Soil Respiration and Carbon Sequestration of an Oak-grass Savanna in California: Roles of temperature, soil moisture, rain events and photosynthesis

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Summary

We quantified the spatial-temporal roles of photosynthesis, temperature and soil moisture on soil respiration of an oak savanna with a combination of field and laboratory measurements. Canopy photosynthesis was quantified from eddy covariance measurements over and under the woodland. Spatial gradients in soil respiration were surveyed with a portable soil respiration chamber. Contributions to soil respiration by autotrophs and heterotrophs were assessed using profiles of CO₂ sensors inserted in the soil under a tree and in the open grassland.

At a given spot, soil respiration was a function of soil moisture and temperature and labile carbon pools associated with decomposing organic matter and recent photosynthetic production. Spatial/temporal variations in soil respiration reflect changes in these controlling factors. Spatial transect studies, for example, showed that soil respiration decreased by 60% as one radiates from a tree to the open grassland. Soil respiration measured under a tree crown reflected the sum of rhizosphere respiration and heterotrophic respiration while soil respiration measured in an open area represented heterotrophic respiration when the grass was dead during the summer. Basal rates of soil respiration diminished over the summer as the soil dried and it stressed photosynthetic and microbial activity. Summer rains, on the other hand, were found to stimulate the activity of latent microbes immediately, thereby pulsing soil respiration by more than a factor of 10 until the upper soil layer dries. Continuous measurements of soil respiration revealed that soil respiration under the tree was decoupled with soil temperature. Soil respiration was strongly correlated with tree photosynthesis, but with a time lag of 7 to 12 hours. These results indicate that photosynthesis drives soil respiration in addition to soil temperature and moisture. Measurements of soil respiration were combined with remote sensing information to upscale soil CO₂ efflux measurements. Cumulative soil respiration was 394 gC m⁻² y⁻¹ in the open area and 616 gC m⁻² y⁻¹ under trees producing a site-average of 488 gC m⁻² y⁻¹.

Keywords: soil respiration, rain pulse, oak-grass savanna

Objectives

We investigated the biotic and abiotic mechanisms controlling soil respiration and soil carbon content of an oak-grass savanna ecosystem. In particular, we examined the roles that spatial and temporal variations in net primary productivity, soil moisture, temperature and rain pulses had on root and microbial respiration from the soil. At the field scale, we assessed soil respiration with three methods. First, we operated an eddy covariance flux system over and under an oak

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savanna to measure soil respiration and ecosystem photosynthesis and respiration (supported by extramural funding, DOE/TCP and WESTGEC). Second, we measured soil respiration continuously under a tree and from an open grassland with a gradient-diffusion system that is based on new solid-state CO$_2$ sensors. And thirdly, we assessed spatial gradients in soil respiration, periodically, across a transect using a chamber-based system. Manipulative studies were conducted by introducing water to soil treatments (in the laboratory and field) to examine switches between autotrophic and heterotrophic respiration and changes in C pool size. Laboratory incubation studies were conducted on soil cores at three temperatures (15°, 25° and 35° C) and two moisture treatments (15 and 30%) to assess the turnover time of soil carbon.

**Approach and Procedures**

Our study was conducted at a field site near Ione, CA. The overstory of the oak savanna consisted of scattered blue oak trees (*Quercus douglasii*). The understory was vegetated by an annual California grassland. Annual temperature is 16.3°C, and the mean annual precipitation is about 559 mm per year. Site details are reported in Xu and Baldocchi (2004).

**Soil Respiration**

Soil CO$_2$ efflux was measured along a 42-m transect between two oak trees at 11 spots using a soil chamber system (LI6400-09, LI-COR Inc, Nebraska, USA). Soil temperature and moisture was measured to interpret the fluxes. Repeated measurements of soil CO$_2$ efflux were made every three to four weeks in order to assess the seasonal variation in respiration due to changes in temperature and moisture.

**Soil CO$_2$ Concentration Profiles**

We used solid-state CO$_2$ sensors (GMT 222, Vaisala, Finland) to measure CO$_2$ profiles in the soil. The sensors were buried at depths of 2 cm, 8 cm and 16 cm (Tang et al. 2003). We deduced respiration rates from the measured profiles of CO$_2$ in the soil using Fick’s First Law of diffusion and theoretical estimates of soil diffusivity, which varied with soil moisture and texture.

**Carbon Turnover Measurements**

Incubation studies were conducted in the Berkeley Biometeorology lab. Soil samples were held at 10% soil moisture at 15°, 25° and 35° C and at 10, 20 and 30% moisture at 15° C. Analytical measurements of CO$_2$ evolution are being made periodically with a flow-through system attached to a Licor 6262 CO$_2$ analyzer; respiration rates were a function of the increase in CO$_2$ concentration, detected by the system, and its volume. Laboratory measurements of soil C/N were performed at the DANR Soils Lab in Davis prior to the incubation and will be measured again at its conclusion.

**Results**

**Spatial/Temporal Variation in Soil Respiration**
Soil Respiration and Carbon Sequestration of an Oak-grass Savanna in California: Roles of temperature, soil moisture, rain events and photosynthesis—Baldocchi

A strong horizontal gradient in soil respiration was measured across a transect that spanned from an oak tree to a patch of open grassland between to widely separated trees throughout the year. Seasonal variations resulted in a reduction in the reference rate near the tree as one transcended from the wet winter period to the dry summer period; during the wet period the spatial gradient in soil respiration as one radiated from a tree (x) could be quantified using $F = 1.88 + \frac{2.13}{x}$; during the dry period, the spatial pattern in respiration was quantified as $F = 0.026 + \frac{2.7}{x}$.

With the CO$_2$ gradient-diffusion system, we were able to quantify the seasonal dynamics of soil CO$_2$ evolution from under the tree and the grassland soil system (fig. 1). An appeal of this experimental design is its power to enable us to quantify the impact of tree photosynthesis on soil respiration in a non-destructive way, in contrast to the destructive xylem girdling method of Hogberg et al. (2001). Three pieces of information can be extracted from figure 1. First, the supply of photosynthate to roots and associated soil microbes elevated respiration rates significantly, compared to measurements made under dead grass. Second, the embellishment of respiration under the trees diminishes with time as soil moisture becomes depleted and inhibits photosynthesis. And, third, summer rainfall events cause a rapid and significant spike in soil respiration, and this spike is attributed to renewal of activity from dormant microbes.

![Figure 1. Seasonal variation of soil respiration under a photosynthesizing oak tree and under an open path of dead grass.](image)

With information on temperature, soil moisture, canopy closure and crown size structure and gradients in respiration between trees, we attempted to upscale the detailed site-specific information. A comparison between the upscaled soil respiration measurements and understory eddy flux measurements (this system samples a footprint of several hundred square meters) shows reasonable agreement through much of the season, day 200 through 365 (fig. 2). Only after a rain pulse was there some discrepancy between the methods. This discrepancy can be expected because there is much uncertainty in diffusivities, soil CO$_2$ and eddy fluxes after a rain event.
Soil Respiration and Carbon Sequestration of an Oak-grass Savanna in California: Roles of temperature, soil moisture, rain events and photosynthesis—Baldocchi

Figure 2. A comparison between upscaled soil respiration measurement, using a transect of soil chambers, and understory eddy covariance measurements.

By combining our spatial/temporal data on soil respiration and stand structure we estimated that the cumulative soil respiration in was 394 gC m$^{-2}$ y$^{-1}$ in the open area and 616 gC m$^{-2}$ y$^{-1}$ under trees with a site-average of 488 gC m$^{-2}$ y$^{-1}$.

**Mechanisms**

Respiration from the dead grassland can be attributed to heterotrophs. They evolve CO$_2$ at low rates (below 1.0 µmol m$^{-2}$ s$^{-1}$) and remain a function of soil temperature as soil moisture is depleted through June, July and September (fig. 3a). In contrast, respiration from under a tree shows much larger values in respiration that seem decoupled from soil temperature. Figure 3b shows that hysteresis between soil respiration and soil temperature occurred over the course of a day.

This hysteresis in soil respiration under a tree is attributed to the production and translocation of photosynthate from the leaves, through the phloem and to the roots and associated microbes. Statistical analysis of lag-correlation coefficients with an inverse Fourier transform revealed that soil respiration peaked about seven to eight hours after the daily peak in daily photosynthesis, and after soil temperature had diminished (fig. 4).
Soil Respiration and Carbon Sequestration of an Oak-grass Savanna in California: Roles of temperature, soil moisture, rain events and photosynthesis—Baldocchi

Figure 3. Comparison between soil respiration, measured with the flux-gradient method, and soil temperature. Measurements were made under a tree and in the open. Data were averaged by hour for a month.
Soil Respiration and Carbon Sequestration of an Oak-grass Savanna in California: Roles of temperature, soil moisture, rain events and photosynthesis—Baldocchi

**Figure 4.** Lag correlation between soil respiration, under a tree, and canopy photosynthesis, measured with the overstory and understory eddy covariance systems.

**Discussion**

Many studies on soil respiration report that soil temperature accounts for less than 70% of its variance. There is a new trend to try and examine the effects of carbon pool sizes and to partition soil respiration into its autotrophic and heterotrophic components. With the open nature of savanna ecosystem and the wide range of conditions it experiences, we were able to tease apart the complex and coupled roles of soil moisture, temperature, growth and recent photosynthesis on soil respiration. These data have the potential to generate a new generation of algorithms for predicting spatial-temporal variations in soil respiration and coupling estimates of soil respiration to photosynthesis, a quantity we can model well and evaluate from space.

Characterizing the effects of rain and photosynthesis on respiration has major implications for how we measure, model and assess annual carbon budgets. Rain pulses can burn off up to 80 gC m$^{-2}$ over a two-week period. Periodic measurements of soil respiration may miss rain events and underestimate the carbon lost. Furthermore, we observed situations in which light rains stimulated microbial respiration, but did not saturate deep into the soil to alter the reading of soil moisture probes much. In these situations, simple algorithms that reflect the role of soil moisture on respiration may be in error.
Soil Respiration and Carbon Sequestration of an Oak-grass Savanna in California: Roles of temperature, soil moisture, rain events and photosynthesis—Baldocchi

References


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