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Tree photosynthesis modulates soil respiration on a diurnal time scale

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Abstract

To estimate how tree photosynthesis modulates soil respiration, we simultaneously and continuously measured soil respiration and canopy photosynthesis over an oak-grass savanna during the summer, when the annual grass between trees was dead. Soil respiration measured under a tree crown reflected the sum of rhizosphere respiration and heterotrophic respiration; soil respiration measured in an open area represented heterotrophic respiration. Soil respiration was measured using solid-state CO_2 sensors buried in soils and the flux-gradient method. Canopy photosynthesis was obtained from overstory and understory flux measurements using the eddy covariance method. We found that the diurnal pattern of soil respiration in the open was driven by soil temperature, while soil respiration under the tree was decoupled with soil temperature. Although soil moisture controlled the seasonal pattern of soil respiration, it did not influence the diurnal pattern of soil respiration. Soil respiration under the tree controlled by the root component was strongly correlated with tree photosynthesis, but with a time lag of 7–12 h. These results indicate that photosynthesis drives soil respiration in addition to soil temperature and moisture.

Keywords: carbon cycle, CO_2 efflux, CO_2 sensor, eddy covariance, savanna

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Introduction

In order to construct global carbon budgets and predict future climate change, a mechanistic understanding of processes and driving factors controlling soil respiration is essential. It has been reported that soil respiration correlates with gross primary productivity (GPP) or canopy photosynthesis (Craine *et al.*, 1999; Hogberg *et al.*, 2001; Janssens *et al.*, 2001; Kuzyakov & Cheng, 2001; Irvine *et al.*, 2005). However, our knowledge in the quantitative correlation between soil respiration and photosynthesis with direct field measurements is still limited because of methodological and instrumentational limitations. First, continuous measurements of canopy photosynthesis can be derived from the eddy covariance method on an hourly basis (Aubinet *et al.*, 2000; Baldocchi, 2003), but simultaneous measurements of soil respiration without disturbance on the similar resolution are difficult. The development of new soil CO_2 sensors, coupled with the flux-gradient method, provides a new method to measure soil respiration continuously (Hirano *et al.*, 2003; Tang *et al.*, 2003). Second, soil respiration consists of functionally different components, rhizosphere respiration (root plus associated respiration from mycorrhizae) and heterotrophic respiration from free-living microbes. Heterotrophic respiration often obscures the correlation between root respiration and photosynthesis. Third, temperature is a sensitive driver for soil respiration in most biomes. The correlation between root respiration and photosynthesis is often confounded with temperature. In this study, we simultaneously measure soil respiration and photosynthesis, assess the difference in soil respiration with and without associated tree roots, and detect the correlation between soil respiration and photosynthesis.

Materials and methods

We conducted a set of experiments over an oak-grass savanna during the summer, when the annual grass

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between widely spaced trees has negligible living parts for autotrophic respiration. The study site (38.4311°N, 120.9660°W and 177 m), one of the AmeriFlux sites for carbon flux studies, is located at the lower foothills of the Sierra Nevada Mountains near Ione, CA, USA. The climate is Mediterranean – hot and dry during the summer and relatively cool and wet during the winter. The overstory consists mainly of scattered blue oak trees (*Quercus douglasii*) with crown cover of 42.4%. The understory grass and herbs are annual species. The soil is the Auburn very rocky silt loam (Lithic haploxerepts).

Soil respiration was continuously assessed using a soil CO_2 gradient measurement system with minimum disturbance. We buried solid-state infrared gas analyzers (GMT 222, Vaisala, Finland) both under a tree and in an open area at 0.02, 0.08 and 0.16 m depth to measure CO_2 profiles in the soil in a continuous manner (Tang *et al*., 2003). The CO_2 profile data were sent to a datalogger (CR-23X, Campbell Scientific Inc., Logan, UT, USA), which was programmed to take samples every 30 s and to compute and store 5 min averages. The system under the tree was 1 m from the tree stem with a diameter at breast height (DBH) of 0.716 m and an average of crown diameter of 13.05 m. The system in the open was 24.5 m away from the above tree and 18 m away from another smaller tree with an average of crown diameter of 6.05 m. Soil respiration in the open was assumed to have negligible influence from trees.

CO_2 flux between any two layers of gradient measurements was computed based on Fick's first law of diffusion. CO_2 diffusivity in soils was computed as a function of soil volumetric water content, soil texture (Moldrup *et al*., 1999), and CO_2 diffusivity in the free air, which was corrected for temperature and pressure (Jones, 1992). CO_2 flux from the soil surface layer was extrapolated based on the linear increase in flux from deep to shallow layers. The temporally continuous gradient measurement systems were complemented by periodical measurements using soil chambers (LI-6400-09, Licor Inc., Lincoln, NE, USA) along a transect for large spatial coverage (Tang & Baldocchi, 2005) and validated that the continuous soil respiration measurements represented soil respiration under the tree and in the open.

Soil temperature and moisture at various locations and depths were measured. Soil temperature at a depth of 0.02, 0.08, and 0.16 m close to the location of CO_2 gradient measurements was correspondingly measured with multiple-level thermocouple sensors. In addition, we also measured soil temperature at a depth of 0.02, 0.04, 0.08, 0.16, and 0.32 m near an eddy covariance tower. Volumetric soil moisture content was measured continuously near the tower at a depth of 0.05, 0.1, 0.2, and 0.5 m in the soil with frequency domain reflectometry sensors (Theta Probe, model ML2-X, Delta-T Devices, Cambridge, UK). Profiles of soil moisture (0–15, 15–30, 30–45 and 45–60 cm) from two locations close to the CO_2 gradient measurement sensors and seven locations elsewhere were also measured weekly and manually using an enhanced time domain reflectometer (Moisture Point, model 917, E.S.I. Environmental Sensors Inc., Victoria, Canada). The meteorological and soil physics data were acquired and logged on CR-23X and CR-10X dataloggers (Campbell Scientific Inc.). The sensors were sampled every second, and half-hour averages were computed and stored on a computer to coincide with the carbon flux measurements.

Two sets of ecosystem-level measurements for net ecosystem carbon exchange (NEE) were made for 30 min integration periods by the eddy covariance method with instruments mounted on a 2 m tower under canopy and a 20 m tower over canopy (Baldocchi *et al*., 2004; Xu *et al*., 2004). Other meteorological data were also measured on the same temporal resolution. Specific data computation and adjustment including spike removal, coordinate rotation, and corrections for storage, low friction velocity, density, and humidity were described in detail in a grassland study adjacent to this site (Xu & Baldocchi, 2004).

Canopy photosynthesis at daytime was derived based on NEE measurements from overstory and understory. Overstory measurements of NEE at daytime were composed of photosynthesis (P_s) and ecosystem respiration (R_{eco}) ($NEE = R_{eco} + P_s$). Unlike many other studies that extrapolate nighttime R_{eco}, which equals to nighttime NEE, to daytime R_{eco} based on temperature response curves (Falge *et al*., 2002), we did not find a good correlation between night-time R_{eco} and temperature in the dry summer. Instead, we derived daytime R_{eco} based on understory measurements of carbon flux. Understory carbon flux in the summer, when there was no carbon uptake by the understory grass, was mainly from soil respiration with a small amount from stem respiration below the height of the measurement tower at 2 m. Therefore, daytime R_{eco} is the sum of understory flux measurements and part of stem respiration. Our preliminary results using chamber measurements for stem respiration indicated that stem respiration was relatively small compared with total soil respiration. We used a fixed rate, 5% of soil respiration, to estimate the contribution of stem respiration above the understory sensor to ecosystem respiration, based on results reported by Chen *et al*. (2003) in a savanna with similar leaf area index, stand density, and basal area. Estimated daytime ecosystem respiration was then used to compute canopy photosynthesis.

In order to reduce sampling errors associated with the meteorological method, we computed diurnal patterns averaged over a month. We analyzed the relationship between soil respiration and canopy photosynthesis based on two independent measurement methods on a diurnal basis. To emphasize the controls of temperature and photosynthesis on soil respiration, we removed other factors such as rain by analyzing data in June, July (except the 31st), and September 2003 only, when there was almost no rain.

Results and discussion

The average rate of photosynthesis over the site decreased from June to September (Fig. 1). The mean diurnal pattern of photosynthesis in June peaked at $-8.8\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ at 12 h. It peaked at $-5.6\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ at 9.5 h in July, and at $-2.9\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ at 9 h in September. Progressive summer drought caused the seasonal reduction in photosynthetic capacity (Xu & Baldocchi, 2003). Influenced by extremely high temperature, high vapor pressure deficit, and low soil moisture content, photosynthesis peaked earlier and shut down quickly during the course of a day from June to September. This gradual shift towards the morning in the timing of peak photosynthesis is consistent with measurements over ecosystems in Mediterranean climates (Wilson *et al*., 2003).

Soil respiration under the tree was five to 10 times greater than that in the open (Fig. 1), indicating a dominant control of root associated respiration on soil respiration. Soil respiration under the tree decreased from an average of $6.25\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ in June to $1.21\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ in September. Soil respiration at the open location decreased from $0.77\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ in June to $0.27\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ in September. The small values of soil respiration in the open were derived only from heterotrophic respiration when the annual grass was dead. Although heterotrophic respiration under the tree might be larger than in the open because of difference in root substrate, root turnover rates, exudates, soil organic matter, and nutrients between under trees and in the open, considering the small magnitude of heterotrophic respiration in the open in the dry summer, we assumed heterotrophic respiration under the tree was also small. Therefore, soil respiration under the tree was largely controlled by rhizosphere respiration.

The seasonal variation of soil respiration during this period was decoupled with the temporal variation in soil temperature, which peaked in July (Fig. 2a–c). However, the decrease in soil respiration was synchronized with the continuous decrease in soil moisture as a result of the prolonged summer drought in the savanna. Soil volumetric moisture measured at 0.1 m depth slightly decreased from $0.125\,\mathrm{m^3\,m^{-3}}$ averaged in June to $0.113\,\mathrm{m^3\,m^{-3}}$ in September (Fig. 2d–f). The seasonal decrease in soil respiration was also consistent with the decrease in photosynthesis as soil water deficits became more severe.

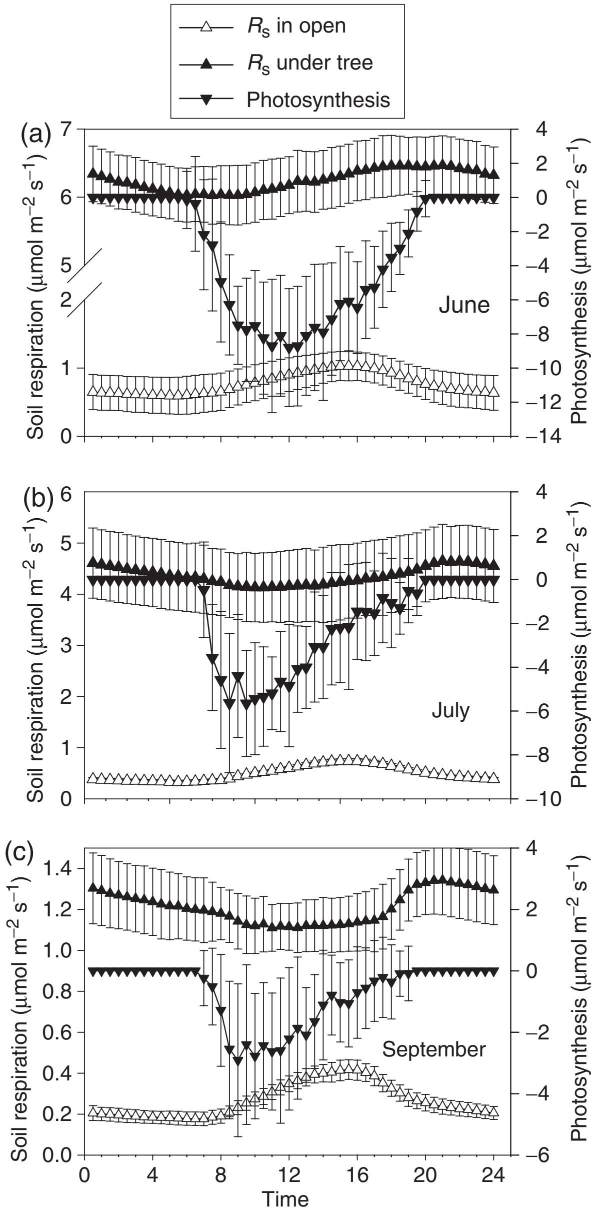

Fig. 1 Diurnal patterns of soil respiration (R_s) in the open, under the tree, and photosynthesis in June (a), July (b), and September (c). Values are averages of 30 days of the month. Error bars indicate standard deviations.

The diurnal variation of soil respiration in the open and under the tree shows a different pattern (Fig. 1). Throughout the experimental period, soil respiration in the open peaked at around 15 h, in phase with the

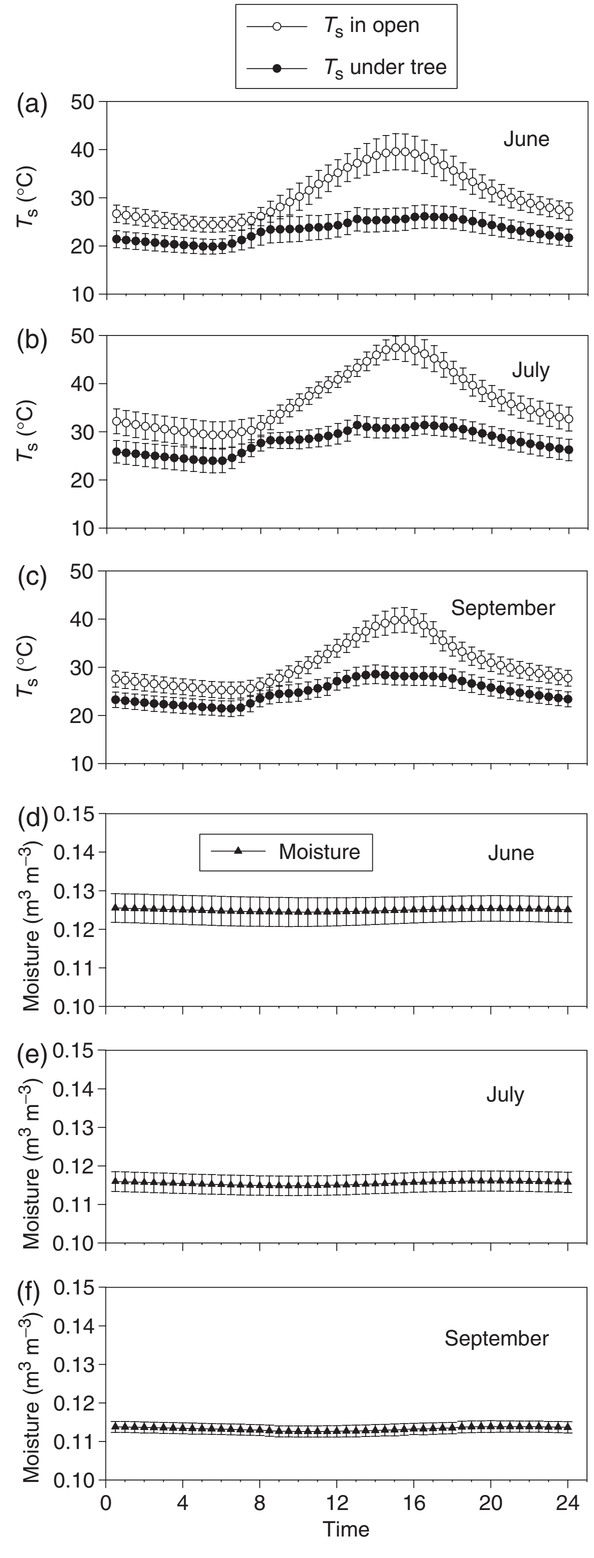

Fig. 2 Diurnal patterns of soil temperature (T_s) in the open and under the tree at 0.08 m in June (a), July (b), and September (c), and diurnal patterns of soil volumetric moisture under the tree at 0.1 m in June (d), July (e), and September (f). Values are averages of 30 days of the month. Error bars indicate standard deviations.

increase in soil temperature at 0.08 m (Fig. 2a–c), suggesting its dominant control by soil temperature. However, soil respiration under the tree was out of phase with soil temperature, indicating another control on root respiration. Although we found that diurnal peaks of soil temperature lagged about 2 h, accompanied by the decrease in amplitude when depth increased from 0.08 to 0.24 m, soil respiration under the tree peaked later than the peak of soil temperature at any layer. Soil respiration under the tree peaked at 18.5 h in June, and around 21 h in July and September, 7–12 h later than the peak of photosynthesis. The diurnal variation of soil moisture was negligible in the dry summer (Fig. 2d–f), indicating that soil moisture was not an influencing factor for soil respiration on a diurnal basis.

After plotting soil respiration against soil temperature at 0.08 m, we found a strong correlation between heterotrophic respiration in the open and soil temperature (Fig. 3a). The sensitivity of heterotrophic respiration to soil temperature decreased from June to September when soil moisture was decreased, indicating a moisture control on the sensitivity.

Soil respiration under the tree, mainly controlled by rhizosphere respiration, had a much weaker relationship with soil temperature at 0.08 m (Fig. 3b). By using different depths of soil temperature measurements, we also found very weak relationships between soil respiration and soil temperature on a diurnal basis ($r^2 < 0.2$). The sensitivity of soil respiration under the tree to temperature decreased from June to September. In July and September, the sensitivities were negative, indicating the decrease in soil respiration with increase in soil temperature. The decoupling of soil respiration under the tree with soil temperature was more significant in September than in June. This decoupling was likely influenced by the continuous decrease in soil moisture before the autumnal rain. We found a counterclockwise hysteresis loop after plotting soil respiration against soil temperature, that is, the change of soil respiration with temperature followed the time of a day (Fig. 3b). Under the same temperature, soil respiration was higher in the late afternoon and evening than in the morning. The difference of soil respiration between 10 and 21 h was 0.4 μmol m^{-2} s^{-1}, or 7% of soil respiration at 10 h averaged in June. The difference was 12% in July and 20% in September. Compared with the absolute value of soil respiration, this difference of soil respiration during a day under the same temperature increased from June to September. This phenomenon suggests that another factor was driving the diurnal variation of soil respiration in addition to soil temperature, which is likely from photosynthesis.

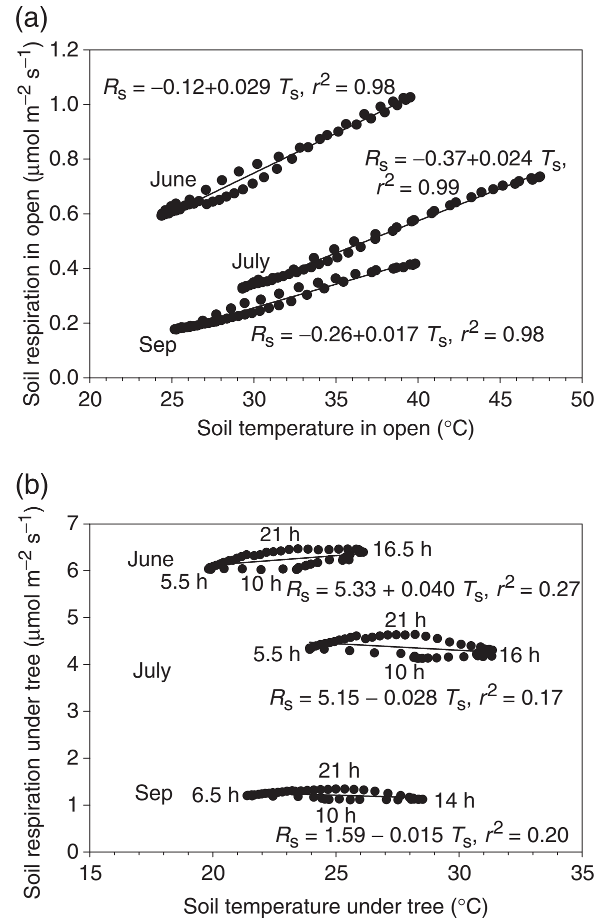

Fig. 3 Soil respiration (R_s) vs. soil temperature at 0.08 m (T_s) in the open (a) and under the tree (b). Values are averages of 30 days of the month. The hour (b) indicates the time of day when a certain data point is measured.

Soil respiration did not show an instantaneous correlation with photosynthesis. However, by applying an inverse Fourier transformation to the soil respiration and photosynthesis time series, we found that soil respiration was strongly correlated with photosynthesis with a time delay at 7–12 h. After shifting photosynthesis forward 7 h in June, 12 h in July, and 11 h in September, soil respiration was proportional to photosynthesis (Fig. 4). The high values of r^2 (0.86–0.93) but low values of regression slopes (absolute values = 0.031–0.062, but were statistically significantly different from 0 with $P < 0.0001$) of the fitted lines in Fig. 4 suggest that soil respiration is dependent on photosynthesis but the sensitivity is low. The intercepts of three fitted lines, decreased from June at 6.19 $\mu mol\,m^{-2}\,s^{-1}$ to September at 1.22 $\mu mol\,m^{-2}\,s^{-1}$, may indicate the decrease in soil respiration from June to September, primarily driven by the further decrease in soil moisture.

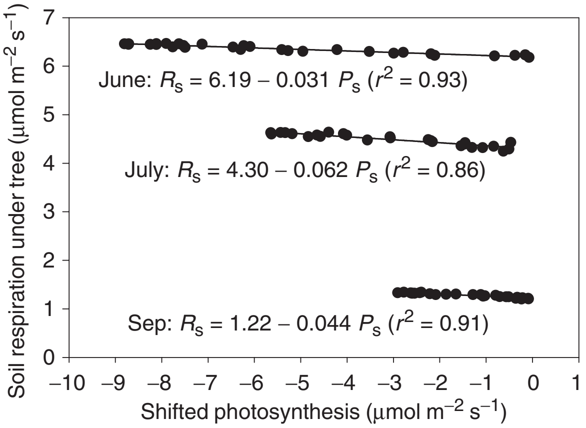

Fig. 4 Correlation between soil respiration (R_s, positive) and photosynthesis (P_s, negative). Photosynthesis was shifted by 7 h in June, 12 h in July, and 11 h in September.

The decoupling of soil respiration under the tree with soil temperature within a day can be explained by the driving of photosynthesis with time lag. Another possible reason for this decoupling could be hydraulic lift (Ishikawa & Bledsoe, 2000), the transfer of water from deep soils to shallower soils by tree roots. However, we did not find significant diurnal variations in soil moisture measured at 0.1, 0.2, and 0.5 m depth ($P < 0.01$). Nor did we find a significant difference of soil moisture measured from 0 to 0.6 m between under the tree and in the open resulting from the hydraulic lift effect ($P < 0.01$).

The dependence of soil respiration on photosynthesis may be because of the source of the respiratory process provided by the photosynthetic process. The 7–12 h of time lag between respiration and photosynthesis may be equivalent to the time needed for the translocation of photosynthetic products (mainly carbohydrates) from leaves to roots via phloem, a conductive tissue for transporting carbohydrates downward. However, the short-time lag may not be because of the real transmission of carbohydrates, but because of the propagation of pressure and concentration fronts, which is faster than the solution itself (Thompson & Holbrook, 2004). Our results suggest that the daytime peak of photosynthesis may stimulate root respiration after the pressure/concentration wave of carbohydrate reaches the roots.

This report is one of the first attempts to quantify the correlation between soil respiration and photosynthesis on a diurnal time scale, based on undisturbed, continuous field measurements without manipulation. The time lag we found is shorter than some carbon isotopic studies that reported 1–4 days (Ekblad & Hogberg, 2001) or 5–10 days (Bowling *et al.*, 2002) of time lag between respiration and air humidity, which correlates with photosynthesis. In addition to our reported time lag within a day, we also have data on a daily basis showing another longer time lag (5–6 days) between respiration and photosynthesis, indicating the influence of daily sums of photosynthesis on respiration (data not shown here). This suggests that photosynthesis may modulate respiration in multiple pathways. Peak photosynthesis within a day influences respiration on a diurnal scale; the daily sum of photosynthesis may influence the day-to-day variation of respiration on a weekly scale. Because the sensitivity of respiration responding to photosynthesis is small, the above time lag and the correlation between respiration and photosynthesis is often suppressed by more sensitive drivers such as temperature and moisture, and is thus not easily detected. However, the correlation we found on a diurnal scale is strong when temperature sensitivity becomes weak in the dry hot summer. Our results suggest that a dynamic mechanism-based carbon model should incorporate the modulation of photosynthesis on soil respiration as a physiological process.

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