Variability in net ecosystem exchange from hourly to inter-annual time scales at adjacent pine and hardwood forests: a wavelet analysis

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Summary  Orthonormal wavelet transformation (OWT) is a computationally efficient technique for quantifying underlying frequencies in nonstationary and gap-infested time series, such as eddy-covariance-measured net ecosystem exchange of CO₂ (NEE). We employed OWT to analyze the frequency characteristics of synchronously measured and modeled NEE at adjacent pine (PP) and hardwood (HW) ecosystems. Wavelet cospectral analysis showed that NEE at PP was more correlated to light and vapor pressure deficit at the daily time scale, and NEE at HW was more correlated to leaf area index (LAI) and temperature, especially soil temperature, at seasonal time scales. Models were required to disentangle the impacts of environmental drivers on the components of NEE, ecosystem carbon assimilation ($A_c$) and ecosystem respiration ($R_E$). Sensitivity analyses revealed that using air temperature rather than soil temperature in $R_E$ models improved the modeled wavelet spectral frequency response on time scales longer than 1 day at both ecosystems. Including LAI improved $R_E$ model fit on seasonal time scales at HW, and incorporating parameter variability improved the $R_E$ model response at annual time scales at both ecosystems. Resolving variability in canopy conductance, rather than leaf-internal CO₂, was more important for modeling $A_c$ at both ecosystems. The PP ecosystem was more sensitive to hydrologic variables that regulate canopy conductance: vapor pressure deficit on weekly time scales and soil moisture on seasonal to interannual time scales. The HW ecosystem was sensitive to water limitation on weekly time scales. A combination of intrinsic drought sensitivity and non-conservative water use at PP was the basis for this response. At both ecosystems, incorporating variability in LAI was required for an accurate spectral representation of modeled NEE. However, nonlinearities imposed by canopy light attenuation were of little importance to spectral fit. The OWT revealed similarities and differences in the scale-wise control of NEE by vegetation with implications for model simplification and improvement.

Keywords: eddy covariance, hardwood forest, multiscale methods, net ecosystem exchange, orthonormal wavelet transformation, Pinus taeda, process-based models, southeastern USA.

Introduction

Net ecosystem exchange of CO₂ (NEE) is controlled by physical and biological processes that vary on multiple temporal scales (Olson et al. 1985, Berner and Lasaga 1989, Keeling et al. 1996, Baldocchi and Wilson 2001, Katul et al. 2001, Schimel et al. 2001, Gruber et al. 2002, Law et al. 2002). Thus, modeling NEE entails replicating measurements rich in spectral properties (e.g., Figure 1). Despite the complex controls on NEE and its components, ecosystem carbon assimilation ($A_c$) and ecosystem respiration ($R_E$), low-dimensional process-based models (i.e., models with few independent variables) remain desirable if prediction is accurately preserved. The challenge lies in creating models that are robust across the time scales of interest with simplifications that do not compromise the spectral characteristics of the model versus those of the measurements. Fourier and wavelet transformation are signal processing techniques used to quantify the spectral characteristics of data that vary across time or space, and are finding increasing application in the analysis and modeling of NEE time series (Baldocchi et al. 2001, Baldocchi and Wilson 2001, Katul et al. 2001, Katul and Siqueira 2002).

There are two primary complications to analyzing the spectral properties of eddy-covariance (EC)-measured NEE using standard Fourier transformation (FT). The first is that EC measurements are contaminated with missing data (“gaps”) caused by rain events, calibration down-time and, often, the suppression of turbulent exchange at night (Falge et al. 2001). The second is that NEE time series are generally nonstationary (Scanlon and Albertson 2001), meaning that the statistical properties of NEE time series change over time (Hui et al. 2003). In contrast to FT, wavelet techniques can efficiently re-
solve the contributions of processes that act on different frequencies in nonstationary and gap-infested EC-measured time series, and are thus a suitable tool for the interpretation and modeling of NEE (Katul et al. 2001). To date, wavelet analysis has not been used to compare the temporal responses of different ecosystems to common environmental drivers, or in conjunction with sensitivity analyses of process-based models.

Here, we employ orthonormal wavelet transformation (OWT) with the Haar basis function to analyze long-term (3.74 year) NEE measurements from a mid-rotation loblolly pine (Pinus taeda L.) plantation (hereafter PP) and a mature oak (Quercus)–hickory (Carya)-dominated hardwood forest (HW). These ecosystems are common on the landscape, serve as a model for succession in the southeastern US piedmont (Oosting 1942), lie adjacent to one another, and experience identical climatic and edaphic conditions. Thus, differential frequency responses to environmental drivers are due primarily to the effects of vegetation, and the motivation for this study was to understand temporal differences in the carbon dynamics of these typical southeastern U.S. ecosystems.

To illustrate, Figure 1 details key processes that are likely to affect a typical NEE spectrum on time scales from hours to years. Vegetation type is likely to alter the frequency distribution and the magnitude of the energetic modes at any given frequency. It is this response that should be captured by process-based models. Figure 2 describes the modeling approach taken here. Variability in environmental drivers, ecosystem characteristics and (potentially) model parameters are transferred by the model to modeled flux variability, which in turn is compared with the measured flux variability. The goal of this study was to find model transfer functions and parameterizations that capture this coupled physical/biological response on many time scales. Thus, our objective was to assess similarities and differences in how environmental and biological con-

Figure 1. A conceptual description of the environmental drivers that impact net ecosystem exchange of CO2 (NEE) at characteristic temporal scales. The abscissa is the time scale in units of years. Thus, $10^2$ is 1 year, and the large signal in the NEE spectrum (the ordinate) represents variability from the annual cycle. Likewise, the peak at $10^{-2.56}$ years represents diurnal variability. The area under the curve is the variance of the NEE time series at each scale. Figures 4–9 have an identical abscissa and should be read in the same fashion as this figure. The factors in bold are considered in this analysis. Abbreviations: $R_n$ = net radiation; PAR = photosynthetically active radiation; VPD = vapor pressure deficit; $T_a$ = air temperature; $T_s$ = soil temperature; and $\theta$ = volumetric soil moisture.

Figure 2. A schematic showing how models transfer variability across different time scales in physical drivers, ecosystem structure and model parameters to variability in fluxes. Here, variability is represented by the energy spectrum as a function of time scale as in Figure 1. Abbreviations: $Q_{10} = ecosystem respiration sensitivity to temperature; R_{10} = reference respiration at 10 °C; V_{max} = maximum carboxylation efficiency; NEE = net ecosystem exchange of CO2; LE = latent heat exchange; PAR = photosynthetically active radiation; VPD = vapor pressure deficit; $\theta$ = volumetric soil moisture; $T = temperature; R_n = net radiation; LAI = leaf area index; and LAD = leaf area density.
controls modulate the NEE spectra of PP and HW by using a combination of data analysis, simplified models and sensitivity analysis.

We briefly contrast the principal strategies for spectral analysis, FT and wavelet transformation, with an example involving synthetic NEE time series. We then show that wavelet spectral and cospectral analysis of environmental and flux data alone is insufficient to isolate the mechanisms that control NEE at all time scales, but does uncover interesting correlations between NEE and environmental drivers at daily and seasonal time scales. The data analysis thus motivated a modeling study to isolate the role of intrinsic variability in physiological attributes (e.g., maximum carboxylation capacity \( V_{\text{max}} \)) and canopy attributes (e.g., leaf area) from variability in environmental drivers on measured fluxes (see Figure 2). We used OWT to test if \( R_E \), \( A_c \) and canopy stratification models of varying complexity replicate the variance of the measured flux signal at time scales from hours to years. After choosing the most robust \( R_E \) model structure, we added complexity to account for processes that act on seasonal to inter-annual time scales, such as the onset of drought and canopy leaf area. Conversely, we employed a sensitivity analysis to determine which environmental drivers most control the \( A_c \) component of NEE on time scales from hours to years. We note that a global analysis on such controls has already been conducted for various biomes (Law et al. 2002); however, an analogous scale-wise or spectral analysis has not been undertaken to date. The goal of the modeling approach was not to find models that replicate every half-hour flux measurement (in this case 65,536 or \( 2^{16} \) potential measurements); rather, it was to find simple models that capture the essential modes of NEE variability to deconvolve the important temporal differences in the carbon cycling function of the two ecosystems.

Materials and methods

Spectral analysis

A detailed description of OWT for flux applications is found in Katul and Parlange (1995). However, for completeness, we review the basic principles with hypothetical examples illustrating the effect of data gaps and time-frequency shifts (i.e., non-stationarity) to demonstrate the advantages of OWT over FT in the analysis of EC time series.

The purpose of spectral analysis is to quantify the underlying energetic (or active) frequencies in a signal that varies in time or space, or both. Fourier transformation, which remains the most popular tool for spectral analysis, separates or “decomposes” a signal into a series of sinusoidal functions of different frequencies such that when all squared amplitudes are summed, the original signal variance is recovered (Parseval’s Identity).

Because the FT basis function is sinusoidal, rapid pulses and transients in the time series, e.g., the introduction of a gap or quick pulses caused by precipitation (Lee et al. 2004), affect all frequencies in the FT even though gaps and wetting events are localized and have clear physical time scales. Another difficulty with the sinusoidal basis function is a trend, linear or otherwise, which also affects all frequencies in the FT, a phenomenon known as red noise. Given that NEE time series are nonstationary (Scanlon and Albertson 2001), sinusoidal basis functions are not the optimum choice.

Wavelet transformation offers a reasonable solution to the aforementioned problems of discontinuity and nonstationarity by employing a finite basis function, called a mother wavelet, in the transformation. The mother wavelet is dilated (expanded and contracted) and translated across the signal and thus quantifies frequency as a function of time and scale. An infinite number of wavelet basis functions exist. The square-shaped Haar wavelet is ideal for analyzing spectral properties of NEE measurements because of its strong locality in the temporal domain (Katul and Parlange 1995, Katul et al. 2001, Scanlon and Albertson 2001) and for the accurate transformation of nonstationary and discontinuous data. An additional advantage of using wavelets for EC time series is that any time-independent bias in the EC measurements will not impact the spectral calculations because of the differencing properties of the wavelets.

In the graphical example in Figure 3, we introduce synthetic time series with “gaps” (Figure 3A) and non-stationarity (Figure 3B). The FT spectra of these signals are shown in Figures 3C and 3D, respectively. There are two distinct peaks in the FT spectra that correspond to the two dominant frequencies in the synthetic signal. Graphically, the sharp discontinuities in the time series (Figure 3A) add energy to the Fourier decomposition at multiple frequencies (Figure 3C). In contrast, the wavelet decomposition returns no measured variance when gaps in the synthetic signal occur (Figure 3E). Figure 3E is the wavelet “half-plane” that represents the frequency–time decomposition of the time series in Figure 3A using the Haar wavelet basis function. The OWT output in subsequent figures represents the mean of the wavelet coefficients at each power of two (excluding zero values generated by gaps) on the scale index (ordinate) of the wavelet half-plane.

For the nonstationary case, the FT in Figure 3D cannot readily determine where a shift in variance in the synthetic signal in Figure 3B occurs, which may be important to understanding ecosystem response to physical or biological drivers such as drought, or leaf-out at HW. The increasing variance of the nonstationary synthetic signal in (Figure 3B) is evident at the same times by a “whitening” of the wavelet half-plane (Figure 3F).

Practices designed to minimize the effects of non-stationarity on computing Fourier coefficients do so at the expense of accuracy. For example, employing short time FT to decompose nonstationary signals introduces errors near the edges of the moving windows that contain the sinusoidal basis function. Also, the size of the window remains arbitrary. Gap-filling techniques to obtain a continuous NEE data series (Falge et al. 2001) bias the spectral properties of NEE by the transfer function of the regression model or by constant values obtained from “look-up” tables.

The wavelet transform is continuous and the translation and dilation of the mother wavelet can occur at all points in the
time series. However, discrete sampling is usually desirable to retrieve a tractable number of wavelet coefficients and to avoid redundant information. The OWT uses a log-spaced discretization while fully preserving measured variance in the flux signal. The OWT allocates most of the coefficients to the rapidly varying (high frequency) scales and less to slowly varying (low frequency) scales. Graphically, in Figures 3E and 3F, OWT coefficients represent the mean of the squared wavelet coefficients at each power of two. For a data series of length $2^N$, OWT returns $2^N$ coefficients distributed across $N - 1$ time scales. Thus, the 3.74-year EC data records with 216 measurements analyzed here result in 15 discrete orthonormal wavelet coefficients representing time scales from 30 min to 1.875 years.

**Study sites**

The PP and HW EC towers lie 750 m apart in the Blackwood Division of the Duke Forest near Durham, North Carolina (35°58′41.430″ N, 79°05′39.087″ W, 163 m a.s.l.). The experimental site also includes EC measurements at a grass-covered forest clearing, not considered here, and the three ecosystems serve as a model of post-agricultural ecosystem succession in the SE US Piedmont (Oosting 1942). The soils are Enon silt loam and Iredell gravelly loam, low-to-moderate fertility Hap-hudalfs found throughout the region. An impervious clay pan underlies the research sites at about 30 cm belowground (Oren et al. 1998). Mean growing season precipitation is 632 ± 130 mm and mean annual precipitation is 1145 ± 180 mm. The measurement period was characterized by an increasingly severe drought that extended from summer 2001 until October 2002. The April–September growing season precipitation was about 1 SD below average in 2001, about 2 SD below average in 2002, and about 1 SD above average in 2000 and 2003. Thus, the measurement period captures well the range of hydrologic conditions experienced by the ecosystems.

The PP was established in 1983 following a clear cut and burn and comprised primarily *P. taeda* with a minor component of *Liquidambar styraciflua* L. and a diverse understory. Ecosystem development has not been managed after planting. Mean canopy height increased from 16 to 18 m, and emergent treetops to 19 m, during the 3.74-year measurement period, another source of nonstationarity at PP. The HW is classified as an uneven-aged (80–100-year-old) oak–hickory forest with *L. styraciflua*, and *Liriodendron tulipifera* L. also contributing to the canopy and similar understory species as at PP. Mean canopy height at HW was 25 m with some emergent treetops reaching to 35 m. More detailed descriptions of PP and HW can be found elsewhere (Ellsworth 1999, Pataki and Oren 2003).

**Eddy covariance measurements**

Fluxes of CO$_2$ and H$_2$O were measured with EC systems comprising triaxial sonic anemometers (CSAT3, Campbell Scientific, Logan, UT) and open-path gas analyzers (LI-7500, Li-Cor, Lincoln, NE) positioned above the canopy at 20.2 m at PP and 39.8 m at HW. Covariances were computed for half-hourly periods, and spurious data were filtered as described by Katul et al. (1997). A closed path gas analyzer (LI-6262, Li-Cor) was employed at PP before May 1, 2001. The Webb-Pearman-Leuning (Webb et al. 1980) correction for

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**Figure 3.** A synthetic time series with simulated gaps (A) and nonstationarity (B) with corresponding Fourier transformations (C, D) and discrete wavelet transformations with the Haar basis function, shown as the wavelet “half-plane” (E, F). The grayscale indicates the magnitude of the wavelet coefficients. The orthonormal wavelet transformation (OWT) output (Figures 4–9) represents the mean of the squared wavelet coefficients at each power of two (excluding zero values generated by gaps) on the “scale index” (ordinate) of the wavelet half-plane.
the effects of air density fluctuations on flux measurement was applied to scalar fluxes measured with the open-path Li-Cor LI-7500. Nighttime data were filtered based on the atmospheric stability threshold (Novick et al. 2004), which filters nighttime data if atmospheric stability is not near-neutral and if the peak of the source-weight function of the flux footprint, calculated using the approximate analytical model of Hsieh et al. (2000), exceeds the ecosystem dimension. The analytical footprint model, and thus the atmospheric stability threshold, is sensitive to friction velocity, sensible heat and ecosystem dimension. The HW flux measurements became available in October 2000. The HW NEE data prior to October 2000 were padded with zeros until 216 data points were obtained. For OWT analysis, it is common to pad series with zeros until a power of two is reached for computational efficiency (Torsen and Compo 1998). These zero-padded coefficients can be identified and removed in the wavelet spectral and co-spectral analyses.

**Micrometeorological measurements**

Micrometeorological variables were sampled every second and averaged every half hour at both ecosystems. Net radiation \( R_{\text{n}} \) (W m\(^{-2}\)) and photosynthetically active radiation (PAR; \( \mu\text{mol photons m}^{-2}\text{s}^{-1} \)) were measured at 22 m at PP and 45 m at HW with Q7 Fritschen-type net radiometers (REBS, Seattle, WA) and Li-Cor LI-190SA quantum sensors, respectively. Air temperature \( T_a \) and relative humidity (RH) were measured at about two thirds canopy height with HMP35C temperature/RH probes (Campbell Scientific). Soil temperature \( \theta_s \) was measured at 10-cm depth at both ecosystems in at least four locations. At PP, volumetric soil moisture \( \theta \) (cm\(^{-3}\)) was measured at four locations around the tower with CS615 soil moisture sensors (Campbell Scientific) that integrate from 0 to 30 cm belowground. At PP, \( \theta \) was taken to be the mean of these values. At HW, \( \theta \) was measured with ThetaProbe soil moisture sensors Type ML1 (Delta-T Devices, Cambridge, U.K.) positioned at 10- and 25-cm depths at 12 locations near the tower. To obtain a single value for \( \theta \) that is comparable to PP, mean \( \theta \) was computed for the 10- and 25-cm depths and these two values were further averaged to obtain site-wide \( \theta \).

**Leaf area index measurements**

At PP, the contribution to leaf area index (LAI; m\(^2\) m\(^{-2}\)) from *P. taeda* and understory trees was calculated based on needle or leaf elongation and litterfall measurements (Oren and Pataki 2001). At HW, LAI was determined with a Li-Cor LAI-2000 plant-canopy analyzer together with litterfall measurements. Leaf area density (LAD) was measured about once a month at about 1-m height increments at PP and at about 2-m increments at HW with a Li-Cor LAI-2000. The full protocol for determining LAI and LAD at PP can be found elsewhere (Oren and Pataki 2001, Pataki and Oren 2003).

**Models**

**Ecosystem respiration**

We estimated \( R_E \) from nighttime EC measurements (taken here to be periods where \( R_n < 0 \) ) in the absence of \( A_c \). We tested simple temperature-based \( R_E \) models for their ability to match the frequency characteristics of the measured \( R_E \), and then adjusted the \( R_E \) models to account for drivers that vary on time scales where the basic models fare poorly.

The popular \( Q_{10} \) respiration model, originally proposed by van’t Hoff (1884), has found wide applicability in soil and ecosystem respiration research (Raich and Schlesinger 1992, Winkler et al. 1996). For the \( Q_{10} \) model:

\[
R_{Q10} = R_{Q10}^{Q(T_{10})} \quad (1)
\]

where \( R_{Q10} \) is the reference respiration rate at 10 °C and \( Q_{10} \) is \( R_E \) sensitivity to temperature. We tested the frequency response of this model against \( R_E \) measurements with both \( T_a \) (abbreviated \( Q_{Q10} \)) and \( T_c \) (\( Q_{Q10} \)) as the independent variable. Slaytor (1906) first found temperature dependence in the \( Q_{10} \) parameter (Lloyd and Taylor 1994), and these observations have subsequently been confirmed for soil and ecosystem respiration (Lloyd and Taylor 1994, Kirschbaum 1995, 2000, Swanson and Flanagan 2001). However, soil respiration predictions based on temperature-insensitive parameters do not differ from those produced by temperature-dependent parameters at PP and HW (Palmeroth et al. 2005); thus we employed the \( Q_{10} \) model for this analysis. We also tested improvements to \( R_{Q10} \) by adding terms to account for \( \theta \), LAI, assimilated carbon and parameter variability (e.g., Janssens and Pilegaard 2003). These models are listed in Table 1 and described in Appendix A.

**Canopy carbon assimilation**

We defined \( A_c \) as the difference between daytime measured NEE and modeled \( R_E \). We considered both single layer (“big leaf”) and multilayer canopy assimilation schemes. In both cases, to a first approximation, \( A_c \) can be described by a Fick’s law analogy:

\[
A_c = g_c C_a \left( \frac{C_i}{C_a} - 1 \right) \quad (2)
\]

where \( g_c \) is canopy conductance to CO\(_2\), \( C_a \) is atmospheric CO\(_2\) concentration, and \( C_i \) is mesophyll CO\(_2\) concentration for the canopy or vertically averaged canopy layer.

This equation has three unknowns. The \( C_i/C_a \) ratio can be solved by employing a “closure” model, which models \( C_i/C_a \) using empirical relationships between stomatal function and environmental conditions. Multiple closure formulations exist (Katul et al. 2000), and we chose three to represent a range of simplifications and biophysical reality.

The simplest model, referred to as the Norman (1982) closure model, assumes a fixed ratio between \( C_i \) and \( C_a \) for the entire canopy:

\[
\frac{C_i}{C_a} = N_c \quad (3)
\]

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This simplification is surprisingly robust and has been upheld by both ecophysiological measurements (Ehleringer 1993, Ellsworth 1999) and models (Baldocchi 1994).

The Ball-Berry model is perhaps the most commonly used closure model (Ball et al. 1987, Collatz et al. 1991). After adjustment for use in Equation 2 (Katul et al. 2000), it takes the form:

\[
\frac{C_i}{C_a} = 1 - \frac{1}{m_R \cdot RH}
\]

where \( m_R \) is a dimensionless parameter meant to approximate both physiological responses and aerodynamic resistance at the leaf surface.

Because RH is a poor driving mechanism for stomatal response and gas exchange (Aphalo and Jarvis 1991, Monteith 1995, Campbell and Norman 1998), Leuning (1995) modified the Ball-Berry model to account for a more appropriate driving variable, vapor pressure deficit (VPD):

\[
\frac{C_i}{C_a} = 1 - \frac{1 - \Gamma}{m_L} \left( 1 + \frac{\text{VPD}}{D_o} \right)
\]

Here, \( m_L \) is analogous to the Ball-Berry \( m_R \), \( \Gamma \) is the leaf CO2 compensation point, and \( D_o \) accounts for species-specific sensitivity to VPD.

The other unknown in Equation 2 is \( g_c \). We modeled \( g_c \) using published relationships of stomatal sensitivity to \( \text{PAR} \) and VPD (Oren et al. 1999) that include data from PP and HW, with an adjustment for soil water limitations:

\[
g_c = \frac{1}{1.6} (m_{\text{PAR}} \cdot \text{PAR} + g_{\text{PAR}})(1 - m \log \text{VPD})g(\theta) \cdot \text{LAI}
\]

The first term converts stomatal conductance to \( \text{H}_2\text{O} \) to stomatal conductance to \( \text{CO}_2 \) by correcting for differences in molecular diffusivity, and \( m_{\text{PAR}} \) and \( g_{\text{PAR}} \) are fitted parameters. Multiplying by LAI converts stomatal conductance to \( g_c \). Parameter \( m \) is about 0.6 for a wide range of temperate plant canopies including PP and HW (Oren et al. 1999), and \( g(\theta) \) is a standard soil moisture reduction function:

\[
g(\theta) = \left\{ \begin{array}{ll}
1 & \text{if } \theta_R > 1 \\
1 - \left( \frac{\theta - \theta_R}{\theta_R} \right) & \text{if } 0 < \theta_R \leq 1
\end{array} \right.
\]

where \( \theta_R \) is the value at which \( \theta \) begins to limit \( g_c \) (Lai and Katul 2000, Novick et al. 2004) and \( \nu \) describes the curvature of the reduction function. For the single-layer canopy representation, \( A_c \) (Equation 2) can be solved for directly by combining Equation 6 with Equations 3, 4, or 5.

To simplify the sensitivity analysis, all parameters for the respiration, canopy conductance and single-layer \( A_c \) models were fit to the entire data sets by nonlinear optimization using the Gauss-Newton algorithm standard in MATLAB, unless otherwise stated. Initial parameter estimates were taken from literature sources where possible.

**Sensitivity analysis**

It is difficult to measure all biophysically important variables across time and space, and it is uncertain if the variability of all environmental drivers contributes to the observed flux variability (see Figure 2). To explore potential model and measurement simplifications, we performed a sensitivity analysis on single-layer \( A_c \) models by replacing measured variability with the global mean of \( \text{PAR}, \text{VPD}, \theta \) and LAI (using maximum LAI for HW models).

In the context of the sensitivity analysis, simple multilayer canopy models, with varying simplifications to the LAD pro-
file, were examined to test if more detailed model transfer functions are necessary (Figure 2) and to investigate the importance of nonlinear responses of \( A_c \) to the light environment of the canopy in wavelet space. We also examined the importance of including temperature and time dependence of the parameters that describe the biochemistry of photosynthesis, namely \( V_{\text{cmax}} \), as potential model simplifications (Campbell and Norman 1998, Ellsworth 2000, Wilson et al. 2001; see Appendix B). For multilayer canopy models, we introduced the Farquhar biochemical model for \( A_c \) as a function of \( C_i \) (Appendix B) and solved a system of three equations with three unknowns \( (A_c, g_c, C_i) \) at each canopy layer. We chose a layer height of 1 m for both ecosystems. Thus, the number of canopy layers increased from 15 to 19 at PP over the data record, and 38 canopy layers were used to describe HW. The canopy layering scheme included emergent trees. Spatial heterogeneity at HW was simplified by using mean LAI-2000 measurements from four directions at each canopy layer and only vertical LAD stratification was considered.

Although \( g_c \) places an important constraint on \( A_c \) (Schäfer et al. 2003), the system of equations in the multilayer model does not independently constrain \( A_c \) by \( g_c \) when \( g_c \) is low. Thus, after solving for multilayer \( A_c \) using Equations 2 and B1–B3, and the Leuning closure model (Equation 5), we adjusted multilayer modeled \( g_c \) with bulk canopy modeled \( g_c \) (Equation 6) and re-calculated \( A_c \) (Schäfer et al. 2003). Hence, the multilayer model only retains the nonlinearities of the leaf \( A_c \) with PAR relationship so that the vertically averaged \( C_i/C_a \) accounts for this nonlinearity. The photosynthetic parameters of the Farquhar model were taken from the literature, and thus may be seen as a “forward” model parameterization. Unlike the canopy conductance and single-layer models, the Farquhar parameters do not take the fitted parameter step described above.

**Results**

**Data analysis**

We normalized the flux and meteorological time series to have zero mean and unit variance for the purposes of the data analysis (Katul et. al 2001). We defined \( A_c \) as negative according to the micrometeorological convention, so negative wavelet cospectra correspond to either correlation with \( A_c \) or anti-correlation with \( R_E \). In the context of Figure 2, this analysis is a direct comparison with the environmental and biological drivers at the left and bottom of the figure, respectively, with the flux response on the right side of the figure.

At the daily time scale, the wavelet cospectrum between \( T_s \) and NEE was more negatively correlated at HW than at PP, but the wavelet cospectra between \( T_{a} \) and NEE were correlated to a similar magnitude at both ecosystems (Figures 4A and 4B). Both PAR and \( R_n \) were correlated to NEE at short time scales at each ecosystem, but the correlation was stronger at PP than at HW at time scales from 6 hours to 2 days. At the seasonal time scale, LAI, \( g_c \) and VPD were more negatively correlated to NEE at HW (Figures 4C and 4D). At both ecosystems, \( \theta \) was positively correlated to NEE at the seasonal time scale, particularly at HW. This corresponds to either correlation between \( \theta \) and \( R_E \) or anti-correlation with \( A_c \) if \( \theta \) is higher during

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**Figure 4.** Normalized wavelet cospectra between net ecosystem exchange of CO2 (NEE) and radiative environmental drivers at PP (A) and HW (B), and between NEE and hydrologic environmental drivers (C, D), noting that the two categories are not independent. The area under the normalized cospectrum represents the correlation coefficient between NEE and the signal analyzed. Abbreviations: PP = loblolly pine plantation; HW = mature oak-hickory dominated hardwood forest; \( R_n \) = net radiation; \( T_{a} \) = air temperature; \( T_s \) = soil temperature; PAR = photosynthetically active radiation; VPD = vapor pressure deficit; \( \theta \) = volumetric soil moisture; LAI = leaf area index; and \( g_c \) = stomatal conductance.
winter periods with low assimilation, as was the case here.

Figure 5 shows that the seasonal variations in fluxes, environmental drivers and ecosystem characteristics dominated the overall variability of the time series. As expected, the wavelet-spectra of LAI showed more concentrated activity at the seasonal time scale at HW when compared with PP given the “square-wave” nature of the LAI dynamics at HW (versus sinusoidal at PP). Figure 5 also shows that hydrologic drivers including θ and VPD were more variable at PP than at HW at weekly to monthly time scales. If these drivers “resonate” with NEE at these scales, there may be differences in the hydrologic function of the two ecosystems.

Direct comparison of NEE spectra with those of environmental drivers (e.g., temperature) or intrinsic drivers (e.g., LAI) may be misleading, because it is unclear how driver variability “injects” variability in NEE through effects on \( A_c \) and \( R_E \). For example, there was a strong seasonal spectral covariance between NEE and LAI (Figure 4), and the normalized wavelet spectra were similar at these time scales for both ecosystems (Figure 5). However, the cospectral and spectral relationship between NEE and LAI and NEE and temperature were similar (Figures 4 and 5). Clearly, variability in LAI and temperature impact NEE variability differently, but LAI and temperature are correlated. Models are necessary to deconvolve such impacts of environmental and intrinsic drivers on NEE and its components.

At PP, \( R_E \) exhibited no spectral gap on weekly to monthly time scales (Figures 6A and 6C) as observed with NEE measurements at this ecosystem (Figure 7) and in spectral analyses that employed the FT and flux gap filling (Baldocchi et al. 2001). Also, the spectral gap in NEE at weekly to monthly time scales was less pronounced at PP than at HW (Figure 7). This suggests that, at PP, \( R_E \) or \( A_c \), or both, are sensitive to the drivers that act on these time scales, namely periodic θ depletion at the weekly time scale, or drought over monthly time scales (Figure 1). Again, models are necessary to examine the mechanistic bases for these responses. In the context of Figure 2, the following is an analysis of model transfer functions and their parameterizations.

Models

Ecosystem respiration Variability in \( R_E \) models did not match measured \( R_E \) variability on time scales shorter than about 1 month (i.e., \( 10^{-1} \) years, Figure 6). The \( R_{EQ10a} \) represented a minor improvement over \( R_{EQ10s} \) on most time scales except for sub-weekly time scales at HW (Figures 6A and 6B). Employing the suggested \( R_E \) model improvements (Table 1, Equations A1–A3) did not influence the model fit on hourly to monthly time scales at either ecosystem (Figures 6C and 6D). At PP, \( R_{EQ} \) (Table 1) improved interannual \( R_E \) model spectral response, and \( R_{EAc} \) (Table 1) improved both annual and interannual model spectral response. The \( R_{ELAI} \) (Table 1) gave better spectral fit on seasonal time scales at HW (Figures 6C and 6D). Parameterizing the \( Q_{10} \) model for each winter and summer season individually (i.e., \( R_{EVPD} \)) improved model fit on annual and interannual time scales at both ecosystems (Figures 6E and 6F). For simplicity, we retain \( R_{EQ10a} \) for NEE model analysis.
Canopy carbon assimilation  Models generally matched measured NEE variability well, but the Ball-Berry closure model performed relatively poorly on time scales from 4 days to years at both ecosystems; the spectral energy of the Ball-Berry model did not match NEE measurements at these time scales (Figures 7A and 7B). Constant $g_c$ resulted in poor model fit on almost all time scales at PP and on all sub-weekly time scales at HW (Figures 7A and 7B). At both PP and HW, there was little difference between the Norman and Leuning model spectra (Figures 7A and 7B), but the latter fit better on inter-annual time scales at PP. We retain the Leuning closure model for the sensitivity analysis, which is meant to quantify which environmental and biological drivers most impact observed NEE, as well as the complexity of transfer functions required to capture NEE measurement variability (Figure 2).

Sensitivity analysis
Photosynthetically active radiation was the most important input for NEE model fit on short (hourly to weekly) time scales at both ecosystems (Figures 7C and 7D); the wavelet coefficients in models without PAR variability did not match the peak node in measured NEE on the daily time scale. At PP, VPD was the most important model input on monthly to bi-monthly time scales, $\theta$ on monthly time scales, and LAI on seasonal to interannual time scales. At HW, simplifying LAI by using its maximum value over-specified NEE model variability on multiple time scales (Figure 7D). The HW ecosystem was generally less sensitive to simplifications in VPD and $\theta$ than the PP ecosystem. However, NEE at HW was sensitive to $\theta$ on weekly time scales (Figure 7D), rather than on monthly time scales as at PP (Figure 7C).
Both ecosystems, particularly HW, were relatively insensitive to dramatic simplifications in LAD (Figures 8A and 8B) for modeling the $C_i/C_a$. Both PP and HW were sensitive to the assumption of temperature independence of the $V_{\text{cmax}}$ parameter on all time scales longer than hours and days, respectively (Figures 8C and 8D). The HW ecosystem was more sensitive than the PP ecosystem to modeling the seasonal dynamics of $V_{\text{cmax}}$ that result from leaf age (Ellsworth 2000, Wilson et al. 2001), particularly at weekly and monthly time scales.

**Discussion**

**Data analysis**

The peak in the wavelet cospectrum between PAR and NEE at the daily time scale at both ecosystems was an expected result of ecosystem light response. The stronger cospectral peak at the daily time scale at PP was due to the poor relationship between PAR and NEE at wintertime in the southeastern USA. The peaks in the cospectrum at the seasonal time scale between both NEE and LAI and NEE and $g_c$ at HW were expected and correspond to the “on–off” LAI seasonality of the deciduous ecosystem. The stronger seasonal correlations between NEE and both $T_a$ and $T_s$ at HW than at PP were unexpected and the models will be used to investigate these responses.

**Ecosystem respiration**

At both ecosystems, the greater variability at half-hourly time scales than at hourly time scales reflects the intermittent nature of EC-measured $R_e$ (Lee 1998), which may include storage and ejection of CO$_2$ from the canopy volume, the dynamic footprint that samples different vegetation patches depending on atmospheric conditions and wind direction, and measurement error in the EC systems (Goulden et al. 1996, Moncrieff et al. 1996). These are important sources of potential error.
(and perhaps bias) in interpreting the $R_E$ component of EC-measured NEE at short time scales. The models did not include stochastic components to account for random measurement error and were not spatially explicit to consider effects of the variable footprint. If the patches of forest differ in either state variables (e.g., $T_a$, $T_s$, or $\theta$) or sensitivity to the state variables (e.g., $R_{10}$, $Q_{10}$), then an ecological model with fixed parameters will always underestimate variability in measured $R_E$.

The PP ecosystem was sensitive to the drivers that act on weekly and monthly time scales as evidenced by the lack of spectral gap in measured $R_E$, but models did not capture variability at sub-monthly time scales at either PP or HW. Independent modeling studies (Schäfer et al. 2003) found that $R_E$ at PP was sensitive to $A_c$, and $\delta^{13}C$ analysis (Andrews and Schlesinger 2001, Mortazavi et al. 2005) showed that aboveground respiration contributes more to $R_E$ at PP than at HW. This analysis further supports the stable isotope analysis of Mortazavi et al. (2005), who showed that aboveground respiration contributes more to $R_E$ at PP compared to HW. This analysis further supports the stable isotope analysis of Mortazavi et al. (2005), who showed that aboveground respiration contributes more to $R_E$ at PP than at HW. For these ecosystems, sensitivity to $T_s$ or $T_a$ at short time scales can be a surrogate for determining how the aboveground fraction contributes to $R_E$.

In summary, models for EC-measured $R_E$ can give the desired spectral response on time steps of months or longer if the proper driving mechanisms are included, but sub-monthly variation in $R_E$ was not well captured in the widely used model formulations. We found that models with “improvements” (Equations A1–A3) often fared worse than simpler models, in-

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**Figure 8.** Wavelet spectral representation of multilayer net ecosystem exchange of CO$_2$ (NEE) models with simplifications in the vertical structure of the vegetation (A, B) and variability of the maximum carboxylation capacity ($V_{cmax}$) parameter (C, D). The abbreviation LAD refers to the model with measured leaf area density (LAD) that varies in time and space. Model LAD employs a simplified variation of LAD that varies in space but not with time. Model $V_{cmax}$ employs a $V_{cmax}$ parameter that varies seasonally and is sensitive to temperature. Model $V_{cmax,t}$ varies with temperature but not time, and model $V_{cmax,c}$ treats $V_{cmax}$ as a constant. Abbreviations: PP = loblolly pine plantation; and HW = mature oak–hickory dominated hardwood forest.
indicating that adding model complexity does not necessarily improve model skill, at least in replicating the spectral response of EC-measured \(R_E\). Simpler model transfer functions may improve spectral fit between models and measurements (see Figure 2). However, modeling parameter variability (e.g., \(R_{EVP2}\)) was an effective step in improving model fit to EC data on longer time scales. This suggests that simple hierarchical models with transient parameters, rather than complicated model transfer functions, may better describe \(R_E\) variability across time.

**Canopy assimilation models**

Models accurately replicated measured variability in NEE on daily to seasonal time scales despite the poor performance in replicating \(R_E\). However, the Ball-Berry closure model generally gave a worse spectral fit than treating \(C_i/C_a\) as a constant (i.e., the Norman model) because of accumulated errors from employing a biophysically unrealistic descriptor of gas exchange, RH, in the model transfer function. This effect was particularly pronounced on longer time scales at PP, where vegetation is active during winter and VPD is lower regardless of RH because of low temperatures. Independent studies have shown the Ball-Berry model to be inadequate for modeling \(A_c\) at PP (Kutal et al. 2000), and the results here extend this finding to longer temporal scales for two different ecosystems. Norman’s assumption of a constant \(C_i/C_a\) was robust at most time scales in both ecosystems, and variability in \(g_s\) dominated variability in \(A_c\). Thus, resolving variability in canopy conductance and not leaf biochemistry was the crucial step in accurately describing the spectral characteristics of NEE at PP and HW.

**Sensitivity analysis**

Our analysis suggests that resolving the temporal dynamics of all variable inputs at both ecosystems may be unnecessary to model the broad spectral response of NEE. For example, on time scales greater than four days, variability of NEE at PP can be explained by variability in \(V\), \(\theta\) and LAI alone, without variability in PAR (Figure 7C). Models of NEE at HW were generally amenable to simplifications in VPD, \(\theta\) and PAR on time scales longer than weeks. The PP ecosystem was relatively more sensitive to hydrologic drivers (i.e., VPD and \(\theta\)). Although HW and a similar forest were found to be relatively insensitive to hydrologic drivers, PP was found to be highly sensitive to these variables (Oren et al. 1998, Oren and Pataki 2001, Pataki and Oren 2003). This study additionally shows that NEE at PP is sensitive to \(\theta\) at longer time scales than HW, and further analysis can clarify these responses.

Measured \(\theta\) was never less than \(\theta_R\) (Equation 7) during the wetter years (2000 and 2003) at either ecosystem. During periods with high PAR (> 1200 \(\mu\)mol m\(^{-2}\) s\(^{-1}\)) in the May–August peak growing season of the mild drought year (2001), \(\theta_R\) was \(0.17 \text{ m}^3 \text{m}^{-3}\) at PP and \(0.16 \text{ m}^3 \text{m}^{-3}\) at HW (model parameters were otherwise fit to the entire data sets to simplify the sensitivity analysis). For the same periods in the severe drought year (2002), \(g_s\) at PP was slightly more sensitive to \(\theta\) (\(\theta_R = 0.19 \text{ m}^3 \text{m}^{-3}\)), whereas \(\theta_R\) at HW did not change. Parameter error is on the order of \(0.005 \text{ m}^3 \text{m}^{-3}\). These parameter values are close to those calculated for a nearby grass clearing (\(\theta_R = 0.19–0.20 \text{ m}^3 \text{m}^{-3}\)) (Lai and Kutal 2000, Novick et al. 2004), and alone suggest minor differences in the onset of drought sensitivity between the ecosystems. However, compared with HW, PP used water less conservatively and experienced longer periods for which \(\theta < \theta_R\). This resulted in the observed sensitivity to \(\theta\) on monthly and weekly time scales at PP and HW, respectively.

In 2001, \(\theta\) was less than \(\theta_R\) for 40% of the high PAR period (372 incidences/933 measurements) at PP, but only 10% of the time at HW (83/808). During the severe drought of 2002, \(\theta\) was less than \(\theta_R\) for nearly the entire peak growing season at PP (93%, 676/727), but less than half of the time at HW (46%, 444/968). Thus, variability in \(\theta\) impacted HW for shorter periods during drought, and this response was elucidated by the model sensitivity analysis. Integrated over the course of a year, there were small differences in mean \(\theta\) between PP and HW (Palmroth et al. 2005), but variability in \(\theta\) has different temporal consequences for NEE in these ecosystems. Modeling efforts should reflect the central role of hydrologic variability on the variability of the terrestrial C cycle in temperate ecosystems (Ollinger et al. 1998, Schäfer et al. 2003), noting that adjacent, edaphically similar ecosystems may have different temporal responses to a common drought.

The PP ecosystem was sensitive to the constant \(V_{\text{max}}\) simplification at most time scales including annual and longer, reflecting the importance of capturing dynamic leaf responses to
the wider range of environmental conditions experienced by the coniferous ecosystem. The sensitivity ofHW to modeling the seasonality of $V_{\text{max}}$ highlights the large variations in this parameter that result from leaf development, aging and senescence throughout the growing season in some of the species at HW (see Figure 4 in Wilson et al. 2001).

Major simplifications in the temporal and spatial profile of LAD did not compromise spectral fit, and this result is particularly evident at HW, where the diverse canopy structure makes any spatially explicit model of LAD a simplification. The simplified canopy profile (LAD$_{s}$) at PP fared worse than when using mean LAD. The LAD$_{s}$ incorporated LAD from only the overstory loblolly pine trees and ignored understory contributions, consequently assuming that all of the leaf area was in the active overstory, and thus overestimated NEE. The added steps of the multilayer $A_{c}$ model in the model transfer function (Figure 2) may be unnecessary to replicate NEE variability at longer time scales, given that the bulk LAI dynamics may dominate over the precise shape of the LAD profile.

In summary, the $A_{c}$ component of NEE models was generally amenable to simplifications of the canopy structure and biochemistry, and Figure 9 summarizes the sensitivity analyses by identifying the time scales at which including variability of environmental drivers most impacts the spectral response of the models. The $R_{b}$ models tested here generally require improvement, possibly by employing nonstationary parameters. In many cases, adding more variables and parameters did not result in improved spectral fit for the NEE models.

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References


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Appendix A: Ecosystem respiration models

We briefly describe additions to the “Q10” \( R_E \) model (Equation 1) that account for potential effects of \( \theta \), LAI and recently assimilated carbon on \( R_E \).

Various models have been used to describe the relationship between \( \theta \) and \( R_E \), and results appear to be highly site specific. Volumetric soil water influences \( R_E \) by reducing plant and microbial activity under dry conditions, and by inhibiting O2 diffusion and thus microbial function under wet conditions. We used a function, \( f(\theta) \), that adjusts \( R_E \) down during dry and wet periods while retaining temperature sensitivity across the range of intermediary \( \theta \):

\[
f(\theta) = \frac{1}{e} \left( 1 - \frac{1}{e} \right) \exp \left( - \left( \frac{\theta - a}{b} \right)^m \right)
\]  

(A1)

The three fitted parameters, \( a \), \( b \) and \( m \), adjust the point along the \( \theta \) scale at which the function reaches its maxima, the slope of the tails, and the shape of the tails, respectively (Figure A1). The model \( R_{EB} \) is obtained by multiplying Equation 1 by Equation A1 (Table 1).

Standing biomass and productivity are important determinants of \( R_E \) at PP and HW (Janssens et al. 2001, Pataki et al. 2003, Mortazavi et al. 2005). The effects of respiring biomass and recently assimilated carbon on \( R_E \) can be modeled hierarchically where \( Q_{10} \) model parameters are a function of respiring biomass, \( A_c \), or environmental drivers, or by adding additional terms to the \( R_E \) model. To keep the analysis simple, we chose the latter. We took LAI to be a surrogate for respiring biomass and added a linear model component (after Reichstein et al. 2003) to \( R_{EQ10a} \):

\[
R_{ELAI} = R_{10Q_{10}^{(T_{\dagger} - 10)/10}} + cLAI + d
\]  

(A2)

where \( c \) and \( d \) are fitted parameters.

It is difficult to determine the effects of \( A_c \) on \( R_E \) using EC because \( A_c \) is not measured directly. The sum of daytime NEE was used as a surrogate for \( A_c \), and data from the literature were used to estimate the optimum window to account for the effects of \( A_c \) on \( R_E \). Andrews et al. (1999) found that respired CO2 in the top 15 cm of soil was depleted in \( ^{13}C \) within 1 week of fumigation in the \( ^{13}C \)-labeled elevated CO2 rings of the FACE experiment at PP. Root respiration of assimilates can occur within 12 h as evidenced by \( ^{14}C \) analysis of 3-m-tall Populus trees, for which the \( ^{14}C \) pulse effect was negligible after 2 weeks (Horwath et al. 1994). Four days was a sufficient window to identify the effect of VPD on \( \delta C_{\dagger} \) through its effect on stomatal conductance and \( A_c \) at PP and HW (Mortazavi et al. 2005). Thus, the 2-week cumulative sum of NEE (NEE$_{cum}$) was considered to be a conservative window for modeling the effects of carbon assimilation on \( R_E \) for both ecosystems, and the model \( R_{EAc} \) takes the same form as Equation A2:

\[
R_{EAc} = R_{10Q_{10}^{(T_{\dagger} - 10)/10}} + h\text{NEE}_{cum} + j
\]  

(A3)

where \( h \) and \( j \) are fitted parameters.

In addition to the above \( R_E \) model improvements, we tested two variations of the \( Q_{10} \) model where the parameters are fit for combined summer and winter periods (abbreviated \( R_{EVPP1} \)), or for each summer and winter period separately (\( R_{EVPP2} \)). These models are meant to resemble a hierarchical model structure, where independent variables influence the parameters of a structurally simple model.

Figure A1. The shape of \( f(\theta) \) from Equation A1 for different \( a \) “scale” (A), \( b \) “slope” (B) and \( m \) “shape” (C) parameters.
Appendix B: Farquhar photosynthesis model

The Farquhar model is described in detail elsewhere (Farquhar et al. 1980, Collatz et al. 1991). Briefly, leaf-level photosynthesis is the product of a system of multiple limitations arising primarily from light-driven electron transport \( J_E \) or ribulose biphosphate carboxylase-oxygenase (Rubisco) activity \( J_C \). Thus:

\[
A_s = \min \left( \frac{J_E}{J_C} \right) \tag{B1}
\]

\[
J_E = \alpha e_m \text{PAR} \frac{C_i - \Gamma}{C_i + 2\Gamma} \tag{B2}
\]

\[
J_C = \frac{V_{\text{max}} (C_i - \Gamma)}{C_i + K_{CO_2} \left( 1 + \frac{O_2}{K_{O_2}} \right)} \tag{B3}
\]

where \( \alpha \) is leaf PAR absorptivity, \( e_m \) is maximum quantum efficiency for CO2 uptake, and PARi is PAR at canopy layer i. We used a simple light attenuation model after Campbell and Norman (1998) to model PARi without consideration of sunlit and shaded foliage or any penumbral effects. Parameter \( \Gamma \) is the leaf CO2 compensation point as in Equation 5, O2 is atmospheric O2 concentration, \( V_{\text{max}} \) is maximum Rubisco activity per unit leaf area, and \( K_j \) describes a temperature-dependent kinetic parameter that takes the form:

\[
K_j = K_{j,25} \exp(\gamma(T_L - 25)) \tag{B4}
\]

where the subscript \( j \) refers to either CO2 or O2, \( K_{j,25} \) is the parameter value at 25 °C, \( \gamma \) is a temperature coefficient and \( T_a \) was used to approximate leaf temperature \( T_L \). We used general Farquhar parameter values from Campbell and Norman (1998) and tested model sensitivity to the temperature dependence (Equation B4) and seasonal variations in the \( V_{\text{max}} \) parameter. At PP, seasonal trends in \( V_{\text{max},25} \) were taken from other studies conducted at the site (Ellsworth 2000). At HW, temporal variations in \( V_{\text{max},25} \) were assumed to follow the relationship between leaf age and \( V_{\text{max}} \) (Wilson et al. 2001). Measured \( V_{\text{max}} \) (Naumburg et al. 2001) was used for understory species in both ecosystems.