was normalized to have zero means (with zeroes in gaps when gapped data were used) and unit variances for cross comparison. MATLAB codes distributed by Ng and Chan (2012) (http://www.cityu.edu.hk/gcacic/hvavelet/) were modified for all wavelet analyses. A 5% significance level against red noise was tested through Monte Carlo simulations (Grinsted et al., 2004).

3. Results

3.1. Oscillations of NEE in time and time scales

The magnitudes of NEE oscillation varied across time scales but were mainly at four scales: the diurnal (i.e., $\frac{1}{2}$ day), the daily, the seasonal, and the annual (Fig. 1). At the annual scale, significant oscillations appeared constant throughout the entire measurement period. Significant oscillations were also observed at seasonal scales and peaked at $ca.$ 170–180 days (i.e., equivalent to the growing season length) continuously throughout the 7-year study period, except the significant oscillations at scales from $ca.$ 40 days to $ca.$ 150 days in 2006, likely because of a large number of short gaps during the growing season. At the daily scale, however, significant oscillations were found during the growing seasons. Oscillations at the diurnal scale were also obvious during the growing seasons (Fig. 1a), but the average oscillation power is much lower than that at the daily scale (Fig. 1b). Oscillations at scales from weekly to monthly were also apparent as a few hotspots (i.e., red areas in the time-scale half-plane with high wavelet power enclosed by thick contours, which represent a 5% significance level against the red noise) in some years. Generally, more variance was distributed at the long scales (seasonal and annual) than at the short scales (diurnal and daily).

3.2. Common power between $Ta$/PAR and NEE

High and significant common power was found at some scales, mainly diurnal, daily, seasonal, and annual, from the XWT time-scale half-planes (Fig. 2). $Ta$ & NEE and PAR & NEE had significantly high common power centered at the daily scale during the growing seasons and annual scale throughout the entire period. PAR & NEE also showed high common power at the diurnal scale, while $Ta$ and NEE showed much fewer pixels on the time-scale half-plane with high common power at this scale. The highest common wavelet power for PAR & NEE happened at the daily scale while the highest common wavelet power for $Ta$ & NEE were found at the annual scale. Significant common oscillations at the seasonal scale were present but not

Fig. 1. Continuous wavelet transform for NEE time series. The left axis is the Fourier period for the scaleogram timescale half-plane and the right plot is the scale-wise wavelet power spectra in log scale. The 5% significance level against red noise is shown as a thick contour. The cone of influence is shown as a thin line. The blue vertical stripes are caused by long data gaps. The redder the color, the higher is the wavelet power.
continuous. From weekly to monthly scales, regions with significant common power were only observed in 2004 and 2007.

3.3. Coherence between Ta/PAR and NEE

The time scales and time periods for the significant coherence were consistent with the high common power and stable phase relationships detected in the time-scale half-planes in the XWT (Fig. 3). Both Ta and PAR were significantly correlated with NEE at the daily scale during the growing season and at the annual scale throughout the time series. At the diurnal scale, the results were not clear due to the influences of data gaps. However, for the last four years, with a smaller number of short gaps (Fig. 3) and gap-filled data (Fig. 4), PAR & NEE were tightly correlated during the growing seasons, while the coherence between Ta and NEE was weak. At intermediate scales (multi-days, multi-weeks, and multi-months), significant coherent regions emerged discontinuously and occasionally for both the WTCs.

3.4. Spectral transfer across scales

The tendency of NEE to have less variation (dampen) or more variation (amplify) than the variability of PAR and Ta varied across scales (Fig. 5). At the <8 h scales, the NEE variability tended to be greater than that of Ta and PAR. Between scales of 10–32 h (i.e., equivalent to diurnal and daily scales), NEE seemed less variable than PAR. However, NEE was more variable than Ta at these scales. NEE oscillated more than PAR and Ta from the scales of approximately two days to one year, except at scales approaching the growing season scale. NEE also oscillated more than Ta and PAR at time scales longer than a year.

3.5. Partial coherence across scales and phase relationships

Partial wavelet coherence had fewer significant oscillations across all scales in the time-scale half-plane, but the observed areas with significant coherence were mostly located at the daily and annual scales (Fig. 5). Out of the COI, Ta & NEE was
continuously and significantly high at the annual scale after removing the effects of PAR. At the daily scale, however, no regions with significant coherence could be detected for Ta & NEE. In contrast, after removing the common dependence on Ta, PAR & NEE was only significant at the daily scale during growing seasons in all years, but not at the annual scale. Additionally, at intermediate scales (multi-day, multi-week, and multi-month), significant PWC regions for PAR & NEE and Ta & NEE were observed for some time durations.

Locked-phase angles often suggest significant correlation between phenomena recorded in the two time series. The phase angles provided by the XWT/CWT time-scale half-plane at the daily scale during the growing season and at the annual scale throughout the entire time series were stable (Figs. 2–4). The phase angles based on data with gaps often deviated from the average trend or, sometimes, totally shifted the average trend, likely due to data gaps affecting the phase angle calculation that is based on an entire cycle. Thus, we describe the phase angles and interpret them based on the analysis of gap-filled data (e.g., Fig. 4). At the daily scale, the phase angles for PAR & NEE are locked nearly anti-phased, while the phase angle for Ta & NEE were locked at ca. 146° (Table 2). At the annual scale, the phase angle for PAR & NEE was locked at −147°, while the phase angles for Ta & NEE were locked nearly anti-phased (Table 2). At the diurnal scale, however, PAR & NEE were approximately anti-phased, while the phase-angles for Ta & NEE were very changeable (Fig. 2). These differences could be caused by PAR and photosynthesis – the major component of NEE – that were not detectable during the nights. We thus made two groups of artificial time series: daytime series (06:00–18:00 h) and nighttime series (18:00–06:00 h), respectively, performed the WTC analyses and calculated the statistic of phase angles again. It turned out that Ta was locked with NEE in-phase in the nighttime series and locked with NEN at ca. 124°, while PAR was locked with anti-phased NEE in the daytime series (Table 2). Based on the NEE sign convention and the fact that more sunlight
Fig. 4. WTC between Fc and NEE (a) and WTC between Ta and NEE (b) of gap-filled data. The 5% significance level against red noise is shown as a thick contour. The cone of influence (COI) is shown as a thin line. The relative phase relationship is shown as arrows. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Fig. 5. Ecosystem spectra transfer (EST) of NEE for PAR and Ta averaged throughout the 7 years across different time scales. The EST shows the tendency of NEE to dampen (less variation) or amplify (more variation) the oscillation of Ta and PAR.
corresponds well with more CO₂ withdrawal from the atmosphere by photosynthesis and the rising temperatures are associated with more CO₂ release by respiration, our the interpretation is that: at the daily scale, PAR synchronizes with NEE without time lag while NEE lagged NEE for 2–3 h. At the annual scale, Ta synchronized with NEE without time lag, while PAR lead NEE ca. 34 days. At the diurnal scale, there is no time lag between the oscillations of PAR and NEE while Ta lagged NEE during cycles where the daytime dominated and synchronized with NEE during nighttime cycles.

3.6. Wavelet coherence and phase relationship for LAI to Ta/PAR and NEE

LAI was highly correlated with NEE at seasonal–annual scales, with Ta and PAR in the growing season scale (e.g., 170–180 days) and the annual scale. LAI was anti-phased (i.e., no time lag) with NEE at the growing season and at the annual scale (Fig. 7), in-phased (no time lag) with Ta, and locked at −68° with PAR (a time lag of ca. 34 days at the annual scale) at the growing season and the annual scale (Fig. 7).

4. Discussions

4.1. NEE variations and regulations

Spectral peaks at daily, seasonal, and annual time scales are the general features in a global NEE time series (Stoy et al., 2009), with a more pronounced pattern for temperate forests (Baldocchi et al., 2001; Braswell et al., 2005; Katul et al., 2001; Richardson et al., 2007). Our wavelet analysis is consistent with their reports.

Climatic variability (e.g., Ta, PAR), centered at the diurnal, daily, and annual scales, plays a dominant role in controlling the total variability in measured fluxes (Figs. 2–4). However, less driving force of Ta and PAR were observed at the seasonal scales. At this scale, significantly high common power was occasionally observed between NEE and the two climatic drivers (Fig. 2), without any significant coherence (Figs. 3 and 4). The EST analysis (Fig. 5) further suggested that NEE is more variable than both Ta and PAR at the growing season scale. This indicates that other variables, physical and biological, might have also contributed to the variance of NEE at this scale. Our analysis on LAI suggests that LAI is likely the main driver for NEE at seasonal scales (Fig. 7; also see Stoy et al., 2005; Baldocchi et al., 2001). The average growing season length at our site is ca. 180 days, indicating a LAI dynamic/cycle of 180 days. This explains why wavelet power also peaks at a scale at ca. 170–180 days (Fig. 1). However, LAI responds to climatic variability and is highly correlated with Ta and PAR at growing season and annual scales (Fig. 7). Therefore, we cannot exclude the regulating effect of Ta and PAR at the seasonal scales.

At other scales (i.e., hourly, weekly, monthly, 2–3 months, and >1 year), Ta and PAR were not likely the major drivers for NEE oscillations, as suggested by the fact that significant common power and coherence were rarely found at these scales (Figs. 2–4). The dynamics of LAI could be responsible for the observed successional oscillation at scales from ca. 42–150 days (Fig. 7a), while turbulence at hourly scales and irregular precipitation events may have played more important roles at scales of a few hours (Baldocchi et al., 2001; Stoy et al., 2005). However, drought events and synoptic weather changes that affect PAR, Ta, humidity, and wind direction may be responsible for hotspot NEE at weekly to monthly, and even longer, time scales (Baldocchi et al., 2001; Stoy et al., 2005). We suspect that the wavelet power hotspots from weekly to seasonal scales in 2007 were likely caused by the heat waves in the summer (http://www.ncdc.noaa.gov/oa/climate/research/2007/jul/jul07.html). At scales longer than a year, NEE seemed more variable than Ta and PAR (Fig. 5). Aggregation at longer time scales from model predictions and long-term measurements have both suggested that variations in environmental drivers (e.g., PAR, Ta, VPD, soil water content, etc.) become progressively less important while variations in the biotic response become progressively more important in determining the carbon fluxes (Richardson et al., 2007; Urbanski et al., 2007). Factors causing such biotic responses may include ecosystem succession, nutrient availability, and disturbances that need years for ecosystems to recover or large-scale climate cycles (e.g., El Nino, La Nina cycles) (Baldocchi et al., 2001; Stoy et al., 2009). We did not observe any significant oscillations at multi-year scales because our site has been stable as a mature forest and experienced no serious disturbance during 2004–2010.

4.2. The unique effects of PAR and Ta across scales

The dominant oscillations or variations of NEE happened at the diurnal, daily, growing season, and annual scales (Fig. 1). Both PAR and Ta are highly related to the NEE variations at these scales. However, PAR and Ta played different roles at each of these scales. PAR is the primary regulator for NEE compared to Ta at the daily scale. First, the co-varying power for PAR & NEE are stronger than those for Ta & NEE at this scale (Fig. 2). PAR has more oscillating power than Ta at the daily scale (Fig. 5), which probably transfers more variation to ecosystem functions. More importantly, there is no delay between the oscillations of NEE and PAR, while Ta lags NEE for ~2–3 h. We speculate that photosynthesis, instead of respiration, dominates the variation of NEE (Fig. 8; Yuan et al., 2010). Photosynthesis is a function of PAR, while respiration is a function of temperature (Kull and Kruijt, 1998; Mueller et al., 2010; Tjoelker et al., 2001). Therefore, PAR and photosynthesis productivity should theoretically be oscillating synchronously whereas Ta and respiration change at similar pace. However, the daily course of Ta often lags the daily course of sunlight and, thus, the daily course of photosynthesis often leads to the daily course of respiration (Baldocchi et al., 2001; Tang et al., 2005). During the growing season at our ecosystem, NEE variation depends strongly on photosynthesis that respiration has contributed less to NEE, resulting in PAR’s dominance.

At the diurnal scale, PAR remained as the primary driver for NEE compared to Ta during growing seasons. Higher common power and more regions with significant coherence were observed for PAR & NEE than for Ta & NEE (Figs. 2–4). Though PAR only functioned as a driver during the daytime, most NEE variation happened during the daytime when photosynthesis dominated (Fig. 6). During the daytime, PAR co-varied with NEE
synchronously, while Ta still lags NEE for 2–3 h. Only during complete nighttime, when photosynthesis was not possible, was Ta the primary driver and it co-varied with NEE with no time lag. Daytime length changes throughout a year but is longer than nighttime during the growing seasons in our ecosystem, further highlighting the importance of PAR in driving NEE at this scale.

At the seasonal scale, Ta replaced PAR as the major driver for NEE. Both Ta and PAR had significant common wavelet power with NEE, occasionally, but had no significant coherence for the entire series. However, LAI, the major direct driver for the NEE oscillations at this scale, is primarily determined by temperature rather than PAR, as suggested by the lags of both LAI and Ta to PAR. Though PAR is also commonly thought as an important driver of Ta as an energy source, LAI seems to respond mostly to temperature. For example, the leaf out/off time is determined by Ta rather than PAR.

At the annual scale, Ta remained as the primary regulator for NEE as compared to PAR. PAR led NEE ca. one month with no delay between NEE & Ta. This could be explained by the strong dependence of LAI/biomass dynamics on Ta; the ca. one-month lag of the LAI biomass (e.g., LAI) development to the progress of sunlight (e.g., PAR) (Fig. 7); and vegetation characteristics (e.g., phenology and LAI) determine the magnitudes and dynamics of gross productivity (Griffis et al., 2003; Penuelas and Filella, 2001). Numerous studies reported that it is Ta, not PAR that served as an important control of the variation of annual carbon fluxes in temperate forests in both time and space (Law et al., 2002; Yu et al., 2013).

The results from the PWC analysis further prove the different roles played by Ta and PAR across temporal scales. The PWC is powerful to provide the “stand-alone” relationship between two time series after removing the effect of a third factor (Ng and Chan, 2012). We observed insignificant partial coherence for Ta & NEE at the daily scale and for PAR & NEE at the annual scale (Fig. 6), suggesting a small or none “stand-alone” effect of Ta at the daily scale and of PAR at the annual scale. In contrast, we observed significant partial coherence for Ta & NEE at the annual scale and for PAR & NEE at the daily scale (Fig. 6), suggesting a significant “stand-alone” effect of Ta at the annual scale and of PAR at the daily scale.

4.3. Measurement uncertainty, nonlinear characteristics, and spectral leakage

Measurement uncertainty could be considered as a part of noise. Ta and PAR could be measured directly with guaranteed accuracy as long as the sensors function normally (±0.2 °C and ±5%, respectively, at 20 °C and normal humidity). The accuracy of LAI from MODIS Collection 5 is ca. 0.66–1.0 (i.e., RMSE) when all biomes are taken into account (Fang et al., 2012; Ryu et al., 2012). The NEE is often contaminated from both random and systematic errors that may mask some oscillating patterns. There is a growing recognition within the EC community that more attention must be paid on quantifying NEE uncertainties. However, it remains a challenging task. The conventional QA/QC protocols for processing the EC data, such as the Webb–Pearman–Leuning corrections, focus on systematic errors, but not random errors. Yet, it is well-known that random error is not normal and not linearly scaled with the magnitudes of fluxes (Richardson et al., 2006). We thus have assumed that the remaining error terms are red noise and applied the Monte Carlo simulations to just report the significant results.

Another uncertainty involved in quantifying the regulatory mechanisms is the nonlinearity embedded in our time series, where the wavelet is not a powerful tool for the processes. For example, ecosystem respiration is usually described as an exponential function of Ta (Eq. (1)), whereas canopy photosynthesis is considered as a hyperbolic function of PAR. To partly solve the problem, we ran XWT (lg (NEE), Ta), WTC (lg (NEE), Ta), XWT (sqt (NEE), PAR), and WTC (sqt (NEE), PAR) to linearize these variables (Figs. S1 and S2 in the Supplementary material). The new results from transformed data are consistent with our original results found in this paper (Figs. 2 vs. S1 and Figs. 3 vs. S2). Therefore, our findings are robust to some potential nonlinear characteristics.

See Figs. S1 and S2 as supplementary file. Supplementary material related to this article can be found in the online version, at http://dx.doi.org/10.1016/j.ecocom.2014.04.005.

Spectral/energy leakage is inherent of wavelet analysis, thus we must consider its effect. Our analysis has revealed significant power and coherence at four bands that peak at diurnal, daily, growing season, and annual scales. Significant results within each band beyond the peak might be caused by energy leakage from the central time scales, though none of these central time scales owned dyadic frequencies in terms of the time resolution (half-hour) of data, which reduces energy leakage (Peng et al., 2009). Therefore, there is no guarantee that all significant frequencies within each band are real components of the data. However, the significant results located at exactly the four central time scales were unlikely caused by energy leaking for neighboring frequencies. Firstly, it is unlikely for energy leakage to produce higher energy than from where it is leaked, even
Fig. 7. WTC for MODIS 8-day composite LAI and NEE (a), PAR (b), and Ta (c). The 5% significance level against red noise is shown as a thick contour. The cone of influence (COI) is shown as a thin line. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)
with multiple source frequencies. Secondly, the original data have clearly revealed significant cycles at these scales (Figs. 8 and S3). Finally, this is consistent with previous studies that frequencies related to these four scales are major components of NEE or microclimatic time series (Baldocchi et al., 2001; Goulden et al., 2004; Stoy et al., 2009).

See Fig. S3 as supplementary file. Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecocom.2014.04.005.

4.4. The implication to ecosystem modeling

Lessons learned from this study suggest that we should consider the proper primary drivers by time scale. Recognizing the time lag between Ta and NEE/photosynthesis at the daily scale and between PAR and NEE at the annual scale in ecosystem modeling will likely improve the estimation of NEE (Dietze et al., 2011; Stoy et al., 2013). Appropriate representation of ecosystem state variables (e.g., LAI, vegetation type) that respond to climatic variables is also pivotal for modeling NEE variation across seasonal/annual scales because they are important regulators of NEE at those scales. At other intermediate scales, it is always a challenge for ecosystem modelers to simulate the NEE variations (Baldocchi and Wilson, 2001; Siqueira et al., 2006; Stoy et al., 2013) due to the irregular and unpredictable events (e.g., precipitation, drought, frontal passages, etc.) that play important roles (Baldocchi et al., 2001; Stoy et al., 2005). Though the proportion of variation of NEE at the intermediate sales is relatively small (Fig. 1), careful records of these events would improve model performance.

5. Conclusions

We employed innovative wavelet tools for spectral analyses at different time scales for seven years of EC measurements. We found that Ta and PAR played different roles at given time scales. At the daily scale during the growing seasons, both PAR and Ta co- varied with NEE with high common power and coherence. However, PAR co-varied with NEE with no time delay and was the primary driver for NEE, while Ta was the minor one and lagged NEE for 2–3 h. This could be explained by the strong dependence of NEE on photosynthesis, the strong dependence of photosynthesis on PAR, and a lag of 2–3 h of the daily course of Ta to PAR. Significant coherence and high common power between Ta and NEE were detected at this scale, likely due to their common dependence on PAR. At the diurnal scales during the growing seasons, PAR is also the major climatic driver as daytime NEE variations overwhelm nighttime NEE variation, except for complete nighttime cycles, where Ta became the primary driver for NEE. At diurnal and daily scales during the non-growing seasons, both the oscillations of Ta and PAR are not significantly correlated with the oscillations of NEE. At the annual scale, high common power and coherence were observed for Ta & NEE and PAR & NEE throughout a year. However, Ta appeared to be the primary driver for NEE and co- varied with NEE synchronously, while PAR led NEE by ca. one month with insignificant influence on NEE after the common dependence on Ta was removed. At the seasonal scale, both Ta and PAR were not directly correlated with NEE, but Ta is likely more important than PAR for regulating NEE, because Ta determines LAI and other biological properties.

Our results supported our hypothesis that PAR is the primary climatic driver at short time scales (e.g., hours to days) and Ta is the primary climatic driver at long time scales (e.g., seasonal/annual). The unique influences of Ta and PAR on NEE by scale will have important implications for future ecosystem modeling on ecosystem NEE.

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