Biogeochemistry (2005) 73: 183–207
DOI 10.1007/s10533-004-5889-6

Spatial–temporal variation in soil respiration in an oak–grass savanna ecosystem in California and its partitioning into autotrophic and heterotrophic components

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Key words: CO_2 efflux, Root respiration, Savanna, Soil respiration, Spatial and temporal variation

Abstract. The spatial upscaling of soil respiration from field measurements to ecosystem levels will be biased without studying its spatial variation. We took advantage of the unique spatial gradients of an oak–grass savanna ecosystem in California, with widely spaced oak trees overlying a grass layer, to study the spatial variation in soil respiration and to use these natural gradients to partition soil respiration according to its autotrophic and heterotrophic components. We measured soil respiration along a 42.5 m transect between two oak trees in 2001 and 2002, and found that soil respiration under tree canopies decreased with distance from its base. In the open area, tree roots have no influence on soil respiration. Seasonally, soil respiration increased in spring until late April, and decreased in summer following the decrease in soil moisture content, despite the further increase in soil temperature. Soil respiration significantly increased following the rain events in autumn. During the grass growing season between November and mid-May, the average of CO_2 efflux under trees was 2.29 μmol m^{-2} s^{-1}, while CO_2 efflux from the open area was 1.40 μmol m^{-2} s^{-1}. We deduced that oak root respiration averaged as 0.89 μmol m^{-2} s^{-1}, accounting for 39% of total soil respiration (oak root + grass root + microbes). During the dry season between mid-May and October, the average of CO_2 efflux under trees was 0.87 μmol m^{-2} s^{-1}, while CO_2 efflux from the open areas was 0.51 μmol m^{-2} s^{-1}. Oak root respiration was 0.36 μmol m^{-2} s^{-1}, accounting for 41% of total soil respiration (oak root + microbes). The seasonal pattern of soil CO_2 efflux under trees and in open areas was simulated by a bivariable model driven by soil temperature and moisture. The diurnal pattern was influenced by tree physiology as well. Based on the spatial gradient of soil respiration, spatial analysis of crown closure and the simulation model, we spatially and temporally upscaled chamber measurements to the ecosystem scale. We estimated that the cumulative soil respiration in 2002 was 394 gC m^{-2} $year^{-1}$ in the open area and 616 gC m^{-2} $year^{-1}$ under trees with a site-average of 488 gC m^{-2} $year^{-1}$.

Introduction

On a global basis, the pool of soil carbon is huge (~1500 GtC) and the magnitude of soil carbon fluxes is large compared with anthropogenic carbon emissions (~68 GtC $year^{-1}$ vs. 5.4 GtC $year^{-1}$) (Raich and Schlesinger 1992;

Raich and Potter 1995; IPCC 2001). In order to construct global carbon budgets, detailed information at the local scale is needed from a diverse range of ecosystems and climate zones because the spatial and temporal variation in soil respiration is high (Rayment and Jarvis 2000; Law et al. 2001; Raich et al. 2002). Upscaling such information is complicated because the great heterogeneity in time and space due to the dynamics and the relative contribution of the autotrophic and heterotrophic processes that maintain metabolism of the plants and decompose dead carbon. On a local basis, the spatial and temporal variations in soil respiration are significant and the sensitivity to environmental conditions (temperature, soil moisture, soil texture) is complex and non-linear (Hanson et al. 1993; Xu and Qi 2001).

Our partial understanding of the spatial and temporal complexity of soil respiration stems from the methods that are available to researchers in the field. Portable soil chambers allow investigators to study treatments and spatial patterns, but they do not allow investigators to make continuous and long-term measurements of soil respiration. In contrast, the understory eddy covariance method (Baldocchi and Meyers 1991; Law et al. 1999a), automated soil chambers (Goulden and Crill 1997; Russell et al. 1998; Scott et al. 1999; Drewitt et al. 2002; Irvine and Law 2002; King and Harrison 2002), and profile measurements from soil CO_2 sensors (Tang et al. 2003; Hirano et al. 2003) provide continuous measurements and parameterization necessary for modeling the temporal patterns of soil respiration. But due to their expense and complexity, they do not allow the investigator to replicate the measurements at many places.

Temporal patterns of soil respiration have been simulated by using the continuous records of temperature, moisture and other variables (e.g., Raich and Schlesinger 1992; Davidson et al. 1998; Epron et al. 1999; Xu and Qi 2001; Treonis et al. 2002). However, the spatial difference of soil respiration within a site and between sites is often not explained by climatic variables, but is modulated by gradients in biological activity and by differences in soil moisture, texture, and chemistry. Methods in quantifying spatial variation in soil respiration are limited and proved to be difficult (Rayment and Jarvis 2000). As a result, compared with studies on the temporal variation in soil respiration, relatively few publications have explored in depth spatial variation in soil respiration and thus indicated our limited understanding on this topic. For example, Goulden et al. (1996), Law et al. (2001) and Xu and Qi (2001) reported significant spatial variation in soil respiration. Hanson et al. (1993) studied the spatial variability in forest floor respiration by investigating the reason from topographically distinct locations. Rayment and Jarvis (2000) correlated spatial variation empirically with the thickness of the dead moss layer. Shibistova et al. (2002) concluded that the spatial variability may be related to root density. Scott-Denton et al. (2003) found a correlation between spatial variation and the distance from trees. These studies cited above reported various determinants for spatial variation in soil respiration over various sites. However, most of these studies have not provided quantitative

analysis on the determinants of spatial variation in soil respiration; nor have they provided spatially upscaling methods.

A major reason for the high spatial variation could be explained by the different contribution of functionally different components of soil respiration such as rhizosphere respiration (including root autotrophic respiration and associated mycorrhizae respiration) and microbial heterotrophic respiration in a vegetation-covered land. The heterogeneity of vegetation coverage, root distribution, soil microbial community, and microclimatic conditions contribute to the spatial variation in soil respiration. Partitioning of soil respiration helps us identify the source of spatial variation. For example, under the same environmental conditions and magnitude of heterotrophic respiration, total soil respiration may differ in areas with greater and less root density. Given the same total soil respiration but different ratio of each component (i.e., root vs. microbes) over space at a certain time, changing of abiotic factors such as soil temperature and moisture over time may cause the spatial difference of total soil respiration because the different components of soil respiration respond differently to abiotic factors. While heterotrophic respiration is driven mainly by soil temperature and moisture, root respiration may be closely affected by the physiology associated with autotrophic respiration. A few reports contended that soil respiration may be controlled more by photosynthesis and productivity than by traditionally believed soil temperature. For example, using isotope techniques, Kuzyakov and Cheng (2001) found rhizosphere respiration is strongly controlled by plant photosynthesis. By conducting a large-scale tree-girdling experiment, Hogberg et al. (2001) concluded that current photosynthesis drives soil respiration in addition to environmental parameters. Janssens et al. (2001) summarized CO_2 flux data from 18 EUROFLUX sites and found soil respiration depends more on forest productivity than on temperature. By conducting shading and clipping experiments, Craine et al. (1999) reported that carbon availability to roots can be more important than temperature in determining soil respiration. These studies indicate that partitioning of soil respiration is a key to understand the driving factors and the mechanism of spatial variation in soil respiration.

Several experimental methods have been used to partition soil respiration and compute the ratio of root (rhizosphere) respiration to total soil respiration (F_a/F). Hanson et al. (2000) reviewed and summarized methods into root biomass measurement, root exclusion methods, and isotopic techniques. They found that F_a/F varies from 10 to 90% depending on vegetation type and season of the year. Most of these methods are destructive, except for the isotopic technique, which is also subject to some limitations and unproved assumptions (Lin et al. 1999; Bowling et al. 2003).

Oak–grass savanna ecosystems in California provide a unique natural laboratory to study spatial variation and partitioning of soil respiration *in situ* and in a non-destructive manner: during the dry summer oak trees are growing while the grass is dead; during the winter the grass grows while the

oak tree is dormant; during the spring, both the grass and trees are growing. The sparse distribution of oak provides natural gaps for studying the spatial pattern of soil respiration, and for separating the contributions of respiration from roots that support photosynthetically active trees and heterotrophic microbes that decompose dead grass. Despite of these characteristics, publications focusing on spatial patterns of soil respiration in the savanna have not been seen.

This paper aims to (1) quantify the spatial variation in soil respiration in the savanna ecosystem; (2) quantify the relative contributions of heterotrophic respiration and autotrophic respiration to soil respiration; (3) describe the seasonal variation in heterotrophic respiration, autotrophic respiration, and F_a/F ratio; (4) analyze the main factors influencing spatial variation in soil respiration; and (5) upscale periodical measurements of soil respiration along a transect to the whole site over a year.

Materials and methods

Site description

The field study was conducted at an oak–grass savanna (38.4311° N, 120.9660° W and 177 m), one of the AmeriFlux sites, located at the lower foothills of the Sierra Nevada Mountains near Ione, California. The climate is Mediterranean – hot and dry with almost no rain during the summer and relatively cool and wet during the winter. Mean annual temperature and precipitation over the recent 30 years at a nearby weather station with similar altitude and vegetation are 16.3 °C and 559 mm, respectively.

The overstory of the savanna consists of scattered blue oak trees (*Quercus douglasii*), with occasional gray pine trees (*Pinus sabiniana)* (3 ha^{-1}). The density of forest stand was 194 stems per hectare, with a mean height of 7.1 m, diameter at breast height (DBH) of 0.199 m, and basal area of 18 m^2 ha^{-1} in 2000 (Kiang 2002). From an Ikonos panchromatic satellite image for this site, with a resolution of 1 m by 1 m, we classified the study site into tree crown areas and open space using the software Geomatica (PCI Geomatics, Canada). The percentage of the ground area covered by the crown area, or crown closure, was 42.4% at this site. The understory landscape has been managed, as the local rancher has removed brush and the cattle graze the herbs. The main grass and herb species include *Brachypodium distachyon*, *Hypochaeris glabra*, *Bromus madritensis*, and *Cynosurus echinatus*.

The oak trees leaf out normally at the end of March. In about 2 weeks, its leaf area index (LAI) reaches its maximum value of about 0.6. The growing of the understory grass is confined in the wet season, usually from November to the middle of May in the next year. The maximum LAI of the grass is around 1.0.

Soils

The soil of the oak–grass savanna is the Auburn very rocky silt loam (Lithic haploxerepts). The soil profile is about 0.75 m deep, and overlays fractured rock. In the open area soils are composed of 48% of sand, 42% of silt, and 10% of clay with a bulk density of 1.64 g cm^{-3}, and 0.92% of C and 0.10% of N. Soils under canopy are composed 37.5% of sand, 45% of silt, and 17.5% of clay with a bulk density of 1.58 g cm^{-3}, and 1.09% of C and 0.11% of N. Soil texture and chemical composition were analyzed at DANR Analytical Laboratory, University of California, Davis.

Environmental measurements

Air temperature and relative humidity were measured with a platinum resistance thermometer and solid-state humicap, respectively (model HMP-45A, Vaisala, Helsinki, Finland). Soil temperature at the depth of 2, 4, 8, 16, and 32 cm were measured with multiple-level thermocouple sensors. 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, UK). 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) from six locations along a transect and three locations elsewhere were also measured weekly and manually using an enhanced time domain reflectometer (Moisture Point, model 917, E.S.I. Environmental Sensors Inc, Victoria, Canada). Ancillary meteorological and soil physics data were acquired and logged on CR-23x and CR-10x dataloggers (Campbell Scientific Inc., Utah, USA). The sensors were sampled every second, and half-hour averages were computed and stored on a computer to coincide with the flux measurements.

Soil respiration measurements

We established a 42.5 m transect between two oak trees in the savanna that traversed an open patch along the east–west direction, starting in June 2001. At the west side of the transect was a big oak tree with DBH of 0.716 m, tree height of 11.65 m, and an average of crown diameter of 13.05 m. The other oak tree at the east side of the transect was smaller, with DBH of 0.398 m, tree height of 11.25 m, and an average of crown diameter of 6.05 m. A schematic of the transect with a background of the Ikonos panchromatic satellite image for the study site is presented in Figure 1.

We inserted 11 soil collars, each with a height of 4.4 cm and a diameter of 11 cm, into the soil along the transect for measuring soil respiration. During the growing season, grasses growing inside the collars were removed but we did

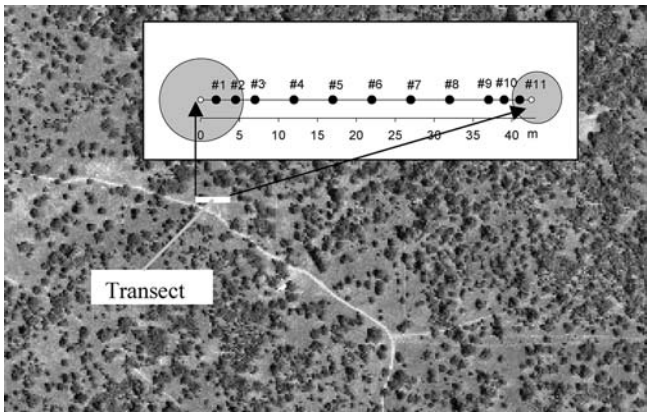

Figure 1. A schematic of the transect with a background of the Ikonos panchromatic satellite image. The resolution of the Ikonos image is 1 m by 1 m. The two gray circles at each side of the transect indicate the crowns of two trees. The 11 dark dots indicate the sample location along the transect where we measured soil respiration.

not disturb the grasses growing surrounding the collars. Thus we presumed that the CO_2 efflux from the collars during the grass growing season was composed of both microbial respiration and grass root respiration that sourced from the grass surrounding the collar with roots reaching beneath the area circled by the collar. The three collars closest to the western tree (#1 to #3) were 2.5 m away from each other, #3 to #9 in the middle of the transect were 5 m away from each other, and #9 to #11 were 2 m away from each other. The distance between the western tree and #1 collar was 2 m, and between #11 collar and the eastern tree was 1.5 m (Figure 1). The purpose of this sampling was to insure that there were samples located in the middle of vertically projected tree crown radii, i.e., the average of #1 and #2 (3.25 m from the tree) was located in the middle of crown radii of the western tree, and #11 (1.5 m from the tree) was located in the middle of crown radii of the eastern tree. In order to study more details about the relationship between soil respiration and location of the measurement, we further installed four more collars between the western tree and #3 in November 2002, so that within 7 m we had seven collars each 1 m away since then.

Soil respiration was measured using a soil chamber (LI6400-09, LI-COR Inc, Nebraska, USA) connected to a portable photosynthesis system (LI-6400, LI-COR Inc, Nebraska, USA) for data collection and storage. Soil temperature at 5 cm depth was measured using the attached soil temperature probe. Soil respiration was measured every 3–4 weeks. Typically, soil respiration was measured along the transect about 3–4 rounds in a day. To catch the diurnal pattern, we measured the transect nine times on August 17 (day 229) and September 6 (day 249), 2001. The paper covers measurement data from July 2001 to December 2002. But we also report additional measurements in July

and August 2003 for studying the relationship between soil respiration and distance from trees.

Temporal and spatial upscaling

In order to estimate the cumulative soil respiration based on periodical measurements, we temporally upscaled periodical measurements based on an empirical equation with soil temperature and moisture as two driving variables. We found that the following functional form with two independent valuables explained best the variation in soil respiration data (Eq. (1)):

$$F = \beta_0 \, e^{\beta_1 T} e^{\beta_2 \theta + \beta_3 \theta^2} \qquad \text{or} \qquad \ln(F) = \ln(\beta_0) + \beta_1 T + \beta_2 \theta + \beta_3 \theta^2, \quad (1)$$

where F (μmol m^{-2} s^{-1}) is the soil CO_2 efflux, T (°C) is the soil temperature, θ (m^3 m^{-3}) is the soil volumetric moisture, and β_0, β_1, β_2, and β_3 are the model coefficients. The equation can be log-transformed to a linear model in order to conduct linear regression to estimate the parameters.

Because of the spatial heterogeneity, we need to spatially upscale chamber measurements of soil respiration to the site scale based on information from the spatial gradients of soil respiration along the transect and crown closure at the study site. We used the average of measurements under the two trees located in the midpoint of crown radii at each side of the transect to represent soil respiration under trees. The average of soil respiration in open areas beyond crown shadow is used to represent soil respiration without the influence from tree roots. Thus, we used crown closure, derived from the Ikonos image, as a weight to spatially average soil respiration over the whole study site. The simple equation can be expressed as Eq. (2):

$$F = F_u \cdot \rho + F_o \cdot (1 - \rho), \quad (2)$$

where F is the soil respiration from the site scale, F_u is the average of soil respiration under trees with tree root component, and F_o is the average of soil respiration in the open without tree root component, and ρ is the crown closure, measured by the vertically projected crown area divided by the whole area.

The average of soil respiration over a crown circle was measured at the midpoint of any radius centered from the stem. Theoretically we can prove the validity of this method if we know the correlation between soil respiration and the distance from stems. Assuming the tree crown is a circle with the radius of R and soil respiration decreases as it radiates from the tree with F_r at any given radius r when $r \leq R$, soil respiration from the circumference with the radius r is $2\pi \, rF_r \, dr$. Thus total soil respiration from the crown area of a tree is

$$F_T = \int_0^R 2\pi r F_r \, dr. \quad (3)$$

If we use an inverse equation to express F_r as a function of r, which was derived by measurements at this site, we have

$$F_r = \beta_0 + \frac{\beta_1}{r}, \tag{4}$$

and thus

$$F_T = \int_0^R 2\pi r\left(\beta_0 + \frac{\beta_1}{r}\right)\mathrm{d}r = \beta_0\pi R^2 + 2\beta_1\pi R. \tag{5}$$

The average of soil respiration rate from the crown area (πR^2) would be

$$\overline{F}_T = \beta_0 + \frac{2}{R}\beta_1. \tag{6}$$

Eq. (6) indicates that if an inverse relationship holds for soil respiration and the distance, the average point of soil respiration over the crown area is located at the midpoint of the radius from the stem.

There are two major assumptions for the upscaling method described in Eq. (2). First, the crown-based average of soil respiration from any tree is the same regardless of the tree size. Second, the inverse equation in Eq. (4) can be applied to any size of trees at this site (but may have different coefficients). Thus, big trees with larger crown areas may have more total soil respiration than small trees, but the average of soil respiration measured at the midpoint could be the same for all trees.

Results and discussion

Soil respiration along the transect

Significant temporal variation in soil respiration was observed between the grass growing season (the wet season, November to mid-May) and the dry season (mid-May to October) when the annual grass is dead. The growing season of oak trees covers half of the wet season (April–May) and the whole dry season. During the wet season, soil CO_2 efflux under trees is composed of tree root respiration, grass root respiration, and microbial respiration, while soil CO_2 efflux from the open area is composed of grass root respiration and microbial respiration. During the dry season, soil CO_2 efflux under trees is composed of tree root respiration and microbial respiration, while soil CO_2 efflux in the open area is only from microbial respiration. We averaged CO_2 efflux over the wet season and over the dry season, respectively, and plotted efflux data along the transect starting from the western end in Figure 2.

Figure 2a indicates that during both the wet and dry season, the spatial variation in soil respiration was significant and reflects the significant influence

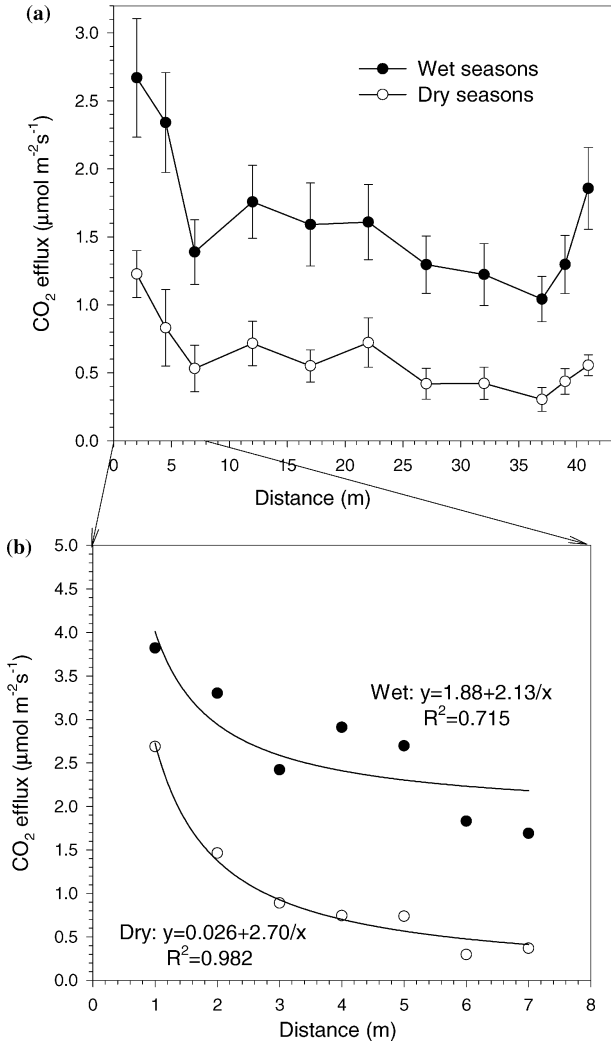

Figure 2. (a) Soil respiration against distance along the transect during the wet and dry seasons, covering from July 2001 to December 2002. Error bars indicate SDs. (b) An inverse equation ($y \sim 1/x$) fits the datapoints within 7 m distance; each datapoint during the wet season is the average over November and December 2002, and during the dry season is the average over July and August 2003.

of respiration from tree roots. Within the distance of 7 m, soil respiration dropped quickly with the increase of distance from the tree. Between 7 and 39 m from the western side, soil respiration varied numerically, but we did not find a significant trend. Between 39 and 42.5 m, soil respiration increased again because of the influence of the smaller tree in the eastern side of the transect.

Table 1. Summary of mean soil respiration, standard deviation (SD) and coefficient of variation (CV) along the whole transect, in the open areas, and under trees during the wet and dry season.

	Distance (m)	Sample number	Season	Mean flux (μmol m^{-2} s^{-1})	SD (μmol m^{-2} s^{-1})	CV (%)
Whole transect	0–42.5	11	Wet season	1.64	0.49	30.1
			Dry season	0.61	0.26	42.1
Open areas	7–39	8	Wet season	1.40	0.24	16.8
			Dry season	0.51	0.15	28.9
Under trees	0–7 and 39–42.5	3	Wet season	2.29	0.41	17.9
			Dry season	0.87	0.34	38.7

Table 1 summarizes the spatial variation in soil respiration along the whole transect, in the open areas, and under trees during the wet and dry season.

By comparing the spatial variation in the open space beyond the crown shadow and the whole transect including oak trees, we found that the coefficient of variation (CV) decreased from 30.1% for the whole transect to 16.8% for the open space during the wet season, and decreased from 42.1 to 28.9% during the dry season. The decrease in spatial variation in the open space is mainly due to the lack of tree roots, because root respiration is an important component of total soil respiration when live roots exist in soils. When we compared the spatial variation between the wet and dry season, we found the standard deviation (SD) during the wet season to be greater than that during the dry season, but CV (SD/mean) during the wet season was smaller than that during the dry season. This is due to the greater magnitude of the mean soil respiration during the wet season. Therefore, normalized by mean values, the spatial variation during the wet season is less than that during the dry season. The decreased variation could be explained by the presence of grass during the wet season. The relative homogeneous grass coverage and grass root respiration during the grass growing season reduced the spatial variation in total soil respiration.

Seasonally, the magnitude of soil respiration at any location was higher during the wet season than during the dry season, even though the average soil temperature at 4 cm during the wet season (12.1 °C in 2002) was much lower than the dry season (24.2 °C in 2002). This seasonal difference in soil respiration and its decoupling with temperature could be explained by the seasonal difference in soil moisture and biological activity. The moisture at 5 cm during the wet season (25.1% volumetric in 2002) was much higher than during the dry season (7.1% in 2002). The suitable moisture condition for vegetative and microbial growth during the wet season contributes to the higher soil respiration. During the dry summer when soil temperature maximizes and inversely correlates with soil moisture, soil is dry and respiration has diminished. In addition to climatic factors, root respiration from grass also contributes to the increase in soil respiration during the wet season.

The ratio of root respiration vs. total soil respiration

The major factors explaining the difference of soil respiration under trees and in the open areas are from tree roots, including those from root respiration, root exudates and microbial community and activity associated with tree metabolism. Here we incorporated these factors into root respiration and assumed that the difference between soil respiration under trees and in the open areas is from oak root respiration. During the wet season, the average of CO_2 efflux under trees was 2.29 μmol m^{-2} s^{-1}, while CO_2 efflux in the open areas was 1.40 μmol m^{-2} s^{-1}. Oak root respiration averaged 0.89 μmol m^{-2} s^{-1} during the wet season, accounting for 39% of total soil respiration (oak root + grass root + microbes). During the dry season the average of CO_2 efflux under trees was 0.87 μmol m^{-2} s^{-1}, while CO_2 efflux in the open areas was 0.51 μmol m^{-2} s^{-1}, inferring that oak root respiration was 0.36 μmol m^{-2} s^{-1}, accounting for 41% of total soil respiration (oak root + microbes). The microbial decomposition accounted for 59% of soil respiration during the dry season.

The root contribution to total soil respiration at this site is lower than the average value of 45.8% for forested land (Hanson et al. 2000). It is also lower than ones in several reports conducted in mixed oak forests or woodlands such as 52% (Kelting et al. 1998), 90% (Thierron and Laudelout 1996), and 84% (Edwards and Rosstodd 1983). We have not seen any other report on this subject from oak savannas. We speculate that the oak roots constitute a relatively low fraction of soil CO_2 efflux because of the sparse distribution of oak trees and consequently a low density of root biomass. Even if roots can extend horizontally beyond the dripline of the trees, the probability of overlapped tree roots from different trees is low in the savanna, consistent with the spherical shape of canopy due to the lack of competition for light.

This sparse canopy structure could be explained by the severe drought in the summer at the savanna. In contrast, other forests or woodlands with less constraints of water have high root densities because roots overlap and compete with roots from different trees. Correspondingly, the contribution of root respiration will also be higher than that from the oak savanna. In addition, the values we reported here are from individual trees, not divided by the area of the whole site. If we consider the root contribution in an ecosystem scale and upscale it to the whole site, the contribution of soil respiration from tree roots to the total soil respiration from the whole site would be smaller since the trees only cover 42.4% of the total site. This is different from many other forested lands with few open areas, where the ratio of root respiration over total soil respiration based on individual trees could directly represent for the root contribution to the whole ecosystem.

We also contend that our estimated ratio of root to total respiration may be at its upper limit for the dry season because we are assuming that heterotrophic respiration in the open equals that under the tree. In reality, we found slightly higher values of soil C and N contents and percentage of silt and clay in soil

texture under trees than in the open. This difference may cause slightly higher heterotrophic respiration under trees, but compared with the root component, this difference in heterotrophic respiration in influencing total respiration is considered to be small. During the wet season with the presence of the grass, the ratio of tree root to total respiration may have another source of error due to slightly different species and density of grass under the tree and in the open. In addition, the litterfall from trees may be an error source for deriving tree root respiration, but this error could be minimum due to relatively small amount of leaf litter (average LAI = 0.6) from the open canopy in the savanna, and almost evenly distributed leaf litter on the surface due to wind blowing in autumn. In addition to above biotic factors, there may be difference in microclimate between under the tree and in the open. However, we did not find significant and systematic difference in soil moisture along the transect at this site with an open canopy and sparse tree density. The difference in soil temperature between under the tree and in the open was minimized by averaging soil respiration measurements over hours of a day and over days of a year.

Our study indicates that the root contribution from oak trees to total soil respiration varies with seasons. This conclusion is often neglected by many studies about root distribution to soil respiration. It is easy to infer that the activity of roots in the growing season is higher than that in the dormant season. In the dormant season root respiration is only from maintenance respiration but during the growing season root respiration consists of maintenance respiration and growth respiration. The maintenance respiration could be higher in the growing season with higher temperature than in the dormant season due to the positive temperature dependence of maintenance respiration (Ryan 1991; Ryan et al. 1996). Because the temperature dependence and moisture dependence of each component of soil respiration differ, the ratio of root respiration over the total respiration could vary with seasons when soil temperature and moisture vary.

Soil respiration vs. distance from trees

In order to investigate more details about the root influence on soil respiration, we plotted soil respiration vs. distance using the high-resolution transect measured within the dripline of the tree. Figure 2b quantifies the influence of tree roots on soil respiration.

Soil respiration decreased with distance radiating from the stem of the tree during both wet and dry seasons. We found an inverse equation (efflux vs. 1/distance) fitted the data. By comparing the curve during the dry season with that during the wet season, we found that the curve of the dry season is lower than that of the wet season, and soil respiration during the dry season decreases more rapidly with distance from trees than that during the wet season. This difference is probably due to the growth of grass during the wet season. During the wet growing season, grass covers both open areas and under trees. The root

respiration from grass contributes to the total soil respiration during the wet season. Thus, soil respiration decreases slower with distance during the wet season due to the relatively homogeneous distribution of grass, i.e., the influence of root respiration on total soil respiration is less during the wet season than during the dry season. During the dry season with no presence of grass, the difference of soil respiration between under trees and in open areas is more significant. In addition to the above analysis of slope, the relatively lower value of the coefficient of determination ($r^2 = 0.715$) for the wet season also indicates that the influence of grass roots reduces the influence of tree roots on total soil respiration. The extremely high r^2 (0.982) during the dry season suggests a strong signal of the correlation between soil respiration and tree roots.

The root pattern under canopy derived from soil respiration measurements is consistent with limited root studies in oak woodlands/savannas with a similar climate. Millikin and Bledsoe (1999) reported that root biomass decreased with increase in distance from a large oak tree with DBH of 0.29 m, and the majority (82%) of root biomass was within the crown area. Jackson et al. (1990) reported 90% of root biomass under oak canopy. We did not find significant signals of root influence on soil respiration beyond the crown area.

This paper does not partition grass root respiration from total soil respiration during the wet season. During the dry season there is no grass root respiration, but during the wet season the grass root respiration is a part of total soil respiration. We found the ratio of tree root respiration over total soil respiration slightly decreased from 41% during the dry season to 39% during the wet season. This small decline may be due to the contribution of grass root respiration to the total soil respiration. Craine et al. (1999) has reported that root respiration accounts for 38–40% of soil respiration in a grassland. In the savanna, the root respiration from the grass may account for less of total respiration than that in the grassland. Further studies on partitioning grass root respiration during the wet season in the savanna are suggested.

Seasonal patterns of soil respiration

Figure 3a shows the season pattern of daytime mean soil respiration in open areas, under trees, and derived tree root respiration as the difference of above two between July 2001 and December 2002. Figure 3b shows the daily mean soil volumetric moisture and soil temperature. The magnitude of soil respiration was low in the summer of 2001. The average rates of soil respiration in July, August, and September before the first rain in the fall 2001 were around 0.30 μmol m^{-2} s^{-1} in the open areas and 0.69 μmol m^{-2} s^{-1} under trees with tree root respiration. After the first rain in the fall, soil respiration dropped after a pulse value, but it then continuously increased until the end of the year. This pattern also corresponded to the increase in soil moisture as autumnal rains commenced. We used dotted lines to indicate the main trend of soil respiration excluding the pulse values following rain events.

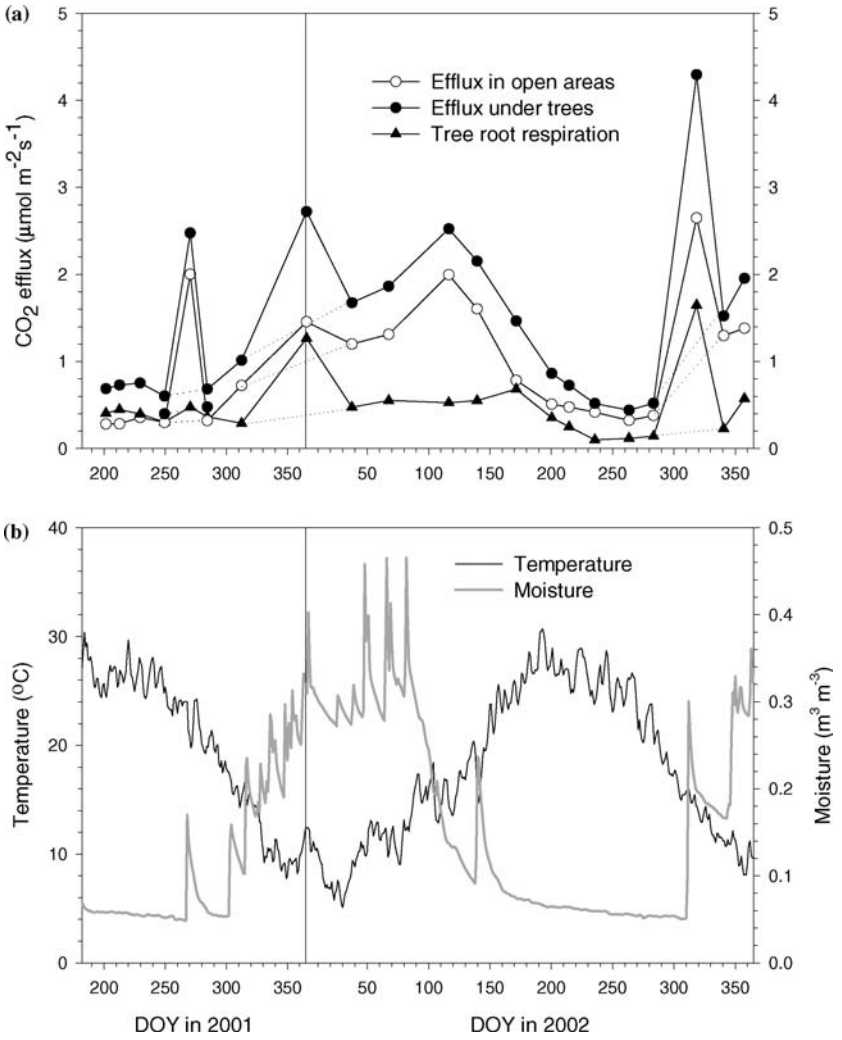

Figure 3. The season pattern of soil respiration in open areas and under trees, and tree root respiration (a), and daily mean soil volumetric moisture at 5 cm depth and soil temperature at 4 cm depth (b) between July 2001 and December 2002. The dotted lines indicate the trend without extreme events.

In 2002 soil respiration rates increased in the spring until late April. By then efflux rates were on the order of 2.00 μmol m^{-2} s^{-1} in the open areas and 2.52 μmol m^{-2} s^{-1} under trees, following the seasonal increase in temperature. On the other hand, soil moisture was not a significant controlling factor because soil moisture remained high (above 0.2 m^3 m^{-3}). After May, the seasonal decrease in soil moisture became a limiting factor to soil respiration. Corresponding with the temporal change in soil moisture, soil respiration rates

declined gradually from the maximum values observed between April and May (excluding pulses) to the minimum values in September, before the start of autumnal rains. By late summer/early autumn in 2002, soil respiration rates diminished to values on the order of 0.32 μmol m^{-2} s^{-1} in the open areas and 0.44 μmol m^{-2} s^{-1} under trees.

Soil respiration demonstrated a pulse effect after the first rainstorm of the season. 7.4 mm of precipitation fell between the night of day 267 and day 268 of year 2001. We did not measure soil respiration during and immediately after the rain, but we measured it on day 270, 2–3 days after the rain and still found a significant pulse value of soil respiration on the order of 2.00 μmol m^{-2} s^{-1} in the open areas and 2.48 μmol m^{-2} s^{-1} under trees compared with 0.30 μmol m^{-2} s^{-1} in the open areas and 0.60 μmol m^{-2} s^{-1} under trees before the rain. The observation of the pulse effect is consistent with continuous eddy flux measurements and soil CO_2 profile measurements after rains (Xu et al. 2004; Xu and Baldocchi 2004) and is an indicative of rapid microbial activity with the introduction of new sources of soil moisture (Birch 1958; Xu et al. 2004). During this transient event, daily mean soil moisture at 5 cm increased from 0.049 m^3 m^{-3} on day 267 to 0.170 m^3 m^{-3} on day 268 of year 2001. We also observed a respiratory pulse in 2002, with the magnitude of 2.65 μmol m^{-2} s^{-1} in the open areas and 4.29 μmol m^{-2} s^{-1} under trees on day 318, after the significant rainstorm on days 311–312, when 51.82 mm of precipitation fell. Figure 3a does not reflect a potential pulse on day 140, 2002 because we measured soil respiration on day 139, the day before the rain.

One and half years of measurement data suggest that although soil respiration during the dry summer indicated a similar pattern in 2001 and 2002 with very low values, the seasonal variation during the wet season between 2 years was different. The timing of the rainfall, particularly of the first and second rain after the summer, is an important factor in understanding the seasonal dynamics of soil respiration in savannas.

Figure 3a also indicates that the oak root respiration rates exhibited less range over the seasons than soil respiration under trees and in the open areas. Root respiration also demonstrated small pulse values, corresponding with the pulses from soil respiration in the open and under trees. In this study we were not able to identify if these derived pulses from roots were biased due to different pulse effects from heterotrophic respiration under trees and in open areas; nor did we observe the time lag between the pulses from root respiration and from heterotrophic respiration. If the pulse values were excluded, root respiration increased gradually from January and maximized in June. It decreased in July and August and then increased slowly until the end of the year.

Diurnal patterns of soil respiration

The seasonal pattern of soil respiration indicated that soil respiration was correlated with soil temperature and moisture on a daily basis. We may use soil

temperature and moisture as driving factors to upscale periodical measurements to the whole season and further to the ecosystem level. In order to explore whether or not the diurnal pattern had such a correlation as in the seasonal pattern, we examined two typical days of soil respiration in the summer.

We plotted the diurnal patterns of soil respiration from 6:00 to 18:00 h (Figure 4a), and soil temperature (Figure 4b) for 2 days, days 229 and 249 in 2001. Soil temperature on day 229 was higher than that on day 249. Spatially, soil temperature in open areas was higher than that under trees due to the shading of trees on sunny days. Soil temperature at 5 cm depth increased from

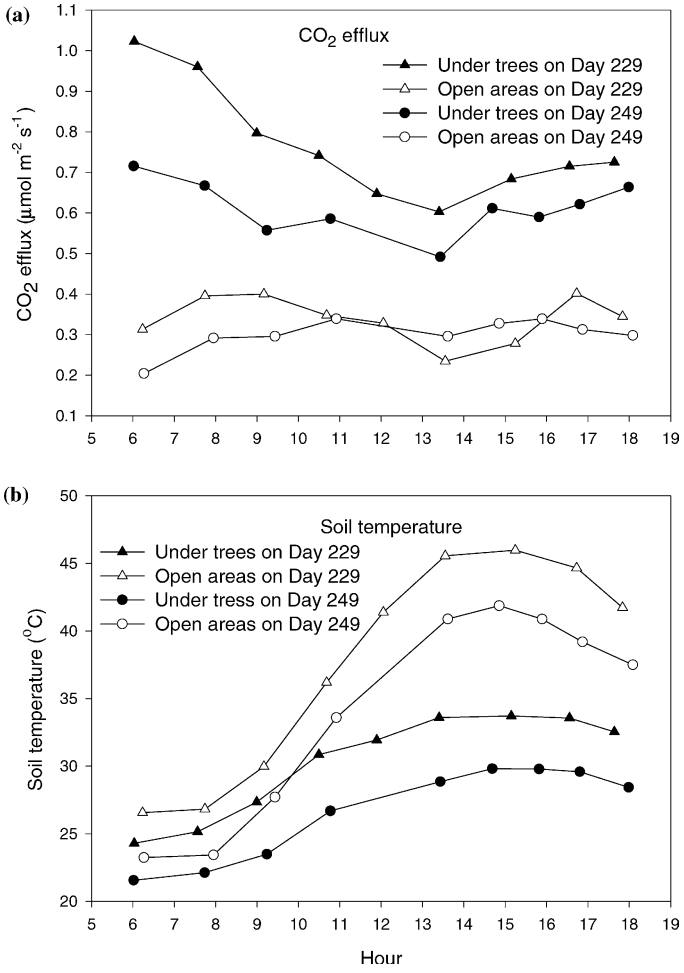

Figure 4. Diurnal patters of soil respiration (a), and soil temperature at 5 cm depth (b) under trees and in open areas on days 229 and 249 in 2001.

24.3 °C and peaked at 33.7 °C between 14:00 and 16:00 h under trees, and increased from 26.6 °C peaking at 50.0 °C in open areas on day 229. Soil temperature on day 249 had a similar trend, peaking at 30.0 °C under trees and at 41.9 °C in open areas. Soil moisture at 5 cm was very low and quite constant with little variation during both days with 0.055 m^3 m^{-3} on day 229, and 0.052 m^3 m^{-3} on day 249.

The average of soil respiration on day 229 was slightly higher than day 249 due to higher soil temperature and probably also due to a little higher soil moisture on day 229 than on day 249. However, the diurnal pattern of soil respiration did not vary correspondingly with soil temperature on either day. Soil respiration under trees decreased from 1.02 μmol m^{-2} s^{-1} at 6:02 h to 0.60 μmol m^{-2} s^{-1} at 13:24 h on day 229 and decreased from 0.72 μmol m^{-2} s^{-1} at 6:01 h to 0.49 μmol m^{-2} s^{-1} at 13:25 h on day 249. In open areas, the decrease in soil respiration from the morning to afternoon during a day was not as significant as under trees. However, soil respiration in the afternoon, when temperature peaked, did not show a corresponding peak in open areas.

The diurnal patters of soil respiration in the summer indicated the decoupling with soil temperature with a higher level of decoupling under trees and a lower level of decoupling in open areas. We speculate two reasons to explain the decoupling. First, root respiration from oak trees may be restrained by a low photosynthetic rate resulting in a decrease in photosynthate supply as the carbon source for respiration, due to stomatal closure caused by extremely high air temperature, high vapor pressure deficit (VPD), and low soil moisture. However, the time lag between photosynthesis and respiration is still unknown. Bowling et al. (2002) reported a lag of 5–10 days between the correlated VPD and ecosystem respiration, observed by carbon isotope. Our limited data suggest that root respiration immediately responded to photosynthesis within a day in the Mediterranean summer.

The second reason for the decoupling may be due to the decreased sensitivity of microbial decomposition responding to extremely high soil temperature (more than 40 °C) and low moisture in open areas. It has been reported that temperature sensitivity of soil respiration may decrease under a high temperature range (Singh and Gupta 1977; Lloyd and Taylor 1994; Kirschbaum 1995). Our measurements of soil respiration (mainly microbial decomposition) in the summer are consistent with above results that the temperature sensitivity could be very low or close to zero under high temperature.

The above two reasons may explain the decoupling of soil respiration with soil temperature on the diurnal basis as well as the difference of diurnal patterns under trees and in open areas: because the coupling of root with photosynthesis outweighs the coupling between soil respiration and temperature, soil respiration decreases in the afternoon under trees; because of high temperature, soil respiration is not sensitive to soil temperature in open areas, but the decoupling is not as significant as that under trees with influences from

roots. Although the decoupling may happen only when the soil is the driest in a year, it suggests a caveat if one wants to extrapolate nighttime soil respiration to daytime respiration in the dry summer solely based on temperature dependence. More evidences of this diurnal decoupling have been observed at this site using continuous measurement data and will be reported in a companion paper (Tang et al. in review).

Temporal upscaling

Although we found that the diurnal variation in soil respiration was not strongly correlated with soil temperature and moisture, we can still use the daily mean soil temperature and moisture to upscale the periodical measurements of soil respiration in order to estimate the annual sum of soil respiration from the site. We found temperature was not the sole factor driving soil respiration. Soil respiration was controlled by both soil moisture and temperature. The influence of moisture on soil respiration was more complex than temperature. In order to remove the temperature effect and examine the single moisture effect on soil respiration, we plotted soil respiration, normalized by soil temperature at a reference value of 25 °C, as a function of soil moisture in open areas and under trees (Figure 5). The normalization was made by a denominator, $\exp(0.02T)/\exp(0.02 \times 25)$, where T is the soil temperature (°C) with a reference value at 25 °C. Here we assumed soil respiration exponentially responded to soil temperature with a coefficient of 0.02 ($Q_{10} = \exp(10 \times 0.02) = 1.22$).

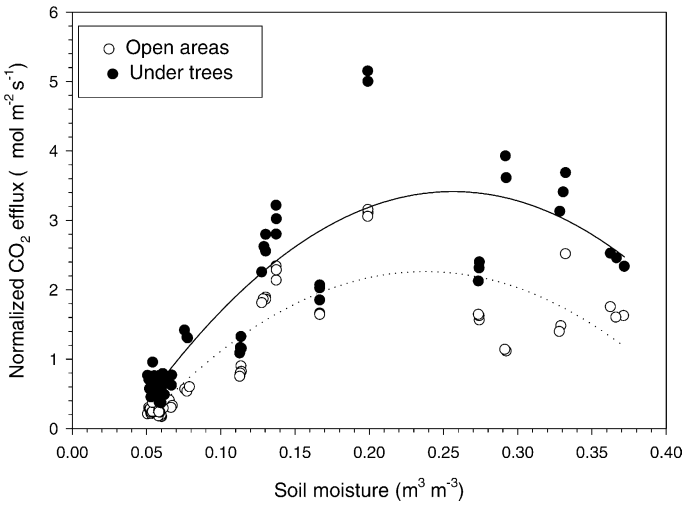

Figure 5. Normalized soil respiration (by soil temperature) vs. soil moisture in the open area and under trees. The dotted line is fitted for open areas and solid line is for under trees.

Figure 5 indicates that soil moisture had two opposite directions influencing soil respiration. When soil moisture was below a critical value (around 25%), soil respiration increased with moisture; it decreased with soil moisture when the moisture was greater than the critical value. The negative correlation at the high rates of soil moisture was probably due to the decrease in soil air porosity and oxygen availability in soils. The outliers around soil moisture of 0.20 $m^3\ m^{-3}$ with extremely high values of soil respiration were probably due to the rain effect.

We used Eq. (1) to estimate the cumulative soil respiration over the seasons with two driving variables, soil temperature and moisture. The temperature term takes the exponential form while the moisture term takes the quadratic form in the exponent to reflect the two opposite influences on soil respiration. We estimated the coefficients by conducting linear regression after log-transform in open areas and under trees, respectively. In the open area, we have $\beta_0 = 0.0599$, $\beta_1 = 0.00958$, $\beta_2 = 28.937$ and $\beta_3 = -60.197$, $r^2 = 0.793$, $n = 64$. Under trees, $\beta_0 = 0.114$, $\beta_1 = 0.0204$, $\beta_2 = 23.823$ and $\beta_3 = -46.696$, $r^2 = 0.798$, $n = 61$.

We plotted the residuals (measured values − fitted values) vs. soil temperature and moisture in open areas and under trees in Figure 6. During the dry summer when soil temperature was higher than 30 °C, moisture lower than 0.1 $m^3\ m^{-3}$, and soil respiration was less than 1 μmol $m^{-2}\ s^{-1}$, the residuals were small, indicating the model well fits the measurement results. In contrast, the residuals increased during the wet season when soil temperature was low but soil moisture was high. This is probably due to the growing of grass with the influence from grass roots. The model does not fit the large values of soil respiration, greater than 4 μmol $m^{-2}\ s^{-1}$, when soil moisture was around 0.2 $m^3\ m^{-3}$, probably because of the rain pulse effect after prolonged drought. The model was unable to simulate the effect of rain pulse on respiration. We separately simulated soil respiration in open space and under trees because with the significant effects from tree roots, the model coefficients would be different between under trees and open areas.

Eq. (1) allows us to investigate Q_{10} when moisture is held constant. Q_{10} is defined as the increasing ratio of soil respiration when temperature is increased by 10 °C. Holding moisture constant, we derived from the Eq. (1) that $Q_{10} = 1.10$ for open areas and $Q_{10} = 1.23$ for measurements under trees. Notice, these Q_{10} values were estimated by measurement data over seasons combining with soil moisture data. The Q_{10} value in the open areas with soil temperature at 5 cm is less than the Q_{10} values from a previous study using continuous soil profile measurement in the summer (Tang et al. 2003). Tang et al. (2003) gave $Q_{10} = 1.27$ for temperature at 8 cm and $Q_{10} = 1.17$ at 2 cm. The small Q_{10} value computed from a bi-variable model in this study and derived from a whole season may only explain diurnal patterns or day-to-day variation within a short period when soil moisture is constant. Under some extreme conditions in dry summer, Q_{10} cannot explain the diurnal pattern under trees, as indicated in Figure 4, due to physiological influences.

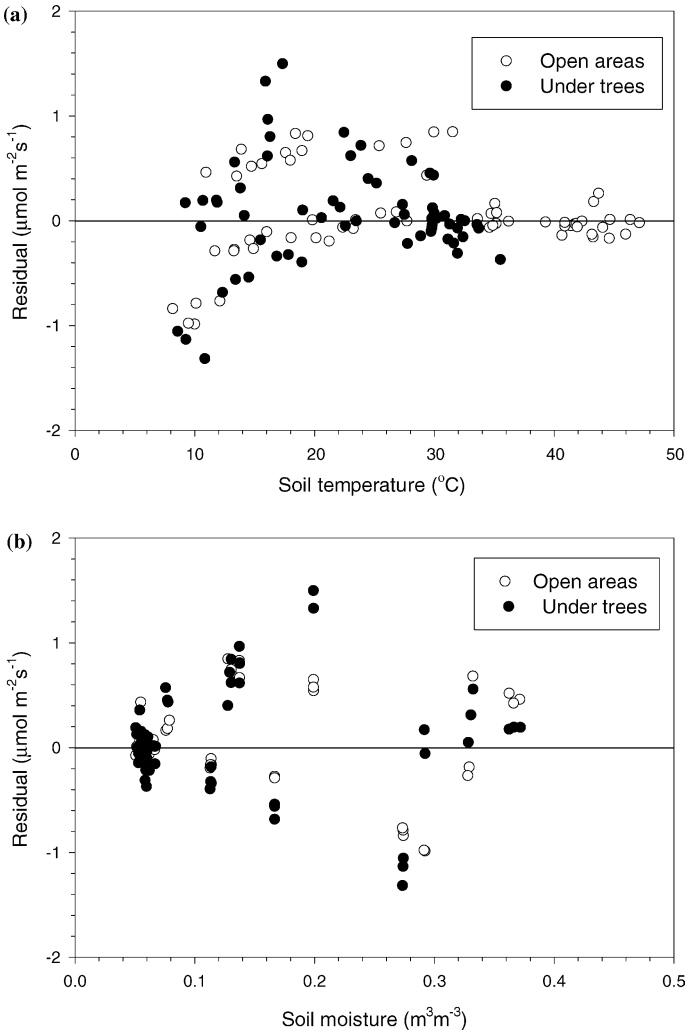

Figure 6. Residuals (measured value − fitted value) vs. soil temperature (a) and vs. moisture (b) in open areas and under trees.

Therefore, when soil moisture varied significantly and was a dominant variable at this site, Q_{10} had little application, although it may explain the temperature sensitivity confounded with soil moisture.

Eq. (1) indicates two opposite effects of soil moisture on soil respiration. The quadratic term of moisture in the exponent indicates that there is a maximum value of soil respiration when $\theta = 0.240\ \mathrm{m^3\ m^{-3}}$ for open areas and $\theta = 0.255\ \mathrm{m^3\ m^{-3}}$ for under trees. Holding soil temperature constant, when volumetric moisture is increased but no more than the maximum, soil

respiration will increase; when volumetric moisture is increased and greater than the maximum, soil respiration will decrease.

We observed pulse values of soil respiration after the rain events through field measurements. Due to periodical measurements of chambers, we were unable to describe in detail the pulse effect following the rain including the magnitude, maximum, and the time lag. To describe and simulate the seasonal pattern of soil respiration including some extreme events, continuous measurements of soil respiration is recommended. Combining chamber measurement and continuous measurements may provide a better understanding of both spatial and temporal patterns of soil respiration.

Spatial upscaling

After temporally upscaling the periodical measurements for estimating the cumulative soil respiration over a year, we need to spatially upscale soil respiration estimated from different places to the site scale because of the spatial heterogeneity of soil respiration. Due to the simplicity and sparseness of plant coverage at this site, we spatially averaged soil respiration under trees and in the open weighted by the crown closure (Eq. (2)). Combining Eqs. (1) and (2) we estimated that the annual soil respiration efflux in 2002 was 394 gC m^{-2} $year^{-1}$ in the open areas and 616 gC m^{-2} $year^{-1}$ under trees. The average of soil respiration from the site was estimated to be 488 gC m^{-2} $year^{-1}$.

The estimated annual CO_2 emission from soil at the savanna is less than ones from other ecosystems such as the estimation of 713 ± 88 gC m^{-2} $year^{-1}$ summarized from Mediterranean woodlands (Raich and Schlesinger 1992). It is in the lower band of a study (760 ± 340 gC m^{-2} $year^{-1}$) synthesized from EUROFLUX projects (Janssens et al. 2001). Our estimation is also less than several studies conducted from forests in the similar Mediterranean climate zones in the western United States such as the estimation of 1089 gC m^{-2} $year^{-1}$ within 9 months from April to December (Xu and Qi 2001) in the adjacent uphill of the Sierra Nevada in California, and 683 gC m^{-2} $year^{-1}$ in a ponderosa pine ecosystem in Oregon (Law et al. 1999b). However, if only the soil respiration under trees at this site is considered, the number (616 gC m^{-2} $year^{-1}$) is close to the one (683 gC m^{-2} $year^{-1}$) in the open forest in Oregon (Law et al. 1999b). The low value of annual soil respiration at this site could be explained by the prolonged drought in the summer controlled by the Mediterranean climate, sparse tree coverage, and grazed grass growing only in the winter and spring with relatively low temperature.

We used crown closure and difference of soil respiration between under the tree and in the open to spatially upscale soil respiration to the ecosystem level. This is the first step to quantify the spatial variation within a site. We found that the average of soil respiration measured under crown areas (Eq. (6)) can represent soil respiration with the root component, and there was no substantial difference of this averaged soil respiration from different trees at this

site with sparse and homogeneous tree species. However, the average of soil respiration under trees may vary with tree size and species. More measurements from more trees are suggested to help spatially upscale soil respiration from a forest ecosystem with a complex canopy composition.

Conclusions

Soil respiration at this study site is composed of microbial heterotrophic respiration, tree root respiration, and grass root respiration during the wet season from November to mid-May, and microbial heterotrophic respiration and tree root respiration during the dry season from mid-May to October. The spatial variation in soil respiration, measured by the chamber method, is mainly explained by the horizontal distribution of tree roots. Under tree canopies, soil respiration decreased with increasing distance from trees. The horizontal gradient of soil respiration is inversely proportional to the distance from trees. In the open area beyond the crown shadow, tree roots have no influence on soil respiration. This pattern allows us to partition tree root respiration from total soil respiration (microbes + tree roots + grass roots during the wet seasons, and microbes + tree roots during the dry season). The contribution of root respiration to total soil respiration varies with seasons, with 39% during the wet season and 41% during the dry season.

The seasonal pattern of soil respiration cannot be explained by temperature alone, but can be explained by the combination of soil moisture and temperature. The diurnal pattern was also influenced by tree physiology. Based on spatial gradient of soil respiration, spatial analysis of crown closure, and a bivariable simulation model, we estimated that the cumulative soil respiration in 2002 was 394 gC m^{-2} $year^{-1}$ in the open areas and 616 gC m^{-2} $year^{-1}$ under trees with a site-average of 488 gC m^{-2} $year^{-1}$.

Portable chamber measurements provide a useful tool to study spatial pattern of soil respiration. Combining spatial gradient of soil respiration and canopy structure derived from the satellite data allows us to upscale soil respiration from field measurement to a crown area, and then to a whole site. This is one of the first attempts to upscale soil respiration using a combined chamber gradient measurements and remote sensing data.

Simulation models with driving factors of soil temperature and moisture explain most temporal variations of soil respiration. Continuous measurements are needed to explain more details in temporal variation, particularly for diurnal patterns and for some extreme events such as rain pulse effects.

Acknowledgments

We thank Liukang Xu for help in fieldwork, and Qi Chen for help in image analysis. We thank Mr. Russell Tonzi for access and use of his ranch. JT is

partly supported by Edward A. Colman Fellowship, W.S. Rosecrans Fellowship at UC Berkeley and the Kearney Soil Science Foundation. DDB acknowledges support by DOE/TCP (DE-FG02-03ER63638), the Kearney Soil Science Foundation, and the California Agricultural Experiment Station.

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