

JGR Biogeosciences

RESEARCH ARTICLE

10.1029/2019JG005148

Key Points:

- The diurnal variation in soil respiration is driven primarily by *PAR* (surrogate for photosynthesis), whereas temperature and soil moisture affect primarily synoptic (8–15 days) and seasonal (15–30 days) variability, respectively
- Soil respiration lagged *PAR* by 1.5 to 3 hr and was independent of vegetation height
- The discrete and nonoverlapping influences from different factors call for a revision of current respiration models so as to realistically capture their temporal domain of influence

Supporting Information:

- Supporting Information S1
- Data Set S1

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Citation:

Mitra, B., Miao, G., Minick, K., McNulty, S. G., Sun, G., Gavazzi, M., et al. (2019). Disentangling the effects of temperature, moisture, and substrate availability on soil CO₂ efflux. *Journal of Geophysical Research: Biogeosciences*, 124. <https://doi.org/10.1029/2019JG005148>

Received 24 MAR 2019

Accepted 6 JUN 2019

Accepted article online 20 JUN 2019

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(continued)

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Disentangling the Effects of Temperature, Moisture, and Substrate Availability on Soil CO₂ Efflux

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Abstract Soil respiration (R_s), the largest carbon emission flux in ecosystems, is usually modeled as an empirically parameterized function of temperature, and sometimes water availability. The likely contribution by other factors, such as carbohydrate substrate supply from photosynthesis, has been recognized, but modeling capacity to use this information is limited. Wavelet transformations of the residuals of a seasonal Q_{10} temperature response model indicated structure at different temporal scales. We hypothesize that this indicates the lack of explicit representation of relevant processes in the models. Using cross-spectral analysis, we found that time series of photosynthetically active radiation explained most of the diurnal variation, temperature, explained variability at multiple time scales (diurnal-synoptic), whereas volumetric soil water content correlated with variability in R_s at scales 15–30 days. The results suggest that the time domains of influence for different driving variables of R_s are discrete, and largely nonoverlapping, and represent functional relationships between soil biological activity and its constraints. Analysis of phase angles showed that R_s lagged photosynthetically active radiation by 1.5–3.0 hr. As this time lag was the same in both young and mature trees, with more than fivefold difference in transport distances, we hypothesize that this finding adds to the body of literature that support the pressure-concentration-wave model of carbohydrate availability in plants.

Plain Language Summary “Soil respiration” (R_s) is the net emission of carbon dioxide (CO₂) from the soil to the atmosphere. R_s has traditionally been quantified as a function of soil temperature, even though it originates from a suite of biological processes in the soil. Recent experimental studies have shown strong dependence of both plant root and microbial activity on plant-internal carbohydrate status. Here we report how different physical (soil temperature and soil moisture) and biological (plant carbohydrate supply, approximated with photosynthetically active radiation [*PAR*]) process covary with soil CO₂ emissions in two forest stands of different age. The individual and pairwise variation in R_s , soil temperature, soil moisture, and *PAR* time series at different frequencies was used to infer causal relationships between them. Environmental factor temperature and soil moisture significantly covaried with R_s at weekly to seasonal time scales, whereas diurnal variability of R_s was attributed to carbohydrate substrate availability. The consistent 1.5- to 3-hr time lag between R_s and *PAR* (as a proxy for carbohydrate availability) did not differ between forests of different stature. We hypothesize that this suggests that carbohydrate availability throughout the plant was regulated by pressure-concentration waves from phloem loading rather than actual mass transport of the loaded carbohydrates.

1. Introduction

Soil respiration (R_s) is an important metric of ecosystem metabolism (Ryan & Law, 2005) and represents the largest source of carbon dioxide (CO₂) emitted to the atmosphere (Barron-Gafford et al., 2011). It represents the aggregate metabolic activity of roots and rhizosphere symbionts (autotrophic respiration, R_a) and free-living microbes in the soil that decompose organic matter (heterotrophic respiration, R_h ; Hanson et al., 2000). Regulated by both environmental and biotic drivers, each of these component processes have different temperature sensitivities. Yet in ecosystem and Earth system models, they are often treated as a single process described with a simple temperature response function (Davidson et al., 2006; Kirschbaum, 1995; Lloyd & Taylor, 1994). While capturing long-term mean system behavior (Carey et al., 2016), the temperature-

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based models lack specificity with regard to underlying mechanisms and are unable to resolve short-term perturbations. As a result, uncaptured variability in soil carbon fluxes remains a key source of uncertainty in global carbon cycle models (Friedlingstein et al., 2006, 2014; Suseela et al., 2012).

Factors such as soil water content (θ) and substrate availability have long been recognized as additional controls on R_s and models incorporating these factors have been analyzed (e.g., Fang & Moncrieff, 2001). For example, the effect of θ has been added to the Q_{10} model as an additive (Chang et al., 2012; Van Meeteren et al., 2007), multiplicative (e.g., Davidson et al., 1998; DeForest et al., 2009) and even a nested term (Miao et al., 2013). While all these formulations can increase model fit, they often lack universality that would apply across sites and environmental conditions, possibly due to other, still unaccounted for processes, for example, transient mineralization spikes triggered by rain pulses in arid sites, known as the “Birch effect” (Jarvis et al., 2007), and hydraulic redistribution (Cardon et al., 2013; Kieft et al., 1987; Xu et al., 2004). Similarly, the importance of substrate supply for R_s has been conclusively established following Hogberg et al. (2001) and has since been confirmed in many ecosystems (Bahn et al., 2009; Baldocchi et al., 2006; Han et al., 2007). However, models accounting for secondary drivers of R_s remain few and site-specific (e.g., Reichstein et al., 2003; Vargas & Allen, 2008).

Another layer of complication to developing multiparameter R_s models is that different controlling variables may operate at different time scales, exhibiting lagged responses, and both direct and indirect effects (e.g., time lags due to diffusion; Kuzyakov & Gavrichkova, 2010; Mencuccini & Holttta, 2010). Combined, these factors affect the time domain of R_s response (Reichstein & Beer, 2008; Vargas et al., 2011). The interaction of these factors and processes is manifest in ontogenetic changes in ecosystem development—as plants grow, progressively colonize the soil volume, and their allocation patterns shift according to changes in limiting resources—the proportionality of different respiration components also changes (Amiro et al., 2010; Desai et al., 2008; King et al., 1999; Magnani et al., 2007; Noormets et al., 2007; Noormets et al., 2012). Yet the direction of the age-related change can vary. Some studies have found increased soil respiration with stand age-driven primarily by increase in root biomass and soil organic carbon (Litton et al., 2003; Xiao et al., 2014), while others have reported decreases in R_s , attributed to decreased fine root activity (Gong et al., 2012; Wang et al., 2002), and yet others have observed no change with stand age (Saiz et al., 2006; Tedeschi et al., 2006).

In the current study, as a first step toward improved understanding of the multitemporal relationship of soil respiration with biotic and abiotic drivers, we analyzed the performance of a conventional Q_{10} function model of soil respiration along the time domain (Braswell et al., 2005). The conventional “lumped” error analysis (e.g., root-mean-square error or Nash-Sutcliffe efficiency; Nash & Sutcliffe, 1970) is blind to any scale dependence (Reusser et al., 2009). The inability to identify the timing of model errors can prevent comprehensive model improvement (Liu et al., 2011). Second, we analyzed the cospectra and phase relationships of R_s with soil temperature (T_s), θ , and photosynthetically active radiation (PAR). The work was carried out in two different-aged loblolly pine plantations with different structural characteristics, and among years with contrasting water availability. The study site was located on drained organic soil in the lower coastal plain of North Carolina, where the relative contributions from different respiratory processes and driving variables were expected to differ. The main objectives of this study were (1) frequency domain error analysis of a temperature response function fit to R_s and (2) analyze the multitemporal relationship of R_s to θ , T_s , and photosynthesis.

2. Methods

2.1. Study Sites

The study site was located near the town of Plymouth in Washington County on the lower coastal plain of North Carolina (35.8°, -76.67°). Owned and managed by Weyerhaeuser NR Company, and known locally as “Parker Tract,” the area is dominated by loblolly pine (*Pinus taeda*) in roughly 1- to 2-km² block plantings. The study sites captured the juvenile precanopy closure and midrotation closed canopy states of stand development.

A network of parallel ditches (90-100 cm deep; 80- to 100-m spacing) were installed to improve stand productivity and reduce stress from high soil water content during wet periods. Based on long-term records (1945-

2010), average annual precipitation across the site was $1,308 \pm 201$ mm, that was distributed uniformly throughout the year (Sun et al., 2010). Mean annual temperature was 15.5°C with the highest and lowest temperatures occurring in July (26.6°C) and January (6.4°C), respectively. Within Parker Tract, two blocks (US-NC1 and US-NC2) of different age were selected for this study (Noormets et al., 2012; Sun et al., 2010). Mean stand age of US-NC1 and US-NC2 in 2005 was 1 and 13 years, respectively. The vegetation structure (height, diameter at breast height, and biomass) differed among the stands (Table 1; Noormets et al., 2012). A complete description of the difference between the two sites has been provided in the online supplement (Text S1 in the supporting information).

2.2. Micrometeorological and R_s Measurements

Meteorological variables measured above canopy at both sites included air temperature (T_a) and PAR (LI-190, Li-Cor, Lincoln, NE, USA; starting June 2010 PAR-Lite, Kipp & Zonen, Delft, Netherlands). PAR was gap-filled by incoming shortwave radiation (SWR_{in}) in 2011 at US-NC1. PAR was used as a substitute for substrate availability, similar to Vargas et al. (2010). Instrument height was 6 m until February 2008 at US-NC1, which was then increased to 11.6m from August 2008 onward. Instrument height at US-NC2 throughout the study period was 22.5 m.

Continuous R_s was measured near the central instrument tower on a permanently installed PVC collar with a soil respiration measurement system that included an automated soil CO_2 efflux chamber (LI8100-104, Licor Inc). The spatial representativeness of the single autochamber was validated against 30 spatially distributed survey measurement locations (Noormets et al., 2012). The instantaneous fluxes, annual integrals, and temporal dynamics were all well captured by the autochamber, lending confidence that the spectral analysis characterizes the stand as a whole.

R_s was measured at the US-NC1 site from 2009 until 2012 and has been continuously monitored at the US-NC2 site since 2005. R_s and micrometeorological data were collected at 30-minute intervals. Gaps in R_s data were due to multiple factors including power problems, system shutdown due to development of excessive humidity inside chambers and high flux coefficient of variation (Miao et al., 2013). On account of significant gaps in the data (>90%) during the growing season, certain years (e.g., 2008 and 2009 in US-NC2) were excluded from our analysis. Soil temperature was measured at 5-cm depth (T_{s5}) with a Campbell CS 107 temperature probe. Volumetric soil water content (θ) in the top 30 cm was measured with a Campbell CS616 (CS) water content reflectometer (time domain reflectometer). Daily average precipitation data for the town of Plymouth, located less than 5 miles from the study site, were obtained from the National Climatic Data Center (NCDC; <https://www.ncdc.noaa.gov/cdo-web/>).

2.3. R_s Modeling

As the site was not water-limited, an exponential Q_{10} function was used to model the half-hourly R_s measurements (van't Hoff, 1898):

$$R_s = R_{\text{ref}} Q_{10}^{(T_s - 10) / 10} \quad (1)$$

Reference respiration, R_{ref} , refers to mean R_s at 15°C while Q_{10} (unit less) quantifies the temperature sensitivity of R_s . As the site remains characteristically warm for most of the year, a 15°C base temperature was used for doubling of respiration with a 10°C increase in temperature. R_{ref} and Q_{10} parameters were obtained by minimizing the residual sum of squares. The difference between measured and modeled R_s was identified as the model residuals (R_r).

2.4. Spectral Analysis

Wavelet spectral decomposition was utilized to analyze the energetic frequencies of R_s and to relate those frequencies with the timescales of variability in biotic and abiotic drivers. As the time series are nonstationary and discontinuous, wavelet transformation (WT) is an appropriate tool for spectral analysis compared to standard Fourier techniques (Cazelles et al., 2008). Mathematical description of the different wavelet analyses incorporated into this study has already been well documented, and therefore, only a brief summary is provided here (Grinsted et al., 2004; Katul et al., 2001; Stoy et al., 2005; Torrence & Compo, 1998; Vargas et al., 2010).

Table 1
Summary of Mean Diameter at Breast Height (dbh) and Height of Pine Trees Greater Than 5" Diameter

Year	US-NC1				US-NC2			
	Pine dbh (cm)	Pine Height (m)	Aboveground biomass (trees; gC/m ²)	Total root biomass (gC/m ²)	Pine dbh (cm)	Pine Height (m)	Aboveground biomass (trees; gC/m ²)	Total root biomass (gC/m ²)
2004		0.2	0.1	0.03	24.5	11.9	3,727	925
2005		0.7	6.1	1.4	25.8	12.6	4,228	1,050
2006	2	1.6	56.5	11.9	26.8	13.5	4,814	1,195
2007	4.3	2.8	269.7	52.8	28	15.1	5,642	1,402
2008	6.5	3.9	529	131.2	28.7	16.0	6,236	1,547
2009 ^a	10.2	5.7	1,204.7	234.60	29.4	16.5	6,741	1,671
2009					30.4	16.6		
2010	10.6	6.9	1,899.1	362.90	31.6	17.4	2,892	720
2011	14.9	8.0	2640	518.5	33.2	17.7	3,182	794
2012	16.7	9.2	3,202.5	643.5	34.4	18.3	3,377	846
2013					35.7	19.0	3,736	946
2014					36.6	19.5	4,252	1,088

Note. Summary of aboveground biomass and total root biomass for both sites (US-NC1 and US-NC2) have also been provided.

^aThinning was conducted at US-NC2 in 2009.

Wavelets are mathematical functions characterized by a mean value of zero and localized in both time (t) and frequency. WT of any time series $x(t)$ involves convolution by a set of subwavelets to produce a third function (Wave(τ, s)), which has both a real and imaginary component as shown below:

$$\text{Wave}(\tau, s) = \sum_t x(t) \frac{1}{\sqrt{s}} \psi^* \left(\frac{t-\tau}{s} \right) \quad (2)$$

where ψ^* is the complex component of the Morlet function (ψ).

WT allows the microscopic analysis of any time series by allowing the time scale to be stretched (or dilated) by scale s (i.e. frequency resolution) along the localized time index τ . WT of R_s therefore offers the advantage of quantifying soil carbon flux as a function of both time and frequency. It allows the flexibility of the local analysis of R_s , whereby it dilates the carbon flux time series to quantify low-frequency oscillations, as well as compresses it to a short function to analyze high-frequency components. However, on account of Heisenberg's uncertainty principle, accurate characterization of both these features (s, τ) at the same time is not always possible.

Continuous wavelet transformation (CWT) analysis with the Morlet basis function (Grinsted et al., 2004) offers a good trade-off between the time and frequency resolutions. The parameter of interest in this complex transformation, wavelet power, is defined as the amount of energy (i.e., average variance) present in the frequency domain at any particular period (i.e., diurnal, synoptic, or phonological). Moreover, WT can also provide insight into the nature of the temporal changes of the different periodic components of R_s over time. This is possible by drawing conclusions about the synchronization between R_s and biotic (photosynthesis, approximated with PAR) as well as abiotic factors (T_{s5}, θ) at different temporal resolutions using cross-WT (XWT).

Analogous to cross correlation at multiple time points, XWT has been successfully applied to analyze the phase relationship between different processes (Grinsted et al., 2004). WT of single time series (R_s, R_t), as well as XWT (R_s and T_{s5}, R_s and θ , and R_s and PAR) generated wavelet power averages along with significance levels of the averages. XWT analysis also produced "heat plots" that provide a graphical representation of the convolution of the two time series. Analysis of the phase difference between R_s and T_{s5}, R_s and θ , and R_s and PAR from the heat maps allows one to quantify causality between response and effector variables, as well as calculate the time lag between the two time series (Banfi & Ferrini, 2012; Grinsted et al., 2004; Vargas et al., 2010). Any delay between R_s and T_{s5}, R_s and θ , or R_s and PAR from the phase difference estimation can provide insight about nature of mechanisms regulating soil carbon flux.

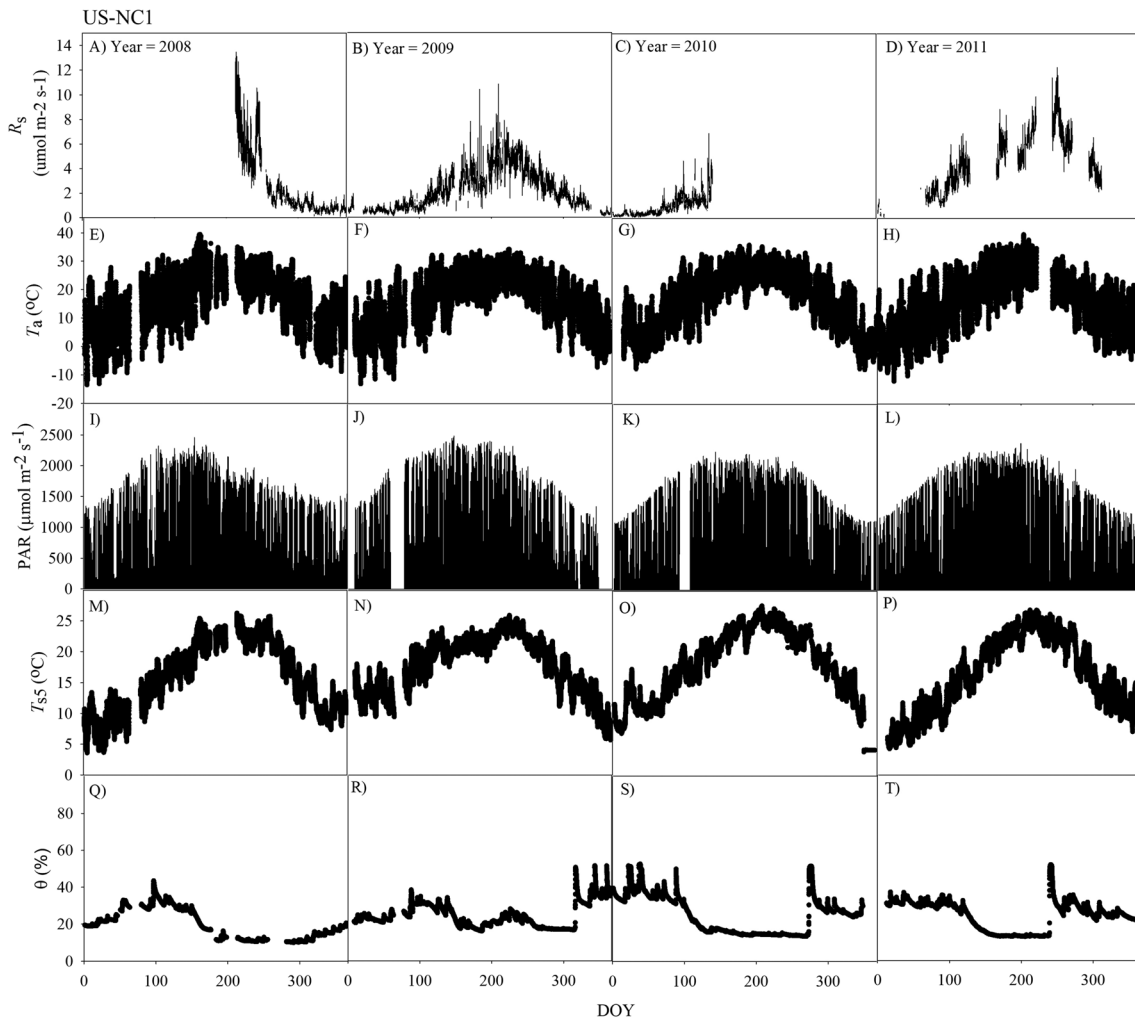


Figure 1. Seasonal variation of (a–d) 30-min soil respiration (R_s), (e–h) air temperature (T_a), (i–l) photosynthetically active radiation (PAR), (m–p) soil temperature at 5 cm depth (T_{s5}), and (q–t) volumetric soil water content at 30-cm depth (θ) for US-NC1 across different years (2008, 2009, 2010, and 2011).

A complete description of the interpretation of the images generated from XWT analysis has been provided in the online supplement (Text S2). The phase difference between PAR and R_s at the diurnal frequency during the growing season (days of year 100–300) was converted to lag time. The statistical significance (5 % significance level) of WT and XWT analyses was analyzed within the cone of influence (COI) using Monte Carlo methods (1000 simulations). The surrogate data required for significance analysis were generated using white noise. The minimum and maximum sampling rates were 3 hr and 100 days, respectively. The maximum sampling rate was not extended beyond 100 days because uncertainty of the wavelet coefficients impacted the cone of influence.

Gaps in R_s and the meteorological data were padded with zeros, which avoids wrap-around effects without introducing additional spectral information (see Considerations in the supporting information). WT and XWT analyses require the data series to be continuous. Therefore, in order to further ensure that the results generated from CWT analyses were robust and not an artifact of padding the time series with zero, we conducted WT (and XWT) analyses of null time series (of white color) with the same gap structure as the observations. This allowed us to identify the frequencies that have significant erroneous power and hence were excluded from subsequent discussions. Uncertainties from gaps and collinearity in data as well as sampling points have been summarized in the online supplement section (Text S3).

All time series were normalized to have zero mean and unit variance prior to wavelet analysis. Nonlinear regression modeling and continuous wavelet analysis were conducted in R (version 3.3.2, R Core Team,

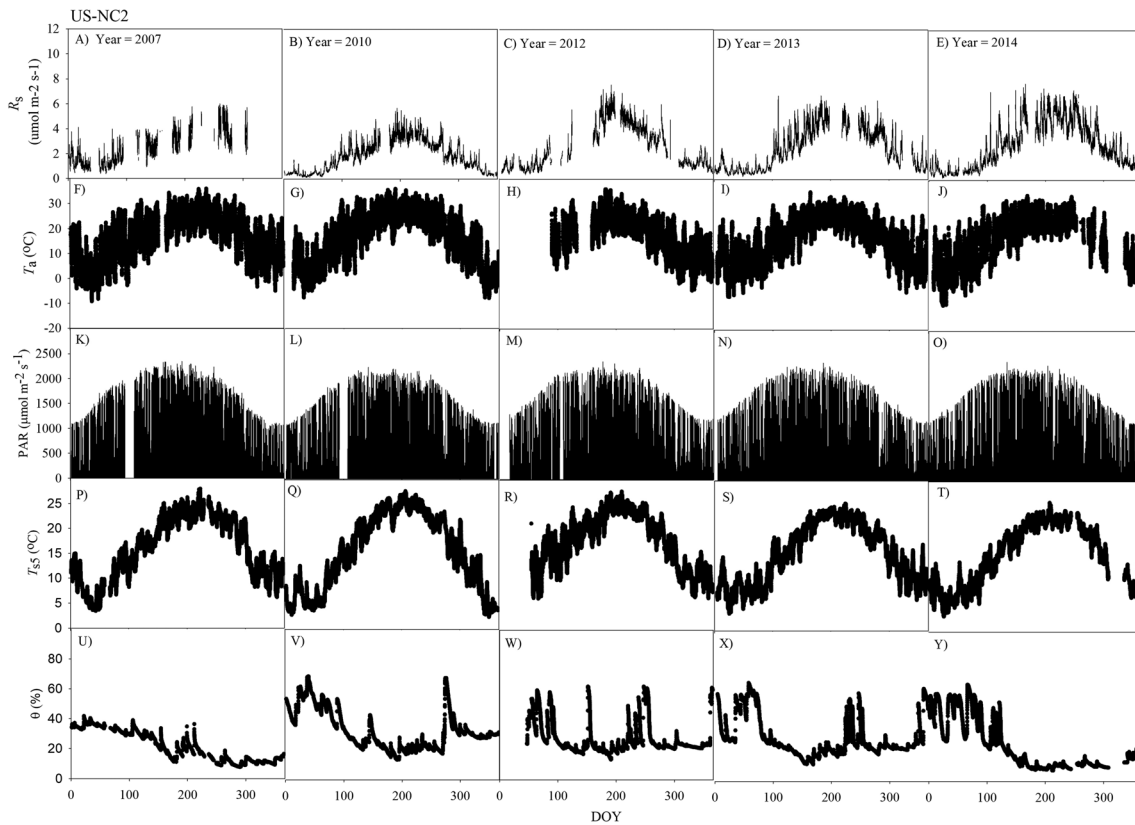


Figure 2. Seasonal variation of (a–e) 30-min soil respiration (R_s), (f–j) air temperature (T_a), (k–o) photosynthetically active radiation (PAR), (p–t) soil temperature at 5-cm depth (T_{s5}), and (u–y) volumetric soil water content at 30-cm depth (θ) for US-NC2 across different years (2007, 2010, 2012, 2013, and 2014).

2016) using the “nlrwr” (Ritz & Streibig, 2008) and “WaveletComp” (Roesch & Schmidbauer, 2014) packages respectively.

3. Results

The study period captured hydrologic variability at both sites (Figure S1 in the supporting information), with annual rainfall ranging from 854 to 1,609 mm (65–123% of 30-year normal). Peak midseason soil CO_2 efflux was greater in US-NC1 than US-NC2 (Figures 1 and 2), ranging from 4 to 11 $\mu\text{mol } CO_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. The annual temperature response to soil captured 75–85% of variability in R_s (extreme site-years are shown in Figure 3a and 3b; other years yielded a similar pattern and are not shown). WT analysis of the residuals of the annual model fit exhibited consistent spectral peaks from diurnal to synoptic and phenological timescales (from a few to 64 days; Figures 3c and 3d). The spectral signatures in the R_s time series produced by WT (Figures 4a–4i) analysis indicate significant cospectral peaks at multiple timescales.

The cospectrum between T_{s5} and R_s shows peaks at diurnal, synoptic, and phenological scale (Figures 4j–4r). The heat plots detected regions of diurnal rhythm during the growing seasons in both young and old stands (Figures 5a–5i), but the phase angle (135°) showed that R_s peaked before T_s at the daily scale (period [days] = 1). There were also other regions of strong common power between R_s and T_s (e.g., 2, 4, and 16 days), but with inconsistent phase angles (Figures 5a–5i).

The cospectra of R_s and θ exhibited significant ($p < 0.05$) peaks at the synoptic (>7 days) and phenological (>30 days) time scales (Figures 4s–4z and 4A1). Areas of high common power (red zones in Figures 6a–6i) between R_s and θ were concentrated either in the early part of the season when soil water content was high or when soil water content peaked after precipitation. However, the phase angles of the R_s - θ relationship varied widely, indicating that at times R_s maxima lagged behind those of θ , and at times they were leading (red zones in Figures 6a–6i).

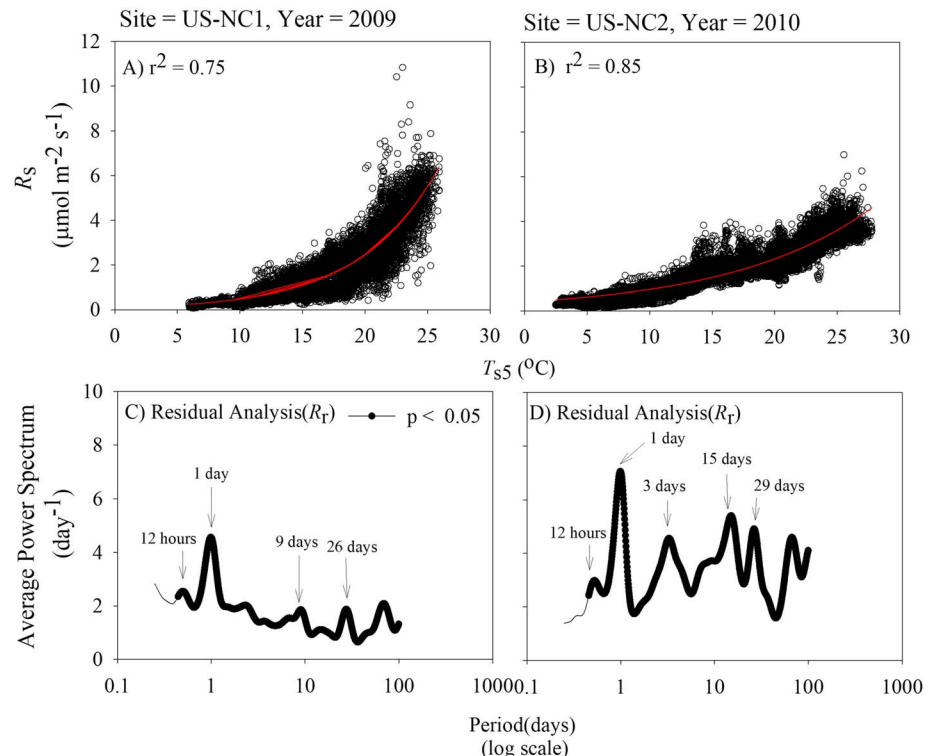


Figure 3. (a and b) Seasonal variation of soil respiration (R_s) against soil temperature (T_{s5}) for two different stands (US-NC1 & US-NC2) and two different years (2009 and 2010) along with the best line of the exponential Q_{10} function fit. The continuous average wavelet power spectra for the residuals (R_r) of the corresponding exponential Q_{10} function fit along with the p -values of the average wavelet power at the (c) US-NC1 and (d) US-NC2 sites. R_r is the difference between the measured and modeled R_s .

Cospectra of R_s and PAR detected very strong and consistent peaks at the diurnal scale at both sites and in each year (Figures 4 A2–A10). The heat maps from cross-spectral transformation showed significant correlation (red zone) at diurnal scale to be very strong and consistent during the growing season (days of year 100–300), whereas at longer timescales the effects were weaker and more intermittent (Figures 7a–7i).

The phase difference between PAR and R_s indicated an in-phase relationship (based on direction of arrows), with PAR leading R_s at the diurnal period. A day is a reasonable amount of time for a PAR/R_s lag if immediate osmoregulatory (i.e., root cells maintaining fluid balance with surroundings) root exudation is a minor factor. This relationship appeared to be consistent across the growing period across all sites and years. However, at the subdaily time scale, a generalization of the trend between PAR and R_s could not be established. PAR and R_s appeared to be out of phase at certain times of the growing season. The average time lag, corresponding to the region of common power between R_s and PAR , at the diurnal scale ranged from 1 to 3 hr (Figure 8). The only outlier was US-NC2 in 2007: an exceptionally dry year, when R_s peaked about 1.5 hr before PAR (Figure 7e).

4. Discussion

4.1. Frequency Domain Error Analysis of a Temperature Response Function Fit to R_s

As soil respiration is a function of stand age (including biomass; Table 1), it was not surprising that CO_2 flux differed between US-NC1 and US-NC2 (Figures 1 and 2; Klopatek, 2002). Analysis of the residuals (Figures 3c and 3d) of the annual temperature relationship (Figures 3a and 3b) highlighted structures at different temporal scales. Average wavelet power spectrum of R_s (Figures 4a–4i) also identified significant peaks at diurnal (12 hr), daily (24 hr), synoptic (7–14 days) and monthly to seasonal scales. These observations are consistent with our understanding of the controls and mechanisms of control of R_s at both diurnal (Heinemeyer et al., 2012; Vargas et al., 2010) and phenological timescales (Baldocchi et al., 2001).

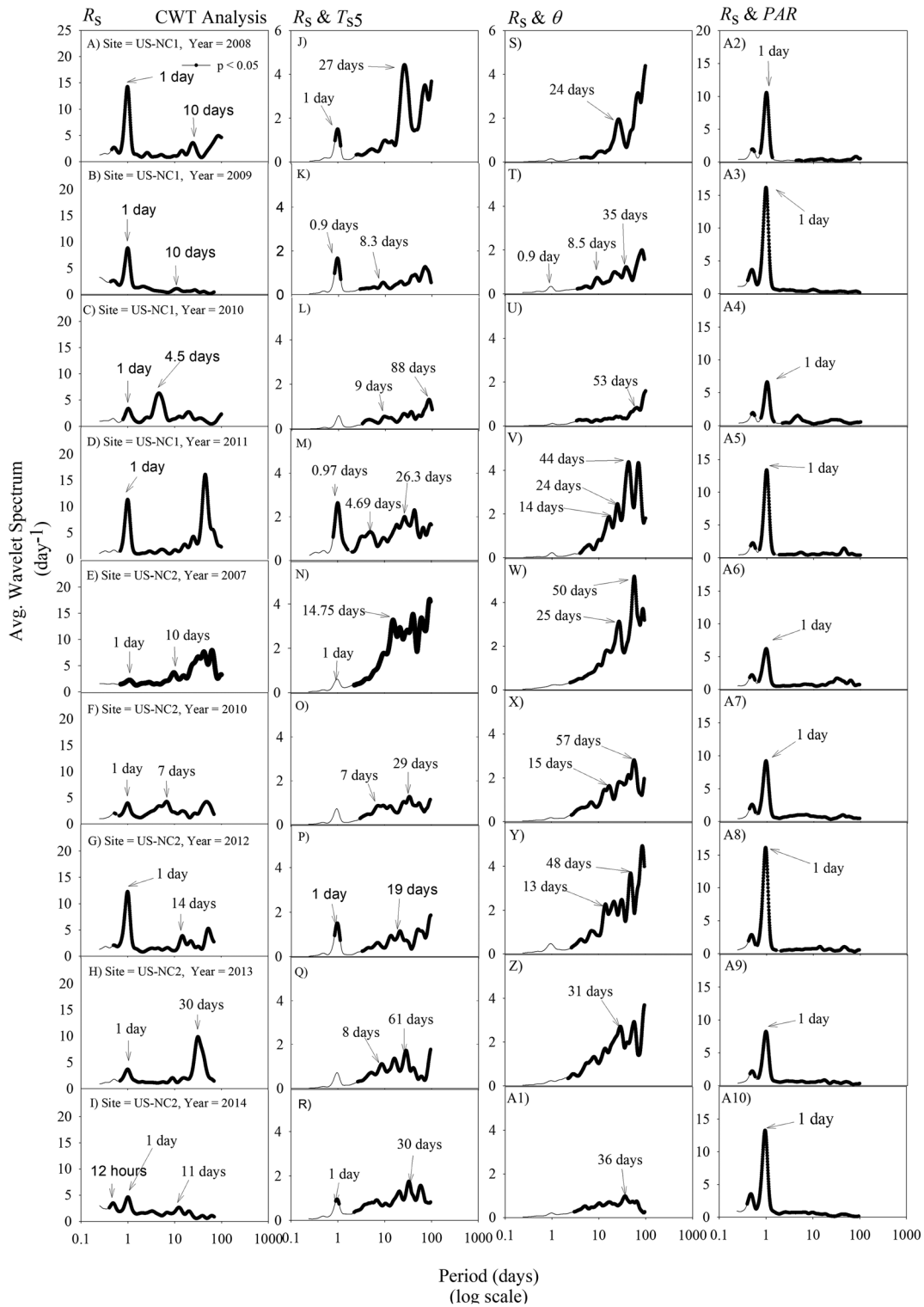


Figure 4. (a-i) Average wavelet power in the frequency domain generated from the wavelet transformation of soil respiration (R_s) at different sites (US NC1 and US NC2) and different years (2007, 2008, 2009, 2010, 2011, 2012, 2013, and 2014) using continuous wavelet (CWT). Cross wavelet transformation (XWT) of soil respiration (R_s) against soil temperature at (j-r) 5-cm depth (T_{s5}), (s-z and 4A1) volumetric soil water content (θ), (A2–A10) photosynthetically active radiation (PAR) at different sites (US-NC1 and US-NC2) and for different years (2007, 2008, 2009, 2010, 2011, 2012, 2013, and 2014). The 5% significance level generated against white noise has also been identified.

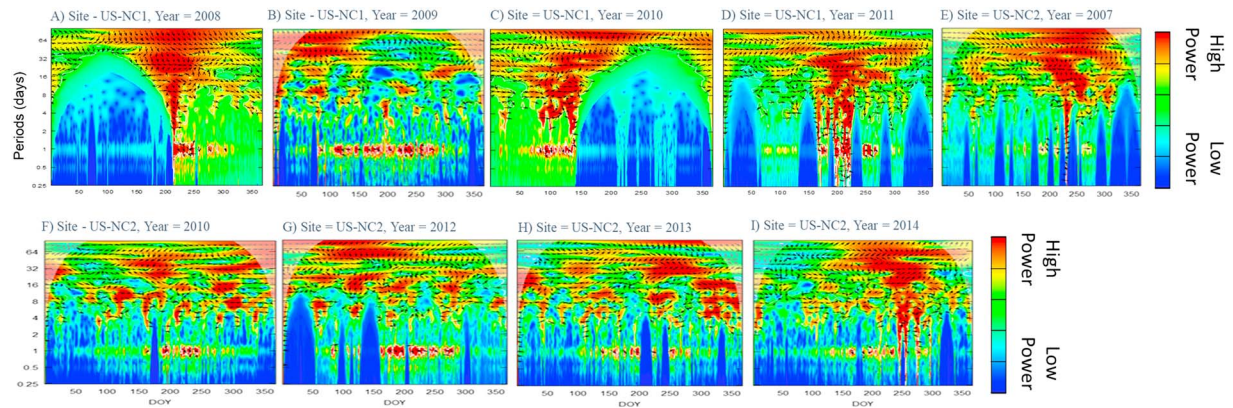


Figure 5. Heat maps highlighting the cross-wavelet transformation (XWT) of soil respiration (R_s) and soil temperature (T_{s5}) at different sites (US-NC1 and US-NC2) for different years. The phase relationship has been identified by arrows. The 5% significance level of the XWT analysis was generated within the cone of influence (COI) against white noise and identified by a white contour lines. COI within the heat plot was identified by a light shade. Additional information to interpreting the heat maps and phase angles are in the online supplement section (Text S2).

The spectral footprints of R_s (Figures 3c and 3d and 4a-4i) suggest the existence of multiple superimposed influences. Earlier studies have proposed that these may include microbial decomposition, phenology, soil water content, and soil temperature (Baldocchi et al., 2001; DeForest et al., 2006; Fierer et al., 2003; Irvine et al., 2008; Xu et al., 2004), to name some. As carbon cycle models currently do not explicitly account for the temporal dimension of different controls, and thus, they do not capture the variability on a number of temporal scales (Dietze et al., 2011; Stoy et al., 2013). As the temperature dependence varies in time (nonconstant Q_{10}), the challenge becomes one of disentangling the confounding effects of these variously lagged effects with different spectral properties.

4.2. The Multitemporal Relationship of R_s With T_s

The annual temperature relationship (equation (1)) did not fully capture temperature dependence on shorter timescales (Figures 3c and 3d). The temporal variability and the difference between short- and long-term temperature sensitivity have been the subject of discussion for well over a decade (Karhu et al.,

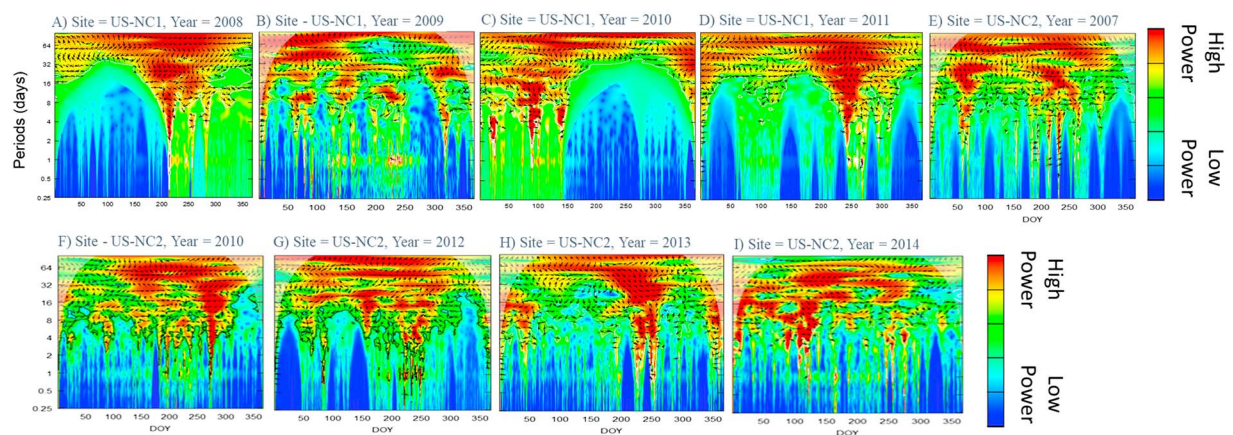


Figure 6. Examples of heat maps highlighting the cross-wavelet transformation (XWT) of soil respiration (R_s) and volumetric soil water content (θ) at different sites (US-NC1 and US-NC2) for different years. The phase relationship has been identified by arrows. The 5% significance level of the XWT analysis was generated within the cone of influence (COI) against white noise and identified by a white contour lines. COI within the heat plot was identified by a light shade. Additional information to interpreting the heat maps and phase angles are in the online supplement section (Text S2).

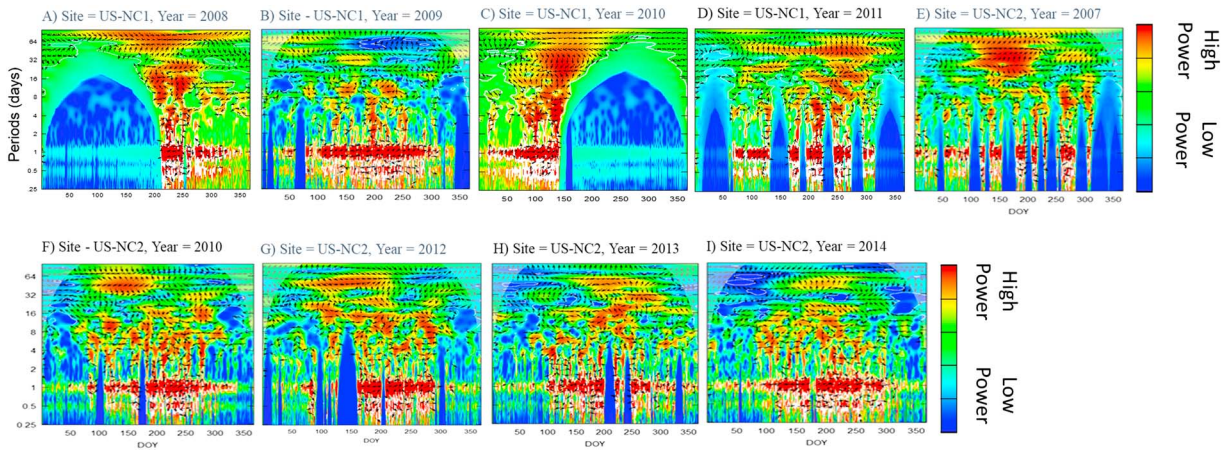


Figure 7. Examples of heat maps highlighting the cross-wavelet transformation (XWT) of soil respiration (R_s) and photosynthetically active radiation (PAR) at different sites (US-NC1 and US-NC2) for different years. The phase relationship has been identified by arrows. The 5% significance level of the XWT analysis was generated within the cone of influence (COI) against white noise and identified by a white contour lines. COI within the heat plot was identified by a light shade. Additional information to interpreting the heat maps and phase angles are in the online supplement section (Text S2).

2014; Mahecha et al., 2010; Subke & Bahn, 2010; Meyer et al., 2018; Yan et al., 2017), but its mechanisms have not been fully established. In the current study, notably, the cospectral peaks were often stronger at weekly to monthly than at daily timescale (Figures 4j-4r). In fact, in some years (2007, 2010, and 2013 at US-NC2 and 2010 at US-NC1) the diurnal peaks were not even statistically significant (Figures 4l, 4n, 4o, and 4q).

The phase angle (averaging at 135°) indicated that R_s peaked before T_s on daily scale, precluding the causal role of temperature in the relationship (Figure 5a-5i). Hysteretic response where T_{s5} leads R_{s5} could be explained by substrate supply (Kuzuyakov & Gavrichkova, 2010; Stoy et al., 2007; Tang et al., 2005), thermal diffusivity (Graf et al., 2008; Pavelka et al., 2007), microbial abundance, soil moisture conditions, and atmospheric turbulence (Flecharth et al., 2007). In contrast, if T_{s5} lags behind R_s , these explanations hold no value.

While divergent temperature sensitivity of the component processes that make up R_s (Conant et al., 2011) could potentially give rise to cospectra we observed, the inconsistent phase relationships at synoptic scales (2-16 days) suggests that the observed relationships were correlative, not directly causal.

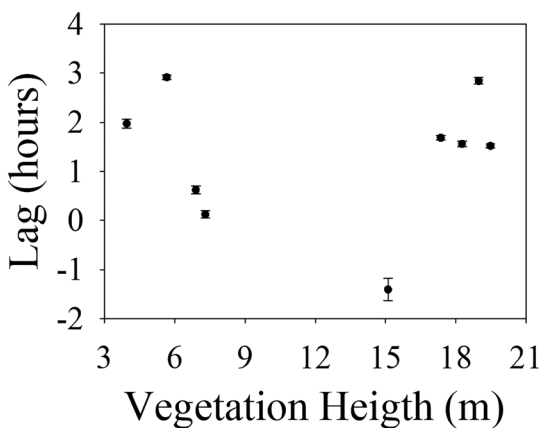


Figure 8. Variation in average lag hours as a function of vegetation height. The lag hours were calculated when soil respiration (R_s) lagged photosynthetically active radiation (PAR) at the diurnal scale across US-NC1 and US-NC2. The lag hours corresponded to zones of significant common power during the growing season (day of year 100–300) at the diurnal scale. Each dot represents a year.

4.3. The Effect of Moisture Availability on R_s

The nonlinear and threshold relationship between R_s and θ makes their cospectra difficult to predict from precipitation and moisture availability data alone (Figures 4s-4z and 4A1). The relationship between R_s and θ also depends on the soil moisture status prior to rainfall, and the moisture demand of the vegetation, which may explain the complex and continuous power spectra at synoptic scales at our two forests with contrasting water needs, rooting profiles, and the balance between auto- and heterotrophic components of R_s (Figures 4s–4z and 4A1).

Furthermore, the nonlinearity of the R_s - θ relationship may have contributed to the inconsistent phase-angle relationships even during periods of high common power (Figures 6a-6i). For example, a positive relationship may have existed when water limitation was initially relieved, but not when moisture availability exceeded a given threshold, often around 50% or relative extractable water (Domec et al., 2012).

4.4. The Effect of PAR on R_s

R_s and PAR co-spectral analysis yielded strong consistency of the spectral peak (Figures 4A2–A10), phase angle (Figures 7a-7i), and time lag (1 to 3

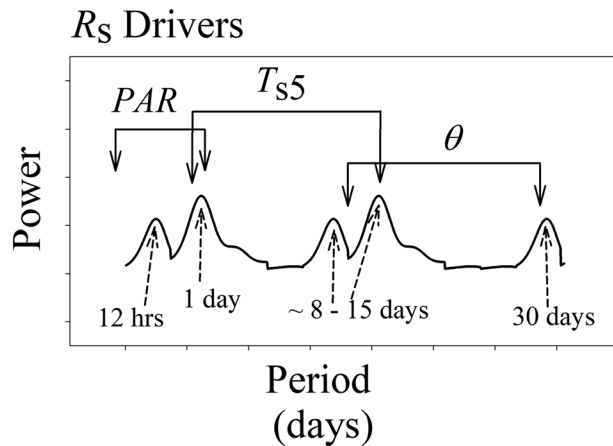


Figure 9. Conceptual figure highlighting the disentanglement between soil respiration (R_s) and its biotic (photosynthesis) and abiotic drivers (volumetric soil water content [θ] and soil temperature (T_{s5}) at different periods (days). Photosynthetically active radiation (PAR) was used as a surrogate for photosynthesis.

hr; Figure 8) at daily scale across years and between the two sites with very different canopy height, structure, and rooting profile (Table 1), suggesting a strong causal relationship. We hypothesize that the connection between R_s and PAR is through photosynthesis, and plant-internal carbohydrate availability for metabolic processes, including rhizosphere activity. Based on the fact that R_s lagged PAR by 1-3 hr (Figure 8), we hypothesize that carbohydrate availability in different plant parts was regulated via pressure-concentration waves (PCW; Thompson & Holbrook, 2003; Zimmerman 1969). The PCW theory postulates that a rapid propagation of turgor and osmotic pressure waves link plant photosynthesis with carbohydrate availability throughout the plant (Thompson & Holbrook, 2003). Similar time series assessment has been done previously to calculate the lag hour between above and belowground plant processes (Gorbenko & Panikov, 1989; Liu et al., 2006; Tang et al., 2005). Our PCW hypothesis must be validated with independent field studies (e.g., pulse labeling and isotope analysis). The alternative view that carbohydrate availability is determined by mass flow requires that a newly synthesized sugar molecule be transported to its destination and has been tested using isotope labeling methods (Mencuccini & Holttta, 2010; Wingate et al., 2010).

This process is dependent on plant phloem length and takes in trees about 1-3 days (e.g., Mencuccini & Holttta, 2010), whereas most of the studies of time lags of carbohydrate transport find improved carbohydrate availability within a few hours of increase in assimilation (Bahn et al., 2008; Baldocchi et al., 2006; Barron-Gafford et al., 2011; Carbone & Trumbore, 2007; Gaumont-Guay et al., 2006; Höglberg et al., 2001, 2009; Liu et al., 2006; Tang et al., 2005). Kuzyakov and Gavrichkova (2010) presented a good summary of this debate. Intermediate lag times (5-24 hr), reported by many authors (e.g., references in Kuzyakov & Gavrichkova, 2010), may be the result of nonsynchronous compound processes (discussed above), and PCW of varying magnitude. At times, additional lags have been invoked to consolidate the shorter observed lags with presumed “true” times of mass flow. For example, Vargas et al. (2011) hypothesized that delays due to diffusion of CO_2 from point of production to point of measurement may explain the observed patterns. However, this may be unnecessary if we consider that carbohydrate availability in rhizosphere may be mediated by PCW, which the findings of the current study lend support for with the highly consistent time lag and phase angles between young and mature trees.

The only outlier in the time lag spectrum was US-NC2 in 2007 (Figure 8). However, it could be reasoned that during this exceptionally dry year, when R_s peaked about 1.5 hr before PAR (Figure 7e), the source of the carbohydrate substrate may have been different, possibly old carbohydrate reserves stored in roots (Richardson et al., 2015). If the increase in the heterotrophic fraction of R_s in the drought year, that we have reported earlier (Noormets et al., 2012), was fully independent of plant-derived new carbohydrate supply, R_s should have lagged in relation to T_s (and PAR), but it did not. This lends support to the idea that the metabolic activity was supported by plant-derived, but not fresh photosynthetic carbon.

4.5. Implications

The time series of soil temperature, water content, and PAR all showed distinct peaks in their cospectra with R_s . PAR correlated with soil respiration at diurnal scale, temperature was significant on diurnal and synoptic time scales, while soil water content dominated at synoptic to seasonal time scales (Figure 9). We hypothesize that multiple controlling factors modulate soil respiration flux across two pine plantations of contrasting age and vegetation structure. These findings are important as they introduce the idea of temporal scale dependence of different driving variables to simulating ecosystem processes, which currently is not done. The traditional models implicitly assume the omnipresence of substrate, to the point where it can be omitted from explicit consideration. Given physiological acclimation in all processes, this assumption may, indeed, be justified when dealing with fluxes at synoptic scales and longer. However, it also invalidates some of the approaches used for interpreting temporal trends. For example, it appears that assessing temperature sensitivity on a daily scale may be meaningless. Combined, our results point to the need to develop spectrally

truthful models of respiration dynamics, ones that would consider the influence of different driving variables at their individual appropriate scale. This may also help us more meaningfully interpret the existing model parameters, metabolic acclimation, rhizosphere interactions, and external episodic perturbations.

5. Conclusions

Wavelet analysis showed that R_s responds to soil temperature (T_{s5}), soil water content (θ), and PAR at different temporal scales. Diurnal variation of soil respiration was driven primarily by PAR , and less by temperature, which was more significant at synoptic time scales, while soil water content dominated at synoptic to seasonal time scales. The result suggests a strong need to move beyond temperature-based quantification of soil carbon flux and develop respiration models that (1) more explicitly consider plant carbohydrate status as a driver of R_s and (2) partition variability between different time domains, with appropriate attribution to different environmental factors. As soil carbon dynamics remains a key uncertainty in ecosystem and Earth system models (Suseela et al., 2012), such a new conceptual representation may alter the estimates of terrestrial carbon fluxes. Furthermore, such spectrally sensitive models may also alter the estimates of vegetation respiration.

List of Abbreviations

Continuous wavelet transformation	— CWT
Cone of influence	— COI
Confidence intervals	— (CI)
Cross-wavelet transformation	— XWT
Earth system models	— ESM
Gross primary productivity	— GPP
Incoming shortwave radiation	— SWR_{in} ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)
National Climatic Data Center	— NCDC
Photosynthetically active radiation	— PAR ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)
Pressure-concentration-wave	— PCW
Wavelet transformation	— WT

List of Symbols

Phase angle	— \emptyset
Air temperature	— T_a ($^{\circ}\text{C}$)
Angular frequency	— w_o
Autotrophic respiration	— R_a
Average volumetric soil water content within the top 30 cm	— θ (%)
Carbon dioxide	— CO_2
Difference between measured and modeled soil respiration	— R_r ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)
Heterotrophic respiration	— R_h
L	— Lag time
Localized time index	— τ
Scale	— s
Soil temperature	— (T_s ; $^{\circ}\text{C}$)
Soil temperature was measured at 5-cm depth	— T_{s5} ($^{\circ}\text{C}$)
Soil respiration at 10°C	— R_{ref}
Soil respiration	— R_s ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)
Time series	— x_t
Temperature sensitivity of soil respiration	— Q_{10}
Temperature-independent component of soil respiration	— R_i

Acknowledgments

Funding for these AmeriFlux core sites was provided by the U.S. Department of Energy's Office of Science. The work was also partly supported by DOE BER-TERES awards 7090112 and 11-DE-SC-0006700, USDA NIFA 2011-67009-20089 and 2014-67003-22068, and U.S. Forest Service Eastern Forest Environmental Threat Assessment Center grants 08-JV-11330147-038 and 13-JV-11330110-081. The authors would like to thank two anonymous referees for their useful comments in revising the manuscript. Data for this paper have been provided as online supplement.

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