

The Use of Newly Assimilated Photosynthates by Soil Autotrophic and Heterotrophic Respiration on a Diurnal Scale

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Abstract

The regulatory role of plant carbohydrate status and root exudation on soil CO₂ efflux has been demonstrated, yet the underlying mechanisms, particularly through root respiration, remain largely theoretical. In this study, we analyzed the cospectral variation of soil autotrophic (Ra) and heterotrophic (Rh) respiration components with key physiological and environmental factors, including gross primary productivity (GPP), photosynthetically active radiations (PAR), soil temperature (Ts) and volumetric water content (VWC), to evaluate their relative contributions in a subtropical mature shortleaf pine forest in the southern United States. The findings reveal a strong diurnal relationship between Rh and both GPP and PAR, in contrast to the weaker and more variable associations observed with Ra. This suggests that substrate availability was a key limitation of Rh on a diurnal basis, and that recently assimilated carbohydrates were directly discharged into the soil via root and mycorrhizal exudates. The consistent 2–4 hour time lag between Rh relative to GPP is consistent with the propagation rate of phloem pressure-concentration waves. While a diurnal peak in Rh-Ts covariance was also detected, the time lag of Rh in relation to Ts varied between positive and negative values, precluding this from being a causal relationship. Ra had a similarly strong cospectral peak with GPP as Rh, but with inconsistent lag, likely because of carbon availability from local starch reserves.

1 Introduction

In the global carbon (C) cycle, soil CO₂ efflux (SR) is a major terrestrial C flux, estimated at 89 Pg C year⁻¹ (range: 68–101 Pg C year⁻¹) (Hashimoto et al., 2023; Jian et al., 2021), approximately nine times greater than annual fossil fuel emissions (Friedlingstein et al., 2022), and serves as the primary pathway for returning plant-assimilated CO₂ to the atmosphere. SR arises from the combined respiration of plant roots, bacteria, and rhizosphere microbes, with carbohydrates (CHO) translocated from photosynthetic tissues playing an essential role in sustaining this flux (Kuzyakov & Gavrichkova, 2010). Autotrophic respiration (Ra), including root and mycorrhizal respiration, is, in principle, directly fueled by CHO translocated belowground (Fenn et al., 2010; Heinemeyer et al., 2012). Heterotrophic respiration (Rh), particularly rhizosphere microbes, is also linked to photosynthesis through above- and belowground detritus production and rhizodeposition, including exudates that provide

30 labile C inputs, which are estimated to be around 1–3% of a forest’s net primary productivity (NPP) (Phillips et al., 2008; Yin
et al., 2014). The recent demonstration of tight coupling between SR and GPP (Han et al., 2014; Heinemeyer et al., 2012;
Mitra et al., 2019) suggests that the pattern is driven by root respiration as mediated by the diurnal fluctuation in plant CHO
status. With Rh being further removed from the CHO source, the primary C inputs (i.e., detritus) varying on a seasonal scale,
and reports of lower temperature sensitivity of Rh than Ra (Reichstein et al., 2005), it has often been viewed as a more
35 invariable, baseline process. However, direct evidence for such differentiation remains limited. Furthermore, most SR
upscaling models do not explicitly consider substrate availability, and confound seasonal and diurnal temperature (Davidson
et al., 2006) and moisture (Davidson et al., 1998; Li et al., 2008) sensitivities (Martin et al., 2012).

The allocation of CHO belowground depends on the relative strength of different C sinks in plants, which, in turn, may be
40 restricted by water and nutrient availability (Jiang et al., 2020; Körner, 2015; Sevanto & Dickman, 2015), physiological state,
and hormones (Herms & Mattson, 1992), all of which vary seasonally and respond to stresses (Gessler & Zweifel, 2024). As
summarized in the “surplus carbon hypothesis” (Prescott et al., 2020), overwhelming evidence supports the view of a passive,
sink-strength-driven nature of C allocation, with implications for C cycling and responses to stressors, such as drought and
nutrient limitations (Prescott, 2022; Prescott et al., 2020). Surplus CHO that are not used in aboveground growth and
45 maintenance can be stored (as starch or lipids), converted to secondary compounds, or translocated from leaves to belowground
compartments, where they can support root and mycorrhizal growth, or be exuded into the soil. The sink-strength-driven
allocation model implies that this process helps regulate CHO concentrations in cells, preventing them from reaching levels
that could become toxic to cellular processes (McClain & Sharkey, 2019). However, quantifying the interactions between
CHO translocation and CO₂ release remains challenging due to the complexity of these mechanisms.

50 The timescale and level of coupling between photosynthetic C uptake and soil processes are confounded by plant physiological
processes that can introduce variable lags to C transport from leaves to different plant organs, including the sink strength of
different tissues, mycorrhizal associations, and the rate of phloem transport (Canarini et al., 2019; Sevanto & Dickman, 2015),
as well as by methodological effects. Much of our current understanding of C allocation originates from stable isotope labeling
55 studies, in which the progressive detection of isotopically labeled C in different tissues has been tracked (e.g., Epron et al.,
2012; Gessler et al., 2007; Höglberg et al., 2008; Kodama et al., 2008; Wingate et al., 2010). These studies show that the newly
assimilated C can be translocated from leaves of a tree to the roots on the order of a day or two (Mencuccini & Hölttä, 2010;
Moyano et al., 2008). Yet, our earlier analysis (Mitra et al., 2019), as well as those of others (Vargas et al., 2011; Vargas et al.,
2010), detected a diurnal cospectral peak between SR and CHO availability, indicated by photosynthetically active radiation
60 (PAR) or net ecosystem exchange (NEE), on the order of hours, which is attributable to plant carbohydrate status responding
via pressure-concentration waves (Thompson & Holbrook, 2004). Finally, additional coupling with potentially variable lags
may be introduced by soil heterotrophs, where the C subsidy by plant exudates may serve as a free substrate for their
metabolism. For example, Yang et al. (2022) demonstrated a strong correlation between microbial respiration and PAR in a

subtropical forest with a lag of a few hours, underscoring the tight coupling between recent photosynthetic inputs and soil
65 microbial activity. Such inputs can also trigger priming of the decomposition of old recalcitrant soil C, by providing energy
(and possibly substrate) for the production of more resource-intensive enzymes (Jilling et al., 2025; Meier et al., 2017).

Here, we report the coherence of Rh and Ra with key physiological and environmental drivers, gross primary productivity
(GPP), PAR, soil temperature, and soil moisture, with the focus on the diurnal timescale. We hypothesized that GPP is the
70 primary driver of diurnal variations in Ra, while soil temperature and moisture predominantly regulate Rh, with influences
spanning diel and synoptic scales. Quantitative understanding of the coupling between respiration components and GPP may
help address key remaining uncertainties in ecosystem carbon cycle models (Lawrence et al., 2019; O’Sullivan et al., 2022).

2 Materials and Methods

2.1 Study Site

75 The study was conducted at the US-CRK Ameriflux site, a fire-managed mature shortleaf pine forest in Davy Crockett National
Forest, TX (31.4629 N, 95.3415 W), in a humid subtropical climate region. The average annual precipitation and annual
temperature are 1148 mm and 19.1 °C, respectively. The soil type at this site is classified as moderately well-drained Latex
loam. The majority of fine root biomass (84%) was concentrated in the top 30 cm of soil at the site (Fig. S1). The site is
maintained through biannual prescribed burning, and the recent burning took place in the winters of 2022 and 2024, although
80 the fire's effect on the measurement area was minimal. The overstory vegetation within the study site is primarily dominated
by shortleaf pine (*Pinus echinata*), with lesser amounts of loblolly pine (*Pinus taeda*), American sweetgum (*Liquidambar
styraciflua*), and post oak (*Quercus stellata*). The stand average tree diameter at breast height was 33.1 ± 1.60 cm, the mean
tree height was 25.8 ± 1.47 m, and the estimated aboveground biomass was 15.4 ± 0.06 kg m⁻² year⁻¹ in 2021.

2.2 Continuous Soil Respiration Measurements

85 Continuous soil respiration measurements were conducted hourly from May 2022 through October 2024 using an infrared gas
analyzer (LI-8100A, LI-COR Biosciences, Lincoln, NE, USA) equipped with three long-term chambers (LI-8100-101 and LI-
8100-104, LI-COR Biosciences). Chambers were installed over shallow (5cm tall) or deep (35 cm) polyvinyl chloride (PVC)
collars. Shallow collars were inserted 2–3 cm into the soil and used to quantify total soil CO₂ efflux (SR), while deep collars
were inserted approximately 25 cm into the soil to sever roots and capture root-excluded heterotrophic soil CO₂ efflux (Rh).
90 Collars were initially installed in April 2022 and relocated in April 2023, October 2023, and June 2024 to maintain effective
root severance in deep collars (Ono et al., 2025). Only periods during which the CO₂ efflux ratio between paired deep and
shallow collars had stabilized, validated against manual survey measurements across five surrounding study plots, were
included in the analysis (McElligott et al., 2016). The paired shallow and deep collars were placed at similar microsites, at a
similar distance (approx. 2–3 m) from the nearest tree, and ensuring that initial soil CO₂ efflux rates would not differ more

95 than 10%. Aboveground vegetation within collars was clipped monthly to maintain bare-soil conditions. The spatial representativeness of the single automated system was further supported by comparison with 25 pairs of similar paired collars at five study plots and measured for three years. Autotrophic respiration (R_a) was estimated by the difference between SR and Rh during periods when Rh was deemed stable. The stable usable estimates of partitioned Rh (and R_a) occurred typically between 3 and 6 months after deep collar insertion (Ono et al., 2025). Soil CO_2 efflux declined during the first 2–3 months of
100 the deep collar insertion as root internal carbohydrate reserves were being depleted. After about 6–8 months, the CO_2 efflux in the deep collars began to increase as the dead roots became additional substrate for heterotrophs.

Six measurement periods (hereafter referred to as campaigns), each spanning approximately 3–4 weeks, were identified from the continuous dataset. They were determined by the simultaneous availability of high-quality gross primary productivity
105 (GPP), SR, Rh, photosynthetically active radiation (PAR), soil temperature (T_s), and volumetric water content (VWC) data. The six campaigns included two early growing seasons (C1, C4), one late growing season (C5), and three dormant or cool seasons (C2, C3, C6) (Table 1, Fig.1). The categorization into seasons was based on physiological state, including canopy leaf area index (LAI), GPP, and SR values, as well as soil temperature and moisture conditions. Importantly, the vegetation was active throughout the year, and the “dormant” periods were characterized merely by lower GPP (and LAI and SR), not their
110 cessation.

2.3 Micrometeorological Parameters

Photosynthetically active radiation (PAR) was measured half-hourly above the canopy at a height of 43 m (PQS1, Kipp & Zonen, Delft, Netherlands). Soil temperature (T_s) and volumetric water content (VWC) were recorded half-hourly at 5 and 20 cm depth with CS108 and CS650 probes, respectively (both by Campbell Scientific, Logan, UT, USA). Half-hourly gross
115 primary productivity (GPP) was estimated by partitioning the net ecosystem exchange of CO_2 into GPP and ecosystem respiration using the nighttime partitioning approach in the “Reddypoc” package in R (Wutzler et al., 2022). Specific details of eddy covariance data processing are reported by Baniya et al. (2025). All parameters were aggregated to hourly values for analysis, to match the frequency of continuous SR data.

120 The leaf area index (LAI) at the site was extracted from the Moderate Resolution Imaging Spectroradiometer (MODIS; MCD15A3H Version 6.1), which provides 4-day composite estimates for a 500-meter pixel centered on the study site (Myneni et al., 2021). Peak LAI estimates were verified against on-site measurements with a LAI-2000 Plant Canopy Analyzer (LI-COR Biosciences) in August 2023. Both estimates matched within $0.2 \text{ m}^2 \text{ m}^{-2}$ (data not shown).

2.4 Data Analysis

125 All data analyses were performed in R (version 4.3.3) (R Core Team, 2024) and implemented in RStudio (version 2023.12.1) (Posit team, 2024).

2.4.1 Quality Control of Soil Respiration Components

Occasional abnormal spikes in the soil respiration data time series were observed, often due to gas analyzer failure or interference from small animals. To ensure the data quality for subsequent analyses, these anomalies were removed using the following quality control criteria: (1) poor model fit for flux calculation ($R^2 < 0.975$), (2) high coefficient of variation ($CV > 1.9$), (3) negative flux values, and (4) insufficient flow rate.

2.4.2 Spectral Analysis

We analyzed the wavelet spectra of soil respiration components (R_a and R_h , or their residuals, r_{Ra} and r_{Rh} ; Section 2.4.3) and their cospectra with environmental and physiological drivers (GPP, PAR, T_s , and VWC) in the time-frequency domain. The most straightforward analysis quantifies the covariance of each flux with the four drivers. However, if we assume, like some earlier analyses have done (Liu et al., 2006; Vargas et al., 2011), that the primary driver of respiration fluxes is temperature, the contribution of additional drivers can be evaluated considering their covariance with the residuals of the temperature response model. Therefore, the cospectral analyses of the residuals were included to verify the consistency of the conclusions. And given that diurnal and synoptic temperature responses of respiration can differ drastically, the residuals were calculated for each (section 2.4.3). The residual analyses were consistent with and confirmed the conclusions based on the cospectral analyses with fluxes R_a and R_h (Figs. S3–S13). Similarly, the spectral analyses were completed for data where campaigns C3–C4 and C5–C6 were not separated into active and dormant periods. The results showed similar cospectral peaks and similar patterns in lag times between respiration components (R_a and R_h) with potential drivers (GPP, PAR, T_s , and VWC). Only the standard deviations of time lags were larger with the longer averaging periods. Therefore, we chose to subdivide the data into 6 instead of 4 campaigns, as the differences in flux magnitudes may also signify changes in underlying physiology.

Briefly, the continuous wavelet transformation was performed using the Morlet wavelet as the basis function (Grinsted et al., 2004). We applied wavelet transformation (WT) for a single time series (e.g., R_h , R_a) and cross-wavelet transformation (XWT) for analyzing the relationship between two time series (e.g., R_h vs GPP), following the methodological framework described by Mitra et al. (2019). The time series data were normalized to zero mean and unit variance, and occasional gaps were filled using zero padding. To align with the temporal scales of interest, the analysis focused on frequencies corresponding to time intervals from 6 hours to 64 days. For the phase angle analysis between effects (i.e., R_h and R_a) and drivers, we focused on the diurnal frequency range (0.5 to 1.5 days). Phase differences within this range were averaged but included only when the spectral peak at the 1-day period was statistically significant ($p < 0.1$). Daily mean phase angles were then converted to time lags (in hours) using $\text{Lag (hours)} = (\text{mean phase angle} \times 24) / (2\pi)$. To prevent introducing artifacts, phase angle values during padded gaps were excluded. The statistical significance of WT and XWT analyses was evaluated within the cone of influence (COI) at a 5% significance level using Monte Carlo methods (100 simulations). The surrogate data for significant analysis was generated using white noise (the color of the noise has little impact on the results; Grinsted et al., 2004; Vargas et al., 2010).

The cospectral analysis was performed using the “analyze.coherency” function in the “WaveletComp” package in R (Roesch & Schmidbauer, 2018).

2.4.3 Residual Analysis

We also analyzed the temperature- and GPP- (or PAR-) controlled components of Ra and Rh by first removing the temperature dependence by exploring the cospectra of the potential drivers with the residuals of the measured and modeled Ra and Rh (r_{Ra} and r_{Rh}) (Liu et al., 2006; Vargas et al., 2011). Ra and Rh were modeled using the Q_{10} function (van't Hoff (1898) as cited in Lloyd and Taylor (1994)):

$$R_{model} = R_{20} \times Q_{10}^{\frac{T_{s5}-20}{10}}, \quad (1)$$

where R_{model} is the modeled respiration component at soil temperature (T_{s5}) at 5 cm depth, R_{20} is the reference respiration at 20 °C, and Q_{10} is the temperature sensitivity coefficient. Spectral analysis of T_{s5} revealed consistent diurnal and weekly peaks across campaigns (Figs. 3M–R; see section 3.2). Therefore, we estimated coefficients (R_{20} and Q_{10}) at two window lengths to isolate temperature responses at these timescales: a daily window to track diurnal variability and a 7-day rolling window to capture slower variability. The corresponding residuals were denoted as r_{Rh_day} (or r_{Ra_day}) and r_{Rh_week} (or r_{Ra_week}), respectively. Coefficients were estimated by minimizing the residual sum of squares through nonlinear least-squares analysis using the “nls_table” function in the “forestmangr” package in R (Braga et al., 2023).

3 Results

3.1 Soil Respiration and Environmental Conditions

Across the six measurement campaigns, SR ranged from 1.69 ± 0.81 to $5.05 \pm 1.03 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, Rh from 1.05 ± 0.40 to $2.46 \pm 0.32 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and Ra 0.43 ± 0.38 to $2.70 \pm 0.84 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Table 1, Figs. 1A–D). Maximum effluxes for SR and Ra were recorded in C1, which corresponded to the highest GPP and LAI (Table 1). On the other hand, lower SR, Rh, and Ra were observed during dormant-season campaigns (C2, C3, and C6). Rh consistently accounted for the majority of SR, contributing 59–86% across campaigns, except for C1, when its contribution was 47%. The Rh:SR ratio was greater during the dormant season (0.79 ± 0.08 , $n = 3$) than the growing season (0.63 ± 0.19 , $n = 3$), but the difference was not statistically significant (one-way ANOVA, $p = 0.26$). VWC during C3 and C4 was among the highest, driven by sustained rainfall in early 2024, whereas C5 and C6 experienced the lowest values due to drought conditions.

Table 1. Mean site conditions and fluxes during the six measurement campaigns (Mean $\pm$ standard deviation). Soil temperature (T_{s5} ; $^{\circ}\text{C}$) and volumetric water content (VWC_5 ; %) at a depth of 5 cm, total soil respiration (SR ; $\mu\text{mol m}^{-2} \text{s}^{-1}$), heterotrophic respiration (R_h ; $\mu\text{mol m}^{-2} \text{s}^{-1}$), autotrophic respiration (R_a ; $\mu\text{mol m}^{-2} \text{s}^{-1}$), the ratio of R_h to SR ($R_h:SR$; unitless), daylight-period gross primary productivity (GPP ; $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$), and leaf area index derived from MODIS (LAI ; $\text{m}^2 \text{m}^{-2}$). Campaigns conducted during active growing seasons are marked with an asterisk (*).

Campaign	Date	T_{s5}	VWC_5	SR	R_h	R_a	$R_h:SR$	GPP	LAI
1*	2022-05-22 ~ 2022-06-09	24.1 ± 2.31	24.2 ± 1.78	5.05 ± 1.04	2.35 ± 0.45	2.70 ± 0.84	0.47 ± 0.08	14.3 ± 2.94	4.18 ± 0.79
2	2023-03-15 ~ 2023-04-05	16.4 ± 2.57	23.4 ± 2.95	1.69 ± 0.81	1.05 ± 0.40	0.51 ± 0.43	0.71 ± 0.15	9.05 ± 2.53	1.68 ± 0.15
3	2024-03-03 ~ 2024-03-31	16.6 ± 2.05	42.6 ± 0.66	1.79 ± 0.63	1.38 ± 0.39	0.44 ± 0.38	0.79 ± 0.16	8.31 ± 2.01	1.17 ± 0.40
4*	2024-04-01 ~ 2024-04-27	19.2 ± 1.93	43.0 ± 0.52	2.15 ± 0.68	1.88 ± 0.42	0.43 ± 0.40	0.84 ± 0.18	11.6 ± 2.29	1.77 ± 0.90
5*	2024-09-03 ~ 2024-09-30	24.7 ± 2.17	10.4 ± 2.14	4.20 ± 0.54	2.47 ± 0.32	1.73 ± 0.42	0.59 ± 0.07	11.1 ± 1.76	2.11 ± 0.41
6	2024-10-01 ~ 2024-10-31	21.8 ± 2.62	4.11 ± 0.90	2.10 ± 0.50	1.78 ± 0.32	0.32 ± 0.31	0.86 ± 0.11	8.21 ± 1.85	1.75 ± 0.29

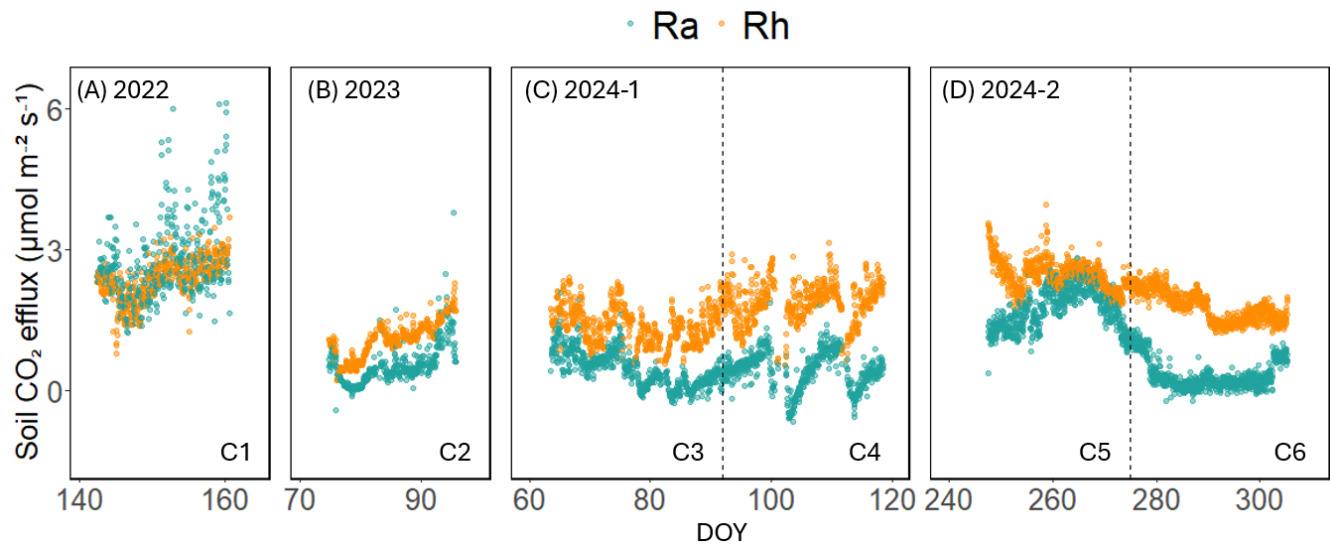


Figure 1. Hourly time series of soil autotrophic respiration (Ra, green) and heterotrophic respiration (Rh, orange) in $\mu\text{mol m}^{-2} \text{s}^{-1}$ across six measurement campaigns (C1–C6) at the US-CRK between 2022 and 2024 (A–D).

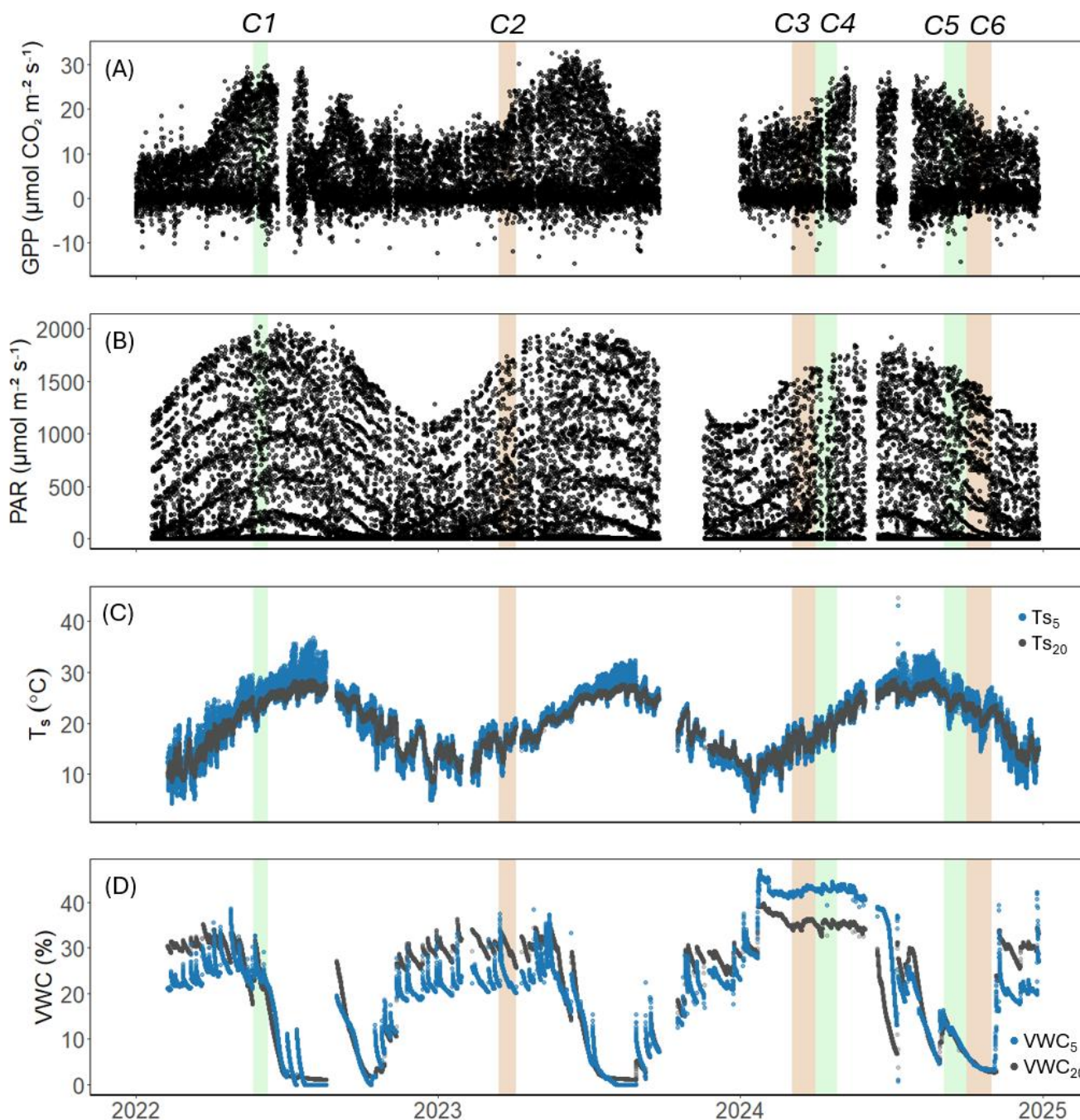


Figure 2. Hourly time series of (A) gross primary productivity (GPP; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), (B) photosynthetically active radiation (PAR; $\mu\text{mol m}^{-2} \text{ s}^{-1}$), (C) soil temperature (T_{s5} and T_{s20} ; $^{\circ}\text{C}$), and (D) volumetric water content (VWC_5 and VWC_{20} ; %) at 5 and 20 cm depth at the US-CRK site from 2022 to 2024. Shaded regions denote the six soil respiration measurement campaigns (C1–C6); green indicates active growing season campaigns, while brown indicates dormant season campaigns.

3.2 Spectral and Cospectral Characteristics

GPP and PAR consistently exhibited significant diurnal and subdiurnal spectral peaks across all six campaigns (Figs. 3A–L).

200 In contrast, Ts_5 displayed both significant diurnal and synoptic peaks, with the latter ranging from weekly to monthly timescales, while VWC_5 varied mostly at the synoptic scale (Figs. 3M–X). Rh showed significant diurnal spectral peaks in all campaigns, with more pronounced and distinct peaks during the growing season (C1, C4, and C5) and C3 (Figs. 4A–F). Synoptic peaks in Rh were also detected. Spectral analysis of Ra showed strong, significant diurnal peaks in C1 and weak but still significant diurnal peaks in C2, C3, and C5, along with detectable synoptic peaks (Figs. 5A–F).

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Cospectral analysis showed that Rh exhibited significant diurnal peaks with GPP and PAR across all campaigns, with stronger diurnal peaks during the growing seasons (C1, C4, and C5) and in C3 (Figs. 4G–R, 6A–L). Ra also exhibited significant diurnal peaks with GPP and both subdiurnal and diurnal peaks with PAR, particularly during C1 and C5 (Figs. 5G–R, 7A–L). Although Ra-GPP cospectral power was slightly greater than that for Rh-GPP in C1 and C2, in C3–C6, Rh-GPP cospectral power
210 exceeded that of Ra-GPP by a factor of 1.2 to 2.6-fold ($p = 0.047$; one-way ANOVA).

Cospectral analysis with Ts_5 demonstrated both significant diurnal and synoptic peaks for both Rh and Ra across campaigns (Figs. 4S–X, 5S–X). Notably, in C2, C3, and C4, cospectral peaks at weekly timescales were stronger than those at the diurnal timescale. While peaks extending beyond monthly timescales were observed for both Rh and Ra with Ts_5 , they fell outside the
215 cone of significance and were excluded from further interpretation. Rh and Ra also exhibited cospectral peaks with VWC_5 at synoptic scales (weekly to monthly). Significant diurnal peaks were detected only during C1, C3, and C4, but these were generally weaker and less consistent than those observed with GPP, PAR, and Ts_5 (Figs. 4Y–A4, 5Y–A4). Overall, their cospectral peaks at weekly scales were stronger than diurnal-scale peaks. The cospectral analysis with Ts_{20} and VWC_{20} also showed a similar pattern with Ts_5 and VWC_5 , though the magnitude of the diurnal peaks was generally smaller (Fig. S2).

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Cospectral analysis of model residuals (r_{Rh_day} and r_{Ra_day} , as well as r_{Rh_week} and r_{Ra_week}) with GPP and PAR showed overall patterns consistent with those of Rh and Ra. Diurnal peaks of r_{Rh_day} and r_{Rh_week} with GPP and PAR were consistently pronounced and significant across campaigns (Figs. S3 G–R, S7 G–R). Both r_{Ra_day} and r_{Ra_week} also exhibited consistently significant diurnal peaks with GPP and PAR (Figs. S4 G–R, S8 G–R), with particularly strong peaks of r_{Ra_day} observed during
225 C5 and C6 (Figs. S4 K, L). The Q_{10} values for model residuals showed large variability across campaigns and between Rh and Ra, with particularly high and uncertain estimates for Ra during campaigns 3 and 4 (no data shown).

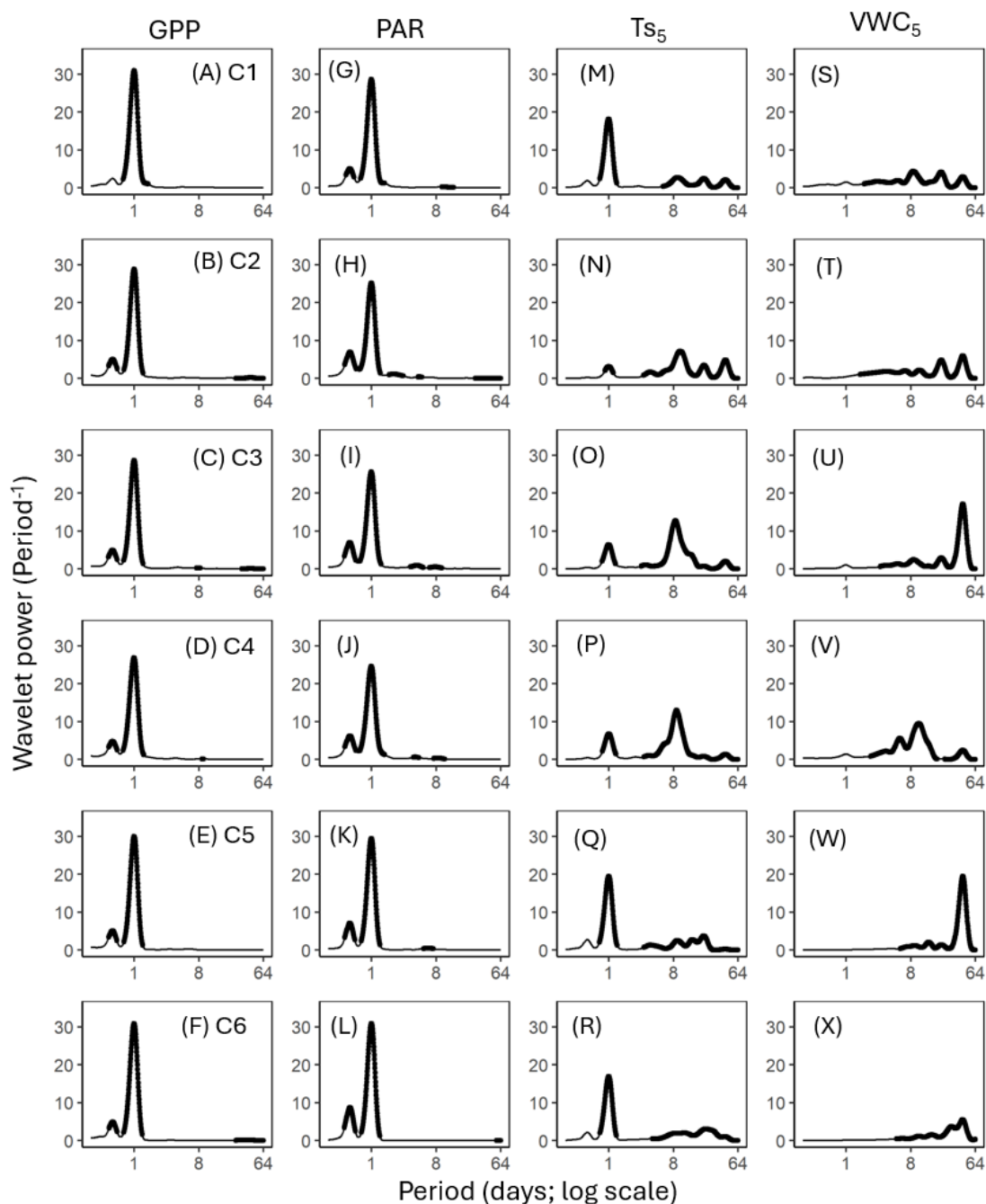


Figure 3. Average wavelet power in the frequency domain (Period; time intervals from 6 hours to 64 days) generated from the wavelet transformation of gross primary productivity (GPP; A–F), photosynthetically active radiation (PAR; G–L), soil temperature (Ts₅; M–R), and volumetric water content (VWC₅; S–X) at 5-cm depth for six campaigns (C1–C6) at US-CRK. The bold contours indicate areas with significant coherence at the 5% level against white noise.

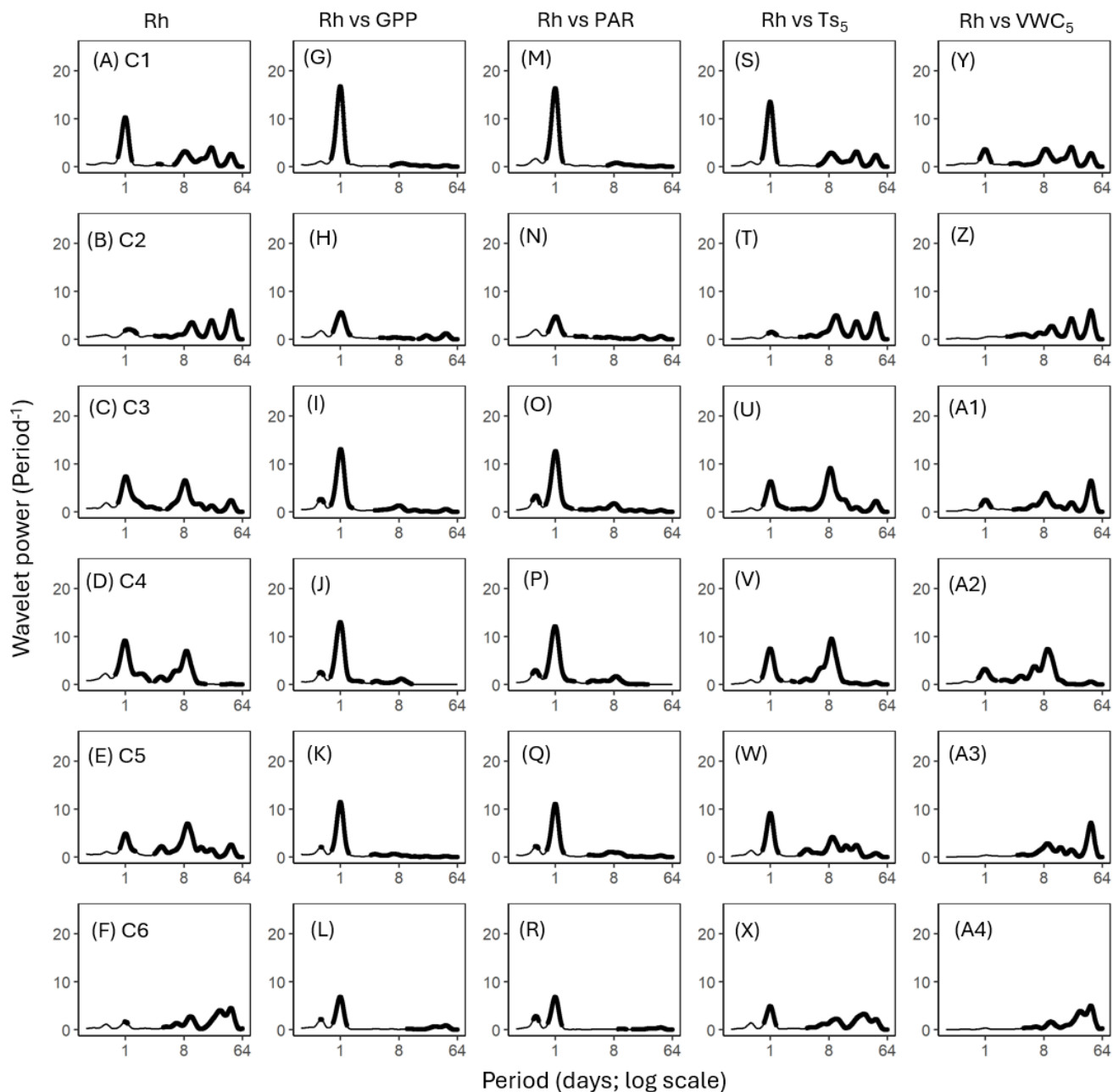


Figure 4. Average wavelet power in the frequency domain (Period; time intervals from 6 hours to 64 days) generated from the wavelet transformation of heterotrophic respiration (Rh; A–F) for six campaigns (C1–C6) at US-CRK. Average wavelet power in the frequency domain generated from the cross-wavelet transformation of heterotrophic respiration (Rh) against gross primary productivity (GPP; G–L), photosynthetically active radiation (PAR; M–R), soil temperature (Ts₅; S–X), and volumetric water content (VWC₅; Y–A4) at 5-cm depth for six campaigns at the US-CRK site. The bold contours indicate areas with significant coherence at the 5% level against white noise.

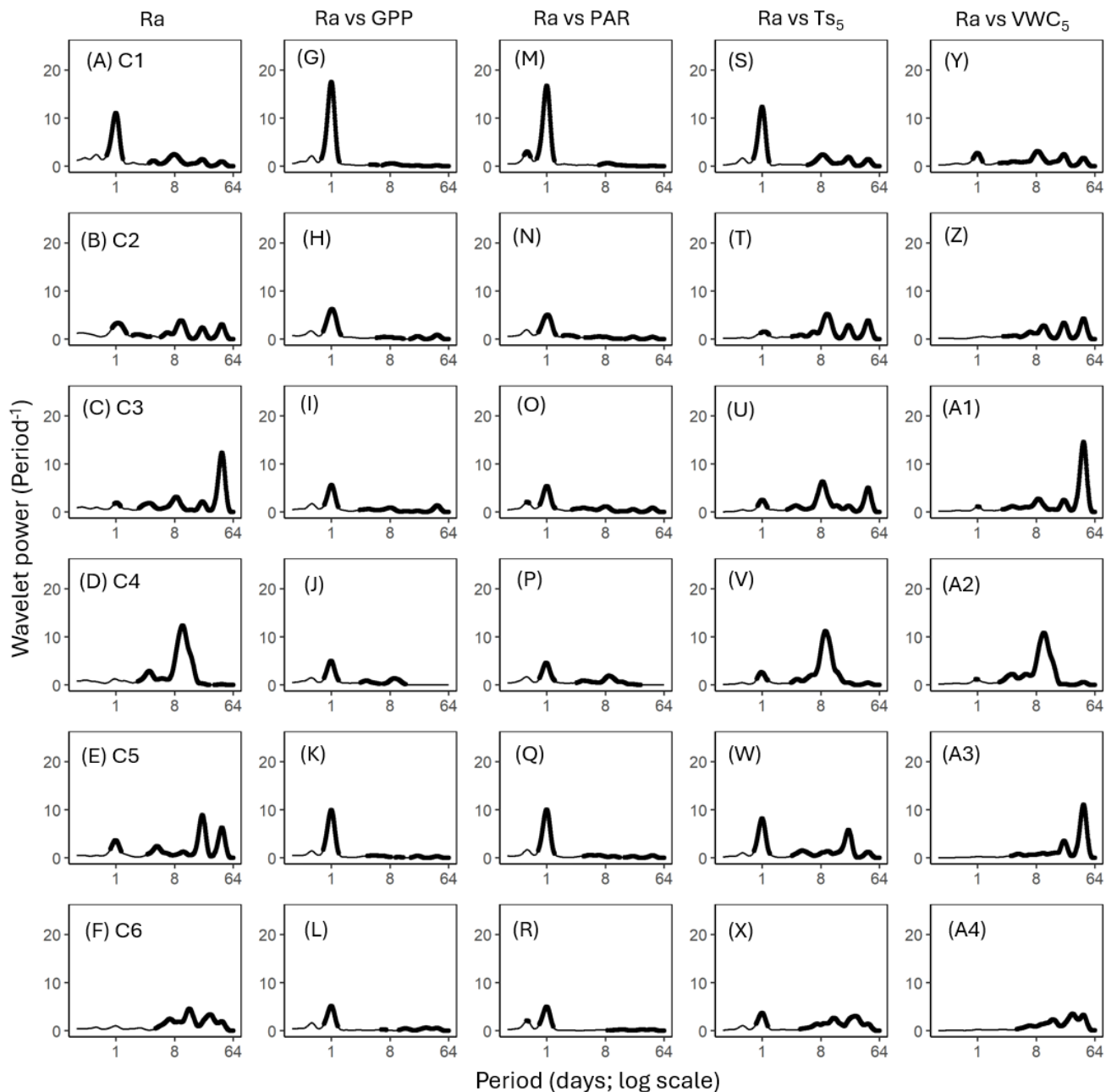


Figure 5. Average wavelet power in the frequency domain (Period; time intervals from 6 hours to 64 days) generated from the wavelet transformation of autotrophic respiration (Ra; A–F) for six campaigns (C1–C6) at US-CRK. Average wavelet power in the frequency domain generated from the cross-wavelet transformation of heterotrophic respiration (Rh) against gross primary productivity (GPP; G–L), photosynthetically active radiation (PAR; M–R), soil temperature (Ts₅; S–X), and volumetric water content (VWC₅; Y–A4) at 5-cm depth for six campaigns at the US-CRK site. The bold contours indicate areas with significant coherence at the 5% level against white noise.

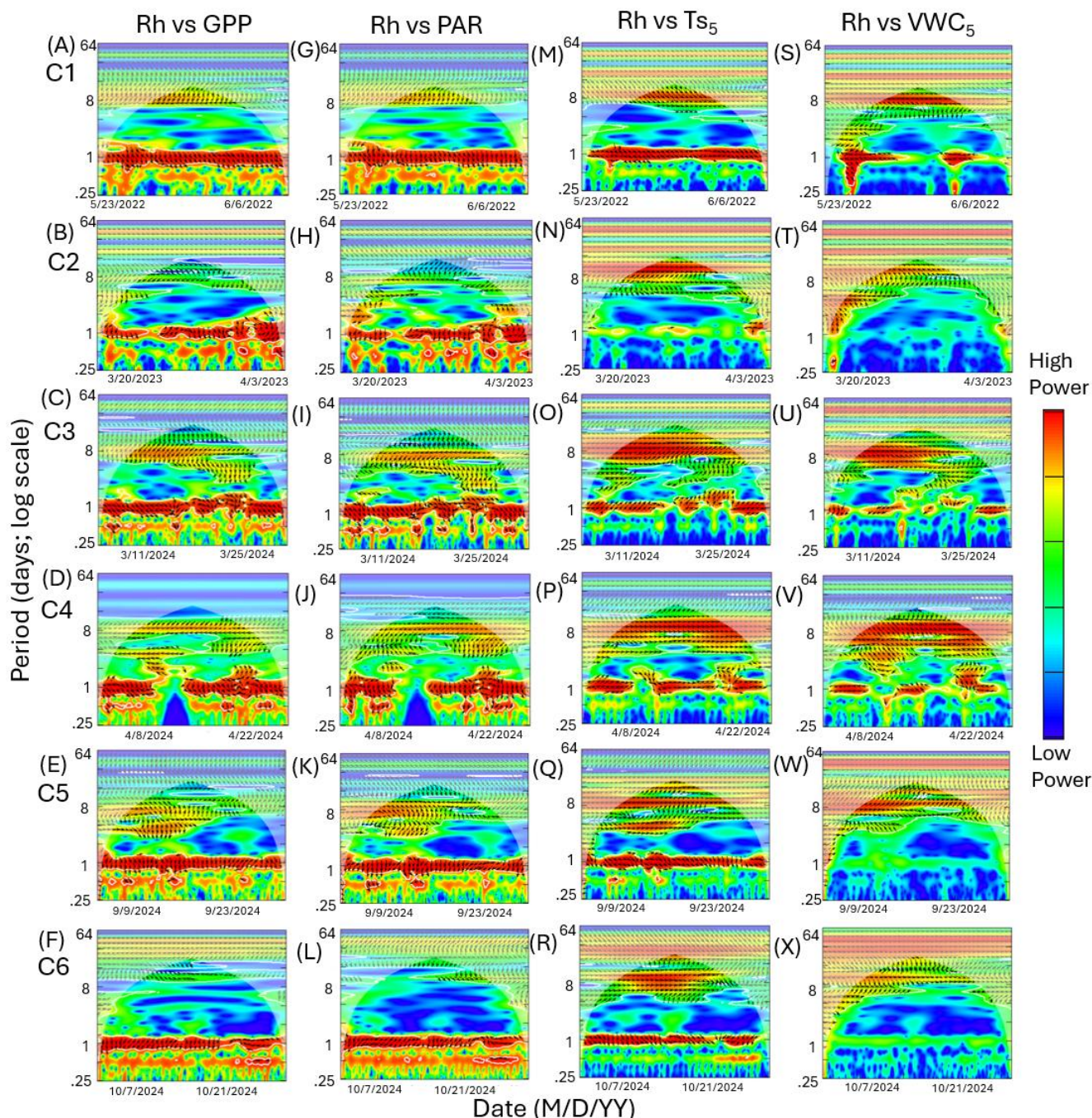


Figure 6. Heatmaps of the cross-wavelet transformation (XWT) of heterotrophic respiration (Rh) against gross primary productivity (GPP; A–F), photosynthetically active radiation (PAR; G–L), soil temperature (Ts₅; M–R), and volumetric water content (VWC₅; S–X) for six measurement campaigns (C1–C6) at US-CRK. Arrows pointing to the right and left represent positive and negative correlations, respectively, without lag. Arrows pointing up-left (positive correlation) and down-right (negative correlation) indicate the response component lags behind the driver, while arrows pointing up-right and down-left indicate that the driver lags behind the response component. The 5% significance level of the XWT analysis was generated within the cone of influence (COI) against white noise and identified by white contour lines. COI within the heat plot is identified with a light shade.

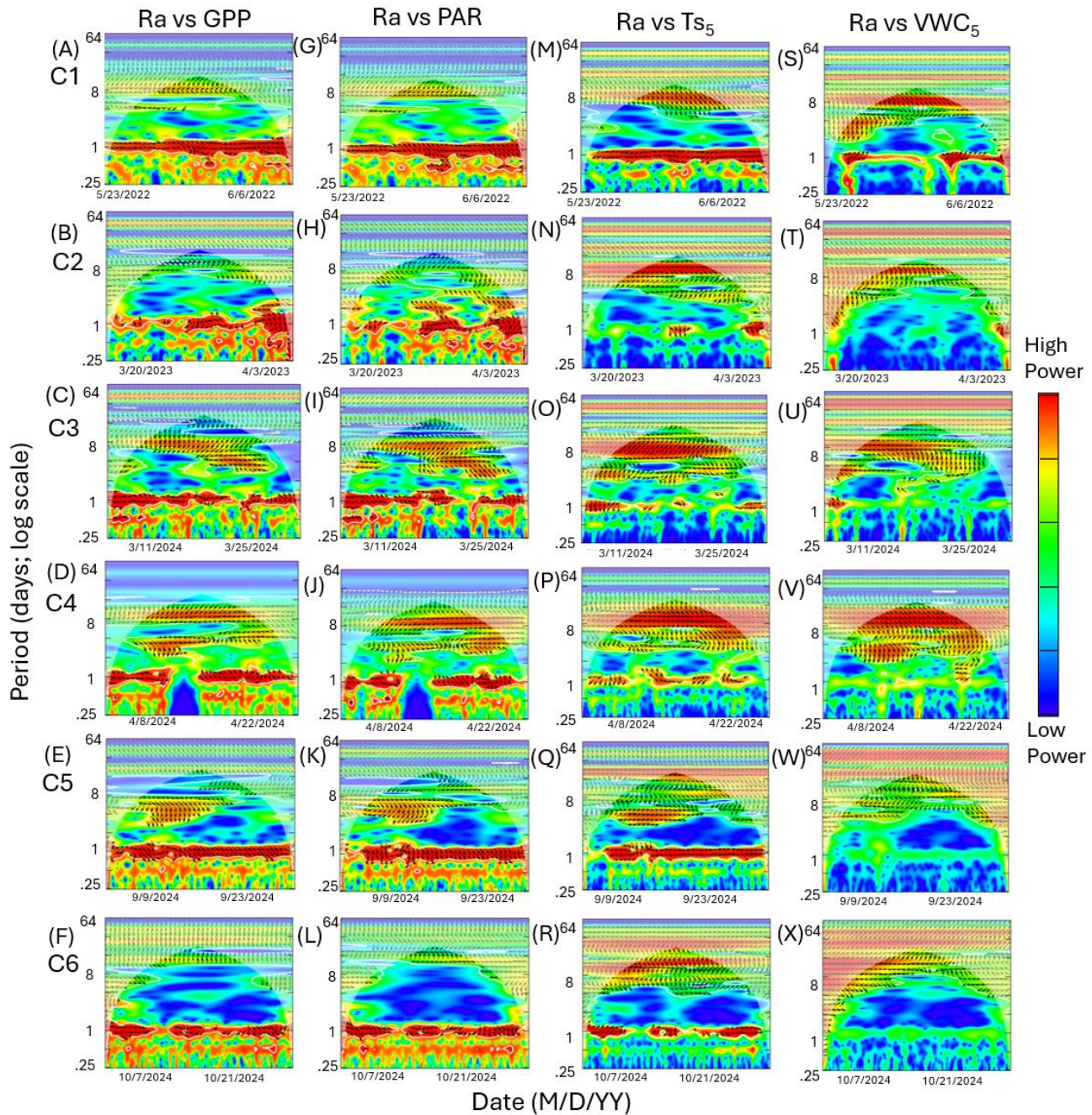
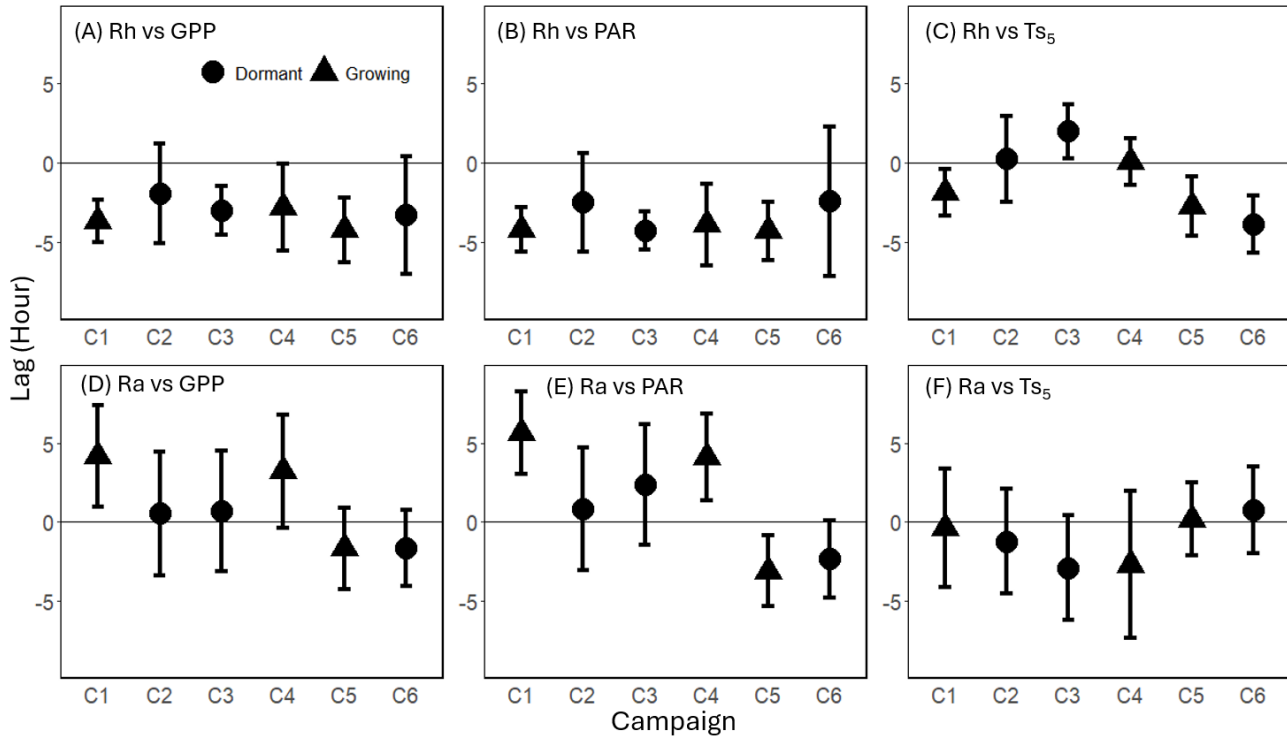


Figure 7. Heatmaps of the cross-wavelet transformation (XWT) of autotrophic respiration (Ra) against gross primary productivity (GPP; A–F), photosynthetically active radiation (PAR; G–L), soil temperature (Ts₅; M–R), and volumetric water content (VWC₅; S–X) for six measurement campaigns (C1–C6) at US-CRK. Arrows pointing to the right and left represent positive and negative correlations, respectively, without lag. Arrows pointing up-left (positive correlation) and down-right (negative correlation) indicate the response component lags behind the driver, while arrows pointing up-right and down-left indicate that the driver lags behind the response component. The 5% significance level of the XWT analysis was generated within the cone of influence (COI) against white noise and identified by white contour lines. COI within the heat plot is identified with a light shade.

3.3 Phase Analysis

At the diurnal frequency range, the phase differences between Rh and both GPP and PAR revealed consistent lag patterns, with Rh lagging behind GPP by 1.9–4.2 hours and behind PAR by 2.5–4.3 hours across campaigns (Figs. 8A, B). In contrast, the phase relationships between Ra and GPP or PAR were more variable, with lag-lead times ranging from -1.7 to +4.2 hours for GPP and -3.1 to +5.7 hours for PAR, showing inconsistent patterns (Figs. 8D, E). Notably, during drought (C5 and C6), the lag time of Ra relative to GPP (C5: -1.7 hour; C6: -1.7 hour) was shorter than that of Rh (C5: -4.2 hour; C6: -3.3 hour). Phase angle analysis using model residuals showed similar results, where r_{Rh_day} lagged GPP by -3.5 ± 0.42 hours on average, except during C2, which exhibited a slight lead of $+0.64 \pm 2.8$ hours, and r_{Rh_week} lagged GPP by -5.7 to -0.02 hours (Figs. S11A, S12A). In contrast, r_{Ra_day} and r_{Ra_week} exhibited greater variability, with lag-lead times ranging from -1.9 to 2.1 hours and from +0.20 to 3.9 hours, respectively (Figs. S11D, S12D). The phase angles between Ts and Rh or Ra also varied, ranging from -3.8 to +2.2 hours for Rh and -3.9 to +1.5 hours for Ra, indicating an inconsistent lag-lead relationship at the diurnal timescale (Figs. 8C, F). Ts₅ consistently lagged behind GPP and PAR by 3.5 ± 1.1 hours and 4.6 ± 1.3 hours, respectively, across all campaigns (Fig. S13).



280 **Figure 8. Mean time lag ($\pm$ standard deviation) between heterotrophic respiration (Rh) in relation to (A) gross primary productivity**
 (GPP), (B) photosynthetically active radiation (PAR), and (C) soil temperature (Ts₅), and between autotrophic respiration (Ra) with
 (D) GPP, (E) PAR, and (F) Ts₅ at the diurnal frequency range (0.5 to 1.5 days) across six measurement campaigns (C1–C6). Phase
 differences were averaged over the diurnal frequency range and included only when the 1-day spectral peak was significant ($p <$
 0.1). Round dots represent dormant season campaigns, while triangles represent growing season campaigns. Positive lag values
 285 indicate that respiration preceded the corresponding driver, while negative values indicate that respiration lagged behind the driver.

4 Discussion

4.1 Limitations and Uncertainties

This study lacks true replication, as measurements were conducted at a single system location. However, we report data from six measurement campaigns that span different seasons, vegetation physiological states, and soil water availability. The spatial representativeness of the continuous autochamber measurements of soil respiration measurements was validated against monthly manual survey measurements from 25 pairs of control and root exclusion collars located in five study plots over three years. A representativeness analysis (Baniya et al., 2025) indicated that the temporal dynamics of the SR, Ra, and Rh, as well as the heterotrophic fraction, were similar among all measurement locations, but the absolute magnitude of SR was slightly greater in plots with greater understory cover. Additionally, the observed Rh:SR ratio (59–86%) was comparable to the 36–84% recorded using the root exclusion method in our previous studies conducted in loblolly pine forest stands in East Texas that also experienced low-intensity prescribed burns with a return interval of 2–5 years (Ono et al., 2025), and consistent with other studies in loblolly pine chronosequences (McElligott et al., 2016) and among different ecosystems globally (Bond-Lamberty et al., 2018).

The partitioning of SR to Ra and Rh using the root exclusion method has its own limitations (Bond-Lamberty et al., 2011), and the partitioned fluxes are not fully independent. Ra and Rh are inherently interconnected through rhizodeposition, root exudation, and mycorrhizal associations (Kuzyakov & Gavrichkova, 2010), and CHO-priming further complicates their separation. In the current study, Rh was expected to be isolated from root activity and diurnal fluctuations in CHO supply. However, respiration from root-excluded soils (i.e., Rh) overall showed a stronger correlation with canopy photosynthetic activity (GPP and PAR) than did the flux attributed to Ra. This unexpected pattern suggests incomplete exclusion, potentially due to ingrowth of fine roots or mycorrhizal hyphae, or root activity below the collar. The influx of labile C compounds (presumably exudates) likely enhanced microbial activity within the collars, thereby coupling Rh with recent photosynthate supply.

Lastly, we acknowledge that this study did not directly quantify root exudation, microbial biomass, or enzyme activity, nor employ isotopic pulse-chase techniques. The inference about microbial activity is based solely on the cospectral analysis of fluxes described above, which, among the alternative approaches available, is considered the preferred tool for analyzing the coupling between plant and soil C dynamics (Mencuccini & Hölttä, 2010).

4.2 Multitemporal Relationship of Rh and Ra with GPP, PAR, Ts, and VWC

The initial hypothesis that Ra would be more sensitive than Rh to GPP on a diurnal scale was not supported by the results. Instead, Rh and r_{Rh} demonstrated strong diurnal correlations with both GPP and PAR, as evidenced by distinct diurnal

cospectral peaks (Figs. 4G–R, S2 G–R, S6 G–R) and heatmaps (Figs. 6A–L, S4 A–L, S8 A–L). The overall stronger diurnal cospectral relationship between Rh and GPP, compared to that of Ra and GPP, along with the consistent lag of Rh relative to GPP, rather than the more variable lag-lead patterns observed in Ra–GPP, suggests that the diurnal cycle of plant carbohydrate status was a key limiting factor for Rh, but was less pronounced for Ra. While Ra and r_{Ra} also exhibited diurnal cospectral peaks with GPP as well as the lag of Ra relative to GPP during C5 and C6 (Figs. 5K–L, S3 K–L), the time lag was reversed (Ra preceding GPP) during the first four campaigns. This suggests that tissue carbon status may have been buffered by starch reserves, as hydrolysis of stored starch can supply soluble sugars to meet the local energy and material demands (Zweifel et al., 2021). The strong response of Rh to plant C status during all measurement campaigns suggests an opportunistic microbial community. This is consistent with the findings of Yang et al. (2022), who reported a similar 2–6.5-hour lag of Rh relative to PAR across a year in a subtropical evergreen broadleaf forest, and contrasted it to a lack of such a pattern in an adjacent open canopy area. However, this contrasts with our initial hypothesis that the diurnal cospectral peaks would be mediated by fine root activity (Mitra et al., 2019). Many earlier studies that observed elevated soil CO₂ efflux closer to trees than away from them (e.g., Noormets et al., 2010; Savage et al., 2013; Tang et al., 2005) also assumed it must have been of autotrophic origin. In light of the results reported here, and those of Yang et al. (2022), Mitra et al. (2019), and Mitra et al. (2020), it should be acknowledged that while autotrophic respiration cannot be ruled out in those cases, there appears to be a rapid transfer of assimilated substrates from plants to soil microbes or simply exudation into the soil medium, and the processing of this newly assimilated carbon can be under microbial metabolic control.

The observed 2–4 hour lag of Rh relative to GPP at the diurnal scale is consistent with previously reported rates of pressure-concentration wave propagation in the phloem (Mencuccini & Hölttä, 2010) and the subsequent release into the rhizosphere (Kuzyakov & Gavrichkova, 2010). Although we did not directly measure exudate composition or microbial community responses, prior studies suggest that such rapid microbial utilization of new carbon inputs is facilitated by readily available substrates, such as soluble sugars and amino acids, that are tightly coupled with photosynthetic dynamics (Canarini et al., 2019). These labile compounds can activate microbes (Cheng et al., 2014; Kuzyakov & Blagodatskaya, 2015), and they can metabolize the compounds within hours (Kuzyakov & Gavrichkova, 2010). Therefore, we interpret it as a change in C availability (C status) in roots, with a likely pulse of exudation that triggered an increase in Rh within hours of enhanced photosynthetic activity, even though the mass flow of assimilates may occur over longer timescales (Liesche et al., 2015).

We did not observe pronounced seasonal differences in the diurnal cospectral peak strengths or lag-lead times for either Rh–GPP or Ra–GPP, in contrast to findings from other earlier studies (Heinemeyer et al., 2012; Yang et al., 2022). The reduced seasonal variation in our evergreen subtropical study site compared to that in deciduous forests is probably associated with the year-round photosynthetic capacity and metabolic activity. We also observed that allocation to non-structural carbohydrates remained positive even during the drought when growth ceased (C5–C6) (Baniya et al., 2025). This is consistent with earlier

reports that photosynthesis is less sensitive to drought than biomass production (Prescott et al., 2020), which may increase belowground carbon allocation and substrate availability to both Ra and Rh (further discussed in Section 4.3).

355 The phase angle differences between Ra and Rh with Ts showed mixed lag and lead relationships. Notably, in C1 and C5, the lag of Rh relative to Ts (1.9 and 2.7 hours, respectively; Fig. 8C) was shorter than its lag relative to GPP (3.7 and 4.2 hours, respectively; Fig. 8A), suggesting a potential functional connection between them (Mitra et al., 2019). However, the cospectral peak height was greater for Rh with GPP than with Ts (16.7 vs 13.5 period⁻¹ in C1, and 11.4 vs 9.1 period⁻¹ in C5; Figs. 4G, S, K, W), and the time lag between Rh and GPP (unlike that between Rh and Ts) was consistent across all campaigns, suggesting that carbohydrate transfer had a greater influence on Rh diurnal dynamics.

360 4.3 Implications and Future Considerations

The consistently strong cospectral peaks between Rh and GPP suggest that surplus photosynthates, not immediately allocated to plant growth, are exuded into the soil, where they appear to support the activity of the opportunistic microbial community. Ecosystem scale estimates of the magnitude of root exudation remain difficult to quantify, but at the current study site, the overall allocation to non-structural carbon compounds exceeded 100 g C m⁻² month⁻¹ in some months (Baniya et al., 2025).
365 How much of it was retained in plants as storage compounds and how much was exuded into the soil, and whether these can be derived from the diurnal magnitudes of each flux (Fig. 1), remains to be determined, but there appears to be ample C available to support the exudation.

The current conclusion that the short-term (diurnal) variability in SR is primarily mediated by Rh and coupled to substrate availability from GPP appears to contrast most earlier interpretations (e.g., Heinemeyer et al., 2012; Savage et al., 2013; Tang et al., 2005), where the evidence appeared to support the link between GPP and Ra. However, in light of the present findings and those by Yang et al. (2022), it is possible that studies where the partitioning between Ra and Rh was based only on proximity to trees (Savage et al., 2013; Tang et al., 2005), without explicit root exclusion, may have measured CO₂ that was produced either by the roots and associated symbionts or by free-living microbes. If C exudation can fuel heterotrophs on a diurnal cycle
375 and prime the decomposition of detritus, then separating these two fluxes conclusively becomes more difficult. Furthermore, if heterotrophic activity draws to a significant degree on newly assimilated photosynthates, it also calls into question the reliability of partitioning plant and microbial respiration based on Keeling plots (Pataki et al., 2003). This is illustrated by the recent study by Yang et al. (2022), who, on one hand, observed diurnal fluctuation only under a tree canopy and not in the open, but because root exclusion treatments were applied in both situations, were still able to attribute the signal to Rh instead
380 of Ra.

Our findings lend support to the “surplus C theory” (Prescott, 2022; Prescott et al., 2020), whereby assimilation in excess of immediate plant needs may be stored or exuded. In the current study, campaigns C2–C6 coincided with low biomass

production, while C1 occurred during high growth (data not shown), yet during all of them, plants were estimated to have had
385 excess non-structural carbohydrates (Baniya et al., 2025). It lends further support to the conclusion that carbon was exuded
into the soil and consumed by heterotrophs. The current study adds to the body of evidence that increased photosynthesis does
not always manifest in increased growth (Jiang et al., 2020), but can instead be exuded into the soil (Klein et al., 2016) or to
mycorrhizal symbionts, where it may actually serve plant needs and support nutrient-acquiring enzymes (Hagenbo et al., 2019).
The magnitude of exudation flux at different physiological states remains to be determined. It is notable that in the current
390 study, this was observed during all six campaigns, spanning early, mid-, and late growing seasons.

The changing magnitudes and diurnal amplitudes of both R_a and R_h (Fig. 1) could be caused by both environmental and
physiological constraints, and carbon allocation to different plant compartments likely responds to both. Future research will
incorporate diel measurements of carbohydrate concentrations in tree and root tissues, isotopic partitioning of soil respiration,
395 and multi-season campaigns to further evaluate the mechanisms underlying these observations.

Code and data availability. Meteorological data at the US-CRK can be downloaded from the Ameriflux database (Noormets, 2024). Continuous soil respiration data and all the code files for the analyses in this manuscript can be found on GitHub via https://github.com/moekaono/CRK_cont_SR.

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Author contribution. MO: Writing – original draft, Visualization, Methodology, Investigation, Software, Formal analysis, Data curation, Conceptualization. BM: Writing – review & editing, Supervision, Methodology, Investigation, Software, Validation, Conceptualization. BB: Software, Investigation, Data curation, Writing – review & editing. DK: Data curation, Writing – review & editing. AN: Writing – review & editing, Supervision, Resources, Validation, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

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Competing interests. The authors declare that they have no conflict of interest.

Acknowledgments. Blaize Britton, Clement Sarpong, Malik Nkrumah, and Seth Massery assisted with soil sampling and soil CO₂ efflux measurements. MO was supported by the ITO Foundation and the McMillan-Ward Fellowship. DK and BB were supported by the Native Plant Society of Texas.

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Financial support. This project was supported by USDA NIFA (award #: 2023-67019-40537), the Cynthia and George Mitchell Foundation, and the U.S. Department of Energy’s Office of Science through the AmeriFlux Management Project (DE-AC02-05CH11231).

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