How soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature

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[1] In this paper, we analyzed 3 years of carbon flux data from continuous eddy covariance measurements to investigate how soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature. The data were acquired over an annual grassland and from the grass understory of an oak/grass savanna ecosystem in California. We observed that ecosystem respiration was an exponential function of soil temperature during the winter wet season and a jump in ecosystem respiration occurred, at comparable temperatures, during the spring growth period. The depletion of the moisture from the soil reservoir, during spring, limited ecosystem respiration after its volumetric water content dropped below a threshold of 0.15 m^3 m^{-3}. The senescence of grass during the summer switched the source of ecosystem respiration to heterotrophic bacteria and fungi. During the summer, respiration proceeded at a low basal rate (about 0.10 to 0.3 g C m^{-2} d^{-1}), except when summer rain events stimulated large dynamic pulses in heterotrophic respiration. Peak respiratory pulses were on the order of 60–80 times baseline and could not be explained by functions that depend on mean soil moisture and temperature. We found that the magnitude of the respiratory pulses was inversely related to its prerain value and that the time constant, describing the exponential decay of the respiratory pulses after the rain event, was a function of the amount of rainfall. The amount of carbon lost, in association with a few summer rain events, was greater at the site with higher primary productivity and soil carbon content. *INDEX TERMS:* 0315 Atmospheric Composition and Structure: Biosphere/atmosphere interactions; 1615 Global Change: Biogeochemical processes (4805); 1866 Hydrology: Soil moisture; 3322 Meteorology and Atmospheric Dynamics: Land/atmosphere interactions; *KEYWORDS:* respiration, carbon balance, savanna, biosphere-atmosphere interactions, eddy covariance

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1. Introduction

[2] Ecosystem respiration provides the energy for the work that is performed by the components of an ecosystem: leaves, stems, roots, fungi, and bacteria. In doing so, it is a major source of carbon to the atmosphere that is equal to or slightly exceeds, in magnitude, gross photosynthesis [*Falge et al.*, 2002; *Janssens et al.*, 2001; *Raich and Schlesinger*, 1992].

[3] Quantifying how ecosystem respiration will respond to environmental perturbations is a crucial step in our quest to predict past and future climates [*Cox et al.*, 2000; *Friedlingstein et al.*, 2003]. For example, small changes in ecosystem respiration, due to global warming, may cause an ecosystem to switch from being a sink to a source of carbon. Such a switch could amplify greenhouse warming by imposing a positive feedback on the climate system [*Cox et al.*, 2000]. On the other hand, if global warming alters the hydrological cycle, causing rainfall to decrease in some regions [*Wetherald and Manabe*, 2002], a positive perturbation in ecosystem respiration, due to global warming, may be dampened.

[4] At present, most models of ecosystem respiration remain highly empirical, in comparison to the mechanistic and validated theories that exist for predicting leaf [*Farquhar et al.*, 1980] and canopy [*Baldocchi and Amthor*, 2001] photosynthesis. This situation arises because numerous factors cause ecosystem respiration to be a complex process to quantify. First, ecosystem respiration is composed of two distinct processes, autotrophic and heterotrophic respiration. Second, the proportional contribution of autotrophic and heterotrophic respiration can vary widely in time and space [*Hanson et al.*, 2000]. Third, these components of ecosystem respiration respond to environmental perturbations differently, and their functional response may depend on current and antecedent conditions. In sum, models of ecosystem respiration must consider its dependence on such

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biotic or abiotic variables as composition and activity of the microbial community, quality and quantity of plant and soil carbon pools, photosynthetic/growth activity, soil moisture, and soil temperature [*Amundson*, 2001; *Hogberg et al.*, 2001; *Janssens et al.*, 2001; *Norman et al.*, 1992]. Because so many biotic and abiotic factors contribute to ecosystem respiration, we also contend that at the field scale its quantification, remains data deficient. In particular, many studies are unable to span across a broad range of environmental and biological conditions that are needed to produce robust empirical regression models for predicting how ecosystem respiration may respond to environmental change.

[5] In lieu of better options, many researchers have attempted to capture the essence of plant and soil respiration by using soil temperature as the main environmental driver. [*Gifford*, 2003; *Lloyd and Taylor*, 1994; *Raich and Schlesinger*, 1992]. However, in general, temperature accounts for <70% of the variance in soil respiration [*Raich and Schlesinger*, 1992]. In semiarid and arid regions, soil moisture is the second most important abiotic variable for predicting ecosystem respiration, as it strongly influences the physiological activity of vegetation and soil microbes [*Qi and Xu*, 2001]. Two approaches are often used to model the influence of soil moisture on respiration. One approach assumes that the impacts of moisture and temperature are multiplicative [*Hanson et al.*, 1993; *Qi and Xu*, 2001; *Reichstein et al.*, 2002b]. However, additional complication may arise if soil moisture changes the temperature sensitivity of respiration [*Qi et al.*, 2002; *Reichstein et al.*, 2002b]. An alternative approach toward modeling the effect of soil moisture on soil respiration assumes that it becomes limited when soil moisture drops below a threshold value [*Davidson et al.*, 1998; *Reichstein et al.*, 2002b; *Rey et al.*, 2002]. However, the threshold values are often site-specific, so no universal value exists.

[6] Another aspect of current respiration models is their assumption of steady state conditions and a reliance on mean environmental variables. In arid and semiarid regions, precipitation often falls as infrequent pulse events [*Noy-Meir*, 1973]. How ecosystem respiration responds to rain pulse events is relatively unknown. We can only surmise that wetting rapidly activates microbial activity on the basis of studies that add water to dry soil in small field plots [*Borken et al.*, 1999; *Liu et al.*, 2002] or in the laboratory [*Birch*, 1958, 1959; *Griffiths and Birch*, 1961; *Halverson et al.*, 2000; *Kieft et al.*, 1987; *Orchard and Cook*, 1983]. Owing to artificial experimental conditions, those experiment results may not reflect what might be occurring in the field, which can be affected by antecedent conditions, nor do these cited studies provide information on the amount of carbon that will be lost from field plots on seasonal timescales. Several recent studies from flux measurements, however, suggest a notable increase in ecosystem respiration immediately after rain events, especially those occurring during the dry season [*Emmerich*, 2003; *Flanagan et al.*, 2002; *Lee et al.*, 2004; *Reichstein et al.*, 2002a; *Xu and Baldocchi*, 2004]. However, little information has been produced on the total carbon respired from rain pulses.

[7] In this paper, we analyze 3 years of carbon flux data from continuous eddy covariance measurements to investigate how soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature. The data were acquired over an annual grassland and the grass understory of an oak/grass savanna ecosystem in the Mediterranean climate zone of California. Long-term and continuous carbon flux measurements were conducted in a region that experiences distinct wet and dry periods and a wide range in air and soil temperature. This combination of conditions enables us to capture the response of ecosystem respiration to changes in soil temperature, soil moisture, and plant and soil carbon pools and to dynamic and infrequent rain pulses. Furthermore, the senescent nature of the grass during the summer eliminates its autotrophic component of respiration and allows us to quantify how heterotrophic respiration will respond to rain pulses at the field scale.

2. Material and Method

2.1. Site Information

[8] The data sets analyzed in this study were produced from the continuous carbon flux measurements at two AmeriFlux sites in California over the past 3 years. One site is an annual grassland [*Xu and Baldocchi*, 2004], located at lower foothills of the Sierra Nevada (38°24.400 N latitude, 120°57.044 W longitude, and 129 m above sea level). The soil is an Exchequer very rocky silt loam (Lithic xerorthents). It contains 30% sand, 57% silt, and 13% clay. Its bulk density at surface layer (0–30 cm) is around 1.43 ± 0.10 g cm^{-3} (n = 27). Total nitrogen and carbon content of the soil were ~0.14 and 1.39%, respectively.

[9] The other site is composed of oak/grass savanna. It is 3 km away from the grassland (38.4311°N latitude, 120.966°W longitude, 177-m altitude) and possesses two distinct layers, with blue oak trees (*Quercus douglasii*) in the overstory and annual grasses in the understory [*Baldocchi et al.*, 2004]. The overstory and understory vegetation operate in and out of phase with each other over the course of a year. The oak trees are deciduous and dormant in the winter wet season, while the grass understory is active only during the winter/spring wet season.

[10] The oak woodland consists of ~194 stems per hectare, whose mean diameter at breast height is 0.199 m and basal area is 18 m^2 ha^{-1}. On the basis of IKONOS imagery we assessed crown closure to be ~40% (Q. Chen et al., A slope adaptive method for separation of terrain and vegetation returns of small-footprint LIDAR in forest area, submitted to *Photogrammetric Engineering and Remote Sensing*, 2004; J. Kim et al., Upscaling CO_2 fluxes from tower to landscape: Overlaying tower flux footprint calculations on high resolution (IKONOS) vegetation density images, submitted to *Agricultural and Forest Meteorology*, 2004). The average height of the oak trees was determined with an airborne laser altimeter. The mean height of the woodland is 10.1 m, and its standard deviation is 4.7 m. Leaf area index of the oak woodland was measured with a plant canopy analyzer (LAI-2000, LI-COR, Inc., Lincoln, Nebraska). Its value was steady during the growing season and equaled 0.6 m^2 m^{-2} [*Kiang*, 2002].

[11] The soil is classified as an Auburn very rocky silt loam (lithic haploxerepts). It contains 43% sand, 43% silt,

and 13% clay. Its bulk density at surface layer (0–30 cm) is around 1.61 ± 0.10 g cm^{-3} (n = 54). Total nitrogen and carbon content of the soil are ~0.11 and 0.95%, respectively. The soil profile at both sites is ~0.5 m deep and overlays fractured rock.

[12] The climate of the region is Mediterranean with clear days, high temperatures, and low humidity, and virtually no rain falls during the summer. In contrast, the winter is relatively cool and wet. The mean annual temperature is 16.3°C, and 559 mm of precipitation fall per year, as determined from over 30 years of data from a nearby weather station at Ione, California.

[13] The grasses at both sites are cool season annual C_3 species. More than 95% of species composition at the site are *Brachypodium distachyon* L., *Hypochaeris glabra* L., *Trifolium dubium* Sibth., *Trifolium hirtum* All., *Dichelostemma volubile* A., and *Erodium botrys* Cav. Owing to the Mediterranean climate, the growing season for the grasses is confined to wet season only, typically from late October to mid-May. No carbon uptake occurred by the grass during the summer because it had senesced.

2.2. Meteorology, Soil, and Other Parameter Measurements

[14] Standard meteorological and soil parameters were measured continuously with an array of sensors. Photosynthetic photon flux density, Q_p, and reflected Q_p were measured with a quantum sensor (Kipp and Zonen PAR-Lite, Delft, Netherlands), and R_n was measured with a net radiometer at the height of 2.5 m (Kipp and Zonen, Delft, Netherlands). Precipitation was measured with a tipping-bucket rain gauge (Texas Electronics, Texas). Air temperature and relative humidity at the height of 2.5 m were measured with a shielded and aspirated sensor (HMP-35 A, Vaisala, Helsinki, Finland). Soil temperatures at the depths of 0.02, 0.04, 0.08, 0.16, and 0.32 m were measured with three multilevel thermocouple sensors. Soil volumetric water content was measured with frequency domain reflectometer probe (ML2x, Delta-T Devices, Burwell, Cambridge, United Kingdom) at depths of 0.05, 0.10, and 0.20 m, with two to three replicates at each depth. Profiles of soil moisture (at the depth of 0–0.15, 0.15–0.30, 0.30–0.45, and 0.45–0.60 m) were measured weekly with a time domain reflectometer (Moisture Point, model 917, Environmental Sciences, Inc., Vancouver, Canada). Nine probes were distributed across the woodland to improve upon our spatial sampling of soil moisture. Soil water potential was estimated based on the soil moisture release curve obtained on soil sample from sites, using a psychrometer (Model WP4, Decagon, Washington). Soil heat flux was obtained by averaging the output of three heat flux plates (model HFP-01, Hukseflux Thermal Sensors, Delft, Netherlands). They were buried 0.01 m below the surface and were randomly placed within a few meters of the flux system. All channels from meteorological and soil sensors, except the rain gauge, were scanned every 5 s with data loggers (Campbell Scientific, Inc., Logan, Utah), and then 30-min mean data were stored.

[15] Leaf area index (LAI) of the grass was determined at intervals of 2–4 weeks, depending on the growth rate of grass. Grass was harvested from four sample plots (0.25 × 0.25 m) in the upwind direction of eddy covariance flux system. Then leaves were separated from the stem, and their areas were measured with a leaf area meter (Li-Cor 3100, Lincoln, Nebraska).

2.3. Flux Measurement and Daytime Ecosystem Respiration Estimation

[16] The fluxes of CO_2 were measured over the grassland and understory at the oak savanna site with the eddy covariance technique [*Baldocchi*, 2003]. The eddy covariance system at both sites was mounted at 2.0 m above the ground. It consisted of a three-dimensional sonic anemometer (Model 1352, Gill Instruments Ltd., Lymington, United Kingdom) and an open path and fast response infrared gas analyzer (IRGA, Li 7500, LI-COR, Inc., Lincoln, Nebraska). The anemometer and the IRGA provide digital output of the fluctuations in three wind components, sonic temperature, water vapor, and CO_2 density. The raw data from each 30-min period were recorded at a rate of 10 Hz into separate files on a laptop computer.

[17] The IRGA was replaced every month with a freshly calibrated one. The CO_2 signal of the IRGA was calibrated against gas mixtures in air that were referenced to standards prepared by National Oceanic and Atmospheric Administration's (NOAA's) Climate Monitoring and Diagnostics Laboratory. The span for the water vapor was calibrated with a dew point generator (Li-610, LI-COR, Inc., Lincoln, Nebraska). Zeros for both CO_2 and water vapor channels were calibrated with 99.99% nitrogen gas. Calibration results showed that the cumulative deviations for zero drift and span change for both CO_2 and water vapor channels over a period of one full year were less than a few percent. Thus shifts of the instruments zero and span can be considered to be insignificant over a month.

[18] Each eddy flux system was powered by eight 12-V DC deep cycle batteries that were charged by eight solar panels (Model SP75, Siemens). The system used ~3 A at 12 V.

[19] Micrometeorological software, developed in house, was used to compute flux covariances from the raw data. Computation procedures included spike removal, coordinate rotation, application of standard gas laws, and correction for air density fluctuations [*Baldocchi et al.*, 1988; *Webb et al.*, 1980]. Following the sign convention in the atmospheric flux community, positive flux covariances represent net carbon gain by the atmosphere and a loss from the ecosystem; conversely, negative values indicate a loss of carbon from the atmosphere and a gain by the ecosystem.

[20] To assess the accuracy of the eddy covariance measurements, we analyzed linear regressions between the sum of latent heat (LE), sensible heat (H), and soil heat flux (G) versus net radiation (R_n). Taking data from the grassland site in year 2002, as an example, we found that the intercept, the slope, and the coefficient of determination were 1.91, 0.91, and 0.98 W m^{-2}, respectively. Even though our energy balance lacks 9% to meet full closure, it is ranked among the highest degree of closure among FLUXNET community on the basis of a survey by *Wilson et al.* [2002]. Our cumulative evaporation data over the dry season (days of year (DOY) 150 to 309) in 2001 from the grassland site also

matched closely the change of soil moisture in the soil profile [*Baldocchi et al.*, 2004].

2.4. Methods for Estimating R_{eco} and Gap Filling

[21] Ecosystem respiration was derived from measurements of net ecosystem carbon exchange using flux partitioning methods described by *Xu and Baldocchi* [2004]. Eddy flux measurements of ecosystem respiration over the annual grassland represent the sum of autotrophic (roots, leaves, and stems) and heterotrophic (bacteria and fungi) respiration. However, during the summer, when the grass is dead, the flux measurements represent respiration by heterotrophs in the soil only. To enlarge our data set on the response of respiration to rain, data from the oak woodland understory are only used when the grass is dead. In general, carbon flux data from this site represent heterotrophic respiration and root respiration. However, pulses from background, after summer rains, and their dynamic decay are indicative of changes in heterotrophic respiration.

[22] For long-term and continuous field measurements, missing data are unavoidable owing to malfunction of the instruments or power failures. We also must reject data when they do not meet specific quality assurance criteria, e.g., extreme statistics and values off scale [*Foken and Wichura*, 1996]. In order to obtain the information on the daily carbon flux data we used the following procedure to fill missing data and replace bad data. For small blocks of missing data (less than an hour) a simple interpolation method was used. Missing data, during nighttime, were filled by using a method established by *Falge et al.* [2002]: An exponential relationship between F_c and soil temperature at depth of 0.04 m (T_{soil}) was generated from periods of high turbulence, defined as when friction velocity (u_*) exceeded 0.1 m s^{-1} [*Xu and Baldocchi*, 2004]. During the nongrowing summer period, all missing, rejected data were filled or replaced by using the exponential relationship.

2.5. Soil Air CO_2 Concentration Measurements

[23] To detect how fast the soil microbial activity can respond to rain events, we buried small solid state, nondispersive infrared gas analyzers (GMT222, Vaisala, Finland) in the soil to measure CO_2 concentration ($[CO_2]$) in situ at soil depths of 0.02, 0.08, and 0.16 m. The sensors were logged continuously and data were averaged at 5-min intervals. Afterward, their output was corrected for temperature using algorithms supplied by the manufacturer. The CO_2 profile measurements were deployed only at the oak savanna woodland site, starting in June 2002. The gradient measurements were applied to Fick's gradient diffusion equation to calculate the CO_2 efflux from the soil. Diffusivities of CO_2 were computed as a function of soil moisture using algorithms developed by *Moldrup et al.* [2003]. Additional information on the concentration profile measurements and flux computations is presented by *Tang et al.* [2003].

2.6. Soil Incubation Studies

[24] Incubation studies were performed on soil samples to determine how heterotrophic respiration and the carbon pool turnover time respond to variations in soil moisture and temperature. Soil samples were collected from the upper 10-cm layer of plots in the open grassland and under the trees after the grass, on 2 July 2003. Soil samples were prepared by (1) removing the organic layer, (2) mixing the soil, and (3) drying the samples. The next day, 100-g samples of soil were placed into incubation jars, moisture was added, and the incubation study was initiated. One set of soil samples were maintained at three temperatures (15, 25, and 35°C) and at constant and low moisture content, representing summer moisture conditions (0.10 g g^{-1}). Another group of samples was evaluated for three moisture treatments (0.10, 0.20, and 0.30 g g^{-1}) at a constant temperature (15°C), representing winter temperature conditions; each treatment consisted of three replicates. Carbon efflux from each incubation jar was measured periodically using a dynamic technique; the method assesses carbon dioxide efflux by measuring the time rate of change in CO_2 as air circulated through a closed system that was connected to a Li-Cor 6262 infrared gas analyzer.

3. Results and Discussion

3.1. Weather Pattern and Grass Phenology

[25] To understand how ecosystem respiration responds to environmental perturbations, we begin by presenting some of the key meteorological and ecophysiological variables, including air temperature, precipitation, soil moisture, and leaf area index. As an example, seasonal variation in daily maximum (T_{max}) and minimum (T_{min}) air temperature and daily precipitation from year 2003 are illustrated in Figure 1.

[26] There were pronounced variations in temperature over a season. Maximum air temperature, T_{max}, for example, ranged from just over 10°C in the winter and early spring to an extreme high of over 40°C in the summer after the grass had senesced (Figure 1a). The wide temperature range encountered by the ecosystem over the course of a couple of days is also worth noting. For example, T_{max} could change as much as 15°C because of air mass movements from the coast or the continent.

[27] Because of the Mediterranean climate, over 95% of precipitation fell between October and April, the typical wet season (Figure 1b). The annual precipitation in 2003 was 434 mm, a below-normal (559 mm) amount. Nevertheless, winter rainfall provided enough moisture to recharge the soil profile. For example, surface layer (0–0.05 m) θ_v was around 0.30 m^3 m^{-3} or higher during the wet season. When the wet season was over, volumetric water content, θ_v, declined within a month to a low steady state value in the range of 0.03–0.05 m^3 m^{-3} (Figure 2a). Vigorous growth of grass, combined with a shallow soil profile, relatively light soil texture, and high evaporative demand, caused a rapid depletion of soil moisture. This large seasonal variation in θ_v, along with the wide range of diel and seasonal temperature, provides us a unique opportunity to better define temperature response and moisture response curves of carbon flux of the ecosystem.

[28] In correspondence with changes in soil moisture, soil water potential varied from around −0.5 MPa in the wet season to the extreme of −16.4 MPa at the end of dry season. We also note that a small change in θ_v in dry summer could result in a large soil water potential change. For instance, 11.5 mm of rain on DOY 214 increased

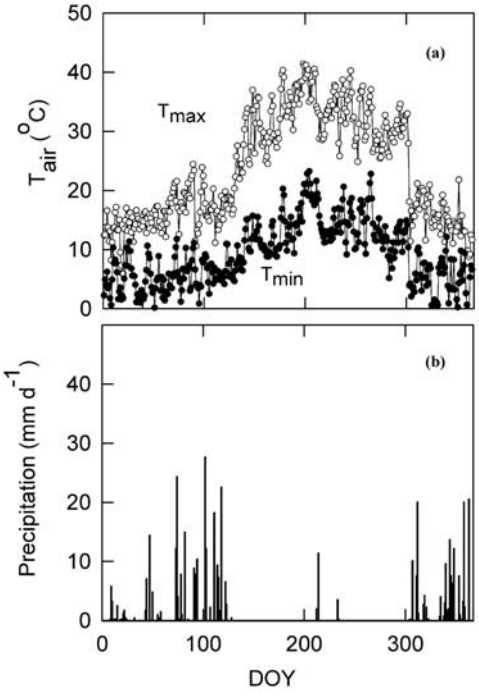

Figure 1. (a) Seasonal variations of maximum (T_{max}) and minimum (T_{min}) air temperature and (b) daily precipitation from the grassland site in 2003.

surface layer soil moisture only by 2.6% (from 4 to 6.6%), but soil water potential jumped from −14.5 to −4.4 MPa.

[29] Because of its shallow rooting depth the grass was unable to tap any moisture from deep layers. Consequently, its phenological development followed soil moisture closely, which, in turn, depended on the rainfall. Grass seed germination normally occurs in the fall, 1 week after a major rain event with total precipitation of at least 15 mm [*Bartolome*, 1979; *Xu and Baldocchi*, 2004]. After germination the grass typically undergoes a period of slow vegetative growth in the wintertime as we can see from seasonal LAI data from both sites (Figure 2b). In general, periodic frosts, low light, and soil temperature limit growth during the winter. In the spring, warming temperatures, longer day length, and ample soil moisture cause grass growth to accelerate. In our study the maximum grass height in the peak growth period (late April to early May) could reach up to 0.55 ± 0.12 m (n = 25) for the grassland site and 0.28 ± 0.06 m (n = 30) for the savanna site. Correspondingly, the maximum LAI of the open grassland was 2.5, and LAI of the grass understory was 1.0. The peak growth period did not last very long, however. The grass quickly senesced around DOY 160 at both sites, shortly after the wet season was over, and most of the available soil moisture was utilized (Figure 2b).

3.2. Impact of Soil Drying Down and Grass Phenology on the Temperature Dependency of Ecosystem Respiration

[30] To investigate the impact of soil moisture deficits on ecosystem respiration, we first developed a temperature function for respiration with the data from the vegetative stage, during the winter, wet season (Figure 3). In the analysis we excluded the data from the exponential growth period (DOY 45–92, Figure 2b) to minimize the confounding effect of growth respiration on the temperature function. An exponential curve fit of daily total respiration on soil temperature yielded a Q_{10} value (the factor by which respiration increases with a 10°C increase in temperature) of 2.3 and a coefficient of variation (r^2) of 0.90. Subsequently, we used this exponential function to evaluate the reference rate of ecosystem respiration (R_{ref}), the rate we would expect if there were no water stress or no growth enhancement.

[31] Data in Figure 4 show the relationship between respiration rates, normalized by temperature (R_{eco}/R_{ref}), and soil volumetric water content (θ_v). This analysis revealed several interesting results. First, when the soil moisture exceeded 0.15 m^3 m^{-3}, a group of data points had a value near 1.0, indicating that moisture was not a limiting factor, and temperature was the main controlling factor. Second, there was a group of data points located above one and as high as 1.5. After careful inspection we found that those points were from the exponential growth period during early spring (from DOY 45 to 92, Figure 2b). Third, normalized rates of ecosystem respiration decreased steadily from 1.0 to almost zero after volumetric soil moisture dropped below a threshold of 0.15 m^3 m^{-3}, which corresponded to a water potential of −0.8 MPa and represented 42% of field capacity. Fourth, rates of ecosystem respiration were close to zero by the time volumetric soil moisture was 0.10 m^3 m^{-3} or −2.0 MPa. Finally, large pulses of normalized values of R_{eco} occurred

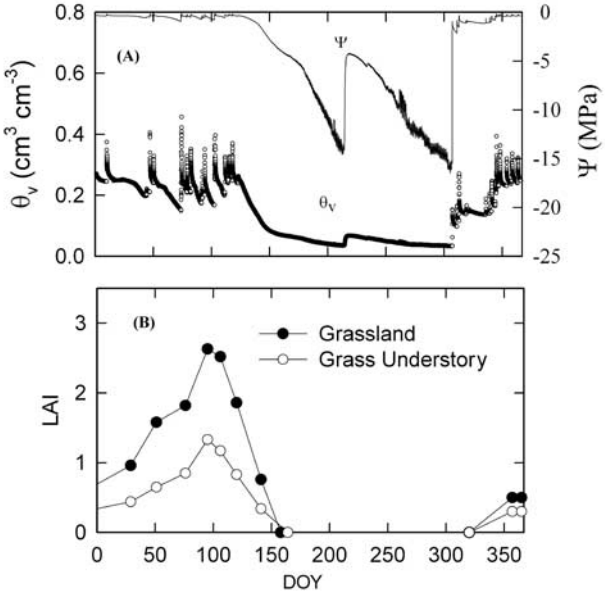

Figure 2. (a) Seasonal variations of soil volumetric water content (θ_v) and soil water potential (Ψ) estimated from soil moisture release curve and (b) grass leaf area index (LAI) from the grassland site and understory grass at oak savanna site. Data were obtained in year 2003.

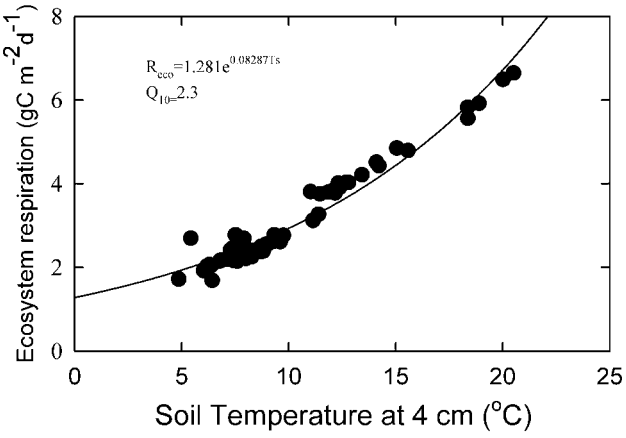

Figure 3. Relationship between soil temperature and ecosystem respiration of an annual grassland when soil moisture was adequate and the grass was in its vegetative stage.

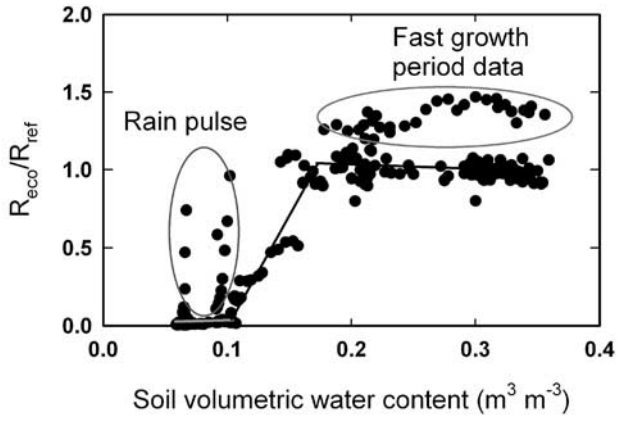

Figure 4. Ratio between ecosystem respiration (R_{eco}) and its reference value (R_{ref}) versus soil volumetric water content (θ_v). Soil moisture was averaged from the depth of 0–0.2 m. R_{ref} was computed from the temperature-dependent Q_{10} function.

when θ_v was below 0.1 m^3 m^{-3}. We suspect that these pulses reflect great stimulation in microbial activity by rain events during dry seasons, as we discuss in section 3.3.

3.3. Impacts and Dynamics of Rain Events on Ecosystem Respiration During Dry Season

[32] In this section, we quantify the dynamic response of soil and ecosystem respiration to moisture by examining data from an incubation study, a specific field case, and by synthesizing data from the numerous rain events we have observed over the past 3 years. Our laboratory incubation studies demonstrate that heterotrophic respiration from soil samples maintained at 15°C increased with increasing soil moisture (Figure 5). For example, 1.6 days after the start of the incubation experiment, CO_2 efflux rates from samples with 0.30 g g^{-1} moisture were more than 2.5 times greater than efflux rates sustained at 0.10 g g^{-1} moisture. Figure 5 also shows that the CO_2 efflux rates decreased with time as the size of the labile carbon pool was depleted. In order to distill and quantify the dynamics of these results, we computed the incubation half time, $t_{1/2}$, which we define as the period for a 50% reduction in CO_2 evolution. Data shown in Table 1 indicate that the incubation half time increased from 18 to 60 days, more than a factor of 3, as soil moisture decreased from 0.30 to 0.10 g g^{-1} (Table 1). These relatively short turnover times suggest that the microbes are digesting a relatively labile pool of carbon [*Amundson*, 2001]. We also conclude that the dynamics of heterotrophic respiration is faster when the soil is wet than when it is dry.

[33] Next, we examine how [CO_2] in the soil air pores changed after a substantial rain event at the oak savanna woodland site (Figure 6). The rain event was on DOY 214 2003, when 12.5 mm of precipitation fell. Prior to this rain event the soil surface layer was extremely dry; the volumetric soil water content was 0.03 m^3 m^{-3}, corresponding to a water potential of −15 MPa. The rain started in the morning around 0500 LT, and it was associated with an almost instantaneous response in soil CO_2 production. In just about an hour, soil [CO_2] at the depth of 0.02 m increased from its background level, near 617 ppm, to 900 ppm (Figure 6 inset). Then for the next half hour the growth rate of soil [CO_2] was as high as 181 ppm min^{-1}. By 0645 LT, soil [CO_2] leveled off at ~7100 ppm. This new equilibrium resulted from the balance between microbial CO_2 production and the diffusion of CO_2 through the wet soil column. Soil [CO_2] at the depths of 0.08 and 0.16 m showed an increase after the rain but at a much slower rate and with a time lag (Figure 6 inset). This increase was presumably caused by the diffusion of CO_2, produced at the surface, into deep layers, since soil moisture at those layers did not show any changes (data not shown).

[34] The fast response time (~1.0 hour) for the initiation of CO_2 production in the soil strongly suggests that even under severe water stress, surviving microbes are poised at a high state of "metabolic alertness" [*De Nobili et al.*, 2001].

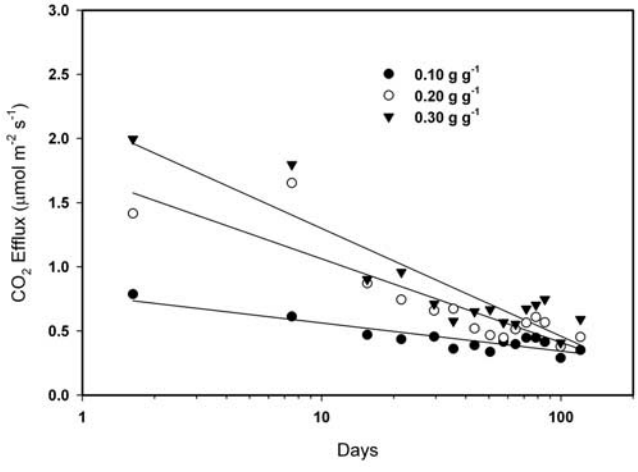

Figure 5. CO_2 efflux measured during a soil incubation study. The soil samples were maintained at 15°C and were exposed to three moisture levels.

Table 1. Information on the Relationship Between Soil Moisture and Soil Incubation Half Time, $t_{1/2}$[a]

Soil Moisture, g g^{-1}	$t_{1/2}$, days
0.1	61.0
0.2	20.7
0.3	18.8

[a]Soil incubation half time, $t_{1/2}$, is the number of days for a 50% reduction in CO_2 efflux. The incubation half time was computed by fitting a log linear regression through the data in Figure 5 ($F(t) = a + b \log(t)$). We then solved simultaneous equations for the cases when $F = 1$ and $F = 0.5$, leading to the following definition of $t_{1/2}$: $\log(t_{1/2}) = (a/2 - a)/b$.

In other words, they can utilize carbon substrates immediately when environmental conditions become favorable, such as when it rains. Several mechanisms may contribute to this rapid production of CO_2 by microbes. Early studies show that during the soil drying process a large amount of "water soluble organic substrate" becomes available by the cracking of organic colloids [*Birch*, 1959]. Subsequent wetting causes microbial cells to release a significant portion of the available substrate, including low molecular weight carbohydrates and other labile C solutes [*Halverson et al.*, 2000]. This is because when microbes are subjected to large change in soil water, potential cell lysis can occur (disruption of cell membrane due to excessive turgor pressure) [*Kieft et al.*, 1987]. Intracellular substrates that are released by cell lysis are subsequently consumed by surviving microbes.

[35] Our eddy covariance measurements of carbon efflux show that R_{eco} was also greatly stimulated after rain events. Two examples from each study site are presented in Figure 7a. The first example was from 2002 after a substantial rain event. The rain event was on DOY 311 and 312, when 61.1 mm of precipitation fell. The rain increased surface layer (0–0.05 m) volumetric soil moisture from 0.023 m^3 m^{-3} on DOY 310 to over 0.35 m^3 m^{-3} on DOY 313. Correspondingly, R_{eco} at the grassland site increased from 0.12 to 7.29 g C m^{-2} d^{-1}, a 60-fold increase. Then daily CO_2 efflux decreased exponentially with time as the soil moisture of the upper layers dried out by evaporation; evaporation from wetted soils normally proceeds at a rate proportional to the inverse of the square root of time [*Denmead*, 1984]. Respiration from the understory of the savanna woodland site showed a similar response to the rain event as the open grassland but with a much weaker peak value. Differences in carbon pool sizes alter the magnitude of the peak rate of respiration, as well as the basal rate [*Sanderman et al.*, 2003]. In this case the savanna site had less decomposing plant biomass and less soil carbon than the grassland site.

[36] A second and different case occurred on DOY 214 2003, when a smaller amount of precipitation fell, 12.5 mm. Soil moisture at the surface layer increased from 0.035 m^3 m^{-3} before to 0.067 m^3 m^{-3} after the rain. Again, R_{eco} increased suddenly. In this case, respiration increased from 0.25 to 6.66 g C m^{-2} d^{-1} for the open grassland and from 0.68 to 3.98 g C m^{-2} d^{-1} for the understory of the savanna. Again, R_{eco} of both ecosystems showed an exponential decrease with time but at a much faster decay rate as compared with the first example. We attribute this observation to the combination of less precipitation and higher soil temperature. It is worthwhile to point out that the peak values of respiration, as induced by the rain, were much higher than R_{eco} from vigorous growth stage when soil moisture was ample [*Xu and Baldocchi*, 2004], even after we accounted for the temperature difference. The strongest R_{eco} pulse was observed on DOY 267 2001 from the grassland site. An 8.9-mm rain event caused an 81-fold increase in R_{eco} (from 0.09 to 7.29 g C m^{-2} d^{-1}).

[37] The enhancement in R_{eco}, determined by the difference in respiration before and after rain events, was inversely related to background R_{eco} (Figure 7b), suggesting a strong dependency of the enhancement on initial condition of the soil moisture. This observation is consistent with some of the laboratory studies. For example, *Birch* [1959] found that the amount of carbon respired after wetting a dry soil is related to how long the soil has remained in a dry condition. Other studies [*Kieft et al.*, 1987; *Orchard and Cook*, 1983] show that the amount of available substrate released from microbial cells is directly proportional to the magnitude of change in water potential when a dry soil is wetted.

[38] We computed the dynamic time constant (τ) to quantify the decay rate of R_{eco} after rain events by fitting the data to the following function:

$$R_{eco} = b_0 + b_1 e^{-t/\tau},$$

with t being the number of days after the rain event. The coefficients, b_0 and b_1, represent the background and the enhancement of R_{eco}. The coefficient τ represents the time required for R_{eco} to decline to $1/e$ (e is the base for natural log) of its peak value. Statistical analysis indicates that τ

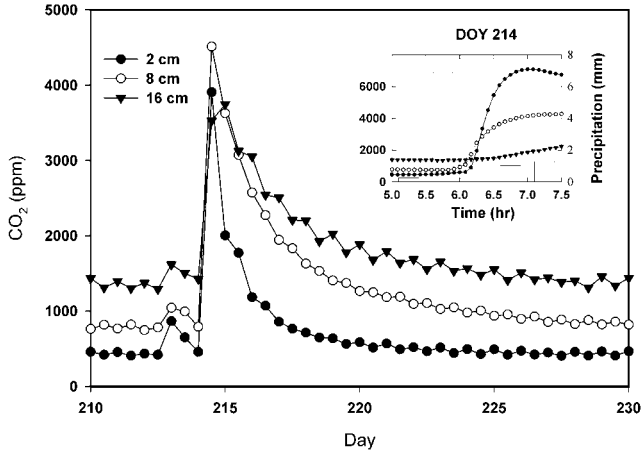

Figure 6. Example of fast response of soil microbial activity to rain events. Data represent changes in soil CO_2 concentration at depths of 0.02, 0.08, and 0.16 m as measured with soil IRGA probes at the savanna woodland site. The rain event was on 2 August (DOY 214) 2003 with total amount 12.5 mm. Inset is enlargement of the rain event to show the different responses for soil air CO_2 concentration at different depths. Also shown in the inset is the time course of precipitation.

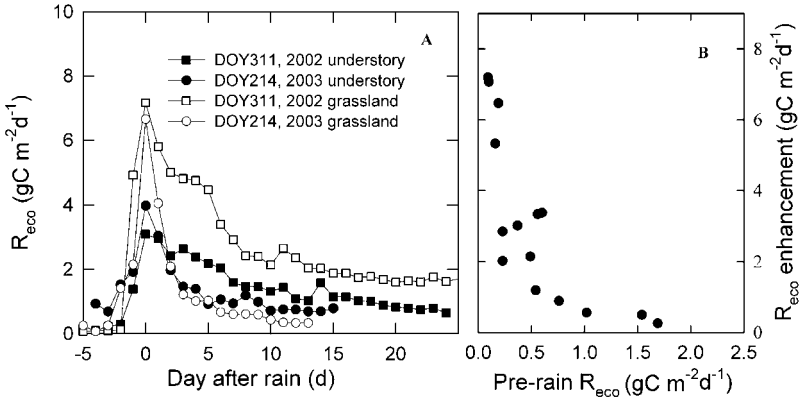

Figure 7. (a) Examples of ecosystem respiration (R_{eco}) response to rain events in the understory of the savanna woodland and the grassland. Data were obtained from continuous eddy covariance carbon flux measurements on DOY 311 2002 at understory and grassland and on DOY 214 2003 at understory and grassland. The two examples show a great stimulation of R_{eco} by rain events and their exponential decay. (b) Enhancements of R_{eco} (the difference in respiration after and before rain events), which were found to be inversely related to prerain R_{eco}.

was a linear function of the amount of rain (Figure 8a) with the coefficient of determination (r^2) equaling 0.90 and 0.97 for the understory and the grassland, respectively. Note that for the same amount of rainfall, τ at understory was longer than for the grassland because shading by the trees lowered the evaporation rate of the soil [*Baldocchi et al.*, 2004].

[39] The total amount of carbon respired from each rain event ranged between 2.1 and 70.1 g C m^{-2}. The total amount of respired carbon was linearly correlated with the amount of precipitation (Figure 8b), and the regression slope was site-dependent; a lower slope was associated with CO_2 efflux from the understory. The linear relationships presented in Figure 8 suggest that for a particular site, moisture was the most limiting factor for carbon decomposition during rain pulse events. Site-dependent differences in the regression slope were partly attributed to the different pool sizes of liable and recalcitrant carbon at the soil surface layers. Our grass biomass production and soil inventory data support this argument; both aboveground net primary productivity (251.5 g C m^{-2}) and soil carbon content (1.39%) of the annual grassland were greater than what was measured at the savanna site (68.7 g C m^{-2} and 0.95%, respectively). This finding is also consistent with a recent study by *Jackson et al.* [2002], who showed that grasslands have more soil organic carbon at the surface layer than that for shrub or woody lands.

[40] The amount of carbon respired from the few summer rain events was not trivial. One instance, when respiration approached 70 g C m^{-2}, was equivalent to almost 10% of gross primary production. It is very likely that the carbon loss associated with one or two rain events could produce more respiration than from the rest of dry season, which typically proceeds at a rate 0.1 and 0.3 g C m^{-2} d^{-1} when the soil is dry [*Xu and Baldocchi*, 2004]. In comparison, *Lee et al.* [2004] recently reported that respiration pulses caused by rain in a temperate deciduous forest constituted $\sim$18 g C m^{-2}, a value approximating 5–10% of its net primary productivity.

[41] The magnitude of the carbon loss by rain pulses is comparable to the annual net carbon exchange of many terrestrial ecosystems, including forest, grassland, and other biomes, as deduced from the FLUXNET http://

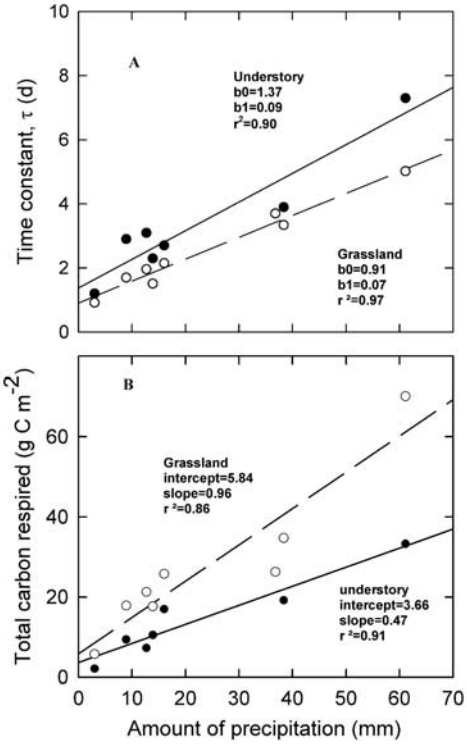

Figure 8. Relationships between the (a) time constant (τ) for R_{eco} decay and (b) total ecosystem carbon loss via stimulated respiration with the amount of precipitation of the rain event for the grassland and the understory of savanna woodland.

www-eosdis.ornl.gov/FLUXNET) data set [*Baldocchi et al.*, 2001]. For example, *Janssens et al.* [2003] found that the average net ecosystem production across European forests was 92 g C m^{-2} yr^{-1}. Thus our study clearly demonstrated that the impact of rain pulses on R_{eco} should not be ignored in the study of carbon balance of terrestrial ecosystems, especially in modeling studies for arid and semiarid ecosystems.

[42] This study is among the first ones to quantify the dynamics of respiration pulses after rain events at the ecosystem level, a process that only can be observed with a continuous flux measurement system. In contrast, manually deployed soil chambers sample the soil respiration at certain time intervals, so they are apt to miss such pulses and to underestimate the integrated amount of carbon lost by the ecosystem. For example, *Knapp et al.* [2002] altered the rainfall pattern at a grassland in Kansas (they exposed the system to fewer, but larger rain events that produced the same total annual precipitation). They found that the altered rainfall pattern reduced soil respiration, which is the opposite of our results, but they sampled soil respiration at weekly intervals and may have missed a significant part of any respiratory pulse.

[43] Our result on R_{eco} pulse has several implications for understanding the global carbon cycle. First, our result, though obtained in California, should be applicable in arid and semiarid ecosystems including tropical grasslands and savanna woodlands, warm desert and semidesert, temperate grassland, and other Mediterranean ecosystems with dry-wet seasons. These lands cover over one third of the Earth's land surface and play a significant role in the global carbon cycle [*Grace and Rayment*, 2000]. Second, precipitation often falls in the forms of pulses in semiarid and arid regions [*Noy-Meir*, 1973], and they experience large year-to-year variation in rainfall [*Knapp and Smith*, 2001]. Using mean soil temperature and moisture will inevitably produce an underestimate in the sum of ecosystem respiration because they do not account for the respiration pulse after rain events. Finally, many climate change scenarios predict a global trend toward increasing extremes in precipitation without changing the total precipitation. Also, two observational studies, based on the past 80-year precipitation data, show such a trend [*Easterling et al.*, 2000; *Karl et al.*, 1995] that may reflect global warming or may be a consequence of natural variation [*Kunkel et al.*, 2003].

4. Conclusion

[44] On the basis of multiyear continuous data sets of carbon flux measurement over two Mediterranean ecosystems we presented information on how ecosystem respiration responds to a slow drying down of soil moisture, a sudden increase in soil moisture, and a rapid change in growth. We have demonstrated that growth respiration sometimes could attribute up to one third of total ecosystem respiration during the fast grass growth period in the early spring. Soil moisture started to limit ecosystem respiration when the volumetric soil water content decreased to below 0.15 m^3 m^{-3}. R_{eco} gradually decreased as soil moisture dropped down to 0.10 m^3 m^{-3}, and then respiration almost shut down when soil moisture further dried down (<0.10 m^3 m^{-3}).

[45] The soil moisture threshold that initiates the reduction in ecosystem respiration was much lower than previously published data. For example, some studies have reported that soil moisture could start to limit the respiration when it dropped to below 75% of field capacity [*Davidson et al.*, 1998; *Rey et al.*, 2002].

[46] During dry seasons, soil microbes respond quickly (within an hour) to a sudden increase in soil moisture from occasional rain events. We observed short-lived but very strong R_{eco} pulse after rain events. The magnitude of the pulse was inversely related to prerain R_{eco}. Even though only a few rain events may occur during the summer of each year, the carbon loss from those rain events is significant. It is comparable to annual net ecosystem CO_2 exchange of many ecosystems [*Janssens et al.*, 2003]. This study demonstrates that it is imperative to have continuous measurement of soil respiration in order to understand the total soil respiration of an ecosystem. Neglecting the pulse effect as stimulated by rain events in modeling study, one would definitely underestimate the soil respiration, especially for arid and semiarid ecosystems.

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