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REGULAR ARTICLE

Herbaceous layer determines the relationship between soil respiration and photosynthesis in a shrub-dominated desert plant community

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Abstract
Aims Although the linkages between aboveground photosynthates production and belowground respiration processes have been well studied, doubts remain as to the extent that photosynthate regulates soil respiration (R_{soil}) and its generality throughout the growing season in a given ecosystem. This study aimed to test whether photosynthesis affected R_{soil} at the diurnal scale and assess how the relation between them changed with changing vegetation composition.

Methods We measured R_{soil} and gross primary productivity (GPP using eddy covariance) in two consecutive growing seasons (2013–2014) in a desert ecosystem, western China. We compared R_{soil} on sunny days with that on adjacent cloudy days in two periods with different vegetation compositions [herbs-shrub coexistence period (HSP) and purely shrubs dominated period (SDP)] to identify how photosynthesis affect R_{soil}.

Results GPP regulated diurnal variations of R_{soil} conspicuously in spite of the strong correlation between soil temperature (T_{soil}) and R_{soil}, but such regulation was limited in HSP. 48.3% of the changes in daytime R_{soil} between sunny and cloudy days was explained by changes in T_{soil} together with changes of GPP in HSP. When spring annuals died, no differences in daily amplitude and average of R_{soil} between sunny and cloudy days were found.

Conclusions Our results suggested that effect of photosynthesis on R_{soil} was not constant throughout the growing season. In the presence of herbaceous plants, R_{soil} was directly related to photosynthesis. These findings highlighted the important role of photosynthesis played in R_{soil} regulation and the importance of community composition in determining the extent that photosynthesis affects R_{soil}.

Keywords Herbaceous layer · Canopy photosynthesis · Soil respiration · Diurnal variation · Community composition

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Introduction

Quantifying ecosystem carbon budgets is essential for a sustainable future because CO_2 plays an active role in Earth's mass & energy budget. Soil respiration (R_{soil}), representing a substantial source of CO_2 emissions to the atmosphere (Raich and Potter 1995), can be a variable carbon flux, making its quantification important for improving our ability to predict ecosystem carbon dynamics (Barron-Gafford et al. 2014). Over the last decade, substantial progress has been made in modeling R_{soil} by moving beyond the relationship between R_{soil} and temperature (see Lloyd and Taylor 1994; Davidson et al. 2006a; Barron-Gafford et al. 2014; Cable et al. 2011; Liu et al. 2019) to develop frameworks and models incorporating with multiple biotic and abiotic effects, such as soil microbial biodiversity (Liu et al. 2018), and antecedent environmental conditions (Barron-Gafford et al. 2014). However, a notable amount of variation in R_{soil} was still unexplained, and there remained significant challenges in mechanistically understanding carbon flux processes in soils. For example, doubts remain as to how aboveground–belowground linkages modulate carbon dynamics (Carbone and Trumbore 2007; Kayler et al. 2010), which has been reported to be largely responsible for the current limit of developing process-based models of R_{soil} at short and medium temporal scales (Vargas et al. 2011; Han et al. 2014). Thus, understanding whether and how canopy photosynthesis regulates R_{soil} has the potential to reveal the underlying determinants of R_{soil} and improve our ability to quantify and predict ecosystem carbon balance in natural setting (Trumbore 2006; Barron-Gafford et al. 2014).

A tight linkage between R_{soil} and aboveground photosynthesis has been widely reported for different ecosystems based on shading (Yan et al. 2011), clipping (Zhou et al. 2007), gridling (Högberg et al. 2001), and/or isotopic labeling experiments (Högberg et al. 2008; Bahn et al. 2009). In particular, the hysteretic relationship between R_{soil} and temperature may partially result from abiotic forcing (Phillips et al. 2011), but may be also tied with the time delay in supply of recently assimilated products (Tang et al. 2005; Liu et al. 2006). R_{soil} usually lags behind canopy photosynthesis hours even days (Tang et al. 2005; Kuzyakov and Gavrichkova 2010; Vargas et al. 2011; Yan et al. 2011; Han et al. 2014). The highly variable lag time between them has been suggested to be associated with plant functional type and the size of the plants (Kuzyakov and Gavrichkova 2010; Vargas et al. 2011), wherein large trees and shrubs tend to produce longer lag time than grasses or herbaceous plants.

Shifts in the distribution of vegetation is a widespread feature of global change, and uncovering the effect of such changes on ecosystem processes (e.g. ecosystem C flux) has been one of the core topics in modern ecology (Metcalfe et al. 2011). For example, shift from grass to woody plants, or vice versa, has been continually occurring in many regions of North and West America and other parts of the world (Van Auken 2000; Jackson et al. 2002; Carbone and Trumbore 2007), due to deforestation, desertification, and woody plant invasion. Ecosystem processes associated with such shifts, including carbon assimilation and plant-specific carbon use and/or allocation (Metcalfe et al. 2011), are modified as a result of changes in canopy structure and plant traits, such as leaf area index, root distribution (Jackson et al. 2000; Schenk and Jackson 2002) and maximum rooting depth (Breecker et al. 2012).

In term of R_{soil}, the distribution and dominance of woody plants relative to grasses may not only influence the extent of photosynthetic influence on R_{soil} but also the speed of the link between aboveground carbon fixation and belowground carbon release. Namely, the effect of photosynthesis on R_{soil} varies with shifting vegetation composition, and this variation may also occur within a growing season owing to differences in plant life history and phenology (Huang and Li 2015). Unfortunately, previous studies associating R_{soil} with aboveground carbon processes have mainly focused on a certain growth period (i.e., pulse labeling studies) or a particular target (e.g., grass or trees), and little is known about its continuity throughout the entire growth season in a mixed vegetation of woody/herb plants (Kuzyakov and Gavrichkova 2010).

In this study, we focused on C fluxes in the Gurbantonggut desert, the second largest desert in China. Its plant community comprises a typical "two-layer" structure (Liu et al. 2019) with considerable inter- or intra-annual variation in composition of herbs and shrubs (Fan et al. 2014; Huang and Li 2015), which provides a unique opportunate to test the effect of community composition on soil C fluxes. The main objectives of this study were to test the effect of canopy photosynthesis on R_{soil} at a diurnal scale and to determine how such effect respond to shifting plant community composition. We accomplished this by automatic measurement of R_{soil} and eddy covariance measurement of ecosystem photosynthesis with high resolution (e.g., hourly) in two consecutive growing seasons (2013 and 2014). We took advantage of natural variations in weather conditions and compared R_{soil} on sunny days with that on adjacent cloudy days in two growing periods with distinct vegetation compositions (the dominance of herbs and shrubs from mid-Arip to late May, and purely shrubs dominance from early June to later October). We hypothesized that diurnal or day-to-day variation in R_{soil} would be driven by a combination of temperature and canopy photosynthesis because canopy photosynthesis provides substrates for root and rhizosphere respiration (Bahn et al. 2008; Han et al. 2014). We also hypothesized that the control of canopy photosynthesis over diurnal R_{soil} would weaken when plant community structure shifted from herbs and shrubs to only shrubs.

Material and methods

Study site

All fieldwork was conducted at the southern margin of the Gurbantonggut Desert, which is approximately 8 km away from the Fukang Station of Desert Ecology, Chinese Academy of Sciences (87°56′ E, 44°17′ N; 475 m a.s.l.). The plains in this area have a continental arid temperate climate with dry hot summers and cold winters. According to the meteorological data recorded in the Fukang Station of Desert Ecology over the last 30-years (1987–2016, data available at http://fkd.cern.ac.cn/), annual mean temperature is 6.6 °C and annual mean precipitation is ~160 mm. The soil is loamy sand (81.7% sand, 16.8% silt, and 1.5% clay) textured with high salinity and alkalinity (electrical conductivity >4dS m^{-1}, pH > 8.2 for a soil solution at a soil:water ratio of 1:5), classified as Aridosols in the FAO/UNESCO soil classification system.

Plants in this area are mainly deep-rooted shrubs, such as *Haloxylon ammodendron*, and well-developed herbaceous plants, with maximal coverage of ca. 60%. More than 60% of the vegetation cover and up to 70–80% of herbaceous plant biomass are contributed by spring annuals from early spring to early summer (Fan et al. 2014). The dominant spring annuals mainly include *Erodium oxyrrhynchum*, *Alyssum linifolium*, and *Nepeta micrantha*, which account for more than 60% of herbaceous cover and 85% of biomass (Huang and Li 2015). Summer annuals and perennial herbs, including *Ceratocarpus arenarius*, *Salsola foliosa*, *Descurainia Sophia*, and *Hyalea pulchella*, usually coexist but only account for a very small portion of community biomass. Phenological observation revealed that spring annuals began to grow immediately after snow melt in late March, matured in early May, and usually died before late May (Fig. 1a). Growth of the dominant shrub *H. ammodendron* is usually slow in May, speeding up in early June until reaching its maximum biomass in late June or early July (Fig. 1b). Hence, the whole growing season could be divided into two periods: one in which herbs and shrubs coexisted (mid-April to late May; hereafter referred to as HSP), and one purely dominated by shrubs (early June to late October; SDP).

Dynamics of shrub leaf area index and herbaceous layer biomass

Shrub leaf area index (LAI) dynamics were determined by combining leaf (assimilating branch) relative growth rate with accumulated leaf biomass as described in Ma et al. (2014). Briefly, relative growth rate was derived from area changes in labeled assimilating branches, which were monitored by photographs at intervals of two weeks. Accumulated leaf biomass was measured using a harvesting method. At the end of the growing season, a 50 m × 3 m transect was randomly selected in the center of the footprint area of the eddy flux tower, and all assimilating branches in this transect were destructively sampled and dried (65 °C) to determine the accumulated leaf biomass. Based on the relationship between surface area and dry biomass, branch biomass was converted to branch area (per unit area). Coupled with variation in relative growth rate, seasonal LAI dynamics were determined.

Herbaceous plants were surveyed from mid-April to early October each year in 10 long-term monitoring quadrats (1 m × 1 m), which were random selected and fixed with iron wire in the footprint area of the flux tower at the beginning of the growing season in 2012. Plant coverage, abundance, and average height for each species were recorded synchronously. The frequency of plant survey was not fixed: at the beginning of the growing season, the biomass of spring ephemeral plants changed rapidly over time, and quadrats were surveyed every 12 days; whereas, when the spring ephemeral plants died, surveying frequency decreased to every 20 days. Finally, the dynamics of herbaceous plant

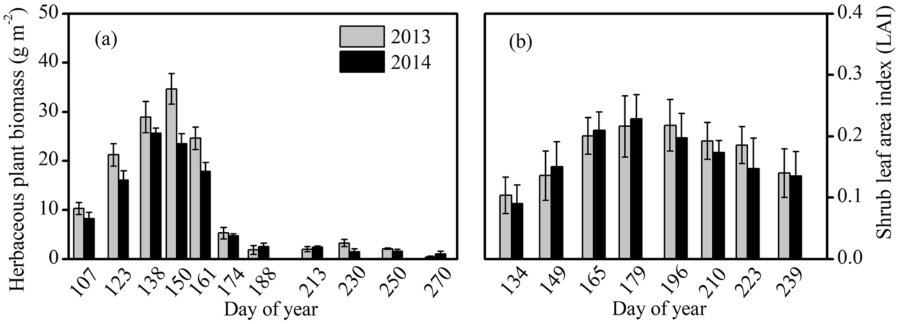

Fig. 1 Seasonal variations of herbaceous plant biomass (a) and shrub leaf area index (LAI, b) in 2013 and 2014

biomass were determined using allometric equations as defined by Huang and Li (2015).

Root system investigation

The intact root system of *H. ammodendron* was excavated to investigate their vertical distribution. In total, five shrubs of approximately average size (average height, 2.15 m; average canopy diameter, 2.85 m) were randomly selected for excavation. A ring ditch with a diameter of 12 m was dug around each selected shrub. The soil surrounding the main root was removed manually at 0.1-m depth intervals to progressively expose the roots. In this way, the root could be traced layer by layer, and the diameter and length of lateral root segments could be measured section by section along the branches of the laterals with calipers and rulers. As the shape of the root segment resembled a cylinder, the root surface area was determined based on the recorded diameters and lengths of all root segments within each 0.1-m soil layer.

Root distribution of herbaceous plants was determined in late May when the biomass of herbaceous plants peaked (Fig. 1). Four quadrats, which were previously used to survey plants, were randomly selected to determine fine root biomass at intervals of 0.1 m.

Eddy covariance measurements

Ecosystem CO_2 flux was monitored in 2013 and 2014 using an open-path eddy covariance (EC) system comprising a 3-D ultrasonic anemometer thermometer (STA-5055, KAIJO Corporation, Tokyo, Japan) and an open-path infrared gas (CO_2/H_2O) analyzer (LI-7500, LI-COR Inc., Lincoln, NE, USA). The former measured instantaneous fluctuations of the horizontal, vertical, and lateral wind speed and the virtual temperature. The latter measured instantaneous fluctuations in the concentration of CO_2 and water vapor. These data were recorded with a data logger (CR23X, Campbell, Scientific Inc., UT, USA) at 30-min intervals. Additional meteorological parameters were measured simultaneously with an array of sensors, including photosynthetically active radiation (PAR) and net radiation (LI-190SB, Li-COR Inc., USA), air temperature and humidity (MP300, Campbell Scientific Ltd., Shepshed, UK), atmospheric pressure (CS106, Campbell Scientific Inc., USA), and precipitation (TE525 tipping bucket gauge, Texas Electronics, TX, USA). Soil temperature (T_{soil}) was measured at six depths: 5, 10, 15, 20, 30, and 50 cm. Two soil heat-flux plates (HFP01SC, Hukseflux, the Netherlands) installed 5 cm below the soil surface monitored soil heat flux. All meteorological data were logged with another CR23X data logger. Soil water content (SWC) of the 0–10 cm soil layer was measured by a conventional balance-weighing and oven drying method at 10 a.m. with six replications.

Flux data processing

Raw EC data were processed in EdiRe (V.1.4.3.1186, www.geos.ed.ac.uk/abs/research/ micromet/EdiRe) to determine net ecosystem CO_2 exchange (NEE). Data processing followed standard methods (Lee et al. 2004) and included despiking, coordinate rotation, auto-detection of the time delay between different sensors, spectral correction for sensor separation and sensor path length, and air density corrections. Additionally, 30-min flux data were rejected if the data were anomalous or measured under stable atmospheric conditions, which might have been derived from sensor maintenance, rain or snow, power failure, or insufficient mixing. Roughly 30–40% of the data were eliminated and gap-filling was required. Small gaps (i.e., less than 2 h) were filled by linear interpolation. Large gaps were filled separately for daytime and nighttime. For daytime, the relationship between photosynthetically active photon flux density and CO_2 flux was used. Gap filling during the night was accomplished using the Lloyd-Taylor function between NEE (representing ecosystem respiration) and T_{soil}. More details on flux data processing, quality control, and gap filling were described in Liu et al. (2012).

Based on the assumption that daytime ecosystem respiration ($R_{eco,day}$) follows the same temperature response as during the night, 30-min $R_{eco,day}$ were determined using the same exponential functions (Lloyd-Taylor equation) developed for gap filling during the night:

$$R_{eco,day} = a \times \exp(b \times T_{siol})$$

where a and b are the fitting coefficients and T_{soil} is soil temperature at 5 cm depth. Parameters for the temperature response of ecosystem respiration in different growing periods are listed in Fig. S1. Gross primary productivity (GPP) was determined by subtracting NEE from R_{eco}.

Soil respiration measurements

R_{soil} was monitored during the growing seasons (April 13–October 24, 2013; April 1–October 22, 2014), with an LI–8150 Automated Soil CO_2 Flux System (LI-COR Inc., USA) equipped with six long-term monitoring chambers (LI-8100-104). Mosaic-distributed shrubs result in high levels of variation in soil physical and chemical characteristics, which are usually known as “fertilized islands” and “salty islands” (Li et al. 2007). To record such variations, which was also observed in R_{soil} (Ma et al. 2012), measurements were taken under the *H. ammodendron* canopy (three monitoring chambers) and in the interplant space (the other three chambers) simultaneously. Shrubs of approximately average crown width and interplant sites where herbaceous plants were uniformly distributed were selected. To minimize disturbance, soil collars were installed at least 24 h prior to measurements and were left in place throughout the experiment. Measurements were taken every 30 min. R_{soil}, at the ecosystem level, was estimated by area-weighted average with ratio of shrubs coverage (0.32) and interplant space (0.68) as weighting factors.

Leaf-level measurements of photosynthetic activity

The photosynthetic light-response curves of the dominant species (*E. oxyrrhynchum* and *H. ammodendron*) were measured using a LI-6400 portable photosynthesis system (LI-COR Inc., USA). In-chamber photosynthetic photon flux density (PPFDi) was controlled by a 20 × 30 mm^2 leaf chamber with a red-blue light source, set as 0, 20, 50, 100, 150, 200, 300, 400, 600, 800, 1200, 1600, 1800, 2000 and 2200 $\mu mol\ m^{-2}\ s^{-1}$. The gas flow rate was set as 400 $\mu mol\ s^{-1}$ and chamber temperature was of 30 °C. A CO_2-injecting device was attached to the system to control reference CO_2 concentration at 400 $\mu mol\ mol^{-1}$. For each species, leaves from three similar-sized individuals were selected and measurements were done in the morning (09:00–12:00) of the sunny days when the biomass of target species peaked (early May for *E. oxyrrhynchum* and late June for *H. ammodendron*). The photosynthetic light response curves were fitted with non-rectangle hyperbola models to obtain typical photosynthetic parameters: maximum net photosynthetic rate (P_{max}), light saturation point (LSP) and light compensation point (LCP). More details about measurements and data processing are described in Xu and Li (2006).

Data analysis

To test the hypothesis that GPP contributes to diurnal or day-to-day R_{soil} variations, we took advantage of natural weather transitions of sunny and cloudy days, and selected all paired days (20 in total) in these two growing seasons satisfying the following two criteria (Han et al. 2014): 1) the two days are adjacent, one was a sunny day and the other was cloudy, (2) no rain occurred during, and in five days before the two adjacent days. Under the conditions tested, it was reasonable to assume that changes in R_{soil} on the two adjacent days were mainly determined by radiation through altering temperature and plant canopy photosynthesis, without any significant shifts in soil moisture, soil organic carbon, and plant condition (e.g., leaf area index and live biomass). We conducted a paired sample *t*-test to test the differences in the mean values of R_{soil} and GPP between the sunny and adjacent cloudy days in the two growing periods (HSP and SDP), as well as the meteorological factors [PAR, relative humidity (RH), T_{soil}, and SWC] between them. Linear and exponential regression analyses were used to evaluate the respective influences of GPP and T_{soil} on daytime soil respiration on sunny and cloudy days respectively. Standardized major axis (SMA) regression analysis was performed to analyze the differences in slope of GPP–T_{soil} between different growing periods. Additionally, multiple (stepwise) linear regression was applied to examine the effect of changes in GPP (ΔGPP) and changes in T_{soil} (ΔT_{soil}) between sunny and cloudy days on the changes in daytime R_{soil} (ΔRsoil). R^2 change, a parameter indicating the contribution of a certain variable (ΔGPP or ΔTsoil) to the variations in Rsoil, was derived from the difference between model R^2 of multiple linear regression with and without a certain variable. In all tests, a significance level of $P = 0.05$ was set.

As soil temperature variations are highly correlated with solar radiation, they would jointly affect GPP. Thus, it is important to determine the direct effect of GPP on R_{soil} (Kuzyakov and Gavrichkova 2010). We accomplished this by separating temperature-dependent component (R_{soil_TD}) from R_{soil} using a similar approach as Liu et al. (2006), and then evaluated the direct effect of GPP on R_{soil} based on a linear regression between GPP and temperature-independent component of R_{soil} (R_{soil_TIN}). Briefly, apart from the well-known role of T_{soil}, many other temperature-independent factors such as photosynthesis, soil moisture, and substrate availability may also affect R_{soil}. Namely, R_{soil} comprises a temperature-dependent component and a temperature-independent component (Liu et al. 2006; Vargas and Allen 2008). We first established exponential functions between R_{soil} and T_{soil} in the two growing periods using data of the nighttime (23:00 and 06:00), during which temperature was assumed to be the only factor controlling R_{soil}. Then, R_{soil_TD} during daytime of sunny days was calculated by these functions based on T_{soil} of the sunny days. Corresponding R_{soil_TIN} was determined by the differences between directly measured R_{soil} and R_{soil_TD}.

SMA regression analyses were carried out with R 3.6.2 (R-package SMATR, http://www.r-project.org/). Other statistical analyses were performed using SPSS 15.0 for Windows (SPSS Inc., Chicago, IL, USA).

Results

Root distribution

The vertical root distributions of herbaceous plants (expressed as root biomass per unit area) and *H. ammodendron* (expressed as surface area of feeder roots per individual plant) are presented in Fig. 2. The maximum rooting depth for herbaceous plants was found to be around 80 cm. The biomass of active absorbing roots decreased with depth, with more than 80% concentrated in the top 30 cm of soil (Fig.2a). In contrast, the main root of *H. ammodendron* extended to ~3 m, close to the 3.3-m groundwater table. More than 80% of absorbing roots were distributed below 40 cm and few feeder roots were found in the upper 0–30 cm (Fig. 2b).

Diurnal variation in R_{soil} and GPP

Diurnal variation in R_{soil} exhibited a single peak on both sunny and cloudy days with flux rates varying from 0.01 μmol·m^{-2} s^{-1} to 1.74 μmol·m^{-2} s^{-1} (Fig. 3). The amplitude of R_{soil} differed considerably between sunny and cloudy days. From April to early June when shrubs coexisted with herbaceous plants, R_{soil} was lower on cloudy days and fluctuated within a relatively narrow range compared with that on sunny days. By contrast, there were no apparent differences in R_{soil} between sunny and cloudy days from mid-June to the end of the growing season, when shrubs dominated. GPP exhibited a bell-shaped curve on a sunny day, but no clear diurnal trend was observed on a cloudy day.

To gain further insight into the diurnal and day-to-day variations in R_{soil} under different radiation conditions and growing periods, data of GPP, R_{soil}, and T_{soil} were averaged from sunny and cloudy days during HSP (7 paired days in total) and SDP (12 paired days in total) (Fig. 4), respectively. Diurnal trends in R_{soil} lagged behind GPP but preceded T_{soil} on sunny days. In the mornings (07:00–09:30), R_{soil} increased gradually with increasing GPP but T_{soil} decreased. In the afternoons, R_{soil} decreased following declining GPP (Fig. 4). Peak values of R_{soil} were observed around 1 h (0–2.5 h) later than that of GPP (Table S1).

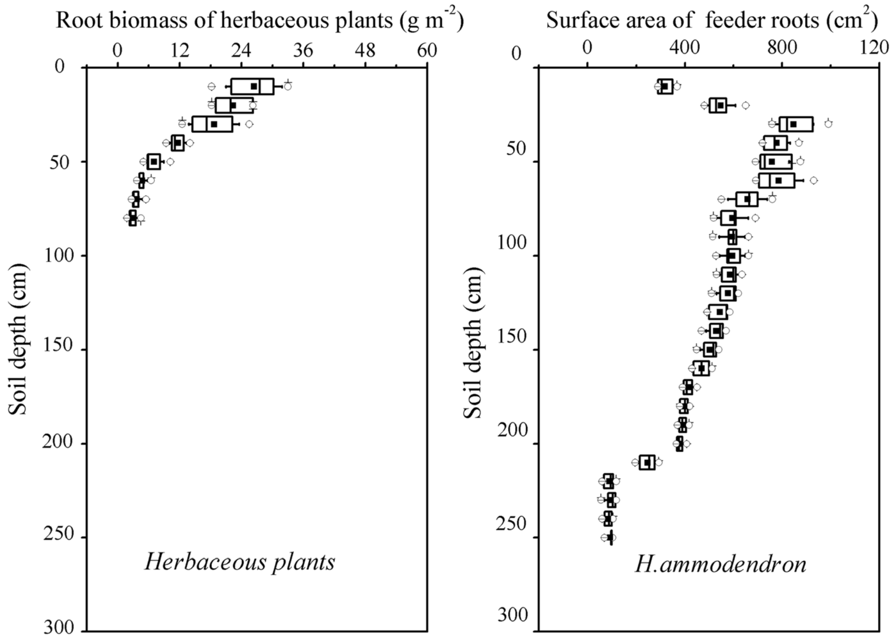

Fig. 2 Vertical distribution of roots for herbaceous plants (expressed as root biomass per unit area, a) and *H. ammodendron* (expressed as surface area of feeder roots per individual plant, b). Data are displayed as boxplots, where center is median, box top and bottom are 25th and 75th percentiles, hollow circles indicate 1th and 99th percentiles, solid squares indicate mean average and whiskers reflect standard deviation. Outliers are denoted with plus signs

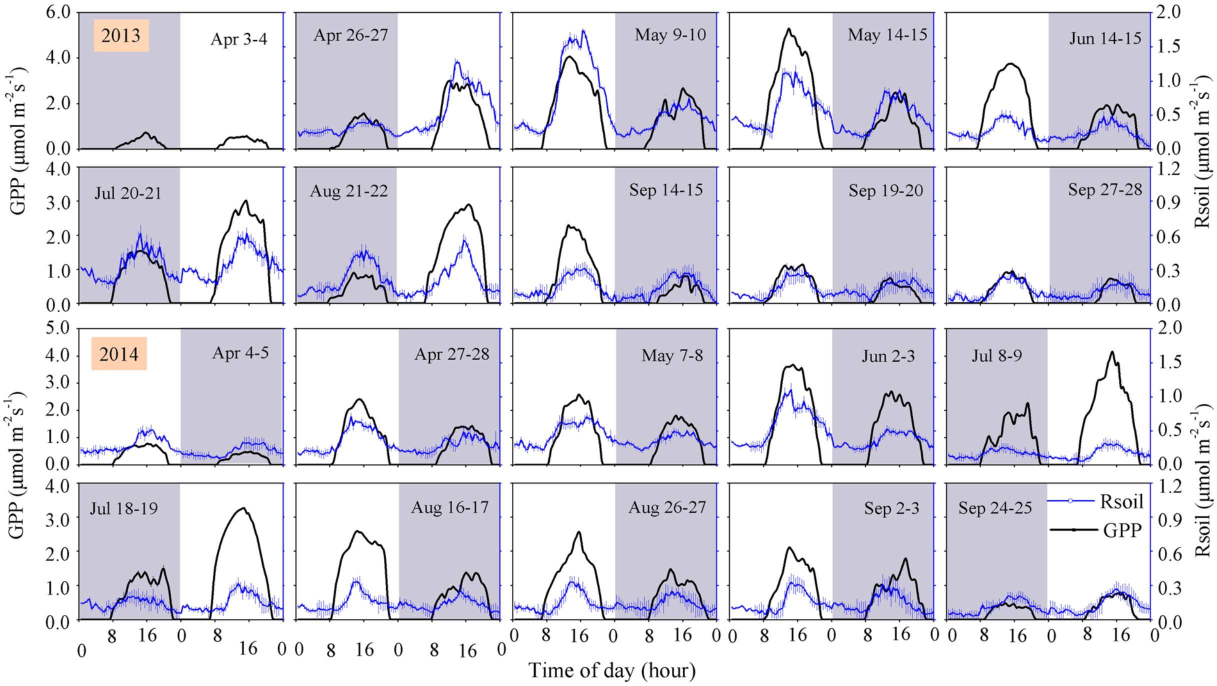

Fig. 3 Diurnal variation in soil respiration (R_{soil}) and gross primary productivity (GPP) on the 20 paired days in the growing seasons of 2013 and 2014. Grey shading indicates the cloudy days and the unshaded parts represented the sunny days. R_{soil} was measured once every 30 min, and data were represented as mean ± standard error ($n = 3$). Data of GPP are represented as 30-min averages

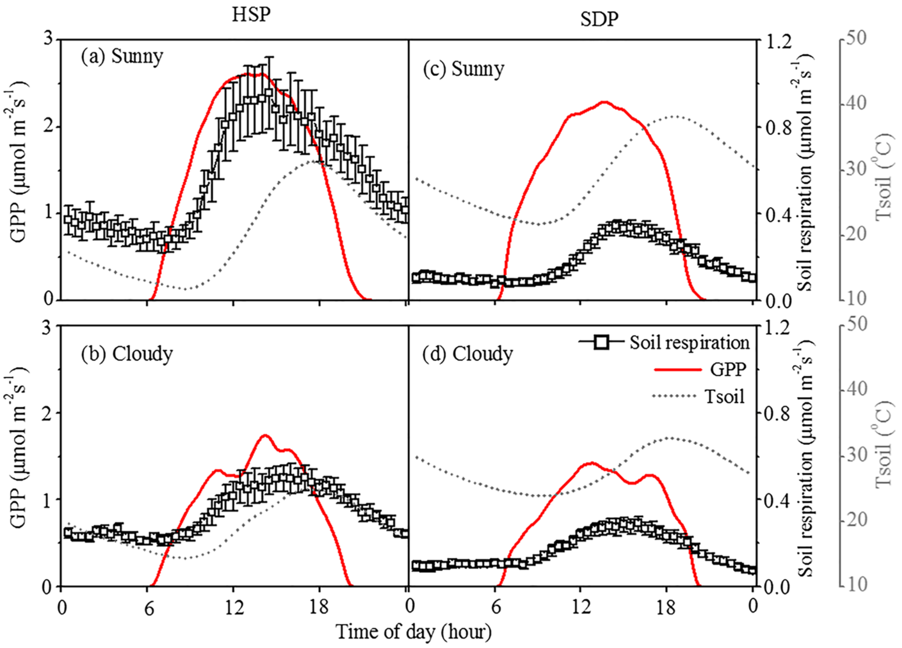

Fig. 4 Averaged diurnal variations of gross primary productivity (GPP), soil respiration (R_{soil}), and soil temperature at 5 cm depth (T_{soil}) on sunny days (a, c) and adjacent cloudy days (b, d) during the herb-shrub coexistence period (HSP, a and b) and shrub-dominated period (SDP, c and d)

Weather conditions and carbon flux on sunny and adjacent cloudy days

On sunny days, PAR was significantly higher than that on corresponding cloudy days for both HSP and SDP (Fig. 5a). Accordingly, averaged T_{soil} was significantly lowered by approximately 2.8 °C in HSP, and about 4.2 °C in SDP on cloudy days, compared to the corresponding sunny days. In contrast, there was no significant difference in SWC and RH between cloudy and sunny days in either period (Fig. 5b and d).

Cloudy conditions significantly lowered the leaf-level photosynthetic rates of dominant plants (Fig. S2) and thereby average values of GPP in both growing periods ($P < 0.001$; Fig. 5e and f). On cloudy days, GPP decreased by 46.09% in HSP (from 1.99 ± 0.23 μmol m^{-2} s^{-1} to 1.07 ± 0.16 μmol m^{-2} s^{-1}) and ~50% in SDP (from 1.89 ± 0.23 μmol m^{-2} s^{-1} to 0.94 ± 0.16 μmol m^{-2} s^{-1}), compared to the corresponding sunny days. Similarly, there was a significant decrease in R_{soil} on cloudy days (0.336 ± 0.033 μmol m^{-2} s^{-1}), compared to corresponding sunny days (0.54 ± 0.07 μmol m^{-2} s^{-1}) in HSP ($P < 0.001$). However, during SDP, R_{soil} was not significantly affected by cloudy conditions (all values were around 0.15 μmol m^{-2} s^{-1}) (Fig. 5f).

Influence of GPP and T_{soil} on daytime R_{soil} variation

Daytime R_{soil} on sunny days was positively correlated with GPP in both growing periods (Fig. 6; $R^2 = 0.518$, $P < 0.001$ in HSP and $R^2 = 0.235$, $P < 0.001$ in SDP) and the slope of R_{soil}–GPP in HSP was significantly higher than that in SDP ($P < 0.001$). On cloudy days, daytime R_{soil} exhibited the same relationship with GPP (Fig. 6; $R^2 = 0.443$, $P < 0.001$ in HSP and $R^2 = 0.250$, $P < 0.001$ in SDP) but no significant difference was observed in the slopes of the linear regression in these two periods ($P = 0.431$). Meanwhile, daytime R_{soil} increased exponentially with T_{soil} ($R^2 = 0.475$, $P < 0.001$ on sunny days and $R^2 = 0.676$, $P < 0.001$ on cloudy days in HSP; $R^2 = 0.485$, $P < 0.001$ on sunny days and $R^2 = 0.425$, $P < 0.001$ on cloudy days in SDP). In HSP, change in R_{soil} between sunny and cloudy days was positively correlated with ΔGPP ($R^2 = 0.229$, $P < 0.001$) and ΔT_{soil} ($R^2 = 0.308$, $P < 0.001$; Fig. 7), respectively. However, ΔR_{soil} only increased with ΔT_{soil} in SDP. Multiple linear regression analysis also suggested that ΔT_{soil} (R^2 change = 0.311, $P < 0.001$; R^2 change indicating the contribution of a certain variable to explanation of the variations in R_{soil}) and ΔGPP (R^2 change = 0.177, $P < 0.001$) together explained 48.3% of the changes in daytime R_{soil} between sunny and cloudy

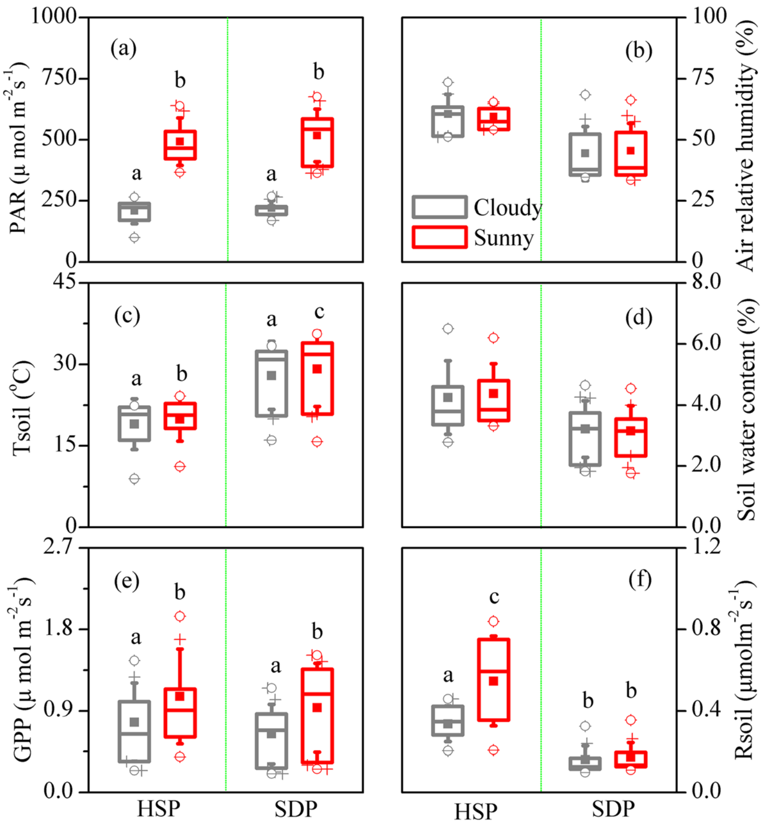

Fig. 5 Comparisons of photosynthetically active radiation (PAR, a), relative humidity (RH, b), soil temperature at 5 cm depth (T_{soil}, c), soil water content (SWC, d), gross primary productivity (GPP, e) and soil respiration (R_{soil}, d) between sunny and adjacent cloudy days. Values are means of sunny and cloudy days in the herb-shrub coexistence period (HSP, $n = 7$) and shrub-dominated period (SDP, $n = 12$). Bars with the same letter do not significantly differ ($P < 0.05$). Data are displayed as boxplots, where center is median, box top and bottom are 25th and 75th percentiles, hollow circles indicate 1th and 99th percentiles, solid squares indicate mean average and whiskers reflect standard deviation. Outliers are denoted with plus signs

days in HSP, whereas only 19.9% of the changes in R_{soil} was explained by change in T_{soil} in SDP (Table 1).

To gain further insight into the direct effect of GPP, R_{soil_TD} (temperature-dependent component of R_{soil}) was removed based on the temperature response function (Fig. S3). Results showed that R_{soil_TIN} (temperature-independent component of R_{soil}) was an important component of R_{soil} in HSP (Fig. 8), with daily average values from 0.058 μmol m^{-2} s^{-1} to 0.81 μmol m^{-2} s^{-1}. More importantly, R_{soil_TIN} was significantly correlated with GPP ($R^2 = 0.854$, $P < 0.001$, Fig. 9).

Discussion

Differed effect of canopy photosynthesis on R_{soil} in different growing periods

Our findings demonstrated that the influence of canopy photosynthesis on R_{soil} differed for the two growing periods, indicating vegetation composition determined the magnitude of R_{soil} and the contribution of GPP to diurnal R_{soil} variations. Given the distinct traits (root distribution and plant height) of dominant plants for these two periods, such different effects of GPP were not surprising. Herbaceous plants survive on rain and snow melt water (Fan et al. 2014; Huang and Li 2015), and their roots are generally concentrated in upper 30 cm soil layer. R_{soil} during HSP was thereby mainly driven by root respiration and corresponding rhizosphere respiration in surface soil layer, which would rapidly respond to changes in aboveground carbon assimilation due to shorter path lengths for photosynthates transport (Tang et al. 2005; Vargas and Allen 2008; Bahn et al. 2009; Han et al. 2014). In contrast, desert shrubs, mainly relying on deep soil water or groundwater for their survival (Dai et al. 2015), extend their roots into deep soil (Fig. 2b; Xu and Li 2006). Considerable R_{soil} was derived from deeper soil layers (Breecker et al. 2012; Hirsch et al. 2002; Davidson et al. 2006b) and the time required for CO_2 assimilation by shrubs, transport of photosynthates to roots, and subsequent diffusion of respired CO_2 from soil would be significantly prolonged (Högberg et al. 2008; Subke et al. 2009). For example, based on a radiocarbon (^{14}C) pulse-chase labeling experiment, Warembourg and Paul (1973) found that

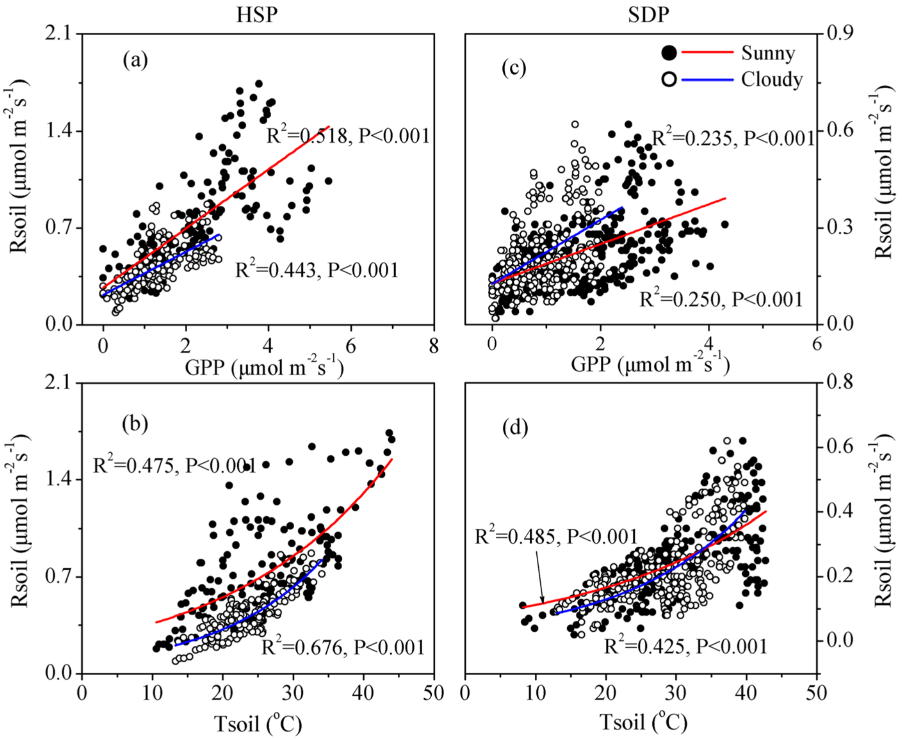

Fig. 6 Relationships between daytime soil respiration (Rsoil) and gross primary productivity (GPP, a and b) and soil temperature (Tsoil, c and d). Red solid lines indicate the fitting lines on sunny days while blue ones indicate fitting lines on cloudy days

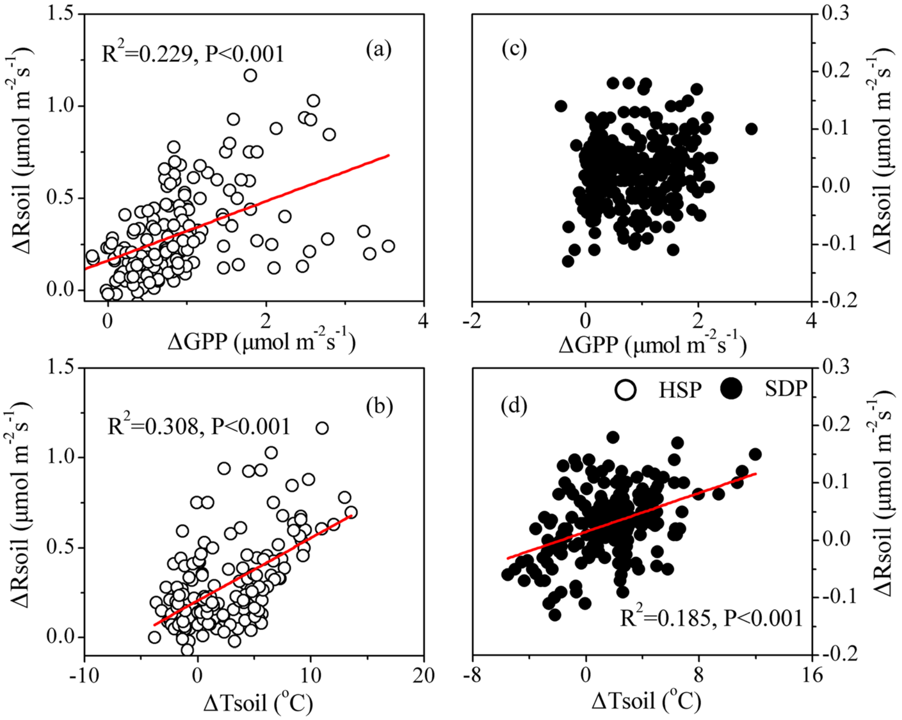

Fig. 7 The response of changes in daytime soil respiration (ΔR_{soil}) between sunny days and adjacent cloudy days to changes in gross primary productivity (ΔGPP) and changes in soil temperature (ΔT_{soil})

Table 1 Parameters of multiple linear regression that explained the changes in soil respiration (ΔR_{soil}, μmol m^{-2} s^{-1}) between sunny and adjacent cloudy days during two distinct growing periods

ΔR_{soil} in herb–shrub coexistence period (HSP)						ΔR_{soil} in shrub-dominated period (SDP)					
Parameters	Coefficient	t	df	*P*	R^2 change [c]	Parameters	Coefficient	t	df	*P*	R^2 change
Constant	0.088	3.622	148	<0.001	–	Constant	0.020	3.357	201	<0.001	–
ΔT_{soil} [a]	0.032	8.625	148	<0.001	0.311	ΔT_{soil}	0.009	6.673	201	<0.001	0.199
ΔGPP [b]	0.139	7.130	148	<0.001	0.177	ΔGPP	−0.007	−1.204	201	0.230	–
Model $R^2 = 0.483$, $F = 70.99$, $P < 0.001$						Model $R^2 = 0.199$, $F = 46.13$, $P < 0.001$					

Model description: $\Delta R_{soil} = a \times \Delta T_{soil} + b \times \Delta GPP + c$

[a] ΔT_{soil} represents changes in soil temperature (°C) at 5 cm depth between sunny days and adjacent cloudy days

[b] ΔGPP represents changes in gross primary production (μmol m^{-2} s^{-1}) between sunny days and cloudy days

[c] R^2 change represents the contribution of a certain variable (ΔGPP or ΔT_{soil}) to the variation in R_{soil}

labeled CO_2 appeared 24 h after pulse labelling at 35 cm depth, while 100 h was needed at 60 cm. The deep rooting pattern of desert shrubs (Fig.2b, Xu et al. 2011) suggests that respired CO_2 would need much longer time to diffuse out of the soil surface.

The nearly synchronous patterns of R_{soil} and canopy photosynthesis in HSP suggested a tight link between recent photosynthates and R_{soil} (Kuzyakov and Gavrichkova 2010; Han et al. 2014). More importantly, it also indicated that the speed for photosynthates translocating from the canopy to belowground might be faster than previously assumed. This finding was consistent with observations reported in many previous studies (Tang et al. 2005; Vargas and Allen 2008; Bahn et al. 2009; Yan et al. 2011; Han et al. 2014). Several potential mechanisms have been suggested to account for the sub-daily level links between plant photosynthesis and R_{soil}. Firstly, the recent photoassimilates might be directly supplied to belowground and utilized in R_{soil} processes with a sufficiently short time to influence diurnal R_{soil} (Kuzyakov et al. 2001; Vargas and Allen 2008; Yan et al. 2011). Secondly, the indirect effect of photosynthesis on root respiration may also be rapid through ion uptake, phloem loading (or unloading), and root exudate production (Thompson and Holbrook 2004; Liu et al. 2006). Information at the physiological level could be rapidly transmitted to roots in the form of concentration or/and pressure waves, which might

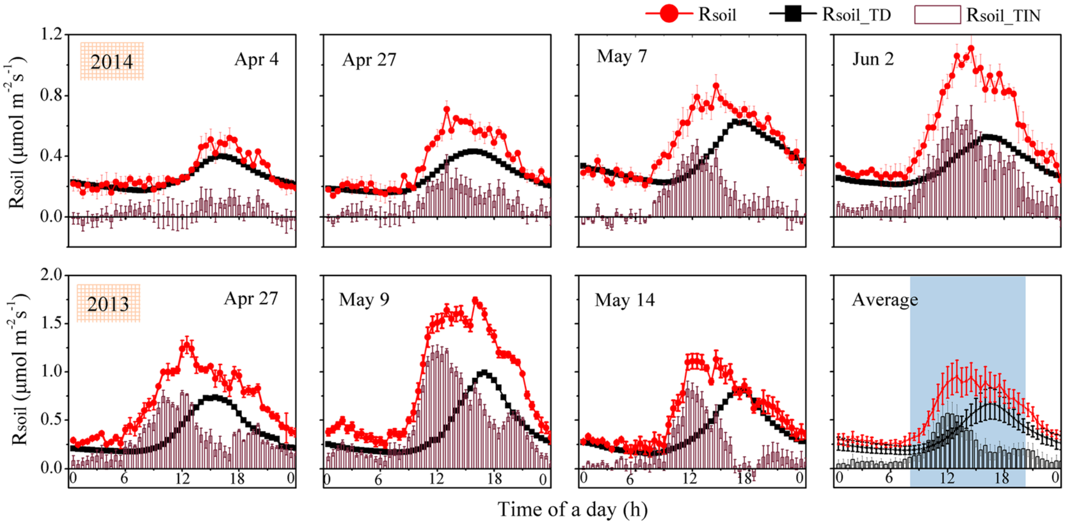

Fig. 8 Diurnal variation in directly observed soil respiration (R_{soil}) and its temperature-dependent (R_{soil_TD}) and temperature-independent components (R_{soil_TIN}) on sunny days in the herb–shrub coexistence period. R_{soil_TIN} was calculated as the difference between observed R_{soil} and the fitted R_{soil_TD}. Error bars of R_{soil_TD} indicate 95% confidence intervals

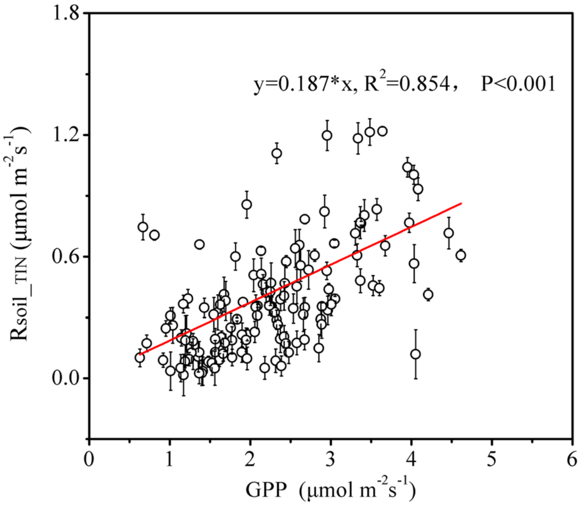

Fig. 9 Temperature-independent component of soil respiration (R_{soil_TIN}) was correlated with gross primary productivity (GPP) in the herb-shrub coexistence period. Error bars denote standard errors of R_{soil_TIN}

trigger immediate responses in the root tips (Thompson and Holbrook 2004; Davidson and Holbrook 2009).

With no significant influence of GPP on R_{soil} at diel timescale in SDP, it is reasonable to expect time lags between photosynthesis and R_{soil} at a timescale >1 day, which has been widely reported for woody vegetation (Högberg et al. 2008; Moyano et al. 2008; Subke et al. 2009; Kayler et al. 2010; Kuzyakov and Gavrichkova 2010). Unfortunately, we were not be able to determine the exact lag time owing to the co-varied multiple factors for regulation of allocation, transport and utilization of photoassimilates, such as plant physiology, growth stages (Kaylor et al. 2010; Kuzyakov and Gavrichkova 2010; Savage et al. 2013) and variable respiration sources (e.g., the fast pool or storage pool; Carbone and Trumbore 2007), which has gone beyond the scope of the current study. Nevertheless, the distinct responses of R_{soil} to decreasing canopy photosynthesis in different growing periods provided evidence that the response speed of R_{soil} to photosynthesis is not constant throughout the growing season. More importantly, in the presence of herbaceous plants, R_{soil} directly responded to canopy photosynthesis on a diurnal scale in this deep-rooted shrub-dominated desert plant community.

Diurnal variation in R_{soil}

We found that R_{soil} significantly reduced on cloudy days in HSP, which resulted from two mechanisms. For one thing, R_{soil} decreased with decreasing T_{soil} (Fig. 5). For another, decreased incoming radiation reduced canopy photosynthesis (Figs. 5 and 9) and the allocation of recent photosynthates to belowground, and finally lowered the rate of R_{soil} (Wan and Luo 2003).

After removing the temperature-dependent component of R_{soil}, changes in daytime R_{soil} were ultimately attributed to the differences in GPP in HSP (Fig. 9). This finding was a valuable addition to the increasing evidence showing that photosynthesis played an important role in regulating diel R_{soil} (Tang et al. 2005; Vargas and Allen 2008; Bahn et al. 2009; Davidson and Holbrook 2009; Kuzyakov and Gavrichkova 2010; Han et al. 2014). Canopy photosynthate regulated R_{soil} mainly via its control over recent photosynthesis substrate supply. First, as discussed above, autotrophic R_{soil} is a direct consequence of root respiration. Second, recent photosynthates via root exudates (sugars or other labile C components) support substantial microbial activity in the rhizosphere, which may significantly decrease without photosynthates supply (Butler et al. 2003; Högberg et al. 2008; Kuzyakov 2010). Moreover, the amount and intensity of labile organic carbon input (by root exudation) potentially varies with plant productivity, and thereby strongly affects the ability of microorganisms to decompose soil organic carbon and the amount of CO_2 emitted to the atmosphere. Hence, it is necessary to incorporate canopy photosynthesis or radiation (a proxy of photosynthesis) as one of the key drivers in R_{soil} modeling (Vargas and Allen 2008; Bahn et al. 2009; Davidson and Holbrook 2009; Kuzyakov and Gavrichkova 2010; Han et al. 2014). Failure to consider these important but hidden regulatory roles of photosynthesis for R_{soil} may lead to erroneous interpretations of belowground processes related to C turnover and of R_{soil} data.

Characteristics and limitations of the current study

Our study has evaluated the influence of canopy photosynthesis on R_{soil} by taking advantage of natural shifts in sunny and cloudy days. Compared with many other indirect methods (e.g., trenching, girdling, or clipping), this approach is based on undisturbed field measurements without any artificial treatments, avoiding the possible alterations of other important factors, such as biomass, LAI, soil organic matter, or moisture content (Fig. 5). Although isotope labeling method has the same advantage as the approach we used, it cannot avoid interference by substrate availability resulted from sudden changes in canopy photosynthesis (Mencuccini and Höltt 2010) and is highly financial costs (Kuzyakov and Gavrichkova 2010). Despite the advantages, the approach used in this study also has some pitfalls. Since we are completely relying on natural weather conditions, the effect of canopy photosynthesis on R_{soil} was only analyzed on 20 pairs of sunny and cloudy days, which did not strictly cover the whole growing season. Moreover, our study may not have been able to disclose the potential influence of phenological changes in plant photosynthesis, allocation of assimilation and other physiological parameters on seasonal R_{soil} variations because of lack of phenological data. Hence, future studies should incorporate leaf - or individual -level physiological changes of dominant plants with a long-term, continueous datasets of CO_2 flux (plant, soil and ecosystem) and combine different approaches, including isotopes, wavelet coherence analysis, and mechanism-based models.

Although this study was carried out in an arid environment, the inconsistent effects of photosynthesis on R_{soil} observed in this study are likely to be pervasive in all other ecosystems experiencing considerable seasonal changes in plant composition and phenology. Given the projected changes in regional climate and vegetation distribution, our findings highlighted the importance of community composition in determining to what extent that photosynthesis are directly related to R_{soil}.

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