Author's response to Reviewer 1 for Manuscript egusphere-2025-2849: “The Use of Newly Assimilated Photosynthates by Soil Autotrophic and Heterotrophic Respiration on a Diurnal Scale”

We thank Reviewer 1 for the valuable comments. We address all comments below and document the resulting changes to the manuscript. The reviewer’s comments are shown in plain typeface, while the author’s responses are highlighted in blue. Revised or added text appears in red. All line numbers refer to the original submitted work. Citations within this response are listed in the References section at the end of the document.

Response to Reviewer #1

1. This study focuses on the diurnal coupling mechanism between soil autotrophic respiration (Ra), heterotrophic respiration (Rh), and photosynthetic carbon allocation in subtropical coniferous forests. It fills the gap in traditional soil respiration models that overlook the dynamic regulation of carbohydrates, and particularly reveals the rapid response of Rh to newly assimilated photosynthates (with a 2-4 hour lag), providing a new perspective for understanding the immediate driving mechanisms of soil carbon fluxes. However, there are still some uncertainties, as detailed below.
   Response 1: We thank the reviewer for the positive and constructive comments.

2. It is necessary to clarify the criteria for determining the stable period (3-6 months) of Rh after the insertion of deep collars, supplement the correlation analysis between the vertical distribution of fine root biomass and collar depth, and explain whether the rhizosphere priming effect has been effectively excluded. The potential biases of the root exclusion method (such as interference of dead root decomposition on Rh) are only briefly mentioned in the "Limitations" section, without discussing whether the differences in the Rh:SR ratio (59%-86%) in the supplementary materials compared with other studies stem from methodological factors.
   Response 2: We will include two references that provide further evidence on the range of Rh:SR in southern pines (McElligott et al., 2016) and more broadly (Bond-Lamberty et al., 2018), as well as a reference to our own earlier study from a similar nearby loblolly pine forest that experienced similar low-intensity fires with a return interval of 2–5 years (Ono et al., 2025). The ratio recorded with the study was the Rh:SR ratio of 36–84% recorded using the root exclusion, which is similar to this study (59–86%). This earlier report (Ono et al., 2025) also includes supplementary material (Fig. S2) demonstrating how the stability of Rh:SR ratio was assessed.

3. Description of wavelet analysis parameters: The basis for selecting the period parameters of the Morlet wavelet and the specific threshold for excluding data outside the "cone of influence (COI)" should be supplemented to ensure the reproducibility of the results.

   Response 3: We used the white noise for the significance analysis, and the cone of influence at a 5% significance level was checked with Monte Carlo methods (100 simulations). We expand the information, after lines 140-141, as shown below. Please also refer to Comment #14 for the selection of noise type.

   > "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)."

4. Calculation of model residuals: The differences in the estimation of Q10 parameters in Formula (1) between daily and weekly scales need to be quantified, and an explanation should be provided for the use of two time windows (day/week) and their impact on residual results.

   Response 4: The Q_{10} and R_{20} parameter values are not central to our main analysis but were included only as a confirmatory analysis for the main cospectram among the total respiration fluxes. We expanded the discussion (Section 2.4.2, after line 128) to clarify why two time windows (daily and weekly) were applied, as follows:

   > "We analyzed the wavelet spectra of soil respiration components (Ra and Rh, or their residuals, r_{Ra} and r_{Rh}; Section 2.4.3) and their cospectra with environmental and physiological drivers (GPP, PAR, Ts, 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 Ra and Rh (Figs. S2–S12)."

Even though we would prefer to leave it out of the final publication, we included a table of the different Q_{10} estimates below. The Q_{10} values vary widely between different campaigns and between Rh and Ra. They also have widely varying standard errors. Furthermore, the Q_{10} of Ra during campaigns 3 and 4 is unreasonably large in both daily and weekly models, given the narrow temperature and wide Ra range. Reporting these necessitates an additional explanation that we have included, following line 203, as shown below.

> "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)."

Even though this further reinforces the main conclusion of our analysis, it is a divergence from the main analysis, and we would prefer to leave it out.

Table. Average apparent Q_{10} (Mean ± standard deviation) estimated with a daily or weekly rolling window for soil heterotrophic (Rh) and autotrophic respiration for analyzing the cospectral dynamics of respective model residuals (r_{Ra_day}, r_{Ra_week}, r_{Rh_day}, and r_{Rh_week}). Campaigns conducted during active growing seasons are marked with an asterisk (*).

	Daily Q_{10} estimate		Weekly Q_{10} estimate	
Campaign	**Rh**	**Ra**	**Rh**	**Ra**
1*	1.70 ± 0.34	0.45 ± 0.17	1.88 ± 0.17	0.64 ± 0.14
2	2.67 ± 1.88	6.94 ± 18.4	1.51 ± 0.12	14.0 ± 18.0
3	3.58 ± 2.05	$4\times10^{9} \pm 2\times10^{10}$	1.88 ± 0.23	$2\times10^{8} \pm 3\times10^{9}$
4*	4.87 ± 3.55	$1\times10^{11} \pm 5\times10^{11}$	2.00 ± 0.14	$2\times10^{27} \pm 5\times10^{28}$
5*	1.16 ± 0.17	1.51 ± 0.30	2.13 ± 0.14	1.55 ± 0.30
6	1.03 ± 0.18	3.94 ± 6.84	1.74 ± 0.21	2.53 ± 1.01

5. Seasonal differences in lag time: The slight advance (+0.64 hours) of Rh relative to GPP in C2 (dormant season) in Figure 8 needs further explanation, whether it is related to microbial metabolic lag under low temperatures or the release of root carbon reserves.
   Response 5: While the mean lag time was smallest during this campaign, it also had the second largest standard deviation. We are unsure if the small difference in the mean lag time can be given much significance, much less attributed to a specific driver.

6. Fluctuation mechanism of Ra: Combined with the positive and negative alternation of Ra lags in Figures S10-S11, it is suggested to supplement the measured data of non-structural carbohydrates (such as starch) in different seasons to verify the "reserve buffer" hypothesis.
   Response 6: Unfortunately, we do not have a matching dataset for non-structural

carbohydrate concentrations. The non-structural carbon study cited below (Baniya et al., 2025), which we added as a paragraph after line 285 (please also see response #24), is a separate analysis with only a partly overlapping study period. Resolving the mechanistic controls of Ra is the focus of our ongoing studies.

> "… We also observed that allocation to non-structural carbohydrates remained positive even during the drought when growth ceased (C5–C6) (Baniya et al., 2025).

7. Interaction of temperature and humidity: Did the high VWC values (42-43%) in C3-C4 inhibit the response of respiration to substrates? It is necessary to analyze the synergistic effect of VWC and GPP to avoid the limitation of single-factor interpretation.
   Response 7: Water availability is expected to be a key regulator of carbon allocation in plants, as well as a modulator of plant and microbial respiration. However, the current analysis does not address sensitivity in the traditional sense (change in respiration per change in VWC), only the consistency of temporal cospectra.

8. Differences from early studies: A clearer comparison should be made between the results of this study (2-3 meters tree distance) and the "tree distance gradient method", attributing the differences to vegetation types (coniferous vs. deciduous) or methodologies (root exclusion vs. spatial substitution).
   Response 8: Thank you for pointing out this connection. We revised the paragraph starting from line 301, and have added some discussion regarding the interpretation of results based on the distance to the tree, as shown below. However, it may be premature to make blanket interpretations about all reports of elevated soil CO_2 efflux in proximity to trees having been due to C transfer to heterotrophs. Until we understand this process more completely or test it explicitly, it may be possible that the C transfer to microbes could vary among different ecosystems or in different environmental settings.

> "However, in light of the present findings and those by Yang et al. (2022), it is possible that studies were 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 CO_2 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 and prime the decomposition of detritus, then separating these two fluxes conclusively becomes more difficult. … 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 of

Ra."

9. It is recommended to discuss the stability of this mechanism under extreme climates (such as drought), and infer the impact of water stress on carbon allocation based on the data of C5 (VWC=10.4%).
Response 9: The sensitivity of phloem transport to water availability is unclear. We noted that the drought in 2024 (C5-C6) did not alter the time lag between Rh and GPP, as shown below, following line 285.

"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)."

Even the size of the cospectral peak did not clearly correlate with drought or active vs dormant season. A larger dataset is required for comprehensive resolving of both spectral and mechanistic patterns.

10. The differences in Rh:SR ratios (47%-86%) among various campaigns in Table 1 require ANOVA analysis to clarify seasonal significance.
Response 10: The mean and standard deviation of Rh:SR ratio between the growing season (0.63 ± 0.19, $n = 3$) and the dormant season (0.79 ± 0.08, $n = 3$) were not significantly different ($p = 0.26$) based on one-way ANOVA analysis. We add this result, followed by lines 160, as follows:

"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, $p = 0.26$)."

11. Soil temperature and humidity were only measured at a 5cm depth, while 84% of fine roots are distributed in the 0-30cm layer (Figure S1). The association between deep root activity and carbon allocation is ignored, which may underestimate the impact of vertical gradients on Ra/Rh.
Response 11: Yes, the increasing time lag of temperature with soil depth could affect spectral analysis. In the current study, we reasoned that processes in the surface soil with >50% of fine roots in the top 10 cm (Fig. S1) and the greatest heterotrophic activity would dominate the respiration signal and any cospectral pattern. We did measure soil temperature and moisture in multiple depths (the 20 cm depth has now been added to

Fig. 2, shown below). For reference, we will also include a supplementary figure (as Fig. S2, shown below) of the cross-wavelet transformation of both Rh and Ra with Ts and VWC at 20 cm (Ts_{20}, VWC_{20}). The results show a consistent pattern with both depths, but the cospectral peaks are more pronounced with the Ts and VWC at 5 cm.

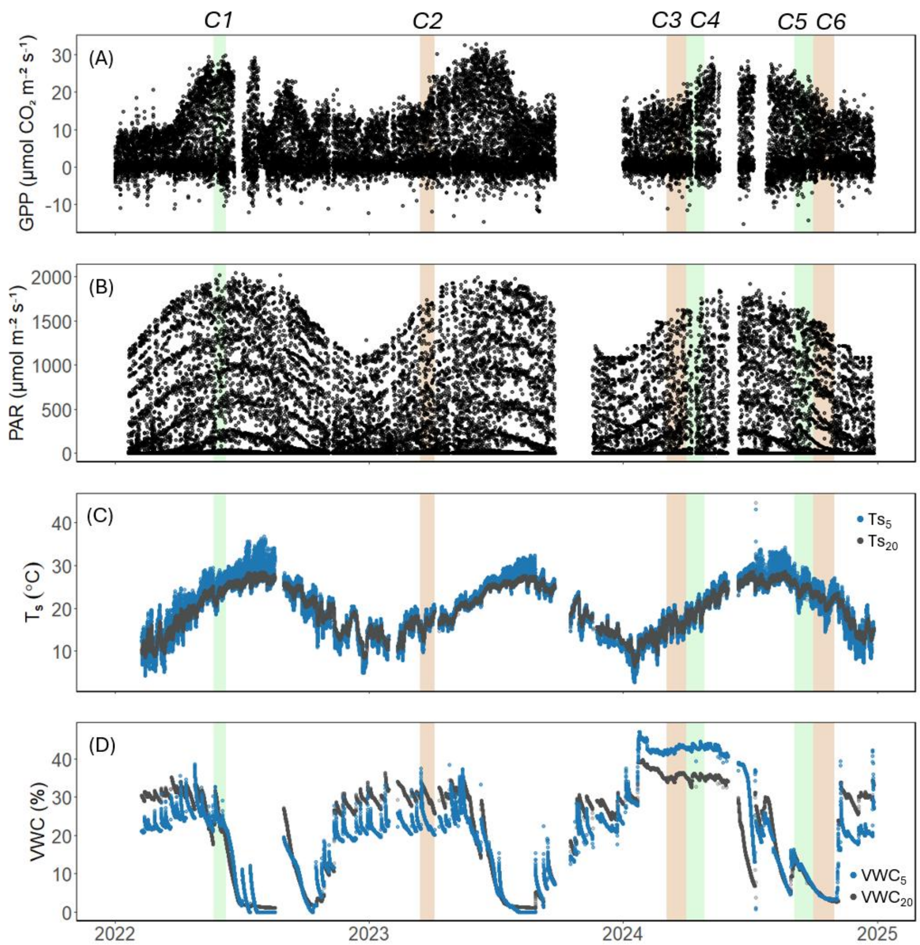

Figure 2. Hourly time series of (A) gross primary productivity (GPP; µmol CO_2 m^{-2} s^{-1}), (B) photosynthetically active radiation (PAR; µmol m^{-2} s^{-1}), (C) soil temperature (Ts_5 and Ts_{20}; °C), and (D) volumetric water content (VWC_5 and VWC_{20}; %) at 5 and 20 cm depth at the US-CRK site 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.

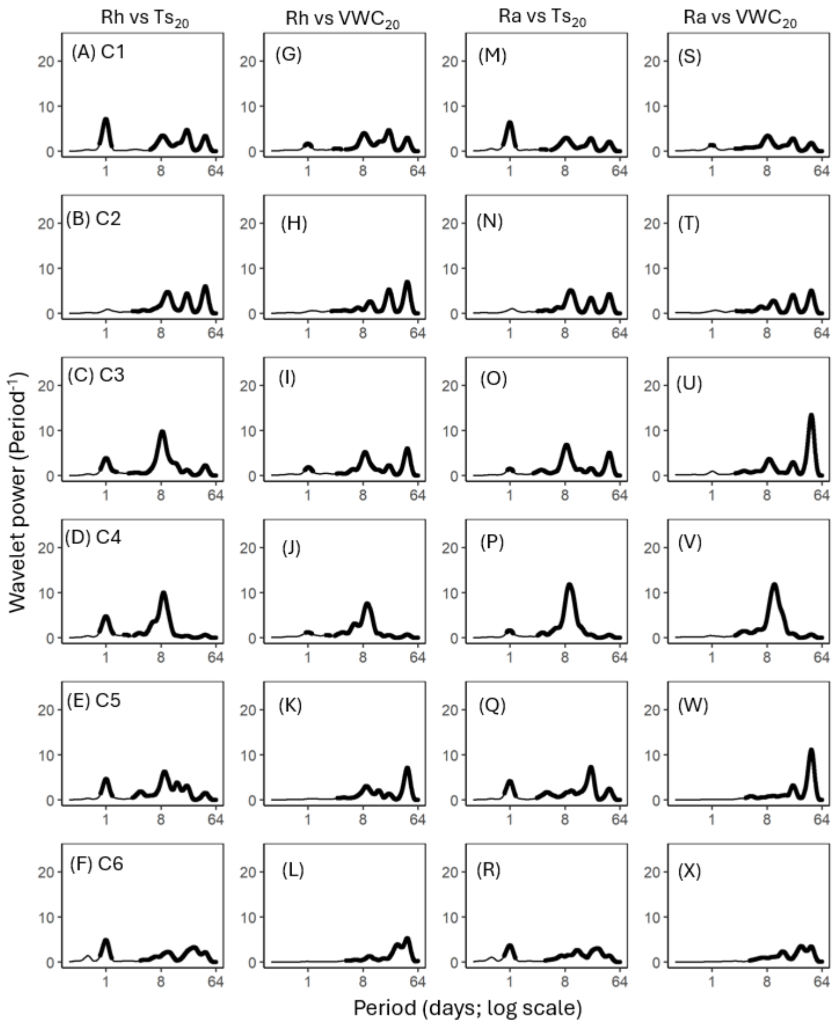

Figure S2. Average wavelet power in the frequency domain (Period; time intervals from 6 hours to 64 days) generated from the cross-wavelet transformation of heterotrophic respiration (Rh) against soil temperature (Ts_{20}; A–F) and volumetric water content (VWC_{20}; G–L) at 20-cm depth, and autotrophic respiration (Ra) against Ts_{20} (M–R) and VWC_{20} (S–X) for six campaigns (C1–C6) at the US-CRK site. The bold contours indicate areas with significant coherence at the 5% level against white noise.

12. Root exudate concentration or isotope labeling data were not measured, so it is impossible to directly prove that the "2-4 hour lag" is caused by carbon input, and the evidence chain is incomplete only through indirect correlation inference.

Response 12: Yes, we do lack this data. The only evidence for the relationship between photosynthesis and CO_2 efflux from the root-excluded soil columns is the consistent cospectral behavior reported in this paper and parallel studies (Yang et al., 2022). As described in the Introduction (lines 59-63), given the temporal lag of pressure-concentration waves and mass flow in the phloem, the flux-based method is considered more powerful than pulse labeling for the interpretation of short-term coupling between photosynthesis and soil processes (Gunina & Kuzyakov, 2022; Mencuccini & Hölttä, 2010). (Admittedly, the exact pathway and regulation of C transfer from leaves to roots and the soil remains to be elucidated). We also add a paragraph at the end of Section 4.1, as follows:

> "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)."

13. When using the Q10 model to isolate temperature effects, the differences in parameter estimation between daily-scale (rRh_day) and weekly-scale (rRh_week) were not quantified. If the weekly-scale parameters smooth out short-term fluctuations, it may artificially amplify the correlation between residuals and GPP, leading to an overestimation of the "substrate-driven" conclusion. However, the actual situation is that I am not familiar with this content, and I would ask other reviewers to comment on it.
    Response 13: This question overlaps partly with question 3 and was addressed above. We have added the Q_{10} values of both daily and weekly scales, and the results show that Q_{10} for Rh did not differ substantially between the two. We applied both methods to account for diurnal and synoptic temperature responses. While the weekly scale may smooth short-term fluctuations, these effects should be captured by the daily-scale analysis, which yielded comparable Q_{10} values. Therefore, we believe that the use of weekly-scale windows did not artificially inflate the correlation between residuals and GPP.

14. In cross-wavelet transformation (XWT), the determination of the "5% significance level" is based on the white noise assumption, but the relationship between soil respiration and environmental factors may have red noise characteristics, leading to misjudgment of significantly correlated regions.
    Response 14: The choice of white noise as a background spectrum was consistent with previous work on the spectral analysis of soil respiration, such as Vargas et al. (2010) and Mitra et al. (2019). Additionally, it has been shown that the color of the noise, including red noise, has little impact on the results of spectral analysis (Grinsted et al., 2004; Vargas et al., 2010). We expand the explanation in lines 140-141, as follows:

"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)."

15. The statement that "the coupling strength between Rh and GPP is 1.2-2.6 times that of Ra" lacks statistical significance testing.
    Response 15: It was statistically significant by one-way ANOVA ($p = 0.047$). We will add this result to the revised manuscript.

16. In the seasonal difference analysis, what are the sample sizes of the growing season and dormant season groups respectively?
    Response 16: Growing season campaigns were during C1, C4, and C5 (n=3) and dormant season campaigns were during C2, C3, and C6 (n=3). Please refer to Table 1.

17. The observed lagged association between Rh and GPP may be driven by third-party factors (such as Ts) (Figure S12 shows that GPP lags behind Ts by 3.5 hours), and confounding effects have not been excluded through methods such as structural equation modeling.
    Response 17: Thank you for pointing this out. The labels on this graph were plotted in the wrong order. We have now corrected the figure and the caption (now Fig. S13), and it now shows that Ts lags behind GPP and PAR.

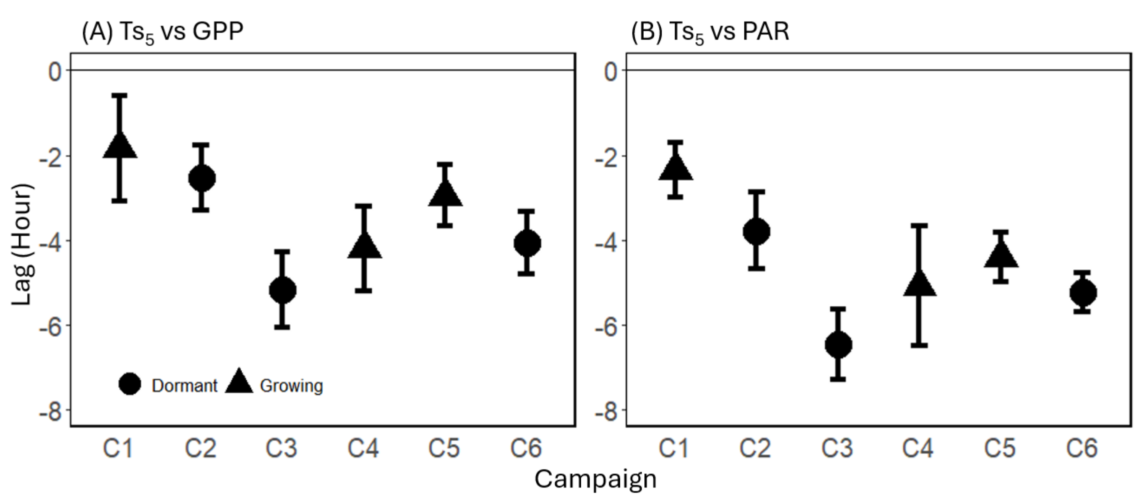

Figure S13. Mean lag times (± standard deviation, in hours) between (A) gross primary productivity (GPP) and soil temperature (Ts_5), and (B) photosynthetically active radiation (PAR), and Ts_5 at the diurnal frequency range (0.5 to 1.5 days) across six measurement campaigns (C1–C6). Phase differences were averaged over the diurnal frequency

range and included only when the 1-day spectral peak was significant ($p < 0.1$). Circular dots represent dormant season campaigns, while triangles represent growing season campaigns. Positive lag values indicate that GPP or PAR lagged behind Ts, while negative values indicate that GPP or PAR preceded Ts.

18. If Rh depends on root exudates and Ra originates from immediate carbon allocation, Ra should respond to GPP more rapidly than Rh, but the results show the opposite. This contradiction has not been reasonably explained, which may be due to methodological biases.
Response 18: This is, indeed, unexpected. We hypothesized that the coupling of SR with GPP would be caused by Ra. As to why Ra would not be as tightly coupled, we have offered a hypothesis as below, by modifying lines 275-277:

> "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)."

Root cells hold carbohydrate reserves (starch and lipids) that can be hydrolyzed based on local metabolic needs, and the soluble sugars so produced may be consumed before any excess can be exported into phloem and released into soil. Thus, the inconsistent cospectral lag does not necessarily indicate a lack of respiratory demand, but rather a local buffer that can more precisely respond to cellular metabolic state. Clearly, the exact mechanism is yet to be elucidated.

19. The study only infers that root exudates drive Rh through the "2-4 hour lag consistent with the propagation rate of phloem pressure-concentration waves", but fails to explain in depth. For example, how do microorganisms quickly utilize newly input carbon sources (such as whether specific functional flora are involved in activation)? Do the chemical compositions of root exudates (such as the proportion of sugars and amino acids) change with photosynthetic dynamics, and what are their differential impacts on Rh?
Response 19: These are details that our study cannot answer. We hypothesize that the rapid up- and down-regulation may indicate bacterial rather than fungal metabolism. We do not have any data to support this, but Kuzyakov and Gavrichkova (2010) showed that labile compounds can activate soil microbes and that they can metabolize the compounds within hours. Furthermore, Canarini et al. (2019) and Yang et al. (2022) have shown, similarly to our current report, that microbial activity is tightly coupled to photosynthesis. We also do not have data about the chemical composition of root exudates, although we have detected diurnal fluctuation in the soluble sugar

concentrations in the soil (a separate study).

20. Why does the significant correlation between rRh_day and GPP in the supplementary materials (Figures S2 and S6) still exist in the dormant season (such as C2), which contradicts the common sense that "carbon input is more active in the growing season", and this abnormal phenomenon has not been discussed.
Response 20: The term "dormant" is misleading, and we have explained it better, as shown below, by expanding lines 105-106. Given the subtropical climate and evergreen canopy, the active and less active periods are defined based on canopy leaf area, soil CO_2 efflux, gross photosynthesis, soil temperature, and moisture. Even though the irradiance and LAI are lower during winter months, photosynthesis continues nevertheless.

> "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 cessation."

21. The high variability in the lag time between Ra and GPP (-1.8 to +4.8 hours) is only attributed to "starch reserves", but without data support.
Response 21: Yes, this is a hypothesis, which remains to be tested.

22. The differences in carbon reserve strategies between coniferous and broad-leaved trees have not been discussed. For example, coniferous trees retain leaves throughout the year, which may have a more stable Ra regulation mechanism.
Response 22: We have added the paragraph to discuss the seasonal and vegetation type differences following line 285, as shown below:

> "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."

23. The study mentions that the coupling between Rh and GPP in this research is stronger than that of Ra, which is opposite to the results of temperate forest studies by Savage et al. (2013), but only attributes it to "vegetation type differences" without in-depth analysis.

Response 23: We have added Yang et al. (2022) to interpret these results. With respect to vegetation type, we added a paragraph highlighting that differences between evergreen and deciduous species are likely due to year-round photosynthetic capacity (please see response #22). Please also refer to response #8 comparing with early studies.

24. In Table 1, the proportion of Ra in C1 (growing season) reaches 53%, while that in C6 (dormant season) is only 15%. Why is Rh still significantly coherent with GPP in the dormant season (Figure S4)? The "source of surplus carbon in non-growing seasons" has not been explained; moreover, the proportion of "surplus carbon" has not been quantified (such as estimated through the flux balance of GPP and Ra/Rh), and only qualitative descriptions are provided, lacking data support.
Response 24: The consistency of the Rh-GPP cospectra across seasons is the main result of the current study. Its independence of the actual flux magnitude and the Rh:Ra ratio underlines the plausibility of the mechanisms proposed. As noted in response #22, the year-round photosynthetic activity (Fig. 2A) provides the C supply. Closing the C budget quantitatively between the non-structural pool and that exuded into the soil, particularly on a diurnal scale, is currently not possible. The closest support we currently have is that NSC flux was estimated to be positive during campaigns C5 and C6, while new biomass growth had ceased due to drought. We have added the discussion following the paragraph in response #22 (after line 285).

> "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)."

25. The reason why the correlation between VWC and respiration in wavelet analysis is extremely weak (VWC-related subgraphs in Figures S2 and S6) has not been explained, which contradicts the general cognition that "soil moisture affects microbial activity", and it is only mentioned in passing as "weak and unstable".
Response 25: We did not find a strong diel correlation between Rh and VWC, but detected a synoptic (weeks to months) relationship across campaigns, which is consistent with the past study (Mitra et al., 2019). However, we did not emphasize this point in this manuscript because (1) we detected the signals on the synoptic

relationship, but this is largely outside the cone of influence (COI), and (2) our focus in this manuscript is on the short-time scale (i.e., the diel relationship).

26. The study indirectly infers photosynthetic carbon input through GPP and PAR, but key indicators such as the concentration, flux, and chemical composition of root exudates, the content of non-structural carbohydrates in leaves and roots, and the allocation path of newly assimilated carbon to Ra and Rh have not been directly measured, resulting in a lack of direct evidence for relevant conclusions.

    Response 26: Quantifying all these components and closing the C allocation budget at different time scales is the ideal, but it would entail methodological, labor, and monetary costs well beyond the scope of the current analysis. We do cite a follow-up study (Baniya et al., 2025) that provides independent lines of evidence and supports the interpretation of the cospectral analysis. Still, we do not have tracing and concentration data at the same resolution as the flux data on which the current work is based.

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