Looking deeper into the soil: biophysical controls and seasonal lags of soil CO₂ production and efflux

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Abstract. We seek to understand how biophysical factors such as soil temperature (T_s), soil moisture (θ), and gross primary production (GPP) influence CO₂ fluxes across terrestrial ecosystems. Recent advancements in automated measurements and remote-sensing approaches have provided time series in which lags and relationships among variables can be explored. The purpose of this study is to present new applications of continuous measurements of soil CO₂ efflux (F₀) and soil CO₂ concentrations measurements. Here we explore how variation in T_s, θ, and GPP (derived from NASA’s moderate-resolution imaging spectroradiometer [MODIS]) influence F₀ and soil CO₂ production (P_s). We focused on seasonal variation and used continuous measurements at a daily timescale across four vegetation types at 13 study sites to quantify: (1) differences in seasonal lags between soil CO₂ fluxes and T_s, θ, and GPP and (2) interactions and relationships between CO₂ fluxes with T_s, θ, and GPP. Mean annual T_s did not explain annual F₀ and P_s among vegetation types, but GPP explained 73% and 30% of the variation, respectively. We found evidence that lags between soil CO₂ fluxes and T_s or GPP provide insights into the role of plant phenology and information relevant about possible timing of controls of autotrophic and heterotrophic processes. The influences of biophysical factors that regulate daily F₀ and P_s are different among vegetation types, but GPP is a dominant variable for explaining soil CO₂ fluxes. The emergence of long-term automated soil CO₂ flux measurement networks provides a unique opportunity for extended investigations into F₀ and P_s processes in the near future.

Key words: lags; moderate-resolution imaging spectroradiometer (MODIS); photosynthesis; soil CO₂ efflux; soil CO₂ production; soil CO₂ sensors; soil respiration.

INTRODUCTION

Understanding the factors that influence patterns of terrestrial CO₂ fluxes across the globe is essential to predict and manage the effects of the human carbon footprint (Magnani et al. 2007). Soil CO₂ efflux (or soil respiration; F₀) constitutes a significant (10–90%) component of CO₂ fluxes from terrestrial ecosystems (Hanson et al. 2000), but the mechanistic understanding of F₀ remains unclear because of the complexity of processes involved. Here we present a synthesis study of the application of continuous automated measurements of soil CO₂ fluxes to identify lags and relationships among biophysical variables. Long-term continuous measurements provide an opportunity to understand how biophysical factors interact to regulate terrestrial CO₂ fluxes and provide an opportunity to explore the timing of biophysical controls on F₀. The application of continuous measurements of multiple biophysical variables will increase with the growth of environmental networks across multiple vegetation types (e.g., FLUXNET, National Ecological Observatory Network [NEON], Integrated Carbon Observation System [ICOS]).

Soil CO₂ efflux provides information about the interaction between soil processes and the atmosphere as an integrated result of biological CO₂ production at the soil surface and changes in soil CO₂ diffusivity in the soil profile. It is the result of the combined contribution of CO₂ production (P_s) in the soil by autotrophic (roots and mycorrhizae) and heterotrophic (decomposers)
components (Hanson et al. 2000, Ryan and Law 2005) and diffusion of CO$_2$ through the porous medium. The diffusion of CO$_2$ in the soil is a function of exogenous factors that affect porosity and tortuosity, such as soil moisture, soil texture, and bulk density (Šimůnek and Suarez 1993, Moldrup et al. 1999, Pumpenan et al. 2003). Consequently, $P_s$ provides information on biological activity because it represents the combined contribution of the autotrophic and heterotrophic components in the soil (Hanson et al. 2000, Ryan and Law 2005). Variation in $P_s$ is mainly dependent on changes in root density, microbial community composition, quality and quantity of soil carbon pools, and photosynthetic activity (Kuzyakov 2006).

The influences of soil temperature ($T_s$) and soil water content ($θ$) have consistently been used to explain variation in $F_0$ at different temporal scales among vegetation types (e.g., Davidson et al. 2000, Curiel Yuste et al. 2003, Reichstein et al. 2003, Ma et al. 2005), and previous reviews have examined the influence of $T_s$ and $θ$ on $F_0$ (Raich et al. 2002, Hibbard et al. 2005, Ryan and Law 2005, Davidson and Janssens 2006). However, in most cases, previous studies have been based on manual CO$_2$ soil chamber measurements that miss multiple days of the year, night measurements, and precipitation events.

Recent technological advances with automated soil respiration chambers have greatly improved the time resolution of $F_0$ measurements (Goulden and Crill 1997, Drewitt et al. 2002, Irvine and Law 2002, Savage and Davidson 2003, Carbone et al. 2008). Alternatively, continuous belowground CO$_2$ concentration measurements using solid-state CO$_2$ sensors provide another method (flux-gradient method) for automated measurement of $F_0$ and $P_s$ (Hirano et al. 2003, Jassal et al. 2004, Tang et al. 2005b, Pumpenan et al. 2008, Vargas and Allen 2008a). The flux gradient method has the advantage that $F_0$, soil CO$_2$ flux at depth $i$ ($F_i$), and $P_s$ can be calculated and compared with other methods (e.g., $F_0$ measured using the soil chamber method). Because of the challenge of measuring soil processes, only a few studies have investigated $F_i$ and $P_s$ (Davidson and Trumbore 1995, Hashimoto and Suzuki 2002, Takahashi et al. 2004, Fierer et al. 2005, Jassal et al. 2005, Pumpenan et al. 2008, Vargas and Allen 2008c), particularly with regard to variation in $T_s$ (Risk et al. 2002, Hashimoto and Komatsu 2006).

Here we used measurements obtained by autochambers and solid-state CO$_2$ sensors in the soil profile to calculate $F_0$ and $P_s$ in four vegetation types at 13 study sites. We concentrated on seasonal variation using mean daily values derived from continuous measurements that captured the seasonal influence of phenology (DeForest et al. 2006), temperature and water (Irvine and Law 2002), and photosynthesis (Högberg et al. 2001, Tang et al. 2005a, Bahn et al. 2009) on soil CO$_2$ fluxes. We investigate the influence of photosynthesis on $F_0$ and $P_s$ among vegetation types using values of gross primary production (GPP) derived from NASA’s moderate-resolution imaging spectroradiometer (MODIS; Running et al. 2004). We used GPP derived from MODIS because not all the sites included in this study have instrumentation of eddy covariance towers to measure GPP. (For a description of the eddy covariance network FLUXNET, see Baldocchi [2008].)

This study is novel in that it uses a unique data set on long-term continuous measurements of $F_0$ and $P_s$ across multiple vegetation types to better understand how biophysical factors regulate soil CO$_2$ fluxes. An advantage of measuring soil CO$_2$ fluxes continuously with automated systems is the possibility to quantify lags between environmental variables and CO$_2$ fluxes (Baldocchi et al. 2006, Gaumont-Guay et al. 2006, Liu et al. 2006, Vargas and Allen 2008a). Using this information we ask two interrelated questions: (1) Are there seasonal lags between $F_0$ and $T_s$, GPP, or $θ$, and if so, do these lags differ among sites and vegetation types? (2) What are the relationships and interactions among $F_0$, $T_s$, $θ$, and GPP within different vegetation types?

Here we test three related hypotheses. $H_1$: Mean annual GPP (derived from MODIS) would be a better predictor of mean annual $F_0$ and $P_s$ than mean annual $T_s$ (measured in situ) across vegetation types. There is increasing evidence of the importance of GPP at multiple vegetation types (Janssens et al. 2001, Reichstein et al. 2003, Bahn et al. 2008), and it is relevant to explore the relationships between remote-sensing estimations and in situ measurements. $H_2$: Lags between $F_0$ and $T_s$ or GPP can provide insights about possible timing of processes associated with autotrophic and heterotrophic components of $F_0$ (e.g., Braswell et al. 1997, McDowell et al. 2004, Baldocchi et al. 2006). We postulate that if $F_0$ increases with $T_s$ and GPP (i.e., in phase with zero lags) there may be a synchronized temporal contribution of autotrophic and heterotrophic activity at the seasonal scale. In contrast, if $F_0$ increases before $T_s$ (i.e., out of phase with positive lags) but after GPP (i.e., out of phase with positive lags) there may be different temporal controls for autotrophic and heterotrophic activity at the seasonal scale. The mechanisms that regulate lags at the seasonal scale could be driven by the different contributions of autotrophic and heterotrophic respiration, which are influenced by plant phenology (DeForest et al. 2006), photosynthesis (McDowell et al. 2004, Baldocchi et al. 2006, Bahn et al. 2009), and rhizosphere dynamics (Bahn et al. 2006, Gaumont-Guay et al. 2008, Vargas and Allen 2008c). $H_3$: The influence of biophysical factors on regulating daily $F_0$ and $P_s$ is different among vegetation types, but general patterns may emerge, providing insights into the mechanisms that control soil CO$_2$ fluxes.

**Materials and Methods**

**Study sites**

We included data from 13 sites in which in situ solid-state soil CO$_2$ sensors are being used and all but two data
sets have been previously published in individual studies (Table 1). Sites were located in six countries between latitudes 61°50' N and 21°12' N and an altitudinal range from 70 to 1850 m above sea level. Mean annual temperatures ranged from 3° to 24°C, and annual precipitation ranged from 250 to 1650 mm (Table 2). All sites measured soil CO\textsubscript{2} concentrations at three or more depths except one grassland site that used automated soil respiration chambers in combination with two soil CO\textsubscript{2} sensors (Table 3). We grouped the study sites by vegetation types including three deciduous forests (DF), four evergreen coniferous forests (ECF), four grasslands (GRA), and two mixed forests (MF; see Table 1). This categorization classification follows physiological and morphological traits, and in most cases grouped sites share similar mycorrhizal associations. Furthermore, the characteristics of evergreen, deciduous, deciduous mixed forest, and grassland are observable from remote-sensing platforms (e.g., MODIS) and are key ecological properties for the determination of photosynthesis and respiration. The results from this study must be corroborated in the future using a larger network of sites with continuous measurements of soil CO\textsubscript{2} fluxes across multiple climatic zones and vegetation types.

**Field measurements of soil CO\textsubscript{2} concentrations**

Soil CO\textsubscript{2} measurements were collected between 2000 and 2007, depending on the study site; dates used in this study are reported in Table 3. At each site, soil CO\textsubscript{2} was continuously measured (mean hourly values) with Vaisala CARBOCAP CO\textsubscript{2} sensors (models GMM 222, GMT 222, GMD 20, or GMP 343; Vaisala, Helsinki, Finland) at multiple depths ranging between 0 and 50 cm (see Table 3). These small silicon-based CO\textsubscript{2} sensors operate on the nondispersive infrared (NDIR) single-beam dual-wavelength principle. The sensors were calibrated periodically against reference gases, and calibration details are reported in the main references for each site (Table 1). In most cases, the sensors were protected either with microporous Teflon tubing or Gore-Tex fiber to avoid possible wetting during rainfall events while allowing free gas exchange. Soil temperatures (in degrees Celsius) were measured at the same depths at which the CO\textsubscript{2} sensors were installed. Soil water content (in cubic meters per cubic meter) was measured either at the same depth as the CO\textsubscript{2} sensors or within the range of their deployment (e.g., 2–16 cm depth). Values of concentration of CO\textsubscript{2} were automatically corrected for temperature in the case of the GMP 343 sensors and corrected for temperature (other than the GMP 343) and pressure using the ideal gas law according to the manufacturer (Vaisala, Helsinki, Finland). To reduce noise of measured CO\textsubscript{2} concentrations being amplified in the calculation of \( F_0 \) and \( P_0 \), we applied a Savitzky-Golay smoothing filter, which preserves peak heights and widths of the original signal. A similar approach was used by Vargas et al. (in press) for continuous measurements of CO\textsubscript{2} concentrations.

**Soil CO\textsubscript{2} efflux and soil CO\textsubscript{2} production**

Soil CO\textsubscript{2} efflux values were obtained using automated soil respiration chambers (sites DF49, HDF88, Hyy, and Stu) or the flux gradient method (for the remaining sites; Table 3). Soil CO\textsubscript{2} production values were calculated from soil CO\textsubscript{2} concentrations using the flux gradient method in all sites. The flux gradient method has been verified using the soil chamber method at each site and is discussed in the main sources for each site (Table 1). Automated soil respiration chambers have been widely used for several years (Drewitt et al. 2002, Savage and Davidson 2003, Pumpanen et al. 2004), and descriptions of these systems at each study site are also available in the main sources provided in Table 1.

When \( F_0 \) or \( P_0 \) values were calculated with soil CO\textsubscript{2} concentrations we used flux gradient theory (DeJong and Schapper 1972). This method is based on Fick’s law of diffusion:

\[
F = -D_s \frac{\partial C}{\partial z}
\]

where \( F \) is the flux density of CO\textsubscript{2} (in micromoles per square meter per second), \( D_s \) is the gaseous diffusion coefficient of CO\textsubscript{2} in the soil (i.e., soil CO\textsubscript{2} diffusivity in square meters per square second), and \( \frac{\partial C}{\partial z} \) is the rate of change of the molar CO\textsubscript{2} concentration (in micro- moles per cubic meter) with depth \( z \) (i.e., the vertical gradient of soil CO\textsubscript{2} concentration). \( D_s \) can be estimated as

\[
D_s = D_a \varepsilon \tau
\]

where \( D_a \) is the CO\textsubscript{2} molecular diffusivity of CO\textsubscript{2} in air, \( \varepsilon \) is the soil air-filled porosity, and \( \tau \) is the tortuosity. The product of \( \varepsilon \tau \) has been defined as the tortuosity factor \( \xi \) (Jury et al. 1991), so that

\[
D_s = D_a \xi.
\]

The effect of temperature and pressure on \( D_a \) is given by

\[
D_a = D_{a0} \left( \frac{T}{T_0} \right)^{1.75} \left( \frac{P_0}{P} \right)
\]

where \( D_{a0} \) is a reference value of \( D_a \) (1.47 \times 10^{-5} \text{ m}^2/\text{s}) at \( T_0 \) (293.15 K) and \( P_0 \) (1.013 \times 10^5 \text{ Pa}) according to Jones (1992). The tortuosity factor can be calculated using several general models (e.g., Moldrup et al. 1999) or measured and evaluated from an empirical relationship developed for each study site (see Hirano et al. 2003, Pumpanen et al. 2003, Jassal et al. 2005). An accurate determination of the diffusivity factor is essential because CO\textsubscript{2} fluxes are influenced by soil moisture, soil texture, and soil bulk density, all of which affect the diffusivity. In this study, we used the site-specific \( \xi \) for sites DF49, HDF88, JP1, JP2, Hyy, and we used the Moldrup model (Moldrup et al. 1999) for the remaining study sites. Although site-specific measurement of the diffusivity is the recommended method, previous studies have found good agreement between \( F_0 \) calculated using
Table 1. Ancillary information of sites included in this study.

<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>Site name</th>
<th>Site ID</th>
<th>Latitude, longitude</th>
<th>Country</th>
</tr>
</thead>
<tbody>
<tr>
<td>DF</td>
<td>Hyytialla</td>
<td>Hyy</td>
<td>61°50’ N, 24°17’ E</td>
<td>Finland</td>
</tr>
<tr>
<td>ECF</td>
<td>Blodgett Forest</td>
<td>Blo</td>
<td>38°53’ N, 120°37’ W</td>
<td>USA</td>
</tr>
<tr>
<td></td>
<td>James Reserve</td>
<td></td>
<td>33°48’ N, 116°46’ E</td>
<td>USA</td>
</tr>
<tr>
<td>GRA</td>
<td>Tonzi Ranch</td>
<td>TonO</td>
<td>38°43’ N, 120°96’ W</td>
<td>USA</td>
</tr>
<tr>
<td>MF</td>
<td>Broadleaf forest</td>
<td>JPI</td>
<td>42°44’ N, 141°44’ E</td>
<td>Japan</td>
</tr>
<tr>
<td></td>
<td>DF49</td>
<td>DF49</td>
<td>49°51’ N, 125°19’ W</td>
<td>Canada</td>
</tr>
<tr>
<td></td>
<td>HDF88</td>
<td>HDF88</td>
<td>49°51’ N, 124°54’ W</td>
<td>Canada</td>
</tr>
<tr>
<td></td>
<td>Larch forest</td>
<td>JPI</td>
<td>42°44’ N, 141°31’ E</td>
<td>Japan</td>
</tr>
<tr>
<td>GRA</td>
<td>Sevilleta LTER</td>
<td>Sev</td>
<td>34°20’ N, 106°43’ W</td>
<td>USA</td>
</tr>
<tr>
<td></td>
<td>Stubai Valley</td>
<td>Stu</td>
<td>47°07’ N, 11°19’ E</td>
<td>Austria</td>
</tr>
<tr>
<td>DF</td>
<td>El Eden</td>
<td>Eden</td>
<td>21°12’ N, 87°11’ W</td>
<td>Mexico</td>
</tr>
</tbody>
</table>

Note: Abbreviations are: DF, deciduous forest dominated by woody vegetation with percent cover >60% and height >2 m and an annual cycle of leaf-on and leaf-off periods; ECF, evergreen coniferous forest land dominated by woody vegetation with percent cover >60% and height >2 m and most trees remain green all year; GRA, grasslands with herbaceous cover, with tree and shrub cover <10%; MF, mixed forests dominated by a mosaic of deciduous and evergreen trees with percent cover >60% and height >2 m; LTER, Long Term Ecological Research center.

Table 2. Climate and soil characteristics of sites included in this study.

<table>
<thead>
<tr>
<th>Site name</th>
<th>Site ID</th>
<th>Elevation (m)</th>
<th>MAP (mm)</th>
<th>MAT (°C)</th>
<th>Soil type</th>
<th>Sand (%)</th>
<th>Silt (%)</th>
<th>Clay (%)</th>
<th>Bulk density (Mg/m³)</th>
<th>Soil porosity (m³/m³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hyytialla</td>
<td>Hyy</td>
<td>181</td>
<td>709</td>
<td>3.8</td>
<td>Haplic podzol</td>
<td>69.2</td>
<td>20</td>
<td>10.8</td>
<td>0.6</td>
<td>0.61</td>
</tr>
<tr>
<td>Blodgett Forest</td>
<td>BloC</td>
<td>1315</td>
<td>1290</td>
<td>9</td>
<td>Ultic haploxeralf</td>
<td>60</td>
<td>28</td>
<td>12</td>
<td>0.58</td>
<td>0.78</td>
</tr>
<tr>
<td>James Reserve</td>
<td>JRh</td>
<td>1640</td>
<td>507</td>
<td>10.3</td>
<td>Entisol</td>
<td>83</td>
<td>10</td>
<td>7</td>
<td>0.9</td>
<td>0.66</td>
</tr>
<tr>
<td></td>
<td>JRw</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.2</td>
<td>0.55</td>
</tr>
<tr>
<td>Tonzi Ranch</td>
<td>TonO</td>
<td>177</td>
<td>562</td>
<td>16.5</td>
<td>Lithic haploxerepts</td>
<td></td>
<td></td>
<td></td>
<td>48</td>
<td>0.38</td>
</tr>
<tr>
<td></td>
<td>TonU</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>37.5</td>
<td>45</td>
<td>17.5</td>
<td>1.58</td>
<td>0.4</td>
</tr>
<tr>
<td>Broadleaf forest</td>
<td>JPI</td>
<td>70</td>
<td>1200</td>
<td>6.5</td>
<td>Volcanogenous regosol</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>0.42</td>
<td>0.8</td>
</tr>
<tr>
<td></td>
<td>DF49†</td>
<td>300</td>
<td>1320</td>
<td>8.3</td>
<td>Humo-ferric podzol</td>
<td>69.3</td>
<td>22.6</td>
<td>8.1</td>
<td>1.05</td>
<td>0.6</td>
</tr>
<tr>
<td>HDF88‡</td>
<td>HDF88</td>
<td>170</td>
<td>1550</td>
<td>9.6</td>
<td>Humo-ferric podzol</td>
<td>85.6</td>
<td>13.1</td>
<td>1.3</td>
<td>1.5</td>
<td>0.43</td>
</tr>
<tr>
<td>Larch forest</td>
<td>JPI</td>
<td>140</td>
<td>1250</td>
<td>7.3</td>
<td>Volcanogenous regosol</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>0.46</td>
<td>0.86</td>
</tr>
<tr>
<td>Sevilleta LTER</td>
<td>Sev</td>
<td>1600</td>
<td>250</td>
<td>13.2</td>
<td>Typic Haplargids</td>
<td>68</td>
<td>22</td>
<td>10</td>
<td>1.51</td>
<td>0.43</td>
</tr>
<tr>
<td>Stubai Valley</td>
<td>Stu</td>
<td>1850</td>
<td>1097</td>
<td>3</td>
<td>Dystric cambisol</td>
<td>41.9</td>
<td>30.8</td>
<td>27.3</td>
<td>0.91</td>
<td>0.66</td>
</tr>
<tr>
<td>El Eden</td>
<td>Eden</td>
<td>10</td>
<td>1650</td>
<td>24.2</td>
<td>Histosol</td>
<td>63</td>
<td>22</td>
<td>15</td>
<td>0.61</td>
<td>0.77</td>
</tr>
</tbody>
</table>

Notes: Soils at JPI and JP2 are classified as sandy loam, which usually contains 65–85% sand and 0–35% silt, with mean values for sand (75%), silt (18%), and clay (7%). Abbreviations: NA, data not available; MAP, mean annual precipitation; MAT, mean annual temperature; LTER, Long Term Ecological Research center.

† The first set of soil characteristic values is for the 0–10 cm horizon; the second set of values is for the 10–50 cm horizon.
‡ The first set of soil characteristic values is for the 0–10 cm horizon; the second set of values is for the 10–60 cm horizon.
the soil chamber method and $F_0$ calculated using the flux gradient method of the Moldrup model (Tang et al. 2005b, Baldocchi et al. 2006, Vargas and Allen 2008a, b, c).

Assuming a constant rate of CO$_2$ production in the upper part of the soil profile, $F_0$ can be calculated as follows (Tang et al. 2005b):

$$F_0 = \frac{z_{i+1}F_i - z_iF_{i+1}}{z_{i+1} - z_i}$$  \hspace{1cm} (5)

where $F_0$, $F_i$, and $F_{i+1}$ are CO$_2$ effluxes (in micromoles per square meter per second) at depths $z_0$, $z_i$, and $z_{i+1}$ (in meters), respectively. This approach has been found to be more reliable than extrapolating the soil CO$_2$ concentrations to the soil surface and using the gradient between the surface and the first level or taking the derivative of the empirically fit concentration–depth curve at $z = 0$ (Amundson et al. 1998). The condition of constant CO$_2$ production in the upper part of the soil profile may not be entirely met in productive ecosystems where CO$_2$ production follows an exponential decay with depth. For each study site we estimated $F_i$ at two depths depending on where the CO$_2$ sensors were deployed (e.g., between 0.08 and 0.16 m; see Table 3).

Once $F_i$ has been calculated for different levels in the soil profile, $P_s$ can be calculated from the difference between the effluxes across adjacent levels as a flux divergence (Simůnek and Suarez 1993):

$$P_s = \frac{F_i - F_{i+1}}{z_{i+1} - z_i}$$  \hspace{1cm} (6)

where $P_s$ is the rate of soil CO$_2$ production (in micromoles per cubic meter per second) in the soil layer between depths $i$ and $i+1$ (Table 3), but the CO$_2$ storage term was ignored in this equation (see Hirano et al. 2003). We used the shallowest layer in which sensors have been installed to calculate $P_s$ (see Table 3), assuming that these shallow depths have the highest root density (see Jackson et al. 1996). All calculations of $F_0$ and $P_s$ were performed using mean hourly values and then averaged as daily mean values for further analyses reported in this study. Similarly, hourly values of $T_s$ and $0$ were averaged as mean daily values and analyses were done using these averages.

Gross primary production

On-site direct measurements of GPP are critical, but we were not able to use GPP derived from eddy covariance towers because not all the sites have these measurements. Thus, to represent the seasonal GPP trend in a systematic way, we used the value-added product derived from MODIS (Running et al. 2004). The product MOD17A2 was used for GPP values (Running et al. 2004), and previous studies have discussed in detail the validation of this product (Turner et al. 2005, Xiao et al. 2005, Zhao et al. 2005, Heinsch et al. 2006). We used MODIS Land Product

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**Table 1. Extended.**

<table>
<thead>
<tr>
<th>Dominant species</th>
<th>Site history</th>
<th>Main source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pinus sylvestris</td>
<td>prescribed burning in 1962</td>
<td>Pumpanen et al. (2008)</td>
</tr>
<tr>
<td>Pinus ponderosa</td>
<td>plantation established in 1990 after clear-cutting control plot</td>
<td>Tang et al. (2005b)</td>
</tr>
<tr>
<td>Bromus tectorum, Elymus elymoides</td>
<td>grazing</td>
<td>Baldocchi et al. (2006)</td>
</tr>
<tr>
<td>Quercus chrysolepis, Calocedrus decurrens, Pinus lambertiana, Arctostaphylos pringlei</td>
<td>natural forest growing after storm damage by a typhoon in 1954</td>
<td>Hirano et al. (2003)</td>
</tr>
<tr>
<td>Brachypodium distachyon, Bromus hordeaceus</td>
<td>slash-burned 1943, planted 1949</td>
<td>Jassal et al. (2005)</td>
</tr>
<tr>
<td>Pseudotsuga menziesii</td>
<td>the larch forest was planted in 1957–1959</td>
<td>Liang et al. (2004)</td>
</tr>
<tr>
<td>Larix kaemferi</td>
<td>human use and cattle grazing until 1973; since then, protected</td>
<td>S. L. Collins, unpublished data</td>
</tr>
<tr>
<td>Bouteloua eriopoda</td>
<td>organic fertilization one cut, grazed in late summer</td>
<td>M. Bahn, unpublished data</td>
</tr>
<tr>
<td>Alchemilla vulgaris, Anthoxanthum odoratum, Festuca rubra, Leontodon hispidus, Trifolium repens</td>
<td>natural forest growing after fire in 1989 and hurricane disturbance in 2005</td>
<td>Vargas and Allen (2008a)</td>
</tr>
</tbody>
</table>
Table 3. Method used to calculate soil respiration ($F_0$) and characteristics of soil CO$_2$ sensor deployments for calculation of soil CO$_2$ production ($P_s$) at the study sites.

<table>
<thead>
<tr>
<th>Site ID, by vegetation type</th>
<th>CO$_2$ sensor model</th>
<th>Period of measurements</th>
<th>Depth of CO$_2$ sensors (cm)</th>
<th>Depth of $P_s$ (cm)</th>
<th>$F_0$ calculation</th>
</tr>
</thead>
<tbody>
<tr>
<td>DF</td>
<td>Eden</td>
<td>GMM 222</td>
<td>1 Jan to 31 Dec 2005</td>
<td>2, 8, 16</td>
<td>8.5 (2) flux gradient</td>
</tr>
<tr>
<td>JP2</td>
<td>GMD 20</td>
<td>22 Jun 2001 to 22 Jun 2002</td>
<td>0, 2, 11, 13</td>
<td>4.3 (1) flux gradient</td>
<td></td>
</tr>
<tr>
<td>TonU</td>
<td>GCT 222</td>
<td>1 Apr 2003 to 16 Apr 2004</td>
<td>2, 8, 16</td>
<td>8.5 (1) flux gradient</td>
<td></td>
</tr>
<tr>
<td>ECF</td>
<td>Bla</td>
<td>GMT 222</td>
<td>3 May to 10 Oct 2005</td>
<td>2, 8, 16</td>
<td>8.5 (1) flux gradient</td>
</tr>
<tr>
<td>DF49</td>
<td>GMM 221</td>
<td>13 Mar to 30 Dec 2003</td>
<td>10, 20, 50</td>
<td>25 (3) automated chambers (6)</td>
<td></td>
</tr>
<tr>
<td>HDF88</td>
<td>GMM 221</td>
<td>28 Jul 2005 to 30 Jul 2006</td>
<td>5, 15, 50</td>
<td>21.3 (3) automated chambers (6)</td>
<td></td>
</tr>
<tr>
<td>Hyy</td>
<td>GMP 343</td>
<td>1 Aug 2004 to 17 Jul 2005</td>
<td>0, 5, 17, 27</td>
<td>6.8 (1) automated chambers (2)</td>
<td></td>
</tr>
<tr>
<td>GRA</td>
<td>JRh</td>
<td>GMM 222</td>
<td>1 Jan to 31 Dec 2006</td>
<td>2, 8, 16</td>
<td>8.5 (4) flux gradient</td>
</tr>
<tr>
<td>Sev</td>
<td>GMM 222</td>
<td>12 Jul to 24 Nov 2007</td>
<td>2, 8, 16</td>
<td>8.5 (3) flux gradient</td>
<td></td>
</tr>
<tr>
<td>Stu</td>
<td>GMM 222</td>
<td>20 Jul 2006 to 20 Jul 2007</td>
<td>5, 10</td>
<td>3.8 (3) automated chambers (1)</td>
<td></td>
</tr>
<tr>
<td>TonO</td>
<td>GMM 222</td>
<td>1 Apr 2003 to 16 Apr 2004</td>
<td>2, 8, 16</td>
<td>8.5 (1) flux gradient</td>
<td></td>
</tr>
<tr>
<td>MF</td>
<td>JP1</td>
<td>GMD 20</td>
<td>29 May 2000 to 20 May 2001</td>
<td>0, 2, 13, 17</td>
<td>4.3 (1) flux gradient</td>
</tr>
<tr>
<td>JRw</td>
<td>GMM 222</td>
<td>1 Jan 2005 to 31 Dec 2006</td>
<td>2, 8, 16</td>
<td>8.5 (4) flux gradient</td>
<td></td>
</tr>
</tbody>
</table>

Notes: $F_0$ was calculated with automated soil respiration chambers or using the flux gradient method. For details on sensor deployment and validation of flux gradients and automated chambers methods see sources in Table 1. Numbers in parentheses represent the number of replicates where $P_s$ was measured. At Stu, $F_0$ was used to calculate $P_s$. The flux gradient method has been validated with the chamber method, and calculated $F_0$ was calibrated spatially with manual and/or automated soil respiration chambers (see sources in Table 1). Abbreviations of vegetation types are: DF, deciduous forest; ECF, evergreen coniferous forest; GRA, grassland; MF, mixed forest. See Table 1 for details on each vegetation type.

Subsets for a $3 \times 3$ km grid at each study site using the average of all nine cells. These were derived from MODIS products generated with Collection 4 from the Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC). Details about preparation of subsets including MODIS data reprocessing, methods, and formats are available online.\textsuperscript{11} Temporal interpolation was used to replace pixels that have quality control flags indicating poor quality. The eight-day MODIS GPP values were extrapolated to daily GPP values (in grams of C per square meter per day) using a Savitzky-Golay smoothing filter. We hereafter refer to the values generated by the product MOD17A2 as GPP.

**Analysis of soil CO$_2$ efflux and production**

To test $H_1$, we calculated mean annual values of the time series of $T_s$, GPP, $F_0$, and $P_s$ for each study site and applied linear regression analysis across sites.

To explore the first question and $H_1$, we used an ordination approach using regression tree analysis (Breiman et al. 1984) to represent $F_0$ or $P_s$. We used daily mean values of $F_0$, $P_s$, $T_s$, GPP, and $\theta$ after including the lags calculated using cross-correlation between variables. Regression tree analysis selects variables that are best able to classify the response ($F_0$ or $P_s$) into distinct clusters through a process known as binary recursive partitioning. This is an iterative process of splitting the data into partitions using the predictor variable ($T_s$, $\theta$, or GPP) that explains the maximum amount of the remaining deviance in the response variable. A minimum node size of 10 was used, meaning no node with fewer than 10 data cases (or data points) was split (Breiman et al. 1984). The advantage of this method is that the tree structure enables interpretation of the explanatory nature of the independent variables. All data analyses were undertaken using MATLAB R2007a (MathWorks, Natick, Massachusetts, USA).

**RESULTS**

**Relationships between $F_0$ or $P_s$ and $T_s$ or GPP at the annual scale**

We did not find significant relationships ($P > 0.1$) between mean annual $T_s$ and mean annual $F_0$ or mean annual $P_s$ when compared among study sites (Fig. 1A, C).
In contrast, we observed a significantly positive relationship between mean annual GPP and mean annual $F_0$ ($P < 0.001$, $r^2 = 0.73$) with a slope of 1.44 $\pm$ 0.27 (mean $\pm$ SE); this positive relationship was also significant ($P < 0.05$) for deciduous and evergreen coniferous forest sites alone (Fig. 1B). We observed a marginally positive relationship between mean annual GPP and mean annual $P_s$ ($P = 0.056$, $r^2 = 0.30$) with a slope of 9.32 $\pm$ 4.4 among all sites, and this positive relationship was also significant ($P < 0.05$) when considering only deciduous and evergreen coniferous forest sites (Fig. 1D).

Cross-correlation analysis

Our results showed that significant ($P < 0.05$) negative lags between 52 and 25 d between $F_0$ and $T_s$ were associated with deciduous forests, indicating that $F_0$ increases before $T_s$ at these sites (Table 4). The largest negative lag was at the oak savanna site in California (TonU), with 52 d, followed by a tropical forest in Mexico (Eden), with 36 d. For mixed forests, the largest negative lag was at the California site (JRw), with 24 d. In contrast, for evergreen coniferous forests sites and grassland sites there were no lags, indicating that $F_0$ was in phase with $T_s$ (Table 4). We observed significant ($P < 0.05$) positive lags between 88 and 5 d between $F_0$ and GPP in deciduous and mixed forests, indicating that $F_0$ increases after GPP at these sites (Table 4). For deciduous forests sites, the largest positive lag was at Eden, with 88 d, followed by TonU. For mixed forest the California site (JRw) had a larger positive lag (29 d) than the Japan sites (5 d). For evergreen coniferous forests sites, we observed negative significant ($P < 0.05$) lags between $F_0$ and GPP, indicating that $F_0$ increases before GPP at these sites. The largest negative lag was at the Finland site (Hyy), with 24 d, followed by the Canadian site (15 d). In contrast, in grasslands sites, there were no lags, indicating that $F_0$ was in phase with GPP (Table 4). We analyzed the cross-correlations between $F_{0SC}$ and $\theta$ and found no lags ($F_{0SC}$ in phase with $\theta$) at any study site (Table 4). The cross-correlations for $P_s$ with $T_s$, GPP, or $\theta$ showed similar seasonal lags as those found for $F_0$ at all study sites.

We tested whether the relationship between $F_0$, $T_s$, and GPP showed lags based on changes in $\theta$. We found that $F_0$ and $T_s$ at evergreen coniferous forests and grassland sites were sensitive with negative lags ($F_0$ peaked before $T_s$) when $\theta$ was $>0.3$ m$^3$/m$^3$ (Fig. 2A). In contrast, the effect of changes in $\theta$ on lags between $F_0$
and GPP was evident when $\theta$ was $>0.25$ m$^3$/m$^3$ where evergreen coniferous forests and grasslands showed negative lags, deciduous forests showed positive lags, and mixed forests were not sensitive to changes in $\theta$ (Fig. 2B).

**Regression trees**

The regression trees for $F_0$ revealed that GPP was the most important parameter for separating high and low values of $F_0$ in deciduous and evergreen coniferous forest sites with critical values of 3.2 and 7.1 g C·m$^{-2}$·d$^{-1}$, respectively (Fig. 3A, B). We observed that the second most important variable for deciduous forests was $h$, but it was $T_s$ for evergreen coniferous forests. For grasslands, the most important parameter to separate high and low values of $F_0$ was $h$, with a critical value of 0.2 m$^3$/m$^3$, while GPP was the secondary variable (Fig. 3C). In contrast, soil temperature was the most important parameter to separate high and low values of $F_0$ in mixed forests (Fig. 3D). In all cases,
higher values of all parameters (when important at each node of the tree) discriminated in favor of higher values of $F_0$. The predicted values of the regression trees for deciduous forests, evergreen coniferous forests, grasslands, and mixed forests explained 67%, 73%, 37%, and 80% of the variance of $F_0$, respectively. The predicted values of all study sites explained 94% of the variance of all observations of daily $F_0$ (Fig. 4A).

The regression trees for $P_s$ revealed that GPP was the most important variable for deciduous forests, with a critical value of 4.4 g C m$^{-2}$ d$^{-1}$, while $\theta$ was a secondary variable associated with higher values of $P_s$ (Fig. 5A). For evergreen coniferous forests, $T_s$ was the most important parameter to separate high and low values of $P_s$ (critical value of 10$^\circ$C), while GPP was a secondary variable with critical values of 9.7 g C m$^{-2}$ d$^{-1}$ for high and 3.4 g C m$^{-2}$ d$^{-1}$ for low values of $P_s$ (Fig. 5B). Similarly, $T_s$ was the most important parameter to separate values of $P_s$ in mixed forests with a critical value of 13.1$^\circ$C, while $\theta$ was a secondary variable.

Fig. 3. Regression trees for daily mean soil respiration ($F_0$) values for: (A) deciduous forests, (B) evergreen coniferous forests, (C) grasslands, and (D) mixed forests. Terminal points of the tree indicate mean $F_0$ values of the cluster. Abbreviations are: GPP, gross primary production (g C m$^{-2}$ d$^{-1}$); $T_s$, soil temperature ($^\circ$C); and SWC, soil water content (m$^3$m$^{-3}$).

Fig. 4. Daily values of (A) predicted soil respiration ($F_0$) vs. observed $F_0$ from regression trees and (B) predicted soil CO$_2$ production ($P_s$) vs. observed $P_s$ from regression trees. The dotted line represents an exact 1:1 relationship; the solid line shows the linear regression of these data.
associated with higher values of $P_s$ (Fig. 5D). In contrast, $\theta$ was the most important variable in grasslands (critical value of 0.2 m$^3$/m$^3$), while GPP was a secondary variable (Fig. 5C). In all cases higher values of all parameters (when important at each node of the tree) discriminated in favor of higher values of $P_s$. The predicted values of the regression trees for deciduous forests, evergreen coniferous forests, grasslands, and mixed forests explained 47%, 33%, 22%, and 77% of the variance of $P_s$, respectively. Consequently, the overall predicted values of all study sites explained 43% of the variance of all observations of daily $P_s$ and underestimate higher values of $P_s$ (Fig. 4B).

**Discussion**

Are there seasonal lags between $F_0$ and $T_s$, $\theta$, or GPP, and if so, do these lags differ among vegetation types?

Biological systems respond to present and past input stimulus, thus processes regulating soil CO$_2$ fluxes can be studied as causal or non-anticipatory systems. Identifying lags is important to the understanding of the manner in which biophysical factors influence processes that regulate variation in terrestrial CO$_2$ fluxes (e.g., Braswell et al. 1997). Here, we focus on seasonal lags (cross-correlation analysis between two one-year-long time series), and our results support the hypothesis that lags between $F_0$ with $T_s$ and GPP provide insights into the role of plant phenology and potentially about the timing of processes associated with autotrophic and heterotrophic components of soil respiration at the seasonal scale.

Seasonal lags between $F_0$ and $T_s$ cause seasonal hysteresis effects that are evident in deciduous, evergreen coniferous, and mixed forest. The amplitude of the seasonal hysteresis and the lag between the time series may depend on the different timing and contributions of autotrophic and heterotrophic components of $F_0$ (Drewitt et al. 2002, Vargas and Allen 2008c). For example, seasonal soil CO$_2$ fluxes at deciduous and mixed forest sites responded after an increase in photosynthesis (positive lags with GPP) but before a peak in temperature (negative lags with $T_s$). Thus it is likely that at these sites the seasonal pattern of $F_0$ is driven first by a substantial increase in autotrophic activity (after inputs from GPP) followed by an increase in heterotrophic activity (after inputs from GPP and an increase in $T_s$). These results support previous observations in which photosynthesis (Baldocchi et al. 2006), phenology (DeForest et al. 2006), and root–rhizomorph dynamics (Burton et al. 1998, Vargas and Allen 2008c) played a role in regulating seasonal soil CO$_2$ fluxes at deciduous and mixed forest sites.

For evergreen coniferous forests (located at high altitudes or latitudes), $F_0$ increases in phase with $T_s$ but before GPP (Table 4). At these sites, the seasonal pattern of $F_0$ may be driven first by a substantial increase in autotrophic activity (after inputs from GPP), followed by an increase in heterotrophic activity (after inputs from GPP and an increase in $T_s$). These results support previous observations in which photosynthesis (Högberg et al. 2001) and temperature (Pumpanen et al. 2008) were found to regulate soil CO$_2$ fluxes in boreal forests.

For grasslands we observed that $F_0$ was in phase with seasonal variation in $T_s$ and GPP because soil CO$_2$ fluxes respond rapidly to changes in photosynthesis and...
influence the intra-seasonal time lags between
and biogeochemical models to better represent the
them in multiple vegetation types.
identify lags at multiple temporal scales and to
2002, Jassal et al. 2008). Further research is needed to
their associated biophysical factors (Irvine and Law
sites across multiple climatic zones and vegetation types,
be regulated by a coupled seasonal timing of autotrophic
measurements can we clearly demonstrate the magnitude of the contribution of each component of soil CO2 fluxes.
We have discussed seasonal lags between soil CO2 fluxes and \( T_s \) or GPP during the year, but the temporal correlation between these variables could change at shorter timescales, depending on the season and changes in \( \theta \). We found that higher \( \theta \) values (>0.3 m^3/m^3) influence the intra-seasonal time lags between \( F_0 \) and \( T_s \) or GPP. These high values could be associated with periods of snowmelt and precipitation events that change the diffusivity of CO2 in the soil, increase nutrient solution in the soil, and influence the photosynthesis rates at the ecosystem scale (Huxman et al. 2004, Xu and Baldocchi 2004). High water levels can also constrain root and microbial metabolism by reducing oxygen availability for respiration. To understand water pulse dynamics it is important to understand how changes in \( \theta \) influence soil CO2 fluxes and their associated biophysical factors (Irvine and Law 2002, Jassal et al. 2008). Further research is needed to identify lags at multiple temporal scales and to understand the biophysical mechanisms that control them in multiple vegetation types.
We believe it is important to include lags in empirical and biogeochemical models to better represent the variation of soil CO2 fluxes. A simple example could be the modification of the empirical relationship between \( T_s \) and \( F_0 \) by including lags at the appropriate temporal scale:

\[
F_0 = B_0 \times \exp(B_1 \times T_s^{(k)})
\]

where \( T_s^{(k)} \) is the time series of \( T_s \) lagged by the appropriate time step (e.g., lag in days for a seasonal scale or lag in hours for a daily timescale). The inclusion of lags in seasonal estimations of \( F_0 \) based on \( T_s \) could reduce potential errors associated with diel and seasonal hysteresis effects (Vargas and Allen 2008c).

What are the relationships and interactions among \( F_0 \), \( T_s \), \( \theta \), and GPP within different vegetation types?
Our results showed that mean annual GPP was a good predictor for mean annual \( F_0 \) and \( P_s \) among our study sites. This result supports previous observations in which GPP overshadows \( T_s \) in determining soil and ecosystem respiration in European forest (Janssens et al. 2001), grasslands (Bahn et al. 2008), and among FLUXNET sites (Reichstein et al. 2003, Baldocchi et al. 2006). The fact that there was a strong relationship between \( F_0 \) and GPP derived independently from remote sensing provides motivation for further studies using GPP derived from remote-sensing platforms.

It is important to recognize that MODIS GPP values represent a different footprint than the site-specific measurements of CO2 fluxes; therefore future studies must require a dense spatial array of soil CO2 measurements to corroborate the results presented in this study. In most cases \( F_0 \) was calibrated spatially using manual soil respiration chambers (see references in Table 1), but may not fully represent the MODIS subset in which GPP was estimated. This is a current challenge as there is a trade-off between frequency of measurements (e.g., daily) and spatial coverage (e.g., plot level vs. landscape) that is limited by human resources, electrical power, and budget. Despite these limitations our results encourage the application of MODIS products for the estimation of soil CO2 fluxes at large geographical distances. Further studies should compile larger data sets and test these observations among sites with different soil, vegetation, and climatic conditions that could help in future global estimates of soil CO2 fluxes.

Cross-correlation analysis showed distinct time lags for each vegetation type, providing insights about the timing of soil CO2 processes. We applied respective lags in the time series, and regression tree analyses showed that the dominant environmental factors influencing soil CO2 fluxes differ between vegetation types. Using daily values, we found that GPP was the dominant variable explaining the variance in \( F_0 \) for deciduous and evergreen coniferous forests, but was the second most important variable for grasslands. In contrast, \( T_s \) was the main variable for mixed forests while \( \theta \) was the dominant variable for grasslands as these are mainly from arid or semiarid regions (but see Bahn et al. 2008). It is known that in arid and Mediterranean ecosystems, precipitation pulses dictate microbial dynamics influencing CO2 fluxes (Ogle and Reynolds 2004, Xu et al. 2004, Kurc and Small 2007, Collins et al. 2008). However, for the mesic grassland site (Stu) GPP was the main regulator of soil CO2 fluxes (data not shown), supporting the importance of this variable in temperate mesic grasslands (Bahn et al. 2008). From regression trees, we could generalize that increased GPP is linked with higher soil CO2 fluxes, and when \( T_s \) and \( \theta \) are relevant, they also promote higher values of \( F_0 \) and \( P_s \) among all vegetation types.

Although we found similar patterns and relationships that regulate \( F_0 \) and \( P_s \), a low percentage of the variance (43%) in \( P_s \) was explained by regression trees in comparison with the 90% explained for \( F_0 \). We present two complementary explanations: (1) parameters other than \( T_s \), GPP, and \( \theta \) are needed to explain the variance in \( P_s \), and (2) there is a larger mismatch between GPP and \( P_s \) because it is difficult to spatially average biophysical processes that act deeper in the soil.
Because $P_a$ is a measurement of biological activity, we postulate that other unmeasured factors, likely of biological origin, may not be fully explained by GPP, $T_a$, and $\theta$ alone (Kuzyakov 2006). Previous studies have shown that fine roots and mycorrhizal rhizosphere dynamics (Missen et al. 2006, Heinemeyer et al. 2007, Gaumont-Guay et al. 2008, Vargas and Allen 2008c) and substrate supply and nutrient availability (Schimel et al. 1994, Ruess et al. 2003) are other biological drivers that influence $P_a$. To date we do not have a common biological variable (other than GPP) among sites (e.g., root production, microbial biomass) that could allow us to test this hypothesis. It is a current challenge to spatially average the biophysical processes that interact deeper in the soil profile, but this information is critical for improving climate models as these processes could influence the regional climate (Lee et al. 2005).

Limitations and future considerations

To better understand the drivers of soil CO2 fluxes, it is necessary to study the distribution of $P_a$ in the soil profile. Although we assumed a constant $P_a$ with soil depth and analyzed $P_a$ values calculated for a shallow depth with higher root density zones, future studies should determine the depth of maximum CO2 production. This is why it is critical to look deeper into the soil to understand the biophysical drivers of $P_a$ suggested in this study. Multiple CO2 sensors in the soil profile allow the calculation of $P_a$ at multiple depths to understand the different contributions over the soil profile (Hashimoto and Suzuki 2002, Hirano et al. 2003, Jassal et al. 2005, Davidson et al. 2006). High spatial sampling resolution is important to understand vertical and horizontal variation in $F_o$ and $P_a$ (Vargas and Allen 2008a, c), especially in complex terrains (Riveros-Iregui et al. 2008). Furthermore, measurement points should follow indicators of biological activity (e.g., maximum root biomass or maximum rooting depth) or biophysical transitions in the soil (e.g., soil horizons) associated with $T_a$ and $\theta$ measurements to better interpret $P_a$ at individual sites or across sites (Pumpanen et al. 2008). We recognize that the flux-gradient method is not always the most appropriate method to estimate $F_0$ in all conditions, and more studies are needed to compare methods and calculate $P_a$ at multiple depths. However, values of $F_0$ obtained using different methods (autochambers vs. flux gradient method) have been shown to yield similar results within the sites included in this study (Tang et al. 2003, 2005b, Liang et al. 2004, Jassal et al. 2005, Baldocchi et al. 2006, Pumpanen et al. 2008, Vargas and Allen 2008a, b, c).

Finally, studies that incorporate complementary measurements are needed to understand the controls of $P_a$ on $F_0$. Examples are the combination of soil CO2 concentration measurements with soil respiration autochambers (Jassal et al. 2005, 2008, Pihlatie et al. 2007), eddy covariance towers (Baldocchi et al. 2006), minirhizotron measurements (Missen et al. 2006, Vargas and Allen 2008b, c), or the possibility of incorporating analyses of natural abundance of radiocarbon (Carbone et al. 2008) and stable isotopes (Bahn et al. 2009) in soil CO2 fluxes. With increasing interest in wireless networks (Allen et al. 2007, Porter et al. 2009) and the emergence of long-term automated soil sensor networks as a result of continental monitoring programs (e.g., FLUXNET, NEON, ICOS), complex spectral analysis of continuous biometeorological measurements can be applied (Vargas et al., in press). We expect that these regional networks and future analyses will provide critical data and input parameters for testing process-based models among multiple vegetation types.

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Literature Cited


