How switches and lags in biophysical regulators affect spatial-temporal variation of soil respiration in an oak-grass savanna

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Complex behavior, associated with soil respiration of an oak-grass savanna ecosystem in California, was quantified with continuous measurements of CO₂ exchange at two scales (soil and canopy) and with three methods (overstory and understory eddy covariance systems, soil respiration chambers, and a below-ground CO₂ flux gradient system). To partition soil respiration into its autotrophic and heterotrophic components, we exploited spatial gradients in the landscape and seasonal variations in rainfall. During the dry summer, heterotrophic respiration was dominant in the senesced grassland area, whereas autotrophic respiration by roots and the feeding of microbes by root exudates was dominant under the trees. A temporal switch in soil respiration occurred in the spring. But the stimulation of root respiration lagged the timing of leaf-out by the trees. Another temporal switch in soil respiration occurred at the start of autumn rains. This switch was induced by the rapid germination of grass seed and new grass growth. Isolated summer rain storms caused a pulse in soil respiration. Such rain events stimulated microbial respiration only; the rain was not sufficient to replenisih soil moisture in the root zone or to germinate grass seed. Soil respiration lagged photosynthetic activity on hourly scales. The likely mechanism is the slow translocation of photosynthate to the roots and associated microbes. Another lag occurred on daily scales because of modulations in photosynthesis and stomatal conductance by the passage of dry and humid air masses.


1. Introduction

How soil respiration will respond to changes in temperature, soil moisture and carbon pools remains a critical question for assessing the carbon balance of ecosystems [Gower, 2003; Granier et al., 2000; Hanson et al., 2004; Law et al., 2003] and for quantifying feedbacks on the climate system [Cox et al., 2000; Friedlingstein et al., 2003; Sitch et al., 2005]. In general, rates of soil respiration are modulated by a large set of edaphic (soil texture, temperature and moisture, carbon and nitrogen content), physiological (photosynthesis), functional (plant functional type, phenological and reproductive stage) and structural (leaf area index) factors [Hanson et al., 2000; Hogberg et al., 2001; Norman et al., 1992; Ryan and Law, 2005]. Additional complications in predicting rates of soil respiration are introduced by the differential and nonlinear responses to environmental perturbations by the soil's autotrophic and heterotrophic respiratory components [Hanson et al., 2000; Raich and Schlesinger, 1992], biophysical switches (leaf-out, senescence, snow, drought) [Granier et al., 2000; Wilson and Baldocchi, 2001] and pulses (rain) [Borken et al., 2003; Huxman et al., 2004; Irvine and Law, 2002; Jassal et al., 2005; Lee et al., 2004; Xu et al., 2004].

[2] In principle, heterotrophic soil respiration increases exponentially with soil temperature and its basal rate, at a reference temperature, is inhibited by extremely dry or wet soil conditions [Hanson et al., 2000; Kelliher et al., 2004; Orchard and Cook, 1983]. Basal rates of heterotrophic respiration also vary as a function of the age and type (e.g., digestibility) of the organic matter in the soil [Gleixner et al., 2005; Grayston et al., 1997; Kelliher et al., 2004; Trumbore, 2000].

[3] Autotrophic soil respiration is a direct consequence of root respiration, so it is coupled to rates of photosynthesis. In practice, it is difficult to disentangle and measure the effect of photosynthesis on autotrophic respiration because root exudates feed microbes, influencing the relative fraction of heterotrophic respiration [Bowling et al., 2002; Gleixner et al., 2005; Grayston et al., 1997; Tang et al., 2005]. Consequently, most relevant studies examine links between soil respiration and photosynthesis, together [Kuzmakov and Larionova, 2005].

[4] The coupling between soil respiration and photosynthesis depends on the timescale at which the two variables are correlated with one another. On annual timescales, soil respiration correlates with gross primary productivity (GPP)
[Janssens et al., 2001; Raich and Tufekciogul, 2000]. On daily to weekly timescales, soil respiration is sensitive to antecedent rates of photosynthesis. Hogberg et al. [2001], for example, girdled a cohort of trees to disrupt the supply of photosynthate to their roots. They reported that a significant reduction in soil respiration occurred five days after the cessation of photosynthesis. Bowling et al. [2002] and McDowell et al. [2004] examined the linkage between soil respiration and natural modulations in photosynthesis—they were imposed by temporal variations in humidity deficits. These cited authors found that daily to weekly variations in photosynthesis were followed by a 5 to 10 day lag in the isotopic signature of soil respiration. More recently, Tang et al. [2005] measured photosynthesis and soil respiration simultaneously, on hourly timescales, and found that soil respiration lagged variations in carbon supply by several hours.

[6] Horizontal and vertical gradients in biophysical drivers of soil respiration will impose spatial variation in soil respiration [Curiel-Yuste et al., 2004; Davidson et al., 1998; Irvine and Law, 2002; Qi and Xu, 2001; Tang and Baldocchi, 2005]. Horizontal and vertical variations in soil respiration are contingent upon how the population of roots, fungi and microbes, and their controlling edaphic variables vary in space [Belnap et al., 2003; Gleixner et al., 2005]. Small-scale variance is produced by respiratory ‘hot spots’ that are associated with clusters of microbes on soil grains, along soil pores, by roots and associated mychorrhizae, and channels formed by vertebrates and invertebrates [Belnap et al., 2003]. At the landscape-scale geographical position of plants and the transition of ensembles of plants into communities and ecosystems causes spatial variation in soil respiration. Spatial switches in the controls and magnitude of soil respiration can be expected as one moves across a landscape between open spaces and the vicinity of plants [Tang and Baldocchi, 2005]. Vertical variations in the production of CO₂ will occur because root [Jackson et al., 1996] and microbial presence and activity, soil temperature and moisture vary with soil depth [Hirsch et al., 2004; Jassal et al., 2004].

[7] The overarching goal of this paper is to quantify how switches and lags in biophysical regulators affect spatial-temporal variations of soil respiration in an oak-grass savanna ecosystem in California. Our experimental approach involves continuous measurements of CO₂ exchange at two scales (soil and canopy) and with three methods (overstory and understory eddy covariance systems, soil respiration chambers and a below-ground, CO₂ flux gradient system).

[8] We use natural spatial gradients in canopy structure and the landscape and seasonal variations in rainfall to partition soil respiration into its autotrophic and heterotrophic components. Californian savanna ecosystems are amenable to this approach. They comprise widely spaced trees, separated by isolated grass patches that are minimally affected by neighboring tree roots [Tang and Baldocchi, 2005]. The natural gradient approach is most capable of separating autotrophic and heterotrophic respiration during the long dry summers when the annual grasses are dead. Then, the predominant source of respiration in open spaces comes from microbial respiration of decaying organic matter. In contrast respiration under the photosynthesizing trees represents the sum of autotrophic respiration by roots and heterotrophic respiration associated with the microbial consumption of root exudates, mychorrhizae, invertebrate metabolism and the decomposition of dead organic matter. To a first-order approximation, we can evaluate the dynamics and magnitude of root respiration by subtracting soil respiration measurements made under a tree from those in the open area. The advantage of the natural gradient approach is its minimal disturbance of the system, as opposed to girdling and trenching studies [Kuzyakov and Larionova, 2005]. Albeit, potential artifacts will exist because of differences in stores of carbon, soil moisture, temperature and texture under the trees and in the open. However, they are minor [Tang and Baldocchi, 2005] and they should not affect the dynamical responses that we report.

[9] With this integrated and continuous measurement approach we have the unique ability to quantify lags between autotrophic respiration and canopy photosynthesis using inverse Fourier transforms [Press et al., 1988]. We are also able to observe and infer switches in the partitioning of soil respiration by autotrophic or heterotrophic respiration that are associated with the landscape and with seasonal changes in soil moisture and phenology and by episodic rain pulses. Information on the pulse dynamics of ecosystem respiration have been assessed in a previous paper [Xu et al., 2004].

2. Site Description

[10] The study was conducted at a pair of field sites located on the lower foothills of the Sierra Nevada Mountains near Ione, California. The study sites are members of the AmeriFlux and FLUXNET networks. The oak savanna field site (Tonzi Ranch) is located at 38.4311°N, 120.966°W. The altitude of the site is 177 m and the terrain is relatively flat. The companion site (Vaira Ranch) is an annual grassland, that is 2 km away (latitude: 38.4133°N; longitude: 120.9508°W; altitude: 129 m). The grassland study started in October, 2000 and the savanna study started in April, 2001.

2.1. Vegetation Characteristics

[11] The woodland overstory consists of scattered blue oak trees (Quercus douglasii) and occasional grey pine trees (Pinus sabiniana). The understory landscape is managed; the rancher removes brush and cattle graze the grass and herbs. The understory consists of exotic annual grasses and herbs; the species include Brachypodium distachyon, Hypochaeris glabra, Bromus madritensis, and Cynosurus echinatus.

[12] A demographic survey on stand structure of the oak woodland was conducted using a multireturn laser altimeter system; the survey extended for a kilometer area centered on the meteorological tower [Chen et al., 2006]. The mean tree height was 9.41 ± 4.33 m, the mean trunk height was 1.75 ± 1.35 m, the mean crown radius was 3.18 ± 1.54 m and the mean basal area was 0.074 ± 0.0839 m² (Q. Chen, personal communication, 2005). The trees covered 40% of the landscape. The mean leaf area index of the savanna woodland has been evaluated using a combination of remote sensing information (CASI, IKONOS, LIDAR)
and allometric relations [Karlik and McKay, 2002]. The leaf area index for this heterogeneous canopy equals 0.706 ± 0.408. This new value is slightly greater than our previously published estimate of projected leaf area index (0.6) that was derived from a 200 m transect using a LICOR-2000 [Kiang, 2002].

Leaf area index of the grasses was measured throughout the growing season using the direct clipping method on 3 to 5 samples, 0.0625 m² in area. The leaf area of each sample was determined with an area meter (LICOR LI 3100 C). The grasses growing at the savanna (Tonzi Ranch) and open grassland (Vaira Ranch) sites exhibited considerable seasonal dynamics and site differences in their leaf area indices (Figure 1). Growth started in the autumn with commencement of the rainy season, but it remained modest during the cold winter season. Grass growth accelerated during spring and peaked around day 100. Afterward, the grass canopy senesced as moisture in the soil reservoir was depleted. No live leaves existed after day 160 in 2003 and after day 125 in 2004. The amount of grass growth differed among the two sites, too. Greater grass production occurred at the open grassland site than in association with the oak trees. These differences are consistent with the observation of greater soil carbon in the open grassland than in the understory at the savanna site (see below).

2.2. Climate
[14] Annual temperature at a nearby weather station with similar altitude and vegetation (Pardee, California) is 16.3°C. The mean annual precipitation is about 559 mm per year (from weather station in Ione, California, that operated between 1959 and 1977). During the 2003 and 2004 study period, the mean air temperature was 16.31°C and 16.18°C, respectively. More precipitation fell during the 2003 study year (616 mm) than during the 2004 study year (485 mm) and essentially no rain falls during the summer months of this Mediterranean climate region. Seasonal trends in sunlight, temperature and humidity are reported elsewhere [Baldocchi et al., 2004].

2.3. Soil Characteristics
[15] The soil of the oak-grass savanna is classified as Auburn rocky silt loam (Lithic haploxerepts; soil survey of Amador Area, California, 1965, USDA, Soil Conservation Service). Physical properties are reported by Baldocchi et al. [2004]. The chemical properties of the soil were surveyed in November, 2003 for the 0.15 m layer below the surface. Under the trees, the percentages of organic matter, organic carbon and nitrogen were, on average, 4.82, 2.80 and 0.286%, respectively. In the space between trees, the soil contained 1.85% organic matter, 1.07% carbon and 0.10% nitrogen. At the nearby annual grassland, the soil contained 1.39% carbon and 0.14% nitrogen.

Seasonal variations in mean soil moisture (between 0 and 0.60 m) and daily mean soil temperature (at 0.08 m) are depicted in Figures 2a and 2b, respectively, for the Tonzi Ranch savanna during 2003. Together, Figures 2a and 2b show that the roots and microbes experience a very wide range of soil moisture and temperature conditions over the course of the year, a fact we exploit to examine responses of autotrophic and heterotrophic respiration components to changes in the environment. Soil moisture was near field capacity during the wet period and experienced minor dry-wet cycles between rain events. In general soil moisture ranged between 30 and 50% at all depths during the wet winter. With the cessation of rainfall (around day 125 in 2003) there was an immediate and dramatic reduction in soil moisture. During the summer dry period, soil moisture at depth below 0.15 m was near 10% and soil moisture in the first layer was below 5%. Daily mean soil temperature, at 0.08 m, experienced a 20°C range over the course of the year. Lowest temperatures, near 10°C, occurred during the winter wet season. During the dry summer, mean daily soil temperature reach exceeded 30°C because latent heat exchange was low [Baldocchi et al., 2004].

3. Methods
3.1. Environmental Measurements
[17] Air temperature and relative humidity were measured with a platinum resistance thermometer and solid-state humicap, respectively (model HMP-45A, Vaisala, Helsinki, Finland). Static pressure was measured with a capacitance analog barometer (model PTB101B, Vaisala, Helsinki, Finland). Soil temperatures were measured with multilevel
thermocouple probes. Volumetric soil moisture content was measured continuously in the field at several depths in the soil with frequency domain reflectometry sensors (Theta Probe model ML2-X, Delta-T Devices, Cambridge, United Kingdom). Sensors were placed at various depths in the soil (5, 10, 20 and 50 cm) and were calibrated using the gravimetric method. Profiles of soil moisture (0–15, 15–30, 30–45 and 45–60 cm) were made periodically and manually using a time domain reflectometer (Moisture Point, model 917, E.S.I Environmental Sensors, Inc, Victoria, British Columbia).

Ancillary meteorological and soil physics data were acquired and logged on CR-23x and CR-10x data loggers (Campbell Scientific Inc., Logan, Utah). The sensors were sampled every second, and half-hour averages were computed and stored on a computer, to coincide with the flux measurements.

Fluxes of carbon dioxide, water vapor and heat between the land and the atmosphere were measured with the eddy covariance method [Baldocchi, 2003]. Wind velocity and virtual temperature fluctuations were measured with a three-dimensional ultrasonic anemometer (Windmaster Pro, Gill Instruments, Lymington, United Kingdom). Carbon dioxide and water vapor fluctuations were measured with an open-path, infrared absorption gas analyzer (model LI-7500, LICOR, Lincoln, Nebraska). The micrometeorological sensors were sampled and digitized ten times per second.

Figure 2. (a) Seasonal variation in soil moisture for four layers at the oak savanna field site. The data were sampled weekly with a segmented time domain reflectometer. (b) Seasonal variation in soil temperature at 0.08 m. Both data sets were acquired in 2003 at the oak savanna field site.
[20] At the savanna site, a set of micrometeorological instruments was supported 23 m above the ground (∼10 m over the forest) on a walk-up scaffold tower. The gas analyzer was mounted 0.35 m below the sonic and 0.25 m to the side of the anemometer. Two other sets of flux measurement instrumentation were mounted about 2 m above the ground in the understory and over the open grassland. Each tower was protected from the cows with an electrical fence.

[21] In-house software was used to process the measurements into flux densities. The software computed covariances between velocity and scalar fluctuations over half-hour intervals. Turbulent fluctuations were calculated using the Reynolds decomposition technique by taking the difference between instantaneous and mean quantities. Mean velocity and scalar values were determined using 30-min records. The computer program also removes electrical spikes and rotates the coordinate system to force the mean vertical velocity to zero. Corrections for the effect of density fluctuations were applied to the scalar covariances that were measured with the open-path sensor using theory developed by Webb et al. [1980].

[22] The fast response CO₂/water vapor sensors were calibrated every three to four weeks against gas standards. The calibration standards for CO₂ were traceable to those prepared by NOAA’s Climate Monitoring and Diagnostic Laboratory. The output of the water vapor channel was referenced to a dew point generator (LI-610, Licor, Lincoln, Nebraska). Over the past three years the calibration zeros and spans have shown negligible drift.

[23] Prior to the experimental set up computations of the flux covariance transfer functions [Moore, 1986] were made to guide the positioning of sensors in the field. Overall transfer correction factors were less than a few percent. Considering uncertainties with applying the transfer functions, we chose not to apply them to our data. We also have reported near closure of the surface energy balance with our instrument setup [Baldocchi et al., 2004].

[24] Data gaps are inevitable and must be filled to compute daily and annual sums of fluxes. We filled data gaps with the mean diurnal average method [Falge et al., 2001]. The diurnal means were computed for consecutive 26-day windows to account for seasonal trends in phenology and soil moisture. The 26-day window corresponds well with a spectral gap in energy fluxes, suggesting that this time window was nearly optimal.

### 3.2. Soil CO₂ Profile Measurements

[25] Soil CO₂ concentrations were measured at depths of 0.02, 0.08, 0.16 and 0.24 m and at two locations. One station was under a mature oak tree and the other was midway between two widely separated trees. The system under the tree was 1 m from a tree; the tree had a diameter at breast height (DBH) of 0.716 m and an average of crown diameter of 13.05 m. The system in the open was 24.5 m away from the above tree and 18 m away from another smaller tree with an average of crown diameter of 6.05 m. CO₂ concentrations measured in the open had negligible influence from trees on the basis of transect measurements of soil respiration using a manual chamber system [Tang and Baldocchi, 2005].

[26] CO₂ concentrations in the soil air were measured by solid-state infrared gas analyzers (Vaisala CarboCap sensors, series GMT 220). The sensors were enshrouded in Gorex, to keep them dry, and were installed in the soil in sealed aluminum tubes that were installed vertically and open only at the sampling depth. In the shallow depths and at the open location we used model GMT 222. These sensors measure CO₂ across the range between 0 and 10000 ppm. Their accuracy is ±(20 ppm + 2% of reading). Under the tree and at depth we used model GMT 221. These sensors operate in the 0 to 2% range and have an accuracy of ±(0.2% + 2% of reading). The concentration readings from the CO₂ sensors were corrected for variations in temperature and pressure using empirical formulae reported by Tang et al. [2003] and CO₂ mole density (C mol m⁻³) was computed using the universal gas law:

\[
C_{\text{mol}} = \frac{C_i P}{RT},
\]

where \(C_i\) is the CO₂ concentration (µmol mol⁻¹), \(P\) is the air pressure (Pa), \(T\) is the soil absolute temperature (K), and \(R\) is the universal gas constant (8.3144 J mol⁻¹ K⁻¹). Calibrations were performed against standard gases traceable to the world standards produced at NOAA’s Climate Monitoring and Diagnostics Laboratory.

[27] The deployment of solid-state CO₂ sensors in the soil has many advantages over the periodic and manual sampling of ports inserted into the soil with syringes, a method many former flux gradient studies used [Hirsch et al., 2004; Jassal et al., 2004; Moncrieff and Fang, 1999; Risk et al., 2002; Takle et al., 2004]. Sampling a finite volume of soil air with a syringe has the potential to smear CO₂ gradient measurements—sampling pulls a volume of air that is subject to a very strong concentration gradients. In rare instances, this sampling problem has been circumvented by inserting long porous tubes horizontally in the soil whose volume exceeds that of the sampling syringe [Jassal et al., 2004]. However, the insertion of this horizontal sampling tube stills disturbs the soil profile. If the air sample is injected into a stream of air that is carried to a gas chromatograph or an infrared gas analyzer, error can be introduced by how well one evaluates the area under the curve in the time signal. Relying on manual sampling prevents one from taking continuous and long-term measurements, as we are able to do with these sensors. In comparison, measuring CO₂ concentrations continuously and at multiple levels enables us to examine the production of CO₂ at depth [Fang and Moncrieff, 1999; Risk et al., 2002] and correlate it with the local and representative temperature and moisture.

[28] One negative aspect of using the solid-state CO₂ sensors is associated with its heating of the soil when the sensor is activated constantly [Hirano et al., 2003; Jassal et al., 2005]. To assess this error, we conducted a set of laboratory studies. We discovered that continual operation of the CO₂ sensors caused a ∼2°C elevation in temperature at the mouth of the sampling tube relative to a column of soil not heated by the CO₂ probe. This degree of warming has the potential to increase soil respiration rates in the vicinity of the heated probe by about 14%, assuming a Q₁₀ of 2.
3.3. Soil CO₂ Efflux

[29] Soil respiration efflux rates were computed using flux gradient theory [Amundson et al., 1998; Hirano et al., 2003; Jassal et al., 2005; Liang et al., 2004; Tang et al., 2003]. In principle, the time rate of change of CO₂ in the soil is a function of the diffusive flux divergence and the source production, as defined by the conservation of mass equation:

\[ \frac{\partial c}{\partial t} = - \frac{\partial F}{\partial z} + S(z). \]  

(2)

In equation (2), \( c \) is the CO₂ molar density, \( F \) is the CO₂ efflux (\( \mu \text{mol m}^{-2} \text{s}^{-1} \)), \( \varepsilon \) is the volumetric air content (air-filled porosity), \( S \) is the source strength (\( \mu \text{mol m}^{-2} \text{s}^{-1} \)) and \( z \) is the depth (m). Using Fick’s law of diffusion we can compute the flux density, where \( F \) is positive when the flux is directed toward the atmosphere, as a function of the molar density gradient and the molecular diffusivity, \( D_s \):

\[ F = D_s \frac{\partial c_{mol}}{\partial z}. \]  

(3)

[30] At steady state conditions, the change in storage is nil (LHS of Equation 2), causing the diffusive flux divergence to be in balance with the source production term:

\[ \frac{\partial F}{\partial z} = S(z). \]  

(4)

If the CO₂ production and molecular diffusivity are constant with depth, the local source production is proportional to the second derivative in the change of CO₂ concentration with depth (\( D_s \frac{\partial^2 c_{mol}}{\partial z^2} = S(z) \)) and the concentration field within the soil is a second-order function of soil depth (\( z \)) [Amundson et al., 1998]:

\[ C_s = \frac{S}{D_s} \left( L_z - \frac{z^2}{2} \right) + C_a. \]  

(5)

We tested this assumption by examining soil CO₂ profiles during the winter, spring and summer, under the tree and in the open. Figure 3 presents data from one case, day 343 at noon. These data, and those not shown, indicate that source profile was generally constant. This assumption allows us to approximate and integrate equation (4) in finite difference form, thereby estimating CO₂ efflux density at the soil surface, \( F(0) \) as

\[ F(0) = \frac{z^2 F_1 - z_1 F_2}{z_2 - z_1}. \]  

(6)

We estimated \( F_1 \) between 0.02 and 0.08 m and \( F_2 \) between 0.08 and 0.16 m.

[31] The CO₂ diffusion coefficient in the soil, \( D_s \), is equal to the product of CO₂ diffusion coefficient in the free air, \( D_{a,ref} \) and the gas tortuosity factor, \( \xi \). The diffusion coefficient in free air, \( D_{a,ref} \), was computed using

\[ D_s = D_{a,ref} (T/293.15)^{1.75} (101.3/P). \]  

(7)

In equation (7), \( T \) is temperature, \( P \) is pressure and \( D_{a,ref} \) is a reference value of \( D_s \) at 20°C (293.15 K) and a pressure of 101.3 kPa; it equals 14.7 mm² s⁻¹. Soil tortuosity was evaluated as a function of volumetric water content and soil texture [Moldrup et al., 1999]:

\[ \frac{D_s}{D_{a,ref}} = \xi = \phi^\beta \left( \frac{\varepsilon}{\theta} \right)^{\alpha \gamma}. \]  

(8)

where \( \gamma \) is the percentage of mineral soil with size >2 μm, \( \beta \) is a constant (2.9), \( \phi \) is the porosity, defined as the sum of the volumetric air content, \( \varepsilon \), and the volumetric water content, \( \theta \). The diffusivity of CO₂ through liquid water was ignored as it is insignificant compared to diffusion through the air spaces [Fang and Moncrieff, 1999; Welsch and Hornberger, 2004].

3.4. Validation

[32] Application of the flux gradient method is not without pitfalls and needs validation before we can use it to interpret differences between soil respiration that was measured at different components of the landscape. Errors in evaluating soil respiration can be introduced by (1) the measurement of soil CO₂ concentration gradients, (2) the theoretical assessment of soil diffusivity in terms of soil moisture and soil porosity, and (3) from the numerical assessment of CO₂ gradients at a discrete and limited number of depths. We assessed potential for error by comparing measurements of soil respiration, using the LICOR 6400 soil respiration system, and fluxes computed with the soil CO₂ flux gradient system (Figure 4). The correspondence between the two methods was very high (\( r^2 = 0.90 \)), but on average the flux gradient effluxes were about 77% of the chamber measurements. The agreement
between the flux profile and soil chamber system is lower than what we reported in our earlier study [Tang et al., 2003], which was confined to the dry season when soil moisture and the diffusivity was more conservative. On the other hand, this level of agreement falls within the bounds reported by Pumpanen et al. [2004], who compared the performance of 20 soil respiration systems over wet sand and Jassal et al. [2005], who compared profile effluxes with soil chambers. In contrast, Liang et al. [2004] report that flux gradient estimate of soil CO$_2$ effluxes, using the same solid-state CO$_2$ sensors were 45% greater than estimates made with an automatic chamber system. In summary, CO$_2$ effluxes, produced by the flux gradient system, are sensitive to soil diffusivity models through their dependence on soil moisture and the measurements of soil moisture. However, the method is robust enough to study spatial and temporal differences with confidence.

While we were unable to replicate the flux profile system in a desired manner because of the cost of sensors, we were able to explore the representativeness of the array by comparing area-weighted averages against eddy covariance measurements made in the forest understory (Figure 5). We weighted efflux measurements made by the flux gradient system in proportion with its representative cover (60% for the system in the open and 40% for system under the tree). Except for a period between days 130 and 200, we observed very close agreement between the two measurement methods as the soil dried. We also saw good correspondence in how the two systems responded to the summer rain event and the commencement of autumnal rainfall. The bias, after day 130, may be explained by the fact that we moved one profile system on day 128 because gophers were churning soil and altering nearby soil properties. Application of the eddy covariance method in the understory is susceptible to its own bias errors. However, several studies have shown it can produce reliable results in open canopies [Baldocchi et al., 2000; Blanken et al., 1998; Janssens et al., 2001; Law et al., 1999; Subke and Tenhunen, 2004].

3.5. Canopy Photosynthesis

Net canopy photosynthesis was measured by taking the difference between simultaneous eddy covariance measurements over and under the canopy [Baldocchi and Vogel, 1996; Baldocchi et al., 1997]. The overstory eddy covariance system measured the difference between gross canopy photosynthesis ($P_g$) and leaf ($R_l$), bole ($R_b$), root ($R_r$) and microbial respiration ($R_m$):

$$F_c \approx -P_g + R_l + R_b + R_r + R_m.$$  \hspace{1cm} (9)

The understory eddy covariance system measured the sum of root and microbial respiration, when the grass was dead:

$$F_u \approx R_r + R_m.$$  \hspace{1cm} (10)

Taking the difference between the two systems yields an approximate measure of net canopy photosynthesis:

$$A_c \approx -P_u + R_l + R_b.$$  \hspace{1cm} (11)

The sign convention is with respect to the atmosphere, so losses of CO$_2$ from the atmosphere reflect gains by the ecosystem. Consequently, $A_c$ has a negative value for carbon uptake.

4. Results and Discussion

4.1. Switches: CO$_2$ Concentration Profiles

CO$_2$ concentrations in the soil exhibited strong horizontal and vertical gradients that varied with time.
First we consider measurements in the open grassland. Starting in spring we observed a rapid diminution of CO$_2$ as the soil dried, the grass senesced and microbial activity was inhibited. Through the spring/summer dry-down (days 120 to 200), we observed a large and significant gradient in CO$_2$ between 0.02 and 0.16 m. Then, CO$_2$ at 0.02 ranged between 10000 and 500 ppm and CO$_2$ at 0.16 m ranged between 20000 and 2000 ppm. During the driest period of the summer/autumn period (to day 290), CO$_2$ was above 400 ppm at 0.02 m and increased in steps of about 200 and 500 ppm down to depths of 0.08 and 0.16 m. The commencement of autumn rains caused an immediate jump in soil CO$_2$ concentration as porosity diminished and microbial activity resumed. During the wet winter, CO$_2$ concentrations above 5000 ppm were common at depths of 0.08 and 0.16 m.

CO$_2$ levels under the tree were more than double those measured in the open grassland, during the spring to summer dry period. However, CO$_2$ concentrations under the tree diminished linearly with time, as drought inhibited photosynthesis and soil respiration. The commencement of winter rains stimulated CO$_2$ production in shallow layer by grass and deeper layers by tree roots. In general, the observed range and the seasonal dynamics of CO$_2$ concentrations in the soil were consistent with recent measurements and model simulations for forests [Jassal et al., 2004; Welsch and Hornberger, 2004].

### 4.2. Switches: CO$_2$ Effluxes

Switches in soil CO$_2$ effluxes were observed and attributed to both spatial and temporal origins. A spatial switch was associated with landscape class. Here, we observed very large and distinct differences whether the

![Figure 5](image-url)

**Figure 5.** Upscaled comparison between soil CO$_2$ efflux measured in the forest understory with the eddy covariance method and the soil CO$_2$ probes. The contributions by the probes were weighted by their fractional area (40% understory, 60% open).

![Figure 6](image-url)

**Figure 6.** Daily averaged CO$_2$ concentrations in the soil over the course of the year. Data are shown for the wet and dry seasons and for locations in the open grassland and under an active tree.
effluxes were measured under a tree or in the open grassland (Figure 7). CO$_2$ effluxes from the open grassland, which primarily consisted of heterotrophic respiration, remained at a low basal level, below 0.5 μmol m$^{-2}$ s$^{-1}$, throughout the dry period after the grass had died. In contrast, soil CO$_2$ effluxes from under the tree were both very dynamic and always larger than soil respiration rates measured in the open space between trees. Effluxes under the tree exceeded 5 μmol m$^{-2}$ s$^{-1}$ during the spring/summer transition when photosynthesis was most active (Figure 8). Afterward a gradual reduction in CO$_2$ efflux occurred as the summer drought reduced photosynthesis. The commencement of winter rains (after day 300) caused another temporal switch in soil respiration under the tree and in the open grassland. This response reflects an enhancement in respiration by the newly wetted microbes and the new grass growth in the savanna understory. However, soil respiration rates under the tree remained greater despite the cessation of photosynthesis by day 300 (Figure 8).

Significant diurnal patterns in soil CO$_2$ efflux were superimposed on the seasonal courses at both locations. They reflect changes in microbial respiration as soil temperatures in the layers under investigation ranged over 15°C on a daily basis [Tang et al., 2005] and diurnal modulations in photosynthesis. A pulse in soil CO$_2$ efflux, near day 215, was associated with a rain event (Figure 7). A ten day relaxation period followed as the soil dried and as readily digestible carbon sources were consumed. Detailed quantification of the temporal dynamics associated with ecosystem respiration after rain pulses is described elsewhere [Xu et al., 2004] and will not be repeated here.

A question about temporal switches that remains involves when root activity under the trees commenced? Did it occur during the dormant period (prior to leaf-out), simultaneously with the initiation of photosynthesis or after leaf expansion? Photosynthetic activity commenced after day 70 in year 2003 (Figure 8). Observations at this site, and across the deciduous forest biome, indicate a close correspondence between the date when canopy photosynthesis initiates and when soil temperature equals mean air temperature [Baldocchi et al., 2005].

A first-order attempt to examine the seasonal variation in autotrophic respiration is produced by comparing nocturnal eddy flux measurements in the savanna understory and at the nearby open grassland (Figure 9). We assume that nighttime respiration from the dry grassland represents heterotrophic respiration associated with the decomposition of organic matter. In comparison, respiration measured with the understory eddy covariance system represents the sum of autotrophic and heterotrophic respiration from a grove of trees in its flux footprint. This CO$_2$ efflux is associated with labile root exudates and more recalcitrant organic matter. During the wet winter, respiration from the grassland exceeded that from the forest understory. This offset is expected because greater grass growth occurred at the open grassland.
site (Figure 1) and the trees were leafless and dormant. These results suggest that root respiration from the oak trees during the dormant period was low. An acceleration in understory soil respiration occurred after day 80 about ten days after when leaf out occurred. However, respiration in the understory of the oak woodland did not exceed that from the open grassland until after day 100. Thus we infer from our data that a delay in autotrophic root respiration occurred about three weeks after the initiation of photosynthesis in the spring. This result suggests that the priority for new carbohydrates went to leaves rather than roots. We also observed that the estimate of autotrophic respiration peaked around day 120, which led the date of peak of photosynthesis, which was near day 150. By day 300, when photosynthetic activity was close to nil, the spatially integrated efflux from the dry grassland and the forest understory were similar.

4.3. Lags

[42] Having CO_2 flux measurements with high temporal resolution enables us to reexamine the coupling of soil respiration to diurnal variations in photosynthesis and to test the hypotheses derived from the analyses of Hogberg et al. [2001] and Bowling et al. [2002] that detect day to week lags between photosynthesis and respiration. Other noteworthy lag responses involve dark respiration of leaves and previous days’ photosynthesis [Whitehead et al., 2004], but these are not evaluated here.

[43] We discovered that soil respiration in July was best correlated, |r = 0.8|, with rates of photosynthesis that were lagged by ten 30-min averaging periods, or 5 hours (Figure 10). These data are consistent with the fact that it takes a finite amount of time for pulses of carbohydrates to flow from the leaves, through the phloem and to the roots [Thompson and Holbrook, 2003]. Nevertheless, direct modeling and measurement studies will be needed to prove this assertion.

[45] Over the course of the summer growing season, the field site experienced an alternating succession of air masses with high and low vapor pressure deficits and air temperature; winds from the southwest were of marine origins and had lower vapor pressure deficits [Zhong et al., 2004], while those coming from the north were continental in origin and were hotter and drier. The pattern of synoptic meteorology modulated canopy photosynthesis (Figure 11) and gave us the opportunity to examine how repeated modulation in photosynthesis altered soil respiration (R_s).

[46] Using daily integrated data we observed that the highest degree of correlation (r = |0.6|) between soil respiration and canopy photosynthesis occurred with a zero lag (Figure 12). A second and less pronounced lag (r = |0.25|) was quantified with a time delay of 14 days. What is deduced from Figure 12 is a correspondence between short (daily) and long (seasonal) trends in photosynthesis and soil respiration. The peak correlation with zero lag is consistent with the intraday lag found in Figure 10. The 14 day lag reflects effect of vapor pressure deficits on photosynthesis (Figure 11) and the low correlation coefficient reflects the effect of diminishing rates of photosynthesis (Figure 8) and autotrophic and heterotrophic respiration. Because photosynthesis was assigned a negative value, negative correlations are indicative of respiration increasing with more photosynthesis.

Figure 10. Lag correlation between soil respiration and canopy photosynthesis for July 2003 (days 182–212). The negative correlation states that an increase in soil respiration is associated with a more negative value in canopy photosynthesis (we adopt an atmospheric framework where a loss from the atmosphere is a gain by the ecosystem).

Figure 11. Correlation between canopy photosynthesis and daily averaged vapor pressure deficit (vpd). Data were confined to the period when photosynthesis was most active. The negative correlation states that an increase in vpd is associated with a more negative value in canopy photosynthesis (we adopt an atmospheric framework where a loss from the atmosphere is a gain by the ecosystem.)
its lower power to modulate soil respiration, as the summer drought proceeds.

5. Conclusions

[47] We have reported how soil respiration of an oak-grass savanna is affected by switches and lags in its autotrophic and heterotrophic components. Such an assessment was possible by combining several continuous flux measurement techniques (the eddy covariance and soil flux gradient measurements) across natural gradients in the landscape.

[48] Switches in soil respiration were associated with spatial and temporal factors. A large switch in respiration occurred during the summer as one transcended from an open grasslands (where heterotrophic respiration was dominant) to the woodland understory (where rates were elevated because of the presence of roots and the feeding of microbes by root exudates). A temporal switch in respiration occurred at the commencement in autumnal rains, with rapid germination of grass seed and new growth. Another temporal switch was associated with leaf out by the trees and the triggering of renewed root activity.

[49] Pulses in soil respiration were associated with frequent and isolated summer rain storms. These events only stimulated microbial respiration, since rainfall only wetted the upper soil surface and the annual grasses were senesced. Furthermore, summer rains were typically not sufficient to replenish soil moisture in the root zone to stimulate physiological activity by the trees.

[50] Lags were associated between variations in photosynthetic activity and soil respiration. The lags were observed on hourly scales because of the slow translocation of photosynthate to the roots and associated microbes, and on daily scales because of modulations in photosynthesis by the passage of dry and humid air masses.

[51] The quantification of nonlinear and hysteretic responses, associated with physiological activity of trees provide a foundation for developing a new generation of soil respiration models that are coupled with well formulated models of photosynthesis [Farquhar et al., 1980] and phloem transport [Thompson and Holbrook, 2003] and the soil environment. Such data sets may also be used to test new dynamic theories such as the threshold delay model [Ogle and Reynolds, 2004].

[52] Finally, we suggest additional studies that may stem from this research. There is a need to examine the seasonal variation in the depth of maximal $\text{CO}_2$ production ($S(z) = \frac{\partial z}{\partial z}$). This can be accomplished with a denser and deeper network of soil $\text{CO}_2$ sensors. Direct and continuous measurements of respired $^{13}\text{CO}_2$ with new tunable diode laser spectrometers will provide additional information whether photosynthetic translocation is stimulating soil respiration directly, or indirectly by supplying carbohydrates to microbes.

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