# On the multi-temporal correlation between photosynthesis and soil CO<sub>2</sub> efflux: reconciling lags and observations

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#### Summary

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• Although there is increasing evidence of the temporal correlation between photosynthesis and soil CO<sub>2</sub> efflux, no study has so far tested its generality across the growing season at multiple study sites and across several time scales.

• Here, we used continuous (hourly) data and applied time series analysis (wavelet coherence analysis) to identify temporal correlations and time lags between photosynthesis and soil CO<sub>2</sub> efflux for three forests from different climates and a grassland.

• Results showed the existence of multi-temporal correlations at time periods that varied between 1 and 16 d during the growing seasons at all study sites. Temporal correlations were strongest at the 1 d time period, with longer time lags for forests relative to the grassland. The multi-temporal correlations were not continuous throughout the growing season, and were weakened when the effect of variations in soil temperature and  $CO_2$  diffusivity on soil  $CO_2$  efflux was taken into account.

• Multi-temporal correlations between photosynthesis and soil CO<sub>2</sub> efflux exist, and suggest that multiple biophysical drivers (i.e. photosynthesis, soil CO<sub>2</sub> diffusion, temperature) are likely to coexist for the regulation of allocation and transport speed of carbon during a growing season. Future studies should consider the multi-temporal influence of these biophysical drivers to investigate their effect on the transport of carbon through the soil–plant–atmosphere continuum.

# Introduction

Canopy photosynthesis ( $F_A$ ) and ecosystem respiration are important fluxes that regulate the carbon balance of terrestrial ecosystems. Soil CO<sub>2</sub> efflux (SR), which includes autotrophic and heterotrophic CO<sub>2</sub> contributions (Hanson *et al.*, 2000; Ryan & Law, 2005), represents the largest source of CO<sub>2</sub> from terrestrial ecosystems to the atmosphere (Raich & Potter, 1995; Schlesinger & Andrews, 2000). Consequently, predictive models of terrestrial carbon cycling depend on an accurate representation of SR for the quantification of carbon fluxes (Vargas *et al.*, 2011).

Traditionally, SR has been represented by a temperaturedependent function (Lloyd & Taylor, 1994), but multiple studies have recognized the importance of changes in soil moisture, as these influence plant and microbial metabolism and change soil CO<sub>2</sub> diffusion rates (Šimůnek & Suarez, 1993; Davidson & Trumbore, 1995; Burton *et al.*, 1998). Recent studies have provided evidence that  $F_A$  influences SR, which challenges the assumption that most of the CO<sub>2</sub> efflux from soils is derived from the decomposition of soil organic matter (Högberg *et al.*, 2001; Kuzyakov & Cheng, 2001). Short-term relationships between  $F_A$  and SR have been consistently reported using girdling techniques (Högberg *et al.*, 2002; Subke *et al.*, 2004), root exclusion by trenching (Hanson *et al.*, 2000; Kuzyakov & Larionova, 2005), clipping (Bremer *et al.*, 1998; Bahn *et al.*, 2006), measurements of natural abundance of ecosystem  $\delta^{13}$ C

(Ekblad & Hogberg, 2001; Bowling *et al.*, 2002), isotopic labeling using <sup>13</sup>C (Carbone & Trumbore, 2007; Högberg *et al.*, 2008; Bahn *et al.*, 2009; Subke *et al.*, 2009) or <sup>14</sup>C (Carbone *et al.*, 2007; Pumpanen *et al.*, 2009), and ecosystem carbon fluxes using the eddy covariance technique (Tang *et al.*, 2005; Baldocchi *et al.*, 2006; Stoy *et al.*, 2007).

Previous studies have reported that the relationship between  $F_A$  and SR varies from hours to multiple days (Kuzyakov & Gavrichkova, 2010; Mencuccini & Holtta, 2010). Thus, it has been argued that the differences in results may come from the different methodologies applied. For example, isotopic techniques track molecules of carbon (<sup>13</sup>C or <sup>14</sup>C) through the soil-plant-atmosphere continuum, whereas soil flux-based techniques relate the variation in  $F_A$  (or a surrogate such as vapor pressure deficit or photosynthetic active radiation) to SR. In general, isotopic labeling techniques have been able to identify the relatively slow (i.e. days to weeks) transport of carbon molecules from  $F_A$  to SR processes (Kuzyakov & Gavrichkova, 2010; Mencuccini & Holtta, 2010). Meanwhile, soil flux-based techniques have been able to identify a strong short-term correlation between  $F_A$  of trees and SR (i.e. hours to < 2 d) because of the high temporal frequency of the measurements (Baldocchi et al., 2006; Stoy et al., 2007). Finally, a strong correlation between FA and SR has also been observed at seasonal and annual intervals (Janssens et al., 2001; Bahn et al., 2008; Vargas et al., 2010b). At the seasonal scale,  $F_A$  and SR appear to be coupled in short-stature vegetation, but decoupled in tall-stature vegetation (Vargas et al., 2010a).

The main goal of this study was to explore at which temporal scales  $F_A$  influences SR using continuous datasets across the growing season of different study sites. Here, we ask two questions: (1) at which time periods (e.g. hours (1 d), days (4 d) or weeks (16 d)) are the temporal correlations (if any) between  $F_A$  and SR most pronounced?; and (2) do the temporal correlations remain constant throughout the growing seasons of different vegetation types, or are they influenced by changes in photosynthetic capacity, soil temperature and soil moisture?

We hypothesize that  $F_A$  influences SR at multiple time periods (potentially from hours to weeks) independent of changes in soil temperature  $(T_s)$  and soil CO<sub>2</sub> diffusivity among different vegetation types. This may be possible because different drivers that influence the allocation and transport speed of carbon through the soil-plantatmosphere continuum could coexist within the growing season. These drivers (e.g. photosynthesis, soil CO2 diffusion,  $T_s$ , phloem transport) have been reviewed recently (Kuzyakov & Gavrichkova, 2010; Mencuccini & Holtta, 2010), but have been identified by the individual original studies only at one particular time. The novelty of our study relies on the analysis at high temporal resolution of  $F_A$  and SR data (hourly intervals), and on the exploration of the possibility of multi-temporal relationships between these fluxes using wavelet coherence analysis (Grinsted et al., 2004; Vargas et al., 2010c) across multiple sites throughout their growing seasons.

## Materials and Methods

#### Study sites

We used continuous hourly measurements of  $F_A$  inferred from net ecosystem exchange (NEE) values using the eddy covariance technique (Goulden *et al.*, 1996; Aubinet *et al.*, 2000), and hourly measurements of SR during the growing season at four study sites (Table 1). Eddy covariance data for this study were drawn from the La Thuile 2007 FLUXNET 2.0v dataset (http://www.fluxdata.org). The La Thuile dataset has been harmonized for gap filling, quality control of NEE values and calculation of  $F_A$  following standardized

 Table 1
 Information on location, elevation, dominant species, maximum canopy height, growing season and history of the sites included in this study

Site name	Site ID	Latitude	Longitude	Elevation (m)	Canopy height (m)	Growing season (DOY)	Site history	Reference
Tonzi Ranch	US-Ton	38.4316	-120.966	177	5.4–14.8	50–160	Grazing	Ma et al. (2007)
Missouri Ozark	US-Moz	38.7441	-92.2	219	17–20	120–210	Undisturbed/85 yr of natural regeneration	Gu et al. (2006); Yang et al. (2007)
Hyytiälä	FI-Hyy	61.8474	24.2948	181	14	150–250	Prescribed burning in 1962	Hari & Kulmala (2005)
Neustift/Stubai Valley	AT-Neu	47.11667	11.3175	970	0.05–1.0	110–265	Organic fertilization three cuts, grazed in late summer	Wohlfahrt <i>et al</i> . (2008)

US-Ton, Mediterranean deciduous forest; US-Moz, temperate broadleaf forest; FI-Hyy, boreal evergreen forest; AT-Neu, temperate grassland. DOY, days of the year of the growing season, defined as the days on which the ecosystem was a net carbon sink for the year 2007 (Churkina *et al.*, 2005). protocols (Reichstein *et al.*, 2005; Papale *et al.*, 2006). This study uses data from the year 2007 across all sites for which both eddy covariance and SR measurements were carried out during the growing season (Supporting Information Methods S1). The SR measurements presented in this study have not been published previously for any site.

The sites included the following: Mediterranean deciduous woodland (US-Ton), temperate broadleaf forest (US-Moz), boreal evergreen forest (FI-Hyy) and temperate grassland (AT-Neu).  $F_A$  was not manipulated directly, but we took advantage of its variation during the whole growing season and explored a range of time scales from days to weeks. Throughout the growing season, rapid changes in  $F_A$ were expected as a result of changes in phenology and synoptic events (e.g. rainfall, cloudiness) that influence atmospheric vapor pressure deficit and stomatal conductance (Baldocchi *et al.*, 2001; Bowling *et al.*, 2002). The growing seasons were defined as the carbon uptake periods (Fig. 1; Table 1), which were the days during which the ecosystem was a net carbon sink (Churkina *et al.*, 2005) for the year 2007.

The deciduous woodland (US-Ton) is located in the lower foothills of the Sierra Nevada Mountains, CA, USA. The site is dominated by *Quercus douglasii* Hook. & Arn., and experiences a Mediterranean-type climate with dry, hot summers and rainy, mild winters (Table 1).  $F_A$  was inferred from NEE measured with a three-dimensional sonic anemometer (Model 1352; Gill Instruments Ltd, Lymington, UK) and an open-path CO<sub>2</sub>/H<sub>2</sub>O infrared gas analyzer (LI7500; Li-Cor Inc., Lincoln, NE, USA) installed above the stand at a height of 23 m (Ma *et al.*, 2007). SR was calculated using

solid-state  $CO_2$  sensors installed at 2, 8 and 16 cm depths using the gradient flux method as described previously (Vargas *et al.*, 2010a). Soil characteristics are defined in Table 2, and more detailed instrumentation and site information can be found elsewhere (Ma *et al.*, 2007).

The temperate broadleaf forest (US-Moz) is located in central Missouri (30 km southeast of Columbia), USA and is dominated by *Quercus alba* L. (Table 1).  $F_A$  was inferred from NEE measured with a three-dimensional sonic anemometer (81000; RM Young, Traverse City, MI, USA) and an open-path CO<sub>2</sub>/H<sub>2</sub>O infrared gas analyzer (LI7500, Li-Cor Inc.) installed at a height of 32 m above the ground (Gu *et al.*, 2006; Yang *et al.*, 2007). SR was calculated using automated SR chambers located within the footprint of the flux tower (Edwards & Riggs, 2003). Soil characteristics are defined in Table 2, and more detailed instrumentation and site information can be found in previous studies (Gu *et al.*, 2006; Yang *et al.*, 2007).

The boreal evergreen forest (FI-Hyy) is located at the Hyytiälä Forestry Field Station, Finland, and is part of the CarboEurope network. This is a managed stand dominated by Scots pine (*Pinus sylvestris* L.), established in 1962 by sowing after the area had first been treated with prescribed burning and mechanical soil preparation.  $F_A$  was inferred from NEE measured with a three-dimensional sonic anemometer (R3IA; Gill Instruments Ltd) and a closed-path CO<sub>2</sub>/H<sub>2</sub>O infrared gas analyzer (LI6262; Li-Cor Inc.) installed above the stand at a height of 23 m. The instrumentation is documented in more detail in Vesala *et al.* (2005). SR was calculated using automatic chambers based on the closed dynamic chamber technique. The soil



**Fig. 1** Normalized values of daily averages of canopy photosynthesis ( $F_A$ ) (a–d), soil temperature at the depth of maximum correlation with soil CO<sub>2</sub> efflux ( $T_s$ ) (e–h), soil water content (SWC) (i–l) and soil CO<sub>2</sub> efflux (SR) (m–p) at four study sites during their respective growing seasons. For descriptions of sites, see Tables 1 and 2. Days of the year (DOY), days after January 1st of the year in which data were collected. Normalization was performed on the basis of the maximum values of daily averages for each variable at each study site.

Site	Site ID	Climate	MAP (mm)	MAT (°C)	Soil type	Sand (%)	Silt (%)	Clay (%)	Bulk density (mg m <sup>-3</sup> )	Soil porosity (m <sup>3</sup> m <sup>-3</sup> )
Mediterranean deciduous forest	US-Ton	Csa	562	16.5	Lithic haploxerepts	37.5	45	17.5	1.58	0.4
Temperate broadleaf forest	US-Moz	Cfa	985	12.11	Hapludalt & argiudoll	10.5	60	29.5	0.9–1.59	0.45
Boreal evergreen forest Temperate grassland	FI-Hyy AT-Neu	Dfc Cfb	709 1097	3.8 3	Haplic podzol Gleyic fluvisol	65.1 41.9	28.3 30.8	6.6 27.3	0.6 0.91	0.61 0.66

MAP, mean annual precipitation; MAT, mean annual temperature. Sand (%) includes soil fraction > 2 mm in FI-Hyy. Climate acronyms are based on the Köppen climate classification.

characteristics are defined in Table 2, and more detailed instrumentation and site information can be found in previous studies (Pumpanen *et al.*, 2003; Hari & Kulmala, 2005; Vesala *et al.*, 2005).

The temperate grassland (AT-Neu) is located in a meadow in the vicinity of the village Neustift in the Stubai Valley, Austria. The vegetation consists mainly of a few dominant graminoids [Dactylis glomerata L., Festuca pratensis Huds., Phleum pratensis L., Trisetum flavescens (L.) Beauv.] and forbs (Ranunculus acris L., Taraxacum officinale G.H. Weber ex Wiggers, Trifolium pretense L., Trifolium repens L., Carum carvi L.). FA was inferred from NEE measured with a three-dimensional sonic anemometer (R3IA; Gill Instruments) and a closed-path infrared gas analyzer (Li-6262; Li-Cor) installed above the grassland at a height of 3 m (Wohlfahrt et al., 2008). SR was calculated using solid-state CO<sub>2</sub> sensors installed at 5 and 10 cm depth, employing the gradient flux method as described previously (Vargas et al., 2010a). Soil characteristics are defined in Table 2, and more detailed instrumentation and site information can be found in previous studies (Bahn et al., 2008; Wohlfahrt et al., 2008).

#### Wavelet analysis

We used wavelet analysis as a time series technique that has been widely applied in the geosciences (Torrence & Compo, 1998) and recently for SR research (Vargas et al., 2010c, 2011). This technique is used to quantify the spectral characteristics of time series that may be nonstationary and heteroscedastic. Previous studies have used Fourier transform (Tang et al., 2005; Baldocchi et al., 2006) and cross-correlation (Stoy et al., 2007; Vargas et al., 2010a) analysis to investigate the spectral properties of SR signals. However, these analyses failed in the presence of nonstationary phenomena (Katul et al., 2001), such as rain pulses, heat waves or freezing events. Most biometeorological variables (e.g. SR,  $F_A$ ) typically violate the stationary assumption underlying the analysis of spectral properties and wavelet analysis is an alternative technique (Torrence & Compo, 1998).

In this study, we explored the temporal correlation between any two time series (e.g. SR with  $F_A$ ) using wavelet coherence analysis (Grinsted et al., 2004) (Methods S1). Previous reports have described the technique in detail for climate studies (Torrence & Compo, 1998; Grinsted et al., 2004) and SR research (Vargas et al., 2010c). Briefly, coherency is roughly similar to classical correlation, but it pertains to the oscillating components in a given time period (e.g. 1 d, 8 d). There are two main advantages of using wavelet coherence analysis. First, it is possible to determine the multi-temporal correlation between two time series. Therefore, one can identify periodicities (e.g. 1 d, 2 d, ..., n d time periods) with high temporal correlations between the two original time series. Second, it is possible to quantify the phase differences or time lags between two time series. Therefore, one can calculate the time lag between two time series at each period that has been identified with high temporal correlation between them.

The phase difference represents whether or not two time series tend to oscillate simultaneously, rising and falling together within a given time period (in phase, and therefore showing no time lags), or rise and fall out of phase within a given time period (therefore showing a time lag between them). From all wavelet coherence analyses, we extracted the percentage of days with significant temporal correlations and calculated the phase difference (time lags) at 1, 2, 4, 8, 12 and 16 d time periods within the cone of influence. The cone of influence is the region in which the wavelet transform suffers from edge effects because of incomplete time locality across frequencies (Torrence & Compo, 1998); thus, the results outside the cone of influence must be interpreted carefully. The statistical significance (5% significance level) of common power between any two time series was assessed within the cone of influence of the wavelet coherence analysis using Monte Carlo simulations of white noise time series (Torrence & Webster, 1999). Further details of the applied wavelet coherence analysis are given in Methods S1.

From a time series analysis approach, the delay between two time series can provide information on the nature and origin of coupling between the processes, and causality under the assumption that the effect must follow the cause. We raise caution over the use of the word 'lag'. In isotope studies, 'lag' has been used to define the time elapsed between the labeling and recovery of the isotope. In this study, the 'lags' associated with the transport of carbon molecules are interpreted as the temporal correlation at different 'time periods'. Here, we interpret subdaily 'lags' (hours) between  $F_A$  and SR, reported by either isotope approaches or flux-based measurements, by exploring the phase difference ('time lag') within the 1 d time period. All analyses were performed using MATLAB R2007a (The MathWorks, Inc., Natick, MA, USA) and wavelet analysis software (Torrence & Compo, 1998; Grinsted *et al.*, 2004).

#### Data analysis

We explored the influence of  $F_A$  or  $T_s$  on SR using wavelet coherence analysis. The assumption from a time series analysis approach is that, if SR responds strongly and rapidly to a change in  $F_A$  (in comparison with  $T_s$ ), it might be expected that  $T_s$  may have less of a role in controlling SR.

We tested the main hypothesis that  $F_A$  influences SR independent of changes in  $T_s$  and soil CO<sub>2</sub> diffusivity. It is important to recognize that the diurnal cycle of solar radiation governs the daily course of air temperature,  $T_s$  and  $F_A$ , which are drivers of SR. In addition, variations in soil water content (SWC) change the diffusivity of CO<sub>2</sub> and thus SR rates (Šimůnek & Suarez, 1993), contributing to confounding effects. Therefore, changes in  $T_s$  and CO<sub>2</sub> diffusivity could mask or overestimate the relationship between  $F_A$  and SR because there could be spurious correlations. Thus, we analyzed the temporal correlation between SRr (representing  $T_s$  and CO<sub>2</sub> diffusion time series independent of SR) and  $F_{Ar}$  ( $T_s$  time series independent of  $F_A$ ).

First, we removed the effect of changes in  $T_s$  on  $F_A$  by fitting independent simple linear regressions for each day calculated from hourly measurements with the form:

$$F_{\rm Ar} = F_{\rm A} - \left(B_1 + B_2 T_S\right)$$
 Eqn 1

where  $B_1$  and  $B_2$  are parameters evaluated for each single day during the growing season based on hourly measurements of  $T_s$  (at the depth of maximum correlation with SR). The depth of maximum correlation of  $T_s$  with SR was calculated throughout the growing season, rather than for each single day, to avoid the inclusion of periodicities as a result of changes in heat transfer in the soil at each site. The goal of this first equation was to remove the periodicities in  $F_A$  associated with changes in  $T_s$  that also influence SR and could be a source of spurious temporal correlations. In other words, the  $F_A$  signal was detrended for changes in  $T_s$ .

Second, we removed the effect of changes in  $T_s$  and  $CO_2$  diffusion on SR using:

$$SRr = SR - [(B_3 exp^{(B4*T_s)})f D_s]$$
Eqn 2

where  $B_3$  and  $B_4$  are parameters evaluated for each single day during the growing season based on hourly measurements of  $T_s$  (at the depth of maximum correlation with SR), and  $fD_s$  represents a function of diffusivity of soil CO<sub>2</sub> in the soil profile calculated using the Moldrup model (Moldrup *et al.*, 1999):

$$\frac{D_{\rm s}}{D_{\rm a}} = \phi^2 \left(\frac{\varepsilon}{\phi}\right)^{\beta \rm S}$$
 Eqn 3

where  $D_a$  is the molecular diffusivity of CO<sub>2</sub> in the air,  $\varepsilon$  is the air-filled porosity,  $\beta$  is a constant ( $\beta = 2.9$ ), S is the percentage of silt plus sand content and  $\Phi$  is the soil porosity. Thus, independent regressions with the form of Eqn 2 were fitted for each day during the growing season, calculated from hourly measurements, as performed for  $F_{Ar}$ . In other words, the SR signal was detrended for changes in  $T_s$  and the diffusivity of soil CO<sub>2</sub>.

Using this conservative approach, we propose that any temporal correlation between  $F_{Ar}$  and SRr (residuals of  $F_A$  and SR) is likely to represent a link between  $F_A$  and SR by removing the effects of changes in temperature and CO<sub>2</sub> diffusion in the soil. Importantly, we used the same depth of  $T_s$  for SRr and  $F_{Ar}$  to avoid the inclusion of artificial periodicities and lags as a result of differences in the time series of  $T_s$  as a response to heat transfer in the soil at each site. Absolute values of  $F_A$  and SR are not the goal and are not relevant in this study because the interpretations are performed in the frequency domain.

#### Results

#### Temporal relationships between SR and $F_A$

Measurements of  $F_A$ ,  $T_s$ , SWC and SR showed large variation in temporal patterns during the growing seasons at all study sites in the time domain (Fig. 1). Importantly, the sites showed a wide range of patterns for these variables as a result of differences in climate and plant phenology. The wavelet coherence analysis showed that the strongest synchrony between  $F_A$  and SR was at the 1 d time period across study sites (Fig. 2a-d; Table 3). This was inferred by extracting the percentage of days with significant temporal correlations (see the Materials and Methods section and Methods S1) between  $F_A$  and SR within the growing season. The dark gray areas in Fig. 2 represent the regions with significant temporal correlations. Within forest sites, the Mediterranean site showed the least synchrony at the 1 d time period (24% significant days during the growing season), followed by the temperate site with 52% significant days, and the boreal site with nearly 83% significant days during the growing season (Table 3). The grassland site showed significant synchrony at the 1 d time period for nearly 56% of the days during the growing season (Table 3). Time periods longer than 1 d (i.e. 4, 8 and 12 d) also showed significant temporal correlations, but most of the synchrony was localized at time periods of less than 12 d (Fig. 2a–d; Table 3). At any time period, the dark gray areas (showing significant correlations in Fig. 2) were not continuous throughout the analyzed period, as gaps were found between them. In other words, at any site and time period, the temporal correlation between SR and  $F_A$ was not constant throughout the growing season.

An advantage of wavelet coherence analysis is the calculation of the phase difference (time lags) between two time series. As explained earlier, the phase difference represents whether or not two time series tend to oscillate simultaneously at a given time period (in phase, showing no time lags) or rise and fall out of phase within a given time period (out of phase, showing a time lag between them). The arrows in Figs 3 and 4 represent the phase difference. Overall, SR and  $F_A$  were in phase (no time lags) at time periods greater than 1 d at all sites (Table 3). By contrast,  $F_A$  preceded SR by between 3 and 7 h (out of phase) within the 1 d time period in the forest sites, but was mostly in phase (0.9 ± 3.9 h) at the grassland site (Table 3). At the 1 d time period, the phase difference (time lag) was not consistent throughout the growing season, as represented by the standard deviation of the phase difference (time lags) in Table 3. In other words, the oscillation between the two time series at the 1 d time period was not constant throughout the growing season as the phase difference varied among days.

#### Temporal relationships between SR and $T_s$

We found a strong synchrony at the 1 d time period between SR and  $T_s$  at all sites, but significant temporal correlations were also found at larger time periods (Fig. 2e–h). The least synchrony at the 1 d time period was found at the Mediterranean site, followed by the temperate and boreal forests, with nearly 26%, 58% and 76% significant days, respectively, during the growing season (Table 3). The grassland site showed synchrony at the 1 d time period for nearly 50% of the days during the growing season (Table 3). Other time periods larger than 1 d (i.e. 4, 8, 12 and 16 d) also showed significant temporal correlation, but most of the synchrony was localized at time periods of less than 12 d (Fig. 2e–h). At any site and time period, the temporal correlation between SR and  $T_s$  was not constant throughout the growing season.

Overall, SR and  $T_s$  were in phase (no time lags) at time periods larger than 1 d. By contrast, SR preceded  $T_s$  by between 5 and 7 h in the forest sites, and was mostly in phase (1 ± 3.9 h) at the grassland site, within the 1 d time

Fig. 2 Wavelet coherence analysis and phase difference between canopy photosynthesis  $(F_A)$  and soil CO<sub>2</sub> efflux (SR), or SR and soil temperature at the depth of maximum correlation with SR ( $T_s$ ). The approximate phase difference is shown by arrows, in phase pointing right and out of phase pointing left. The shades for power values are from white (low values) to dark gray (high values). Black contour lines represent the 5% significance level, and the thick black line indicates the cone of influence that delimits the region not influenced by edge effects. Days of the year (DOY), days after January 1st of the year in which data were collected.



**Table 3** Percentage and mean phase differences or time lags ( $\pm$  1 SD) within days with significant correlation between soil CO<sub>2</sub> efflux and canopy photosynthesis (SR–*F*<sub>A</sub>), soil CO<sub>2</sub> efflux and soil temperature (SR–*T*<sub>s</sub>) or residuals of soil CO<sub>2</sub> efflux and canopy photosynthesis (SRr–*F*<sub>A</sub>), soil CO<sub>2</sub> efflux and soil temperature (SR–*T*<sub>s</sub>) or residuals of soil CO<sub>2</sub> efflux and canopy photosynthesis (SRr–*F*<sub>A</sub>), solic CO<sub>2</sub> efflux and soil temperature (SR–*T*<sub>s</sub>) or residuals of soil CO<sub>2</sub> efflux and canopy photosynthesis (SRr–*F*<sub>A</sub>), solic CO<sub>2</sub> efflux and solic temperature (SR–*T*<sub>s</sub>) or residuals of soil CO<sub>2</sub> efflux and canopy photosynthesis (SRr–*F*<sub>A</sub>), solic CO<sub>2</sub> efflux and solic temperature (SR–*T*<sub>s</sub>) or residuals of solic CO<sub>2</sub> efflux and canopy photosynthesis (SRr–*F*<sub>A</sub>), solic CO<sub>2</sub> efflux and solic temperature (SR–*T*<sub>s</sub>) or residuals of solic CO<sub>2</sub> efflux and canopy photosynthesis (SRr–*F*<sub>A</sub>), solic CO<sub>2</sub> efflux and solic temperature (SR–*T*<sub>s</sub>) or residuals of solic CO<sub>2</sub> efflux and canopy photosynthesis (SRr–*F*<sub>A</sub>), solic CO<sub>2</sub> efflux and canopy photosynthesis (SRr–*F*<sub>A</sub>), solic CO<sub>2</sub> efflux and solic temperature (SR–*T*<sub>s</sub>) or residuals of solic CO<sub>2</sub> efflux and canopy photosynthesis (SRr–*F*<sub>A</sub>), solic CO<sub>3</sub> efflux and canopy photosynthesynthesynthesynthesynthesynthesynthesynthesy

		SR–F <sub>A</sub>		SR-T <sub>s</sub>		SRr–F <sub>Ar</sub>		
Time-period	Site ID	% of days	Time lag (h)	% of days	Time lag (h)	% of days	Time lag (h)	
1 d	US-Ton	23.8	-3.0 ± 1.1	26.6	6.9 ± 1.2	29.9	-5.7 ± 1.5	
	US-Moz	51.6	-7.6 ± 2.4	58.2	6.9 ± 2.2	30.8	-11.8 ± 3.0	
	FI-Hyy	82.9	$-4.0 \pm 0.8$	75.7	5.1 ± 1.2	60.4	-5.1 ± 1.2	
	AT-Neu	55.7	$-0.9 \pm 3.9$	49.5	1.0 ± 3.9	38.8	$-0.8 \pm 5.3$	
2 d	US-Ton	0.5	0	2.4	0	16.4	0	
	US-Moz	2.7	0	9.3	0	10.7	0	
	FI-Hyy	0	0	1.4	0	0	0	
	AT-Neu	9.9	0	21.2	0	13.0	0	
4 d	US-Ton	4.9	0	0	0	7.2	0	
	US-Moz	0	0	12.5	0	0	0	
	FI-Hyy	0	0	5.8	0	16.8	0	
	AT-Neu	18.2	0	9.0	0	4.7	0	
8 d	US-Ton	0	0	0	0	0	0	
	US-Moz	7.6	0	23.25	0	0	0	
	FI-Hyy	0	0	0	0	0	0	
	AT-Neu	6.3	0	13.7	0	0	0	
12 d	US-Ton	0	0	0	0	0	0	
	US-Moz	31.5	0	37.6	0	32.8	0	
	FI-Hyy	0	0	0	0	0	0	
	AT-Neu	0	0	0	0	0	0	
16 d	US-Ton	0	0	0	0	0	0	
	US-Moz	0	0	0	0	15.6	0	
	FI-Hyy	0	0	0	0	0	0	
	AT-Neu	0	0	5.6	0	0	0	

Results are extracted from the dark gray areas in the wavelet coherence analysis of Figs 3 and 4.  $T_s$ , soil temperature at the depth of maximum correlation with SR at each site (US-Ton, 16 cm depth; US-Moz, 10 cm depth; FI-Hyy, 2 cm depth; AT-Neu, 5 cm depth). For details on the calculation of SRr– $F_{Ar}$ , see the Materials and Methods section. US-Ton, Mediterranean deciduous forest; US-Moz, temperate broadleaf forest; FI-Hyy, boreal evergreen forest; AT-Neu, temperate grassland.

A negative time lag means that the response of the first variable is behind, by x number of hours, the response of the second variable.

period (Table 3). At the 1 d time period, the phase difference (time lag) was not constant throughout the growing season, and is represented by the standard deviation of the phase difference (time lags) in Table 3.

# Temporal relationships between SR and $F_A$ accounting for confounding effects

To test the hypothesis that  $F_A$  influences SR independent of variation in  $T_s$  and soil CO<sub>2</sub> diffusivity (i.e. confounding effects), we tested the temporal correlation between SRr and  $F_{Ar}$ . In general, we found a decrease in the temporal synchrony between SRr and  $F_{Ar}$  at the 1 d time period (Fig. 3), in comparison with the temporal correlation at that time period between SR and  $F_A$  (Fig. 2a–d). The least synchrony at the 1 d time period was found at the Mediterranean and temperate sites, followed by the boreal forest, with nearly 30%, 30% and 60% significant days, respectively, during the growing season (Table 3). The grassland site showed synchrony at the 1 d time period for nearly 39% of the days during the growing season

(Table 3). Importantly, at any site and time period, the temporal correlation between SRr and  $F_{Ar}$  was not constant throughout the growing season.

The influence of  $F_{Ar}$  on SRr at the 1 d time period was independent of changes in  $T_s$  or soil moisture across study sites (Fig. 4). Furthermore, it was independent of the magnitude of  $F_{Ar}$  at the forest sites, but was dependent on the magnitude of  $F_{Ar}$  at the grassland site. For the grassland site, days with significant temporal correlation between SRr and  $F_{Ar}$  showed significantly higher  $F_{Ar}$  than days without significant temporal correlation (*t*-test, P = 0.0039).

When calculating the phase difference (time lags) between SRr and  $F_{Ar}$ , our results were consistent with previous observations for SR and  $F_A$ . Overall, SRr and  $F_{Ar}$  were in phase (no time lags) at time periods of more than 1 d at all sites (Table 3). We found that  $F_{Ar}$  was out of phase at the forest sites as it preceded SR by between 5 and 11 h within the 1 d time period. By contrast, this relationship was mostly in phase (no time lags) at the grassland site within the 1 d time period (Table 3). Similarly, within the 1 d time period, the phase difference (time lag) was not



**Fig. 3** Wavelet coherence analysis and phase difference between soil CO<sub>2</sub> efflux (SRr) and canopy photosynthesis ( $F_{Ar}$ ) after removing the effect of soil temperature and soil CO<sub>2</sub> diffusivity for soil CO<sub>2</sub> efflux, and soil temperature for canopy photosynthesis. For details on the calculation of SRr and  $F_{Ar}$ , see the Materials and Methods section. The approximate phase difference is shown by arrows, in phase pointing right and out of phase pointing left. The shades for power values are from white (low values) to dark gray (high values). Black contour lines represent the 5% significance level, and the thick black line indicates the cone of influence that delimits the region not influenced by edge effects. Days of the year (DOY), days after January 1st of the year in which data were collected.

constant throughout the growing season, and is represented by the standard deviation of the phase difference (time lags) in Table 3.

#### Discussion

Our findings based on time series analysis show that  $F_A$  influences SR at multiple temporal scales during the growing season at three forest sites with different climates and at a temperate grassland. Importantly, the temporal correlations between  $F_A$  and SR (at any time period), and the phase difference (time lags) with the 1 d time period, were neither uniform nor constant throughout the growing season at any study site.

These results suggest that: (1) the link between  $F_A$  and SR may not be constant throughout the growing season; and (2) different drivers (e.g. photosynthesis, soil CO<sub>2</sub> diffusion,  $T_s$ , phloem transport) that influence the allocation and transport speed of carbon through the soil-plant-atmosphere continuum are likely to coexist within a

growing season, explaining the multiple time periods and time lags observed at the study sites.

The temporal correlation between  $F_A$  and SR was most consistent at the 1 d time period for all vegetation types. This suggests an influence of daily photosynthesis on SR and supports the observations from different methods in forests (Baldocchi et al., 2006; Högberg et al., 2008; Subke et al., 2009) and grasslands (Staddon et al., 2003; Carbone & Trumbore, 2007; Bahn et al., 2009). Furthermore, the phase difference (time lag) at the 1 d time period provides insights into the nature and origin of coupling between these processes. This is supported because the delay between two time series could provide information on the coupling between the processes, and causality is inferred under the assumption that the effect must follow the cause. For example, in forests, FA increases before SR, suggesting two potential mechanisms: (1) a fast transport of recent photosynthate carbon molecules from the canopy to the forest soil (Högberg et al., 2008; Dannoura et al., 2011); or (2) the propagation of pressure concentration waves in the phloem of these tall trees (Mencuccini & Holtta, 2010). Importantly, pressure concentration waves may be present only when the osmotic pressure is high relative to turgor differences, and is highly variable among species (Thompson & Holbrook, 2003). In grasslands, the phase difference (near zero lags) supports the observation of a strong link between recent photosynthetic products and SR at the 1 d time period (Bahn et al., 2009).

The fact that SR responds ahead of  $T_s$  at the 1 d time period in forests could be interpreted as the combination of the following: (1) temperature may have less of a role in controlling SR at this time period during the growing season in forests; and (2) autotrophic respiration may dominate the SR signal during the growing season in forests. By contrast, SR is nearly in phase with  $T_s$  in the grassland at the 1 d time period. These results indicate that autotrophic respiration dominates during the growing season, but this contribution is highly variable (Epron *et al.*, 2001; Irvine *et al.*, 2008; Ruehr & Buchmann, 2010). Furthermore, this variability indicates that the synchrony between  $F_A$  and SR is not constant within the growing season (Fig. 3).

It is important to consider the potential confounding effects of soil CO<sub>2</sub> diffusivity and  $T_s$  on SR. Without considering changes in these variables, the influence of  $F_A$  on SR can be over-represented at most sites. This can be observed by comparing the significant temporal correlation (dark gray areas) between Fig. 2(a–d) and Fig. 3. Thus, this study emphasizes the importance of incorporating the effect of  $T_s$  and soil CO<sub>2</sub> diffusivity to avoid misinterpretation of the temporal correlation and potential confounding effects (Davidson *et al.*, 1998; Stoy *et al.*, 2007). By incorporating the effects of changes in  $T_s$  and soil CO<sub>2</sub> diffusivity, we observed a reduced but still important correlation between



**Fig. 4** Normalized time series of canopy photosynthesis ( $F_A$ ), soil temperature, soil water content and soil CO<sub>2</sub> efflux (SR) across the growing season at the study sites. The gray areas show days with significant temporal correlation between CO<sub>2</sub> efflux (SRr) and canopy photosynthesis ( $F_{Ar}$ ) at the 1 d time period extracted from Fig. 3. Normalization was based on Eqn 5 in Supporting Information Methods S1 with the form: X = [X-(mean(X))]/std(X), where X represents the values of the time series analyzed (e.g. soil CO<sub>2</sub> efflux or  $F_A$ ). Days of the year (DOY), days after January 1st of the year in which data were collected.

 $F_{Ar}$  and SRr (Fig. 3). Although the temporal correlation was reduced, our results show that the generality of the conclusions is consistent with the initial approach (relationship between  $F_A$  and SR; Fig. 2a–d; Table 3).

It is critical to recognize that the time lags at the 1 d time period are not constant over the growing season (expressed as standard deviations in Table 3 and by the arrows in Figs 2 and 3). Recent reviews have compiled information about forests and grasslands, reporting mean time lags within the 1 d time period (Kuzyakov & Gavrichkova, 2010; Mencuccini & Holtta, 2010) that are consistent with those given in Table 3. However, most of the studies (isotope- or flux-based) compiled by these reviews have focused their attention at only one particular time (i.e. isotopebased studies), or are limited by the time series analysis employed (i.e. flux-based studies using cross-correlation or Fourier analysis), limiting the capacity to explore the variation across the growing season. A possible explanation for the variation in time lags within the 1 d time period is the response to the daily variation in stomatal conductance, carbon storage effects in plants and changes in photosynthesis during the course of the growing season (Hartley et al.,

2006) as a result of drought stress (Ruehr *et al.*, 2009). Our results show that the influence of  $F_A$  on SR at the 1 d time period occurs under multiple environmental conditions. Only at the grassland site were higher photosynthesis rates associated with significant temporal correlation with SR (Fig. 4). This could be explained by the fast transport of carbon in grasslands controlled by photosynthesis, and therefore the sensitivity to changes in environmental conditions, such as shading (Bahn *et al.*, 2009). We believe that these results raise research questions on why, when and how these relationships occur across different ecosystems and time scales under nonstationary weather conditions and with future climate variability.

Our results show that, by using time series analysis in conjunction with continuous efflux measurements, from either automated chambers or networks of soil CO<sub>2</sub> gradients, it is possible to explore the temporal correlation between  $F_A$  and SR. Our results are novel because they reconcile apparent discrepancies from isotope-based and flux-based observations. As discussed earlier and in recent reviews (Kuzyakov & Gavrichkova, 2010; Mencuccini & Holtta, 2010), different methods may identify different

mechanisms on how  $F_A$  influences SR. In this study, we showed that, from a time series approach, it is possible to identify all the time periods and time lags associated with these fluxes, as reported by previous studies (see Introduction). However, the multi-temporal correlations in time periods and time lags are not uniform throughout the growing season, showing that the strong link between  $F_A$ and SR is not constant in time. Further research is needed to obtain a comprehensive SR theory that considers the multi-temporal influence of biological (i.e. photosynthesis) and physical (i.e. soil CO<sub>2</sub> diffusion,  $T_s$ ) drivers on SR.

#### Potential limitations and future considerations

Our study presents an advance over previous analyses using Fourier transform and cross-correlation techniques to study the influence of  $F_A$  on SR, because they fail in the presence of nonstationary phenomena, such as rain pulses and heat waves, that are present during a growing season (Katul et al., 2001). Wavelet analysis overcomes this issue by using a window size that is not fixed, and varies as a function of frequency, with an optimal trade-off between time and frequency resolution. An advantage of wavelet coherence analysis is that it finds regions in time and frequency domains in which two time series co-vary, but do not necessarily have high common power (Grinsted et al., 2004). As a disadvantage, the fact that these two time series may not necessarily have high common power could lead to an overinterpretation of the magnitude of the temporal influence of  $F_A$  on SR. Furthermore, our analysis may not have been able to remove all the influence of physical factors (i.e.  $T_s$ , soil CO<sub>2</sub> diffusivity) on the periodicity of the signals, and may show temporal correlations where there are none (Stoy et al., 2007). We tried to overcome this limitation by removing the effects of  $T_s$  and soil CO<sub>2</sub> diffusivity by fitting independent equations for each day and by limiting our study to the growing season. Using a different depth of  $T_s$ (other than that with the highest correlation) in these fitting equations changes the temporal relationships as a result of the introduction of a heat transfer component into the signal processing (Vargas et al., 2010c), but does not change the overall conclusion of the multi-temporal relationship presented in this study.

Because biophysical factors influence  $F_A$  and SR at multiple temporal scales, multiple approaches are needed to better understand the temporal correlation between these fluxes (Bahn *et al.*, 2010). Most isotope labeling studies have been performed on short-term campaigns and their results have focused on the identification of the correlation between  $F_A$  and the recovery of the isotope signal via SR. These studies are expensive and difficult to perform; however, future campaigns could be longer or repetitive across seasons to track carbon molecules and identify fast and slow transport rates under different weather conditions (i.e. non-

stationary) and  $F_A$  rates. Repeated labeling, coupled with flux-based measurements (e.g. eddy covariance, soil CO<sub>2</sub> flux gradients and automated SR chambers) and the use of time series analysis, could help in our understanding of the fate of recently assimilated carbon and its role on SR. Finally, long-term deployment of isotope and CO<sub>2</sub> flux (plant and soil) measurements (Wingate *et al.*, 2010), with manipulations of photosynthesis (Bahn *et al.*, 2009) or physical properties of the soil (e.g. changes in SWC) (Thomey *et al.*, 2011), may enable a better understanding of the above-ground links with SR at multiple temporal scales.

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# **Supporting Information**

Additional supporting information may be found in the online version of this article.

Methods S1 Soil  $CO_2$  efflux measurements and wavelet analysis.

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