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Ecosystem photosynthesis regulates soil respiration on a diurnal scale with a short-term time lag in a coastal wetland

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ABSTRACT

Although increasing evidence has provided that soil respiration is strongly related to recent canopy photosynthesis, doubts remain as to the extent to which primary productivity controls soil respiratory and the speed of the link between soil respiration and photosynthesis. Based on the automated measurements of soil respiration and eddy covariance measurements of ecosystem photosynthesis (i.e. gross primary production, GPP) in a coastal wetland, we assessed the speed of link between ecosystem photosynthesis and soil respiration on the diurnal scale, and quantified the control of the ecosystem primary production on diurnal soil respiration. On the diurnal scale, the time of daily peak soil respiration lagged GPP but preceded soil temperature on both sunny and cloudy days. Daytime soil respiration was significantly linearly correlated with GPP with a lag of 1.5 h on sunny days and 1 h on cloudy days, respectively. By taking advantage of the natural shift of sunny and cloudy days without disturbance to the plant-soil system, our results also indicated that the changes in soil temperature and GPP together explained 53% of the changes in daytime soil respiration rates between sunny days and adjacent cloudy days. Under the same soil temperature, changes in soil respiration rates were strongly correlated with changes in GPP between sunny days and adjacent cloudy days. We therefore conclude that recent canopy photosynthesis regulates soil respiration on a diurnal scale with a short-term time lag. Thus, it is necessary to take into account the influence of photosynthesis on soil respiration in order to accurately simulate the magnitude and variation of soil respiration, especially at short and medium temporal scales.

1. Introduction

It is well documented that soil respiration may lag canopy photosynthesis by times that vary from hours to weeks in different ecosystems including forests (Högberg et al., 2001; Tang et al., 2005; Baldocchi et al., 2006; Moyano et al., 2008; Wingate et al., 2010), grasslands (Bahn et al., 2008, 2009; Yan et al., 2011; Vargas et al., 2011a) and croplands (Kuzyakov and Cheng, 2001, 2004; Han et al., 2007). The highly variable time lags between photosynthesis and soil respiration might be controlled by the species, transport distance (plant height and phloem path-length), root depth, plant physiology and growth stage, and environmental conditions (Davidson and Holbrook, 2009; Kuzyakov and Gavrichkova, 2010; Mencuccini and Hölttä, 2010; Wingate et al., 2010). For example, leaf metabolism including the switch between a mobile sugar and a transient immobile carbon pool determined the interaction between assimilation and soil respiration on a diurnal timescale (Barthel et al., 2011). The lag time was shorter for grasses and shrubs than for trees, because tree height slightly affected the lag with increasing delay of 0.1 day m^{-1} (Davidson and Holbrook, 2009; Kuzyakov and Gavrichkova, 2010). In addition, gas diffusion through soil imposed a lag between the time of CO_2 production at depth and release from the soil surface (Stoy et al., 2007; Phillips et al., 2011), which also influenced the time lags. Consequently, the time lag between the fixation of a carbon molecule during photosynthesis and its respiration belowground contains real information about plant physiology and carbon use as well as the degree to which plant and soil are coupled (Kayler et al., 2010).

The time lags between photosynthesis and soil respiration provide evidence of close links between recent photosynthate supply and soil respiration at different timescales. In contrast to the indirect connection between temperature and soil respiration, the tight linkage between photosynthesis and soil respiration processes is direct (Kuzyakov and Gavrichkova, 2010). Soil respiration is

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derived from heterotrophic and autotrophic sources. In principle, autotrophic soil respiration is a direct consequence of root respiration, so it is coupled to rates of photosynthesis (Baldocchi et al., 2006). Meanwhile, the flux of recent photosynthate supports substantial microbial activity in the rhizosphere, which can in turn influence the relative fraction of heterotrophic respiration (Cardon et al., 2002; Tang et al., 2005). Consequently, half or more of the soil respiration is driven directly by recent photosynthesis, which challenges the assumption that most of the soil respiration is derived from the decomposition of soil organic matter (Kuzyakov and Cheng, 2001; Bhupinderpal-Singh et al., 2003; Högberg and Read, 2006). Therefore, any short-term changes of assimilation rates caused by day/night light cycles may potentially control the diurnal dynamics of soil respiration (Kuzyakov and Cheng, 2004).

Although important, this fact has been overlooked in most soil respiration studies because temperature variations are highly correlated with solar radiation, which mask the direct effect of photosynthesis on substrate availability in soil, especially on diurnal scale (Tang et al., 2005; Gaumont-Guay et al., 2008; Kuzyakov and Gavrichkova, 2010). For example, the diurnal soil respiration is controlled by the photosynthesis cycle together with temperature changes (Kuzyakov and Cheng, 2001; Davidson and Holbrook, 2009; Phillips et al., 2011), so it is difficult to distinguish the degree to which canopy processes and temperature influence root activity, which can easily lead to erroneous conclusions on temperature relations (Moyano et al., 2008). Moreover, although soil temperature of soil respiration is important for modellingpurposes, it might be inadequate to account for the diurnal variation of soil respiration (Tang et al., 2005; Liu et al., 2006). Therefore, further studies are needed to better quantify the effect of canopy photosynthesis on soil respiration especially at short and medium temporal scales (Tang et al., 2005; Moyano et al., 2008; Kuzyakov and Gavrichkova, 2010).

Furthermore, previous studies have provided evidence that soil respiration is strongly related to recent canopy photosynthesis on different time scales ranging from several hours to several days using phloem girdling (Ekblad and Högberg, 2001; Högberg et al., 2001), shading and clipping (Wan and Luo, 2003; Yan et al., 2011), root exclusion by trenching (Kuzyakov and Larionova, 2005; Gaumont-Guay et al., 2008), and isotopic labelling studies of photosynthate (Kuzyakov and Cheng, 2001, 2004; Ekblad et al., 2005; Högberg et al., 2008; Barthel et al., 2011; Wingate et al., 2010). However, doubts remain as to the extent to which primary productivity controls soil respiratory and the speed of the link between soil respiration and photosynthesis (Gaumont-Guay et al., 2008; Kayler et al., 2010). For instance, the immediate link of soil respiration to photosynthesis is still uncertain on the diurnal scale (Bahn et al., 2009). Therefore, current major challenges remain ahead of us for developing process-based models of soil respiration at short and medium temporal scales, including the lags and transport of carbon from photosynthesis to soil respiration (Vargas et al., 2011b).

The development of automated soil respiration measurements and eddy covariance (EC) techniques with high temporal resolution enables us to examine the role of photosynthesis supply in modulating soil respiration on the diurnal timescale. We hypothesized that ecosystem photosynthesis can regulate soil respiration at hourly temporal resolution. To test these hypotheses, we selected 12 paired days during the growing season in a coastal wetland under the following two criteria: (1) the two days are adjacent, one is a sunny day, and another is a cloudy day; (2) no rain occurs during the two adjacent days. We hypothesized that (1) live biomass and leaf area index (LAI) have no large shifts within the two adjacent days; (2) soil moisture has no significant difference between the two adjacent days because no rain occurs; (3) soil organic carbon (SOC) and plant litterfall have not changed substantially within the short term. Therefore, by limiting variability from these factors, we expected during such conditions the radiation condition exerted a major control on soil respiration by altering temperature and plant photosynthetic activity. The purpose of this study was to (1) assess the speed of link between ecosystem photosynthesis and soil respiration on the diurnal scale; (2) quantify the control of the ecosystem primary production on diurnal soil respiration in a coastal wetland.

2. Materials and methods

2.1. Site description

The experiment was conducted during the growing season (from mid April to early November) of 2012 at Yellow River Delta Ecological Research Station of Coastal Wetland (37° 45′ 50″N, 118° 59′ 24″E), Chinese Academy of Sciences. The original vegetation of coastal wetlands in the Yellow River Delta is composed of halophytic plant communities predominated by herb and shrub species, such as *Phragmites australis*, *Suaeda salsa*, and *Imperata cylindrical* (Han et al., 2013). The terrain of the station is quite flat, with relatively homogeneous vegetation dominated by reed (*Phragmites australis*), which usually bud during the end of March and the first 10 days of April, and head in the middle 10 days of October (Xie et al., 2011; Han et al., 2013). The climate in the Yellow River Delta is a warm-temperate and continental monsoon climate with distinctive seasons. The annual average temperature is 12.9 °C, and the average annual precipitation is 550–640 mm, with nearly 70% of the precipitation falling between May and September. During the rainy season, surface ponding is often observed in *Phragmites australis* community, following heavy rainfall events. Generally, the soil type of coastal wetlands in the Yellow River Delta gradually varies from fluvo-aquic to saline soil, and the soil texture is mainly sandy clay loam (Nie et al., 2009).

2.2. Soil respiration measurements

Soil respiration was recorded continuously using a LI-8100 automated soil CO_2 flux measurement system and LI-8150 multiplexer with four 8100-104 long-term chambers (Li-Cor Inc, Lincoln, NE, USA). Four soil collars with a height of 11.4 cm and diameter of 21.3 cm were inserted into the soil one week before the first measurement. Living weeds inside the collars were carefully clipped from the soil surface. The soil collars were left in place throughout the entire study period (from mid April to early November). Each collar was measured at least once every 2 h during the growing season. The chamber was closed for 120 s and the linear increase of CO_2 concentration in the chamber was used to estimate soil respiration. In 2012, the greatest daily rainfall of 71.8 mm occurred on 6 August because of Typhoon Damrey. Consequently, soil respiration could not be measured from the August to mid-October because surface water flooded the soil collars.

2.3. EC measurements

Ecosystem CO_2 fluxes were measured using a paired EC system mounted 3.0 m above the soil surface. The EC system included a three-axis sonic anemometer (CSAT-3, Campbell Scientific Inc., USA) and open path infrared gas analyzer (IRGA, LI-7500, Li-COR Inc., USA). The flux data were recorded at 10 Hz by a datalogger (CR1000, Campbell Scientific Inc., USA) at 30 min intervals. Raw EC data collected from a Campbell Scientific datalogger were processed with EdiRe (v.1.4.3.1186) from the University of Edinburg (Scotland) to determine net ecosystem CO_2 exchange (NEE) with an