

Are ecosystem carbon inputs and outputs coupled at short time scales? A case study from adjacent pine and hardwood forests using impulse–response analysis

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ABSTRACT

A number of recent studies have attributed a large proportion of soil respiration (R_{soil}) to recently photoassimilated carbon (C). Time lags (τ_{PR}) associated with these pulses of photosynthesis and responses of R_{soil} have been found on time scales of hours to weeks for different ecosystems, but most studies find evidence for τ_{PR} on the order of 1–5 d. We showed that such time scales are commensurate with CO_2 diffusion time scales from the roots to the soil surface, and may thus be independent from photosynthetic pulses. To further quantify the role of physical (i.e. edaphic) and biological (i.e. vegetative) controls on such lags, we investigated τ_{PR} at adjacent planted pine (PP) and hardwood (HW) forest ecosystems over six and four measurement years, respectively, using both autocorrelation analysis on automated soil surface flux measurements and their lagged cross-correlations with drivers for and surrogates of photosynthesis. Evidence for τ_{PR} on the order of 1–3 d was identified in both ecosystems and using both analyses, but this lag could not be attributed to recently photoassimilated C because the same analysis yielded comparable lags at HW during leaf-off periods. Future efforts to model ecosystem C inputs and outputs in a pulse–response framework must combine measurements of transport in the physical and biological components of terrestrial ecosystems.

Key-words: *Pinus taeda*; canopy conductance; eddy covariance; soil respiration; Southeastern United States.

INTRODUCTION

Soil respiration (R_{soil}) is the largest terrestrial source of CO_2 to the atmosphere and currently represents an annual flux an order of magnitude larger than that from anthropogenic fossil fuel emissions (Schimel 1995; Schlesinger 1997). Quantifying the processes that control the dynamics of R_{soil} is thus critical to understanding the global carbon (C) cycle

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and the climate system. Despite its importance, there is a general lack of agreement on how R_{soil} responds to environmental drivers and photosynthetic C inputs across short and long time scales (Reichstein *et al.* 2005a,b; Davidson & Janssens 2006). These difficulties arise from the multifactorial nature of the processes that control the magnitude and variability of R_{soil} , and the affiliated time lags between environmental drivers and ecosystem responses (Table 1).

In boreal and temperate ecosystems, R_{soil} is thought to be determined primarily by soil temperature (T_{soil} , see Appendix Table A1 for a list of abbreviations) (Lloyd & Taylor 1994). Soil moisture (θ) often plays an important role at the dry and wet ends of its distribution (Davidson, Belk & Boone 1998; Mielnick & Dugas 2000; Palmroth *et al.* 2005). In addition to the well-studied effects of T_{soil} and θ , a number of recent studies have investigated the role of photosynthesis in determining the magnitude and variability of R_{soil} after some time lag (τ_{PR}), suggesting that within-ecosystem carbon transport may be critical for understanding the biosphere–atmosphere exchange of C (Högberg *et al.* 2001; Ryan & Law 2005).

If models of R_{soil} are to incorporate photosynthetic inputs of C (Högberg *et al.* 2001), it is necessary to understand how these two fluxes are coupled. The τ_{PR} reflects the sum of the time scales of C transport in the biological (τ_{B}) and soil (or physical, τ_{P}) components of the ecosystem (Fig. 1). The former includes the time required for C to travel from leaf to phloem to root or endomycorrhizal surface; respiration from these sources is often considered to be the ‘autotrophic’ component of R_{soil} . The latter consists of CO_2 diffusion in the soil air space after production from either autotrophic or heterotrophic sources. Studies employing stable isotope, radioisotope or automated ecosystem flux measurements in forested or savanna ecosystems generally find evidence for τ between photosynthesis and R_{soil} or ecosystem respiration (R_{eco}) on the order of hours (Tang, Baldocchi & Xu 2005), to days (Table 1) or even weeks (Mikan *et al.* 2000; Baldocchi, Tang & Xu 2006). However, no study to our knowledge has quantified the different roles of τ_{B} and τ_{P} in determining τ_{PR} .

Table 1. A summary of studies that investigated the relationship between aboveground processes and soil respiration (R_{soil}) or ecosystem respiration (R_{eco}) in forest and savanna ecosystems using non-destructive methods. PP and HW refer to the planted pine and hardwood forests in the Duke Forest, NC, respectively

Study	Lag (d)	Method	Ecosystem
Horwath, Pretzinger & Paul (1994)	2–3	^{14}C	<i>Populus eumericana</i>
Mikan <i>et al.</i> (2000)	Multiple	^{14}C	<i>P. eumericana</i>
Tang <i>et al.</i> (2005)	5–6 ^a	EC/flux gradient	<i>Quercus douglasii</i> savanna
Baldocchi <i>et al.</i> (2006)	Multiple	EC/flux gradient	<i>Q. douglasii</i> savanna
Ekblad & Hogberg (2001)	1–4	$\delta^{13}\text{C}$	Boreal mixed coniferous
Bowling <i>et al.</i> (2002)	5–10	$\delta^{13}\text{C}$	6 W US coniferous forests
Barbour <i>et al.</i> (2005)	3 ^b	$\delta^{13}\text{C}$	<i>Nothofagus solandri</i>
Knohl <i>et al.</i> (2005)	4–5	$\delta^{13}\text{C}$	Mixed deciduous
Mortazavi <i>et al.</i> (2005)	3–4 ^c	$\delta^{13}\text{C}$	PP and HW
Andrews <i>et al.</i> (1999)	< 7	$\delta^{13}\text{C}$	PP/FACE experiment

^aTang *et al.* (2005) also found evidence for a 7–12 h time lag between photosynthesis and R_{soil} .

^bHoneydew at tree base.

^cFor leaf, plant and ecosystem respiration.

PP, planted pine; HW, hardwood; EC, eddy covariance; W US, western United States; FACE, free-air carbon dioxide enrichment.

We note that R_{soil} comprises, on average, 70% of R_{eco} across temperate forested ecosystems (Janssens *et al.* 2001), such that τ between photosynthesis and R_{eco} may largely reflect τ between photosynthesis and R_{soil} . Whereas the signal of photosynthesis has been shown to be present in

R_{soil} measurements (Table 1), it remains unclear how τ_{P} and τ_{B} interact to influence τ_{PR} because both can vary with edaphic conditions and vegetative function.

A first-order estimate of τ_{P} can be determined from dimensional analysis:

$$\tau_{\text{P}} = \frac{Z_{\text{R}}^2}{d_{\text{mol,diff}}} \quad (1)$$

where Z_{R} is the root-zone depth and $d_{\text{mol,diff}}$ is the molecular diffusivity of CO_2 in the soil, which depends on its molecular diffusivity in free atmosphere (d_{atm}) and tortuosity (ξ). While tortuosity is difficult to measure in porous media dominated by macropores (Suwa *et al.* 2004), an estimate of ξ can still be obtained using the Millington–Quirk relationship:

$$\xi = \frac{(\eta - \theta)^{10/3}}{\eta^2} \quad (2)$$

where η is soil porosity. As a case study, consider a situation where soil temperature is 20 °C such that $d_{\text{atm}} \sim 0.14 \text{ cm}^2 \text{ s}^{-1}$ and Z_{R} is small (e.g. 0.3 m) in a silt loam with $\eta = 0.54$. Based on these parameters, the time scales of CO_2 diffusion from the root zone may vary between 1.5 and 6.0 d or longer for typical seasonal soil moisture states (Fig. 2), thus overlapping with literature estimates that may be interpreted as τ_{B} or both τ_{B} and τ_{P} (Table 1).

In addition to the likely similarities between the magnitudes of τ_{P} and τ_{B} , biological storage of C and phenological effects may complicate the estimation of τ_{PR} and its variability. For example, tree-girdling studies have found large and rapid decreases in the magnitude of R_{soil} after girdling (Högberg *et al.* 2001; Subke *et al.* 2004), variable responses that depend on stand composition (Andersen *et al.* 2005), or weak signals (Edwards & Ross-Todd 1979; Binkley *et al.* 2006). The variability in these responses may reflect the role of plant-stored C (Binkley *et al.* 2006) and thus may vary seasonally. For example, Cisneros-Dozal, Trumbore & Hanson (2006) traced an industrial pulse of ^{14}C through an

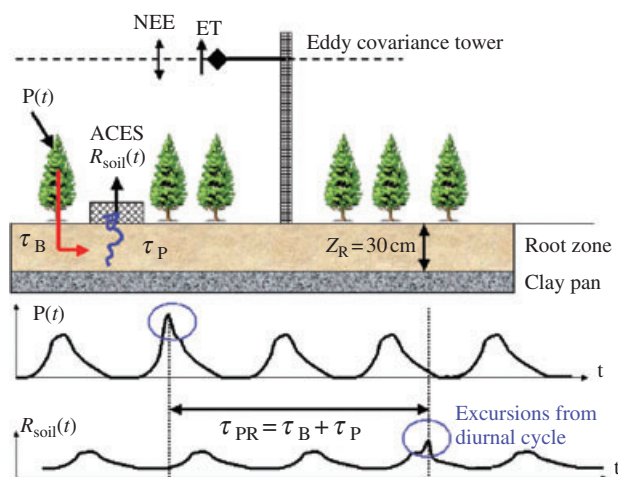


Figure 1. Top: A conceptual diagram of CO_2 entry (via photosynthesis, P) and exit (via soil respiration, R_{soil}) in a forested ecosystem. Time lags due to transport (τ) in the biological (τ_{B}) and physical (τ_{P}) components of the ecosystem are shown. The τ_{P} is purposely shown as tortuous. The general location of the eddy covariance (EC) and automated CO_2 efflux systems (ACES) in this experiment is presented. The rooting depth and most respiratory activity in the study ecosystems are constrained by a clay pan at ca 30 cm as indicated. Bottom: Hypothetical time series of photosynthesis $P(t)$ and soil respiration $R_{\text{soil}}(t)$ are shown for illustration. The impulse–response analysis attempts to determine the lag time between an impulse in photosynthesis, defined as an anomalous excursion from the diurnal cycle, and its response in the soil respiration (defined here as an anomalous excursion from the background state set by the instantaneous soil temperature and soil moisture series) using the cross-correlation function. The time separation between anomalous excursions in the soil respiration can also be determined from an autocorrelation analysis.

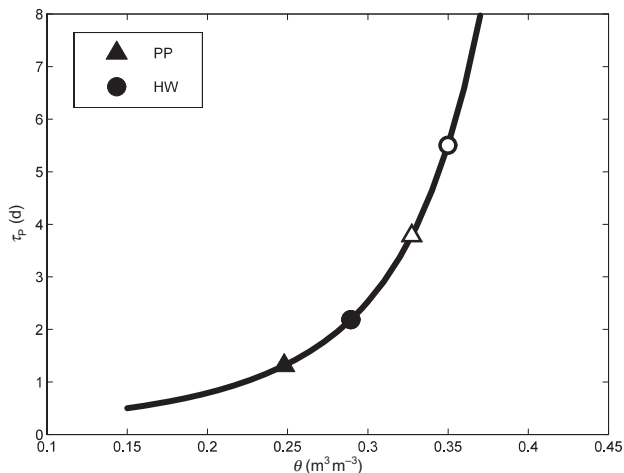


Figure 2. Estimated transport time of gas-phase soil CO_2 (τ_p) for typical growing season (solid symbols) and non-growing season periods at the planted pine (PP) and hardwood (HW) forest ecosystems using mean seasonal soil moisture (θ) under unsaturated conditions. The τ_p for PP is denoted by triangles and HW by circles.

oak-hickory forest, and found that root respiration was generated from stored non-structural carbohydrates before the growing season and by recent photoassimilates near the peak of the growing season. Other variables likely to influence the velocity and seasonality of τ_B include distance from assimilation site to respiring tissue, phloem temperature and sap viscosity, and C sink strength and size, and plant allocation (McDowell *et al.* 2004; Barbour *et al.* 2005).

Thus, the coupling between photosynthesis and R_{soil} depends on τ_p and τ_B , both of which may vary because of the biological and physical properties of the ecosystem. Some of these variables can be controlled for by studying adjacent ecosystems with similar meteorological and edaphic characteristics, but with different phenology.

Here, we examine time lags between canopy level flux measurements and R_{soil} for multiple years in planted pine (PP) and hardwood (HW) forest ecosystems in the Duke Forest, NC. Specifically, we investigate the coupling between photosynthesis and R_{soil} at shorter (e.g. daily) time scales (Table 1) to determine the 'pulse-response' relationship that may exist between ecosystem C inputs and outputs using continuous non-invasive flux measurements (Fig. 1). The study ecosystems are adjacent with identical climate and similar soil type, rooting depth, annual R_{soil} and bulk soil C (K. Johnsen, unpublished results), such that differences in observed ecosystem dynamics are attributable to vegetative activity (Stoy *et al.* 2006a,b). The strong role of T_{soil} and θ in controlling R_{soil} at the daily time step at PP and HW has been well established (Palmroth *et al.* 2005). *The purpose of the present study is to investigate the additional role of aboveground processes via canopy photosynthesis on R_{soil} by extending a recent methodology proposed by Baldocchi *et al.* (2006) that employed automated measurements of canopy level and soil fluxes.*

The PP and HW study ecosystems may represent a best-case scenario for disentangling the roles of τ_B and τ_p in controlling the coupling between photosynthesis and R_{soil} in forests. A clay pan at ca 30 cm (Oren *et al.* 1998) constrains the vertical root distribution at both ecosystems (Fig. 1), such that τ_p is likely to be small but similar at these two stands – at least in terms of the seasonal variation in τ_p due to seasonal variations in soil moisture. Canopy activity is strongly diminished at PP when air temperature is less than 10 °C (Schäfer *et al.* 2002), but remains otherwise active during winter. However, canopy activity is entirely absent at HW during winter when the canopy is without leaf. Such periods can be investigated as a control case. In addition, near-continuous eddy covariance (EC) photosynthesis estimates and R_{soil} measurements from automated carbon efflux systems (ACES, Butnor *et al.* 2003) are available for 6 years at PP and 4 years at HW, making it possible to investigate several combinations of phenological situations and climatic conditions.

Briefly, EC measures the turbulent flux of CO_2 (net ecosystem exchange, NEE), water vapour (evapotranspiration, ET) and momentum between the biosphere and atmosphere (Baldocchi *et al.* 2001). Near-continuous, defensible long-term EC-based estimates of canopy C uptake by photosynthesis and ecosystem C loss through respiration can be derived using a variety of 'flux partitioning methods', which have been validated against independent and model-based canopy photosynthesis and ecosystem respiration measurements for the study ecosystems by Stoy *et al.* (2006b). Estimates of photosynthesis can also be derived using water flux measurements by assuming that transpiration dominates ET in forested ecosystems (during leaf-on periods in the case of HW forests) and that canopy water loss is coupled to CO_2 gain through stomatal function.

METHODS

Site description

The study ecosystems lay adjacent on Enon silt loam, a low fertility Hapludalf typical of the Southeastern United States (SE US) Piedmont, with a transition to Iredell gravelly loam in parts of HW (Pataki & Oren 2003). PP was established in 1983 and is comprised primarily of *Pinus taeda* L. with some emergent *Liquidambar styraciflua* L. Canopy height was 19 m in 2005. HW is an 80- to 100-year-old mixed deciduous forest dominated by oak (*Quercus*) and hickory (*Carya*) species. Canopy height averaged 25 m with emergent treetops reaching over 35 m. The canopies of both ecosystems are characterized by a diverse understory, and thus a large vertical distribution of leaf area (Stoy *et al.* 2005).

R_{soil} measurements

R_{soil} was measured using two ACES (US patent 6 692 970) developed by the United States Department of Agriculture (USDA) Forest Service (Butnor *et al.* 2003). The ACES

coupled an infrared gas analyser (IRGA, EGM-3; PP Systems, Amesbury, MA, USA) with a chamber-based multi-port design to iteratively measure CO₂ efflux from either stem or soil. ACES R_{soil} measurements were easily corrected to give a consistent response for different soil types, and the system has been lab-calibrated against known CO₂ efflux rates (Butnor & Johnsen 2004; Butnor, Johnsen & Maier 2005). The chambers included a pressure equilibration port to ensure that chamber and atmospheric pressure differences do not compromise accurate flux measurements.

For each ACES, 15 measurement chambers and one reference chamber were sampled by the IRGA. Chambers were sampled for 9 min after a 1-min purge, such that individual chambers were sampled every 160 min (ca 2.7 h). For this study, R_{soil} measurements were available from six chambers at PP and eight chambers at HW. The remaining chambers were used to measure stem respiration or R_{soil} in fertilized plots and were not considered here. We were interested in examining the pulse–response relationship between photosynthesis and R_{soil} , and thus used the average of R_{soil} normalized between 0 and 1 for each chamber for each 2.7 h measurement interval in this analysis.

The ACES at PP was located in Plot 8 of the Duke FACE study some 400 m south-southwest (SSW) of the EC system located in Plot 1 (Palmroth *et al.* 2005; Stoy *et al.* 2006a). The portion of PP surrounding Plot 1 (i.e. within the EC flux footprint) had slightly lower C flux magnitude than the rest of the forest, such that the magnitude of measured NEE was some 50 g C m⁻² y⁻¹ lower than the plot as a whole (Oren *et al.* 2006). We assumed that, although the absolute quantities of R_{soil} sampled by the ACES may not represent R_{soil} of the EC measurement footprint at PP, the temporal pattern of R_{soil} does not vary systematically at this uniformly

planted stand. At HW, the ACES chambers were situated within 50 m of the EC measurement tower in an area commonly enveloped by the flux footprint.

ET and EC measurements

We note again that EC systems measure the biosphere/atmosphere flux of both water (i.e. ET) and CO₂ (NEE), and that R_{soil} is an important component of NEE. To avoid the inherent correlations that exist between two measurements that both capture soil CO₂ efflux, we used estimates of ET rather than NEE as a surrogate for canopy photosynthesis when photosynthesis exists. The fundamental relationship between ecosystem C and H₂O follows from considering the Fick's law relationship between canopy conductance (G_c) and gross ecosystem productivity (GEP), itself related to canopy photosynthesis (Goulden *et al.* 1997; Stoy *et al.* 2006b):

$$GEP = -\varepsilon G_c \left(1 - \frac{C_i}{C_a}\right) \quad (3)$$

where ε is a conversion factor to account for differences in diffusivity between H₂O and CO₂ (1/1.6), and C_i/C_a is the ratio of leaf mesophyll to atmospheric (CO₂), and is related to vapour pressure deficit (D) both at short and long time scales at PP and HW (Leuning 1995; Katul, Leuning & Oren 2003; Mortazavi *et al.* 2005). G_c dominates ET at the study ecosystems (Stoy *et al.* 2006a), and the relationship between ET and GEP is extremely strong; using monthly averages, $P < 10^{-3}$ at both ecosystems with $r^2 = 0.83$ and 0.95 at PP and HW, respectively (Fig. 3). ET is comprised entirely of evaporation (E) in the absence of G_c [i.e. during winter in the deciduous HW or when G_c is limited by air

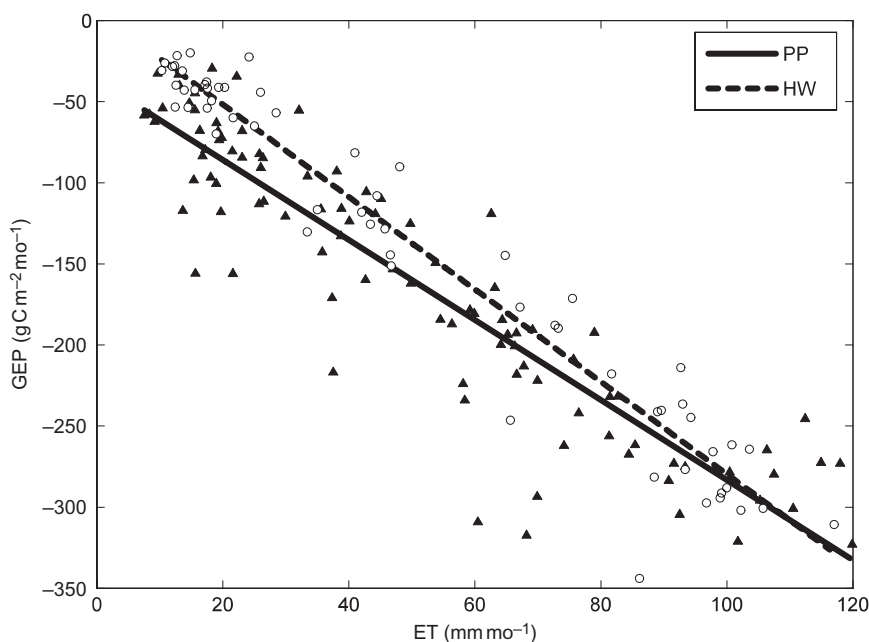


Figure 3. The relationship between measured evapotranspiration (ET) and estimated gross ecosystem productivity (GEP) at the planted pine (PP, closed triangles) and hardwood (HW, open circles) forest study ecosystems at the monthly time scale.

temperatures of less than 10 °C at PP (Schäfer *et al.* 2002)]. Ecosystem E is dominated by E from the soil surface, which is primarily an energy-limited process when θ is high (Brutsaert 1982), as found during wintertime periods in both ecosystems (Stoy *et al.* 2006a). As an independent check, we also analysed time lags in the relationship between photosynthetically active radiation (PAR) and R_{soil} . PAR was strongly related to GEP on hourly to daily time scales at both ecosystems (Stoy *et al.* 2005).

ET was measured using EC systems comprised of triaxial sonic anemometers (CSAT3; Campbell Scientific, Logan, UT, USA) and open-path infrared gas analysers (IRGA, LI-7500; Li-Cor, Lincoln, NE, USA) positioned at 20.2 m at PP and at 39.8 m at HW. A closed-path gas analyser (LI-6262; Li-Cor) was employed at PP before 1 May 2001 (Katul *et al.* 1997b). The Webb–Pearman–Leuning correction (Webb, Pearman & Leuning 1980) for the effects of air density fluctuations on flux measurements was applied to scalar fluxes measured with the open-path LI-7500 (Li-Cor). More information on measurement details and data quality assurance can be found elsewhere (Katul *et al.* 1997a; Detto & Katul 2007; Stoy *et al.* 2006a,b).

Data analysis

We seek to examine the lag relationship between photosynthetic C assimilation and R_{soil} . For this analysis, it is necessary to estimate both τ_B and τ_P . We did so by performing two analyses that differ in their underlying assumptions and data inputs:

1 Memory analysis on measured R_{soil} . The basic assumption in the memory analysis is that internal autocorrelation in the R_{soil} time series on short time scales is due to autocorrelation in the physical drivers of R_{soil} and variations in carbon input. Hence, by removing the effects of the physical drivers (and their memory) on R_{soil} , the memory in the residual series may reflect the memory injected by the carbon input (which is zero for the HW during winter, but finite for summer runs at both ecosystems). Algorithmically, an autocorrelation analysis on R_{soil} for every week of the measurement period was used to determine the time lags at which the time series is no longer autocorrelated. Significant correlation (abbreviated σ) was determined using the classic approach of Anderson (1942) as described in Salas *et al.* (1988) and demonstrated in more detail in Appendix B. We then estimated τ_B by examining autocorrelation in the residual R_{soil} time series (R_{res}) after removing the effects of soil transport due to diffusion and heterotrophic respiration due to soil temperature using

$$R_{\text{res}} = R_{\text{soil}} - R_{10} Q_{10}^{\frac{T_{\text{soil}} - 10}{10}} f(\tau_P) \quad (4)$$

where $f(\tau_P) = \xi^{-1}$, to represent the dominant effects of tortuosity (and hence soil moisture) in controlling the variability of soil CO₂ diffusion (Fig. 2). Palmroth *et al.* (2005) found that the Q_{10} function describes the tempera-

ture response of R_{soil} better than alternate formulations after Lloyd & Taylor (1994) or Arrhenius (1889) at the study ecosystems. R_{res} reflects the time separation in anomalous events, taken here to mean events not explained by soil temperature and soil moisture, and as an indicator of τ_B . It is important to note that both autotrophic and heterotrophic respiration is likely to respond to both T_{soil} and θ , possibly in a similar manner. However, to conservatively identify any pulse–response events due to τ_B , we removed the effects of T_{soil} and θ from R_{soil} after Eqn 4 for the purpose of the residual analysis.

2 A cross-correlation analysis between ET or PAR and R_{soil} or R_{res} . In essence, this cross-correlation analysis is conceptually analogous to the analysis reported in Tang *et al.* (2005) & Baldocchi *et al.* (2006). We computed (σ) for time lags of up to 6 d using a 10 d moving window. This analysis ensured that at least 30 data points were included in the computation of σ , noting that if all ACES chambers were averaged, then nine measurements were available daily. We note that a correlation analysis of periodic time series inherently induces both positive and negative correlation (e.g. Appendix Fig. B1c); we are interested in those cases when an increase or decrease in aboveground activity induces an affiliated increase or decrease in belowground activity, respectively.

All time series showed evidence of diurnal variability, and the auto- or cross-correlations of time series that share diurnal variations may be ‘contaminated’ by the diurnal cycle. We removed the diurnal trend of (i.e. ‘detrended’) the T_{soil} , ET and PAR time series using a Fourier transformation/Lorentz thresholding methodology (Katul & Vidakovic 1998; Wesson, Katul & Siqueira 2003) described in more detail in Appendix B.

R_{soil} is strongly controlled by T_{soil} at the study ecosystems (Palmroth *et al.* 2005); therefore significant autocorrelation in the T_{soil} signal or cross-correlation between T_{soil} and aboveground surrogates for photosynthesis may result in artificial σ . We removed from the analysis all time periods for which significant autocorrelation or cross-correlation with detrended T_{soil} was present. Despite the strict requirements for data acceptability, the length of the data record ensured that a wide variety of environmental and phenological conditions were sampled. We separated the analysis into summer (May–August) and winter (November–February) to investigate the periods where canopy photosynthesis is absent at HW.

RESULTS AND DISCUSSION

Ecological measurements

To motivate the analysis of σ between R_{soil} , edaphic, and aboveground driving variables, we first described the features of the data record. The R_{soil} , T_{soil} , θ and ET time series for the 2000–2004 time period have been described elsewhere (Palmroth *et al.* 2005; Stoy *et al.* 2006a; Katul *et al.* 2007); we reiterate some of the basic trends as a background

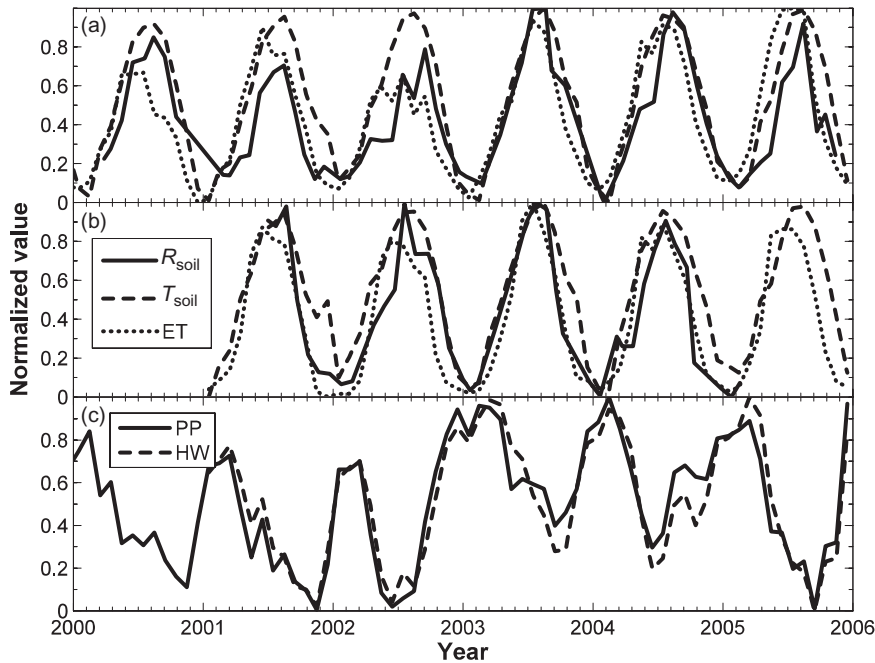


Figure 4. The monthly average of soil respiration (R_{soil}), soil temperature (T_{soil}) and canopy conductance (G_c) at the planted pine [PP, (a)] and hardwood [HW, (b)] forest ecosystems. Time series were normalized to have a maximum of 1 and minimum of 0 for comparison. (c) Normalized soil moisture (θ) measurements at the PP and HW ecosystems.

for later interpretation. We then investigate autocorrelation in the R_{soil} and R_{res} time series, as well as cross-correlations between both R_{soil} and R_{res} and the surrogates of photosynthesis, ET and PAR.

At both ecosystems, R_{soil} , T_{soil} and ET increased and θ decreased during the growing seasons of the measurement period (Fig. 4). Maximum monthly R_{soil} during the severe drought in 2002 was observed during a period of high T_{soil} when ET was relatively low compared with similar periods during other growing seasons (Fig. 4a,b). PP is a drought-sensitive ecosystem, and reductions in G_c and, thereby,

photosynthesis are observed when θ is less than $0.2 \text{ m}^3 \text{ m}^{-3}$ (Oren *et al.* 1998; Stoy *et al.* 2005).

Memory analysis

The 10 d R_{soil} time series were autocorrelated at time scales of ca 1.5–3 d on average in the study ecosystems during both summer and winter (Fig. 5a). These are approximately the time scales associated with C transport from photosynthesis and R_{soil} at the study ecosystems (Mortazavi *et al.* 2005) and other ecosystems (Table 1), but

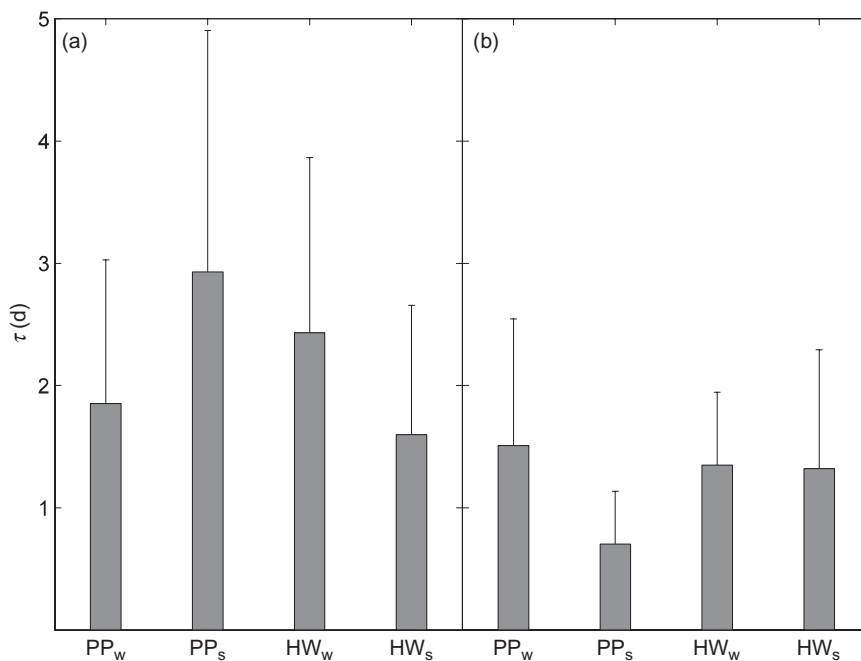


Figure 5. (a) The mean value at which 10 d R_{soil} autocorrelation functions cross the positive correlation threshold of Anderson (1942). PP refers to the planted pine ecosystem, HW the hardwood forest, s to summer and w to winter. (b) Same as (a) but for R_{soil} residual time series (R_{res}) obtained after removing the effects of physical turnover times after Eqn 3.

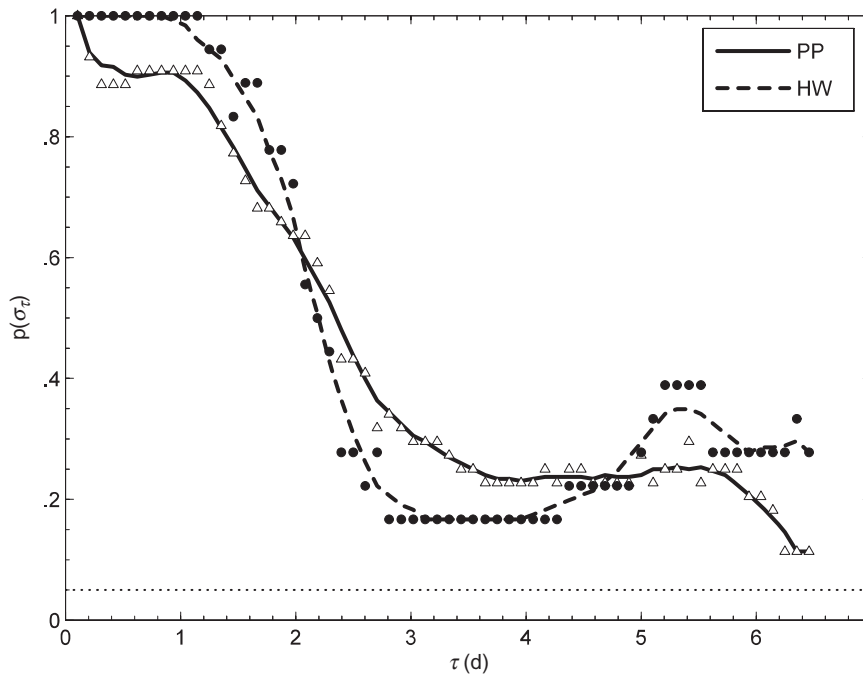


Figure 6. The probability (p) of observing a significant autocorrelation (σ) at lag time τ in detrended 10 d soil temperature (T_{soil}) time series at the planted pine (PP) and hardwood (HW) forest ecosystems. Significant autocorrelation of a random time series would be expected 5% of the time as indicated by the dashed line.

we note that a time lag of similar length is also present at HW in winter when photosynthetic inputs are absent (Fig. 5a).

After removing the effects of T_{soil} and ξ via Eqn 4, the mean R_{soil} autocorrelation (i.e. R_{res}) drops to ca 0.7–1.5 d with strong variability that is not related to θ ($P > 0.1$) (Fig. 5b). The only significant difference between any two distributions of τ is between R_{soil} and R_{res} for summertime periods at PP (two sample t -test, $P < 0.05$). As a whole, this analysis may suggest that τ_{B} is on the order of one day, but this value is shorter than estimated by previous studies (Andrews *et al.* 1999; Mortazavi *et al.* 2005). More importantly, autocorrelations at HW during winter are comparable with other periods at both ecosystems. Therefore, rather than representing biological autocorrelation, R_{res} seems to retain some memory from the physical system, likely due to the strong autocorrelation in the variable to which it responds most strongly, T_{soil} . In short, the non-linear temperature response of R_{soil} means that any mild residual memory in T_{soil} can disproportionately impact the autocorrelation of the residual R_{soil} . This analysis also demonstrates the sensitivity of the ‘memory’ in respiration to the detrended soil temperature memory, even after taking into account the relationship between T_{soil} and R_{soil} using Eqn 3.

The probability (p) of observing significant autocorrelation (σ) at some time lag, abbreviated $p(\sigma_{\tau})$, for the detrended T_{soil} time series is unity at time lags of up to 1 d at PP and up to 3 h (i.e. 1 time step) at HW (Fig. 6). The $p(\sigma_{\tau})$ decreases rapidly at ca 2 d at both ecosystems, and is greater than the $p(\sigma_{\tau})$ of a random signal for all periods of up to 6 d. The strong memory in T_{soil} (Fig. 6) at time scales of ca 2 d corresponds to the memory of the R_{soil} and R_{res} time series (Fig. 6). It is clear from this analysis that τ_{B}

may be difficult to estimate because of multiple and overlapping time scales that appear to be strongly affected by physical drivers, mainly the memory in soil temperature. Again, this memory in T_{soil} is not surprising as a first-order estimate of thermal lags τ_{thermal} in the rooting zone may be determined by

$$\tau_{\text{thermal}} = \frac{Z_{\text{R}}^2}{d_{\text{mol,T}}} \quad (5)$$

where $d_{\text{mol,T}}$ is the molecular diffusivity of heat in the soil (roughly, $d_{\text{mol,T}} \approx 250 \text{ cm}^2 \text{ d}^{-1}$ for a clay soil at intermediate soil moisture) resulting in $\tau_{\text{thermal}} = 3.5 \text{ d}$. These results suggest that the conceptual anomalous excursions in the respiration time series of Fig. 1 are masked by τ_{thermal} and may not reflect anomalous excursions in photosynthesis but anomalous excursions in the soil heat flux.

Cross-correlation analysis

To independently assess these findings, we investigated next the correlations of both R_{soil} and R_{res} with surrogates of photosynthesis as a check on the idea that internal system autocorrelation masks the relationship between ecosystem C inputs and outputs at short time scales at the study ecosystems.

The $p(\sigma_{\tau})$ for the cross-correlation of both R_{soil} and R_{res} , and either detrended ET or detrended PAR (see Appendix B) was often greater than that of a random signal at time lags of up to 6 d (Fig. 7). We note that significant autocorrelation in the detrended T_{soil} time series was nearly always evident at a time lag of 36 h or less (Fig. 6); therefore, $p(\sigma_{\tau})$ was computed for longer periods allowing us

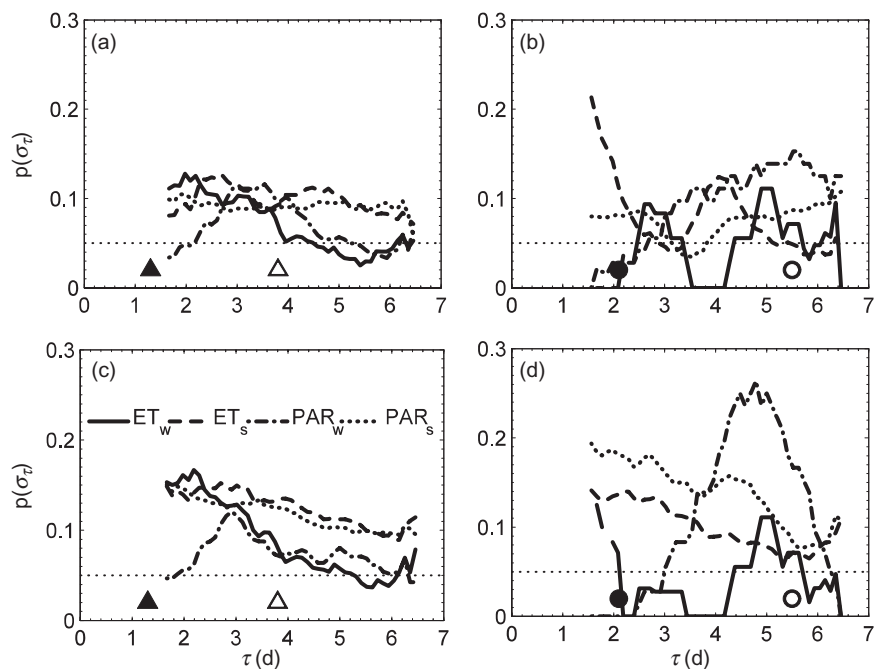


Figure 7. The probability (p) of observing a significant correlation (σ) between soil respiration (R_{soil}) and evapotranspiration (ET) or photosynthetically active radiation (PAR) at time lag τ at the planted pine [PP, (a)] and hardwood [HW, (b)] forest ecosystems during peak winter (w, November–February) and summer (s, May–August) periods. ET_w , ET_s , PAR_w and PAR_s are denoted by solid, dashed, dash-dot and dotted lines, respectively. Driving variables were detrended as discussed in the Appendix. Significant correlation between random time series would be expected 5% of the time as indicated by the dashed line. Approximate time scales of soil CO_2 diffusion after Fig. 2 are indicated by the symbols. (c & d) Same as (a & b) but using R_{soil} residuals (R_{res}) after Eqn 3.

to focus on the possible effects of photosynthesis on R_{soil} . Seasonal differences in $p(\sigma_\tau)$ were evident at both ecosystems and are suggestive of a complex relationship between edaphic and aboveground drivers and R_{soil} .

The $p(\sigma_\tau)$ at PP was between 0.05 and 0.15 for most time lags during both summer and winter for the relationship of both R_{soil} (Fig. 7a) and R_{res} (Fig. 7c) with the surrogates for photosynthesis. During winter, $p(\sigma_\tau)$ between surrogates for photosynthesis and both R_{soil} and R_{res} tended to decrease at ca 3–4 d (indicated by the open triangle), which is similar to the estimated value of τ_p for typical winter θ (Fig. 2) when the soil is not saturated.

This result was also apparent at HW. The $p(\sigma_\tau)$ between PAR and R_{res} decreased rapidly at a time lag of ca 5 d during non-growing season periods, similar to the τ_p during non-saturated mean wintertime soil conditions (Figs 2 & 7d). This response differed from $p(\sigma_\tau)$ between surrogates of photosynthesis and R_{soil} during summer, which has a peak at 4 d for the case of ET and 5.5 d for the case of PAR (Fig. 7b). Thus, it is clear that parts of the ‘physical’ signal are removed via Eqn 3, but it is difficult to fully remove τ_p from the time series as suggested by previous results (Figs 5 & 6). This complicates the estimation of τ_B . Again, we assume that there are no direct photosynthetic C inputs during winter at HW, and that ET is comprised entirely of E. These results demonstrate that the full effects of the physical system act on multiple time scales and are difficult to remove from the R_{soil} time series at these two ecosystems. There are no clear peaks in $p(\sigma_\tau)$ that correspond to an unambiguous relationship between photosynthesis and R_{soil} , even after removing the physical effects of diffusion via equation 3 (i.e. R_{res}).

Combined results from both ecosystems suggest that aboveground inputs mediate existing time lags between R_{soil} and physical drivers because $p(\sigma_\tau)$ differs for summer and

winter periods when canopy photosynthesis is absent at HW. Whereas a ‘signature’ of canopy inputs may be present in as much as the summer $p(\sigma_\tau)$ may be different from that in winter (Fig. 7), it is difficult to deconvolve the time scales at which canopy processes interact with R_{soil} . This is due in part to the long memory in the physical drivers that tend to mask any variations in C input.

Summary

Thus, whereas C outputs via R_{soil} may be dominated by recent photosynthetic C inputs at both of our study sites (Andrews *et al.* 1999; Mortazavi *et al.* 2005; Taneva *et al.* 2006) and others (Table 1), understanding these dynamics based on a pulse–response time series framework may not be possible for ecosystems in which time scales of C transport in the physical and biological components of the ecosystem overlap. Independent estimates from other types of analyses (e.g. Table 1) remain essential for quantifying τ_B , and future studies should isolate potential lags between photosynthesis and C evolution at the root or endomycorrhizal surface. Likewise, measuring the simultaneous profiles of subsurface CO_2 concentration, soil moisture and soil temperature at short time steps (say under 10 min) permits us to estimate directly the subsurface CO_2 production profile (e.g. see formulations in Suwa *et al.* 2004) to better model τ_p . Thus, a measurement scheme that captures the time scales at which respiration and CO_2 transport occur will provide the necessary temporal and spatial resolution to track the movement (and storage) of CO_2 through the biological and physical components of the ecosystem using process-based CO_2 production and transport models. Such models may take advantage of, for example, the simple formulations for tortuosity and soil respiration employed

here. In addition, the cross-correlation analysis at various layers between CO₂ production profiles and photosynthesis (or its surrogates) and forest floor fluxes should permit further constraints on τ_B . This method may prove to be promising because of recent advances in solid-state subsurface CO₂ concentration measurements at unprecedented short time scales (e.g. Tang *et al.* 2005).

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APPENDIX

Appendix A

A list of abbreviations can be found in Table A1.

Table A1. A list of abbreviations with units and definitions

Abbreviation	Units	Definition
ACES		Automated carbon efflux system
C_i	ppm	Leaf internal CO_2 concentration
C_a	ppm	Atmospheric CO_2 concentration
d_{atm}	$\text{cm}^2 \text{s}^{-1}$	Molecular diffusivity of CO_2 in the free atmosphere
$d_{\text{mol,T}}$	$\text{cm}^2 \text{d}^{-1}$	Molecular diffusivity of heat in the soil
$d_{\text{mol,diff}}$	$\text{cm}^2 \text{d}^{-1}$	Molecular diffusivity of soil CO_2
D	kPa	Vapour pressure deficit
EC		Eddy covariance
ET	mm time^{-1}	Evapotranspiration
FT		Fourier transform
G_c	$\text{mol m}^{-2} \text{s}^{-1}$	Canopy conductance to CO_2
GEP	$\text{g C m}^{-2} \text{s}^{-1}$	Gross ecosystem productivity
HW		Hardwood forest ecosystem

Table A1. Continued

Abbreviation	Units	Definition
NEE	$\text{g C m}^{-2} \text{s}^{-1}$	Net ecosystem exchange of CO_2
p	Fraction	Probability
$p(\sigma_z)$	Fraction	The probability of observing significant autocorrelation at some time lag
PAR	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Photosynthetically active radiation
PP		Planted pine ecosystem
Q_{10}		Temperature sensitivity of soil respiration
R_{10}	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Base soil respiration at $T_{\text{soil}} = 10^\circ \text{C}$
R_{eco}	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Ecosystem respiration
R_{soil}	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Soil respiration
R_{res}	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Residual soil respiration after removing the physical effects due to temperature and diffusion using equation 1
SE US		Southeastern United States
T_{soil}	$^\circ \text{C}$	Soil temperature
Z_R	m	Rooting depth
ϵ		Ratio of the binary molecular diffusivity of $\text{CO}_2/\text{H}_2\text{O}$
θ	$\text{m}^3 \text{m}^{-3}$	Soil moisture
η	$\text{m}^3 \text{m}^{-3}$	Soil porosity
ξ		Tortuosity
σ		Significant autocorrelation
τ	d	Time lag
τ_B	d	Time lag in the biological (i.e. vegetative) components of the ecosystem
τ_P	d	Time lag in the physical components of the ecosystem
τ_{PR}	d	Time lag between photosynthesis and soil respiration
τ_{thermal}	d	Thermal lag in the rooting zone

Appendix B

The time series of environmental drivers and R_{soil} measurements showed strong diurnal variability (Palmroth *et al.* 2005; Stoy *et al.* 2006a) and any correlation analysis between such time series would result in significant relationships at regular intervals. To avoid this situation, we removed the diurnal signal from the 2.7 h data by computing the Fourier transform (FT) of the solar zenith angle time series and removing the dominant frequencies from the time series of the environmental drivers. The diurnal mode of variability may be partially described by more than one Fourier coefficient (Fig. B1a); we used a Lorenz thresholding approach (Katul & Vidakovic 1998; Wesson *et al.* 2003) to ensure full removal of the most energetic frequencies, that is, those that describe diurnal variability (Fig. B1a,b). The detrended time series were then reconstructed using the inverse FT, and cross-correlation analysis was performed. Significance was determined using the approach of Anderson (1942) (Fig. B1c).

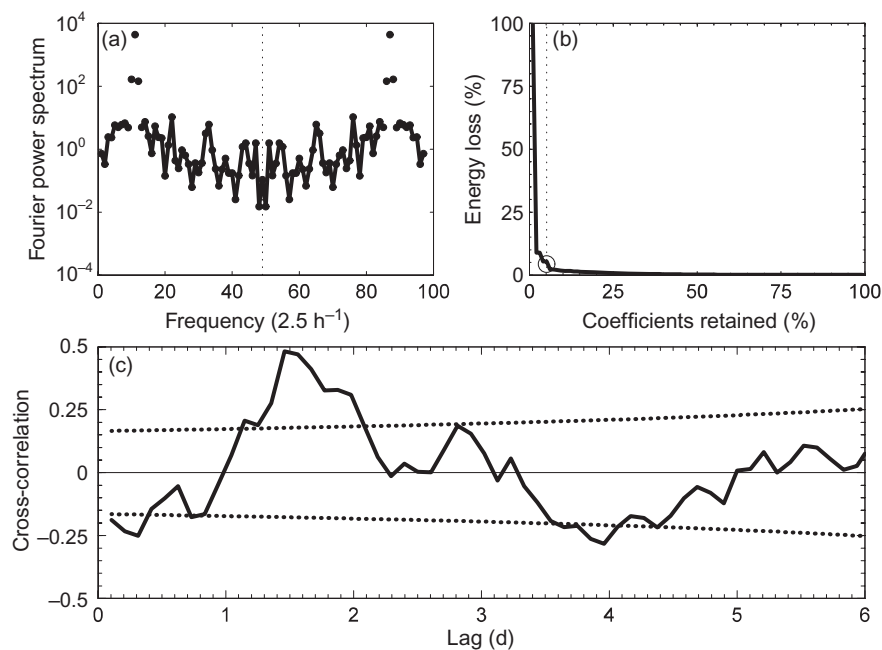


Figure B1. (a) The Fourier transform (FT) of a 10 d solar zenith angle time series with a 2.7 h measurement interval. The Nyquist frequency is denoted by the dotted line. Coefficients that describe the energetic diurnal frequencies were removed using the Lorenz thresholding methodology demonstrated in panel (b); coefficients for which the slope of the energy loss curve was greater than 1 were removed and the detrended time series of flux and environmental drivers were reconstructed using the inverse FT. (c) An example of the cross-correlation analysis between canopy conductance (G_c) and soil respiration (R_{soil}) from chamber 1 of the automated carbon efflux system (ACES) at the planted pine (PP) forest during a 10 d period in April 2000. Significance was determined using the 95% probability threshold (dashed line) described by Anderson (1942).